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Research article

Evolutionary, genomic, and biogeographic characterization of two novel xenobiotics-degrading strains affiliated with *Dechloromonas*

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ABSTRACT

Xenobiotics are generally known as man-made refractory organic pollutants widely distributed in various environments. For exploring the bioremediation possibility of xenobiotics, two novel xenobiotics-degrading strains affiliated with *Azonexaceae* were isolated. We report here the phylogenetics, genome, and geo-distribution of a novel and ubiquitous *Azonexaceae* species that primarily joins in the cometabolic process of some xenobiotics in natural communities. Strains s22 and t15 could be proposed as a novel species within *Dechloromonas* based on genomic and multi-phylogenetic analysis. Pan-genome analysis showed that the 63 core genes in *Dechloromonas* include genes for dozens of metabolisms such as nitrogen fixation protein (*nifU*), nitrogen regulatory protein (*glnK*), dCTP deaminase, C4-dicarboxylate transporter, and fructose-bisphosphate aldolase. Strains s22 and t15 have the ability to metabolize nitrogen, including nitrogen fixation, *NirS*-dependent denitrification, and dissimilatory nitrate reduction. Moreover, the novel species possesses the EnvZ-OmpR two-component system for controlling osmotic stress and QseC-QseB system for quorum sensing to rapidly sense environmental changes. It is intriguing that this new species has a series of genes for the biodegradation of some xenobiotics such as azathioprine, 6-Mercaptopurine, trinitrotoluene, chloroalkane, and chloroalkene. Specifically, glutathione S-transferase (*GST*) and 4-oxalocrotonate tautomerase (*praC*) in this novel species play important roles in the detoxification metabolism of some xenobiotics like dioxin, trichloroethene, chloroacetyl chloride, benzo[a]pyrene, and aflatoxin B1. Using data from GenBank, DDBJ and EMBL databases, we also demonstrated that members of this novel species were found globally in plants (e.g. rice), guts (e.g. insect), pristine and contaminated regions. Given these data, *Dechloromonas* sp. strains s22 and t15 take part in the biodegradation of some xenobiotics through key enzymes.

1. Introduction

Xenobiotics are generally known as man-made refractory organic pollutants [1] and they indeed have harmful health effects on living organisms [2, 3]. Most of them can easily be found in various environments (e.g. soils, sediments, and water bodies) and persist in the environment for months and years [4]. Nonetheless, many biogenic compounds can be biodegraded rapidly [5, 6]. Biodegradation is considered an important way to remove most toxic xenobiotics released into the environment [4] and microorganisms *in situ* are key players in different xenobiotics-polluted conditions [5, 6, 7]. For this reason, the interest in studying the metabolic potential of biodegrading xenobiotics using microbes for bioremediation purposes has increased, especially in unidentified microorganisms having the xenobiotics-metabolizing capability.

As a member of *Azonexaceae*, the genus *Dechloromonas* has been described in the bacterial nomenclature as a chlorate and perchlorate reducer [8, 9, 10, 11]. For instance, *D. agitata* CKB has been well studied as a model microorganism capable of reducing per(chlorate) [12]. So far, *Dechloromonas* spp. were studied for their capability to reduce nitrate and nitrite [10, 11, 13, 14, 15]. Members from *Dechloromonas* are also demonstrated as phosphate accumulating organisms in phosphorus-removing reactors [16, 17, 18]. Additionally, several *Dechloromonas* strains have been identified as anaerobic Fe (II)- and hydrogen-oxidizing bacteria [13, 14, 19, 20, 21]. They also exhibited a broad range of oxidizing capabilities to simple organic acids, hexoses, reduced humic substances, alcohol, and hydrogen sulphide when nitrate as an electron acceptor was added [22]. Moreover, it is noted that some *Dechloromonas* isolates

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were reported to take part in remediating Se- and As-contaminated environments [23, 24].

Many *Dechloromonas* members have demonstrated exceptional biodegradation potential for xenobiotic compounds. For example, some of them are known for their ability to degrade benzene and polycyclic aromatic hydrocarbons under anaerobic conditions such as *Dechloromonas* sp. strain JJ [22, 25, 26, 27, 28]. Moreover, they also have the ability to degrade linear alkylbenzene sulfonate and chlorophenol in anoxic environments [29, 30]. Thus, members from *Dechloromonas* have great potential for biodegrading xenobiotics. However, few studies about *Dechloromonas* having the ability to biodegrade complex xenobiotics were reported. In the current study, two novel xenobiotics-degrading strains s22 and t15 were isolated from pond water. We investigated their evolution, genome assembly, and biogeography. This study is a supplement to provide a better understanding of the distribution and xenobiotics-degrading potential of members from *Dechloromonas*.

2. Materials and methods

2.1. Isolation and genomic sequencing

Strains s22 and t15 were isolated from pond water in China. Aliquots (100 μL) of collected pond water were diluted serially 10-fold and an additional 100 μL of the three dilutions (10^{-4}, 10^{-5}, and 10^{-6}) were spread onto 2216E agar plates (pH 7.6–7.8). These 2216E agar plates include the following ingredients (grams per liter): Tryptone, 5.0; Yeast extract, 1.0; Ferric phosphate, 0.005; and Agarose, 15. Of this media, 1.0 L filtered seawater was added as a solvent. All plates were incubated at 25 °C for the next 3 days in order to examine microbial growth. The colonies having different morphological features were streaked individually onto 2216E agar plates and incubated again for another 3 days at 25 °C for growth. This process was repeated three times for purification. Purified bacterial strains were further cultured in marine broth 2216E overnight to cultivate enough bacterial cells for cryopreservation (−80 °C with the addition of 30% glycerol). For DNA extraction of strains s22 and t15, two grams of cells were collected in 2216E solid medium at the exponential growth phase using bamboo stickers of 20 cm, and their genomic DNA was extracted using TIANamp Bacteria DNA Kit (TIANGEN, Beijing, China) following the manufacturer's instructions. NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, United States) was used to measure DNA concentrations and purity. High-quality DNA of strains s22 and t15 was sent to the Beijing Genomics Institute (BGI, Shenzhen, China) for whole-genome sequencing using Illumina HiSeq 2500.

2.2. Genomic assembly and annotation

The quality of raw sequencing data was trimmed and filtered using Trimmomatic at default settings [31]. Quality-filtered and trimmed reads were assigned to de novo assemble using SPAdes assembler with default parameters [32]. In order to check the completeness, contamination, and heterogeneity of assembled genomes of strains s22 and t15, CheckM [33] and Anvi'o software [34] were applied. Other *Azonexaceae* species genomes were obtained from the NCBI genomes database and related genomic information was listed in the supplementary table S1. Genes prediction on all genomes used in this study was carried out with Prodigal [35] involved in Prokka [36] with default settings to characterize the genomic traits and make FAA protein files compatible for downstream metabolic reconstruction. Furthermore, genome annotations and functional categories were measured based on rapid annotation using the subsystem technology (RAST) server [37], KEGG, and blastp.

2.3. Phylogenetic analysis

In order to determine the phylogenetic placement of two novel strains s22 and t15, multiple sequence alignments of 16S rRNA genes were carried out on CLUSTALW using MEGA X software with default parameters [38]. The complete 16S rRNA gene sequences of strains s22 and t15 were extracted from their draft genomes. Phylogenetic tree based on 16S rRNA gene sequences of strains s22 and t15 as well as other type strains belonging to the family *Rhodocyclales* was constructed using the maximum-likelihood (ML) algorithms. *Rhodospirillum rubrum* ATCC 11170^T was used as the outgroup. Bootstrap values were calculated based on 1000 replications. Moreover, species tree reconstruction based on all lineal homologous genes of total 28 *Azonexaceae* genomes (s22, t15, and 26 genomes downloaded from GenBank database) was performed using OrthoFinder2 with STAG algorithm [39]. Additionally, single-copy genes from 28 *Azonexaceae* genomes were selected to construct the evolutionary tree using Anvi'o software [40] with default settings.

2.4. Comparative genomics and metabolic reconstruction

The online tool JSpeciesWS [41] was arranged to calculate average nucleotide identity (ANI) values and aligned nucleotides percentages (ANP) among the genomes of two novel strains (s22 and t15) and type strains from *Azonexaceae*. The GGD calculator from the DSMZ server [42] was used to measure in silico genome–genome distances (GGDs) among the genomes. Furthermore, CompareM (https://github.com/dparks1134/CompareM) was applied to calculate amino acid identity (AAI) among the genomes. All generated plots were performed with R [43] using the ggplot2 package [44]. Pan-genome analysis was carried out with Roary using the parameters *-e*, *–mafft*, *-p* 8 [45] and the meta-pangenomic workflow of Anvi'o with default settings [34, 40]. In order to visualize all comparative genome information, the program anvi-interactive in Anvi'o software [34, 40] was used. The metabolic reconstructions based on the results of gene prediction were executed using Adobe Illustrator 2019 (Adobe).

2.5. Biogeographic distribution of Dechloromonas strains

In order to better understand the environmental distribution of *Dechloromonas* sp. strains s22 and t15, the Integrated Microbial Next Generation Sequencing (IMNGS, https://www.imngs.org) server was applied with a minimum DNA size of 200 bp and the set threshold of 97% using complete 16S rRNA gene sequences [46]. A total of 422,877 samples from different niches (e.g. air, soil, sediment, water bodies, and guts) in IMNGS server were assigned to study the abundant and biogeographic characterizations of *Dechloromonas* sp. strains s22 and t15. Besides, the biogeographic distribution of 16S rRNA gene sequences of other *Dechloromonas* strains was also investigated.

2.6. Data accessibility

These Whole Genome Shotgun projects of two strains affiliated with *Dechloromonas* have been deposited at the DDBJ/ENA/GenBank under the accession WYCU00000000 (s22) and WYCV00000000 (t15). The versions described in this paper are version WYCU01000000 (s22) and WYCV01000000 (t15).

3. Results and discussion

3.1. Phylogenetic placement of two novel strains affiliated with Dechloromonas

Using the blastn tool, s22 and t15 were closely related to each other (16S rRNA identity: 100%). Moreover, s22 and t15 were closer to members from *Dechloromonas* (16S rRNA identity: >96.04%) than to the type strains belonging to *Azonexus* (Figure 1A). It is noted that two strains (s22 and t15) 16S rRNA genes shared the highest sequence similarity of 96.86% with *D. agitata* CKB^T. This identity was lower than the set threshold of 97% for species demarcation, indicating s22 and t15 may be novel species affiliated with *Dechloromonas*. Additionally, 16S rRNA gene-based phylogeny tree showed that two strains (s22 and t15) were

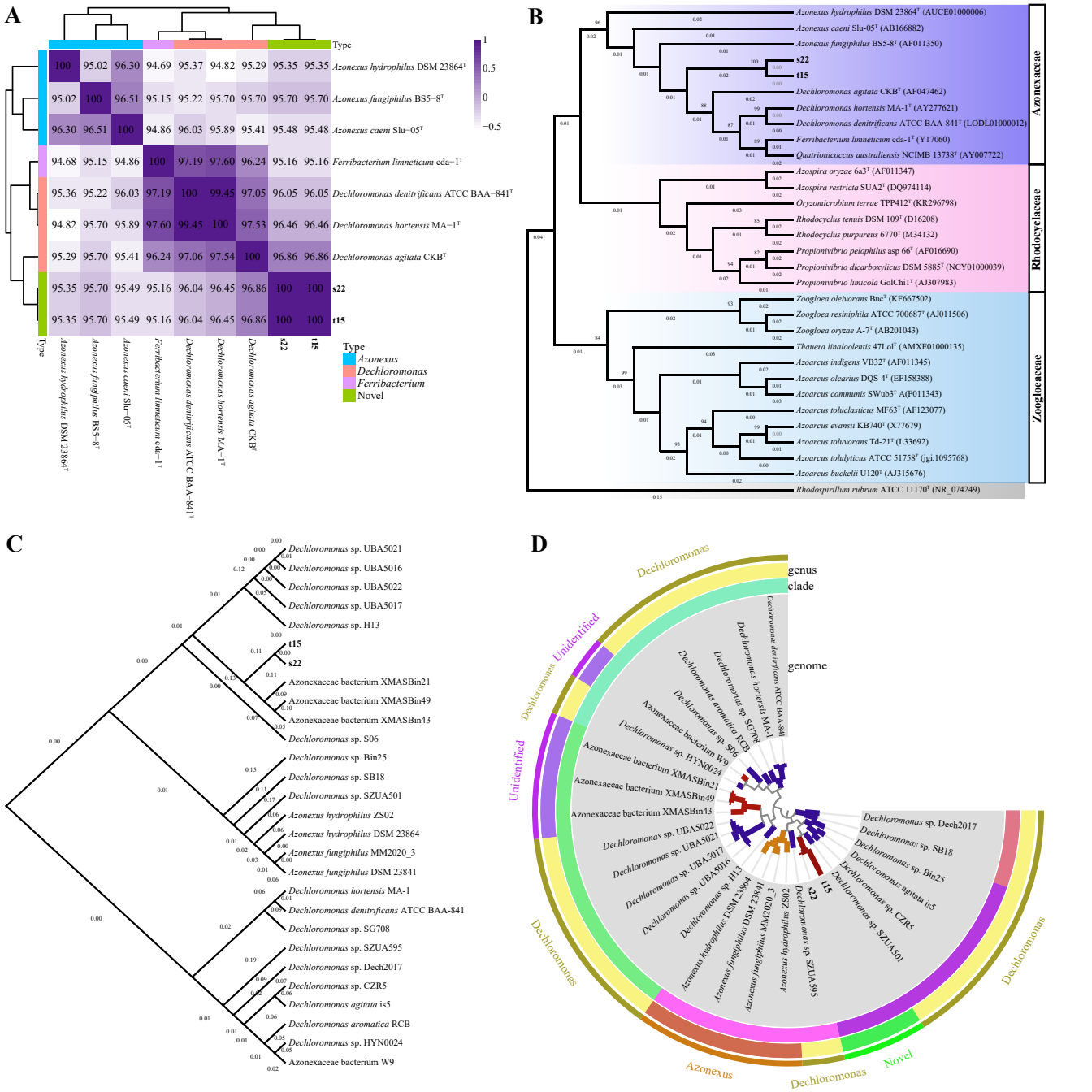

Figure 1. Phylogenetic placement of strains s22 and t15 belonging to family *Azonexaceae*. (A) A heatmap on the basis of 16S rRNA genes similarities. (B) Maximum-likelihood tree based on the 16S rRNA gene of Rhodocyclales. *Rhodospirillum rubrum* ATCC 11170^{T} was used as the outgroup. (C) Species tree of all lineal homologous genes among 28 *Azonexaceae* genomes using OrthoFinder2 with STAG algorithm. (D) Evolutionary reconstructions according to single-copy genes from 28 *Azonexaceae* genomes using Anvi'o software.

located at the adjacent position of type strain *D. agitata* CKB^{T} (Figure 1B). Species tree and single-copy genes-based phylogenetic analysis also reflected two strains (s22 and t15) clustered tightly with *Dechloromonas* strains (Figure 1C, D), which redetermined that s22 and t15 were closer to *D. agitata* (ANI: 76.67% for both; ANP: 49.74% and 49.75%, respectively; AAI: 81.04% and 81.40%, respectively; GGD: 21.50% for both) than to other *Azonexaceae* strains (Figure 2). The average ANI, AAI, and GGD values among the *Dechloromonas* species were ~76%, ~80%, and ~21%, respectively, which are at the lower end of the 62–100% range for interspecies demarcation [47]. On this basis, strains s22 and t15 can be suggested as a new species in the genus *Dechloromonas*.

3.2. Genomic features of two novel strains of Dechloromonas

No plasmid was detected in the genomes of strains s22 and t15. The genomic size of strains s22 and t15 were 3,575,474 bp and 3,590,015 bp, respectively (Table 1). The average G+C content is 58.4%. The final annotation of strains s22 and t15 resulted in 3,183 and 3,173 genes, respectively. 3,127 and 3,173 predicted coding sequences (CDS) were distributed throughout the strains s22 and t15, respectively. A total of 55 RNA sequences, including 2 rRNA genes (16S and 23S) and 53 tRNA genes, were found in strain s22. For strain t15, 67 RNA sequences (4 rRNA genes and 63 tRNA genes) were detected.

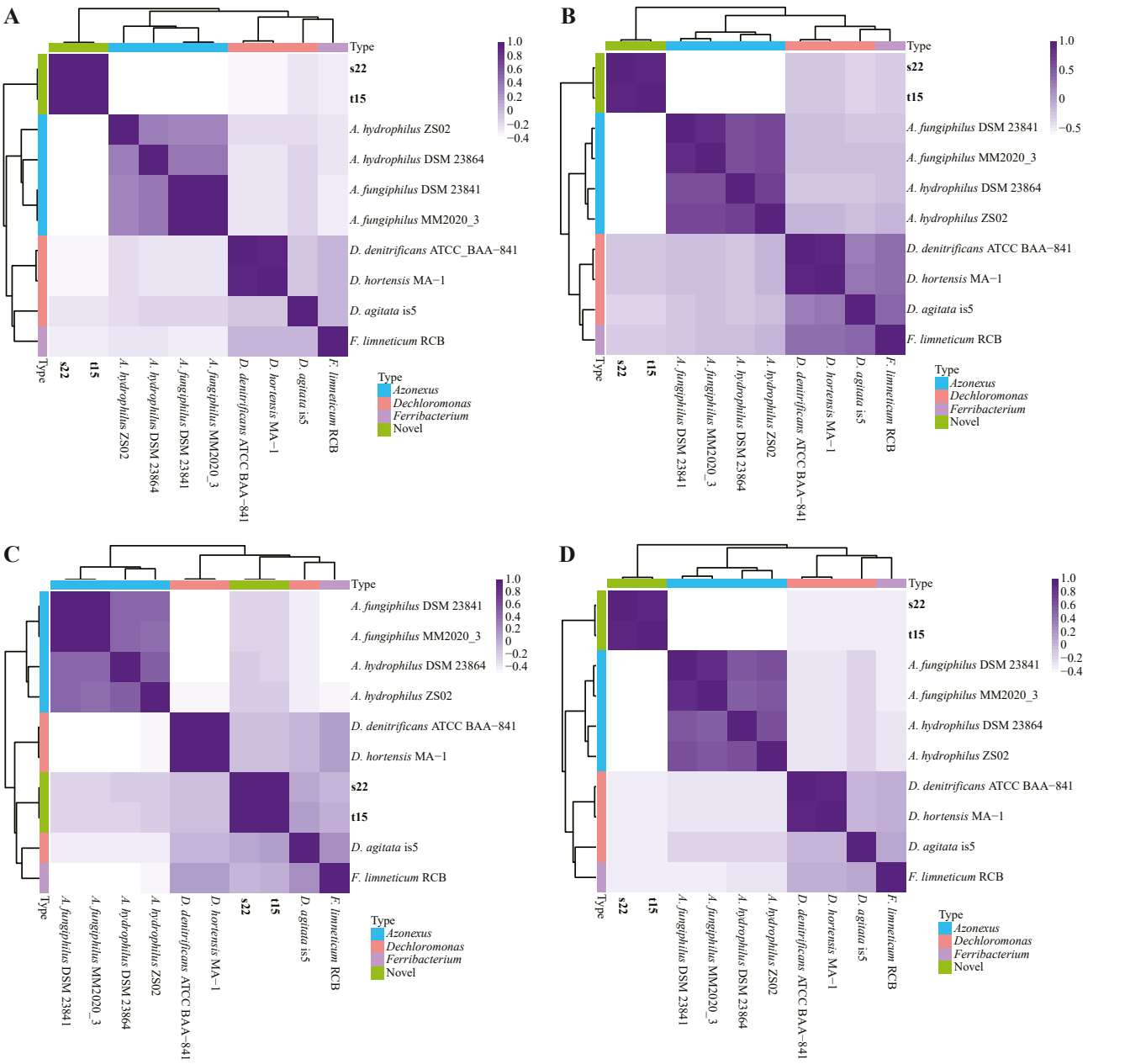

Figure 2. Genomics characteristics of family *Azonexaceae*. Heatmaps based on (A) average nucleotide identity (ANI), (B) aligned nucleotides percentages, (C) average amino acid identity (AAI), and (D) genome–genome distance (GGD) for all the sequenced genomes from family *Azonexaceae*.

3.3. Pan-genome analysis

Genomic comparison of the 5 *Dechloromonas* genomes (s22, t15, is5, MA-1, and BAA-841) was based on pan-genome analysis (Figure 3). Among the 5 *Dechloromonas* strains analyzed, the 20,670 coding sequences (CDS) of the 5 *Dechloromonas* genomes clustered into 8,754 protein clusters (PCs). The number of core and pan genes were 63 and 13,607, respectively. The 63 core genes in *Dechloromonas* include genes for nitrogen fixation protein (*nifU*), nitrogen regulatory protein (*glnK*), dCTP deaminase, C4-dicarboxylate transporter, fructose-bisphosphate aldolase, and malate dehydrogenase (*mdh*). Succinate dehydrogenase/fumarate reductase and thioredoxin 1 were also present in the core genome. With the addition of other *Dechloromonas* strains, a significant change in the core and pan-genome size occurred (Fig. S1), which suggested a large genomic variation among the species within *Dechloromonas* [48].

3.4. Energy metabolism and environmental information processing

Nitrate as an electron acceptor plays a significant role in the respiration and bioactivity of microbiological cells [49]. The

Table 1. General genomic features of strains s22 and t15.

Feature	Strain s22	Strain t15
Genome size (bp)	3,575,474	3,590,015
GC content (%)	58.52	58.25
Number of CDS	3,127	3,105
Number of Gene	3,183	3,173
Number of rRNA	2	4
Number of tRNA	53	63
Number of Repeat region	1	3

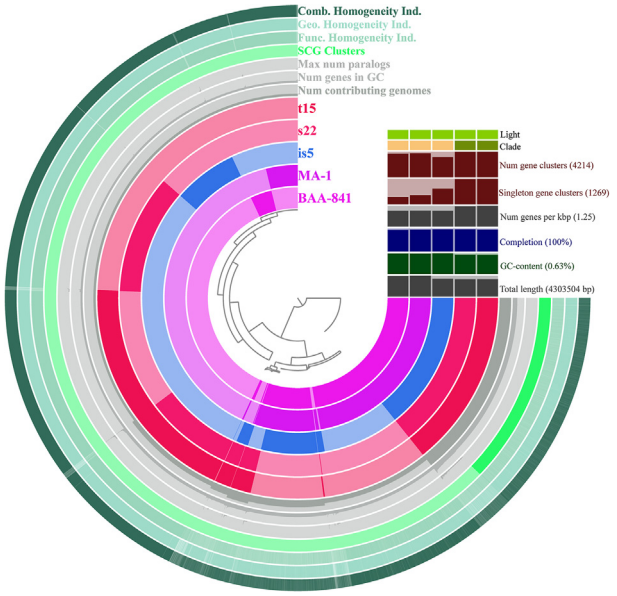

Figure 3. Communality and uniqueness in the *Azonexaceae* pangenome as derived from the clustering of 5 *Dechloromonas* genomes based on 8,754 protein clusters (PCs). Each radial layer represents a genome or a default parameter, and each bar in a layer represents the occurrence of a PC (dark presence, light absence).

oxidation-reduction of members from *Dechloromonas* needs the supplement of nitrate [22]. Strains s22 and t15 both contain 25 genes associated with nitrogen metabolism. The metabolic pathways of these genes mainly include nitrogen fixation, *NirS*-dependent denitrification, and dissimilatory nitrate reduction (Figure 4). Additionally, strains s22 and t15 could uptake and utilize urea due to the presence of urea ABC transporter (*UrtABCDE*) and urease (*UreABCDEFG*). The most abundant genes involved in nitrogen utilization are nitronate monooxygenase (*npd*, 3 copies for each strain) that converts nitroalkane into nitrite. With the presence of ABC transporter *CysPUWA*, strains s22 and t15 cells could uptake SO_4^{2-} and $S_2O_3^{2-}$ from extracellular environments. Assimilatory sulfate reduction (sulfate => H_2S) pathway and sox system represent the key sulfur metabolic pattern of strains s22 and t15.

Despite the lack of genes encoding for NtrY, strains s22 and t15 encode the NarX-NarL two-component system and the GlnL-GlnG system for the regulation of nitrate metabolism. Moreover, strains s22 and t15 possess the EnvZ-OmpR two-component system for controlling osmotic stress and QseC-QseB system for quorum sensing such as the regulation of motility [50, 51, 52]. The identified two-component regulatory systems can help these organisms to rapidly sense environmental changes [52]. Furthermore, strains s22 and t15 have the PhoR-PhoB two-component system for the detection of inorganic phosphate limitation, which may be useful to sense nutrient enrichment and depletion [53]. Lastly, the RegB-RegA two-component system detected in strains s22 and t15 can be used for electron transfer and aerobic respiration in addition to regulating nitrogen assimilation.

3.5. Xenobiotics biodegradation and metabolism

Dechloromonas sp. strains s22 and t15 possess many genes involved in xenobiotics biodegradation and metabolism that may play an important role in the detoxification of xenobiotics (Table S2). Strains s22 and t15 have a complete biodegradation pathway of azathioprine and 6-Mercaptopurine, which are oral immunosuppressants and have many pathogenic risks [54, 55]. Additionally, it is intriguing that this novel species has a series of genes that catalyzes the first step of xenobiotics biodegradation. For instance, with the presence of genes encoding *UbiX*, phenol can be catalyzed into 4-Hydroxybenzoate. Trinitrotoluene can be degraded into 2-Hydroxylamino-2,6-dinitrotoluene or 4-Hydroxylamino-2,6-dinitrotoluene by genes encoding *NfnB* and *NemA*. The two novel strains also

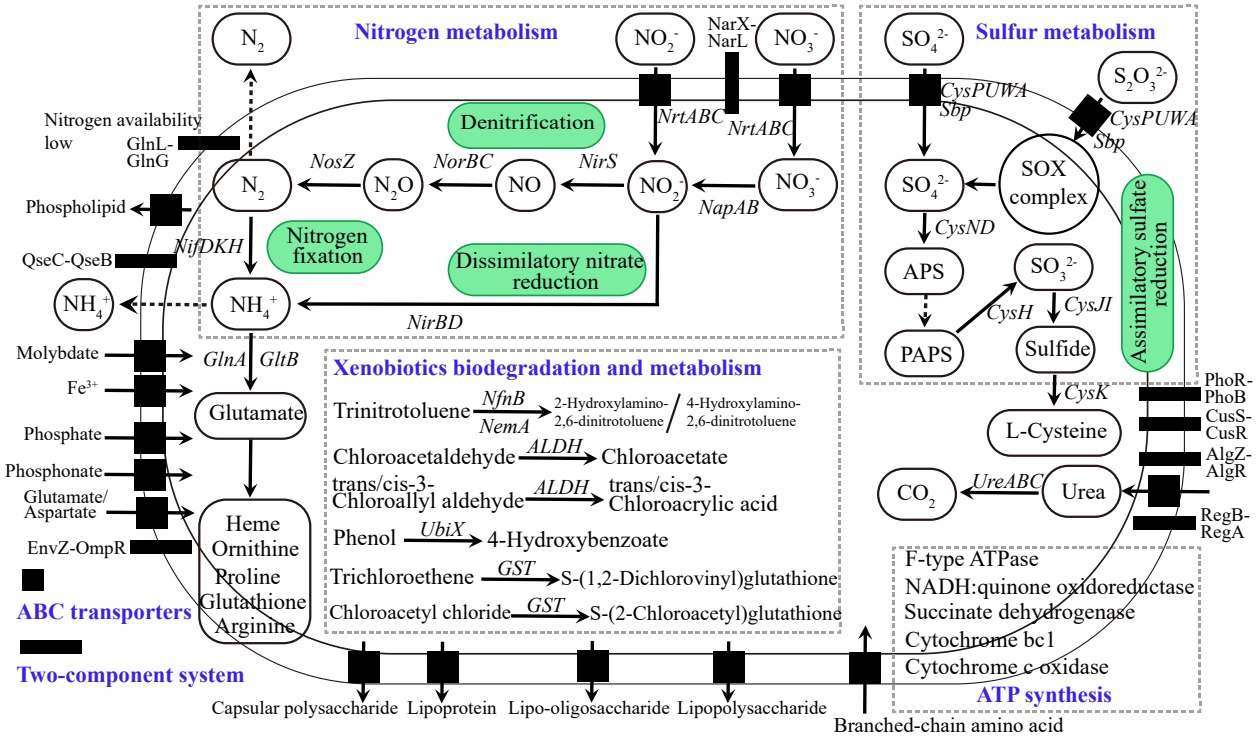

Figure 4. Vary shared metabolic pathways of strains s22 and t15 illustrating predicted ABC transporters, two-component system, nitrogen metabolism, sulfur metabolism, and xenobiotics biodegradation and metabolism. Genes arranged in glutathione S-transferase also take part in degrading benzo[a]pyrene, bromobenzene, naphthalene, 1-nitronaphthalene, aflatoxin B1, and 1,2-Dibromoethane.

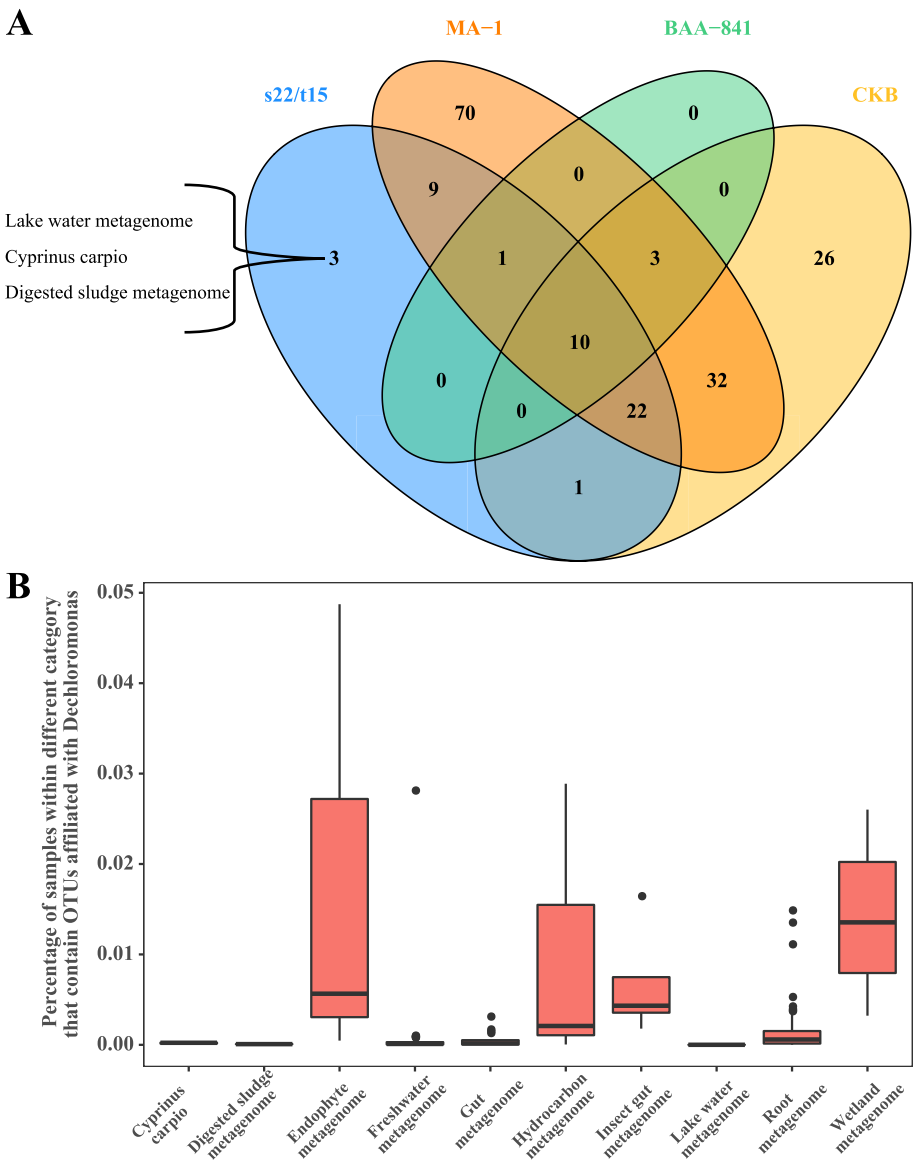

Figure 5. Biogeographic distribution and abundance profiles of *Dechloromonas* strains in kinds of samples. (A) Venn diagram of different categories that contain OTUs affiliated with *Dechloromonas*. (B) Abundance of OTUs belonging to strains s22 and t15 in 10 representative samples.

take part in the downstream metabolism of degrading xenobiotics. In the late stage of benzoyl-CoA degradation, 3-Hydroxy-pimeloyl-CoA can continue to catalyze. The results of the genome analysis showed that *Ferribacterium limneticum* strain RCB harbored more genes required for xenobiotics degradation than other *Azonexaceae* strains. Even so, for chloroalkane and chloroalkene degradation, strains s22 and t15 can biodegrade chloroacetaldehyde and trans/cis-3-Chloroallyl aldehyde due to genes arranged in aldehyde dehydrogenase (*ALDH*). Genomic analysis also showed that *D. denitrificans* ATCC BAA-841, *D. hortensis* MA-1, and *D.* sp. CZR5 had this gene to take part in biodegrading chloroalkane and chloroalkene (Table S2). Moreover, strains s22 and t15 take part in the last two steps of the process of caprolactam degradation before entering the benzoate degradation. It is noted that a key enzyme named 4-oxalocrotonate tautomerase (*praC*) also joins in xenobiotics degradation such as dioxin, xylene, and some aromatic compounds. Moreover, glutathione S-transferase (*GST*) which is a major Phase II enzyme plays a significant role in the detoxification metabolism of exogenous substances [56]. Genes arranged in *GST* take part in degrading trichloroethene, chloroacetyl chloride, benzo[a]pyrene, bromobenzene, naphthalene, 1-nitronaphthalene, aflatoxin B1, and 1,2-Dibromoethane (Figure 4 and Fig. S2). These multifunctional enzymes may play an essential role as the cometabolic potential of some xenobiotics in microbial communities. It is important to note that *Dechloromonas* spp. have the ability to degrade xenobiotics and related metabolisms should be characterized deeply in the future. To some extent, the cometabolism within microbial communities can determine the fate of xenobiotic compounds in nature [57]. In addition, potential functional genes involved in the isolates should be explored due to the incomplete annotation of xenobiotics-degrading metabolic pathways. In the future, more works should focus on the discovery of novel xenobiotics-degrading enzymes and microorganisms.

It is reported that *Dechloromonas* spp. are facultative anaerobic nitrate-reducing bacteria and are known as aromatic compound-degrading bacteria [25]. They are frequently present in aerobic/anaerobic WWTPs [58, 59, 60, 61], where they contribute to the degradation of organic compounds and removal of N and P under aerobic and anaerobic conditions. For strains s22 and t15, apart from reducing nitrate, degrading some aromatic compounds and accumulating polyphosphate, they could be used to remove some poisonous medicines such as azathioprine and

6-Mercaptopurine to reduce pathogenic risk, as well as some small molecular xenobiotics in the wastewater treatment. To sum up, strains s22 and t15 possess a broad range of metabolisms integral to the wastewater treatment ecosystem. The rationale behind the use of this novel species to treat wastewater lies in their ability to (i) biodegrade some xenobiotics through key enzymes like *GST* and *praC*; (ii) use the EnvZ-OmpR two--component system for controlling osmotic stress and QseC-QseB system for quorum sensing to rapidly sense environmental changes; (iii) acclimatize and survive in plants, guts, pristine and contaminated regions.

3.6. Global distribution and abundance of Dechloromonas bacteria

Generally, it was consistent with our results that members of the genus *Dechloromonas* are ubiquitous and have been isolated and identified from almost all screened environments (e.g. lake and river sediments, paper and pulp mill waste, groundwater, soil as well as invertebrate guts) as shown in Supplementary Table S3 and Fig. S3 [19, 62 ,63]. Investigation of biogeographical characterization of strains s22 and t15 based on IMNGS analysis showed that the target 16S rRNA genes were determined (at >97% similarity) in 760 environmental samples (Table S3). It is intriguing that bacteria closely related with strains s22 and t15 could exist in three distinct geographical samples (Figure 5A), including lake water metagenome from Australia (e.g. SRR2516495), *Cyprinus carpio* gut metagenomes from China (e.g. ERR238326), and digested sludge metagenome from China (e.g. SRR3068598). The target 16S rRNA genes of this new species were abundant in plants (e.g. rice), guts (e.g. insect), water bodies (e.g. lake), and hydrocarbon-contaminated regions (Figure 5B). The presence and relative abundances of *Dechloromonas* sp. strains s22 and t15 provide evidence that this new species is more abundant in rice endotrophic metagenomes (e.g. 0.0487% in SRR1197948) than other *Dechloromonas* species (Table S3). Moreover, there was a report that *Dechloromonas* could be dominant in the rice rhizospheric microbial community with the supplement of nitrate [64]. Thus, it can be inferred that s22 and t15 as facultative anaerobes take part in the metabolic process in plant organisms, animal guts, pristine and contaminated environments, and most especially, they are associated with detoxification metabolism of xenobiotics.

4. Conclusion

In the present study, strains s22 and t15 were proposed as novel species within *Dechloromonas*. They played important roles in the biodegradation of some xenobiotics through key enzymes like *GST*. They possess the EnvZ-OmpR two-component system for controlling osmotic stress and QseC-QseB system for quorum sensing to rapidly sense environmental changes. Pan-genome analysis showed that there are 63 core genes in *Dechloromonas* and revealed the potential survival strategies of strains within *Dechloromonas* dwelling in eutrophic and polluted environments. Moreover, biogeographic characterization underlined members of this novel species are found globally in plants, guts, pristine and contaminated regions. The foregoing findings provide a deeper understanding of the biogeographic distribution and the xenobiotics-degrading potential of members from *Dechloromonas*.

Declarations

Author contribution statement

Shuangfei Zhang: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Charles Amanze, Xueduan Liu, Yili Liang: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

Chongran Sun, Kai Zou, Shaodong Fu, Yan Deng: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

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Data availability statement

These Whole Genome Shotgun projects of two strains affiliated with Dechloromonas have been deposited at the DDBJ/ENA/GenBank under the accession WYCU00000000 (s22) and WYCV00000000 (t15). The versions described in this paper are version WYCU01000000 (s22) and WYCV01000000 (t15).

Competing interest statement

The authors declare no conflict of interest.

Additional information

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