

A New Panther Worm Spotted in Japan, *Hofstenia sugashimaensis* sp. nov. (Xenacoelomorpha: Acoela)

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Hofstenia Bock, 1923, the type genus of Hofsteniidae, was originally established for *H. atroviridis* Bock, 1923, from Misaki, Kanagawa Prefecture, Japan. This study describes *Hofstenia sugashimaensis* sp. nov., discovered in water tanks at the Sugashima Marine Biological Laboratory (Nagoya University) and Toba Aquarium, both situated at the mouth of Ise Bay in Mie Prefecture, along the Pacific coast of central Japan. Morphologically, it resembles *H. miamia* Corrêa, 1960 (commonly known as the “three-banded panther worm”) but is distinguished by two transverse bands and dorsal midline markings based on intra- and interspecific comparisons. Phylogenetic analysis of partial sequences of the cytochrome *c* oxidase subunit I, 18S rRNA, and 28S rRNA supports its genetic distinction from *H. miamia*.

Key Words: Acoela, aquarium, taxonomy, Pacific, phylogeny, Xenacoelomorpha.

Introduction

The family Hofsteniidae includes six species across four genera, most of which are found in shallow waters (Hooge et al. 2007; Hookabe et al. 2024). An exception is *Hoftherma hatsushimaensis* Hookabe, Jimi, Furushima, and Fujiwara, 2024 recently described from a deep-sea hydrocarbon seep (Hookabe et al. 2024). Within this family, *Hofstenia* Bock, 1923 is the only non-monospecific genus, comprising three accepted species: *H. atroviridis* Bock, 1923, *H. miamia* Corrêa, 1960, and *H. arabiensis* Beltagi and Mandura, 1991. From Japanese waters, *H. atroviridis*, the type species described from Misaki, Kanagawa, is the only named species in *Hofstenia*. Although *Hofstenia* species resembling *H. miamia* have been reported from Japan in various sources, including the Toba Aquarium Blog (<https://aquarium.co.jp/diary/2014/02/9488>; in Japanese), their species identity remains unclear.

Among the three species of the genus, only *H. miamia* has so far been established as a laboratory research model for developmental and regeneration studies. Owing to the phylogenetic position of Xenacoelomorpha as a sister group to Nephrozoa (Protostomia + Deuterostomia), *H. miamia* provides valuable insights into the early evolution of bilaterians (Cannon et al. 2016; Kimura et al. 2021). As a genetically tractable model, *H. miamia* is supported by molecular resources, including a high-quality genome and

transcriptome (Srivastava et al. 2014; Gehrke et al. 2019). It is well suited for laboratory culture, producing abundant and accessible embryos (Kimura et al. 2021). Additionally, *H. miamia* exhibits the remarkable ability to undergo whole-body regeneration using putatively pluripotent stem cells (Srivastava 2022). These potentials, combined with a solid systematic framework, make *Hofstenia* species an ideal organism for evo-devo studies.

In this study, we obtained specimens of panther worms from tanks at the Sugashima Marine Biological Laboratory, Nagoya University (NU-MBL) and Toba Aquarium. Based on external/internal morphological observation, we describe a new species of *Hofstenia* and provide its phylogenetic position within the genus using multiple gene markers.

Materials and Methods

A total of 21 acoel specimens were collected from two sources: a tank at Toba Aquarium in 2014 and a tank at NU-MBL, which is supplied with seawater directly pumped from nearshore waters around Sugashima Island, Mie, Japan, in 2024 (Fig. 1). In addition, one specimen of *Hofstenia* species was collected from subtidal sandy sediments in Mizugama, Okinawa, Japan, on 12 November 2024 by Satoshi Shimooka (SS), which was provisionally identified based on molecular barcoding.

Living specimens were photographed using digital cam-

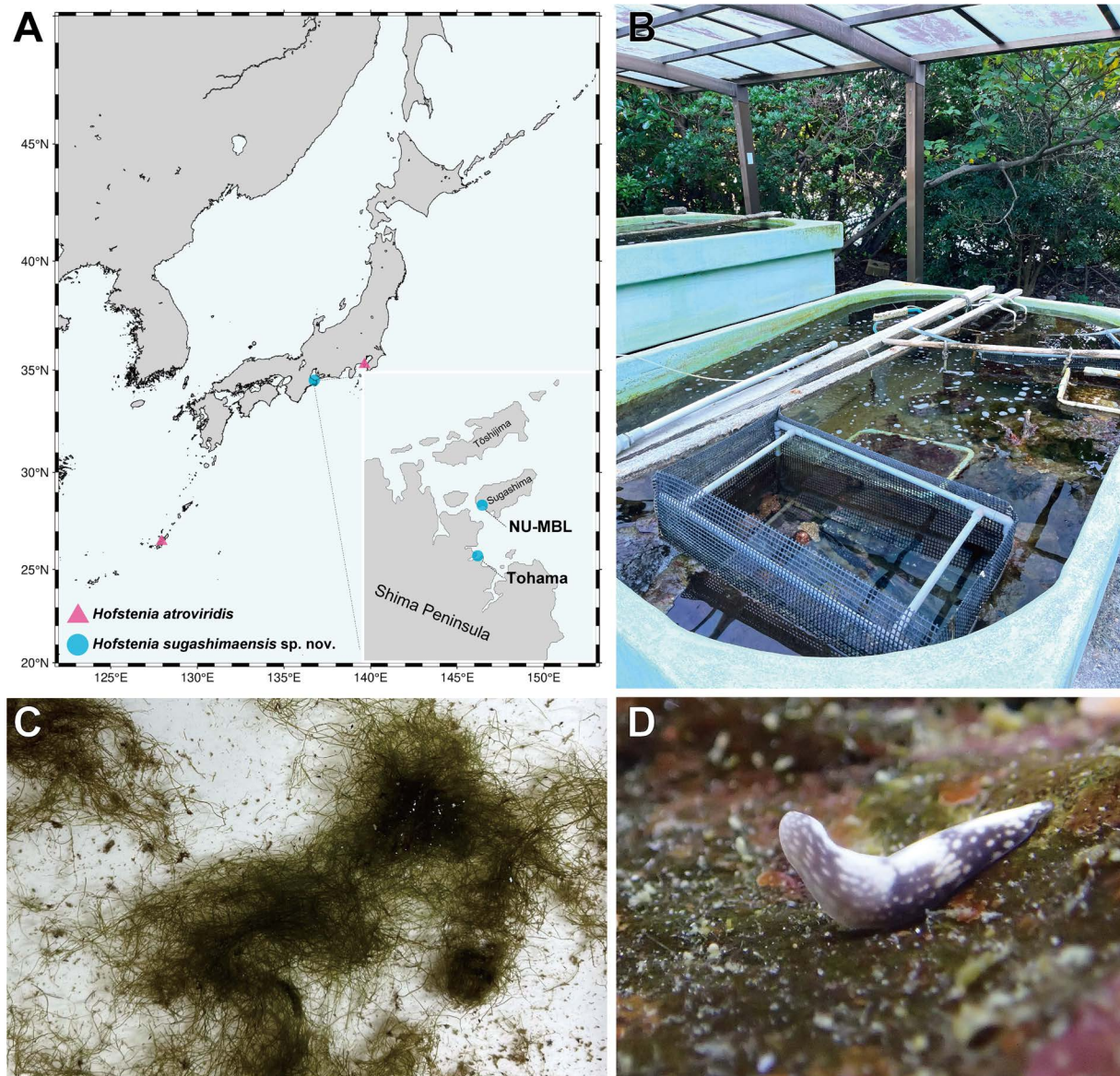


Fig. 1. Sampling locations and habitat of *Hofstenia* spp. collected from Japan. A, Map showing the geological distribution of *H. atroviridis* and *H. sugashimaensis* sp. nov.; B, outdoor tanks at the Sugashima Marine Biological Laboratory, Nagoya University (NU-MBL); C, *Bryopsis* green algae densely growing within the tanks, where *H. sugashimaensis* sp. nov. was found; D, *H. sugashimaensis* sp. nov. found from the tank at Toba Aquarium.

eras (OM SYSTEM/Olympus Tough TG-2 and TG-6). Specimens were fixed in 70% (Toba Aquarium) or 99% ethanol (NU-MBL) for DNA extraction. For histological analysis, specimens were anesthetized with 3.5% MgCl_2 in seawater, fixed in Bouin's fluid for 24 hours, and subsequently preserved in 70% ethanol. Paraffin-embedded samples were sectioned at 7 μm and stained with hematoxylin and eosin.

The methods for DNA extraction, PCR amplification for partial sequences of the cytochrome *c* oxidase subunit I (COI), 18S rRNA (18S), and 28S rRNA (28S), Sanger sequencing, nucleotide alignment, removal of ambiguous sites, and maximum likelihood phylogenetic analysis based on maximum likelihood followed the procedures described in Hookabe et al. (2024); six species in *Xenoturbella* Westblad, 1949 were used as outgroup taxa. Newly obtained sequences were deposited in GenBank, with accession numbers listed in

Table 1. Additional sequences of other acoels were retrieved from GenBank (see Hooge et al. 2007; Hookabe et al. 2024).

Results

Systematics

Genus *Hofstenia* Bock, 1923

Diagnosis (emended). Hofsteniidae with pharynx 1/4–1/2 of the body length; pharynx musculature well developed; seminal vesicles enclosed in a thick muscular wall; body bulky, without dorsal longitudinal furrows.

***Hofstenia sugashimaensis* sp. nov.**

[English name: Sugashima panther worm; Japanese name:
Sugashima-hyōmon-uzumushi]
(Figs 2–4)

Hofstenia sp. Sugashima: Hookabe et al. 2024: figs 1b, 2.

Material examined. Holotype: NMST-Xe 753, unsectioned complete specimen, fixed in Bouin's fluid, collected

Table 1. GenBank accession numbers for DNA sequences newly obtained in this study.

Species	Locality	GenBank accession numbers		
		COI	18S	28S
<i>Hofstenia atroviridis</i>	Okinawa	PX438083	PX561023	PX530453
<i>Hofstenia sugashimaensis</i> sp. nov. SG_4	NU-MBL	—	—	PX561029
<i>Hofstenia sugashimaensis</i> sp. nov. SG_5		PX441373	—	—
<i>Hofstenia sugashimaensis</i> sp. nov. SG_6		PX441366	—	PX561027
<i>Hofstenia sugashimaensis</i> sp. nov. SG_7		PX441368	—	PX561030
<i>Hofstenia sugashimaensis</i> sp. nov. SG_8		PX441365	—	PX561031
<i>Hofstenia sugashimaensis</i> sp. nov. SG_9		PX441364	—	PX561032
<i>Hofstenia sugashimaensis</i> sp. nov. SG_10		PX441372	—	PX561033
<i>Hofstenia sugashimaensis</i> sp. nov. SG_11		PX441369	—	PX561034
<i>Hofstenia sugashimaensis</i> sp. nov. SG_T1		PX441367	—	—
<i>Hofstenia sugashimaensis</i> sp. nov. SG_T2		—	—	PX561035
<i>Hofstenia sugashimaensis</i> sp. nov. SG_T3		—	—	PX561036
<i>Hofstenia sugashimaensis</i> sp. nov. SG_T4		PX441371	PX561024	PX561028
<i>Hofstenia sugashimaensis</i> sp. nov. SG_T5		PX441370	PX561025	PX561037
<i>Hofstenia sugashimaensis</i> sp. nov. SG_T7		—	—	PX561038
<i>Hofstenia sugashimaensis</i> sp. nov. TB-T8	Toba Aquarium	—	—	PX640993



Fig. 2. Living specimens of *Hofstenia sugashimaensis* sp. nov. from NU-MBL. A, Whole specimen, dorsal view; B, whole specimen, ventral view; C, color pattern variations. Abbreviations: AP, anterior patch; MO, mouth opening; PP, posterior patch; 1stML, first dorsal longitudinal midline; 1stTB, first transverse band; 2ndML, second dorsal longitudinal midline; 2ndTB, second transverse band.

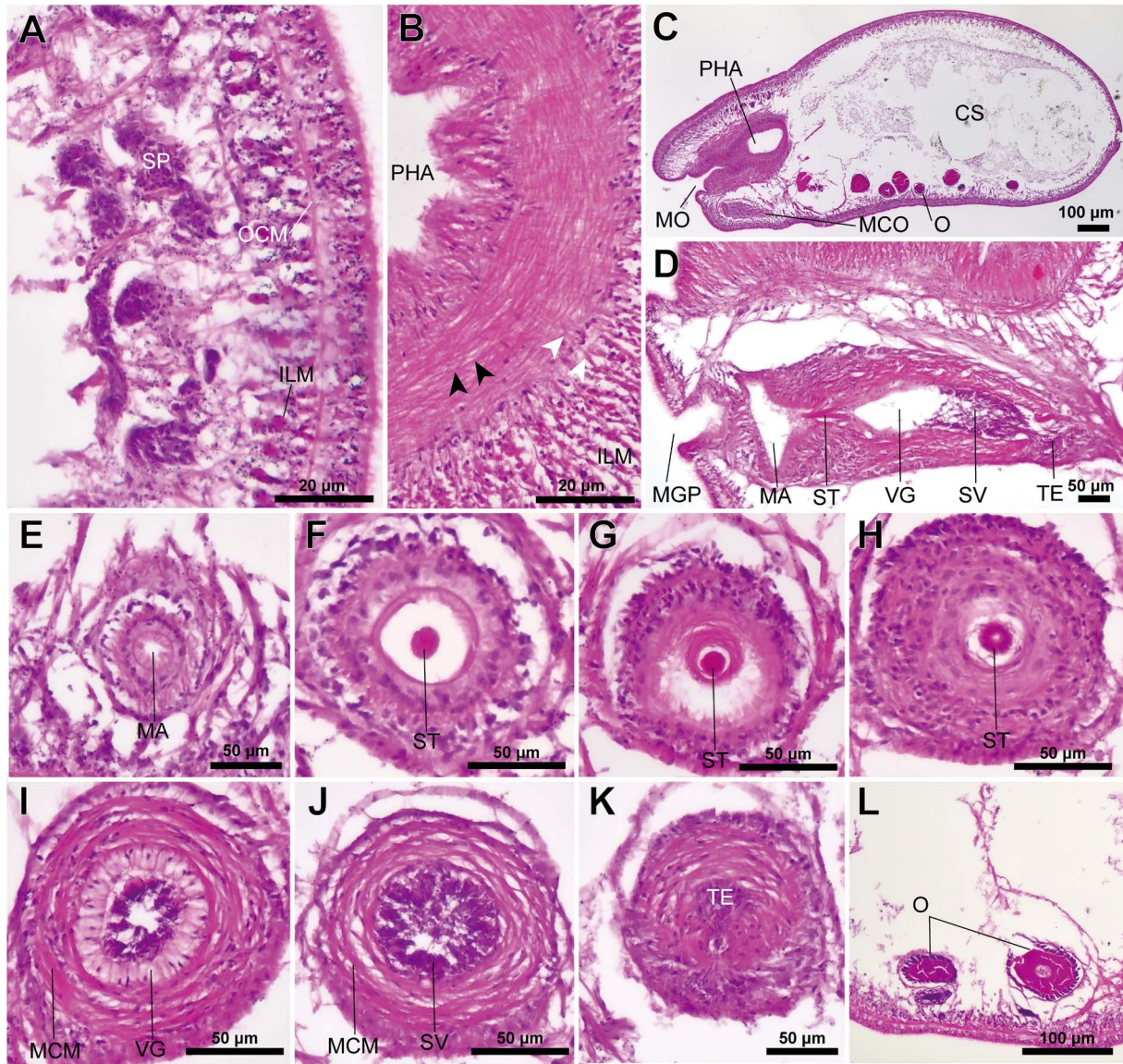


Fig. 3. Histological micrographs of *Hofstenia sugashimaensis* sp. nov., paratype, NSMT-Xe 756, transverse sections (A, B, E–L), paratype, NMST-Xe 757, sagittal sections (C, D). A, Body wall; B, pharyngeal musculature, black arrowheads pointing to circular muscles of pharynx and white arrowheads pointing to radial muscles of pharynx; C, whole body; D, male copulatory organ; E, male antrum; F, anterior part of penis stylet; G, middle part of penis stylet; H, posterior part of penis stylet; I, vesicula granulorum; J, seminal vesicle; K, testes; L, oocytes. Abbreviations: CS, digestive central syncytium; ILM, body-wall inner longitudinal muscle layer; MA, male antrum; MCM, circular muscle layer of male copulatory organ; MCO, male copulatory organ; MGP, male gonopore; MO, mouth opening; O, oocytes; OCM, body-wall outer circular muscle layer; PHA, pharynx; SP, sperm; ST, penis stylet; SV, seminal vesicle; TE, testes; VG, vesicula granulorum.

on 24 November 2024 by Naoto Jimi and SS, from an outside tank at the NU-MBL (Fig. 1). Paratypes: NMST-Xe 754, unsectioned complete specimen, fixed in 99% ethanol, collected on the same date and locality as the holotype; NMST-Xe 755, unsectioned complete specimen, fixed in 70% ethanol, collected on 7 February 2014 by Takeya Moritaki, from a tank at Toba Aquarium, where rubble and rocks in the intertidal zone of Tohama, Arashima, Toba, Mie Prefecture, Japan were kept; NMST-Xe 756, serial transverse sections, 12 slides, collected on the same date and locality as the holotype; NMST-Xe 757, serial sagittal sections, seven slides, collected on the same date and locality as the holotype.

Description. *External morphology.* Specimens approximately 5–6 mm long when contracted and 9–11 mm long

when elongated (Fig. 2A–C). Mouth opening anteriorly sub-terminal (Fig. 2B). Body bulky, dark brown overall, decorated with a distinctive pattern of cream to pale yellow markings (Fig. 2). Dorsally, numerous white dots densely packed at anterior tip, from which first longitudinal white midline extends along anterior 1/5–1/4 of body length; both lateral margins of first midline speckled with white dots (Fig. 2A). First midline interrupted by first transverse white band located in second quarter of body length; first band connected to second longitudinal white midline, which expands laterally and eventually forming second transverse white band at anterior 3/4 of body length (Fig. 2A). On both lateral margins of second midline, sparse white dots scattered against dark brown background (Fig. 2A). Posterior to second band,

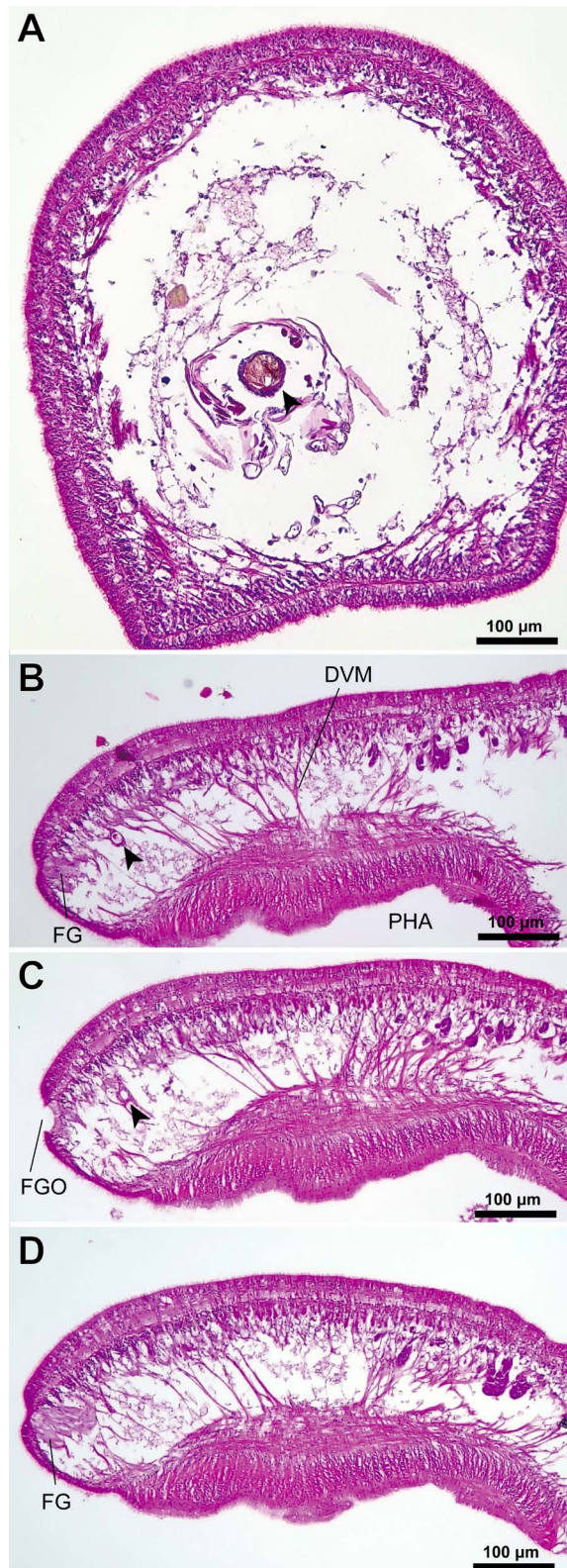


Fig. 4. Histological micrographs of *Hofstenia sugashimaensis* sp. nov., paratype, NMST-Xe 756, transverse section (A), paratype, NMST-Xe 757, sagittal sections (B–D). A, Statocyst; B, frontal glands and statocyst; C, frontal glands opening; D, frontal glands. Black arrowheads (A–C) point to a statocyst. Abbreviations: DVM, dorsoventral muscles of body wall; FG, frontal glands; FGO, frontal glands opening; PHA, pharynx.

white dots becoming less dense but reappear at the posterior tip of the body, forming posterior patch (Fig. 2A). Eyespots not observed.

Internal morphology. Body wall consisting of epidermis, outer circular and inner longitudinal muscles (Fig. 3A); parenchyma and epithelium of pharynx present (Fig. 3A, B). Pharynx 1/4–1/3 body length (Fig. 3C), with folded ciliated epithelium containing gland cells; musculature well developed, thickened with numerous circular muscle fibres; radial muscle fibres present (Fig. 3B). Male gonopore opening ventral side of mouth opening; male copulatory organ located ventral side of pharynx (Fig. 3D), consisting of male antrum (Fig. 3D, E), eversible penis with 18–22 penis stylets (Fig. 3D, F–H), vesicula granulorum (Fig. 3D, I), and seminal vesicle (Fig. 3D, J). Penis stylets about 75 µm in length (Fig. 3D). Seminal vesicle enclosed in a muscular wall (Fig. 3J); seminal vesicle muscular wall without dense radially developed muscle fibres (Fig. 3J). Testes diffuse (Fig. 3D, K), extending to posterior region of male copulatory organ. Female gonopore absent. Ovaries paired laterally and situated ventrally (Fig. 3C, L), extending from just posterior to male copulatory organ to approximately three-quarters of body length; oocytes measuring 70–80 µm in maximum diameter (Fig. 3L). Statocyst positioned near anterior tip of body (Fig. 4A–C). Frontal glands formed by elongated cylindrical gland cells, located at anterior tip of body (Fig. 4B, D), with a ciliated pore opening slightly ventrally (Fig. 4C).

Variation. The new species exhibits a consistent body color pattern observed across multiple specimens. This pattern consists of a cream to pale yellow anterior patch, a first longitudinal midline, a first transverse band, a second longitudinal midline, a second transverse band, and a posterior patch, all set against a brown background (Fig. 2A, B). While the intensity and distribution of the mottling vary among individuals, the overall pattern appears uniform (Fig. 2C).

Etymology. The specific name *sugashimaensis* derives from the type locality, Sugashima Island, Toba, Mie Prefecture.

Phylogeny. In the resulting phylogenetic tree (Fig. 5), *Hofstenia sugashimaensis* sp. nov. was placed within the Hofsteniidae clade. Within this clade, a sister relationship between *H. sugashimaensis* sp. nov. and the clade formed by *H. atroviridis* and *H. miamia* was supported by a low ultra-fast bootstrap value (UFboot) of 62%. The specimen of *H. atroviridis* collected from Okinawa formed a clade with the topotype specimen from Misaki, Kanagawa, Japan (Fig. 5); the two specimens differed by 4.7% in uncorrected *p*-distance based on COI.

We additionally sequenced the specimen from Toba Aquarium. Due to preservation in 70% ethanol for more than 10 years, only a partial 28S fragment (395 bp) was obtained (GenBank accession no. PX640993). This sequence was identical to that of NU-MBL specimens and differed from congeners, supporting its identification as *H. sugashimaensis* sp. nov.

Distribution and habitat. This species was found among green algae *Bryopsis* J.V. Lamouroux densely growing within an outdoor tank at the NU-MBL (Fig. 1A). The tank contained rubble and rocks encrusted with sessile ani-

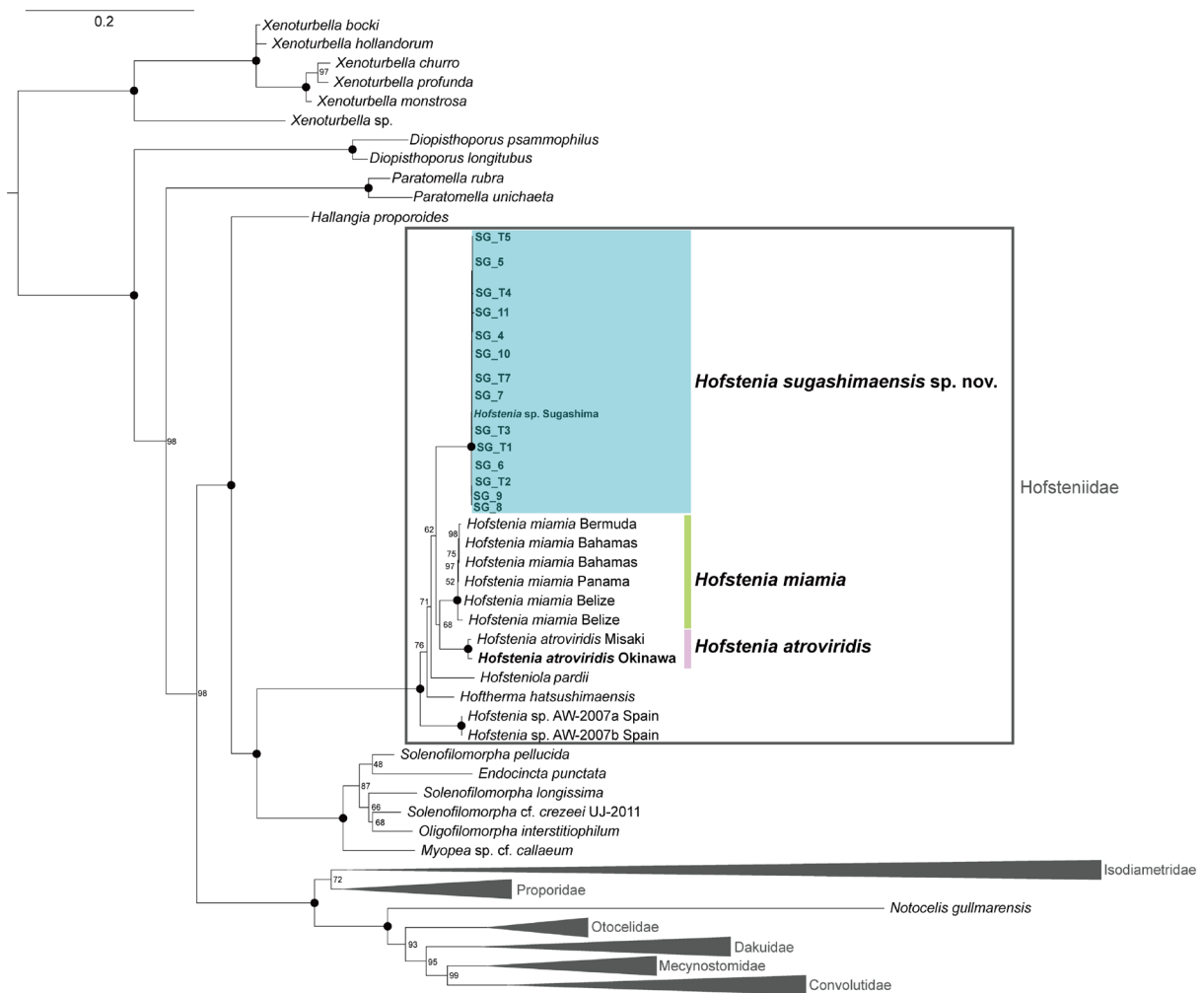


Fig. 5. Maximum-likelihood phylogenetic tree of the selected families in Acoela based on concatenated sequences of COI (636bp), 28S (1759bp) and 18S (1338bp). Solid circles indicate full support (100%) of ultrafast bootstrap value obtained using IQ-TREE software (Trifinopoulos et al. 2016).

mals (e.g., octocorals and sponges) that were collected as by-catch using fishery gill nets in Ise Bay and maintained with a flow of natural seawater (Fig. 1B, C). Additionally, specimens were collected from a tank at the Toba Aquarium, where rubble and rocks in the intertidal zone of Tohama, Arashima, Toba, Mie Prefecture, Japan are kept (Fig. 1A).

Remarks. The new species is placed within Hofsteniidae based on the following morphological characteristics: the subterminal position of the mouth opening (Fig. 2B), a muscular pharynx approximately 1/4–1/3 of body length, the anterior and ventral positioning of the male copulatory organ relative to the pharynx (Fig. 3C, D), and the absence of a female gonopore. Our phylogenetic analysis strongly supports the monophyly of Hofsteniidae with 100% UFboot (Fig. 5), within which the new species is included.

Hofstenia sugashimaensis sp. nov. shows the diagnostic characteristics of *Hofstenia*, including a pharynx measuring 1/4–1/3 of the body length, well-developed pharyngeal musculature (Fig. 3B), seminal vesicles enclosed in a thick muscular wall (Fig. 3J) [N.B.: mistakenly listed as “not enclosed in a muscular wall” in table 1 of Hookabe et al. (2024)], and a bulky body lacking dorsal longitudinal furrows (Fig.

2A, C). Morphologically, *Hofstenia* is similar to *Hoftherma* Hookabe, Jimi, Furushima, and Fujiwara, 2024 but can be distinguished by the absence of dorsal longitudinal furrows (Fig. 2A, C). This distinction is further supported by our phylogenetic analyses, where the three *Hofstenia* species (*H. atroviridis*, *H. miamia*, and *H. sugashimaensis* sp. nov.) form a clade that does not include *Hoftherma hatsushimaensis*.

Hofstenia comprises *H. arabiensis*, *H. atroviridis*, and *H. miamia*, with *H. beltagii* Steinböck, 1966 and *H. minuta* Palombi, 1928 considered species inquirenda (Tyler et al. 2006–2025). *Hofstenia sugashimaensis* sp. nov. differs from these species by its larger body size (up to 11 mm when extended), proportionally shorter pharynx (0.25–0.33 of body length), and slightly fewer penis stylets (18–22 vs. 20–25 in the others; see Hooge et al. 2007; Beltagi and Mandura 1991). The penis stylets of *H. sugashimaensis* sp. nov. (75 µm) are longer than those of *H. miamia* from Curaçao (40 µm) but comparable to those of *H. miamia* from Belize and *H. atroviridis* (cf., Hooge et al. 2007).

The body color pattern of *H. miamia* is typically characterized by three white transverse bands, differing from *H. sugashimaensis* sp. nov. by the absence of the first longitudi-

nal white midline. Specimens of *H. miamia* from sediment of *Thalassia* Banks ex König in Belize and filamentous algae in the Bahamas (Hooge et al. 2007) resemble *H. sugashimaensis* sp. nov. but lack the first longitudinal midline, further distinguishing the new species. Examination of more than ten specimens of *H. sugashimaensis* sp. nov. confirmed consistent differences in external and internal morphology, supporting its recognition as a distinct species.

Among *Hofstenia* species, a panther-like body color pattern—dark pigmentation with irregular white bands and spots—has been reported in *H. miamia* and *H. beltagii*. For *H. miamia*, Hooge et al. (2007) showed body color variation, with the most common pattern being three white transverse bands, either solid or somewhat discontinuous (Hooge et al. 2007). Specimens of *H. miamia* collected from decaying mangrove leaves in Panama and Belize clearly differ from *H. sugashimaensis* sp. nov. in having three thin white transverse bands and lacking the first longitudinal white midline (cf., Hooge et al. 2007: fig. 3, pls 1–29). In contrast, specimens found in sediments with *Thalassia* in Belize (Hooge et al. 2007: fig. 3, pls 30, 31) and on filamentous algae in the Bahamas (Hooge et al. 2007: fig. 3, pls 32, 33) extremely resemble *H. sugashimaensis* sp. nov., in their anterior body coloration, which forms a pale area resembling the first transverse band as in *H. sugashimaensis* sp. nov. However, *H. sugashimaensis* sp. nov. shares a distinct first longitudinal white midline in multiple specimens, whereas *H. miamia* from the Bahamas and Belize features laterally paired patches or lacks the midline pattern.

Discussion

Interestingly, two hofsteniid species, *H. miamia* and *H. sugashimaensis* sp. nov., exhibiting similar body color patterns, have evolved in comparable habitats dominated by filamentous algae in the Pacific and Caribbean/Atlantic Oceans. According to Steinböck (1966), the taxon inquirendum *H. beltagii*, which also exhibits a panther-like body color pattern, occurs among macroalgae in the Red Sea. Hooge et al. (2007) suggested that *H. miamia* may represent a case of aposematic coloration, mimicking the similarly colored, unpalatable nudibranch *Navanax aenigmaticus* (Bergh, 1893), which is occasionally found in the Caribbean (Hooge et al. 2007). Supporting this hypothesis, a nudibranch—likely *Haloo japonica* (Pilsbry, 1895)—displaying a body color remarkably similar to that of *H. sugashimaensis* was observed on filamentous green algae (*Bryopsis* sp.) during our study in Sugashima. A robust molecular phylogeny will clarify whether these patterns share a single origin or evolved independently due to similar environmental pressures.

Data Availability Statement

All data supporting the findings of this study are included in the published article. The sequences used in this study have been deposited in DDBJ/GenBank/ENA under the

accession numbers referred to in the text.

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Author Contributions

Natsumi Hookabe: Conceptualization; Resources; Investigation; Visualization; Writing – original draft; Writing – review & editing. Satoshi Shimooka: Resources; Investigation; Writing – review & editing. Takeya Moritaki: Resources; Investigation; Writing – review & editing. Naoto Jimi: Resources; Investigation; Writing – review & editing.

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Declaration

Competing interests. The authors declare no conflicts of interest.

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