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First Record of the Predatory Leech *Whitmania laevis* (Hirudinea: Hirudiniformes: Hirudinidae) from the Ryukyu Islands, Japan, with New Insights into the Phylogenetic Relationships within *Whitmania*

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Leeches of the predatory genus *Whitmania* Blanchard, 1888 were collected from Yonaguni Island in the Ryukyu Islands, Japan, and are identified as *W. laevis* (Baird, 1869). This represents the first record of this species from the Ryukyu Islands. Molecular phylogenetic analyses, which were performed using mitochondrial cytochrome *c* oxidase subunit I, tRNA^{Cys}, tRNA^{Met}, 12S rRNA, tRNA^{Val}, and 16S rRNA markers, reveal that the Yonaguni population of *W. laevis* is genetically close to the Taiwanese populations. The mitochondrial phylogeny also shows that *W. laevis* is a sister species of *W. edentula* (Whitman, 1886), which is indigenous to the Japanese Archipelago.

Key Words: Hirudinida, Arhynchobdellida, molecular phylogeny, East Asia.

Introduction

Species of the genus *Whitmania* Blanchard, 1888 are predatory leeches that feed on freshwater snails (Takahashi 1931; Lai and Chen 2004, 2010; Luo et al. 2022). This genus comprises six species, most of which are endemic to the Sino-Japanese region (Sawyer 1986; Tan and Zhao 2001). Among those species, only *W. laevis* (Baird, 1869) has a wide distribution across South and East Asia including the Southern Russian Far East (Moore 1927a; Lukin 1976; Yang 1996; Nesemann and Sharma 2001; Lai and Chen 2010). This species was originally described based on a specimen with an undetermined locality kept at the British Museum of Natural History (hereinafter, BMNH; now Natural History Museum, London) (Baird 1869). However, its type locality was later determined to be China by examination of the type and additional specimens at BMNH (Blanchard 1896). Additionally, *W. pigra* (Whitman, 1884), which has type localities in Japan (Whitman 1886), was synonymized with the continental *W. laevis.*

Whitmania laevis was once recorded from Lake Biwa, central Honshu, Japan following Blanchard's taxonomic treatment (Oka 1917). However, following re-evaluation of morphological differences among *Whitmania* species, *W. pigra* was resurrected as a distinct species, and *W. laevis* was considered to only be distributed in continental China and Taiwan, and not to be endemic to the Japanese Archipelago (Oka 1932). Recent molecular phylogenetic analyses also corroborated the distinct taxonomic accounts of *W. pigra* and *W. laevis* (Phillips and Siddall 2009; Ye et al. 2015; Pan and Jiang 2019).

Whitmania leeches were collected from Yonaguni Island, which is the westernmost island of the Ryukyu Islands, Japan and is approximately 110 km from Taiwan. Their taxonomic status is determined by morphological examination and molecular phylogenetic analyses based on mitochondrial sequence data. Additionally, the phylogenetic position of *W. edentula* (Whitman, 1886), of which type localities are in Japan, is estimated for the first time by these molecular phylogenetic analyses.

Materials and Methods

Sampling. Leeches were collected from Yonaguni Island in 2014. Geographical coordinates for the sites were obtained using a Garmin eTrex® GPS unit. Specimens were relaxed by the gradual addition of absolute ethanol (EtOH) to freshwater, and then fixed in absolute EtOH. For DNA extraction, botryoidal tissue was removed from the posterior part around the caudal sucker of each specimen, and then preserved in absolute EtOH. The remainder of the body was fixed in 10% formalin, and preserved in 70% EtOH.

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Six measurements were taken: body length (BL) from the anterior margin of the oral sucker to the posterior margin of the caudal sucker; maximum body width (BW); oral sucker length (OL), from the anterior to the posterior margin of the sucker; oral sucker width (OW), from the right to the left margin of the sucker; caudal sucker length (CL), from the anterior to the posterior margin of the sucker; and caudal sucker width (CW), from the right to the left margin of the sucker. Examination, dissection and drawing of the specimens were conducted using a Leica M125 stereoscopic microscope with a drawing tube. The leech specimens examined in this study were deposited in the Zoological Collection of Kyoto University (KUZ).

The somite numbering convention is based on Moore (1927b): body somites are denoted by Roman numerals, and the annuli in each somite are given alphanumeric designations.

Additionally, four *Whitmania* species, i.e., *W. acranulata* (Whitman, 1886), *W. edentula*, *W. laevis* and *W. pigra*, were collected from Japan, Taiwan, and Korea for the molecular phylogenetic analyses (Table 1).

Whitmania acranulata: KUZ Z5152, Zhuangwei Township, Yilan County, Taiwan (24.77139°N, 121.77889°E), 5 February 2013; KUZ Z5153, Jiaoxi Township, Yilan County, Taiwan (24.78806°N, 121.75139°E), 5 February 2013.

Whitmania edentula: KUZ Z5156, Motomiya-sebiuchi, Motomiya, Fukushima, Japan (37.51667°N, 140.38583°E), 10 June 2013; KUZ Z5157, Minara, Toon, Ehime, Japan (33.78750°N, 132.87500°E), 23 August 2013; KUZ Z5165, Asahimachi-kamijominamiwari, Nirasaki, Yamanashi, Japan (35.67241°N, 138.44414°E), 6 July 2014.

Whitmania laevis: KUZ Z5149, Jinshan District, New Taipei City, Taiwan (25.24383°N, 121.60983°E), 4 February 2013; KUZ Z5150, Yilan City, Yilan County, Taiwan (24.75514°N, 121.77400°E), 5 February 2013; KUZ Z5151, Zhuangwei Township, Yilan County, Taiwan (24.77144°N, 121.77858°E), 5 February 2013; KUZ Z5154, Dounan Township, Yulin County, Taiwan (23.67667°N, 120.45228°E), 10 February 2013; KUZ Z5155, Guoxing Township, Nantou County, Taiwan (24.06058°N, 120.93419°E), 11 February 2013; KUZ Z5158, Gunseo-myeon, Yeongam, Jeollanam-do, Korea (34.78147°N, 126.64839°E), 7 November 2013.

Whitmania pigra: KUZ Z5148, Yamami, Minamichita, Aichi, Japan (~34.72°N, ~136.90°E), 20 July 2011.

Molecular phylogenetic and genetic distance analyses. The phylogenetic positions of the newly collected specimens were investigated based on the concatenated data of several mitochondrial markers, cytochrome *c* oxidase subunit I (COI), and tRNA^{Cys}, tRNA^{Met}, 12S rRNA, tRNA^{Val}, and 16S rRNA (tRNA^{Cys}–16S). Genomic DNA extraction, polymerase chain reaction, and cycle sequencing reaction methods were performed as described by Nakano and Lai (2016, 2017). A total of 28 sequences were newly obtained and deposited with the International Nucleotide Sequence

Table 1. Samples used for molecular analyses. Locality and voucher or isolate information on the vouchers is accompanied by the International Nucleotide Sequence Databases (INSD) accession numbers of the markers. Sequences marked with an asterisk (*) were obtained for the first time in this study.

Taxon	Locality	Voucher/ isolate #	INSD accession #	
			COI	tRNA^{Cys}–16S
Whitmania				
W. laevis	Japan: Ryukyu Islands, Yonaguni Island (24.45064°N, 122.95425°E)	KUZ Z5159	LC811612*	LC811626*
W. laevis	Japan: Ryukyu Islands, Yonaguni Island (24.44956°N, 122.95272°E)	KUZ Z5162	LC811613*	LC811627*
W. laevis	Taiwan: New Taipei City, Jinshan District (25.24383°N, 121.60983°E)	KUZ Z5149	LC811606*	LC811620*
W. laevis	Taiwan: Yilan County, Yilan City (24.75514°N, 121.77400°E)	KUZ Z5150	LC811607*	LC811621*
W. laevis	Taiwan: Yilan County, Zhuangwei Township (24.77144°N, 121.77858°E)	KUZ Z5151	LC811608*	LC811622*
W. laevis	Taiwan: Yulin County, Dounan Township (23.67667°N, 120.45228°E)	KUZ Z5154	LC811609*	LC811623*
W. laevis	Taiwan: Nantou County, Guoxing Township (24.06058°N, 120.93419°E)	KUZ Z5155	LC811610*	LC811624*
W. laevis	China: Shaanxi Province	—	KM655839	KM655839
W. laevis	South Korea: Jeollanam-do, Yeongam, Gunseo-myeon (34.78147°N, 126.64839°E)	KUZ Z5158	LC811611*	LC811625*
W. acranulata	Taiwan: Yilan County, Zhuangwei Township (24.77139°N, 121.77889°E)	KUZ Z5152	LC811601*	LC811615*
W. acranulata	Taiwan: Yilan County, Jiaoxi Township (24.78806°N, 121.75139°E)	KUZ Z5153	LC811602*	LC811616*
W. acranulata	China: Shaanxi Province	—	KM655838	KM655838
W. acranulata	China	CSU-MG-10	OQ076773	OQ076773
W. edentula	Japan: Fukushima, Motomiya, Motomiya-sebiuchi (37.51667°N, 140.38583°E)	KUZ Z5156	LC811603*	LC811617*
W. edentula	Japan: Ehime, Toon, Minara (33.78750°N, 132.87500°E)	KUZ Z5157	LC811604*	LC811618*
W. edentula	Japan: Yamanashi, Nirasaki, Asahimachi-kamijominamiwari (35.67241°N, 138.44414°E)	KUZ Z5165	LC811605*	LC811619*
W. pigra	Japan: Aichi, Minamichita, Yamami (~34.72°N, ~136.90°E)	KUZ Z5148	LC811614*	LC811628*
W. pigra	China: Shangdon Province	—	EU304459	EU304459
W. pigra	China	—	MW659834	—
W. pigra	China	—	MW659836	—
W. pigra	China	CSU-MG-11	OQ076768	OQ076768
W. pigra	China?	HSYC2014	MN729556	—
Hirudo nipponia	China	—	KC667144	KC667144

Databases (INSD) through the DNA Data Bank of Japan (Table 1).

As in previous studies (Phillips and Siddall 2009; Shen et al. 2011; Ye et al. 2015; Xu et al. 2016; Pan and Jiang 2019; Müller et al. 2022) and preliminary phylogenetic analyses (not shown), eight total sequences of two *Whitmania* species and one sequence of a blood-sucking *Hirudo nipponia* Whitman, 1886, which was selected as the outgroup, were retrieved from INSD and included in the dataset for our analyses (Table 1). The COI alignment was trivial, as no indels were observed. The tRNA^{Cys}–16S sequences were aligned using MAFFT v. 7.467 with the L-INS-i option (Katoh and Standley 2013). The lengths of the COI and tRNA^{Cys}–16S aligned datasets were 1271 and 1017 bp, respectively.

Phylogenetic trees were inferred with maximum likelihood (ML) and Bayesian inference (BI) methods. The best-fit partition scheme and substitution models were identified with AICc using IQ-TREE v. 1.6.12 (Nguyen et al. 2015) as follows: COI 1st position, $GTR + I + G$; COI 2nd position, $F81 + I$; COI 3rd position, $GTR + G$; and all of tRNA^{Cys}–16S, $GTR + G$. The ML phylogeny was inferred using IQ-TREE and nonparametric bootstrapping (BS) was subsequently conducted with 1000 replicates. The BI tree and Bayesian posterior probabilities (PP) were obtained using MrBayes v. 3.2.6 (Ronquist et al. 2012). Two independent runs of four Markov chains were conducted for one million generations and the tree was sampled every 1000 generations. Parameter estimates and convergence were checked using Tracer v. 1.7.1 (Rambaut et al. 2018), and the first 10% of trees were discarded as burn-in.

Pairwise comparisons of uncorrected *p*-distances for COI sequences (1271 bp) between *W. laevis* and its most closely related species, and within *W. laevis* were calculated using MEGA X (Kumar et al. 2018). All missing positions were eliminated for each sequence pair.

Whitmania laevis (Baird, 1869)
[Japanese name: Gohon-sesuzi-biru]
(Figs 1–3)

Material examined. In total six specimens were collected from rice paddy located to the south of Mt. Kuburadake, Yonaguni Island, Ryukyu Islands, Japan on 19 March 2014: KUZ Z5159, Z5160, 24.45064°N, 122.95425°E, by Yoshiko Yamane; KUZ Z5161–Z5164, 24.44956°N, 122.95272°E, by Takafumi Nakano. Three specimens, KUZ Z5159, Z5162, Z5164, were dissected.

Description. Body firm, muscular, cephalic region small, from prostomium to somite XI with width increasing significantly in posterior direction, then from somite XII with constant width in posterior direction, ventrally flattened (Figs 1A, B, 2A, C). Oral sucker small, ovate, OL 1.4–1.8 mm, OW 1.3–1.8 mm (Figs 1B, 2C). Caudal sucker ventral elliptic, CL 2.9–4.6 mm, CW 3.8–5.3 mm (Figs 1B, 2G).

Somite I completely merged with prostomium (Fig. 2A). Somite II uniannulate (Fig. 2A). Somite III uni- or biannulate, $(a1 + a2) = a3$, a3 sometimes with slight dorsal furrow (Fig. 2A). Somites IV and V generally biannulate, $(a1 + a2) = a3$, $(a1 + a2)$ generally with slight dorsal furrow (Fig. 2A, B); somite V forming posterior margin of oral sucker (Fig. 2C). Somite VI dorsally triannulate, $a1 > a2 < a3$, or a1 sometimes with obvious furrow, $a1\ (b1 = b2) > a2 < a3$; ventrally biannulate, $(a1 + a2) > a3$ (Fig. 2A–C). Somite VII quadrannulate, $a1 > a2 = b5 = b6$ (Fig. 2A–C), or sometimes $a1\ (b1 = b2$ dorsally$) > a2 = b5 = b6$. Somites VIII–XXIII quinquannulate, $b1 = b2 = a2 = b5 = b6$ (Fig. 2A–E). Somite XXIV quinquannulate, $b1 = b2 = a2 = b5 = b6$, or quadrannulate, $b1 = b2 = a2 < a3\ (b5 = b6)$ (Fig. 2F, G). Somite XXV quadrannulate, $b1 = b2 = a2 = a3$ (Fig. 2F, G). Somite XXVI biannulate, $(a1 + a2) > a3$, $(a1 + a2)$ sometimes with slight furrow (Fig. 2F); $(a1 + a2)$ being ventrally last complete annulus. Somite XXVII uniannulate (Fig. 2F). Anus at posterior margin of XXVII (Fig. 2F).

Male gonopore in anterior margin of, or middle of somite XI b6 (Fig. 2D). Female gonopore in anterior margin of somite XII b6 (Fig. 2D). Gonopores separated by ≤ 5 annuli (Fig. 2D).

Eyespots in 5 pairs, in parabolic arc (Fig. 2A, B); 1st pair on II; 2nd pair on III or III $(a1 + a2)$; 3rd pair on IV $(a1 + a2)$; 4th pair on V $(a1 + a2)$; 5th pair on VI a2. Sensillae developed, 1 row on every annulus. Somital papillae developed, generally 6 papillae detected on a2 of each somite in VII–XXVII (Fig. 2A, B, E, F).

Nephridiopores in 17 pairs, one each situated ventrally at posterior margin of b2 of each somite in VIII–XXIV (Fig. 2C, D, G).

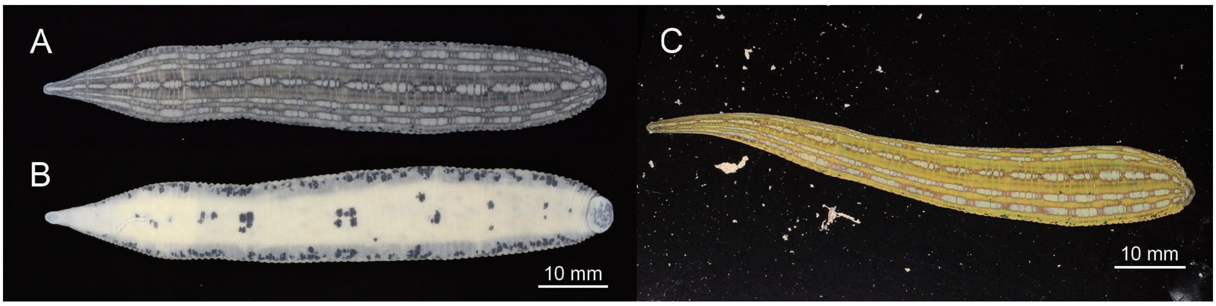

Fig. 1. *Whitmania laevis*, from Yonaguni Island, Ryukyu Islands, Japan, mature individual KUZ Z5159. A, Dorsal view of the preserved specimen; B, ventral view of the preserved specimen; C, dorsal view of the live animal.

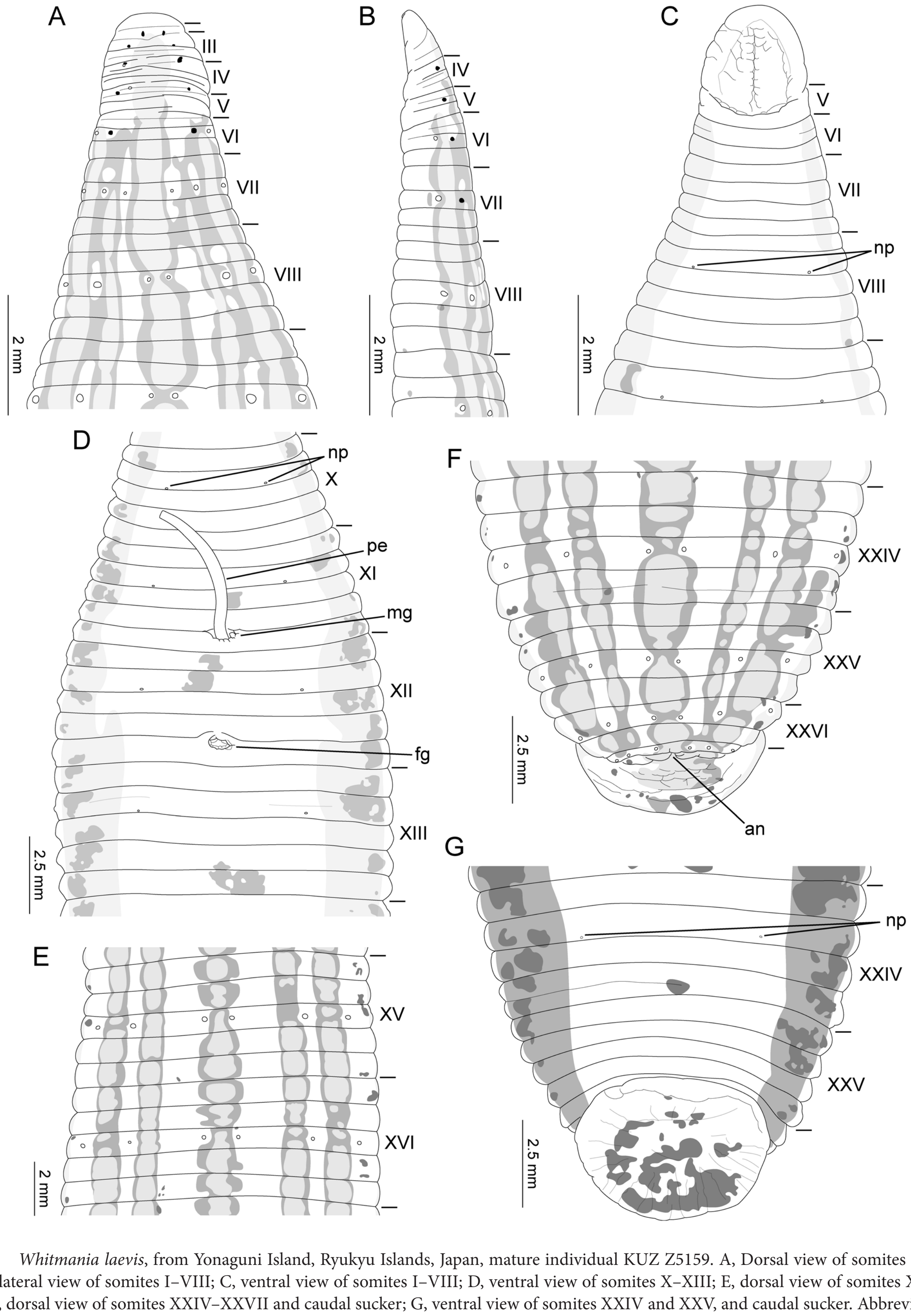

Fig. 2. *Whitmania laevis*, from Yonaguni Island, Ryukyu Islands, Japan, mature individual KUZ Z5159. A, Dorsal view of somites I–VIII; B, left lateral view of somites I–VIII; C, ventral view of somites I–VIII; D, ventral view of somites X–XIII; E, dorsal view of somites XV and XVI; F, dorsal view of somites XXIV–XXVII and caudal sucker; G, ventral view of somites XXIV and XXV, and caudal sucker. Abbreviations: an, anus; fg, female gonopore; mg, male gonopore; np, nephridiopore; pe, penis.

One median longitudinal furrow on ventral surface of oral sucker (Fig. 2C). Three rudimental jaws in oral cavity, 1 dorsal and 2 ventrolateral; salivary papillae undetectable; distichodont. Pharynx reaching to IX b2–b5. Crop reaching to XIX b2, giving rise to 1 pair of crop ceca (post-crop ceca) in XIX b1–b2 to XX b5–XXII b2 (Fig. 3A). Terminal end of intestine forming sphincter between intestine and rectum, in XXI a2 to XXII b1–b5.

Testisacs in 9 or 10 pairs (Fig. 3B): 1st pair in XIII b5–b6 to XIV b2 (left testisac undetectable in KUZ Z5159); 2nd

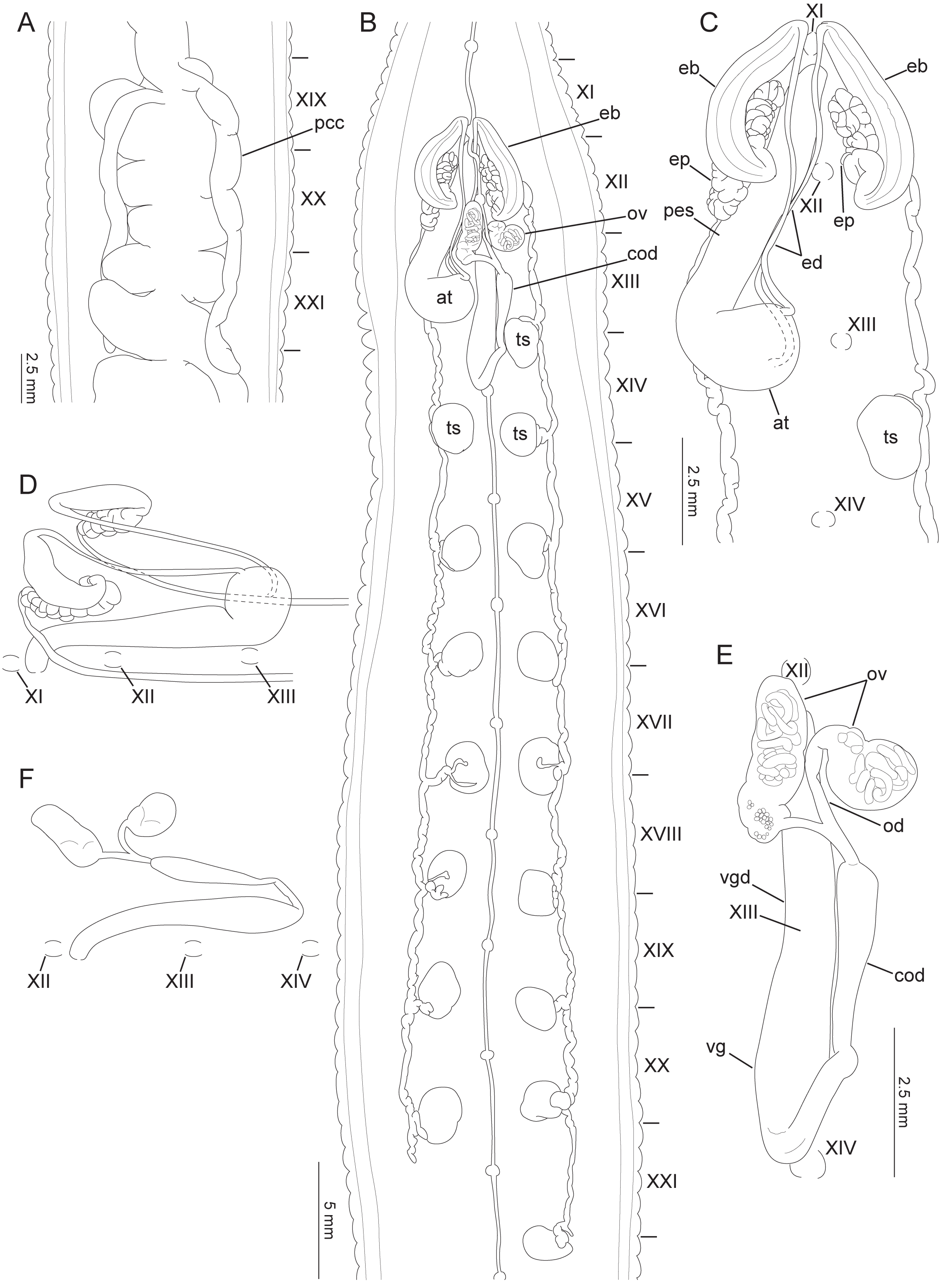

Fig. 3. *Whitmania laevis*, from Yonaguni Island, Ryukyu Islands, Japan, mature individual KUZ Z5159. A, Ventral view of crop terminal and intestine with post-crop ceca; B, dorsal view of reproductive system, including ventral nervous system; C, dorsal view of male median reproductive system, including positions of ganglia XI–XIV; D, schematic drawing of left lateral view of male median reproductive system, including positions of ganglia XI–XIII; E, dorsal view of female reproductive system, including positions of ganglia XII–XIV; F, schematic drawing of left lateral view of female reproductive system, including positions of ganglia XII–XIV. Abbreviations: at, atrium; cod, common oviduct; eb, ejaculatory bulb; ed, ejaculatory duct; ep, epididymis; od, oviduct; ov, ovisac; pcc, post-crop ceca; pes, penis sheath; ts, testisac; vg, vagina; vgd, vaginal duct.

pair in XIV a2–b5 to XV b1; 3rd pair in XV a2–b5 to XVI b1; 4th pair in XVI a2–b5 to XVI b6–XVII b1; 5th pair in XVII a2–b6 to XVII b6–XVIII b2; 6th pair in XVIII a2–b5 to XVIII b6–XIX b1; 7th pair in XIX a2–b6 to XIX b6–XXb1; 8th pair in XX a2–b5 to XX b6–XXI b1; 9th pair in XXI a2–b6 to XXII b1–b2 (left testisac undetectable in KUZ Z5159); 10th pair (detected in KUZ Z5164 only) undeveloped, in XXII b5 and b6. Paired epididymides developed, globular or fusiform (Fig. 3B, C). Ejaculatory bulbs developed, elongated, fusiform (Fig. 3B–D); in large individuals (KUZ Z5159 and Z5162), in XI a2–XII b1 to XII a2–b6, occupying 6 or 7 annuli; in smaller individual (KUZ Z5164), in XI b5–b6 to XII b1–b2, occupying 4 annuli. Ejaculatory ducts narrow, running toward male atrium in XI a2–b5 to XII b2–XIII b5 (Fig. 3B–D); right duct crossing ventrally beneath nerve cord. Male atrium continuous with penis sheath (Fig. 3B–D). Penis sheath hook-like, U- or L-shaped, reaching to XIII b1–b6, then turning anteriorly to male gonopore (Fig. 3B–D).

Paired ovisacs ellipsoidal or globular, in XII b5–XIII b1 to XIII b1–b2 (Fig. 3B, E, F). Oviducts short (Fig. 3B, E, F); right oviduct crossing ventrally beneath nerve cord; both oviducts converging into common oviduct in XII b6 or XIII b2. Common oviduct thick, long, descending to female vagina in XII b6–XIII b2 to XIII b5–XIV a2 (Fig. 3B, E, F). Female vagina continuous to vaginal duct, tubular, in XII b6 to XIII b5–XIV a2 (Fig. 3B, E, F); vaginal cecum absent.

Coloration. In life, dorsal surface olive green with 5 discontinuous whitish-green longitudinal stripes, all stripes bordered in brown, each stripe fully or slightly faded on a2 of each mid-body somite (Figs 1C, 2E); several irregular black markings present on lateral margins; ventral surface tannish with black lateral margins, black markings present on lateral margins and caudal sucker, several irregular black markings also present on mid-ventral surface. Color faded in preservative, but longitudinal stripes and markings still present (Figs 1A, B, 2G).

Natural history. All individuals were found crawling in water of a paddy field at night.

Japanese name. The Japanese name "Gohon-sesuzi-biru," which was proposed by Ohno (1998), is adopted herein. This name is likely to be derived from its five (= "gohon-", 五本) dorsal (= "-se-", 背) longitudinal stripes (= "-suzi", 筋); "biru" (or "hiru") means a leech in Japanese.

Phylogenetic position and genetic distances. The ML (ln $L=-7516.22$; not shown) and BI (ln $L=-7559.22$; Fig. 4) trees had congruent topologies. The monophyly of each of the four *Whitmania* species was well supported: *W. acranulata* (BS =100%, PP = 1.0), *W. edentula* (BS = 100%, PP = 1.0), *W. laevis* (BS = 98%, PP = 1.0), and *W. pigra* (BS = 86%, PP = 0.98). Monophyly of three *Whitmania* species, i.e., *W. pigra*, *W. laevis*, and *W. edentula*, was well supported (BS = 94%, PP = 1.0). *Whitmania laevis* formed a monophyletic lineage with *W. edentula* (BS = 98%, PP = 1.0). The Taiwanese and Yonaguni *W. laevis* formed a distinct clade from the continental *W. laevis* sequences

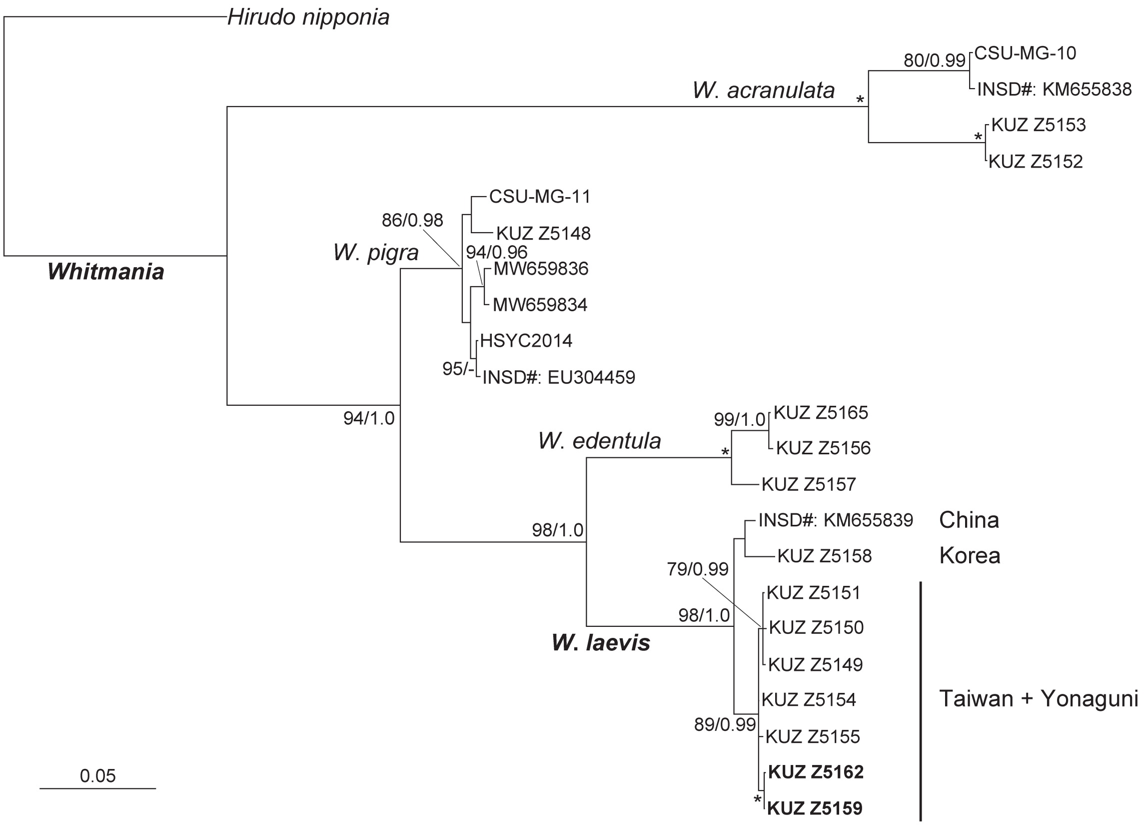

Fig. 4. Bayesian inference tree for 2288 bp of mitochondrial COI, tRNA^{Cys}, tRNA^{Met}, 12S rRNA, tRNA^{Val}, and 16S rRNA markers. Numbers on nodes indicate bootstrap (BS) values for maximum likelihood ≥ 70% and Bayesian posterior probabilities (PP) ≥ 0.95. Asterisks denote nodes with BS = 100%, PP = 1.0.

(BS = 89%, PP = 0.99).

The pairwise COI uncorrected *p*-distances between *W. laevis* and *W. edentula* were 10.5%–11.9%. The intraspecific COI variations within *W. laevis* were as follows: 0.2%–0.7% within the Taiwanese and Yonaguni populations; 2.1% between the Korean and continental Chinese sequences; and 1.8%–3.5% between the Taiwanese + Yonaguni and continental specimens.

Remarks. The *Whitmania* leeches collected from Yonaguni Island were identified as *W. laevis* based on the presence of the following characteristics, which were also reported by the prior studies (Blanchard 1896; Moore 1927a; Yang 1996; Lai and Chen 2010): dorsal surface with five discontinuous whitish-green longitudinal stripes and several irregular black markings, ventral surface with black markings on lateral margins and caudal sucker; male gonopore at XI b6 and female gonopore at XII b6; paired epididymides globular or fusiform; penis sheath hook-like; oviducts short; common oviduct long, descending to female vagina; vaginal duct tubular; vaginal cecum absent. The results of our molecular analyses supported the taxonomic account of the Yonaguni *Whitmania* specimens determined by those morphological features. The results showed close genetic relationships between the Yonaguni and Taiwanese populations. This occurrence report provides the first record of *W. laevis* from the Ryukyu Islands (see Itoh 2003). It remains uncertain whether *W. laevis* on Yonaguni Island was introduced from Taiwan or anywhere else in recent years, but nonetheless, it is noteworthy that the Yonaguni specimens have unique COI sequences.

The large *W. laevis* specimens from Yonaguni Island possess nine pairs of testisacs. However, the Chinese and Taiwanese specimens had 11 pairs of testisacs (Yang 1996; Lai and Chen 2010) and those from eastern India had 10 pairs of testisacs (Moore 1927a). Although the small specimen (KUZ Z5164) possesses 10 pairs of testisacs, the last pair seemed to be rudimentary. The reduced number of testisac pairs may be a shared feature of the *W. laevis* population endemic to Yonaguni Island.

The present phylogenies revealed a sister relationship between *W. laevis* and *W. edentula* for the first time. This relationship is consistent with the morphological similarities in female genital organs between the two species (Whitman 1886), both of which have a thick common oviduct directly descending to the vagina and a tubular vagina and vaginal duct. The calculated uncorrected *p*-distances between *W. laevis* and *W. edentula* were above 10%, and thus met the average interspecific variations detected among the hirudinid predatory species of *Haemopis* Savigny, 1822 (Kvist et al. 2023). Therefore, *W. laevis* and *W. edentula* should both receive distinct species status within *Whitmania*. Three of the five *Whitmania* species, i.e., *W. acranulata*, *W. edentula*, and *W. pigra*, were originally described from Japan. Therefore, their topotypic DNA data and morphological features are essential to reveal the true species richness and evolutionary history of this predatory genus endemic to South and East Asia.

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Authors Contributions

Takafumi Nakano: Conceptualization; Data curation; Funding acquisition; Investigation; Resources; Visualization; Writing – original draft; Writing – review & editing. Yi-Te Lai: Resources; Validation; Writing – review & editing. Hong-Yul Seo: Resources; Validation; Writing – review & editing. Chiaki Kambayashi: Formal Analysis; Funding acquisition; Writing – original draft; Writing – review & editing.

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Declarations

Competing interests. The authors declare no conflicts of interest.

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