Reclassification of a *Polynucleobacter cosmopolitanus* strain isolated from tropical Lake Victoria as *Polynucleobacter victoriensis* sp. nov.

Martin W. Hahn, Johanna Schmidt, Grace Ssanyu Asiyo, Nikos C. Kyrpides, Tanja Woyke and William B. Whitman

**Abstract**

The genus *Polynucleobacter* (family *Burkholderiaceae*) is phylogenetically subdivided into at least four subclusters. One of those, subcluster PnecC, was recognized as a cryptic species complex. Here we test by comparative genome analyses whether subcluster PnecD, currently solely represented by the species *Polynucleobacter cosmopolitanus*, also represents such a cryptic species complex. The genome sequences of the two *P. cosmopolitanus* strains, MWH-Molso2\(^T\) and MWH-VicM1, were determined. The latter strain was also characterized in the previous description of *P. cosmopolitanus*. These two strains originate from a temperate lake located in Austria and from the large tropical Lake Victoria located in East Africa, respectively. Strains MWH-Molso2\(^T\) and MWH-VicM1 possess quite small genomes of 1.78 and 1.63 Mbp, respectively, and share similar G+C values of 44.1 and 43.1 mol%, respectively. Both strains encode only a single copy of the ribosomal operon, and their 16S rRNA genes differ only in four positions, equalling a sequence similarity of 99.74%. Both genomes possess characteristics indicating evolutionary genome streamlining, such as high coding densities of 93.9 and 94.6% of bases, respectively. Average nucleotide identity (ANI) comparisons of the genomes of the two strains resulted in a value of 78.4%, suggesting that each of the strains represents a separate species. Our investigation suggests that PnecD represents an additional cryptic species complex within the genus *Polynucleobacter* that was not resolved by 16S rRNA gene sequence analyses. We propose reclassification of strain MWH-VicM1 as *Polynucleobacter victoriensis* sp. nov., with type strain MWH-VicM1\(^T\)(=DSM 21486\(^T\)=JCM 32005\(^T\)).

The genus *Polynucleobacter* and the species *Polynucleobacter necessarius* were described by Klaus Heckmann and Helmut J. Schmidt as obligate endosymbionts of ciliates [1]. Diversity studies by cultivation-independent methods revealed that bacteria closely related to *P. necessarius* are typically present in the water column of lakes [2], ponds [3] and running waters [4], and that these bacteria frequently occur in such systems with high cell numbers [5]. Isolation of strains [6], investigations of environmental samples by fluorescence in situ hybridization (FISH) [3, 7], and cultivation experiments with endosymbiotic *P. necessarius* [8] indicated that *Polynucleobacter* bacteria dwelling in the water column of freshwater systems represent free-living bacteria and not obligate symbionts of ciliates [9]. Recent genome comparisons between an endosymbiotic and a free-living *Polynucleobacter* strain revealed lifestyle-specific genomic signatures, including, for instance, the presence of a large number of pseudogenes and about 30% reduction in genome size of the obligate endosymbiont [10].

A large number of *Polynucleobacter* strains could be isolated from freshwater systems and were characterized by sequencing of phylogenetic markers [6, 11, 12]. Based on phylogenetic analyses of 16S rRNA genes, the strains were grouped into the subclusters PnecA, PnecB (including PnecB1 and PnecB2), PnecC and PnecD [3, 6]. These subclusters are characterized by inter- and intra-subcluster 16S rRNA sequence similarity values of <98% and ≥99%, respectively [6, 9]. Recent investigations demonstrated that subcluster PnecC represents a cryptic species complex of currently seven described species and an unknown but presumably large number of undescribed species [13–16], which cannot be resolved by analysis of 16S rRNA gene sequences. Presently, it is not known if the other three...
**Polynucleobacter** subclusters also represent such cryptic species complexes.

Subcluster PnecD is currently represented exclusively by the species *Polynucleobacter cosmopolitanus* [17]. The description of this species included the characterization of five strains forming a monophyletic lineage and sharing 16S rRNA sequence similarities \( \geq 99.3 \% \). Owing to generally weak growth of all *Polynucleobacter* strains in artificial medium (see Suppl. Mat. Fig. S2 in [9]) and the difficulty in extracting sufficient genomic DNA for pairwise DNA–DNA reassociation experiments, investigations on genomic coherence of the five strains were omitted. Instead the five strains were preliminarily described as members of the species *P. cosmopolitanus* [17].

In the study presented here, we investigated the genomic similarity of two strains previously included in the species *P. cosmopolitanus* [17]. These strains are the type strain MWH-MoIso2\(^T\) isolated from Lake Mondsee, Austria, and the tropical strain MWH-VicM1 isolated from Lake Victoria near Kampala, Uganda [6]. Both strains were cultivated by using the filtration–acclimatization method and NSY medium [18] as described previously [6]. A comprehensive phenotypic and chemotaxonomic characterization of both strains was included in the previous species description [17]. Based on large genomic differences revealed by comparative genome analyses, we conclude that the two strains represent different species and propose to establish MWH-VicM1\(^T\) as the new type strain of *P. victoriensis* sp. nov.

**GENOMIC CHARACTERIZATION OF STRAINS MWH-MOISO2\(^T\) AND MWH-VICM1\(^T\)**

Genomic DNA of both strains MWH-MoIso2\(^T\) and MWH-VicM1\(^T\) was extracted from biomass grown in liquid NSY medium as described previously [19] and used for genome sequencing. DNA of strain MWH-MoIso2\(^T\) was sequenced by Illumina MiSeq. Paired-end sequencing (2×150 bp) of a fragment library resulted in about 1.2×10\(^8\) quality filtered reads with a mean length of 148 bp. Sequence assembly and subsequent closure of some gaps resulted in six contigs with a total length of 1.78 Mbp (Table 1). Sequencing coverage was about 100-fold.

Strain MWH-VicM1\(^T\) was sequenced at the DOE-Joint Genome Institute as part of the Genomic Encyclopedia of Type Strains, Phase III (KMG–III) study [20] using the Illumina HiSeq 2000 1TB platform. Paired-end sequencing (2×150 bp) of a fragment library resulted in about 7.4×10\(^8\) quality filtered reads. Assembly of reads resulted in three contigs with a total sequence length of 1.63 Mbp and a sequencing coverage of about 680-fold.

The obtained genome sequences of the two strains, MWH-MoIso2\(^T\) and MWH-VicM1\(^T\), were annotated using the IMG/ER annotation pipeline [21]. The IMG Genome IDs of the two genomes are 2642422582 and 2710264786, respectively. Both genome sequences were also deposited in GenBank/EMBL/DDBJ (accession numbers NJGG00000000 and FYEX00000000, respectively). Gene-finding using the JGI annotation pipeline [22, 23] resulted in 1822 and 1677 ORFs in strains MWH-MoIso2\(^T\) and MWH-VicM1\(^T\), respectively (Table 1).

Despite neither genome being closed, the obtained genome sizes are expected to be quite close to the real genome sizes of the two respective strains. Owing to the high sequencing coverage, the whole or almost the whole genome of the strains should be represented by reads. Previous independent sequencing of two very closely related *Polynucleobacter asymbioticus* strains isolated from the same habitat at a time interval of 4 years and differing only in 22 single nucleotide polymorphisms clearly resulted in the same genome size despite different sequencing technologies and strategies being used [24]. On the other hand, many *Polynucleobacter* strains contain a few repetitive sequences, which include insertion elements, giant genes with repetitive sequence elements and the translation elongation factor Tu gene present as two identical copies in all *Polynucleobacter* genomes investigated so far. Such repetitive sequences frequently do not assemble properly and form contigs in the size range of 0.1–2.0 kbp. Such contigs originating from repetitive sequences are usually characterized by coverage values of two-, three- or fourfold the mean coverage of the whole genome. Contigs smaller than 1 kbp are discarded by the IMG annotation pipeline, and thus do not contribute to the final genome size values of draft genomes. In general, such repetitive sequences not assembling properly results in underestimations of the real genome size; however, analyses of several *Polynucleobacter* genome assemblies suggest that the underestimation is usually in the range of about 1 to 5 kbp, which equals in typical *Polynucleobacter* genomes in underestimations of genome size by less than 0.4 %.

Among the free-living *Polynucleobacter* strains with sequenced genomes, strain MWH-VicM1\(^T\) has the smallest genome size. Both genomes show signatures of evolutionary genome streamlining previously described for another free-living *Polynucleobacter* strain [25] but lack large numbers of pseudogenes, a known signature for reductive genome evolution in obligate endosymbionts [10, 26]. Genome streamlining in these two investigated PnecD strains is indicated, for instance, by the high coding densities of the genomes of strains MWH-MoIso2\(^T\) and MWH-VicM1\(^T\) of 93.9 and 94.6 %, respectively. Such high coding densities have not been reported, so far, for other members of the family *Burkholderiaceae* not affiliated with the genus *Polynucleobacter*. The IMG system [21] contains currently (March 2017) 811 genomes of *Burkholderiaceae* (single cell genomes were excluded) bacteria not affiliated with the genus *Polynucleobacter*. Among these genomes, only seven (0.9 %) had coding densities >90 %, and the mean coding density was 85.1 %. By contrast, genomes of free-living *Polynucleobacter* strains usually possess coding densities >92 % [13, 14, 16, 19, 24, 25, 27].
The two genome sequences presented here are the first for *Polynucleobacter* genomes of strains affiliated with subcluster PnecD [6]. All previously published *Polynucleobacter* genome sequences represent strains belonging to subcluster PnecC [13, 14, 16, 24, 25]. The sizes of the two PnecD genomes presented in this study and the 18 previously published genomes of free-living *Polynucleobacter* strains affiliated with subcluster PnecC (Fig. 1 and [24]) differ. All published genomes of free-living *Polynucleobacter* strains are characterized by genome sizes >2 Mbp, while the two PnecD genomes possess sizes of ≤1.78 Mbp (Table 1). Unpublished genome size data of PnecC strains prove that there is no systematic difference in genome size between PnecD and PnecC strains (M. W. Hahn et al., unpublished data). Interestingly, the genome of the free-living (planktonic) strain MWH-VicM1 is only 66 kbp larger than the genome of the obligate endosymbiont *P. necessarius* STIR1 [10] and is even smaller than genomes of a few other endosymbiotic *Polynucleobacter* strains recently presented [26]. This suggests that genome sizes in obligate endosymbiotic and free-living *Polynucleobacter* strains are not necessarily very different. Thus genome size neither is a systematic trait discriminating all PnecC and PnecD strains, nor does it discriminate between free-living and endosymbiotic *Polynucleobacter* strains.

Both of the PnecD strains lack a gene cluster encoding an anoxygenic photosynthesis system previously found in the type strains of *Polynucleobacter duraquae* [14] and *P. wuianus* [16]. Interestingly, *P. cosmopolitanus* strain MWH-Molsos2TF encodes a special variant of rhodopsins (xanthorhodopsins) that is also found in the obligate methylotroph *Candidatus Methylomumilus turicensis* [28] with an amino acid identity of 82 %. These xanthorhodopsins are light-driven proton pumps tuned to green light, which could represent an adaptation to the light conditions in more productive systems [29]. Rhodopsin genes were only found in 1 [27] of the 18 genomes of planktonic *Polynucleobacter* strains and in none of the endosymbiotic strains [10, 26] investigated previously. Strain MWH-Molsos2T encodes flagella, which strain MWH-VicM1T lacks. Both strains encode an ABC-type Fe3+ transport system but no FeoAB transporters for uptake of Fe2+ ions. This reflects very well the alkaline pH conditions of their habitats [6, 13]. Neither strain encodes a cytochrome bd-I terminal oxidase (CydAB) [14–16] or a fumarate reductase (FrdABCD) found in some PnecC genomes [14–16]. Thus, both PnecD strains lack these features typically suggesting adaptation to low oxygen concentrations and facultative anoxygeniosis, respectively.

Analysis of genome similarity between *P. cosmopolitanus* MWH-Molsos2T and strain MWH-VicM1T by ANI [30, 31] using the IMG system [21] resulted in a value of 78 % ANI (Fig. 1). By contrast, pairwise ANI comparisons with genomes of PnecC strains resulted in values of about 72 % ANI, and ANI values shared by strain MWH-VicM1T with the type strains of two *Cupriavidus* species were about 70 %. The alignment fractions from which these ANI values resulted were 78, 41–46 and 12–15 % of the genome size of strain MWH-VicM1T for the comparisons with strain MWH-Molsos2T (intra-PnecD comparison), for comparisons with PnecC strains, and for comparisons with *Cupriavidus* spp. strains, respectively. Both the ANI values [24] and the alignment fraction data indicate that strain MWH-VicM1T shares more homologous genes with the other PnecD strain than with PnecC strains or the closest relatives outside of the genus *Polynucleobacter*.

<table>
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<th>Genome size (Mbp)</th>
<th>Scaffolds</th>
<th>G+C content (mol%)</th>
<th>GenBank/EMBL/DDBJ accession no.</th>
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FL, Free-living; E, endosymbiotic.
Fig. 1. Phylogenetic position of strain MWH-VicM1<sup>T</sup>. (a) Maximum-likelihood (ML) tree calculated with eight concatenated housekeeping gene sequences. Sequences of the type material of <i>P. necessarius</i> [1] could not be included owing to the unavailability of the culture containing this endosymbiont [14]. Instead, sequences of two other <i>P. necessarius</i> strains were included, one of which is most likely identical with the type material of the species [14]. Bootstrap values are shown from left to right for neighbour-joining (NJ), ML and maximum-parsimony (MP) trees calculated with the same sequence set. Pairwise ANI values for whole genome comparisons of strain MWH-VicM1<sup>T</sup> with the other shown taxa are given. Bar, 0.1 substitution per nucleotide position. (b) ML tree calculated with 16S rRNA gene sequences and pairwise 16S rRNA sequence similarity values of strain MWH-VicM1<sup>T</sup> with the other taxa shown. Bootstrap values are shown from left to right for NJ, ML and MP trees calculated with the same sequence set. Bar, 0.01 substitution per nucleotide position. NA, Not available.
PHYLOGENY

As shown previously, phylogenetic reconstructions based on 16S rRNA gene sequences placed strains MWH-Molsso2T and MWH-VicM1T in subcluster PnecD of the genus Polynucleobacter [6]; however, the sequences of this ribosomal gene are too similar (99.74 %) to provide suitable phylogenetic resolution (Fig. 1b). In order to establish a phylogenetic reconstruction with a higher resolution, multilocus sequence analysis based on eight housekeeping genes defined previously [14, 27] was performed. In all but one case (endosymbiotic P. necessarius strain Ammermann, [14]), these genes were extracted from the genomes of the type strains of all previously described PnecC species, from two PnecC strains representing two separate undescribed PnecC species [32, 33], and from the two PnecD strains investigated here. The genomes of two Cupriavidus strains [34, 35] served as outgroup. Concatenation of partial gene sequences resulted in an alignment length of 6249 alignment positions. Neighbour-joining, maximum-likelihood and maximum-parsimony trees were calculated by using the software MEGA7 [36] (Fig. 1b). The obtained multilocus trees confirm the separation of the investigated strains in the two subclusters, PnecC and PnecD, and demonstrate that the phylogenetic distance between the two PnecD strains is similar to distances between distinct PnecC species.

ECOLOGY AND BIOGEOGRAPHY

Strain MWH-VicM1T was isolated from a tropical lake. Like PnecC strains also isolated from tropical freshwater systems [37], it lacked the ability to grow at temperatures of 4–6 °C. On the other hand, the strain showed a higher maximum growth temperature (38 °C) than all other PnecD or PnecC strains isolated from habitats located in temperate climatic zones [9, 15–17, 27, 38–40]. Both traits hint at a thermal adaptation of strain MWH-VicM1T to tropical or at least to warmer climate conditions [41]. For tropical PnecC strains a restricted geographical range was indicated by cultivation-independent investigations [37]. The clade formed by these tropical strains could not be detected in Central European habitats but was detected in Ugandan habitats. Similarities between thermal adaptation and biogeography of PnecC strains and strain MWH-VicM1T are obvious. However, characterization of additional strains of the new species are needed to determine if the geographical range of the new species is really restricted in a way similar to that in the PnecC strains.

CRYPTIC SPECIES COMPLEX

The ANI results of the comparisons of the genomes of strains MWH-Molsso2T and MWH-VicM1T stand in strong contrast to the sequence similarity of their 16S rRNA genes (Fig. 1). A very similar discrepancy between ANI values and 16S rRNA gene similarities is well documented for several strains affiliated with subcluster PnecC [13, 27]. Only two of the five strains included in the description of P. cosmopolitanus [17] have had their genomes sequenced so far; thus, one can only speculate whether the remaining three strains also represent separate species. A recent investigation on four free-living Polynucleobacter strains included in the emended description of P. necessarius [9] revealed that these strains represent four separate species [14]. Sequence comparisons based on partial glutamine synthetase (glnA) gene sequences may provide hints as to whether or not the three other P. cosmopolitanus strains [17] actually represent novel species. A previous investigation on PnecC strains suggested that strains sharing ANI values <85 % also share glnA sequence similarities <94 % [13]. Analyses of the five glnA sequences (accession numbers FR732027, FR732028, FR732031, FR732033 and FR821089) of PnecD strains included in the previous description of the species P. cosmopolitanus resulted in an average sequence similarity of 92.3 %, a minimum value of 88.9 % and a maximum value of 97.7 %. All of the ten pairwise comparisons but the maximum value were below 94 % sequence similarity. The partial glnA sequences of strains MWH-Molsso2T and MWH-VicM1T shared a similarity of 92.7 %, slightly above the mean value of all comparisons. These results indicate that it is quite likely that not only strains MWH-Molsso2T and MWH-VicM1T represent separate species, and support the assumption that subcluster PnecD represents a second cryptic species complex within the genus Polynucleobacter.

PROPOSAL OF THE NEW SPECIES POLYNUCLEOBACTER VICTORIENSIS SP. NOV.

The performed ANI analyses and the phylogenetic reconstructions show that the previously described species P. cosmopolitanus contains at least two distinct species. The determined value of 78.4 % ANI (Fig. 1a) lies far below the threshold range of 93–96 % ANI suggested to demarcate strains representing separate species [31, 42, 43]. Furthermore, comparison of the revealed phylogenetic distances between the two investigated PnecD strains with distances between distinct species within subcluster PnecC confirms the separation of the two strains into two species (Fig. 1a). We propose to establish the new species P. victoriensis sp. nov. to harbour strain MWH-VicM1T. Future genome sequence-based investigations are needed to reveal whether the other three strains included in the description of P. cosmopolitanus really belong to this species, whether they also belong to the new species proposed here, or whether they represent separate, so far undescribed species.

Strain MWH-VicM1T can be discriminated from Polynucleobacter strains not affiliated with subcluster PnecD by the presence of the fatty acid C12:0 3-OH, which in Polynucleobacter strains has so far been detected exclusively in all investigated strains affiliated with subcluster PnecD [17]. A genotypic trait of all so far investigated strains affiliated with subcluster PnecD is the presence of the
signature sequence 5′-AA(T/G)CCCT(A/T)AGGG-GAAA-3′ within the 16S rRNA gene (Escherichia coli positions 181–197) [44]. Strain MWH-VicM1T can be discriminated from the type strain of *P. cosmopolitanus*, which also belongs to subcluster PnecD, by its ability to assimilate malonic acid, as well as by growth at 38°C and lack of growth at 5°C [17].

**DESCRIPTION OF POLYNUCLEOBACTER VICTORIENSIS SP. NOV.**

*Poly nucleobacter victor iensis* (vic.to.r.en’sis. N.L. masc. adj. victor iensis of or belonging to Lake Victoria, the lake from which the type strain was isolated).

The description is based on phenotypical data of Hahn [6] and Hahn *et al.* [17], on chemotaxonomical data of Hahn *et al.* [17] and on genomic data presented in the present study (Table 1). Contains free-living *Poly nucleobacter* strains dwelling in the water column of freshwater systems. Cells are short curved rods, 0.4–1.1 µm in length and 0.3–0.5 µm in width, depending on cultivation conditions. Chemo-organotrophic, aerobic, and weak anaerobic growth was observed. Colonies grown on NSY agar are non-pigmented, circular and convex with smooth surface. Growth occurs up to 38°C but not at 5°C. Growth occurs in 0–0.5 % (w/v) NaCl. Assimilates acetate, propionate, pyruvate, malate, malonate, fumarate, succinate, oxaloacetate, L-alanine and L-cysteine. Weak assimilation of D-galactose and D-galacturonic acid. Does not assimilate glycolate, glyoxylic acid, D-sorbitol, D-fructose, L-sorbose, L-sorbose, L-sarseagine, L-glutamate, L-serine or betaine. Major fatty acids of the strain are summed feature 3, including C16:1ω7c and iso-C15:1 2-OH, C18:1ω7c, C16:0 and C12:0 3-OH.

The type strain is MWH-VicM1T (=DSM 21487T=JCM 32005T), which was isolated from Lake Victoria near Kampala, Uganda. The species epithet indicates the origin of the type strain but does not indicate that the distribution of the taxon is restricted to a certain geographical area or a certain freshwater system. The draft genome of the type strain is 43.1 mol%.

**References**

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Conflicts of interest

The authors declare that there are no conflicts of interest.

Ethical statement

The presented study does not include any experimental work with humans or vertebrates.
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