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A New Species of *Oscillatoria imperialis* sp. nov. (Oscillatoriales, Cyanobacteria) from the Imperial Palace Grounds, Tokyo, Japan

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Abstract. We describe *Oscillatoria imperialis* sp. nov. (Oscillatoriales, Cyanobacteria) from the Imperial Palace Grounds, Tokyo, Japan. The species resembles *O. princeps* morphologically but differs in having broader trichomes that maintain nearly uniform width to the ends and in exhibiting markedly slower gliding motility. Phylogenetic analyses of 16S rRNA sequences recover *O. imperialis* as a distinct, well-supported clade within genus *Oscillatoria* sensu stricto, with affinity to *O. kawamurae*. Predicted ITS secondary structures—particularly the D1-D1′ Helix and V2 region — also distinguish *O. imperialis* from *O. princeps*.

Keywords: cyanobacteria, Imperial Gardens, *Oscillatoria imperialis*, *Oscillatoria princeps*, ITS secondary structure, 16S rRNA phylogeny.

Introduction

During a flora survey of microalgae on 2 August 2022, we observed a continuous cyanobacterial mat covering the downstream reach of the artificial stream from Ōtaki Waterfalls to Hakuchō-bori Pond, and much of the pond surface itself, within the Imperial Palace Grounds (Tokyo, Japan). Microscopy revealed dominance by a single *Oscillatoria* species closely resembling *O. princeps* Vaucher ex Gomont but with conspicuously thicker trichomes that remain nearly constant in width along their length. Because *O. princeps*—the type species of *Oscillatoria*—was recently epitypified (Mühlsteinová and Guiry, 2018) and characterized morphologically and genetically (Mühlsteinová *et al.,* 2018), we compared the Imperial Palace material against the epitype concept and allied taxa using morphology and molecular data (16S rRNA and ITS secondary structure).

Materials and Methods

Sampling and microscopy

Material was collected by A.T. from a benthic mat at the bottom of Hakuchō-bori Pond (Imperial Gardens, Imperial Palace Grounds, Tokyo, Japan) on 2 August 2022. In situ measurements were: electrical conductivity 375 μS cm^{-1}, pH 7.62, and water temperature 29.3 °C. Living material was observed the following day by light microscopy (Eclipse 50i, Nikon) and imaged with a CMOS camera (Floyd-4K, Wraymer). After observation, the specimen was fixed in formalin and deposited in TNS (TNS AL-63292m). The pond is fed by a small artificial stream from the Ōtaki artificial waterfall. The cyanobacterial mat (~0.5 cm thick) covered the riverbed from mid-reach to the pond.

Genomic DNA extraction and whole-genome amplification

Five thalli were isolated under an inverted microscope (AX10, Zeiss) and transferred to 1.5-mL microtubes, then stored at −20 °C. Whole-genome

amplification (WGA) was performed on thalli directly using the REPLI-g Mini Kit (Qiagen) following Lepère *et al.* (2011). Amplified products were stored at −20 °C and assigned identifiers Ak2081–Ak2084 (successful WGA samples are indicated below).

PCR amplification, sequencing, and assembly

An initial PCR (set I) of the 16S rRNA region employed primers PLG-1.3 (Urbach *et al*., 1992) and PitsE-cyanR (Ernst *et al*., 2003). Reactions (25 μL) contained 1 × Q5 Reaction Buffer (New England Biolabs), 200 μM each dNTP, 0.25 μM of each primer, 0.5 U Q5 High-Fidelity DNA Polymerase, and 1 μL template. Cycling: 98 °C 30 s; 35 cycles of 98 °C 10 s, 60 °C 15 s, 72 °C 60 s; final extension 72 °C 7 min. In the initial PCR, contamination was observed in the sequencing results. Therefore, new specific primers were designed based on the sequencing results, and new PCRs were performed. PCRs used five primer sets: (A) Oscillatoria-Kokyo-1150f + PitsE-cyanR; (B) Oscillatoria-1360f + PitsE-cyanR; (C) 27f (Lane 1991) + Oscillatoria-Kokyo-1150r; (D) 27f + Oscillatoria-579r; (E) Oscillatoria-Kokyo-1490f + PitsE-cyanR (Table 1). Amplicons were inspected on 1% agarose gels. Direct Sanger sequencing employed BigDye Terminator chemistry on an ABI 3130xl with primers in Table 1. Contigs were assembled in ChromasPro and manually curated.

Phylogenetic analyses and ITS secondary-structure prediction

16S rRNA sequences from our samples and related taxa were aligned (manual curation), and maximum-likelihood (ML) and neighbor-joining (NJ) trees were inferred in MEGA v12 (Kumar *et al.,* 2024) with the best-fit substitution model selected by AICc. Node support was assessed with 500 bootstrap replicates (ML and NJ). Sequences of *Microcoleus* and relatives served as outgroups. For ITS, we predicted RNA secondary structure with RNAfold (ViennaRNA Package v2.x: Gruber *et al.* 2008; Lorenz *et al.,* 2011) in standard minimum-free-energy mode (25 °C) and with Mfold (Zuker, 2003), retaining dot-bracket and EPS (RNAplot) outputs. To address known ITS secondary-structure, we constrained: (i) D1′→D2 unpaired; (ii) D2 unpaired; (iii) D1-D1′ pairing internal only; (iv) no pairing between pre- and post-tRNA-Ile; (v) no upstream pairing for positions ≥ tRNA-Ala. The DIV value developed by Villanueva *et al*. (2024) was calculated to determine whether each clone in the ITS region is an ortholog or a paralog.

Results

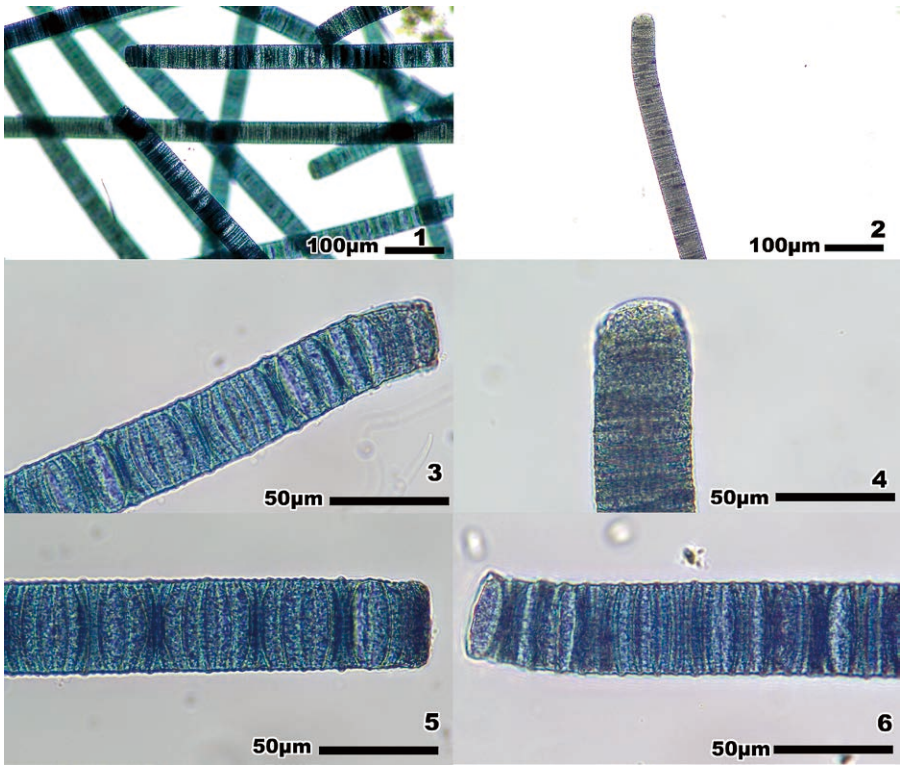
Taxonomic treatment

Oscillatoria imperialis Tuji & Niiyama sp. nov.

Holotype. TNS AL-63292m (fixed in formalin and preserved as a liquid collection), collected from a cyanobacterial mat at Hakuchō-bori Pond, Imperial Gardens, Tokyo, Japan, 2 August 2022.

Table 1. List of primers used for PCR and sequencing in this study

Primer name	Sequences	Reference	PCR set	Sequencing
PLG1.3 (CYA108F)	ACGGGTGAGTAACRCGTRA	Urbach *et al.* 1992	I	I
pits-CyanR	CTCTGTGTGCCAAGGTATC	Ernst *et al*. 2003	I, A, B, C	I, A, B, C
Oscillatoria-Kokyo-1150f	AGATCGAAGCTTGCAACTCAGCTTCG	This study	A	A, B, E
Oscillatoria-1360f	TCACACCATGGGAGCTGGTTTAG	This study	B	A, B
27f	AGAGTTTGATCMTGGCTCAG	Lane 1991	C, D	
Oscillatoria-Kokyo-1150r	TTCACGAAGCTGAGTTGCAAGCTTC	This study	C	
Oscillatoria-579r	TGGGAATTCCCTCTACCCATACTG	This study	D	
Oscillatoria-Kokyo-1490f	ACCTRCCTTGCTGATGATCGATAC	This study	E	A, B, E
905r	CCGTCAATTCATTTGAG	This study		I, C
r1L	GTATTACCGCGGCTGCTGG	Lane 1991		C, D



Figs. 1–6. *Oscillatoria imperialis*. Living material before formalin-fixation of a speciemen TNS AL-63292.

Type locality. Hakuchō-bori Pond and adjacent artificial stream, Imperial Palace Grounds (Tokyo, Japan).

Etymology. From Latin imperialis (pertaining to the Imperial Palace), referring to the type locality.

Diagnosis. Trichomes long, rigid, almost straight, 34–42 µm mid-trichome, nearly uniform in width to the ends, slow-gliding; cells discoid, short, with fine granulation; apical cells truncate to sub-hemispherical, sometimes hyaline; sheath absent. Differs from *O. princeps* by broader trichomes that do not markedly taper, and by slower motility; differs from *O. kawamurae* Negoro by attached habit and absence of aerotope-like gas vesicles.

Description. Thallus dark blue-green to black, forming mats along silty substrates of a slow stream and small pond. Trichomes olive to dark blue-green, long, rigid, almost straight, not constricted at cross-walls, of nearly constant width or rarely slightly tapered at the ends, 34–42 µm wide and 27–36 µm wide at the ends, without sheath, sometimes with terminal slight bends, slowly gliding. Cells discoid, short, about 1/6–1/10 times as long as wide, 3.8–7.6 µm long, containing fine granules. Apical cells truncate to depressed hemispherical, without calyptra.

Ecology. Occurs on silty, low-flow substrates subject to seasonal scouring; site co-occurs seasonally with *Spirogyra* spp. and large benthic *Nitzschia* spp.; clean-water macroindicators [e.g., *Riverina jigongshanensis* (F.Nan & S.Xie) C.W.Vieira & G.W.Saunders and fireflies *Nipponoluciola cruciata* (Motschulsky), *Aquatica lateralis* (Motshulsky)] were found nearby.

Phylogenetic analysis of 16S rRNA

Two WGA products (Ak2081, Ak2083) yielded 16S sequences. In ML and NJ analyses, *O. imperialis* (Ak2081, Ak2083) formed a well-supported monophyletic clade within *Oscillatoria* s. str. (bootstrapvalues 100 for NJ and 99 for ML), sister to a clade comprising multiple *O. kawamurae* se-

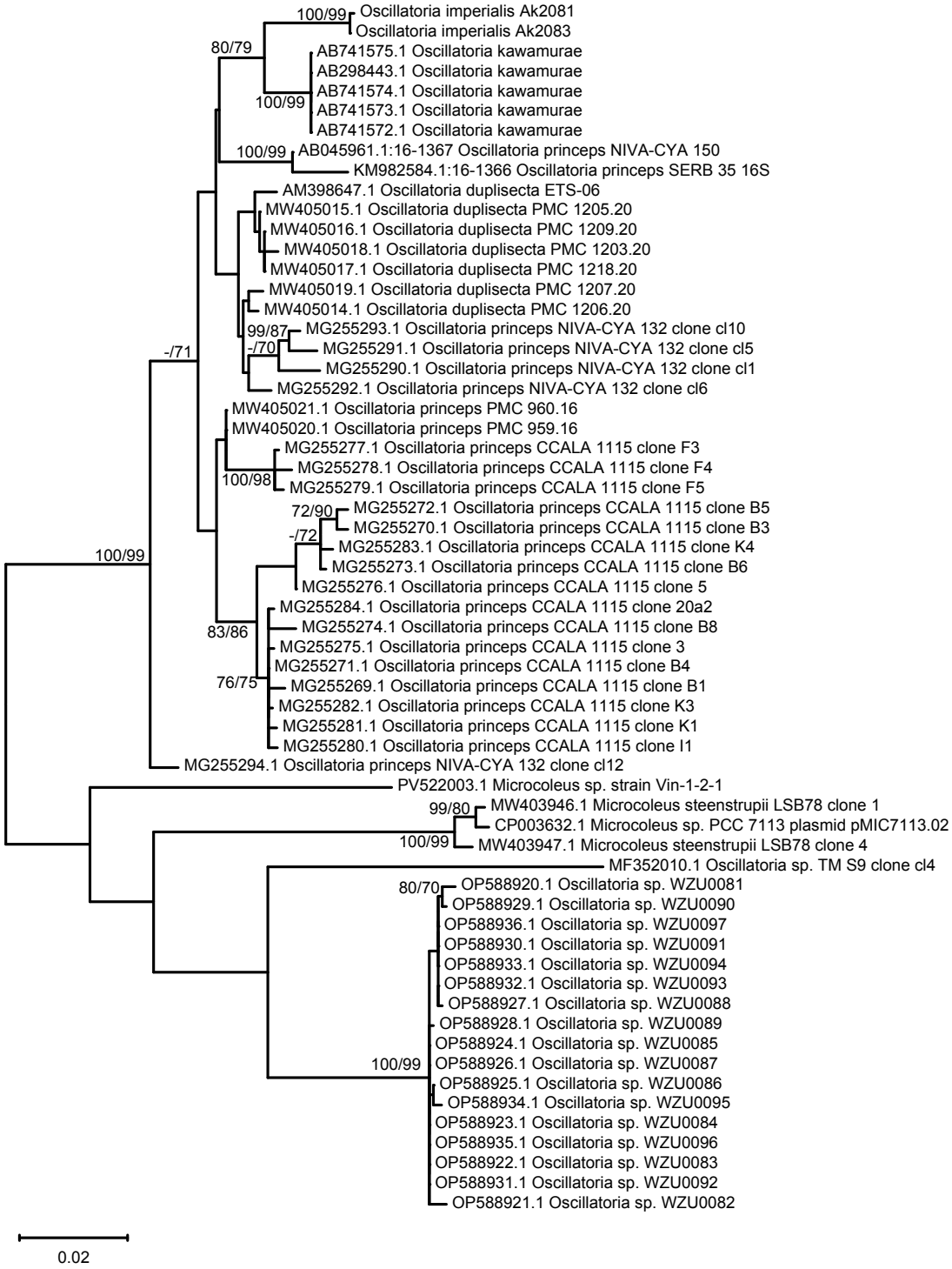


Fig. 7. Phylogenetic tree of *Oscillatoria imperialis* and related taxa determined using the Maximum Likelihood (ML) method with 16S rRNA genes. NJ/ML bootstrap support values are represented on branches (only values above 70 are shown).

quences (bootstrap values 80 for NJ, 79 for ML) (Fig. 7). The reference strain *O. princeps* CCALA 1115 grouped nearby within *Oscillatoria* s. str.

Secondary structure of ITS region

From Ak2081 we obtained a 1,858-bp fragment spanning 16S-ITS; the 16S segment (1,438 bp) was excluded, leaving 420 bp of ITS structure prediction. tRNA features were identified with tRNAscan-SE (Chan *et al.,* 2021; tRNA-Ile, positions 180–253; tRNA-Ala, 281–353) and used to delimit visualization windows and constraint intervals. The D1 and D1′ regions corresponding to the motifs of Iteman *et al.* (2000) and Tuji and Niiyama (2018) were recognized. Immediately downstream of D1′ we detected a region differing by one base from Iteman *et al.* (2000), which we assign to D2. In keeping with the Methods, we enforced the following constraints during folding: positions 113–135 and 136–143 unpaired; D1 allowed to pair internally only; no pairing between pre- and post-tRNA-Ile; and no upstream pairing with positions ≥ 354. Because complete sequencing from the upstream of 16S to the downstream of 23S was not achieved (cf. Tuji and Niiyama, 2018), analyses were performed under these predefined constraints.

A linear arc diagram summarizing the ITS secondary-structure architecture of Ak2081 at 25 °C is provided in Fig. 8, and the RNAplot-style 2D structure in Fig. 9. The V2 region reported by Iteman *et al.* (2000) and Tuji and Niiyama (2018) between tRNA-Ile and tRNA-Ala was also recovered (Figures 8, 9). The D1–D1′ domain formed two long stems with a large terminal hairpin, whereas V2 resolved as a short stem-loop. Downstream of tRNA-Ala we detected a three-stem motif. Although its position corresponds to Box B sensu Iteman *et al.* (2000), the motif differs in detail. Because more distal regions (e.g., the Box A spacer and D4) were not available in our data, further comparisons were not attempted.

Comparative structures of the D1 and D1′ regions for *O. imperialis* (Ak2081, Ak2083) and *O. princeps* (CCALA 1115 clones; NIVA-CYA 150 and NIVA-CYA 132) are shown in Figure 10. A large terminal hairpin of 10–17 nt was observed, together with single-base mismatches immediately after D1 and within the eight bases preceding D1′, as well as one mismatch on each side of the D1–D1′ hairpin. In NIVA-CYA 150 (MG25585) no mismatch was present on the D1′ side, whereas in CCALA 1115 (MG255277) two bases on the D1 side and one on the D1′ side were mismatched. Variation among clones of CCALA 1115 likely reflects clonal heterogeneity. Because three mismatches were shared by all clones except NIVA-CYA 150, we infer broadly similar secondary structures among the remaining clones. Given that NIVA-CYA 150 is phylogenetically distant (Fig. 7), it may represent a separate species. V2-region structures for *O. imperialis* (Ak2081, Ak2083) and *O. princeps* (CCALA 1115 clones F3, F4, F5) are shown in Figure 11; among available CCALA 1115 clones, only F3–F5

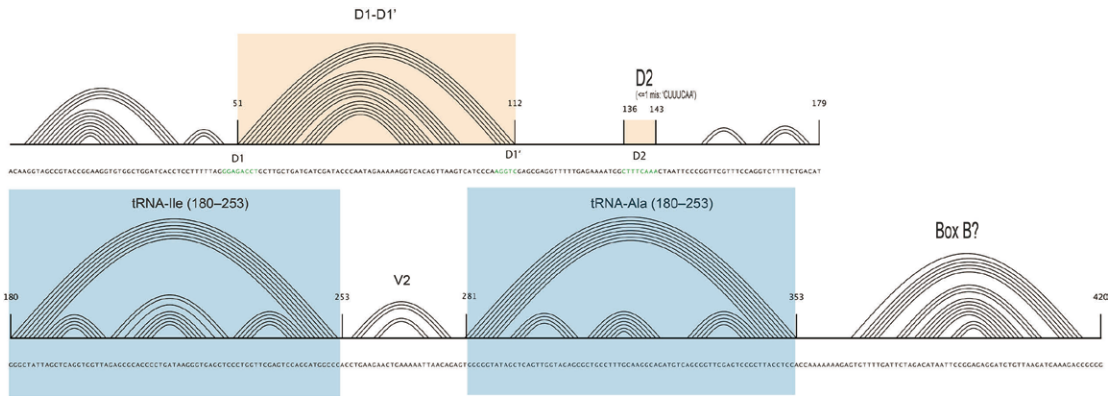


Fig. 8. Linear arc diagram of the ITS secondary-structure architecture at 25 °C for *Oscillatoria imperialis* Ak2081.

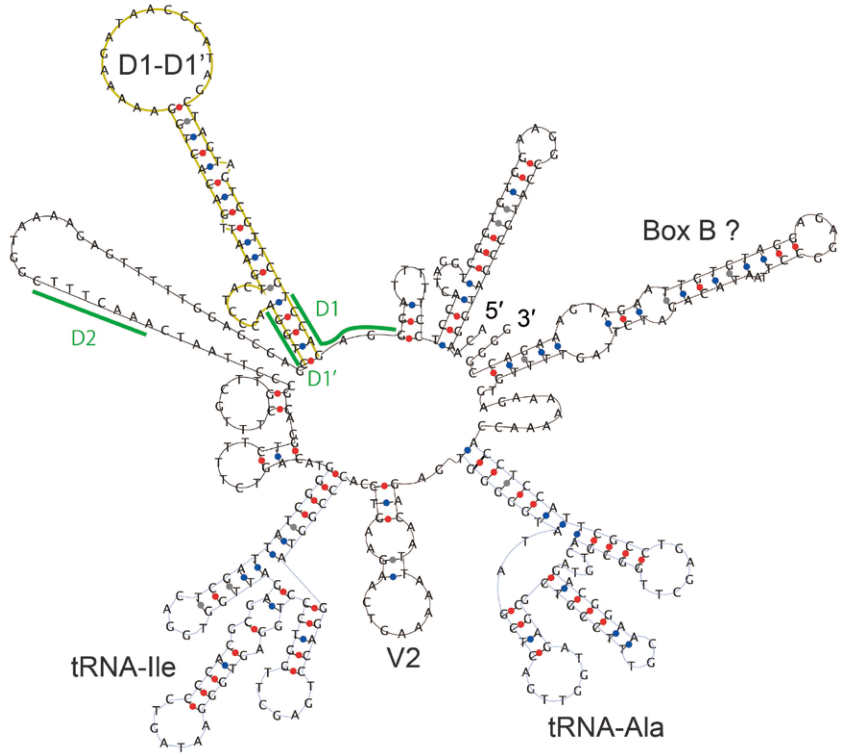


Fig. 9. RNAplot-style 2D secondary structure of the ITS region showing D1, D1′, D1–D1′ region, D2, tRNA-Ile, V2 region, tRNA-Ala and BOX B like region. *Oscillatoria imperialis* Ak2081.

covered V2. Ak2081 and Ak2083 were identical to each other, as were F3–F5. Although *O. imperialis* and *O. princeps* differed by only one nucleotide (asterisk in Fig. 11), the predicted secondary structures were markedly different.

Discussion

Oscillatoria imperialis vs *O. princeps*

Morphologically, *O. imperialis* has wider trichomes that maintain nearly uniform width to the ends and differ from *O. princeps* (Figs. 1–6). The distinction between the two taxa was also shown in phylogentic tree (Fig. 7) and ITS secondary structure (Fig. 11).

Comparative structures of the D1–D1′ Helix, *O. princeps* CCALA1115 is broadly divided into three types of clones (Fig. 10). Clones F3, F4 and F5 possess both tRNA-Ile and tRNA-Ala, clone K4 possesses only tRNA-Ile, and clone B3 possesses neither (Table 2) Clones K4 and B3 form a 3-base pair stem (Table 2, Fig 10). Clones F3, F4 and F5 possess relatively low DIV values and are closer to *O. imperialis* (Ak2081 and Ak2083) (Table 2). Furthermore, clones K3 and B3 are paralogous but could not be definitively determined due to limited information from related species.

The conserved regions of the D1–D1′ domain in strains and clones were analyzed by dividing them into four zones. Zone A contains the basal clamp and variable unmatched nucleotides. Zone D includes the terminal hairpin and a stem of several bases. Zones B and C were separated at the site of a single-base mismatch in Ak2083 (Fig. 10). Since the 5’ side of the D1–D1′ region is more susceptible to evolutionary influence, analysis focused on the 5’ side bases (Table 2). For each zone, we analyzed the 5’-side region exhibiting a higher evolutionary rate (Villanueva *et al*., 2024) as demonstrated by their ΔG-based D1’ Index (DIV) analysis (Table 2).

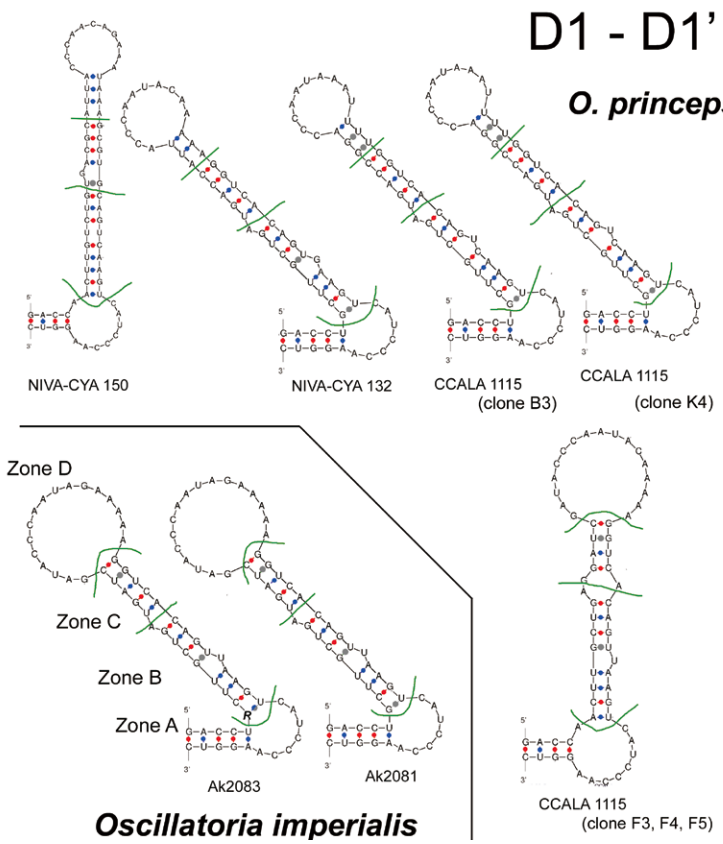


Fig. 10. Secondary structures of the D1–D1′ Helix among *Oscillatoria imeprialis* (Ak2081 and Ak2083), *O. princeps* strain CCALA 1115 (clone F3: MG255277, clone B3: MG255270, clone K4: MG25583), *O. princeps* strain NIVA-CYA 150 (MG25585) and *O. princeps* strain NIVA-CYA 132 (MG255293).

In *O. imperialis* (Ak2081 and Ak2083) and the ortholog candidate *O. princeps* CCALA1115 (clones F3, F4 and F5), 'U' substitutes for 'A' in zone A and 'U' substitutes for 'G' in zone C, resulting in mismatches in both cases. In zone B of the *O. imperialis* sequences, Ak2081 had 'G' while Ak2083 had R (A or G). In *O. princeps* CCALA1115 (clones F3, F4 and F5), it is 'A', while in other *O. princeps* CCALA 1115 clones it is 'G'. Therefore, it is highly likely that polymorphism exists at this base in *O. imperialis* (Ak2081 and Ak2083). The two nucleotide differences found between *O. imperialis* and *O. princeps* CCALA 1115 (epitype strain for this taxon) are considered significant differences as they affected pairing, supporting their classification as distinct species. *O. princeps* NIVA-CYA 150 and NIVA-CYA 132 showed even greater differences

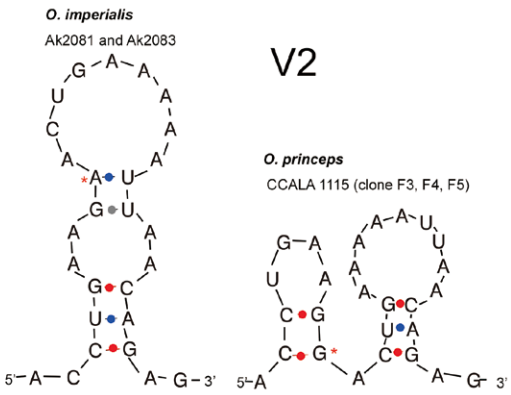


Fig. 11. The secondary structure of V2 region. *Oscillatoria imeprialis* (Ak2081 and Ak2083) and *O. princeps* strain CCALA 1115 (clone F3: MG255277, F4: MG255278, F5: MG255279).

Table 2. DIV values for the D1–D1′ Helix, presence/absence of tRNA, and sequences for zones A–D. Red text dindicates differences from *O. imperialis* (Ak2081). Uppercase letters denote matches, while lowercase letters indicate mismatches.

taxa	strain / clone	DIV	tRNA-Ile	tRNA-Ala	zone A	zone B	zone C	zone D
O. imperialis	Ak2081	0.71	+	+	GACCU	GCUUG	CUGa U	GAUC gauacccaauagaaaaa
O. imperialis	Ak2083	0.71	+	+	GACCU	RCUUG	CUGa U	GAUC gauacccaauagaaaaa
O. princeps	CCALA1115 (clone F3, F4, F5)	0.85	+	+	GACCa	ACUUG	CUGa gGAUC	gauacccaauacaaaaa
O. princeps	CCALA 1115 (clone K4)	0.88	+	-	GACCU	GCUUG	CUGa U	GACC G-GAcccaauaaau---
O. princeps	CCALA 1115 (clone B3)	0.88	-	-	GACCU	GCUUG	CUGa U	GACC G-GAcccaauaaau---
O. princeps	NIVA-CYA 132	0.54	+	-(?)	GACCU	GCUUG	CUGa U	GACC AUUacccaauacaa---
O. princeps	NIVA-CYA 150	0.61	-(?)	-(?)	GACCa	AUUUGuCUG	UgACGC	aUUAcccaacagaaa--

than CCALA1115 (Table 2).

In studies of freshwater algal assemblages under anthropogenic disturbance, *O. princeps* has been reported as a species that thrives under polluted water conditions (Miranda and Krishnakumar, 2015). The classical compilations of algae tolerant to organic pollution rank the genus *Oscillatoria* highly among pollution-tolerant taxa; although the species *O. princeps* is not always singled out, it appears within the tolerant species list (Palmer, 1969). The habitat of *O. imperialis* discovered this time, in contrast to *O. princeps* known as a pollution-tolerant species, is free from pollution loads and inhabited by the red algae *Riverina jigongshanensis* and fireflies (*Nipponoluciola cruciata* and *Aquatica lateralis*), both known as indicator organisms for clean water species. *O. imperialis* has not been found outside its type locality to date. Therefore, further research is needed to determine its indicator value.

The habitat where this *O. imperialis* was found has a silty substrate and slow-moving currents, dominated seasonally by *Spirogyra* spp. (Niiyama and Tuji, 2014) or large *Nitzschia* spp. (Tuji and Niiyama, 2014). It is thought that heavy rainfall floods wash away most of these, resulting in pronounced seasonal changes where a single species forms a pure community. Within Japan, clear-water locations in rivers with such gentle silty substrates are generally limited to spring areas. However, while spring areas are typically cold and maintain constant temperatures, the sampling site in this study reached a high temperature of 39 °C, indicating a different environment. This unique environment within the Imperial Palace is considered to characterize this species.

Oscillatoria imperialis vs *O. kawamurae*

O. kawamurae is widely recognized as phytoplankton in East Asia, including Lake Biwa (Thu *et al.,* 2020). Trichomes float solitary and are exceptionally thick, measuring 60–80 μm in width, making them clearly visible to the naked eye. It differs significantly from other *Oscillatoria* species because it possesses aerotope-like gas vesicles structure within the cell. No planktonic species of the genus *Oscillatoria* have been found other than *O. kawamurae*. Genetic analysis of *O. imperialis* revealed that this species belongs to the same clade as *O. kawamurae*. Unlike *O. kawamurae, O. imperialis* does not exhibit gas vesicle structures and was found as attached algae. *O. kawamurae* is cultured at very high nutrient concentrations (Thu *et al.,* 2020), and cannot be cultured in media such as CT medium typically used for planktonic cyanobacteria (Pers. inf.). The life cycle of *O. kawamurae* is poorly understood, but it may proliferate as an attached algal species in muddy, nutrient-rich areas and become planktonic in response to environmental changes. The close relationship between *O. imperialis* and *O. kawamurae* may serve as a starting point for research into *O. kawamurae*, which possesses highly specialized characteristics.

Acknowledgments

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皇居から見いだされたシアノバクテリア(Oscillatoriales)の一新種 *Oscillatoria imperialis* sp. nov.

辻　彰洋・新山優子

皇居・白鳥堀からシアノバクテリアの新種*Oscillatoria imperialis* sp. nov.を記載した．本種の形態は*O. Princeps*に似るが，トリコームがより太く端が細くならない，また動きが遅い点で異なる．本新種はまた16S rRNAによる系統解析やITS領域の二次構造でも*O. princeps*と区別される．