

A Taxonomic and Metabolic Blueprint for the Phylum “*Zixibacterota*”

by

Aman Verma

A Thesis submitted to the

Faculty of Graduate and Postdoctoral Studies

of the University of Manitoba

in partial fulfilment of the requirements of the degree of

Master of Science

Department of Microbiology

University of Manitoba

Winnipeg

Copyright © 2026 by Aman Verma

Table of Contents

Chapter	Chapter Title	Page
	Abstract	i
	Acknowledgements	lii
	List of Tables	iv
	List of Figures	v
	List of Abbreviations	vi
I	Introduction	1
II	Literature Review	
	1. <i>Biodiversity exploration in the age of environmental genomics</i>	4
	2. <i>Scope of the uncultivated microbial world</i>	5
	3. <i>Classifying and naming the uncultivated majority</i>	6
	4. <i>Introduction to “Zixibacterota”</i>	8
	5. <i>Phylogenetic Placement and Evolutionary Novelty of “Zixibacterota”</i>	9
	6. <i>Geographic and Environmental Distribution of “Zixibacterota”</i>	10
	7. <i>A Deeper Dive into “Zixibacterota” Metabolic Versatility</i>	12
	8. <i>Syntrophy, microbial interactions, and ecological significance of “Zixibacterota”</i>	16
	9. <i>Conclusions and Future Directions</i>	20
III	Research Manuscript	
	<i>Introduction</i>	22
	<i>Methods</i>	
	i. <i>Genome collection, quality assessment and taxon set definition</i>	24
	ii. <i>Phylogenomic analyses and taxonomic assignment</i>	26
	iii. <i>Overall genome-relatedness indices</i>	27
	iv. <i>16S rRNA gene phylogeny</i>	28
	v. <i>Parsimony based homoplasy indices</i>	29
	vi. <i>Substitution saturation analyses</i>	29
	vii. <i>Metabolic annotation and pathway reconstruction</i>	31
	viii. <i>Identification and classification of hydrogenase genes</i>	32
	ix. <i>Identification of iron metabolism genes</i>	34
	x. <i>Identification of Alternative Complex III operons</i>	34
	xi. <i>Delineation of the ActB1 domain</i>	36

	<i>xii. Phylogenetic analysis of ActB1</i>	37
	<i>Results and Discussion</i>	
	<i>A cohesive taxonomic framework for “Zixibacterota”</i>	38
	<i>Reconciling nucleotide–amino acid tree discordance</i>	40
	<i>“Zixibacterota” genomes encode a conserved diderm cellular architecture</i>	41
	<i>Conserved heterotrophic central metabolism supports oxidative carbon utilization</i>	44
	<i>Respiratory chain architectures indicate adaptation to oxic–suboxic environments</i>	46
	<i>Lineage-specific sulfur and putative iron metabolism suggest ecological diversification</i>	50
	<i>Distribution of [NiFe] hydrogenases indicates redox buffering and lineage-specific energy strategies</i>	53
	<i>Nitrate reduction and denitrification are sporadic rather than conserved “Zixibacterota” traits</i>	54
	<i>Arsenic detoxification pathways are broadly conserved across the phylum</i>	57
	<i>Trehalose biosynthesis pathways exhibit a phylogenetically discontinuous distribution</i>	59
	<i>Ecological and evolutionary implications</i>	60
	<i>Conclusions</i>	63
	<i>Tables</i>	65
	<i>Figures</i>	102
	<i>References</i>	108
IV	<i>Conclusions</i>	118
Appendix 1	<i>Supplementary Figures</i>	120

Abstract

Uncultivated microorganisms revealed through metagenomics have substantially expanded the bacterial and archaeal tree of life and uncovered previously unrecognized microbes that contribute to biogeochemical cycling. Among these, the phylum “*Zixibacterota*” (*syn.* “*Zixibacteria*”, *Ca.* Zixiibacteriota) represents a phylogenetically distinct bacterial lineage with a broad global distribution across subsurface environments spanning salinity and redox gradients. Heterotrophic lifestyles and respiratory versatility have been proposed for members of “*Zixibacterota*”, but these inferences were based on few genomic reconstructions. Consequently, evolutionary relationships, metabolic diversity, and ecological strategies within the phylum remain unresolved. Here, I establish a taxonomic framework for “*Zixibacterota*” and apply lineage-resolved metabolic reconstructions to assess whether key physiological traits are conserved at the phylum level or partitioned among lineages. Phylogenomic analyses based on conserved marker-gene sets and concatenated supermatrices resolved evolutionary relationships, with taxonomic boundaries supported by overall genome relatedness indices. Under this framework, “*Zixibacterota*” currently comprise one class, ten Orders, twenty-one families, one hundred and eight genera, and two hundred and two species represented by at least one medium- or high-quality genome. Comparative analyses indicate that members of the phylum are likely diderm, rod-shaped cells with Type IV pilus systems. Central metabolism is uniformly heterotrophic and oxidative across the phylum, and energy conservation universally includes aerobic to microaerobic electron-transport chains, hydrogen metabolism, together with conserved iron acquisition and homeostasis. In contrast, alternative complex III-aa₃

oxidase systems, sulfate reduction, and polysaccharide degradation are likely restricted to specific lineages, which underpins ecological diversification across redox-stratified environments. Together, this study provides a genome-resolved framework for “*Zixibacterota*” evolution and ecology.

Acknowledgements

I would like to express my sincere gratitude to my advisor, Dr. Marike Palmer, Assistant Professor, Department of Microbiology, University of Manitoba, for her invaluable guidance, encouragement, and supervision throughout my thesis work. I am grateful for her insightful discussions, constructive advice, and continuous support throughout this research journey.

I would also like to extend my appreciation to my current and past lab members, Ben Kilbrei, Ayush Sharma, Tiana Steeves, and Nate Poitras, for their constant support, both professionally and personally. Their help, encouragement, and camaraderie made this experience truly rewarding.

Finally, I would like to thank my parents for their unconditional support, encouragement, and belief in me throughout my years of study and during the process of conducting and writing this thesis. This achievement would not have been possible without them.

Thank you.

List of Tables

Table	Table Title	Page
1	Proposed nomenclature and etymology of “ <i>Zixibacterota</i> ” taxa.	65

List of Figures

Figure	Figure Title	Page
1	Maximum-likelihood phylogenies based on four concatenated marker datasets.	102
2	Pairwise ANI and AAI comparisons among Order s of “ <i>Zixibacterota</i> ” and outgroup phyla.	103
3	Predicted physiological and metabolic traits across the phylum “ <i>Zixibacterota</i> ”.	104
4	Phylogenetic analysis of the ActB1 catalytic domain from ACIII.	105
5	Model of respiratory electron transfer in “ <i>Zixibacterota</i> ” lineages encoding an ACIII–cytochrome aa ₃ supercomplex.	106
S1	Phylogenetic placement of “ <i>Zixibacterota</i> ” and closely related outgroup phyla inferred using the GTDB-Tk classify workflow.	120
S2	Venn diagram illustrating the overlap and uniqueness of marker genes among the GTDB-Tk, UBCG3, and BcgTree marker sets.	121
S3	Maximum-likelihood phylogeny of 16S rRNA gene sequences from the phylum “ <i>Zixibacterota</i> ” and closely related bacterial phyla.	122
S4	Substitution saturation plots	124

List of Abbreviations

AAI:	Average Amino-acid Identity
ACIII:	Alternative Complex III
ANI:	Average Nucleotide Identity
BCGTree:	Bacterial Core Gene Tree
DNRA:	Dissimilatory nitrate reduction to ammonium
eggNOG:	Evolutionary Gene Genealogy Non-Supervised Orthologous Groups
GEBA-MDM:	The Genomic Encyclopedia of Bacteria and Archaea – Microbial Dark Matter (GEBA-MDM)
GTDB:	Genome Taxonomy Database
HMM:	Hidden Markov Model
ICNP:	International Code of Nomenclature of Prokaryotes
IMG/M:	Integrated Microbial Genomes & Microbiomes
KEGG:	Kyoto Encyclopedia of Genes and Genomes
LLTP:	Landfill Leachate Treatment Plant
MAG:	Metagenome-assembled genome
OGRI:	Overall Genome Relatedness Indices
SAG:	Single-cell amplified genomes
SINA:	SILVA Incremental Aligner
TCA:	Tricarboxylic Acid Cycle
UBCG:	Up-to-date Bacterial Core Gene

Chapter 1: Introduction

The scale of prokaryotic diversity on Earth remains profoundly underestimated. Global diversity models predict that Earth harbours approximately 10^{12} bacterial species, yet fewer than 30,000 have been described and named (Iqbal et al., 2024). Scaling-law analyses suggest that microbial species-abundance distributions follow power-law patterns, indicating a vast and largely unsampled biosphere (Wong et al., 2020). A recent survey of over 92,000 metagenomes showed that most discoverable prokaryotic lineages remain hidden within unbinned contigs that standard genome-recovery workflows fail to capture (Prasoodanan et al., 2026). At the phylum level alone, an estimated 145 bacterial phyla await valid recognition from existing datasets (Prasoodanan et al., 2026). These findings highlight that microbial exploration remains in its early stages, with much of the tree of life still inaccessible to both culture-based and genome-resolved approaches (Castelle and Banfield, 2018).

A major challenge in translating genomic discoveries into biological understanding is the lack of a nomenclatural framework for uncultivated lineages, as this limits effective communication. The International Code of Nomenclature of Prokaryotes (ICNP) requires viable type strains to be deposited in international culture collections. This requirement excludes most known microbial diversity from nomenclatural standing (Palmer et al., 2022). As a result, microbiologists often rely on alphanumeric placeholders and informal names that lack the stability, precision, and priority protections provided by the rules of nomenclature (Palmer et al., 2022). This communication barrier has become a major obstacle in microbial systematics (Palmer et al., 2022). The recent establishment of the

SeqCode, which allows genome sequences to serve as nomenclatural types, provides a solution to this gap (Hedlund et al., 2022).

The candidate phylum "*Zixibacterota*" (*syn.* "*Zixibacteria*", *Ca.* Zixiibacteriota) illustrates both the opportunities and challenges of this expanding view of prokaryotic diversity. Initially recovered as the "RBG-1" lineage from Colorado River aquifer sediments, the phylum has since been detected in aquatic, terrestrial, and subsurface environments across multiple continents (Liu et al., 2023; Castelle et al., 2013; Savvichev et al., 2023; Wong et al., 2020; Hillyer et al., 2023). Genome-resolved analyses consistently place "*Zixibacterota*" as a deeply branching bacterial lineage. However, its exact phylogenetic position varies depending on the analytical approaches used (Liu et al., 2023; Castelle et al., 2013). This uncertainty is common among lineages with limited intermediate relatives (Hedlund et al., 2015). Currently, The Genome Taxonomy Database (GTDB; Parks et al., 2026) recognizes multiple Orders within the phylum, but all remain represented by placeholder identifiers and lack validly published names. This taxonomic uncertainty limits our ability to communicate accurately about the ecological roles and metabolic capabilities of the group, which emerging evidence suggests are extensive and widespread (Wong et al., 2020).

This thesis addresses these challenges through two complementary approaches. The first is a literature review that summarizes current knowledge of the uncultivated majority of prokaryotes and "*Zixibacterota*" specifically, including its currently understood phylogenetic placement, global distribution, metabolic versatility, and role in syntrophic microbial networks. The second is a research manuscript that establishes a genome-based taxonomy for the phylum and performs systematic comparative analyses of metabolic potential across

representative genomes. Together, I provide a taxonomic and metabolic framework for a lineage that, despite its broad environmental significance, has lacked the foundation required for rigorous scientific communication.

Chapter 2: Literature Review

1. Biodiversity exploration in the age of environmental genomics

For most of microbiology's history, our view of the microbial world was constrained to what could be grown in the laboratory. Cultivation-independent surveys based on 16S rRNA gene amplicons began to expose a vast diversity beyond cultured isolates but offered limited resolution (Castelle and Banfield, 2018). The bacterial and archaeal domains contain vast reservoirs of uncultured diversity that have only recently become accessible through cultivation-independent environmental genomics. The shift from marker-gene surveys to genome-resolved metagenomics and single-cell genomics transformed microbial biodiversity exploration entirely (Jiao et al., 2020). These approaches now allow organism-level genomic analysis directly from complex environmental samples without cultivation, recovering both metagenome-assembled genomes (MAGs) and single-cell amplified genomes (SAGs) (Jiao et al., 2020).

Major international projects illustrate the pace of change. The Genomic Encyclopedia of Bacteria and Archaea – Microbial Dark Matter (GEBA-MDM) project targeted habitats rich in undescribed microbial lineages. This approach nearly quintupled genomic novelty per genome recovered (Hedlund et al., 2015). Crucially, unbinned sequence data indicate that current genomic inventories substantially underestimate total microbial richness. An estimated 145 bacterial phyla remain undiscovered but are potentially recoverable from existing datasets (Prasoodanan et al., 2026). These findings redefine what we mean by microbial biodiversity. Far from being well sampled, much of microbial diversity remains invisible to both culture-based and standard genome-resolved approaches. Contemporary

biodiversity exploration is therefore an enterprise of ongoing discovery, and the total extent of the microbial tree of life remains unknown.

2. Scope of the uncultivated microbial world

Current estimates indicate that more than 99% of bacterial and archaeal species have not been obtained in pure culture (Jiao et al., 2020). More recently, an analysis of over 90,000 publicly available metagenomes predicted approximately 705,000 bacterial and 27,000 archaeal species-level groups (Prasoodanan et al., 2026). Most of this diversity was inferred from unbinned contigs that are typically overlooked by standard workflows (Prasoodanan et al., 2026). The study also identified soils and aquatic environments as major hotspots of undiscovered microbial diversity (Prasoodanan et al., 2026). This uncultivated majority represents the dominant fraction of prokaryotic diversity across all habitats on Earth (Iqbal et al., 2024). Understanding who these organisms are and what functions they perform is one of the central challenges in modern microbiology.

Cultivation remains essential for confirming predicted functions, obtaining isolates for experimental manipulation, and establishing type strains for traditional taxonomic practices (Hedlund et al., 2015). When successful, cultivation provides something that genome sequences alone cannot: viable organisms for physiological, genetic, and biochemical characterization. However, despite decades of success in cultivating prokaryotes, we are limited in our understanding of what makes current unculturable microbes amenable to cultivation.

At the same time, cultivation-independent approaches have transformed our understanding of the uncultivated majority. Genome-resolved metagenomics led to the discovery of the Candidate Phyla Radiation and Asgard archaea. These discoveries fundamentally reshaped the tree of life and placed Eukaryotes within Archaea (Castelle and Banfield, 2018). Metatranscriptomics and stable-isotope probing have further revealed which genes are expressed in natural communities and which organisms actively participate in specific biogeochemical processes (Hedlund et al., 2015).

For lineages such as “*Zixibacterota*”, genome reconstruction has uncovered a wide range of predicted metabolic capabilities before a single isolate was obtained. These include sulfate reduction, iron and arsenic redox transformations, and syntrophic interactions (Liu et al., 2023; Castelle and Banfield, 2018). In short, cultivation remains indispensable for mechanistic validation. However, genome-resolved approaches have become the primary means of understanding the ecology, evolution, and metabolic potential of the uncultivated majority.

3. Classifying and naming the uncultivated majority

Classification of prokaryotes under the International Code of Nomenclature of Prokaryotes (ICNP) has historically required a viable type strain deposited in two international culture collections on different continents (Hedlund et al., 2022; Hedlund et al., 2015). This requirement excludes most known microbial diversity from established nomenclatural systems. As a result, 66% of currently recognized phyla and 76% of species

in the GTDB lack a cultivated representative and thus lack names with standing in nomenclature (Prasoodanan et al., 2026).

The *Candidatus* concept was introduced as a provisional designation for well-characterized but uncultivated taxa. However, these names have never had standing under the ICNP (Ernster and Rodriguez-R, 2025). There was also no regulation of the names during name formation, and proposed *Candidatus* names were often proposed without designation of nomenclatural types. The limitations of this approach became increasingly apparent as genome-resolved studies expanded. Today, more than 96,000 GTDB species are represented only by alphanumeric placeholder identifiers (Ernster and Rodriguez-R, 2025).

The SeqCode was developed to address this gap. It allows genome sequences, including those derived from isolates, MAGs, and SAGs, to serve as nomenclatural types (Hedlund et al., 2022). The application of the SeqCode operates through a public registration system and follows established rules governing name formation and priority (Hedlund et al., 2022). By decoupling nomenclature from cultivation, SeqCode enables the valid publication of names for uncultivated prokaryotes (Hedlund et al., 2022).

Workflows now integrate genome quality assessment, genome-based classification, ANI calculations, and semi-automated name generation through third-party tools, which provides names that can be curated in the SeqCode Registry (Ernster and Rodriguez-R, 2025). The phylum “*Zixibacterota*” illustrates this transition. The lineage was initially recognized within the *Candidatus* framework, as the “RBG-1” candidate phylum, based on a reconstructed genome and environmental 16S rRNA gene surveys (Castelle et al., 2013; Liu

et al., 2023). As SeqCode adoption increases, lineages once known only by alphanumeric placeholders are increasingly receiving stable and citable names. This improves communication across disciplines and facilitates integration of the uncultivated majority into microbial systematics.

4. Introduction to “*Zixibacterota*”

Among the newly recognized lineages revealed through sequence-based approaches, the candidate bacterial phylum “*Zixibacterota*” (*syn. “Zixibacteria”, Candidatus Zixibacteriota*) stands out as a deeply branching and metabolically versatile group. Evidence increasingly suggests that members of this phylum play important roles in biogeochemical cycling across diverse ecosystems (Liu et al., 2023; Castelle et al., 2013; Savvichev et al., 2023; Wong et al., 2020; Hillyer et al., 2023). The lineage was first described as the “RBG-1” group from aquifer sediments adjacent to the Colorado River (Castelle et al., 2013). Since then, “*Zixibacterota*” have been recovered from a broad range of terrestrial and marine environments and are frequently associated with oxic–anoxic interfaces, metal-impacted sediments, and syntrophy-dependent microbial consortia (Deng et al., 2024; Liu et al., 2023).

A second reason “*Zixibacterota*” are of particular interest is that they connect two major themes in contemporary microbial ecology. The first is the exploration of deeply branching uncultivated lineages across the tree of life. The second is the investigation of how such organisms contribute to coupled carbon, nitrogen, sulfur, and metal cycling in energy-

limited environments (Deng et al., 2024; Caesar et al., 2021; Savvichev et al., 2023; Liu et al., 2023).

5. Phylogenetic Placement and Evolutionary Novelty of “*Zixibacterota*”

As with many lineages of life with limited representative genomes in public databases, the robust evolutionary placement of “*Zixibacterota*” was initially challenging and depended heavily on the phylogenetic marker chosen for this purpose. In the concatenated ribosomal protein tree, the “RBG-1” lineage formed a highly supported monophyletic clade (100% support from bootstrap bipartitions) branching as a deep outgroup to the *Bacteroidetes/Chlorobi* superphylum (Castelle et al., 2013). In the 16S rRNA gene tree, however, placement was markedly different: “RBG-1” clustered with low support near *Nitrospirae* and *Elusimicrobia*, and its full-length 16S rRNA gene shared less than 83% sequence identity with any named bacterial phylum (Castelle et al., 2013). These placement discrepancies are typical of deeply branching lineages that lack intermediate relatives to break up long branches, and they underscore why concatenated protein phylogenies became the preferred framework for establishing phylum-level status (Castelle et al., 2013).

The extent of genomic novelty initially assigned to the phylum was also substantial. Among the predicted proteins in the original “RBG-1” genome, only 12.8% matched closest relatives within the *Bacteroidetes/Chlorobi* superphylum, while 7.6% were most like proteins from the distantly related *Caldithrix abyssi*, indicating a large proportion of genes with no close functional homologs (Castelle et al., 2013). Subsequent phylum-wide surveys expanded this view considerably. Compiling 135 medium- and high-quality “*Zixibacterota*”

MAGs from publicly available metagenomes across diverse environments, resolved at least eight Order -level groups within the phylum (Liu et al., 2023). The dispersal of traits across multiple Order s suggests that ecologically relevant functions within “*Zixibacterota*” are phylogenetically widespread rather than restricted to a single specialist lineage (Liu et al., 2023).

The same pattern of undersampled diversity recurs at the system level. In Laptev Sea cold-seep sediments, the “Bin19” genome grouped with other “*Zixibacterota*” but shared only 60.84% average amino acid identity with its closest relative confirming that substantial lineage diversity remains unsampled (Savichev et al., 2023). In landfill leachate treatment systems, four “*Zixibacterota*” MAGs formed discrete lineages relative to 34 reference genomes from the GTDB, further expanding known diversity while also suggesting that local selective pressures can drive phylogenetic differentiation (Deng et al., 2024).

6. Geographic and Environmental Distribution of “*Zixibacterota*”

To date, “*Zixibacterota*” genomes or its 16S rRNA sequences have been recovered from every continent. A systematic screen of the IMG/M database using a phylum-level 16S rRNA identity threshold (>75%) identified 710 unique occurrences across 17 environment types, spanning diverse natural habitats (Liu et al., 2023). Geographically these recoveries include sites across North America (Colorado aquifer, Hanford subsurface), Europe (Laptev Sea, Baltic Sea, Movile Cave), Asia (mangrove sediments of southern China, Beibu Gulf tidal flats, Tibetan Plateau wetlands, Japanese deep subsurface), Australia (Shark Bay hypersaline mats, Derwent estuary), and Africa (soils) (Liu et al., 2023; Castelle et al., 2013;

Savvichev et al., 2023; Wong et al., 2020; Hillyer et al., 2023). This broad geographic range, combined with the fact that the lineage rarely dominates any single community, suggests a persistent but low-abundance cosmopolitan distribution rather than endemic restriction to a specific region.

The recurrent association of “*Zixibacterota*” with subsurface environments is well supported across multiple surveys. Subsequent recoveries extend to cold methane seep sediments in the Laptev Sea, deep terrestrial subsurface fluids at the Sanford Underground Research Facility, and groundwater systems (Savvichev et al., 2023; Casar et al., 2021). These environments share features that likely shape “*Zixibacterota*” ecology: limited energy availability, reduced or fluctuating oxygen concentrations, and dependence on syntrophic or fermentative partnerships (Castelle et al., 2013; Savvichev et al., 2023).

Several lines of evidence indicate that “*Zixibacterota*” are tolerant of heavy metal and metalloid stress. In the Derwent Estuary, a site with legacy zinc, lead, arsenic, and mercury contamination, “*Zixibacterota*” were significantly enriched at the most metal-loaded sites alongside sulfur-metabolizing taxa (Hillyer et al., 2023). Multi-omics profiling showed that sediment mercury concentration was the single best predictor of microbial metabolite profile shifts at those sites, directly linking “*Zixibacterota*” presence to metal stress gradients (Hillyer et al., 2023).

7. A Deeper Dive into “*Zixibacterota*” Metabolic Versatility

The metabolic repertoire of “*Zixibacterota*” is unusually broad for an uncultivated phylum. The reconstructed RBG-1 population genome from aquifer sediment contained genes associated with glycolysis, a complete oxidative TCA cycle, and oxidative phosphorylation, including a cytochrome bc1-type complex III and an alternative complex III linked to an aa3-type oxidase. It also contained an ADP-forming acetyl-CoA synthetase, suggesting the potential for substrate-level ATP generation (Castelle et al., 2013). Metabolic reconstruction further identified genes associated with iron and arsenic redox transformations, hydrogen metabolism, nitrite reduction, and fermentation to propionate, acetate, ethanol, and butyrate (Castelle and Banfield, 2018). The NfnAB iron-sulfur flavoprotein complex, the MvhADG/HdrABC hydrogenase complex, and multiheme cytochromes were also identified as putative electron-transfer components (Castelle and Banfield, 2018). Collectively, these features indicate that the RBG-1 population had the genomic potential to use multiple respiratory and fermentative pathways under different redox conditions. However, because RBG-1 was reconstructed from metagenomic data rather than sequenced from an axenic culture, these predictions should be interpreted as characteristics of the reconstructed population genome and not necessarily as traits shared by all members of the lineage.

Later system-specific genomes strengthened this idea that several “*Zixibacterota*” can switch between different types of metabolisms depending on conditions. In the landfill leachate treatment plant (LLTP) study, one “*Zixibacterota*” MAG affiliated with the “FEB-12” family of Order “GN15”, carried dissimilatory sulfate reduction pathway (*dsrAB*), low-affinity

aa₃-type oxidase, high-affinity bd-type oxidase, and a wide array of redox enzymes connected to carbon, nitrogen, sulfur, hydrogen, iron, and arsenic metabolism (Deng et al., 2024). The coexistence of sulfate reduction genes with two terminal oxidases spanning different oxygen affinities is particularly notable because it suggests that some “*Zixibacterota*” are not obligate anaerobes but can exploit oxygen at different concentrations depending on microzone conditions (Deng et al., 2024). Cold-seep “Bin19” from the Laptev Sea also appeared to be equally broad and versatile in its predicted metabolisms. It contained glycolysis, the pentose phosphate pathway, the TCA cycle, sulfate reduction, and a complete oxidative phosphorylation pathway (Savvichev et al., 2023). What makes this “broad” is not the presence of any single pathway, but the simultaneous retention of respiratory modules that span fully aerobic, microaerophilic, anaerobic respiratory, and fermentative modes, along with the genetic machinery to move between them.

The strongest and most recovered metabolic signal, at least in the “*Zixibacterota*” genomes documented so far, is the capacity for dissimilatory sulfate reduction. This trait has been confirmed across at least five independent studies spanning disparate environments. In Shark Bay hypersaline mats, three “*Zixibacterota*” genomes related to Order “GN15” harboured *dsrAB* and *aprAB* (Wong et al., 2020). In tidal mudflats, six “*Zixibacterota*” MAGs carried sulfite reduction genes as part of sulfur-cycling communities (Ye et al., 2023). In the LLTP, “*Zixibacterota*” accounted for 34-94% of the total sulfate-reducing microorganism abundance across treatment units, and the four “*Zixibacterota*” MAGs of the “FEB-12” family contained a complete pathway for dissimilatory sulfate to sulfide reduction (Deng et al., 2024). In cold-seep sediments, “Bin19” encoded the full sulfate reduction pathway, unlike

the earlier RBG-1 genome (Savvichev et al., 2023). In hydrothermal systems, reductive *dsrB* sequences were assigned to “*Zixibacterota*” alongside known sulfate reducers (Zhong et al., 2022). The repeated detection of this pathway across all studied environments makes dissimilatory sulfate reduction the most robustly supported metabolic function in some of the representatives of the phylum.

Genes for nitrogen transformations have been detected in some “*Zixibacterota*” genomes, but the representation of genes involved in the full nitrogen cycle is incomplete. The expanded metabolic reconstruction of “RBG-1” included nitrate and nitrite reduction capacity (Castelle and Banfield, 2018). In the LLTP, “*Zixibacterota*” encoded and transcriptionally expressed *norBC* and *nosZ*, genes involved in the reduction of nitric oxide to nitrous oxide and nitrous oxide to dinitrogen (Deng et al., 2024). Critically, they lacked *narGHI* (nitrate reductase) and *nirKS* (nitrite reductase), meaning their denitrification potential is restricted to the last two steps of the pathway (Deng et al., 2024). In Beibu Gulf tidal flats, “*Zixibacterota*” MAGs carried genes for nitrite reduction to ammonia, and one MAG showed potential for nitrogen fixation (Ye et al., 2023). Across the phylum, nitrogen cycle gene content is variable and never covers a complete denitrification pathway in any single genome. This partial nature of components coding for roles in the nitrogen cycle, if biologically present and not a contamination artefact, is ecologically significant because it positions “*Zixibacterota*” as metabolic complements to other taxa that encode the missing upstream steps, such as *Pseudomonadota* in the LLTP (Deng et al., 2024).

The predicted capacity for iron and arsenic redox transformations was noted in the earliest metabolic reconstruction and reinforced by later studies detecting “*Zixibacterota*”

among iron-cycling taxa in deep subsurface fluids and hydrothermal systems (Castelle and Banfield, 2018; Casar et al., 2021). In hydrothermal vent MAGs, “*Zixibacterota*”-associated genomes encoded *mtrAB* (porin-cytochrome modules for extracellular electron transfer) and the reductive TCA cycle, suggesting chemolithoautotrophic iron-linked metabolism (Zhong et al., 2022).

The most unusual metal-related specialization, however, is mercury methylation. Among 135 medium- and high-quality “*Zixibacteria*” MAGs, 18 genomes (13.3%), carried *hgcA* with conserved motifs and were distributed across six orders (Liu et al., 2023). These genomes lacked the Wood-Ljungdahl pathway and instead encoded cobalamin-dependent methionine synthase (MetH), which was hypothesized to provide the methyl group for transfer to HgcA, the corrinoid-binding protein involved in mercury methylation (Liu et al., 2023). This genomic and structural evidence supports the potential for mercury methylation, but it has not yet been confirmed experimentally in a cultivated “*Zixibacterota*” representative. In the mangrove sediments examined by Liu et al. (2023), methylmercury reached a maximum concentration of 3.27 ng/g, but this community-level measurement cannot be attributed specifically to “*Zixibacterota*”. The ecological significance lies in the possibility that “*Zixibacterota*” contribute to the production of methylmercury, a bioaccumulative compound that can move through aquatic food webs and pose risks to fish, wildlife, and humans, particularly through consumption of contaminated seafood. These same MAGs also encode benzoyl-CoA reductase, an enzyme that enables anaerobic degradation of aromatic hydrocarbons (Liu et al., 2023). The ecological implication is not that methylmercury assists hydrocarbon breakdown, but rather that these MAGs from

mangrove sediments encode both benzoyl-CoA reductase and mercury methylation genes, suggesting that hydrocarbon adaptation provides a selective advantage in these environments while mercury methylation occurs independently (Liu et al., 2023). This co-occurrence of hydrocarbon adaptation and mercury methylation within a single uncultivated lineage illustrates how genome-resolved approaches reveal unexpected metabolic combinations that would be difficult to recover through cultivation-based surveys alone.

Beyond the pathways above, “*Zixibacterota*” is also predicted to contribute to the breakdown of complex organic carbon. In Baltic Sea sediments, transcripts mapping to CAZyme and peptidase ORFs assigned to “*Zixibacterota*” indicated active involvement in extracellular carbohydrate and protein degradation (Zinke et al., 2019). In Derwent Estuary sediments under heavy metal loading, “*Zixibacterota*” were enriched alongside metabolic shifts toward fermentation, polysaccharide degradation, and sulfur metabolism (Hillyer et al., 2023). These observations connect the fermentation pathways predicted from genomes to measurable activity in situ.

Overall, the ecological significance of “*Zixibacterota*” is therefore best captured not by any single pathway, but by their ability to integrate multiple elemental cycles within the same cells and across different redox regimes (Castelle and Banfield, 2018; Deng et al., 2024; Liu et al., 2023).

8. Syntrophy, microbial interactions, and ecological significance of “*Zixibacterota*”

A recurring theme across “*Zixibacterota*” research is that the lineage appears in network- or interaction-based interpretations more often than as a stand-alone dominant taxon. In mangrove subsurface sediments, “*Zixibacterota*” MAGs carrying *hgcA* and sulfate reduction genes also encoded traits linked to interspecies electron transfer, including multiheme cytochromes, conductive structures, and hydrogen metabolism (Liu et al., 2023). These features are consistent with a syntrophic lifestyle in energy-limited anoxic sediment. The strongest proposed partnership here is with *Syntrophobacterales*: positive co-occurrence, shared interspecies electron transfer features, and the absence of cobalamin biosynthesis in Hg-methylating “*Zixibacterota*” all suggest metabolic dependence on syntrophic partners for cofactor supply and possibly energetic support (Liu et al., 2023).

The mangrove microbial active functional module (mAFM) study broadened this view from pairwise syntrophy to community assembly, predicting previously unrecognized interactions between “*Zixibacterota*” and *Chloroflexota* and arguing that obligate metabolic dependencies are a major reason these organisms remain uncultivated (Du et al., 2022). The same study placed “*Zixibacterota*” into sulfur-cycle interaction cohorts where exchanged metabolites and hydrogen transfer complete pathway modules that no single lineage encodes alone (Du et al., 2022).

Engineered systems provide parallel evidence. In the LLTP study, “*Zixibacterota*” and *Pseudomonadota* repeatedly occupied the same network modules (Deng et al., 2024). Functional reconstruction revealed complementarity: “*Zixibacterota*” produced sulfide and carried some denitrification genes (*norBC*, *nosZ*) while *Pseudomonadota* contributed sulfur oxidation and nitric oxide production (Deng et al., 2024). The ecological role of

“Zixibacterota” in that system therefore depends on interaction complementarity rather than stand-alone metabolism. In anammox dynamic membrane bioreactors, “RBG-1”-affiliated *“Zixibacterota”* were among putative dissimilatory nitrate reduction to ammonium (DNRA) bacteria, showing positive correlations with fermentative and denitrifying partners in the biofilm community (Zhu et al., 2024). In high-salinity produced-water systems, *“Zixibacterota”* formed part of the symbiotic network associated with improved process stability (Yan et al., 2023).

The ecological significance of these interactions becomes clearer when distinguishing natural from engineered contexts. In natural systems, *“Zixibacterota”* appear as cooperative members of microbial consortia, not as dominant primary producers or independent specialists. Their recurring presence in cold seeps, mangrove subsurface sediments, hypersaline mats, and hydrothermal vent communities places them within communities shaped by steep redox gradients and overlapping element cycles (Savvichev et al., 2023; Wong et al., 2020; Zhong et al., 2022). In estuary sediments, they were enriched alongside shifts toward biofilm formation and metal tolerance, suggesting a role in community-level stress adaptation (Hillyer et al., 2023). A key dimension of this natural-system ecology is variable oxygen dependence across the phylum. The earliest reconstructed genome, RBG-1 from aquifer sediment, encoded a low-affinity aa₃-type terminal oxidase and alternative complex III but lacked high-affinity oxidases, suggesting adaptation to microoxic rather than fully anaerobic conditions (Castelle et al., 2013). Later MAGs from LLTP (“FEB-12”, Order “GN15”) carried both low-affinity caa₃-type and high-affinity bd-type terminal oxidases, a configuration that would allow the same organism to

respire oxygen across a broad concentration range while simultaneously maintaining sulfate reduction capacity (Deng et al., 2024). At the community level, this respiratory diversity tracks habitat redox status: in Beibu Gulf tidal flats, “*Zixibacterota*” MAGs were exclusive to anoxic mudflats and absent from oxic sandflats, confirming that oxygen availability is a primary filter on their distribution within natural systems (Ye et al., 2023). Together, these patterns indicate that “*Zixibacterota*” are not uniformly anaerobic but span a spectrum of oxygen tolerance that varies by lineage and micro-environment, which directly shapes where and how they engage in syntrophic partnerships.

In engineered systems, the role becomes more functionally consequential but also more ambivalent. In landfill leachate treatment, “*Zixibacterota*” contribution to nitrogen and sulfur removal, generated H_2S and N_2O as byproducts, making them both functional contributors and potential operational risks (Deng et al., 2024). This duality surfaces in other engineered contexts too: in saline anaerobic sludge, “*Zixibacterota*” increased under salt stress and benefitted from betaine amendment (Zhang et al., 2025). In anammox systems, they contributed biofilm-linked DNRA functions (Zhu et al., 2024).

A broader ecological conclusion follows: “*Zixibacterota*” are not passengers in these communities. In natural settings, they function as metabolic integrators within distributed networks, sustaining coupled sulfur, nitrogen, and carbon transformations that no single lineage performs alone. In engineered systems, the same properties can enhance system performance or introduce operational challenges depending on how their activity scales with reactor conditions and community composition. Natural systems select for “*Zixibacterota*” through redox gradients, sulfur availability, and heavy metal exposure, while

engineered systems intensify those same pressures through sulfate loading, salinity, pollutant pulses, and hydraulic disturbance (Deng et al., 2024). Their ecological significance therefore appears to lie in how their syntrophic lifestyle and metabolic flexibility allow them to stabilize or disrupt biogeochemical flows depending on environmental structure and partner availability.

9. Conclusions and Future Directions

“Zixibacterota” have transitioned from members of the “microbial dark matter” to a lineage of clear ecological relevance. Their broad environmental distribution, and metabolic flexibility point to a generalist lifestyle adapted to chemically dynamic environments. Increasing evidence suggests they function within cooperative microbial networks rather than as isolated metabolic units.

Advances in genome-resolved metagenomics, functional annotation, metabolic modeling, and structural prediction have enabled these insights despite the absence of cultivated representatives. However, current understanding remains limited by the relatively small number of genomes. This leaves intra-phylum diversity, evolutionary relationships, and ecological strategies incompletely resolved.

To interrogate this phylum and communicate more effectively about the diversity encompassed in this group, the development of a robust, evolution-informed taxonomy and systematic exploration of metabolic diversity across lineages is required. Future experimental approaches, including enrichment and co-cultivation strategies, will be

essential to validate genomic predictions and resolve physiological traits. Finally, given their involvement in environmentally significant processes such as greenhouse gas production and mercury transformation, understanding and potentially managing “*Zixibacterota*” activity will be important for both biogeochemical research and environmental biotechnology.

Chapter 3: Research Manuscript

Introduction

Metagenomics has uncovered a vast, uncultured diversity of prokaryotes, revealing numerous microbial lineages that traditional cultivation approaches fail to capture (Hedlund et al., 2015). This involves surveys based on metagenome-assembled genomes (MAGs) and unbinned contigs that have identified deeply branching lineages (Prasoodanan et al., 2026; Castelle and Banfield, 2018). These studies have also revealed previously unrecognized contributors to major biogeochemical cycles (Prasoodanan et al., 2026; Castelle and Banfield, 2018). Many of these underexplored lineages exhibit streamlined biosynthetic capacities, unusual metabolic repertoires and strong ecological interdependencies; features that complicate both their cultivation and taxonomic placement (Castelle and Banfield, 2018). Genome-centered approaches therefore provide a critical framework for documenting and characterizing microbial diversity that would otherwise remain inaccessible. The importance of such efforts has intensified in the context of accelerating climate change, land degradation, and habitat fragmentation, which all threaten the loss of prokaryotic diversity before many species can be identified or studied (Dominguez-Bello et al., 2025; Cavicchioli et al., 2019; Jimenez et al., 2026). These challenges underscore the importance of genome-resolved surveys for establishing baseline knowledge of microbial diversity and metabolic potential across Earth's ecosystems (Jimenez et al., 2026).

Among these uncultivated groups, the phylum "*Zixibacterota*" (syn. "*Zixibacteria*", *Ca. Zixiibacteriota*) has emerged as a phylogenetically distinct bacterial lineage with broad

environmental distribution and a potentially significant influence on element cycling. “*Zixibacterota*” were first identified as the “RBG-1” lineage from aquifer sediments of the Colorado River (USA), where a genome reconstruction predicted a metabolically versatile lifestyle (Castelle et al., 2013; Castelle and Banfield, 2018). Since then, members of the phylum have been recovered from diverse environments, including estuarine and mangrove sediments, groundwater, deep subsurface mines, cold seeps, hypersaline microbial mats and hydrothermal settings (Wong et al., 2020; Casar et al., 2021; Liu et al., 2023; Savvichev et al., 2023; Deng et al., 2024; Zhong et al., 2022). These detections span geographically distinct regions across North America, Europe and Asia, as well as the Atlantic, Pacific, Indian and Arctic Oceans (Li et al., 2025; Bryukhanov et al., 2025; Qu et al., 2024; Zhang et al., 2025; Goh et al., 2022; Baker et al., 2015). Genome-resolved studies further indicate metabolic capabilities linked to sulfur, nitrogen, iron and carbon cycling, together with flexible respiratory strategies that likely support persistence across fluctuating redox gradients (Castelle et al., 2013; Wong et al., 2020; Casar et al., 2021; Savvichev et al., 2023; Deng et al., 2024; Zhong et al., 2022).

Despite increasing recognition of the phylum, current understanding of “*Zixibacterota*” and its classification remains limited. When the name “*Zixibacteria*” was first assigned, no nomenclatural types were designated for the phylum, and the lack of guidance on nomenclature for the uncultivated prokaryotes resulted in inconsistent naming of taxa. Genome Taxonomy Database (GTDB) release R226 recognizes one class and ten orders within the phylum, all represented by alphanumeric placeholder names and lacking cultivated representatives. Moreover, most available inferences regarding their physiology

are derived from a limited number of genomes. As a result, our understanding of their biology, the evolutionary relationships among these lineages, and the extent to which major metabolic traits are conserved or lineage-restricted, remain unresolved.

Here, I address these gaps by establishing a genome-based taxonomic framework for “*Zixibacterota*” and systematically investigate its metabolic potential. Phylogenomic analyses based on multiple complementary amino acid bacterial marker sets consistently recovered “*Zixibacterota*” as a monophyletic lineage, with taxonomic boundaries further supported by overall genome relatedness metrics. Comparative genome analyses revealed a suite of conserved structural and metabolic traits, including a diderm cell envelope, Type IV pili and a heterotrophic oxidative central metabolism, alongside lineage-specific metabolic modules such as alternative complex III (ACIII)-aa₃ oxidase supercomplexes, sulfate reduction and polysaccharide degradation. Together, this integrated approach provides a robust evolutionary and functional foundation for understanding the diversification, ecology and biogeochemical roles of “*Zixibacterota*”.

Methods

Genome collection, quality assessment and taxon set definition

Publicly available genomes assigned to “*Zixibacterota*” and closely related taxa were retrieved from release R226 of the Genome Taxonomy Database (GTDB) (Parks *et al.*, 2022). Genome completeness and contamination estimates based on CheckM2 (Chklovski *et al.*, 2023), together with associated metadata including genome size, GC content, contig count, transfer RNA (tRNA) gene counts, genome recovery source, and country of origin, were

obtained from the GTDB bac120 metadata file. Corresponding genome assemblies were downloaded using the NCBI Datasets command-line interface (O’Leary et al., 2024). These data were complemented with additional MAGs recovered in the Palmer laboratory at the University of Manitoba, Winnipeg (Ben Kilbrei, *personal communication*) from saline springs along the western shores of Lake Winnipegosis, Manitoba, as well as unpublished, preliminarily classified “*Zixibacterota*” MAGs provided by the Banfield laboratory, University of California, Berkeley (Jill Banfield, *personal communication*).

Ribosomal RNA genes were predicted from both “*Zixibacterota*” genomes and selected outgroup genomes using *barrnap* (Seemann, 2013) with the --reject 0.1 option to retain partial and fragmented sequences. Transfer RNA genes in unpublished MAGs were predicted using tRNAscan-SE v2.0.12 (Chan *et al.*, 2021).

Genome quality was assessed based on CheckM2 completeness and contamination estimates in conjunction with the presence of 5S, 16S, and 23S rRNA genes, and the number of tRNA genes. Genomes with $\geq 50\%$ completeness and $\leq 10\%$ contamination were classified as medium quality, whereas genomes with $\geq 90\%$ completeness, $\leq 5\%$ contamination, the presence of 5S, 16S, and 23S rRNA genes, and encoding tRNA genes for at least 18 amino acids were classified as high quality based on the criteria provided before (Bowers et al., 2017; Hedlund et al., 2022). Only medium- and high-quality genomes were retained for downstream analyses, and the entire dataset consisted exclusively of genomes meeting these quality criteria.

Genomes were provisionally classified using the GTDB Toolkit (GTDB-Tk) v2.4.0 (Chaumeil *et al.*, 2022) to confirm their assignment to the phylum “*Zixibacterota*” and identify appropriate outgroup taxa. This was done by using the GTDB-Tk classify workflow with default settings, which uses pplacer to place genomes into an approximate maximum-likelihood reference tree derived from the masked concatenated alignment of the bac120 markers. The resulting reference tree was retained for further interrogation. Appropriate outgroup genomes were selected from neighbouring putative GTDB phylum-level lineages to enable robust rooting of phylogenomic trees.

Phylogenomic analyses and taxonomic assignment

Aligned conserved marker sets were extracted using three established phylogenomic pipelines: the GTDB-Tk bac120 dataset (120 amino acid sequences of markers; Chaumeil *et al.*, 2022), the UBCG3 dataset (92 nucleotide sequences of markers; Kim *et al.*, 2018), and the BCGTree v1.2.1 dataset (110 amino acid sequences of markers; Ankenbrand and Keller, 2016). Concatenated supermatrices were constructed for four marker sets (full list of marker sets available in online supplemental tables, see data availability section) using FASconCAT-G v1.06.1 (Kück and Longo, 2014): i) the bac120 amino acid dataset, ii) the UBCG3 nucleotide dataset, iii) the translated UBCG3 markers to produce the UBCG3 amino acid marker set, and iv) the BCGTree amino acid marker set. During the concatenation of these data matrices with FASconCAT-G, the optimal substitution models were determined for each partition using ProtTest v3.4 (Darriba *et al.*, 2011), whereas the nucleotide dataset was

analysed under a GTR+F model with independent parameter optimization applied per partition. The obtained partition files and concatenated supermatrices were used for tree reconstruction.

Maximum-likelihood phylogenies were inferred using IQ-TREE v2.4.0 (Minh *et al.*, 2020), under a partition scheme in which each marker was treated as a separate partition as specified in a partition file. Partitioned analyses were performed using the ‘-Q’ option, which applies an edge-linked proportional partition model allowing each partition to have its own evolutionary model parameters while sharing a common tree topology and branch-length framework (Lopez *et al.*, 2002). Node support was assessed using ultrafast bootstrap (UFBoot) (Hoang *et al.*, 2018) and Shimodaira–Hasegawa approximate likelihood ratio tests (SH-aLRT) (Shimodaira and Hasegawa, 1999), each with 1,000 replicates. Topological congruence among trees derived from the different marker sets was used to evaluate the robustness of inferred relationships and to guide taxonomic delineation.

Overall genome-relatedness indices and support for taxon boundaries

Genome-based similarity metrics were used to evaluate support for phylogenetically inferred taxonomic boundaries. Protein-coding genes were predicted from genome assemblies using Prokka v1.14.6 (Seemann, 2014), which employs Prodigal v2.6.3 (Hyatt *et al.*, 2010), and the resulting amino acid sequence files (.faa) were used for average amino acid identity (AAI) calculations. Pairwise AAI values were calculated using the *aai.rb* script from the Enveomics Toolbox (Rodriguez-R and Konstantinidis, 2016), whereas average

nucleotide identity (ANI) values were calculated directly from genome assemblies (.fna files) using FastANI v1.33 (Jain et al., 2018).

Custom Python scripts (*allvsall_aai.py* and *allvsall_ani.py*) were developed to automate all-versus-all genome comparisons. These scripts executed pairwise AAI calculations using the Enveomics script and pairwise ANI calculations using FastANI for all genome pairs and subsequently compiled the results into genome similarity matrices. The resulting AAI and ANI matrices were visualized as clustered heatmaps using a custom R script implemented with the pheatmap package (Kolde, 2019). Custom scripts used for pairwise comparisons, matrix generation, and visualization are provided in the Supplementary Note 1.

16S rRNA gene phylogeny

Predicted 16S rRNA gene sequences were extracted as nucleotide sequences using BEDtools v2.31.1 “*getfasta*” subcommand (Quinlan and Hall, 2010) and aligned with the SINA aligner v1.2.12 (Pruesse et al., 2012), with unaligned positions removed prior to downstream analyses. A maximum-likelihood phylogeny was inferred using IQ-TREE v2.4.0, with ModelFinder (–m MFP) employed to select the best-fitting nucleotide substitution model (Kalyaanamoorthy et al., 2017). Node support was assessed using UFBoot and SH-aLRT tests with 1,000 replicates each.

Parsimony based homoplasy indices

Parsimony-based measures of homoplasy were calculated using PAUP* v4.0a (build 169; Swofford, 2002). For each dataset (amino acid marker sets: GTDB-AA, BCGTree-AA, and UBCG3-AA; and nucleotide marker sets: UBCG3-NT, including all codon positions as well as first and second codon positions only), heuristic maximum-parsimony searches were performed using tree-bisection–reconnection (TBR) branch swapping with 50 random addition replicates and a maximum of 10 trees retained per step.

Following each heuristic search, the set of most-parsimonious trees retained in memory was used to calculate tree statistics in PAUP*. Consistency Index (CI) and Retention Index (RI) were computed using the ‘pscores / ci ri’ command, which summarizes these indices across the retained most-parsimonious tree set. The Homoplasy Index (HI) was subsequently calculated as $HI = 1 - CI$. These values therefore reflect the degree of homoplasy present in the optimal parsimony tree space for each dataset rather than a single representative topology.

Substitution saturation analyses

Substitution saturation was assessed for concatenated marker supermatrices using R v4.3.2. Nucleotide and amino acid analyses were performed separately using custom R scripts, with nucleotide analyses implemented using the ape package v5.8.1 (Paradis and Schliep, 2019) and amino acid analyses using the phangorn package v2.11.1 (Schliep, 2011).

For nucleotide datasets, partition boundaries were derived from the FASconCAT-G partition file to define gene-wise blocks. Each partition was further subdivided into four site categories: all sites, and codon positions 1, 2, and 3, respectively, determined relative to the partition start position. Pairwise uncorrected genetic distances were calculated in ape using “`dist.dna(dsub, model = "raw", pairwise.deletion = TRUE)`”. Model-corrected distances were computed under the TN93 substitution model using “`dist.dna(dsub, model = "TN93")`”. Substitution saturation was quantified by ordinary least squares (OLS) regression of TN93-corrected distances against uncorrected p-distances for each partition and site category, with slope and R^2 used as summary statistics. To assess saturation in low-divergence regions, additional regressions were performed using only pairwise comparisons within the 95th percentile of p-distances. Partition-level estimates were summarised using both inverse-variance weighting and length-weighted averaging based on the number of ungapped alignment positions per partition. Pairwise calculations used pairwise deletion for sites containing gaps or ambiguous characters.

For amino acid datasets (GTDB-AA, UBCG3-AA, and BCGTree-AA), uncorrected distances were computed using Hamming distances implemented in phangorn “`(dist.hamming(tmp_subset, ratio = TRUE))`”. Model-corrected amino acid distances were estimated using maximum-likelihood distances in phangorn (“`dist.ml(seg, model = mdl)`”), with substitution models specified per partition according to the FASconCAT-G partition file. Partition-aware mapping of alignment sites to site-pattern indices was applied to ensure correct subset extraction within compressed site-pattern matrices. For each partition,

corrected distances were regressed against uncorrected distances using OLS, and slope and R^2 values were recorded.

All analyses were implemented in custom R scripts (nt_saturation_by_partition.R for nucleotide datasets and aa_saturation_partitioned.R for amino acid datasets; R v4.3.2). These scripts generated pairwise distance tables, regression plots, and partition-level summaries. Final aggregated estimates were obtained using length-weighted pooling across partitions, and for nucleotide datasets, additional inverse-variance weighted summaries were calculated for slope and R^2 values. All scripts and parameter settings are provided in the Supplementary Note 2 to ensure reproducibility.

Metabolic annotation and pathway reconstruction

Metabolic potential was predicted for all medium- and high-quality genomes using eggNOG-mapper v2.1.12 (Cantalapiedra *et al.*, 2021). Predicted protein sequences were functionally annotated against the eggNOG database, and KEGG Orthology (KO) identifiers were retrieved for all detected genes that code for enzymes. For each genome, KO profiles were compiled and used for pathway reconstruction and visualisation in KEGG Mapper web-tool (Kanehisa and Yato, 2022).

The presence and completeness of central metabolic and energy-conserving pathways were evaluated based on KEGG Orthology (KO) assignments, and key metabolic traits were manually curated. KO-based metabolic profiles were first generated at the individual genome level and subsequently aggregated at the species level to account for

within-species genomic variation. For species represented by multiple genomes, a consensus approach was applied, whereby a gene or metabolic trait was considered present if detected in $\geq 70\%$ of genomes within that species; otherwise, it was scored as absent. For species represented by multiple genomes, a consensus approach was applied whereby a gene or metabolic trait was considered present if detected in $\geq 70\%$ of genomes within that species; otherwise, it was scored as absent. For higher taxonomic ranks (genus, family, order, and class), trait distributions were summarized using a majority-rule consensus ($\geq 50\%$) based on the represented lower-level taxa. This consensus was used to summarize trait distributions for comparative analyses and visualization. The thresholds were used to reduce the effect of presence due to potential genomic contamination and annotation artefacts while detecting consistent lineage-level signal. KO-based metabolic profiles were subsequently compared across taxa to identify shared and lineage-specific traits, as well as broader patterns of metabolic similarity and differentiation within the lineages in the phylum.

Identification and classification of hydrogenase genes

Hydrogenase genes were identified using hidden Markov model (HMM) searches against curated hydrogenase models from HydDB (Søndergaard et al., 2016). Predicted protein sequences from each genome were queried using HMMER v3.4 (*hmmsearch*) (Finn et al., 2011) against three HydDB HMM profiles corresponding to the major hydrogenase classes: [FeFe], [NiFe], and [Fe]-only hydrogenases.

To enable genome-resolved analyses, a custom Python workflow was implemented to perform independent *hmmsearch* queries for each genome against the HydDB HMM profiles. Searches were conducted and class-specific domain bit-score thresholds recommended by HydDB were applied (50 for [FeFe], 120 for [NiFe], and 54.4 for [Fe]-only hydrogenases). Outputs were recorded as tabular and domain-level files, from which candidate hydrogenase sequences were extracted.

All candidate hydrogenase sequences were concatenated into a single dataset for downstream classification. Functional classification was performed using DIAMOND BLASTP v2.0.15 (Buchfink et al., 2021) against the HydDB reference protein database, formatted using *diamond makedb*. Searches were conducted in ultra-sensitive mode, retaining a maximum of one target sequence per query. Hydrogenase class and group assignments were inferred from the top-scoring homolog based on HydDB annotations.

To minimise false positives, results were filtered using HydDB-recommended sequence identity thresholds. Hits assigned to [NiFe] hydrogenases were retained at $\geq 50\%$ amino acid identity for Group 4 and $\geq 30\%$ for Groups 1–3. [FeFe] hydrogenases were retained at $\geq 45\%$ identity, and [Fe]-only hydrogenases at $\geq 50\%$ identity. The combined use of HMM-based detection and sequence similarity-based classification enabled sensitive identification of divergent homologs while maintaining robust functional assignment. The resulting curated dataset was used for downstream analyses of hydrogenase diversity and distribution across “*Zixibacterota*” genomes.

Identification of iron metabolism genes

Genes involved in iron metabolism were identified using FeGenie (Garber et al., 2020), a bioinformatic pipeline for the detection of iron-related genes in microbial genomes. Predicted protein sequences from “*Zixibacterota*” genomes were used as input. FeGenie performs HMM-based homology searches using HMMER against a curated database of protein families associated with iron metabolism, including pathways involved in iron oxidation, iron reduction, iron transport, iron storage, and siderophore biosynthesis and uptake. Resulting annotations were parsed to identify candidate iron metabolism genes in each genome. Gene presence–absence profiles were subsequently summarised across the dataset to assess the distribution of iron-related metabolic capabilities within “*Zixibacterota*” lineages.

Identification of Alternative Complex III operons in “*Zixibacterota*”

The presence of Alternative Complex III (ACIII) in respiratory electron transport was predicted in “*Zixibacterota*” genomes using a combined homology and profile-based approach. Protein sequences corresponding to the ACIII operon from the previously characterised “*Zixibacterota*” genome “RBG-1” (Castelle et al., 2013), including the core subunits ActA–ActF and associated terminal oxidase components, were used as reference queries. Each reference protein was searched against protein sequences of all “*Zixibacterota*” genomes using DIAMOND BLASTP with an e-value threshold of 1×10^{-10} and a minimum query coverage of 60%.

To improve detection of divergent homologs, initial BLAST-based retrieval was used to expand lineage-specific sequence diversity, which was subsequently incorporated into HMM profiles for sensitive and comprehensive identification of ACIII subunits. Candidate sequences were retrieved using SeqKit v2.3.0 (Shen *et al.*, 2016) and grouped by individual subunits of ACIII and terminal oxidases. Redundant sequences were removed using CD-HIT v4.8.1 at 95% sequence identity (Fu *et al.*, 2012) to reduce overrepresentation bias and improve the quality of downstream alignments and HMM construction. Non-redundant sequences were aligned using MAFFT v7.526 (Kato and Standley, 2013), and poorly aligned regions were trimmed using TrimAl v1.5.rev1 (Capella-Gutiérrez *et al.*, 2009). HMM profiles were constructed for each subunit using HMMER (*hmmbuild*), and individual models for ActA–ActF and terminal oxidase components were combined into a unified profile database. This database was queried against the “*Zixibacterota*” protein sequences using HMMER (*hmmsearch*), and domain-level outputs were used for downstream operon detection and subsequent analyses.

HMM hits were parsed using custom Python scripts, and subunit-specific bit score thresholds were applied to minimize false positives (ActA ≥ 100 , ActB ≥ 120 , ActC ≥ 80 , ActD ≥ 50 , ActE ≥ 50 , ActF ≥ 80 , and terminal oxidase subunits ≥ 100). Thresholds were empirically defined based on preliminary inspection of HMMER score distributions across representative genomes, using the separation between high-confidence syntenic ACIII operon hits and lower-scoring non-specific protein homologs. These cutoffs reflect differences in conservation among ACIII subunits, with more conserved subunits requiring higher stringency and more variable subunits requiring relaxed thresholds to retain true

homologs while excluding spurious matches. Hits were grouped by genome and ordered based on locus identifiers extracted from protein headers. Putative ACIII operons were defined as gene clusters spanning ≤ 5 loci and containing core ACIII subunits. The co-localisation of terminal oxidase genes within these clusters was used to classify operons as either ACIII-only or ACIII-associated with terminal oxidases. Operon coordinates and gene composition were recorded, and gene order was standardised to ensure consistent orientation of terminal oxidase loci relative to ACIII clusters.

Delineation of the ActB1 domain

The catalytic region of the ACIII ActB subunit (ActB1) was defined based on conserved domain architecture. Reference ActB proteins from phylogenetically diverse bacteria, including the “*Zixibacterota*” genome “RBG-1”, were analysed alongside ActB homologs from 20 representative “*Zixibacterota*” genomes. These sequences were queried against the NCBI non-redundant (nr) protein database using BLASTP to qualitatively inspect domain architectures and validate domain consistency across diverse homologs. This step served as an exploratory assessment of domain organization rather than boundary inference. The ActB1 region was defined as the conserved N-terminal segment encompassing the MopB-like domains and terminating immediately prior to the linker region connecting to the C-terminal PsrB-like Fe–S domain. Based on these manually defined coordinate boundaries, ActB1 regions were extracted from reference and representative sequences using SeqKit (*subseq*).

To enable comprehensive identification of the ActB1 catalytic region across all detected “Zixibacterota” ActB homologs, a domain-aware extraction strategy was employed. First, ActB1 sequences derived from the manually curated reference set (20 representative genomes) were used to define conserved catalytic boundaries. These sequences were then combined with full-length ActB proteins identified from the complete “Zixibacterota” dataset and aligned using MAFFT with the DASH algorithm (Rozewicki et al., 2019).

Conserved ActB1 regions were subsequently delineated across the full alignment using profile-based detection with HMMER (*hmmsearch*), ensuring consistent identification of the catalytic domain across divergent homologs. The resulting ActB1 sequences were extracted to generate a final curated dataset for phylogenetic analysis.

Phylogenetic analysis of ActB1

Phylogenetic analyses were conducted using ActB1 sequences from “Zixibacterota” together with reference homologs. Sequences corresponding to the quinone reductase complex (Qrc) subunit QrcB, which is evolutionarily related to ActB1 (Venceslau et al., 2010), were included as outgroups. Multiple sequence alignment was performed using MAFFT-DASH, and maximum-likelihood phylogenies were inferred using IQ-TREE v2.4.0 with automatic model selection using ModelFinder (–m MFP). Branch support was assessed using UFBoot and SH-aLRT tests with 1,000 replicates each.

Results and Discussion

A cohesive taxonomic framework for “*Zixibacterota*”

Preliminary GTDB-Tk classification revealed that the most closely related phyla to “*Zixibacterota*” are “*Latescibacteriota*”, “*JAAXHH01*”, “*Edwardsbacteria*”, “*TA06*”, “*TA06_A*” and “*4572-55*” (Supplementary Figure 1). Building on this initial placement, we reconstructed phylogenomic relationships using a comprehensive dataset of medium- and high-quality genomes from GTDB and this study, together with these outgroup phyla identified during preliminary classification. Phylogenomic inference was independently performed using three complementary bacterial marker sets (GTDB bac120, UBCG3 and BCGTree).

To evaluate the overlap in markers among these pipelines, PFAM and TIGRFAM terminology was normalized across the marker sets to assess the shared content across datasets. This analysis revealed a conserved core of 65 markers common to all three frameworks (Supplementary Figure 2), predominantly consisting of ribosomal proteins and other essential components of transcriptional, translational, and replicative machinery (Supplementary Table 1). Despite this shared backbone, each marker set also incorporated distinct gene complements and alignment strategies. The application of multiple phylogenomic frameworks therefore provides a robust basis for inference, ensuring that recovered topologies are not artefacts caused by the selection of any single marker or methodological assumption.

Across all amino acid sequence marker-based trees, the phylogenies could consistently be rooted with the outgroup taxa as monophyletic and distinct from the “*Zixibacterota*” lineage, supporting the placement of “*Zixibacterota*” as a discrete phylum. Concordance among bacterial marker-set phylogenies was used to delimit putative taxonomic boundaries at order, family and genus-level, where branches with UFBoot ≥ 95 and SH-aLRT ≥ 0.8 were considered strongly supported (Figure 1). OGRI provided independent support for these phylogenetically defined boundaries. Pairwise ANI and AAI clustering patterns were concordant with the amino acid phylogenies, with genomes assigned to the same phylogenomic groups forming coherent similarity clusters in ANI/AAI space (Figure 2). These concordant clusters corroborated rank assignments, with ANI and AAI serving as supporting evidence for the delineation of taxa across ranks. This framework yielded a classification comprising 1 class, 10 orders, 21 families, 109 genera and 210 species represented by at least one medium- or high-quality genome (Supplementary Table 2). Species and their higher taxa represented by high-quality genomes (based on checkM2 metrics) were then named and described (Table 1 and Supplementary note 3).

To ensure nomenclatural robustness under SeqCode guidelines, we prioritized genomes with high completeness and minimal contamination that also contained near-complete 16S and 23S rRNA genes, along with tRNA complements covering at least 18 amino acids. Taxonomic assignments were further constrained by congruence between a 16S ribosomal RNA gene phylogeny (Supplementary Figure 3) and amino acid-based phylogenomic placements. Within this framework, taxon names were assigned based on geographic origin and, where supported by genomic context, inferred metabolic traits. This resulted in

proposing names for 65 species, 51 genera, 16 families, 8 orders, 1 class, and the phylum itself (Supplementary Table 3). Remaining taxa lacking recoverable rRNA genes despite otherwise representing high-quality genome assemblies, as well as those represented only by medium-quality genomes, were retained as alphanumeric placeholders to preserve representation of the full genomic diversity captured in this study.

Reconciling nucleotide–amino acid tree discordance

The phylogeny inferred from the UBCG3 nucleotide (NT) marker set was discordant with those inferred from the amino acid (AA) sequence-based marker sets (GTDB-AA, UBCG3-AA and BCGTree-AA). Specifically, in the NT tree, a clade comprising the outgroup phyla “TA06”, “TA06_A” and “4572-55”, together with one “*Edwardsbacteria*” representative, was recovered nested within the “*Zixibacterota*” radiation. In contrast, all AA-based trees consistently recovered “*Zixibacterota*” and these outgroups as reciprocally monophyletic.

To test whether the discordant NT placement reflects a reconstruction artefact, we quantified homoplasy and substitution saturation on matched datasets. The homoplasy index ($HI = 1 - CI$) was highest for the NT matrices (0.944 for all codon positions and 0.926 for positions 1+2), whereas AA datasets showed substantially lower HI values (0.813, 0.809 and 0.802 for GTDB-AA, UBCG3-AA and BCGTree-AA, respectively). These results indicate greater homoplasious signal in the NT data—particularly when third positions are included—

consistent with increased susceptibility to non-phylogenetic clustering driven by convergent or parallel substitutions.

Substitution-saturation analyses were consistent with the view that inclusion of highly saturated third codon positions contributed to the discordant NT topology (Supplementary figure 4). For AA datasets, and for NT datasets excluding third codon positions (pos1+2), uncorrected p-distances and model-corrected distances retained strong linear relationships, indicating limited saturation across the sites used for inference. By contrast, datasets dominated by third codon positions exhibited reduced correspondence between uncorrected and corrected distances, consistent with substantial saturation at third positions; such saturation erodes historical signal and can promote artefactual placements in phylogenies.

Taken together—elevated NT homoplasy, evidence of third-position saturation, and very low AAI between “*Zixibacterota*” and the outgroups—the most parsimonious explanation is that the NT-based discordance reflects a reconstruction artefact driven primarily by saturated third codon positions rather than genuine phylogenetic relatedness. Accordingly, AA-based phylogenies were treated as the more reliable representation of “*Zixibacterota*”–outgroup relationships.

“*Zixibacterota*” genomes encode a conserved diderm cellular architecture and cell structures associated with environmental interactions

Having established a robust phylogenomic framework for the phylum, we next examined the genomic basis of its cellular architecture and metabolic potential (Figure 3; Supplementary Table 4 and 5). Although a $\geq 50\%$ majority-rule consensus was used to summarize trait distributions across taxonomic ranks, not all majority-supported traits were interpreted as lineage-defining characteristics. Traits exhibiting substantial variation among constituent taxa were interpreted conservatively to avoid overgeneralizing metabolic capabilities. Comparative genomic analyses across 210 species representatives revealed a highly conserved diderm cell-envelope architecture encoded throughout the phylum. Nearly all genomes encoded canonical lipopolysaccharide transport and outer membrane biogenesis systems, including the lipopolysaccharide transport machinery (Lpt), β -barrel assembly components centered on BamA-associated partners, lipoprotein trafficking systems (Lol), and complete peptidoglycan biosynthesis pathways. Conservation of genes for the synthesis of UDP-GlcNAc, UDP-MurNAc, CMP-Kdo, and GDP-mannose further supports widespread capacity for lipopolysaccharide/core oligosaccharide and peptidoglycan assembly, collectively indicate a likely diderm envelope organization across the phylum.

Genes associated with rod morphogenesis were broadly conserved across the phylum, including *rodA/mrdB* and *mreB*, while *rodZ* and *mreC* displayed more variable distributions. In parallel, canonical Type IV pilus machinery and a chemotaxis gene repertoire were retained across the phylum, and flagellar biosynthesis genes were detected in 158 of 210 species representatives. Flagellar systems were particularly prevalent in orders “*Omnivagifaeales*” (*syn.* GN15; 112/122 species representative genomes),

“*Sulfurireductorales*” (syn. JAABVY01; 7/9), “*Telluricrassaminales*” (syn. UBA10806; 11/17), “*Cuniculidesidentales*” (syn. WJJR01; 13/16), and “*Cryptaquifericales*” (syn. UM-FILTER-46-8; 4/4), suggesting that motility and environmental sensing represent widespread ecological interaction strategies within the phylum. The widespread retention of motility, attachment, and sensory systems suggests that many members of the phylum are adapted to actively explore and exploit chemically heterogeneous environments. Such capabilities would facilitate migration along nutrient and redox gradients, colonization of particles and surfaces, and rapid responses to fluctuating physicochemical conditions.

The pervasive conservation of these envelope and interaction systems has important evolutionary implications. “*Zixibacterota*” retain the full suite of molecular machinery required to construct and maintain a canonical diderm cell envelope. The near-universal distribution of genes for Lpt, Bam, and Lol systems across all examined species representatives indicates that the diderm state is not a lineage-specific innovation but likely an ancestral and evolutionarily stable characteristic of the phylum. This inference is consistent with the earliest description of the lineage from genome RBG-1, from aquifer sediments, which reported the presence of outer membrane proteins and a Gram-negative-like cellular organization (Castelle et al., 2013). Taken together, these findings suggest that the evolutionary success of “*Zixibacterota*” has been built upon a conserved structural framework that combines a diderm envelope with extensive capacities for environmental sensing, motility, and surface interactions.

Conserved heterotrophic central metabolism supports oxidative carbon utilization

Genes encoding central carbon metabolism pathways were remarkably conserved across the phylum and was overwhelmingly consistent with a heterotrophic, respiratory lifestyle. Most genomes encoded glycolysis/gluconeogenesis, pyruvate oxidation to acetyl-CoA, complete or near-complete tricarboxylic acid cycle, and a conserved non-oxidative pentose phosphate pathway coupled with phosphoribosyl pyrophosphate biosynthesis (Supplementary Table 4). These findings collectively support respiratory carbon oxidation as a core metabolic strategy throughout the phylum.

This conserved framework was complemented by widespread capacities for carbohydrate metabolism and substrate interconversions. The 4- α -glucanotransferase gene *malQ*, involved in maltose and maltodextrin metabolism, was encoded by 143 of 210 species representatives, while glycogen phosphorolysis (*glgP*) was encoded by 165 of 210 genomes, suggesting widespread capacities for glycogen metabolism and transient carbon storage utilization (Figure 3 and Supplementary Table 4). In addition, genes associated with short-chain fatty acid catabolism, particularly pathways funneling propanoyl-CoA into central metabolism, were broadly distributed. The prevalence of these genes suggests that many “*Zixibacterota*” can exploit chemically diverse organic substrates while maintaining access to intracellular carbon reserves during periods of resource limitation. Rather than occupying narrowly defined nutritional niches, members of the phylum appear equipped for opportunistic utilization of fluctuating carbon pools across a wide range of environmental settings.

Genes mediating acetaldehyde–ethanol interconversion were also common. The propanol-preferring alcohol dehydrogenase (*adhP*) and the bifunctional aldehyde/alcohol dehydrogenase (*adhE*) occurred in at least one form in 121 of 210 species representatives and were particularly prevalent in the orders “*Zixibacterales*” (*syn.* MSB-5A5;14/26), “*Telluricrassaminales*” (14/17), and the families “*Omnivagifaeceae*” (54/85), and “*Altundifaecaceae*” (*syn.* PGXB01;17/23) (Figure 3 and Supplementary Table 4). These enzymes are frequently associated with fermentative metabolism, redox balance, and the utilization of low-molecular-weight fermentation products, suggesting that many lineages retain the capacity to supplement respiratory metabolism with alcohol-associated redox transformations under oxygen-limited conditions.

The widespread occurrence of alcohol dehydrogenase genes further points to a potential role for “*Zixibacterota*” in community-level carbon exchange networks. Members of the phylum have been identified as important degraders of organic matter in hydrocarbon seep sediments, where fermentation products such as ethanol can serve as electron donors for sulfate-reducing microorganisms (Zhao et al., 2022). Metabolite exchange modeling in mangrove sediments similarly predicted frequent transfers of ethanol and acetaldehyde between phyla and identified “*Zixibacterota*” as active participants in these exchanges, particularly in association with *Desulfobacterota* (Du et al., 2024). Consistent with these observations, the original genomic reconstruction of the RBG-1 lineage identified multiple alcohol dehydrogenase genes and proposed the capacity for both ethanol fermentation and ethanol respiration (Castelle et al., 2013). Collectively, these findings suggest that alcohol metabolism may represent an important interface through which “*Zixibacterota*” engage in

syntrophic interactions, functioning either as producers of ethanol that support partner organisms or as consumers of fermentation products generated elsewhere within microbial communities.

Respiratory chain architectures indicate adaptation to oxic–suboxic environments

Respiratory metabolisms emerged as one of the most conserved physiological features of the phylum (Figure 3). Nearly all genomes encoded NADH dehydrogenase (Complex I), succinate dehydrogenase/fumarate reductase components (Complex II), and complete F-type ATP synthases, likely indicating that respiration constitutes a foundational metabolic strategy throughout “*Zixibacterota*”. This widespread conservation suggests that, despite extensive diversification in substrate utilization and environmental distribution, the phylum has retained a common energy metabolism framework centered on membrane-associated electron transport and oxidative phosphorylation.

In contrast to the highly conserved genes encoding upstream components of the respiratory chain, terminal oxidase gene repertoires exhibited substantial lineage-specific variation. Cytochrome aa_3 -type oxidases were encoded by 114 of 210 species representatives and particularly in those within the orders “*Omnivagifaeales*” (67/122), “*Telluricrassaminales*” (13/17) and “*Cuniculidesidentales*” (10/16). Cytochrome cbb_3 -type oxidases, which possess high oxygen affinity and are typically associated with microoxic respiration, were common in the order “*Undifaeales*” (*syn.* CAIYYT01; 6/10) and the family “*Fundimaricultoraceae*” (*syn.* JAAZOE01; 5/10). Cytochrome bd oxidases, commonly linked

to oxygen stress tolerance and low-oxygen adaptation, were common in several lineages, including the orders “*Undifaecales*” (9/10) and “*Sulfurireductorales*” (7/9), and the family “*Altundifaeceae*” (16/23). The coexistence of genes for terminal oxidases with distinct oxygen affinities and physiological roles suggests that many “*Zixibacterota*” lineages are adapted to environments characterized by fluctuating oxygen availability rather than permanently oxic conditions. Such respiratory versatility would be advantageous in aquifers, hydrothermal systems, and other redox-stratified habitats where oxygen concentrations vary across fine spatial and temporal scales (Savvichev et al. 2023; Zhong et al. 2022; Castelle et al., 2013).

A second notable feature of the respiratory landscape was the widespread occurrence of genes coding for Alternative Complex III (ACIII). ACIII genes were identified in 122 of 210 species representatives and were common within the orders “*Omnivagifaecales*” (79/122), “*Sulfurireductorales*” (8/9), “*Telluricrassaminales*” (14/17), and “*Cuniculidesidentales*” (8/16). The presence of ACIII genes in “*Zixibacterota*” is particularly notable because the complex has been proposed to contribute to the proton motive force through mechanisms distinct from the Q-cycle of canonical bc_1 complexes, potentially including electron bifurcation (Refojo et al., 2012). Importantly, all ACIII gene-containing genomes retained the characteristic subunits in conserved synteny, indicating strong evolutionary preservation of operon organization across divergent lineages (Supplementary Table 6 and 7). This conservation suggests that ACIII likely represents a stable and functionally important component of respiratory metabolism within the phylum rather than a sporadically acquired accessory system.

To verify the evolutionary identity of these complexes, we reconstructed a maximum-likelihood phylogeny of ActB1 protein sequences recovered from “*Zixibacterota*” genes together with reference ActB1 homologs from diverse bacterial taxa (Figure 4 and Supplementary table 8). Across the dataset, ActB sequences exhibited a conserved modular architecture comprising an N-terminal molybdopterin-binding MopB-like catalytic region, followed by a variable linker region and a C-terminal polysulfide reductase PsrB-like iron-sulfur domain. In several sequences, an additional N-terminal MoCo/4Fe-4S cofactor-associated Tat translocation extension domain (MoCo_extend_TAT) was detected upstream of the MopB-like region, consistent with previously reported ActB domain architectures (Majumder et al., 2013; Refojo et al., 2012). The ActB1 region was defined as the conserved N-terminal segment encompassing the MopB-like domains and terminating immediately prior to the linker region connecting to the C-terminal PsrB-like Fe-S domain. Based on these coordinates, ActB1 regions were extracted from reference and “*Zixibacterota*”-representative sequences. Restricting downstream analyses to this conserved catalytic region reduced alignment ambiguity and improved phylogenetic resolution among divergent homologs. Among the 122 species representing genomes, 111 contained full-length ActB1 sequences suitable for phylogenetic analysis, whereas incomplete or truncated sequences were excluded to avoid artefacts associated with partial gene recovery. In the resulting tree, “*Zixibacterota*” ActB1 sequences formed a coherent group nested within the broader ActB1 family. Although the “*Zixibacterota*” group is paraphyletic, insufficient representation of lineages outside of the phylum is included to infer horizontal transfer events or directions

(Figure 3). The resulting ActB1 phylogeny therefore provides robust phylogenetic support for ACIII-identity across the phylum.

Gene neighborhood analysis further revealed that 87 of the 122 ACIII-encoding genomes also exhibited conserved synteny between ACIII components and cytochrome aa_3 oxidase subunits. This co-localization suggests potential functional coupling or coordinated regulation between these respiratory modules, consistent with previously proposed ACIII– aa_3 supercomplex formation in other bacterial systems (Figure 5) (Sun et al., 2018; Lorencik et al., 2021; Refojo et al., 2010). In the remaining genomes, the absence of detectable ACIII– aa_3 oxidase synteny may reflect incomplete genome assembly rather than true biological decoupling, given variable genome completeness across the dataset.

Recent structural studies have further highlighted the significance of ACIII as a distinct respiratory complex. Cryo-electron microscopy of the ACIII– aa_3 supercomplex from *Flavobacterium johnsoniae* revealed an electron-transfer architecture fundamentally different from the canonical cytochrome bc_1 pathway, including a unique arrangement of iron–sulfur clusters and heme cofactors (Sun et al., 2018). These findings, together with experimental evidence demonstrating functional flexibility within the complex (Lorencik et al., 2021), indicate that ACIII represents a specialized solution to respiratory electron transfer that has evolved independently of the classical bc_1 complex.

The respiratory repertoires of “*Zixibacterota*” suggest that this alternative strategy has been retained alongside canonical pathways rather than replacing them outright. Cytochrome bc_1 complexes were present in 117 species representatives, frequently co-

occurring with ACIII in the same genomes. The persistence of both systems raises the possibility of respiratory modularity, whereby alternative electron-transfer routes can be deployed under different environmental conditions. Similar arrangements have been reported in *Rhodothermus marinus* and *Chloroflexus aurantiacus*, where ACIII and bc₁ complexes contribute to distinct respiratory configurations (Refojo et al., 2010, 2012). Although the physiological roles of these complexes have not yet been functionally verified in “*Zixibacterota*”, their broad distribution and evolutionary conservation suggest that respiratory flexibility has been an important driver of ecological adaptation across the phylum.

Lineage-specific sulfur and putative iron metabolism suggest ecological diversification

Two major metabolic traits—dissimilatory sulfate reduction and putative iron redox transformations—exhibited pronounced phylogenetic structuring within “*Zixibacterota*”. This suggests that these functions represent lineage-specific ecological specializations rather than ancestral, phylum-wide capabilities. Genes encoding the dissimilatory sulfate reduction pathway were highly conserved within “*Sulfurireducterales*” (9/9) and found within the families “*Altundifaecaceae*” (17/23) and “*Fundimaricultoraceae*” (5/10) of the order “*Omnivagifaeales*” (Figure 3 and Supplementary Table 4). Notably, genomes affiliated with “*Sulfurireducterales*” were recovered exclusively from sulfidogenic environments, including pelagic sediments, cold seeps, hydrothermal vents, hypersaline microbial mats, fracture fluids, deep groundwaters, and saline springs. This strong habitat association is consistent

with sulfate reduction representing a key energy-conserving strategy in sulfur-rich and anoxic ecosystems.

Beyond the genomic evidence, independent metagenomic, metatranscriptomic, and network analyses reinforce the ecological significance of sulfur metabolism in "*Zixibacterota*". In a landfill leachate treatment system, "*Zixibacterota*" genomes accounted for 34% to 94% of sulfate-reducing microorganisms across treatment units, with high transcriptional expression of *dsrAB* confirming active dissimilatory sulfate reduction (Deng et al., 2024). Network analyses revealed likely syntrophic relationships in which "*Zixibacterota*" produced sulfide while *Pseudomonadota* oxidized it (Deng et al., 2024). Parallel evidence from Laptev Sea cold seep metagenomes showed that "*Zixibacterota*" genomes encoded complete sulfate reduction pathways and were proposed as syntrophic partners of anaerobic methanotrophic archaea (Savvichev et al., 2023). Their detection in hypersaline microbial mats as likely sulfate reducers further underscores their global distribution in sulfidogenic environments (Wong et al., 2020). Together, these findings indicate that "*Zixibacterota*" participate in sulfur-based syntrophy across a wide range of anoxic habitats, consistent with the lineage-restricted distribution we observed.

Genes involved in iron acquisition and putative iron redox processes were both widespread across the phylum and had lineage-level structuring (Figure 3 and Supplementary Table 9). Genes encoding TonB and Exb family proteins were broadly conserved throughout the phylum, while the ferrous iron transporter gene, *feoB*, was detected in 152 of 210 species representatives. Genes for additional uptake systems, including *yfeAB*, showed variable but recurrent distribution across multiple lineages.

Siderophore-associated transporters such as *pirA* and *fpvCDE* were detected, with *pirA* present in 86 of 210 species representatives, including 58 of 122 "*Omnivagifaeales*" and 8 of 17 "*Telluricrassaminales*" genomes. These findings suggest that iron limitation represents a pervasive selective pressure across diverse environmental niches occupied by these taxa.

Putative iron oxidation potential was further indicated by the detection of genes coding for Cyc2 homologs in several families, including "*Fundimaricultoraceae*" (6/10), "*Altundifaeaceae*" (11/23), "*Sulfurireductoraceae*" (4/4), and "*Cuniculidesidentaceae*" (6/14). Sequence classification using FeGenie Cyc2 hidden Markov models assigned these predominantly to Cluster 3, for which functional characterization remains limited. The only verified Cluster 3 representative was an acidophilic *Leptospirillum* with an unusually divergent sequence, and Keffer et al. (2021) therefore cautioned that iron oxidation is less certain for Cluster 3 than for other Cyc2 clades. Although the shared fused cytochrome-porin architecture suggests that these "*Zixibacterota*" homologs can participate in iron redox transformations, genomic data alone cannot confirm iron oxidation activity. Nevertheless, the phylogenetically structured distribution of Cyc2 suggests that iron-associated electron transfer may contribute to the ecology of several "*Zixibacterota*" lineages. This possibility is further supported by the presence of genes encoding MtrAB iron oxidoreductase in some "*Zixibacterota*" MAGs from hydrothermal vent sediments (Zhong et al., 2022) and genes associated with the Mtr-like pathway identified in the RBG-1 genome (Castelle et al., 2013).

Distribution of [NiFe] hydrogenases indicates redox buffering and lineage-specific energy strategies

Genes encoding the cytosolic [NiFe] Group 3 hydrogenases were widely but unevenly distributed across the phylum, indicating lineage-specific diversification of hydrogen-based redox balancing mechanisms (Figure 3 and Supplementary Table 10). Predicted Group 3b hydrogenases were the most prevalent and dominated in several major lineages, including the orders “*Omnivagifaeales*”, “*Sulfurireductorales*”, and “*Telluricrassaminales*”, suggesting a broad role in cytosolic redox homeostasis and reversible electron transfer under fluctuating environmental conditions. In contrast, genes coding for Group 3c hydrogenases were present in the orders “*Undifaeales*” and “*Cuniculidesidentales*”, indicating additional functional diversification of hydrogen metabolism across phylogenetic lineages (Supplementary Table 10). This distribution is consistent with the original RBG-1 genome reconstruction, which identified a cytoplasmic MvhADG/HdrABC [NiFe] hydrogenase complex – a Group 3 [NiFe] hydrogenase – together with an NfnAB transhydrogenase, where hydrogen oxidation was proposed to provide reducing equivalents to the respiratory chain via reduced ferredoxin (Castelle et al., 2013). Widespread occurrence of genes encoding Group 3 [NiFe] hydrogenases therefore suggests that hydrogen metabolism contributes to intracellular redox buffering in “*Zixibacterota*”, particularly in environments characterized by intermittent electron donor availability and fluctuating terminal electron acceptor conditions. This interpretation is consistent with the prevalence of these lineages in hydrothermal, and subsurface ecosystems, where steep and temporally dynamic redox gradients are common. The presence of genes for Group 3b

hydrogenases in sulfate-associated lineages such as “*Sulfurireductorales*” is particularly notable. Metabolite exchange models in mangrove sediments have proposed that “*Zixibacterota*” may utilize hydrogen generated during organic acid oxidation to support sulfate reduction (Du et al., 2024).

In contrast to the widespread distribution of genes encoding cytosolic hydrogenases, membrane-bound [NiFe] Group 1 hydrogenase genes were rare across the phylum. When present, Group 1a hydrogenase genes were restricted to the family “*Aquiterrivaceae*” (*syn.* RBG-16-43-9), suggesting a more specialized capacity for hydrogen oxidation linked to respiratory energy conservation under defined ecological conditions. The scarcity of genes encoding Group 1 enzymes relative to Group 3 hydrogenases indicates that hydrogen metabolism in “*Zixibacterota*” is primarily oriented toward redox balancing rather than obligate hydrogen-dependent lithotrophy, with only limited lineage-specific expansion into respiratory hydrogen oxidation. This restricted distribution is consistent with observations from other uncultivated lineages, where genes for Group 1 hydrogenases are typically associated with narrow respiratory niches and specific electron donor utilization strategies (Wong et al., 2020). Collectively, these patterns support a model in which hydrogen metabolism represents a flexible auxiliary energy system within “*Zixibacterota*”, complementing respiratory electron transport and central carbon metabolism.

Nitrate reduction and denitrification are sporadic rather than conserved “*Zixibacterota*” traits

Earlier metabolic reconstructions proposed a potential role for “*Zixibacterota*” in nitrogen-based respiration, based on the presence of genes encoding a copper-containing nitrite reductase (*NirK*) and a divergent NXR-like oxidoreductase in the original RBG-1 genome (Castelle et al., 2013). Transcriptomic evidence for denitrification gene expression in landfill leachate-derived populations also provided some evidence for this role (Deng et al., 2024). However, expanded genomic sampling in this study demonstrates that genes coding for nitrate reduction and canonical denitrification are not conserved features of the phylum.

Nitric oxide reductase genes (*norBC*) were identified in only 11 of 210 species representatives, and genes encoding respiratory nitrate reductase/nitrite oxidoreductase catalytic subunits (*narG/narZ/nxrA* and *narH/narY/nxrB*) were detected in only 16 of 210 genomes. Neither gene set showed lineage-level conservation, with positive detections scattered across individual genomes rather than clustering within defined phylogenetic groups. The copper-nitrite reductase gene (*NirK*) was detected in 34 of 210 genomes but similarly lacked lineage-level conservation (Figure 3 and Supplementary Table 4). These genes were not preferentially recovered from medium-quality genomes, where incomplete assemblies could produce both false negatives through gene fragmentation and false positives through contamination; instead, detections were distributed across both high-quality and medium-quality assemblies without phylogenetic structure, consistent with sporadic distribution across the phylum rather than a systematic detection artefact.

In the absence of genes for downstream denitrification enzymes (*norBC*, *nosZ*) in most *NirK*-positive genomes, nitrite reduction in “*Zixibacterota*” more likely serves a

detoxification or redox-balancing function than a respiratory role — a possibility already noted in the original RBG-1 description (Castelle et al., 2013). The sparse and phylogenetically unstructured distribution of nitrate reduction and denitrification genes contrasts sharply with the lineage-conserved patterns observed for sulfate reduction, Cyc2-mediated iron oxidation, and acetaldehyde-ethanol interconversion, suggesting that denitrification has not been a major axis of ecological differentiation within the phylum. Given that previous genomic characterisations of "*Zixibacterota*" were based on very few genomes (Castelle et al., 2013; Castelle and Banfield, 2018), the metabolic capabilities attributed to the phylum may reflect strain-specific gene acquisitions (Deng et al., 2024) or overgeneralisation from limited genomic sampling. The 210-genome dataset instead indicates that "*Zixibacterota*" are predominantly organotrophic respiratory generalists that do not depend on nitrate as a terminal electron acceptor, relying instead on oxygen (via their diverse terminal oxidases) and, in specific lineages, on sulfate reduction.

Ubiquitous polysaccharide degradation capacity supports roles in carbon turnover

Genes associated with polysaccharide degradation were broadly distributed across the phylum. Endoglucanases were identified in 134 of 210 species representatives, including the orders "*Undifaeales*" (9/10), "*Omnivagifaeales*" (70/122), "*Sulfurireducterales*" (9/9), "*Zixibacterales*" (17/26), "*Telluricrassaminales*" (14/17), and "*Cuniculidesidentales*" (10/16). β -glucosidases exhibited a similarly widespread but more variable distribution across the phylogeny, further supporting the prevalence of glycan-depolymerizing

capabilities within the phylum (Supplementary Table 4). The broad occurrence of glycoside hydrolase genes suggests that degradation of plant- or detritus-derived polysaccharides may represent an important ecological role for many “*Zixibacterota*” members. Combined with oxidative respiratory metabolism and extensive motility systems, these findings are consistent with participation in organic matter turnover within heterogeneous ecosystems. Our finding of broad endoglucanase and beta-glucosidase gene distributions across the phylum considerably expands the known substrate range. Some genomes of “*Zixibacterota*” have also been predicted to be metabolically flexible heterotrophs capable of degrading polysaccharides and glycoproteins derived from algal cell walls, storage compounds, and extracellular polymeric substances (Hillyer et al., 2023). This combined evidence positions “*Zixibacterota*” as participants in the initial and intermediate stages of organic matter turnover in their habitat.

Arsenic detoxification pathways are broadly conserved across the phylum

Genes associated with arsenic detoxification were unexpectedly widespread throughout the phylum, indicating that resistance to metalloid stress represents a common physiological requirement rather than a lineage-restricted capability. The thioredoxin-dependent arsenate reductase gene *arsC* was identified in 148 of 210 species representatives, while arsenite S-adenosylmethionine methyltransferase genes (*AS3MT/arsM*) were detected in 123 of 210 genomes (Figure 3 and Supplementary Table 4). Together, these enzymes constitute a two-tier detoxification system in which arsenate

[As(V)] is first reduced to the more reactive arsenite [As(III)] via thiol-dependent redox cycling, followed by enzymatic methylation to mono-, di-, and trimethylated arsenicals, including volatile species such as trimethylarsine (Messens and Silver, 2006; Chen et al., 2017). These methylated derivatives are substantially less toxic and more readily removed from the cell, representing an additional layer of detoxification downstream of reduction.

The broad distribution of *arsC* and *AS3MT* genes suggests that arsenic stress is a pervasive selective pressure across diverse “*Zixibacterota*” habitats. This pattern is consistent with the ecological distribution of the phylum across subsurface, hydrothermal systems, and other geochemically dynamic environments where arsenic commonly co-occurs with sulfide- and iron-rich conditions. In such settings, arsenic speciation is tightly coupled to redox fluctuations, making detoxification systems particularly advantageous for survival in transiently toxic niches.

The widespread conservation of genes for arsenic detoxification pathways is consistent with previous genomic findings. The original RBG-1 genome encoded a deeply branching oxidoreductase of the dimethyl sulfoxide reductase superfamily that clustered with arsenite oxidase (*arxA*) and arsenate reductase (*arrA*) genes, suggesting capacity for arsenic redox transformations (Castelle et al., 2013). Although the predicted catalytic binding pocket differed from characterized ArxA and ArrA homologs, the presence of a TAT signal peptide and a [4Fe-4S] cluster motif supported a metal(loid) redox function for the enzymes encoded by these genes (Castelle et al., 2013). The broad presence of *arsC* and *AS3MT* genes across the phylum suggests that arsenic detoxification, rather than energy conservation from arsenic redox chemistry, is the primary selective pressure. However, given

the geochemical association of arsenic with sulfidic and iron-rich sediments, the co-occurrence of arsenic resistance with sulfate reduction, putative Cyc2-mediated iron metabolism, and flexible respiratory chains is consistent with adaptation to polymetallic, redox-dynamic environments.

Trehalose biosynthesis pathways exhibit a phylogenetically discontinuous distribution consistent with ecological contingency

Trehalose biosynthesis genes (*otsAB*, *treT*, *TPS*) were detected in 88 of 210 “*Zixibacterota*” species with a discontinuous phylogenetic distribution, indicating that trehalose production is not a conserved lineage-specific trait (Supplementary Table 4). Unlike glycogen — a broadly conserved carbon storage polymer — trehalose functions as a compatible solute and stress protectant that stabilizes proteins and membranes under osmotic, thermal, oxidative, cold, and desiccation stress (Vanaporn and Titball, 2020).

Trehalose-encoding genomes were recovered from hydrothermally influenced sediments, estuaries, deep-sea deposits, groundwater, soils, wastewater, and microbial mats. Although these habitats share episodic physicochemical fluctuation, they differ in the predominant stress type (e.g., salinity, temperature, redox shifts, energy limitation), suggesting that no single protective mechanism is universally optimal. The presence of trehalose across such varied contexts therefore implies a role within a broader, functionally redundant suite of stress-response strategies, deployed conditionally alongside alternative compatible solute systems.

The discontinuous distribution further argues against strict vertical inheritance: trehalose pathways appear present where they confer context-dependent benefits and absent in closely related lineages that may rely on other protective strategies. This pattern aligns with the view that trait evolution in heterogeneous environments is shaped by functional redundancy and ecological contingency rather than taxonomic conservation alone (Zhang et al., 2023). Together, these observations support a model in which “*Zixibacterota*” possess a vertically inherited core of housekeeping functions (like glycolysis, TCA cycle, respiratory complexes, diderm envelope biogenesis) while stress tolerance constitutes a flexible, evolutionarily labile trait layer — with trehalose as one of several alternative strategies rather than a phylum-defining feature.

Ecological and evolutionary implications

This reconstruction based on 210 species-representative genomes transforms the understanding of the phylum “*Zixibacterota*” from a qualitative narrative of versatile heterotrophs inhabiting dynamic environments into a quantitative, lineage-resolved framework that distinguishes conserved phylum-level traits from derived ecological specializations. Comparative genomics reveals that “*Zixibacterota*” likely share a conserved diderm cell envelope, oxidative central carbon metabolism, and core respiratory machinery including NADH dehydrogenase, succinate dehydrogenase, and F-type ATP synthase, which likely formed part of the ancestral physiological framework of the phylum.

In contrast, predicted ecological diversification within “*Zixibacterota*” appears to have proceeded along multiple, partially independent functional axes. First, respiratory strategies differ markedly among lineages, with distinct combinations of terminal oxidases (aa₃, cbb₃, and bd) and complex III variants (bc1, ACIII, or both) defining lineage-specific electron transport architectures. Second, carbon utilization capacities vary substantially, ranging from widespread polysaccharide degradation potential to differential distributions of glycogen turnover and acetaldehyde–ethanol interconversion pathways. Third, environmental sensing and motility systems, including flagella, chemotaxis, and Type IV pili, exhibit pronounced lineage-level variation, suggesting differences in how taxa respond to environmental heterogeneity. Fourth, genes encoding systems that facilitate interactions with inorganic geochemical cycles are unevenly distributed across the phylogeny, with sulfate reduction, iron acquisition and putative iron oxidation (Cyc2), arsenic detoxification, and siderophore transport systems concentrated in specific lineages. Finally, hydrogen metabolism, predominantly predicted to be mediated by cytosolic [NiFe] Group 3 hydrogenases, exhibits strong lineage-level partitioning, whereas membrane-bound Group 1 hydrogenases are rarely encoded and phylogenetically restricted. Together, these patterns indicate that “*Zixibacterota*” are not a collection of metabolically equivalent heterotrophs but rather a diverse radiation that has diversified through repeated modifications of a conserved physiological foundation.

Their occurrence across habitats as disparate as mangrove sediments, estuaries, cold seeps, hydrothermal vents, groundwater aquifers, hypersaline microbial mats, and hydrocarbon-contaminated soils (Liu et al., 2023) suggests a long history of adaptation to

environmentally heterogeneous conditions. In such systems, spatial and temporal fluctuations in oxygen availability, redox chemistry, sulfur species, iron minerals, and metal(loid) concentrations are expected to promote metabolic specialization and the occupation of distinct ecological niches. The recurrent coexistence of flexible respiratory chains, microaerobic terminal oxidases, sulfur metabolism, iron acquisition systems, arsenic resistance pathways, motility, and complex carbohydrate degradation suggests adaptation to subsurface-associated redox interfaces.

A key advance of this study is that such ecological structuring was not resolvable from the limited genomic sampling analysed previously. The original RBG-1 genome lacked flagella and sulfate reduction — absences that could have been interpreted as phylum-level characteristics but are now understood to represent lineage-specific distributions (Castelle et al., 2013). Conversely, ACIII was noted in RBG-1, but whether it was a phylum-wide feature or a lineage-specific adaptation remained unclear (Castelle et al., 2013). The quantitative prevalence of ACIII across 58% of species representatives, its strong phylogenetic coherence within multiple major orders, and its coexistence with bc1 complexes in several lineages establish ACIII as a major, phylogenetically structured respiratory feature of the phylum rather than an isolated genomic curiosity. A similar pattern emerged for hydrogen metabolism. The RBG-1 genome encoded a cytoplasmic MvhADG/HdrABC hydrogenase complex whose functional significance could not be assessed from a single genome (Castelle et al., 2013). Our 210-genome dataset demonstrates that hydrogenase genes are broadly distributed yet sharply partitioned by subtype, indicating that hydrogen cycling in the

phylum likely functions predominantly as an intracellular redox-buffering system rather than a primary lithotrophic energy-conserving strategy.

A key limitation of this study is that genome completeness varies across the dataset, with 85 of the 210 species-representative genomes classified as medium-quality based on CheckM2 metrics. As a result, some apparent absences of metabolic genes or pathways may reflect the incompleteness of the genomes or contig fragmentation rather than true biological absence. This is particularly relevant for traits with patchy phylogenetic distribution, where partial pathway recovery can bias interpretations of lineage-specific losses. Accordingly, conclusions regarding the absence of specific functions should be interpreted cautiously, whereas the identification of widespread and phylogenetically coherent traits is robust to genome completeness variation. Despite this caveat, the present dataset captures substantially greater phylogenetic breadth than previous predictions and likely still underestimates the full metabolic diversity of the phylum.

Conclusions

Recent large-scale surveys suggest that substantial uncultivated diversity remains within bacterial lineages related to “*Zixibacterota*” (Prasoodanan et al., 2026), and emerging evidence for unexpected metabolic traits such as mercury methylation (Liu et al., 2023) within “*Zixibacterota*” indicates that additional functional capacities remain to be discovered. This dataset generates several testable hypotheses: whether lineages encoding both bc1 and ACIII can remodel electron routing in response to redox conditions, whether

Cyc2-bearing lineages catalyze iron redox transformations at oxic–anoxic interfaces, and whether alcohol interconversion operates as a redox-balancing valve under oxygen limitation. Resolving these questions will require integrated metatranscriptomic, proteomic, cultivation-based, and geochemical approaches targeting environments enriched in “*Zixibacterota*”.

Data Availability

Supplementary data and scripts generated and used in this study are available at <https://doi.org/10.6084/m9.figshare.33191157>.

Tables:

Table 1. Proposed nomenclature and etymology of “*Zixibacterota*” taxa.

Taxon	Nomenclatural information
Phylum <i>Zixibacterota</i>	Synonyms: Zixibacteria Syllabication: Zi.xi.bac.ter.o'ta Nomenclatural type: <i>Zixibacter</i> Etymology: N.L. masc. n. <i>Zixibacter</i> , a bacterial genus; -ota, ending to denote phylum; N.L. neut. pl. n. <i>Zixibacterota</i> , the phylum of the genus <i>Zixibacter</i> .
Class <i>Zixibacteria</i>	Synonyms: MSB-5AS Syllabication: Zi.xi.bac.te'ri.a Nomenclatural type: <i>Zixibacter</i> Etymology: N.L. masc. n. <i>Zixibacter</i> , a bacterial genus; -ia, suffix to denote a class; N.L. neut. pl. n. <i>Zixibacteria</i> , the class of the genus <i>Zixibacter</i> .
Order <i>Zixibacterales</i>	Synonyms: MSB-5AS Syllabication: Zi.xi.bac.te.ra'les Nomenclatural type: <i>Zixibacter</i> Etymology: N.L. masc. n. <i>Zixibacter</i> , a bacterial genus; -ales, suffix to denote an order; N.L. fem. pl. n. <i>Zixibacterales</i> , the order of the genus <i>Zixibacter</i> .
Family <i>Zixibacteraceae</i>	Synonyms: RBG-1 Syllabication: Zi.xi.bac.te.ra'ce.ae Nomenclatural type: <i>Zixibacter</i> Etymology: N.L. masc. n. <i>Zixibacter</i> , a bacterial genus; -aceae, suffix to denote a family; N.L. fem. pl. n. <i>Zixibacteraceae</i> , the family of the genus <i>Zixibacter</i> .
Genus <i>Zixibacter</i>	Synonyms: RBG-1 Syllabication: Zi.xi.bac'ter Nomenclatural type: <i>Zixibacter originalis</i> Etymology: N.L. pref. Zixi-, an arbitrarily formed prefix; N.L. masc. n. bacter, a rod; N.L. masc. n. <i>Zixibacter</i> , an arbitrarily formed bacterial genus name.

Species <i>Zixibacter originalis</i>	Synonyms: RBG-1 sp000447245 Syllabication: o.ri.gi.na'lis Nomenclatural type: GCA_000447245.1 Etymology: L. masc. adj. <i>originalis</i>, original
Family <i>Aquiterrivitaceae</i>	Synonyms: f__RBG-16-43-9 Syllabication: A.qui.ter.ri.vi.ta'ce.ae Nomenclatural type: <i>Aquiterrivita</i> Etymology: N.L. fem. n. <i>Aquiterrivita</i>, referring to the type genus <i>Aquiterrivita</i>; -aceae, ending to denote a family; N.L. fem. pl. n. <i>Aquiterrivitaceae</i>, the <i>Aquiterrivita</i> family.
Genus <i>Aquiterrivita</i>	Synonyms: RBG-16-43-9 Syllabication: A.qui.ter.ri.vi'ta Nomenclatural type: <i>Aquiterrivita orifaecis</i> Etymology: L. fem. n. <i>aqua</i>, water; L. fem. n. <i>terra</i>, earth, soil; L. fem. n. <i>vita</i>, life; N.L. fem. n. <i>Aquiterrivita</i>, “life of water and earth,” a genus of organisms associated with aquatic and soil settings.
Species <i>Aquiterrivita orifaecis</i>	Synonyms: RBG-16-43-9 sp022865345 Syllabication: or.i.fae'cis Nomenclatural type: GCA_022865345.1 Etymology: L. fem. n. <i>ora</i>, shore; L. fem. n. <i>faex</i>, sediment; N.L. gen. n. <i>orifaecis</i>, “of shore-sediment,” referring to origin from lagoon/shoreline sediments.
Species <i>Aquiterrivita humiaquae</i>	Synonyms: RBG-16-43-9 sp030692925 Syllabication: hu.mi.a'quae Nomenclatural type: GCA_030692925.1 Etymology: L. fem. n. <i>humus</i>, ground; L. fem. n. <i>aqua</i>, water; N.L. gen. n. <i>humiaquae</i>, “of groundwater,” referring to organism's origin from groundwater.
Species <i>Aquiterrivita arvi</i>	Synonyms: RBG-16-43-9 sp035543035 Syllabication: ar'vi Nomenclatural type: GCA_035543035.1 Etymology: L. gen. sg. <i>arvi</i>, of soil

Genus <i>Aestuariivita</i>	Synonyms: JAOUFL01 Syllabication: Aes.tu.a.ri.i.vi'ta Nomenclatural type: <i>Aestuariivita litoris</i> Etymology: L. neut. n. <i>aestuarium</i>, estuary; L. fem. n. <i>vita</i>, life; N.L. fem. n. <i>Aestuariivita</i>, "life of the estuary," referring to a genus of organisms associated with estuarine surface sediments.
Species <i>Aestuariivita litoris</i>	Synonyms: JAOUFL01 sp029858245 Syllabication: li'to.ris Nomenclatural type: GCA_029858245.1 Etymology: L. neut. gen. n. <i>litoris</i>, of the shore
Family <i>Hydrofaecaceae</i>	Synonyms: f__SM1-73 Syllabication: Hy.dro.fae.ca'ce.ce Nomenclatural type: <i>Hydrofaecis</i> Etymology: N.L. fem. n. <i>Hydrofaecis</i>, referring to the type genus <i>Hydrofaecis</i>; -aceae, ending to denote a family; N.L. fem. pl. n. <i>Hydrofaecaceae</i>, the <i>Hydrofaecis</i> family.
Genus <i>Hydrofaecis</i>	Synonyms: CAIVRH01 Syllabication: Hy.dro.fae'cis Nomenclatural type: <i>Hydrofaecis lymphisediminis</i> Etymology: Gr. neut. n. <i>hydōr</i> (ὑδωρ), water; L. fem. n. <i>faex</i>, sediment; N.L. fem. n. <i>Hydrofaecis</i>, "of water sediment," referring to a genus of organisms associated with freshwater sediments.
Species <i>Hydrofaecis lymphisediminis</i>	Synonyms: CAIVRH01 sp903908285 Syllabication: lym.phi.se.di.mi'nis Nomenclatural type: GCA_903908285.1 Etymology: L. fem. n. <i>lympa</i>, water; L. neut. n. <i>sedimen</i>, sediment; N.L. gen. n. <i>lymphisediminis</i>, of water sediment
Family <i>Frigidiorantaceae</i>	Synonyms: f__SM23-73-2 Syllabication: Fri.gi.di.ro.ran.ta'ce.ae Nomenclatural type: <i>Frigidiorans</i> Etymology: N.L. masc. n. <i>Frigidiorans</i>, organisms from cold seeps; -aceae, ending to denote a family; N.L. fem. n. <i>Frigidiorantaceae</i>, the family of the genus <i>Frigidiorans</i>

Genus <i>Frigidiorans</i>	Synonyms: SM23-73-2 Syllabication: Fri.gi.di.ro'rans Nomenclatural type: <i>Frigidiorans frigilaticis</i> Etymology: L. masc. adj. <i>frigidus</i>, cold; L. pres. part. <i>rorans</i>, dripping or trickling, referring to a seep; N.L. masc. n. <i>Frigidiorans</i>, organisms from cold seeps
Species <i>Frigidiorans frigilaticis</i>	Synonyms: SM23-73-2 sp030615745 Syllabication: fri.go.ri.la.ti'cis Nomenclatural type: GCA_030615745.1 Etymology: L. neut. n. <i>frigus</i>, cold, chill; L. masc. n. latex, fluid, liquid; N.L. masc. n. <i>frigilaticis</i>, "of cold liquid," referring to the organism's origin from cold seep environments.
Order <i>Undifaeales</i>	Synonyms: CAIYYT01 Syllabication: Un.di.fae.ca'les Nomenclatural type: <i>Undifaecis</i> Etymology: N.L. fem. n. <i>Undifaecis</i>, referring to the type genus; –ales, ending to denote an order; N.L. fem. pl. n. <i>Undifaeales</i>, order of the genus <i>Undifaecis</i>
Family <i>Undifaecaceae</i>	Synonyms: CAIYYT01 Syllabication: Un.di.fae.ca'ce.ae Nomenclatural type: <i>Undifaecis</i> Etymology: N.L. fem. n. <i>Undifaecis</i>, referring to the type genus; –aceae, ending to denote a family; N.L. fem. pl. n. <i>Undifaecaceae</i>, family of the genus <i>Undifaecis</i>
Genus <i>Undifaecis</i>	Synonyms: CAIYYT01 Syllabication: Un.di.fa.e'cis Nomenclatural type: <i>Undifaecis limiphila</i> Etymology: L. femn. <i>unda</i>, water; L. femn. n. <i>faex</i>, sediment; NL. femn. n. <i>Undifaecis</i>, of aquatic sediment.
Species <i>Undifaecis limiphila</i>	Synonyms: CAIYYT01 sp903930455 Syllabication: li.mi'phi.la Nomenclatural type: GCA_903838755.1 Etymology: L. masc. n. <i>limus</i>, mud, clay or slime; N.L. fem. adj. suff. <i>-phila</i>, friend, loving; N.L. fem. adj. <i>limiphila</i>, mud-loving, referring to this organisms' association with freshwater sediments

Species <i>Undifaecis laciphila</i>	Synonyms: CAIYYT01 sp026397575 Syllabication: la.ci.'phi.la Nomenclatural type: GCA_026397575.1 Etymology: L. masc. n. <i>lacus</i>, lake; N.L. fem. adj. suff. <i>-phila</i>, friend, loving; N.L. fem. adj. <i>laciphila</i>, “lake-loving,” referring to the recovery of the organism from lake sediments
Genus <i>Occultisediminis</i>	Synonyms: JADJGC01 Syllabication: Oc.cul.ti.se.di'mi.nis Nomenclatural type: <i>Occultisediminis lutiphilum</i> Etymology: L. masc. adj. <i>occultus</i>, hidden; L. neut. n. <i>sedimen</i>, sediment; N.L. neut. n. <i>Occultisediminis</i>, “of hidden sediment,” referring to a genus of organisms originating from concealed sediments.
Species <i>Occultisediminis cloacae</i>	Synonyms: JADJGC01 sp020853795 Syllabication: clo.a'cae Nomenclatural type: GCA_020853795.1 Etymology: L. gen. n. <i>cloacae</i>, “of a sewer,” denoting wastewater origin.
Species <i>Occultisediminis lutiphilum</i>	Synonyms: JADJGC01 sp016708315 Syllabication: lu.ti.phi'lum Nomenclatural type: GCA_016708315.1 Etymology: L. neut. n. <i>lutum</i>, mud; Gr. adj. <i>philos</i> (φίλος), loving; N.L. neut. n. <i>lutiphilum</i>, “mud-loving,” referring to a genus of organisms originating from activated sludge
Genus <i>Profundifaecis</i>	Synonyms: JAGLUH01 Syllabication: Pro.fun.di.fae'cis Nomenclatural type: <i>Profundifaecis abyssalis</i> Etymology: L. masc. adj. <i>profundus</i>, deep; L. fem. n. <i>faex</i>, sediment; N.L. fem. n. <i>profundifaecis</i>, of deep sediment
Species <i>Profundifaecis abyssi</i>	Synonyms: JAGLUH01 sp023134875 Syllabication: a.bys'si Nomenclatural type: GCA_030631605.1 Etymology: L. gen. n. <i>abyssi</i>, “of the abyss,” referring to the organism’s origin from abyssal/deep-sea environment

Genus <i>Sediminisessor</i>	Synonyms: JBECKX01 Syllabication: Se.di.mi.ni.ses'sor Nomenclatural type: <i>Sediminisessor auranticorii</i> Etymology: L. neut. n. <i>sedimen</i>, <i>sediminis</i>, sediment; L. masc. n. <i>essor</i>, dweller; N.L. masc. n. <i>Sediminisessor</i>, dweller of sediment
Species <i>Sediminisessor litoris</i>	Synonyms: JBECKX01 sp040235515 Syllabication: li'to.ris Nomenclatural type: GCA_040235515.1 Etymology: L. neut. gen. n. <i>litoris</i>, of the shore
Species <i>Sediminisessor auranticorii</i>	Synonyms: JBECKX01;s__ Syllabication: au.ran.ti.co'ri.i Nomenclatural type: (bin.206.fasta_GLS9S) Etymology: L. masc. adj. <i>aurantius</i>, orange; L. neut. n. <i>corium</i>, layer or coating; N.L. gen. n. <i>auranticorii</i>, "of the orange layer," referring to the orange coating over the saline spring sediment from which the organism was recovered.
Order <i>Sulfurireductorales</i>	Synonyms: JAABVY01 Syllabication: Sul.fu.ri.re.duc.to.ra'les Nomenclatural type: <i>Sulfurireductor</i> Etymology: N.L. masc. n. <i>Sulfurireductor</i>, referring to the type genus <i>Sulfurireductor</i>; –ales, ending to denote an order; N.L. fem. pl. n. <i>Sulfurireductorales</i>, order of the genus <i>Sulfurireductor</i>.
Family <i>Sulfurireductoraceae</i>	Synonyms: JAABVY01 Syllabication: Sul.fu.ri.re.duc.to.ra'ce.ae Nomenclatural type: <i>Sulfurireductor</i> Etymology: N.L. masc. n. <i>Sulfurireductor</i>, referring to the type genus <i>Sulfurireductor</i>; –aceae, ending to denote a family; N.L. fem. pl. n. <i>Sulfurireductoraceae</i>, family of the genus <i>Sulfurireductor</i>.
Genus <i>Sulfurireductor</i>	Synonyms: JAABVY01 Syllabication: Sul.fu.ri.re.duc'tor Nomenclatural type: <i>Sulfurireductor halomattae</i> Etymology: L. neut. n. <i>sulfur</i>, sulfur; L. masc. n. <i>reductor</i>, reducer; NL. masc. n. <i>Sulfurireductor</i>, sulfur reducer.

Species <i>Sulfurireductor thermosedis</i>	Synonyms: JAABVY01 sp011056555 Syllabication: ther.mo.se'dis Nomenclatural type: GCA_011056555.1 Etymology: Gr. fem. n. <i>thermē</i> (θερμή), heat; L. fem. n. <i>sedes</i>, seat, site; N.L. masc. n. <i>thermosedis</i>, “of a heated site,” referring to origin from hot-spring sediments or other heated environments.
Species <i>Sulfurireductor halomattae</i>	Synonyms: JAABVY01 sp014730285 Syllabication: ha.lo.mat'tae Nomenclatural type: GCA_014730285.1 Etymology: Gr. masc. n. <i>hāls</i> (ἅλς), salt; L. fem. n. <i>matta</i>, mat; N.L. gen. n. <i>halomattae</i>, “of a salt mat,” referring to the organism’s origin from a hypersaline microbial mat environment.
Genus <i>Hydrocrassaminis</i>	Synonyms: WJMC01 Syllabication: Hy.dro.cras.sa.mi'nis Nomenclatural type: <i>Hydrocrassaminis mattifaecis</i> Etymology: Gr. neut. n. <i>hydōr</i> (ὑδωρ), water; L. neut. n. <i>crassamen</i>, sediment; N.L. fem. n. <i>Hydrocrassaminis</i>, of water sediment
Species <i>Hydrocrassaminis mattifaecis</i>	Synonyms: WJMC01 sp014728145 Syllabication: mat.ti.fae'cis Nomenclatural type: GCA_014728145.1 Etymology: L. fem. n. <i>matta</i>, mat; L. fem. n. <i>faex</i>, sediment; N.L. gen. n. <i>mattifaecis</i>, “of the mat sediment,” referring to organism's origin from microbial mats in hypersaline waters.
Family <i>Hypofontaceae</i>	Synonyms: f__JAHJOQ01 Syllabication: Hy.po.fon.ta'ce.ae Nomenclatural type: <i>Hypofons</i> Etymology: N.L. masc. n. <i>Hypofons</i>, referring to type genus <i>Hypofons</i>; -aceae, ending denoting a bacterial family; N.L. fem. pl. n. <i>Hypofontaceae</i>, the family containing the genus <i>Hypofons</i>.
Genus <i>Hypofons</i>	Synonyms: JAHJOQ01 Syllabication: Hy.po.fons Nomenclatural type: <i>Hypofons crepaturifontis</i> Etymology: Gr. prep. hypo- (ὑπό), under, beneath; L. masc. n. <i>fons</i>, spring, source; N.L. masc. n. <i>Hypofons</i>, a genus of organisms from beneath-surface water sources.

Species <i>Hypofons crepaturifontis</i>	Synonyms: JAHJOQ01 sp018820315 Syllabication: cre.pa.tu.ri.fon'tis Nomenclatural type: GCA_018821285.1 Etymology: L. fem. n. crepatura, crack, fissure; L. masc. n. fons, spring; N.L. gen. n. crepaturifontis, "of the fissure-spring," referring to groundwater emerging through rock fractures.
Genus <i>Salsilaticis</i>	Synonyms: JAJRZO01 Syllabication: Sal.si.la'ti.cis Nomenclatural type: Salsilaticis manitobensis Etymology: L. masc. adj. salsus, salty; L. masc. n. latex, fluid, water; N.L. masc. n. Salsilaticis, "of salty water," referring to organisms recovered from saline aquatic environments.
Species <i>Salsilaticis thermofontis</i>	Synonyms: JAJRZO01 sp024275215 Syllabication: ther.mo.fon'tis Nomenclatural type: GCA_024275215.1 Etymology: Gr. fem. n. thermē (θέρμη), heat; L. masc. n. fons, spring; N.L. gen. n. thermofontis, "of a hot spring," referring to origin from a hydrothermal vent.
Species <i>Salsilaticis manitobensis</i>	Synonyms: JAJRZO01; s__ Syllabication: ma.ni.to.ben'sis Nomenclatural type: (bin.187.fasta_MP62F_HA) Etymology: N.L. masc. adj. manitobensis, from Manitoba, referring to the geographic origin of the organism.
Order <i>Cuniculidesidentales</i>	Synonyms: WJJR01 Syllabication: Cu.ni.cu.li.de.si.den.ta'les Nomenclatural type: Cuniculidesidens Etymology: N.L. masc. n. Cuniculidesidens, referring to the type genus Cuniculidesidens; -ales, ending to denote an Order; N.L. fem. pl. n. Cuniculidesidentales, Order of the genus Cuniculidesidens.
Family <i>Cuniculidesidentaceae</i>	Synonyms: WJJR01 Syllabication: Cu.ni.cu.li.de.si.den.ta'ce.ae Nomenclatural type: Cuniculidesidens Etymology: N.L. masc. n. Cuniculidesidens, referring to the type genus Cuniculidesidens; -aceae, ending to denote a family; N.L. fem. pl. n. Cuniculidesidentaceae, family of the genus Cuniculidesidens.

Genus <i>Cuniculidesidens</i>	Synonyms: JACRMA01 Syllabication: Cu.ni.cu.li.de'si.dens Nomenclatural type: <i>Cuniculidesidens acidiaquae</i> Etymology: L. masc. n. cuniculus, an underground tunnel, excavation; L. pres. part. desidens, settling down; NL. masc. n. <i>Cuniculidesidens</i>, "one that settles in tunnels," referring to a genus of organisms associated with underground or subsurface environment
Species <i>Cuniculidesidens humilis</i>	Synonyms: JACRMA01 sp036170655 Syllabication: hu'mi.lis Nomenclatural type: GCA_036170655.1 Etymology: L. masc. adj. humilis, "low-lying", referring to the organism's occurrence in low-lying subsurface environment
Species <i>Cuniculidesidens acidiaquae</i>	Synonyms: JACRMA01 sp021813505 Syllabication: a.ci.di.a'quae Nomenclatural type: GCA_021843385.1 Etymology: L. masc. adj. acidus, acidic, sour; L. fem. n. aqua, water; N.L. gen. n. <i>acidiaquae</i>, "of acidic water," referring to the organism's origin from acid mine drainage
Species <i>Cuniculidesidens aquiferis</i>	Synonyms: JACRMA01 sp016235085 Syllabication: a.qui.fe'ris Nomenclatural type: GCA_016235085.1 Etymology: N.L. masc. n. aquifer, water-bearing layer; N.L. gen. n. <i>aquiferis</i>, "of the aquifer," referring to origin from groundwater.
Genus <i>Inferivivens</i>	Synonyms: DATKYL01 Syllabication: In.fe.ri.vi'vens Nomenclatural type: <i>Inferivivens argillae</i> Etymology: L. masc. adj. inferus, low, below, underneath; L. pres. part. vivens, living; N.L. fem. n. <i>Inferivivens</i>, "living underneath," referring to a genus of organisms living in subsurface or lower environments
Species <i>Inferivivens argillae</i>	Synonyms: DATKYL01 sp036397555 Syllabication: ar.gil'lae Nomenclatural type: GCA_036397555.1 Etymology: L. gen. n. <i>argillae</i>, "of clay," referring to the organism's origin from agricultural soil.

Species <i>Inferivivens halosedis</i>	Synonyms: DATKYL01;s__ Syllabication: ha.lo.se'dis Nomenclatural type: (bin.046.fasta_MP62F_HA) Etymology: Gr. masc. n. hál̓s (ἅλς), salt; L. fem. n. sedis, seat, place; N.L. fem. n. halosedis, "place of salt," referring to the organism's origin from saline spring sediment.
Genus <i>Tenebrivita</i>	Synonyms: JACQFV01 Syllabication: Te.ne.bri.vi'ta Nomenclatural type: Tenebrivita aquifugax Etymology: L. fem. n. tenebra, obscurity; L. fem. n. vita, life; N.L. fem. n. Tenebrivita, "life in obscurity," referring to a genus of organisms dwelling in obscured environments
Species <i>Tenebrivita aquifugax</i>	Synonyms: JACQFV01 sp040752595 Syllabication: a.qui.fu'gax Nomenclatural type: GCA_040752595.1 Etymology: L. fem. n. aqua, water; L. fem. adj. fugax, transient; N.L. fem. adj. aquifugax, "of transient water," referring to the organism's origin from groundwater
Species <i>Tenebrivita humi</i>	Synonyms: JACQFV01 sp035559435 Syllabication: hu'mi Nomenclatural type: GCA_035559435.1 Etymology: L. gen. n. humi, of soil
Species <i>Tenebrivita subaquae</i>	Synonyms: JACQFV01 sp016199865 Syllabication: sub.a'quae Nomenclatural type: GCA_016199865.1 Etymology: L. prefix sub-, under, beneath; L. fem. n. aqua, water; N.L. gen. n. subaquae, "of the water beneath," referring to the organism's origin from groundwater.
Genus <i>Hydrocultor</i>	Synonyms: JBFMFQ01 Syllabication: Hy.dro.cul'tor Nomenclatural type: Hydrocultor puteilaticis Etymology: Gr. neut. n. hydōr (ὕδωρ), water; L. masc. n. cultor, inhabitant, dweller; N.L. masc. n. Hydrocultor, inhabitant of water

Species <i>Hydrocultor puteilaticis</i>	Synonyms: JBFMFQ01 sp040752075 Syllabication: pu.te.i.la.ti'cis Nomenclatural type: GCA_040752075.1 Etymology: L. masc. n. puteus, well; L. masc. n. latex, liquid; N.L. gen. n. puteilaticis, "of well-liquid," referring to origin from groundwater.
Family <i>Saxicoloniaceae</i>	Synonyms: f__JAJRUJ01 Syllabication: Sax.i.co.lo.ni.a'ce.ae Nomenclatural type: Saxicolonia Etymology: N.L. fem. n. Saxicolonia, referring to the type genus Saxicolonia; –aceae, ending to denote a family; N.L. fem. pl. n. Saxicoloniaceae, family of the genus Saxicolonia.
Genus <i>Saxicolonia</i>	Synonyms: JAJRUJ01 Syllabication: Sax.i.co.lo'ni.a Nomenclatural type: Saxicolonia sulfivorans Etymology: L. neut. n. saxum, rock, stone; L. fem. n. colonia, colony, settlement; N.L. fem. n. Saxicolonia, "settlement of rock," referring to a genus of organisms associated with rocky environments
Species <i>Saxicolonia sulfivorans</i>	Synonyms: JAJRUJ01 sp024277855 Syllabication: sul.fi.vo'rans Nomenclatural type: GCA_024277855.1 Etymology: L. neut. n. sulfur, sulfur; L. pres. part. vorans, devouring, consuming; N.L. part. adj. sulfivorans, "sulfur-devouring," referring to the organism's potential ability to utilize sulfur compounds and its origin from a black smoker environment.
Genus <i>Hypovivens</i>	Synonyms: JAGVQM01 Syllabication: Hy.po.vi'vens Nomenclatural type: Hypovivens fossorivivens Etymology: Gr. prep. hypo- (ὑπό), under, beneath; L. fem. pres. part. vivens, living; N.L. fem. n. Hypovivens, a genus of organisms dwelling in subsurface or subterranean environments.
Species <i>Hypovivens fossorivivens</i>	Synonyms: JAGVQM01 sp020051695 Syllabication: Fos.so.ri.vi'vens Nomenclatural type: GCA_020051695.1 Etymology: L. masc. n. fossor, digger, excavator, miner; L. pres. part. vivens, living; N.L. part. adj. fossorivivens, "living of the digger," referring to an organism inhabiting excavated or subsurface environments, such as fracture fluids.

Order <i>Telluricrassaminales</i>	Synonyms: UBA10806 Syllabication: Tel.lu.ri.cras.sa.mi.na'les Nomenclatural type: <i>Telluricrassaminis</i> Etymology: N.L. neut. n. <i>Telluricrassaminis</i>, referring to the type genus <i>Telluricrassaminis</i>; –ales, ending to denote an Order ; N.L. fem. pl. n. <i>Telluricrassaminales</i>, Order of the genus <i>Telluricrassaminis</i>.
Family <i>Telluricrassaminaceae</i>	Synonyms: UBA10806 Syllabication: Tel.lu.ri.cras.sa.mi.na'ce.ae Nomenclatural type: <i>Telluricrassaminis</i> Etymology: N.L. neut. n. <i>Telluricrassaminis</i>, referring to the type genus <i>Telluricrassaminis</i>; –aceae, ending to denote a family; N.L. fem. pl. n. <i>Telluricrassaminaceae</i>, family of the genus <i>Telluricrassaminis</i>.
Genus <i>Telluricrassaminis</i>	Synonyms: UBA10806 Syllabication: Tel.lu.ri.cras.sa.mi'nis Nomenclatural type: <i>Telluricrassaminis paleosedis</i> Etymology: L. fem. n. <i>tellus</i>, earth, ground; L. neut. n. <i>crassamen</i>, sediment; NL. neut. n. <i>Telluricrassaminis</i>, of ground sediment.
Species <i>Telluricrassaminis paleosedis</i>	Synonyms: UBA10806 sp001775395 Syllabication: pa.le.o.se'dis Nomenclatural type: GCA_001775395.1 Etymology: Gr. masc. adj. <i>palaiós</i> (παλαιός), ancient, old; L. fem. n. <i>sedes</i>, seat, place; N.L. gen. n. <i>Paleosedis</i>, “of an ancient place,” referring to the organism’s origin from background sedimentary environment representing ancient deposition.
Genus <i>Sediministilla</i>	Synonyms: JAZGHS01 Syllabication: Se.di.mi.nis.til'la Nomenclatural type: <i>Sediministilla pelagisediminis</i> Etymology: L. neut. n. <i>sedimen</i>, sediment; L. fem. n. <i>stilla</i>, droplet; N.L. fem. n. <i>Sediministilla</i>, “droplet of sediment,” referring to a genus of organisms associated with fine sediment in marine environment.
Species <i>Sediministilla pelagisediminis</i>	Synonyms: JAZGHS01 sp036481315 Syllabication: pe.la.gi.se.di.mi'nis Nomenclatural type: GCA_036481315.1 Etymology: L. neut. n. <i>pelagus</i>, sea; L. neut. n. <i>sedimen</i>, sediment; N.L. n. <i>pelagisediminis</i>, of sea sediment

Genus <i>Crassaminisepulta</i>	Synonyms: JAHEDG01 Syllabication: Cras.sa.mi.ni.se.pul'ta Nomenclatural type: <i>Crassaminisepulta fluminis</i> Etymology: L. neut. n. crassamen, sediment; L. fem. adj. sepulta, buried, immersed; N.L. fem. n. <i>Crassaminisepulta</i>, a genus of organisms dwelling "buried in sediment," reflecting their origin from sediment.
Species <i>Crassaminisepulta fluminis</i>	Synonyms: JAHEDG01 sp024641335 Syllabication: flu'mi.nis Nomenclatural type: GCA_024641335.1 Etymology: L. gen. n. fluminis, of the river
Genus <i>Absconsiterra</i>	Synonyms: GCA-020348065 Syllabication: Ab.scon.si.ter'ra Nomenclatural type: <i>Absconsiterra aestuarifaecis</i> Etymology: L. masc. adj. absconsus, hidden; L. fem. n. terra, earth, land; N.L. fem. n. <i>Absconsiterra</i>, "of hidden land," referring to a genus of organisms associated with hidden sedimentary environment.
Species <i>Absconsiterra aestuarifaecis</i>	Synonyms: GCA-020348065 sp020348065 Syllabication: aes.tu.a.ri.fae'cis Nomenclatural type: GCA_020348065.1 Etymology: L. neut. n. aestuarium, estuary; L. fem. n. faex, sediment; N.L. gen. n. <i>aestuarifaecis</i>, of estuarine sediment
Species <i>Absconsiterra aestuarii</i>	Synonyms: GCA-020348065 sp020344055 Syllabication: aes.tu.a'ri.i Nomenclatural type: GCA_020344055.1 Etymology: L. gen. n. <i>aestuarii</i>, of the estuary
Family <i>Absconsisediminaceae</i>	Synonyms: f__4484-95 Syllabication: Ab.sco.nsi.se.di.mi.na'ce.ae Nomenclatural type: <i>Absconsisediminis</i> Etymology: N.L. masc. n. <i>Absconsisediminis</i>, type genus of the family; -aceae, ending to denote a family; N.L. fem. pl. n. <i>Absconsisediminaceae</i>, the family of the genus <i>Absconsisediminis</i>.

Genus <i>Absconsisediminis</i>	Synonyms: g_4484-95 Syllabication: Ab.sco.nsi.se.di'mi.nis Nomenclatural type: <i>Absconsisediminis obscurimattae</i> Etymology: L. masc. adj. absconsus, hidden; L. neut. n. sedimen, sediment; N.L. masc. n. <i>Absconsisediminis</i>, of hidden sediment
Species <i>Absconsisediminis obscurimattae</i>	Synonyms: 4484-95 sp002085375 Syllabication: ob.scu.ri.mat'tae Nomenclatural type: GCA_029932605.1 Etymology: L. fem. adj. obscura, obscure; L. fem. n. matta, mat, covering; N.L. gen. n. <i>obscurimattae</i>, “of an obscure mat,” referring to the organism’s recovery from a microbial mat in hydrothermal sediment.
Genus <i>Sediminicrypta</i>	Synonyms: JBBIRK01 Syllabication: Se.di.mi.ni.crypta Nomenclatural type: <i>Sediminicrypta thermofontis</i> Etymology: L. neut. n. sedimen, sediment; Gr. fem. n. kryptē (κρύπτῃ), hidden place; N.L. fem. n. <i>Sediminicrypta</i>, “hidden place of sediment,” referring to a genus of organisms inhabiting obscure sediment environment
Species <i>Sediminicrypta thermofontis</i>	Synonyms: JBBIRK01 sp037441845 Syllabication: ther.mo.fon'tis Nomenclatural type: GCA_037441845.1 Etymology: Gr. fem. n. thermē (θερμῇ), heat; L. masc. n. fons, spring; N.L. gen. n. <i>thermofontis</i>, of a hot spring
Genus <i>Cryptosedes</i>	Synonyms: JAGGSN01 Syllabication: Cryp.to.se'des Nomenclatural type: <i>Cryptosedes thermopelagi</i> Etymology: Gr. masc. adj. kryptós (κρυπτός), hidden; L. fem. n. sedes, seat, settlement; N.L. fem. n. <i>Cryptosedes</i>, of hidden settlement
Species <i>Cryptosedes thermopelagi</i>	Synonyms: JAGGSN01 sp021159005 Syllabication: ther.mo.pe'la.gi Nomenclatural type: GCA_021159005.1 Etymology: Gr. fem. n. thermē (θερμῇ), heat; L. neut. n. pelagus, sea; N.L. gen. n. <i>thermopelagi</i>, “of the warm sea,” referring to the organism’s origin from a marine hydrothermal system.

Genus <i>Fermentidolii</i>	Synonyms: JAAYTW01 Syllabication: Fer.men.ti.do'li.i Nomenclatural type: <i>Fermentidolii digestorium</i> Etymology: L. neut. n. fermentum, fermentation; L. neut. n. dolium, large jar or vat; N.L. neut. n. fermentidolii, of the fermentation vessel
Species <i>Fermentidolii digestorium</i>	Synonyms: JAAYTW01 sp012517955 Syllabication: di.ges.to'ri.um Nomenclatural type: GCA_012517955.1 Etymology: L. neut. adj. digestorium, “pertaining to digestion,” referring to the organism’s origin from an anaerobic digestion system.
Genus <i>Abditiinfera</i>	Synonyms: JAAEQD01 Syllabication: Ab.di.ti.in.fe'ra Nomenclatural type: <i>Abditiinfera halomarinae</i> Etymology: L. masc. adj. abditus, hidden, secret; L. fem. adj. infera, low, beneath; N.L. fem. n. Abditiinfera, “the hidden one beneath,” referring to a genus of organisms inhabiting concealed or subsurface sedimentary environments.
Species <i>Abditiinfera halomarinae</i>	Synonyms: JAAEQD01 sp963668625 Syllabication: Ha.lo.ma.ri'nae Nomenclatural type: GCA_963668625.1 Etymology: Gr. masc. n. hals (ἅλς), salt; L. fem. adj. marina, of the sea; N.L. gen. n. halomarinae, of the saline sea
Order <i>Omnivagifaecales</i>	Synonyms: GN15 Syllabication: Om.ni.va.gi.fae.ca'les Nomenclatural type: <i>Omnivagifaecis</i> Etymology: N.L. fem. n. Omnivagifaecis, referring to the type genus <i>Omnivagifaecis</i>; –ales, ending to denote an Order ; N.L. fem. pl. n. <i>Omnivagifaecales</i>, Order of the genus <i>Omnivagifaecis</i>.
Family <i>Omnivagifaecaceae</i>	Synonyms: f_FEB-12 Syllabication: Om.ni.va.gi.fae.ca'ce.ae Nomenclatural type: <i>Omnivagifaecis</i> Etymology: N.L. fem. n. Omnivagifaecis, referring to the type genus <i>Omnivagifaecis</i>; –aceae, ending to denote a family; N.L. fem. pl. n. <i>Omnivagifaecaceae</i>, family of the genus <i>Omnivagifaecis</i>.

Genus <i>Omnivagifaecis</i>	Synonyms: JAJRTA01 Syllabication: Om.ni.va.gi.fae'cis Nomenclatural type: <i>Omnivagifaecis aestuariisuperficie</i> Etymology: L. fem. adj. omnivaga, wandering everywhere; L. fem. n. faex, sediment; NL. fem. n. <i>Omnivagifaecis</i>, an organism that wander across all types of sedimentary environments.
Species <i>Omnivagifaecis alorisubrepens</i>	Synonyms: JAJRTA01 sp023132995 Syllabication: al.go.ri.sub.re'pens Nomenclatural type: GCA_030630835.1 Etymology: L. masc. n. alor, cold; L. pres. part. subrepens, creeping beneath, seeping; N.L. part. adj. alorisubrepens, referring to an organism associated with cold-seep.
Species <i>Omnivagifaecis thermovaporis</i>	Synonyms: JAJRTA01 sp024278515 Syllabication: ther.mo.va.po'ris Nomenclatural type: GCA_024278515.1 Etymology: Gr. fem. n. thermē (θέρμη), heat; L. masc. n. vapor, steam; N.L. gen. n. thermovaporis, referring to origin from hydrothermal-vent environments.
Species <i>Omnivagifaecis aestuariisuperficie</i>	Synonyms: JAJRTA01 sp029860345 Syllabication: es.tu.a.ri.i.su.per.fi'ci.ei Nomenclatural type: GCA_029860345.1 Etymology: L. neut. n. aestuarium, estuary; L. fem. n. superficies, surface; N.L. gen. n. aestuariisuperficie, of the estuarine surface.
Species <i>Omnivagifaecis frigorisubrepens</i>	Synonyms: JAJRTA01 sp030605565 Syllabication: fri.go.ri.sub.re'pens Nomenclatural type: GCA_030605565.1 Etymology: L. neut. n. frigus, cold; L. pres. part. subrepens, creeping beneath, seeping; N.L. part. adj. frigorisubrepens, referring to origin in cold-seep.
Genus <i>Hydrocauma</i>	Synonyms: JAJRUL01 Syllabication: Hy.dro.cau'ma Nomenclatural type: <i>Hydrocauma camini</i> Etymology: Gr. neut. n. hydōr (ὕδωρ), water; L. neut. n. cauma, heat; N.L. neut. n. <i>Hydrocauma</i>, “heated water,” a genus of organisms associated with hydrothermal systems.

Species <i>Hydrocauma camini</i>	Synonyms: JAJRUL01 sp024277795 Syllabication: ca.mi'ni Nomenclatural type: GCA_024277795.1 Etymology: L. gen. n. camini, “of a vent,” denoting organisms’ origin from hydrothermal vent.
Genus <i>Thermocaminus</i>	Synonyms: JAJRZL01 Syllabication: Ther.mo.ca.mi'nus Nomenclatural type: Thermocaminus camini Etymology: Gr. fem. n. thermē (θέρμη), heat; L. masc. n. caminus, vent; N.L. masc. n. Thermocaminus, a genus of organisms associated with hydrothermal vent.
Species <i>Thermocaminus camini</i>	Synonyms: JAJRZL01 sp024275255 Syllabication: ca.mi'ni Nomenclatural type: GCA_024275255.1 Etymology: L. gen. n. camini, “of a vent,” denoting organisms’ origin from hydrothermal vent.
Genus <i>Maricultor</i>	Synonyms: JANQPI01 Syllabication: Ma.ri.cul'tor Nomenclatural type: Maricultor coralli Etymology: L. neut. n. mare, sea; L. masc. n. cultor, dweller; N.L. masc. n. Maricultor, a genus of organisms dwelling in marine environments.
Species <i>Maricultor coralli</i>	Synonyms: JANQPI01 sp028289585 Syllabication: co.ral'li Nomenclatural type: GCA_028289585.1 Etymology: L. gen. n. coralli, “of coral,” referring to origin from coral skeleton.
Genus <i>Fervidicultor</i>	Synonyms: JARGFS01 Syllabication: Fer.vi.di.cul'tor Nomenclatural type: Fervidicultor limivulcani Etymology: L. adj. fervidus, boiling, very hot; L. masc. n. cultor, dweller, inhabitant; N.L. masc. n. Fervidicultor, a genus of organisms inhabiting hot/geothermal environments.

Species <i>Fervidicultor limivulcani</i>	Synonyms: JARGFS01 sp029211095 Syllabication: li.mi.vul.ca'ni Nomenclatural type: GCA_029211095.1 Etymology: L. masc. n. limus, mud; L. masc. n. Vulcanus, Roman god of fire, volcano; N.L. gen. n. limivulcani, “of the mud of a volcano,” referring to the organism’s origin from a pool on the surface of a mud volcano.
Genus <i>Pelagicultor</i>	Synonyms: JAUXCD01 Syllabication: Pe.la.gi.cul'tor Nomenclatural type: Pelagicultor gelidisubrepens Etymology: L. neut. n. pelagus, open sea; L. masc. n. cultor, dweller; N.L. masc. n. Pelagicultor, a dweller of the open sea.
Species <i>Pelagicultor gelidisubrepens</i>	Synonyms: JAUXCD01 sp030619085 Syllabication: Ge.li.di.sub.re'pens Nomenclatural type: GCA_030619085.1 Etymology: L. masc. adj. gelidus, cold; L. pres. part. subrepens, oozing/creeping from below; N.L. part. adj. gelidisubrepens, “cold-seeping,” referring to organisms recovered from a cold seep.
Genus <i>Lacicultor</i>	Synonyms: JAWXAN01 Syllabication: La.ci.cul'tor Nomenclatural type: Lacicultor mattilaci Etymology: L. masc. n. lacus, lake; L. masc. n. cultor, dweller; N.L. masc. n. Lacicultor, a dweller of lakes.
Species <i>Lacicultor mattalaci</i>	Synonyms: JAWXAN01 sp034439475 Syllabication: Mat.ti.la'ci Nomenclatural type: GCA_034439475.1 Etymology: L. fem. n. matta, mat; L. masc. n. lacus, lake; N.L. gen. n. mattilaci, “of the lake mat,” referring to the organism’s origin from a microbial mat in a lake.
Genus <i>Altisessor</i>	Synonyms: QNAD01 Syllabication: Al.ti.ses'sor Nomenclatural type: Altisessor muriae Etymology: L. neut. n. altum, deep sea; L. masc. n. sessor, inhabitant; N.L. masc. n. Altisessor, an inhabitant of the deep sea.

Species <i>Altisessor muriae</i>	Synonyms: QNAD01 sp034659415 Syllabication: mu.ri'ae Nomenclatural type: GCA_034659415.1 Etymology: L. gen. n. muriae, “of brine,” referring to the organism recovered from a deep-sea brine pool
Genus <i>Aequoricultor</i>	Synonyms: QQUK01 Syllabication: Ae.quo.ri.cul'tor Nomenclatural type: <i>Aequoricultor exudans</i> Etymology: L. neut. n. aequor, ocean; L. masc. n. cultor, inhabitant; N.L. masc. n. <i>Aequoricultor</i>, a dweller of the ocean.
Species <i>Aequoricultor calidifontis</i>	Synonyms: QQUK01 sp024276275 Syllabication: ca.li.di.fon'tis Nomenclatural type: GCA_024276275.1 Etymology: L. masc. adj. calidus, hot; L. masc. n. fons, spring; N.L. gen. n. <i>calidifontis</i>, “of a hot spring,” referring to origin from a hydrothermal vent.
Species <i>Aequoricultor rimarum</i>	Synonyms: QQUK01 sp024278935 Syllabication: ri.ma'rum Nomenclatural type: GCA_024278935.1 Etymology: L. gen. pl. n. rimarum, “of (seafloor) fissures,” denoting recovery from venting cracks at plate boundaries.
Species <i>Aequoricultor thermanum</i>	Synonyms: QQUK01 sp024280215 Syllabication: ther.ma'rum Nomenclatural type: GCA_024280215.1 Etymology: L. gen. pl. n. thermanum, “of hot waters,” referring to origin from hydrothermal vent.
Species <i>Aequoricultor oceanicus</i>	Synonyms: QQUK01 sp913009765 Syllabication: o.ce.a'ni.cus Nomenclatural type: GCA_937900185.1 Etymology: L. masc. adj. oceanicus, "oceanic," belonging to the ocean

Genus <i>Haloinhabitans</i>	Synonyms: WJMS01 Syllabication: Ha.lo.in.ha'bi.tansN omenclatural type: <i>Haloinhabitans</i> <i>lixivii</i> Etymology: Gr. masc. n. hálς (ἅλς), salt; L. pres. part. <i>inhabitans</i>, inhabiting; N.L. masc. n. <i>Haloinhabitans</i>, “inhabiting salt,” referring to organisms recovered from hypersaline environments.
Species <i>Haloinhabitans tapetis</i>	Synonyms: WJMS01 sp014727815 Syllabication: ta.pe'tis Nomenclatural type: GCA_014727815.1 Etymology: L. gen. n. <i>tapetis</i>, “of a mat,” referring to organism's recovery from a microbial mat in hypersaline waters.
Species <i>Haloinhabitans lixivii</i>	Synonyms: WJMS01 sp034003725 Syllabication: li.xi'vi.i Nomenclatural type: GCA_034003725.1 Etymology: L. gen. n. <i>lixivii</i>, “of leachate,” referring to organism's recovery from landfill leachate.
Genus <i>Marisediminis</i>	Synonyms: B120-G9 Syllabication: Ma.ri.se.di'mi.nis Nomenclatural type: <i>Marisediminis</i> <i>oceanisediminis</i> Etymology: L. neut. n. <i>mare</i>, sea; L. neut. n. <i>sedimen</i>, sediment; N.L. fem. n. <i>Marisediminis</i>, “of sea sediment”, refering to a genus of organisms associated with marine sediments.
Species <i>Marisediminis thermosediminis</i>	Synonyms: B120-G9 sp003641415 Syllabication: ther.mo.se.di.mi'nis Nomenclatural type: GCA_003641415.1 Etymology: Gr. fem. n. <i>therme</i> (θερμη), heat; L. neut. n. <i>sedimen</i>, sediment; N.L. gen. n. <i>thermosediminis</i>, “of hot sediment,” referring to origin from deep-sea hydrothermal vent sediments.
Species <i>Marisediminis oceanisediminis</i>	Synonyms: B120-G9 sp019038695 Syllabication: o.ce.a.ni.se.di.mi'nis Nomenclatural type: GCA_019038695.1 Etymology: L. masc. n. <i>oceanus</i>, ocean; L. neut. n. <i>sedimen</i>, sediment; N.L. gen. n. <i>oceanisediminis</i>, “of ocean sediment,” referring to the organism’s origin from marine sediments.

Species <i>Marisediminis halopiscinae</i>	Synonyms: B120-G9 sp034659895 Syllabication: ha.lo.pis.ci'nae Nomenclatural type: GCA_034659895.1 Etymology: Gr. masc. n. hális (ἅλς), salt; L. fem. n. piscina, pool; L. gen. sg. piscinae; N.L. gen. n. halopiscinae, “of a salt pool,” referring to origin from a deep-sea brine pool.
Genus <i>Arviculor</i>	Synonyms: DAISVY01 Syllabication: Ar.vi.cul'tor Nomenclatural type: Arviculor humi Etymology: L. neut. n. arvum, soil; L. masc. n. cultor, dweller, inhabitant; N.L. masc. n. Arviculor, a genus of organisms dwelling in soil.
Species <i>Arviculor humi</i>	Synonyms: DAISVY01 sp036826635 Syllabication: hu'mi Nomenclatural type: GCA_036826635.1 Etymology: L. gen. n. humi, of soil
Genus <i>Liquorivivens</i>	Synonyms: DAOSXA01 Syllabication: Li.quo.ri.vi'vans Nomenclatural type: Liquorivivens cloacalis Etymology: L. masc. n. liquor, liquid; L. pres. part. vivens, living; N.L. fem. n. Liquorivivens, one living in liquid environments.
Species <i>Liquorivivens cloacalis</i>	Synonyms: DAOSXA01_sp035380245 Syllabication: clo.a.ca'lis Nomenclatural type: GCA_035380245.1 Etymology: L. fem. adj. cloacalis, pertaining to a sewer(wastewater), referring to the organism's origin from wastewater.
Genus <i>Gelidisediminis</i>	Synonyms: DAOUUR01 Syllabication: Ge.li.di.se.di'mi.nis Nomenclatural type: Gelidisediminis cryosubrepens Etymology: L. masc. adj. gelidus, cold; L. neut. sedimen, sediment; L. neut. gen. sediminis; N.L. fem. n. Gelidisediminis, of cold sediment

Species <i>Gelidisediminis cryosubrepens</i>	Synonyms: DAOUUR01 sp030668045 Syllabication: cry.o.sub.re'pens Nomenclatural type: GCA_030668045.1 Etymology: Gr. neut. n. krýos (κρύος), cold; L. pres. part. subrepens, to seep; N.L. fem. part. adj. cryosubrepens, referring to an organism associated with cold seeps.
Genus <i>Phreatofons</i>	Synonyms: DATKJY01 Syllabication: Phre.a.to.fons Nomenclatural type: Phreatofons aquiferis Etymology: Gr. neut. n. phrear (φρέαρ), well; L. masc. n. fons, source; N.L. masc. n. Phreatofons, a genus of organisms associated with groundwater sources.
Species <i>Phreatofons aquiferis</i>	Synonyms: DATKJY01 sp040753875 Syllabication: a.qui.fe'ris Nomenclatural type: GCA_040753875.1 Etymology: N.L. masc. n. aquifer, water-bearing layer; N.L. gen. n. aquiferis, “of the aquifer,” referring to origin from groundwater.
Genus <i>Humisedens</i>	Synonyms: DATKXK01 Syllabication: Hu.mi.se'dens Nomenclatural type: Humisedens humi Etymology: L. fem. n. humus, soil; L. pres. part. sedens, settling; N.L. fem. n. Humisedens, a genus of organisms residing in soil.
Species <i>Humisedens humi</i>	Synonyms: DATKXK01 sp035529075 Syllabication: hu'mi Nomenclatural type: GCA_035529075.1 Etymology: L. gen. n. humi, of soil
Genus <i>Terricultor</i>	Synonyms: DATMWY01 Syllabication: Ter.ri.cul'tor Nomenclatural type: Terricultor Etymology: L. fem. n. terra, earth, land, soil; L. masc. n. cultor, dweller; N.L. masc. n. Terricultor, a genus of organisms dwelling in soil.

Species <i>Terricultor solicola</i>	Synonyms: DATMWY01 sp035562415 Syllabication: so.li.co'la Nomenclatural type: GCA_035562415.1 Etymology: L. neut. n. solum, soil, ground; L. masc. n. suff. -cola, inhabitant; N.L. masc. n. solicola, "soil-dweller," referring to origin from soil.
Genus <i>Floccicultor</i>	Synonyms: g_FEB-12 Syllabication: Floc.ci.cul'tor Nomenclatural type: Floccicultor flocculorum Etymology: L. masc. n. floccus, floc, tuft; L. masc. n. cultor, dweller; N.L. masc. n. Floccicultor, a genus of organisms dwelling in flocculated biomass of engineered aquatic systems.
Species <i>Floccicultor dolii</i>	Synonyms: FEB-12 sp003105265 Syllabication: do'li.i Nomenclatural type: GCA_003105265.1 Etymology: L. gen. n. dolii, "of the vat," referring to recovery of the organism from a bioreactor vessel used in wastewater treatment.
Species <i>Floccicultor flocculorum</i>	Synonyms: FEB-12 sp016708025 Syllabication: flo.c.cu.lo'rum Nomenclatural type: GCA_016708025.1 Etymology: L. masc. dim. n. flocculus, a small floc/tuft; N.L. gen. pl. n. flocculorum, "of the flocs," referring to origin from activated-sludge floc aggregates.
Genus <i>Pontisediminis</i>	Synonyms: G963664195 Syllabication: Pon.ti.se.di'mi.nis Nomenclatural type: Pontisediminis pelagifaecis Etymology: L. masc. n. pontus, sea; L. neut. n. sedimen, sediment; N.L. fem. n. Pontisediminis, of sea sediments.
Species <i>Pontisediminis pelagifaecis</i>	Synonyms: G963664195 sp963664195 Syllabication: pe.la.gi.fae'cis Nomenclatural type: GCA_963664195.1 Etymology: L. neut. n. pelagus, sea; L. fem. n. faex, sediment; N.L. gen. n. pelagifaecis, "of sea-sediment," referring to origin from marine sediments.

Genus <i>Phreatomarina</i>	Synonyms: GCA-020346225 Syllabication: Phre.a.to.ma.ri'na Nomenclatural type: <i>Phreatomarina maricrassaminis</i> Etymology: Gr. neut. n. phrear (φρέαρ), well; L. fem. adj. marina, of the sea; N.L. fem. n. <i>Phreatomarina</i>, a genus of organisms associated with groundwater and marine settings.
Species <i>Phreatomarina marifaecis</i>	Synonyms: GCA-020346225 sp020346225 Syllabication: ma.ri.fae'cis Nomenclatural type: GCA_020346225.1 Etymology: L. neut. n. mare, sea; L. fem. n. faex, sediment; N.L. gen. n. <i>marifaecis</i>, “of sea-sediment,” referring to the organism’s origin from marine sediment.
Species <i>Phreatomarina maricrassaminis</i>	Synonyms: GCA-020346225 sp020351995 Syllabication: ma.ri.cras.sa.mi'nis Nomenclatural type: GCA_020351995.1 Etymology: L. neut. n. mare, sea; L. neut. n. crassamen, sediment; N.L. gen. n. <i>maricrassaminis</i>, “of marine sediment,” referring to origin from marine sediments.
Species <i>Phreatomarina puteilaticis</i>	Synonyms: GCA-020346225 sp040756055 Syllabication: pu.te.i.la.ti'cis Nomenclatural type: GCA_040756055.1 Etymology: L. masc. n. puteus, well; L. masc. n. latex, liquid; N.L. gen. n. <i>puteilaticis</i>, “of well-liquid,” referring to origin from groundwater.
Genus <i>Bothynifaecis</i>	Synonyms: JACZWU01 Syllabication: Bo.thy.ni.fae'cis Nomenclatural type: <i>Bothynifaecis scrobis</i> Etymology: L. masc. n. bothynus, trench; L. fem. n. faex, sediment; N.L. fem. n. <i>Bothynifaecis</i>, of trench sediments.
Species <i>Bothynifaecis abyssi</i>	Synonyms: JACZWU01 sp022562075 Syllabication: ab.ys'si Nomenclatural type: GCA_022562075.1 Etymology: L. gen. n. abyssi, “of the abyss,” referring to origin from trench depths.

Species <i>Bothynifaecis fossisediminis</i>	Synonyms: JACZWU01 sp022571845 Syllabication: fos.si.se.di.mi'nis Nomenclatural type: GCA_022571845.1 Etymology: L. fem. n. fossa, trench; L. neut. n. sedimen, sediment; N.L. gen. n. fossisediminis, of trench sediment.
Species <i>Bothynifaecis scrobis</i>	Synonyms: JACZWU01 sp022571985 Syllabication: scro'bis Nomenclatural type: GCA_022571985.1 Etymology: L. gen. n. scrobis, “of a trench,” referring to origin from trench sediments.
Genus <i>Effluvium</i>	Synonyms: JAFGNW01 Syllabication: Ef.flu'vi.um Nomenclatural type: Effluvium lixivia Etymology: L. neut. n. effluvium, flowing out/outlet; N.L. neut. n. Effluvium, a genus associated with liquid outflows.
Species <i>Effluvium lixivii</i>	Synonyms: JAFGNW01 sp028715215 Syllabication: li.xi.vi'i Nomenclatural type: GCA_028715215.1 Etymology: L. gen. n. lixivii, “of leachate,” referring to origin from landfill leachate.
Genus <i>Aquiferus</i>	Synonyms: JAGGTI01 Syllabication: A.quin.fe'rus Nomenclatural type: Aquiferus putei Etymology: L. fem. n. aqua, water; L. masc. adj. inferus, lower, beneath; N.L. masc. n. Aquiferus, a genus of organisms associated with waters from below (groundwater).
Species <i>Aquiferus putei</i>	Synonyms: JAGGTI01 sp040752815 Syllabication: pu.te'i Nomenclatural type: GCA_040752815.1 Etymology: L. gen. n. putei, “of a well,” referring to groundwater origin.

Genus <i>Multihabitans</i>	Synonyms: JAGNLV01 Syllabication: Mul.ti.ha.bi'tans Nomenclatural type: <i>Multihabitans thermoaquae</i> Etymology: L. masc. adj. multus, many; L. pres. part. habitans, dwelling, living; N.L. fem. n. <i>Multihabitans</i>, a genus occurring across multiple habitats
Species <i>Multihabitans cloacae</i>	Synonyms: JAGNLV01 sp017999435 Syllabication: clo.a'cae Nomenclatural type: GCA_017999435.1 Etymology: L. gen. n. <i>cloacae</i>, "of a sewer," denoting wastewater origin.
Species <i>Multihabitans thermoaquae</i>	Synonyms: JAGNLV01 sp041742355 Syllabication: ther.mo.a'quae Nomenclatural type: GCA_041742355.1 Etymology: Gr. fem. n. thermē (θέρμη), heat; L. fem. n. aqua, water; N.L. gen. n. <i>thermoaquae</i>, referring to origin from hot spring water.
Genus <i>Elaterifaecis</i>	Synonyms: FEB12; g__ Syllabication: E.la.te.ri.fae'cis Nomenclatural type: <i>Elaterifaecis harenae</i> Etymology: L. neut. n. elater, spring; L. fem. n. faex, sediment; N.L. fem. n. <i>Elaterifaecis</i>, referring to the organisms recovered from spring sediment.
Species <i>Elaterifaecis harenae</i>	Synonyms: g_(<i>Elaterifaecis</i>); s__ Syllabication: ha.re'nae Nomenclatural type: (bin.142.fasta_MP62F_HA) Etymology: L. gen. n. <i>harenae</i>, "of sand," referring to the sandy habitat from which the organism was recovered.
Genus <i>Appulsifaecis</i>	Synonyms: FEB12; g__ Syllabication: Ap.pul.si.fae'cis Nomenclatural type: <i>Appulsifaecis halofaecis</i> Etymology: L. masc. n. appulsus, approach, landing; L. fem. n. faex; N.L. fem. n. <i>Appulsifaecis</i>, a genus of organisms living upon or settled onto sediment surfaces.

Species <i>Appulsifaecis halofaecis</i>	Synonyms: FEB12; g__s__ Syllabication: ha.lo.fae'cis Nomenclatural type: (bin.170.fasta_GLS202F_HA) Etymology: Gr. masc. n. h́als (ἅλς), salt; L. fem. n. faex, sediment; N.L. gen. n. halofaecis, "of salty sediment," referring to the organism's origin from saline spring sediment.
Family <i>Fundimaricultoraceae</i>	Synonyms: f__JAAZOE01 Syllabication: Fun.di.ma.ri.cul.to.ra'ce.ae Nomenclatural type: Fundimaricultor Etymology: N.L. masc. n. Fundimaricultor, referring to the type genus Fundimaricultor; -aceae, standard suffix denoting a family; N.L. fem. pl. n. Fundimaricultoraceae, the family of the genus Fundimaricultor.
Genus <i>Fundimaricultor</i>	Synonyms: DAOUTW01 Syllabication: Fun.di.ma.ri.cul'tor Nomenclatural type: Fundimaricultor algorirorans Etymology: L. masc. n. fundus, bottom; L. neut. n. mare, sea; L. masc. n. cultor, dweller; N.L. masc. n. Fundimaricultor, a dweller of the sea bottom.
Species <i>Fundimaricultor algorirorans</i>	Synonyms: DAOUTW01 sp030668485 Syllabication: al.go.ri.ro'rans Nomenclatural type: GCA_030668485.1 Etymology: L. masc. n. algor, cold; L. masc. pres. part. rorans (from roro), dripping/seeping; N.L. part. adj. algorirorans, originisms from a cold seep.
Genus <i>Alticultor</i>	Synonyms: JAGLON01 Syllabication: Al.ti.cul'tor Nomenclatural type: Alticultor sediminis Etymology: L. neut. n. altum, deep sea; L. masc. n. cultor, dweller; N.L. masc. n. Alticultor, a dweller of the deep sea.
Species <i>Alticultor sediminis</i>	Synonyms: JAGLON01 sp023138975 Syllabication: se.di'mi.nis Nomenclatural type: GCA_023138975.1 Etymology: L. gen. n. sediminis, "of sediment," referring to the organism's origin from deep-sea sediment.

Species <i>Alticultor cloacae</i>	Synonyms: JAGLON01 sp041394985 Syllabication: clo.a'cae Nomenclatural type: GCA_041394985.1 Etymology: L. gen. n. cloacae, "of a sewer," referring to organism's origin from wastewater.
Genus <i>Fontimaricultor</i>	Synonyms: JAUUYJ01 Syllabication: Fon.ti.ma.ri.cul'tor Nomenclatural type: Fontimaricultor gelidifontis Etymology: L. masc. n. fons, spring; L. neut. n. mare, sea; L. masc. n. cultor, dweller; N.L. masc. n. Fontimaricultor, a dweller of sea springs/seeps.
Species <i>Fontimaricultor gelidifontis</i>	Synonyms: JAUUYJ01 sp030588275 Syllabication: ge.li.di.fon'tis Nomenclatural type: GCA_030588275.1 Etymology: L. masc. adj. gelidus, cold; L. masc. n. fons, spring; N.L. gen. n. gelidifontis, "of a cold spring," referring to organism's origin from a marine cold seep.
Species <i>Fontimaricultor salinarum</i>	Synonyms: JAUUYJ01;s__ Syllabication: sa.li.na'rum Nomenclatural type: (bin.089.fasta_MP62F_HA) Etymology: L. fem. n. salina, salt spring, salt pit; L. gen. pl. n. salinarum, "of salterns," referring to the organism's origin from saline spring sediments.
Genus <i>Marinisediminis</i>	Synonyms: JAZGGI01 Syllabication: Ma.ri.ni.se.di'mi.nis Nomenclatural type: Marinisediminis luti Etymology: L. masc. adj. marinus, marine; L. neut. n. sedimen, sediment; N.L. masc. n. Marinisediminis, of marine sediment
Species <i>Marinisediminis luti</i>	Synonyms: JAZGGI01 sp036480375 Syllabication: lu'ti Nomenclatural type: GCA_036480375.1 Etymology: L. gen. n. luti, "of mud," referring to organism's origin from marine sediment.

Family <i>Rimiculatoraceae</i>	Synonyms: f__JACZUZ01 Syllabication: Ri.mi.cul.to.ra'ce.ae Nomenclatural type: Rimiculator Etymology: N.L. masc. n. Rimiculator, referring to the type genus Rimiculator; –aceae, ending to denote a family; N.L. fem. pl. n. Rimiculatoraceae, family of the genus Rimiculator.
Genus <i>Rimiculator</i>	Synonyms: JAJRPJ01 Syllabication: Ri.mi.cul'tor Nomenclatural type: Rimiculator calidifontis Etymology: L. fem. n. rima, fissure/cleft; L. masc. n. cultor, dweller/inhabitant; N.L. masc. n. Rimiculator, a dweller of seafloor fissures.
Species <i>Rimiculator calidifontis</i>	Synonyms: JAJRPJ01 sp024280775 Syllabication: ca.li.di.fon'tis Nomenclatural type: GCA_024280775.1 Etymology: L. masc. adj. calidus, hot; L. masc. n. fons, spring; N.L. gen. n. calidifontis, “of a hot spring,” referring to origin from a hydrothermal vent.
Species <i>Rimiculator thermarum</i>	Synonyms: JAJRPJ01 sp024280835 Syllabication: ther.ma'rum Nomenclatural type: GCA_024280835.1 Etymology: L. fem. pl. n. thermae, hot waters; N.L. gen. pl. n. thermarum, “of hot waters,” referring to origin from hydrothermal vent.
Family <i>Altundifaecaceae</i>	Synonyms: f__PGXB01 Syllabication: Alt.un.di.fae.ca'ce.ae Nomenclatural type: Altundifaecis Etymology: N.L. fem. n. Altundifaecis, referring to the type genus Altundifaecis; –aceae, ending to denote a family; N.L. fem. pl. n. Altundifaecaceae, family of the genus Altundifaecis.
Genus <i>Altundifaecis</i>	Synonyms: PGXB01 Syllabication: Alt.un.di.fae'cis Nomenclatural type: Altundifaecis aquiferis Etymology: L. masc. adj. altus, deep; L. fem. n. unda, water; L. fem. n. faex, sediment; N.L. fem. n. Altundifaecis, “of deep aquatic sediment,” a genus of organisms associated with deep, sediment-rich waters.

Species <i>Altundifaecis aquiferis</i>	Synonyms: PGXB01 sp002838945 Syllabication: a.qui'fe.ris Nomenclatural type: GCA_002838945.1 Etymology: N.L. neut. n. aquifer, an aquifer; N.L. gen. n. aquiferis, "of an aquifer," referring to origin from groundwater.
Species <i>Altundifaecis calidisediminis</i>	Synonyms: PGXB01 sp003641425 Syllabication: Ca.li.di.se.di'mi.nis Nomenclatural type: GCA_011040955.1 Etymology: L. fem. n. calida, hot water; L. neut. n. sedimen, sediment; N.L. gen. n. calidisediminis, "of hot water sediment," referring to organism's recovery from marine hydrothermal sediment.
Species <i>Altundifaecis humiaquae</i>	Synonyms: PGXB01 sp040752235 Syllabication: hu.mi.a'quae Nomenclatural type: GCA_040752235.1 Etymology: L. fem. n. humus, ground; L. fem. n. aqua, water; N.L. gen. n. humiaquae, "of groundwater," referring to organism's origin from groundwater.
Genus <i>Ingeniaricola</i>	Synonyms: CALAMC01 Syllabication: In.ge.ni.a.ri'co.la Nomenclatural type: Ingeniaricola reactri Etymology: L. masc. n. ingeniarius, engineer; L. masc. n. -cola, inhabitant; N.L. masc. n. Ingeniaricola, a dweller of engineered systems.
Species <i>Ingeniaricola reactri</i>	Synonyms: CALAMC01 sp937925655 Syllabication: re.ac'tri Nomenclatural type: GCA_937925655.1 Etymology: L. gen. n. reactri, "of a reactor," referring to origin from an engineered system.
Genus <i>Hypogicultor</i>	Synonyms: DYGG01 Syllabication: Hy.po.gi.cul'tor Nomenclatural type: Hypogicultor humiaquae Etymology: L. masc. adj. hypogeus, underground; L. masc. n. cultor, dweller; N.L. masc. n. Hypogicultor, "an underground dweller," referring to organisms recovered from groundwater.

Species <i>Hypogicultor humiaquae</i>	Synonyms: DYGG01 sp020724775 Syllabication: hu.mi.a'quae Nomenclatural type: GCA_020724775.1 Etymology: L. fem. n. humus, ground; L. fem. n. aqua, water; N.L. gen. n. humiaquae, "of groundwater," referring to organism's origin from groundwater.
Species <i>Hypogicultor telluriaquae</i>	Synonyms: DYGG01 sp040753495 Syllabication: tel.lu.ri.a'quae Nomenclatural type: GCA_040753495.1 Etymology: L. fem. n. tellus, earth, ground; L. fem. n. aqua, water; N.L. gen. n. telluriaquae, "of earth's water," referring to origin from groundwater.
Genus <i>Alticolonus</i>	Synonyms: JAAERC01 Syllabication: Al.ti.co.lo'nus Nomenclatural type: Alticolonus gelidifontis Etymology: L. neut. n. altum, sea; L. masc. n. colonus, settler/dweller; N.L. masc. n. Alticolonus, a dweller of the sea (marine environment).
Species <i>Alticolonus gelidifontis</i>	Synonyms: JAAERC01 sp030667525 Syllabication: ge.li.di.fon'tis Nomenclatural type: GCA_030667525.1 Etymology: L. masc. adj. gelidus, cold; L. masc. n. fons, spring; N.L. gen. n. gelidifontis, "of a cold spring," referring to organism's origin from a marine cold seep.
Genus <i>Laticicrassaminis</i>	Synonyms: JAFGTT01 Syllabication: La.ti.ci.cras.sa'mi.nis Nomenclatural type: Laticicrassaminis fluviatilis Etymology: L. masc. n. latex, water/liquid; L. neut. n. crassamen, sediment; N.L. masc. n. Laticicrassaminis, of water sediment.
Species <i>Laticicrassaminis fluviatilis</i>	Synonyms: JAFGTT01 sp016933955 Syllabication: flu.vi.a'ti.lis Nomenclatural type: GCA_016933955.1 Etymology: L. masc. adj. fluviatilis, "riverine", referring to river sediment.

Genus <i>Crepaturiliquoris</i>	Synonyms: JAGVEJ01 Syllabication: Cre.pa.tu.ri.li.quo'ris Nomenclatural type: <i>Crepaturiliquoris rimarum</i> Etymology: L. fem. n. crepatura, fissure/crack; L. masc. n. liquor, liquid; N.L. masc. n. <i>Crepaturiliquoris</i>, “of fissure fluid,” referring to organisms originating from fracture fluids.
Species <i>Crepaturiliquoris rimarum</i>	Synonyms: JAGVEJ01 sp020058225 Syllabication: ri.ma'rum Nomenclatural type: GCA_020058225.1 Etymology: L. gen. pl. n. rimarum, “of fissures,” i.e., fracture fluids.
Genus <i>Crassaminicultor</i>	Synonyms: JAPLUR01 Syllabication: Cras.sa.mi.ni.cul'tor Nomenclatural type: <i>Crassaminicultor lacus</i> Etymology: L. neut. n. crassamen, sediment; L. masc. n. cultor, dweller; N.L. masc. n. <i>Crassaminicultor</i>, a dweller of sediments.
Species <i>Crassaminicultor lacus</i>	Synonyms: JAPLUR01 sp026397505 Syllabication: lac'us Nomenclatural type: GCA_026397505.1 Etymology: L. gen. n. lacus, of a lake
Genus <i>Edaphocultor</i>	Synonyms: JBFZV01 Syllabication: E.da.pho.cul'tor Nomenclatural type: <i>Edaphocultor humi</i> Etymology: Gr. neut. n. edaphos (ἔδαφος), soil, ground; L. masc. n. cultor, dweller; N.L. masc. n. <i>Edaphocultor</i>, a dweller of soil.
Species <i>Edaphocultor humi</i>	Synonyms: JBFZV01 sp041306185 Syllabication: hu'mi Nomenclatural type: GCA_041306265.1 Etymology: L. gen. n. humi, of soil

Genus <i>Calidifonticola</i>	Synonyms: JBGSH01 Syllabication: Ca.li.di.fon.ti'co.la Nomenclatural type: <i>Calidifonticola thermarum</i> Etymology: L. masc. adj. calidus, hot; L. masc. n. fons, spring; L. masc. n. -cola, dweller; N.L. masc. n. Calidifonticola, a dweller of hot springs.
Species <i>Calidifonticola thermarum</i>	Synonyms: JBGSH01 sp041752195 Syllabication: ther.ma'rum Nomenclatural type: GCA_041752195.1 Etymology: L. gen. pl. n. thermarum, “of hot waters,” referring to origin from hot spring water.
Genus <i>Undicultor</i>	Synonyms: UNRQ01 Syllabication: Un.di.cul'tor Nomenclatural type: <i>Undicultor lacus</i> Etymology: L. fem. n. unda, water; L. masc. n. cultor, dweller; N.L. masc. n. Undicultor, a dweller of waters (used here for freshwater lineages).
Species <i>Undicultor lacus</i>	Synonyms: UNRQ01 sp900498245 Syllabication: lac'us Nomenclatural type: GCA_900498245.1 Etymology: L. gen. n. lacus, of a lake
Species <i>Undicultor aquae</i>	Synonyms: UNRQ01 sp937867135 Syllabication: a'quae Nomenclatural type: GCA_937867135.1 Etymology: L. gen. n. aquae, “of water,” referring to organism's recovery from freshwater.
Order <i>Cryptaquificales</i>	Synonyms: UM-FILTER-46-8 Syllabication: Crypt.a.qui.fe.ri'ca.les Nomenclatural type: <i>Cryptaquiferis</i> Etymology: N.L. masc. n. Cryptaquifer, referring to the type genus <i>Cryptaquifer</i>; –ales, ending to denote an Order ; N.L. fem. pl. n. Cryptoquificales, Order of the genus <i>Cryptaquifer</i>.

Family <i>Cryptaquifericaceae</i>	Synonyms: UM-FILTER-46-8 Syllabication: Crypt.a.qui.fe.ri'ci'cae Nomenclatural type: <i>Cryptaquiferis</i> Etymology: N.L. masc. n. <i>Cryptaquifer</i>, referring to the type genus <i>Cryptaquifer</i>; –aceae, ending to denote a family; N.L. fem. pl. n. <i>Cryptaquifericaceae</i>, family of the genus <i>Cryptaquifer</i>.
Genus <i>Cryptaquiferis</i>	Synonyms: UM-FILTER-46-8 Syllabication: Crypt.a.qui'fe.ri Nomenclatural type: <i>Cryptaquiferis fundivagus</i> Etymology: Gk. masc. adj. <i>kryptós</i> (κρυπτός), hidden; NL. masc. n. <i>aquifer</i>, water-bearing layer; N.L. masc. n. <i>Cryptaquiferis</i>, of hidden aquifer
Species <i>Cryptaquiferis fundivagus</i>	Synonyms: UM-FILTER-46-8 sp002791595 Syllabication: fu.n.di.va'gus Nomenclatural type: GCA_002791595.1 Etymology: L. masc. n. <i>fundus</i>, bottom, depth; L. masc. adj. <i>vagus</i>, wandering, roaming; N.L. masc. adj. <i>fundivagus</i>, “one whose wandering pertains to or belongs to the bottom,” referring to the organism’s origin from groundwater
Genus <i>Cryptofontis</i>	Synonyms: WJIR01 Syllabication: Cryp.to.fon'tis Nomenclatural type: <i>Cryptofontis salariphilus</i> Etymology: Gk. masc. adj. <i>kryptós</i> (κρυπτός), hidden, concealed; L. masc. n. <i>fons</i>, spring, source; N.L. masc. n. <i>Cryptofontis</i>, of hidden spring
Species <i>Cryptofontis salariphilus</i>	Synonyms: WJIR01 sp014730175 Syllabication: sa.la.ri'phi.lus Nomenclatural type: GCA_014730175.1 Etymology: L. masc. adj. <i>salaris</i>, of or pertaining to salt; Gr. adj. suff. –<i>philos</i> (φίλος), loving; N.L. masc. adj. <i>salariphilus</i>, “salt-loving,” referring to the organism’s origin from hypersaline microbial mat
Genus <i>Tectifontis</i>	Synonyms: WJII01 Syllabication: Tec.ti.fon'tis Nomenclatural type: <i>Tectifontis halocola</i> Etymology: L. masc. adj. sg. <i>tectus</i>, hidden; L. masc. n. <i>fons</i>, spring, source; N.L. masc. n. <i>Tectifontis</i>, of the hidden spring

Species <i>Tectifontis halocola</i>	Synonyms: WJIJ01 sp014730345 Syllabication: ha.lo'co.la Nomenclatural type: GCA_014730345.1 Etymology: Gr. masc. n. hálς (ἅλς), salt, sea; L. masc. n. suff. -cola, inhabitant; N.L. masc. n. halocola, salt-dweller, referring to the organism's origin from a hypersaline spring.
Genus <i>Aquilatens</i>	Synonyms: JALSTH01 Syllabication: Aq.ui.la'tens Nomenclatural type: Aquilatens maricola Etymology: L. fem. n. aqua, water; L. masc. adj. latens, hidden, secret; N.L. masc. n. Aquilatens, "hidden water," referring to a genus of organisms originating from hidden water sources.
Species <i>Aquilatens maricola</i>	Synonyms: JALSTH01 sp026983835 Syllabication: ma.ri'co.la Nomenclatural type: GCA_026983835.1 Etymology: L. neut. n. mare, sea; L. masc. n. suff. -cola, inhabitant; N.L. masc. n. maricola, "sea-dweller," referring to the organism's origin from marine environment
Order <i>Sediminivales</i>	Synonyms: JAUVRN01 Syllabication: Se.di.mi.ni.vi.ta'les Nomenclatural type: Sediminivita Etymology: N.L. fem. n. Sediminivita, referring to the type genus Sediminivita; -ales, ending to denote an Order ; N.L. fem. pl. n. Sediminivales, the Sediminivita Order .
Family <i>Sediminivaceae</i>	Synonyms: JAUVRN01 Syllabication: Se.di.mi.ni.vi.ta'ce.ae Nomenclatural type: Sediminivita Etymology: N.L. fem. n. Sediminivita, referring to the type genus Sediminivita; -aceae, ending to denote a family; N.L. fem. pl. n. Sediminivaceae, the Sediminivita family.
Genus <i>Sediminivita</i>	Synonyms: DAIOGN01 Syllabication: Se.di.mi.ni.vi'ta Nomenclatural type: Sediminivita faecis Etymology: L. neut. n. sedimen, sediment; L. fem. n. vita, life; N.L. fem. n. Sediminivita, "life of sediment," referring to a genus of organisms associated with sedimentary habitats.

Species <i>Sediminivita faecis</i>	Synonyms: DAIOGN01 sp036745245 Syllabication: fae'cis Nomenclatural type: GCA_036745245.1 Etymology: L. gen. n. faecis, of sediment
Order <i>Aequorexudantales</i>	Synonyms: DG-27 Syllabication: Ae.quor.ex.u.dan.ta'les Nomenclatural type: Aequorexudans Etymology: N.L. fem. n. Aequorexudans, referring to the type genus Aequorexudans; –ales, ending to denote an Order ; N.L. fem. pl. n. Aequorexudantales, Order of the genus Aequorexudans.
Family <i>Aequorexudantaceae</i>	Synonyms: DG-27 Syllabication: Ae.quor.ex.u.dan.ta'ce.ae Nomenclatural type: Aequorexudans Etymology: N.L. fem. n. Aequorexudans, referring to the type genus Aequorexudans; –aceae, ending to denote a family; N.L. fem. pl. n. Aequorexudantaceae, family of the genus Aequorexudans.
Genus <i>Aequorexudans</i>	Synonyms: DG-27 Syllabication: Ae.quor.ex.u'dans Nomenclatural type: Aequorexudans gelidifontis Etymology: L. neut. n. aequor, the surface of the sea; L. fem. pres. part. exudans (from exudo), exuding/oozing; N.L. fem. n. Aequorixudans, exuding from the sea surface.
Species <i>Aequorexudans gelidifontis</i>	Synonyms: DG-27 sp030605835 Syllabication: ge.li.di.fon'tis Nomenclatural type: GCA_030605835.1 Etymology: L. masc. adj. gelidus, cold; L. masc. n. fons, spring; N.L. gen. n. gelidifontis, “of a cold spring,” referring to organism's origin from a marine cold seep.
Order <i>Speluncicultorales</i>	Synonyms: DSPP01 Syllabication: Spe.lun.ci.cul.to'ra.les Nomenclatural type: Speluncicultor Etymology: N.L. masc. n. Speluncicultor, referring to the type genus Speluncicultor; –ales, ending to denote an Order ; N.L. fem. pl. n. Speluncicultorales, Order of the genus Speluncicultor.

Family <i>Spelunciculoraceae</i>	Synonyms: DSPP01 Syllabication: Spe.lun.ci.cul'to.ra'ce.ae Nomenclatural type: Speluncicultor Etymology: N.L. masc. n. Speluncicultor, referring to the type genus Speluncicultor; –aceae, ending to denote a family; N.L. fem. pl. n. Spelunciculoraceae, family of the genus Speluncicultor.
Genus <i>Speluncicultor</i>	Synonyms: DSPP01 Syllabication: Spe.lun.ci.cul'tor Nomenclatural type: Speluncicultor specus Etymology: L. fem. n. spelunca, cave; L. masc. n. cultor, inhabitant, dweller; N.L. masc. n. Speluncicultor, a cave-dweller, referring to association with cave environments.
Species <i>Speluncicultor specus</i>	Synonyms: DSPP01 sp022614805 Syllabication: spe'cus Nomenclatural type: GCA_022614805.1 Etymology: L. gen. n. specus, “of a cave,” referring to organism's recovery from a cave gallery wall diverticulum.
Species <i>Speluncicultor arvi</i>	Synonyms: DSPP01 sp035574275 Syllabication: ar'vi Nomenclatural type: GCA_035574275.1 Etymology: L. gen. n. arvi, of a soil

Figures:

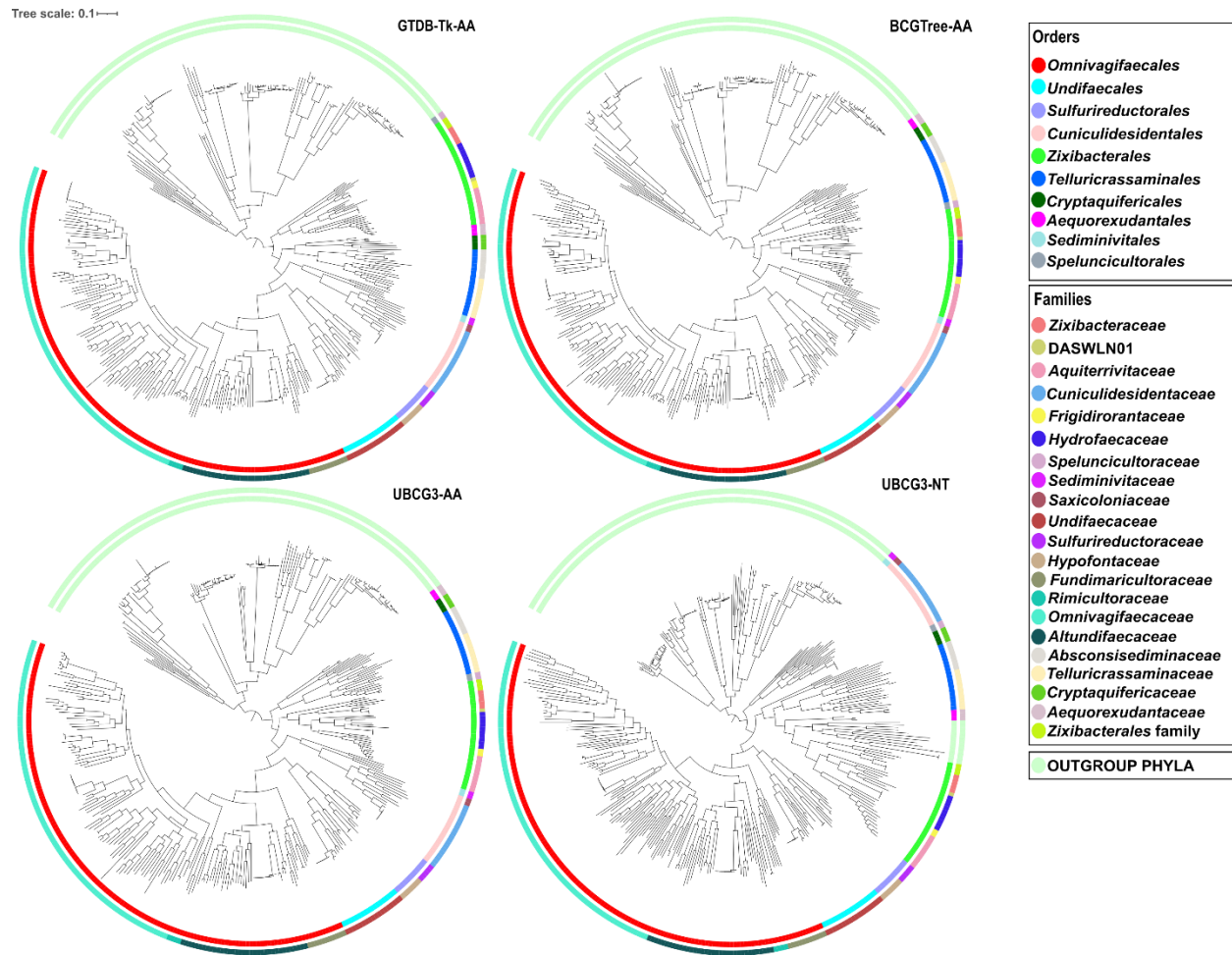


Figure 1. Maximum-likelihood phylogenetic trees based on four concatenated marker datasets. BCGTree, GTDB-Tk, UBCG3-AA, and UBCG3-NT labels indicate the phylogenomic pipeline and marker sets analyzed for resolving Order and family level diversity within the phylum “*Zixibacterota*”. Coloured strips indicate distinct lineages at the Order level (inner strip) and family level (outer strip), while outgroup phyla are combined and represented in light green.

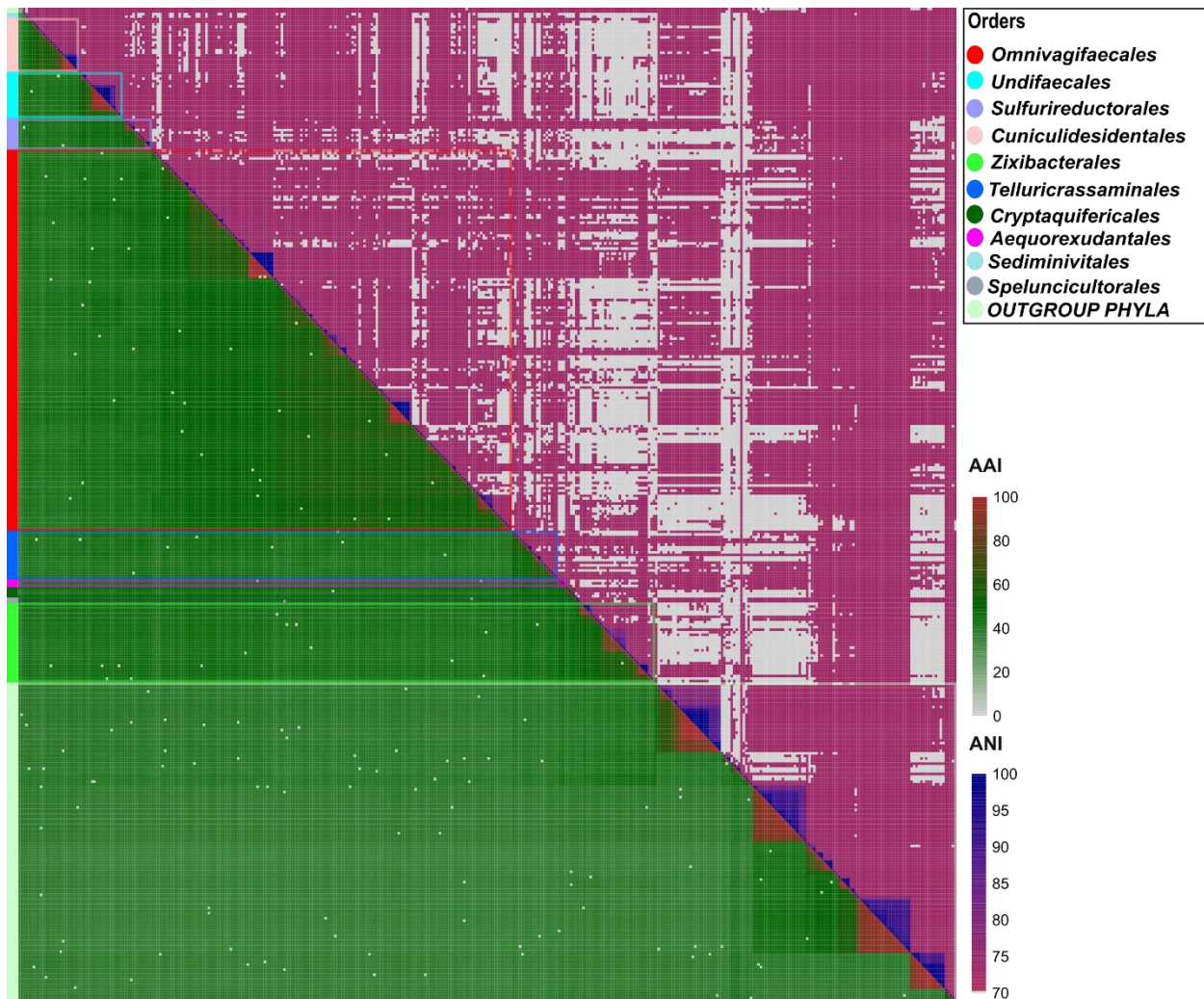


Figure 2. Pairwise ANI and AAI comparisons among Order s of “Zixibacterota” and outgroup phyla. The heatmap shows average nucleotide identity (ANI; top right triangle) and average amino acid identity (AAI; bottom left triangle) values calculated between representative genomes. Colours denote distinct Order -level lineages within “Zixibacterota”, whereas outgroup phyla are shown in a single colour.

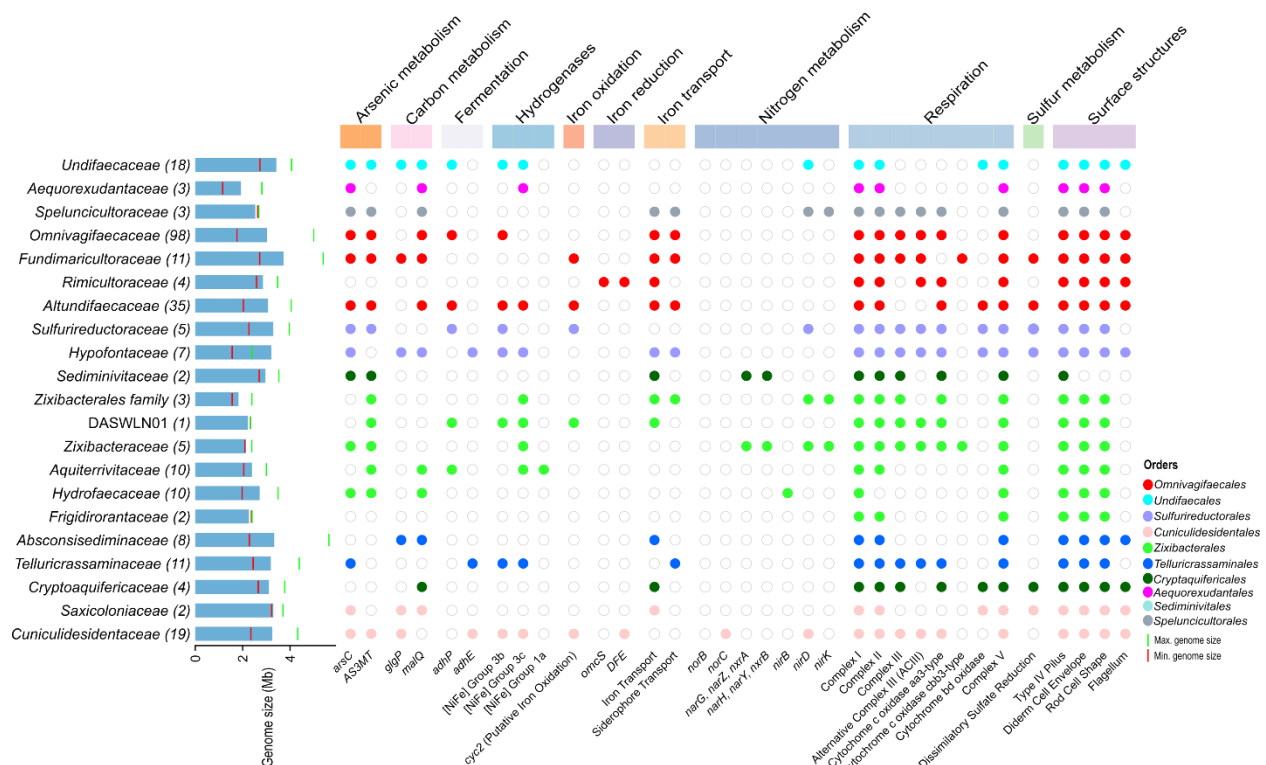


Figure 3. Predicted physiological and metabolic traits across the phylum "Zixibacterota". Presence or absence of genome-inferred traits is summarized at the family level using a majority-rule consensus (>50%) based on genomic analyses. Numbers in parentheses following family names indicate the number of genomes used for trait inference. Filled circles denote the presence of genes or pathways associated with the indicated metabolic trait, whereas empty circles indicate their absence. Families are ordered according to the phylogenomic classification presented in this study. The colour of each filled circle corresponds to the Order in which the trait is inferred to be present, as indicated in the legend. Abbreviations: *arsC*, arsenate reductase; *AS3MT*, arsenite methyltransferase; *glgP*, glycogen phosphorylase; *malQ*, 4- α -glucanotransferase; *adhP*, alcohol dehydrogenase; *adhE*, aldehyde-alcohol dehydrogenase; *cyc2*, Cyc2 cytochrome c; DFE, genes encoding a *Desulfovibrio ferrophilus*-like flavin-based extracellular electron transfer

complex involved in dissimilatory iron reduction; *norB*, nitric oxide reductase; *norC*, nitric oxide reductase cytochrome *c* subunit; *narG/narZ/nxrA*, nitrate reductase/nitrite oxidoreductase α subunit; *narH/narY/nxrB*, nitrate reductase/nitrite oxidoreductase β subunit; *nirB*, nitrite reductase (NADH) large subunit; *nirD*, nitrite reductase (NADH) small subunit; *nirK*, copper-containing nitrite reductase (NO-forming).

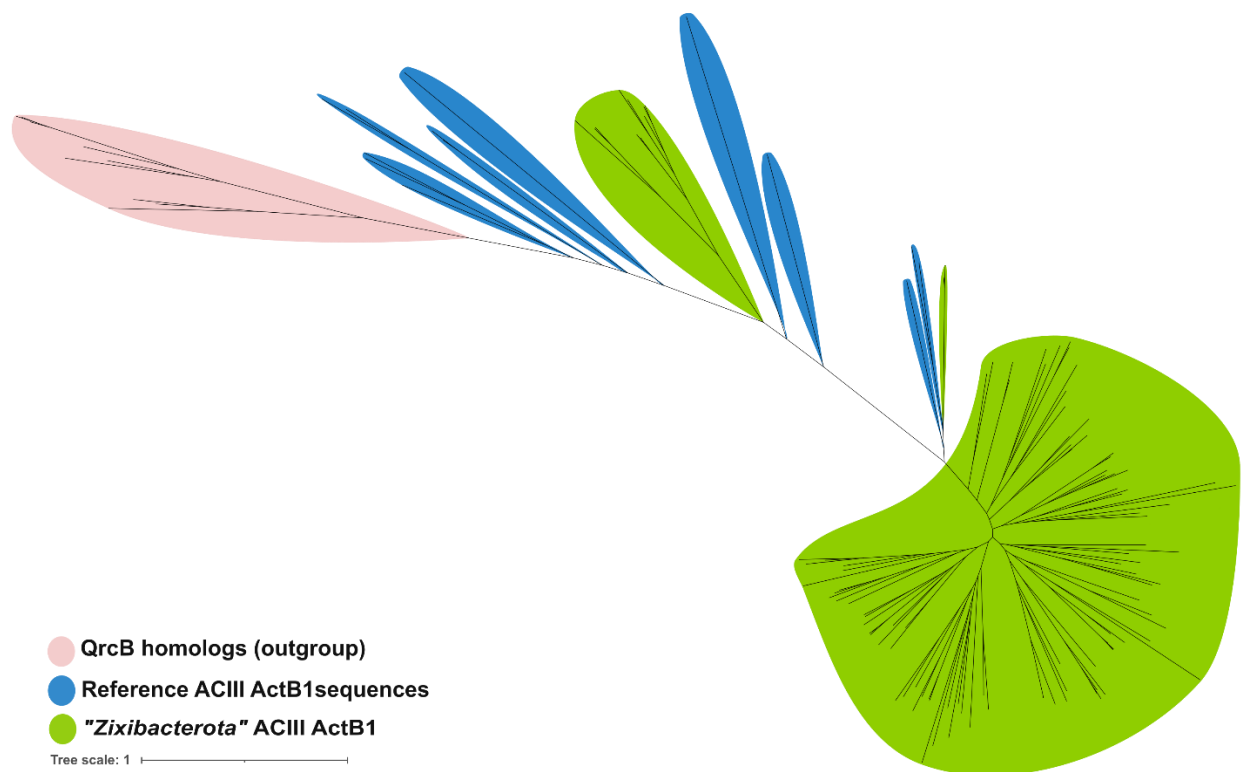


Figure 4. Phylogenetic analysis of the ActB1 catalytic domain from ACIII. Unrooted maximum-likelihood phylogeny of ActB1 sequences derived from "Zixibacterota" genomes and reference ACIII ActB proteins from diverse bacterial lineages. The QrcB homologs is used as an outgroup. Coloured branches indicate sequence origin, with "Zixibacterota" ActB1 sequences shown in green, reference ActB1 sequences in blue, and QrcB outgroup

sequences in pink. The clustering of “*Zixibacterota*” sequences within the ActB1 clade supports the presence of canonical ACIII complexes in these genomes.

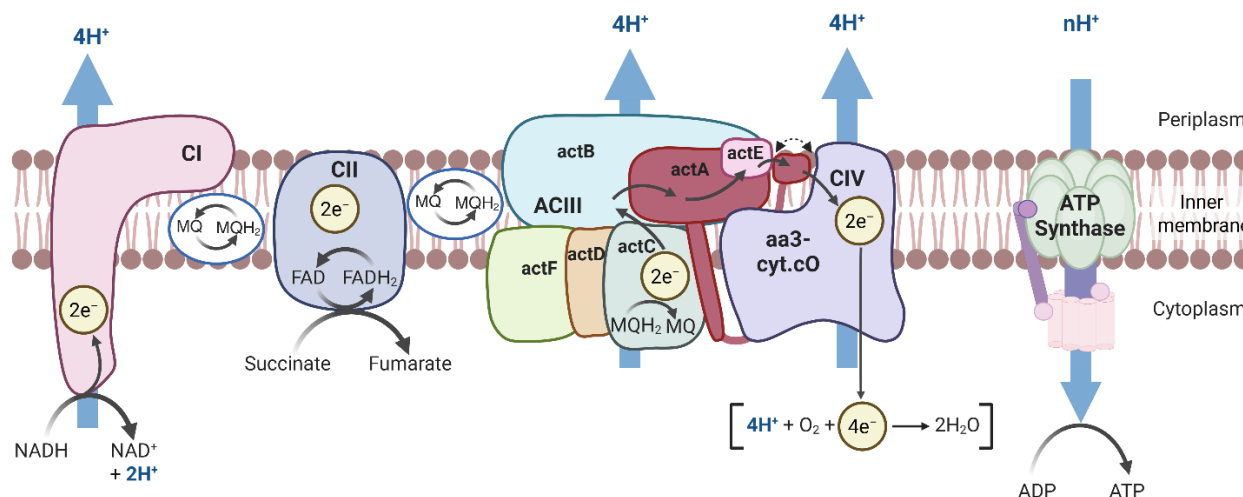


Figure 5. Model of respiratory electron transfer in “*Zixibacterota*” lineages encoding an ACIII–cytochrome aa₃ supercomplex. Electrons derived from NADH oxidation enter the membrane quinone pool through Complex I, reducing menaquinone (MQ → MQH₂), while additional electrons are supplied via Complex II during succinate oxidation. Reduced menaquinol is oxidized by Alternative Complex III (ACIII; ActABCDEF). Within ACIII, the ActC subunit is proposed to mediate MQH₂ oxidation, initiating electron transfer through the cytochrome chain from ActB to ActE. Electrons are subsequently transferred from the terminal heme of ActA to the adjacent cytochrome aa₃ oxidase (Complex IV) forming a putative ACIII–cytochrome aa₃ respiratory supercomplex, which catalyzes the reduction of molecular oxygen to water. The combined activities of Complex I, ACIII, and Complex IV are predicted to contribute to generation of the transmembrane proton motive force, which drives ATP synthesis via ATP synthase. Arrows indicate electron flow, while blue arrows

denote proton translocation across the membrane. This model is inferred from conserved genomic components identified in "*Zixibacterota*" genomes. The proposed electron transfer pathway within ACIII and its interaction with cytochrome aa_3 are adapted from the mechanistic model of Sun *et al.* (2018). Abbreviations: 'CI', Complex I (NADH:quinone oxidoreductase); 'CII', Complex II (succinate dehydrogenase); 'ACIII', Alternative Complex III; 'CIV', Complex IV; 'aa3-cyt.cO', cytochrome aa_3 oxidase; 'MQ', menaquinone; 'MQH₂', menaquinol.

References

1. Ankenbrand, M.J., and Keller, A. 2016. bcgTree: automatized phylogenetic tree building from bacterial core genomes. *Genome*. 59(10): 783–791.
2. Buchfink, B., Reuter, K., and Drost, H.G. 2021. Sensitive protein alignments at tree-of-life scale using DIAMOND. *Nat. Methods*. 18(4): 366–368.
3. Cantalapiedra, C.P., Hernández-Plaza, A., Letunic, I., Bork, P., and Huerta-Cepas, J. 2021. eggNOG-mapper v2: functional annotation, orthology assignments, and domain prediction at the metagenomic scale. *Mol. Biol. Evol.* 38(12): 5825–5829.
4. Capella-Gutiérrez, S., Silla-Martínez, J.M., and Gabaldón, T. 2009. trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics*. 25(15): 1972–1973.
5. Casar, C.P., Momper, L.M., Kruger, B.R., and Osburn, M.R. 2021. Iron-fueled life in the continental subsurface: deep mine microbial observatory, South Dakota, USA. *Appl. Environ. Microbiol.* 87(20): e00832-21.
6. Castelle, C.J., and Banfield, J.F. 2018. Major new microbial groups expand diversity and alter our understanding of the tree of life. *Cell* 172(6): 1181–1197.
7. Castelle, C.J., Hug, L.A., Wrighton, K.C., Thomas, B.C., Williams, K.H., Wu, D., Tringe, S.G., Singer, S.W., Eisen, J.A., and Banfield, J.F. 2013. Extraordinary phylogenetic diversity and metabolic versatility in aquifer sediment. *Nat. Commun.* 4: 2120.
8. Chan, P.P., Lin, B.Y., Mak, A.J., and Lowe, T.M. 2021. tRNAscan-SE 2.0: improved detection and functional classification of transfer RNA genes. *Nucleic Acids Res.* 49(16): 9077–9096.

9. Chaumeil, P.A., Mussig, A.J., Hugenholtz, P., and Parks, D.H. 2022. GTDB-Tk v2: memory friendly classification with the genome taxonomy database. *Bioinformatics*. 38(23): 5315–5316.
10. Chklovski, A., Parks, D.H., Woodcroft, B.J., and Tyson, G.W. 2023. CheckM2: a rapid, scalable and accurate tool for assessing microbial genome quality using machine learning. *Nat. Methods*. 20(8): 1203–1212.
11. Darriba, D., Taboada, G.L., Doallo, R., and Posada, D. 2011. ProtTest-HP: fast selection of best-fit models of protein evolution. *Bioinformatics*. 27(8): 1164–1165.
12. Deng, C., Chen, T., Qiu, Z., Zhou, H., Li, B., Zhang, Y., Xu, X., Lian, C., Qiao, X., and Yu, K. 2024. A mixed blessing of influent leachate microbes in downstream biotreatment systems of a full-scale landfill leachate treatment plant. *Water Res*. 253: 121310.
13. Du, H., Pan, J., Zou, D., Huang, Y., Liu, Y., and Li, M. 2022. Microbial active functional modules derived from network analysis and metabolic interactions decipher the complex microbiome assembly in mangrove sediments. *Microbiome* 10: 224.
14. Ernster, N.M., and Rodriguez-R, L.M. 2025. A practical guide on environmental genomics for prokaryotic systematics. *Syst. Appl. Microbiol*. 48(5): 126643.
15. Finn, R.D., Clements, J., and Eddy, S.R. 2011. HMMER web server: interactive sequence similarity searching. *Nucleic Acids Res*. 39(suppl_2): W29–W37.
16. Fu, L., Niu, B., Zhu, Z., Wu, S., and Li, W. 2012. CD-HIT: accelerated for clustering the next-generation sequencing data. *Bioinformatics*. 28(23): 3150–3152.
17. Garber, A.I., Nealson, K.H., Okamoto, A., McAllister, S.M., Chan, C.S., Barco, R.A., and Merino, N. 2020. FeGenie: a comprehensive tool for the identification of iron

genes and iron gene neighborhoods in genome and metagenome assemblies. *Front. Microbiol.* 11: 499513.

18. Goh, Y.K., Zoqratt, M.Z.H.M., Ayub, Q., and Ting, A.S.Y. 2022. Discovering naturally-occurring microbiota in disease suppressive soil: potential role of biological elements in suppressing *Ganoderma boninense*. *Biol. Control* 165: 104787.
19. Hedlund, B.P., Chuvochina, M., Hugenholtz, P., Konstantinidis, K.T., Murray, A.E., Palmer, M., Parks, D.H., Probst, A.J., Reysenbach, A.L., Rodriguez-R, L.M., and Rossello-Mora, R. 2022. SeqCode: a nomenclatural code for prokaryotes described from sequence data. *Nat. Microbiol.* 7(10): 1702–1708.
20. Hedlund, B.P., Dodsworth, J.A., and Staley, J.T. 2015. The changing landscape of microbial biodiversity exploration and its implications for systematics. *Syst. Appl. Microbiol.* 38(4): 231–236.
21. Hillyer, K.E., Raes, E., Bissett, A., and Beale, D.J. 2023. Multi-omics eco-surveillance of bacterial community function in legacy contaminated estuary sediments. *Environ. Pollut.* 318: 120857.
22. Hoang, D.T., Chernomor, O., Von Haeseler, A., Minh, B.Q., and Vinh, L.S. 2018. UFBoot2: improving the ultrafast bootstrap approximation. *Mol. Biol. Evol.* 35(2): 518–522.
23. Hyatt, D., Chen, G.L., LoCascio, P.F., Land, M.L., Larimer, F.W., and Hauser, L.J. 2010. Prodigal: prokaryotic gene recognition and translation initiation site identification. *BMC Bioinformatics* 11(1): 119.

24. Iqbal, S., Begum, F., Ullah, I., Jalal, N., and Shaw, P. 2025. Peeling off the layers from microbial dark matter (MDM): recent advances, future challenges, and opportunities. *Crit. Rev. Microbiol.* 51(1): 1–21.
25. Jain, C., Rodriguez-R, L.M., Phillippy, A.M., Konstantinidis, K.T., and Aluru, S. 2018. High throughput ANI analysis of 90K prokaryotic genomes reveals clear species boundaries. *Nat. Commun.* 9: 5114.
26. Jiao, J.Y., Liu, L., Hua, Z.S., Fang, B.Z., Zhou, E.M., Salam, N., Hedlund, B.P., and Li, W.J. 2021. Microbial dark matter coming to light: challenges and opportunities. *Nat. Sci. Rev.* 8(3): nwaa280.
27. Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., Von Haeseler, A., and Jermini, L.S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat. Methods* 14(6): 587–595.
28. Kanehisa, M., Sato, Y., and Kawashima, M. 2022. KEGG mapping tools for uncovering hidden features in biological data. *Protein Sci.* 31(1): 47–53.
29. Katoh, K., and Standley, D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30(4): 772–780.
30. Kim, J., Na, S.I., Kim, D., and Chun, J. 2021. UBCG2: up-to-date bacterial core genes and pipeline for phylogenomic analysis. *J. Microbiol.* 59(6): 609–615.
31. Kolde, R. 2019. pheatmap: pretty heatmaps. R package version 1.0.12.

32. Kück, P., and Longo, G.C. 2014. FASconCAT-G: extensive functions for multiple sequence alignment preparations concerning phylogenetic studies. *Front. Zool.* 11: 81.
33. Li, Z., Wei, T., He, L., Qian, H., Zhu, Y.G., and Wang, Y. 2025. Genomic potential for mercury biotransformation in marine sediments across marginal slope to hadal zone. *Nat. Commun.* 16: 8655.
34. Liu, S., Hu, R., Peng, N., Zhou, Z., Chen, R., He, Z., and Wang, C. 2023. Phylogenetic and ecophysiological novelty of subsurface mercury methylators in mangrove sediments. *ISME J.* 17(12): 2313–2325.
35. Liu, S., Hu, R., Peng, N., Zhou, Z., Chen, R., He, Z., and Wang, C. 2023. Phylogenetic and ecophysiological novelty of subsurface mercury methylators in mangrove sediments. *ISME J.* 17(12): 2313–2325.
36. Lopez, P., Casane, D., and Philippe, H. 2002. Heterotachy, an important process of protein evolution. *Mol. Biol. Evol.* 19(1): 1–7.
37. Majumder, E.L., King, J.D., and Blankenship, R.E. 2013. Alternative complex III from phototrophic bacteria and its electron acceptor auracyanin. *Biochim. Biophys. Acta Bioenerg.* 1827(11–12): 1383–1391.
38. Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A., and Lanfear, R. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Mol. Biol. Evol.* 37(5): 1530–1534.
39. O’Leary, N.A., Cox, E., Holmes, J.B., Anderson, W.R., Falk, R., Hem, V., Tsuchiya, M.T., Schuler, G.D., Zhang, X., Torcivia, J., and Ketter, A. 2024. Exploring and retrieving

sequence and metadata for species across the tree of life with NCBI Datasets. *Sci. Data*. 11(1): 732.

40. Pan, W., Zhou, Y., Xie, H., Liang, L., Zou, G., Du, L., and Guo, X. 2024. Plant and microbial response in constructed wetland treating tetracycline antibiotic polluted water: evaluating the effects of microplastic size and concentration. *Chemosphere* 353: 141553.
41. Paradis, E., Blomberg, S.P., Bolker, B., Brown, J., Claude, J., Cuong, H.S., Desper, R., and Didier, G. 2019. ape: analyses of phylogenetics and evolution. R package.
42. Parks, D.H., Chuvochina, M., Rinke, C., Mussig, A.J., Chaumeil, P.A., and Hugenholtz, P. 2022. GTDB: an ongoing census of bacterial and archaeal diversity through a phylogenetically consistent, rank normalized and complete genome-based taxonomy. *Nucleic Acids Res.* 50(D1): D785–D794.
43. Prasoodanan, Pk V., Maistrenko, O.M., Fullam, A., Mende, D.R., Kartal, E., Coelho, L.P., Spang, A., Bork, P., and Schmidt, T.S. 2026. Unbinned contigs expand known diversity in the global microbiome. *Nat. Microbiol.* 2026: 1–3.
44. Pruesse, E., Peplies, J., and Glöckner, F.O. 2012. SINA: accurate high-throughput multiple sequence alignment of ribosomal RNA genes. *Bioinformatics*. 28(14): 1823–1829.
45. Quinlan, A.R., and Hall, I.M. 2010. BEDTools: a flexible suite of utilities for comparing genomic features. *Bioinformatics*. 26(6): 841–842.

46. Refojo, P.N., Teixeira, M., and Pereira, M.M. 2012. The alternative complex III: properties and possible mechanisms for electron transfer and energy conservation. *Biochim. Biophys. Acta Bioenerg.* 1817(10): 1852–1859.
47. Rodriguez-R, L.M., and Konstantinidis, K.T. 2016. The enveomics collection: a toolbox for specialized analyses of microbial genomes and metagenomes. *PeerJ Preprints.* e1900v1.
48. Rozewicki, J., Li, S., Amada, K.M., Standley, D.M., and Katoh, K. 2019. MAFFT-DASH: integrated protein sequence and structural alignment. *Nucleic Acids Res.* 47(W1): W5–W10.
49. Savvichev, A.S., Rusanov, I.I., Kadnikov, V.V., Beletsky, A.V., Zakcharova, E.E., Samylina, O.S., Sigalevich, P.A., Semiletov, I.P., Ravin, N.V., and Pimenov, N.V. 2023. Biogeochemical activity of methane-related microbial communities in bottom sediments of cold seeps of the Laptev Sea. *Microorganisms* 11(2): 250.
50. Schliep, K.P. 2011. phangorn: phylogenetic analysis in R. *Bioinformatics.* 27(4): 592–593.
51. Seemann, T. 2013. barrnap 0.3: bacterial/archaeal ribosomal RNA predictor.
52. Seemann, T. 2014. Prokka: rapid prokaryotic genome annotation. *Bioinformatics* 30(14): 2068–2069.
53. Shen, W., Le, S., Li, Y., and Hu, F. 2016. SeqKit: a cross-platform and ultrafast toolkit for FASTA/Q file manipulation. *PLoS ONE.* 11(10): e0163962.
54. Shimodaira, H., and Hasegawa, M. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Mol. Biol. Evol.* 16(8): 1114–.

55. Søndergaard, D., Pedersen, C.N., and Greening, C. 2016. HydDB: a web tool for hydrogenase classification and analysis. *Sci. Rep.* 6: 34212.
56. Tamura, K., and Nei, M. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.* 10(3): 512–526.
57. Venceslau, S.S., Lino, R.R., and Pereira, I.A. 2010. The Qrc membrane complex, related to the alternative complex III, is a menaquinone reductase involved in sulfate respiration. *J. Biol. Chem.* 285(30): 22774–22783.
58. Wilgenbusch, J.C., and Swofford, D. 2003. Inferring evolutionary trees with PAUP. *Curr. Protoc. Bioinformatics.* 1: 6.4.
59. Wong, H.L., MacLeod, F.I., White III, R.A., Visscher, P.T., and Burns, B.P. 2020. Microbial dark matter filling the niche in hypersaline microbial mats. *Microbiome* 8: 135.
60. Yan, B., Jiang, L., Zhou, H., Atakpa, E.O., Bo, K., Li, P., Xie, Q., Li, Y., and Zhang, C. 2023. Performance and microbial community analysis of combined bioreactors in treating high-salinity hydraulic fracturing flowback and produced water. *Bioresour. Technol.* 386: 129469.
61. Ye, Y.L., Ma, K.J., Fu, Y.H., Wu, Z.C., Fu, G.Y., Sun, C., and Xu, X.W. 2023. The heterogeneity of microbial diversity and its drivers in two types of sediments from tidal flats in Beibu Gulf, China. *Front. Mar. Sci.* 10: 1256393.
62. Zang, H., Tong, X., Yuan, L., Zhang, Y., Zhang, R., Li, M., and Zhu, R. (no year given). A possible mechanism for selenium hyperaccumulation: selenium-induced

recruitment of specific rhizobiome and endophytes in *Cardamine hupingshanensis*. SSRN 4237119.

63. Zhang, H., Zhao, D., Wu, Q.L., and Zeng, J. 2025. Environment selected microbial function rather than taxonomic species in a plateau saline-alkaline wetland. Appl. Environ. Microbiol. 91(7): e02206-24.
64. Zhang, Z., Wan, J., Ye, G., Wang, Y., Bai, Y., and Yan, Z. 2025. Effects of salinity and betaine addition on anaerobic granular sludge properties and microbial community succession patterns in organic saline wastewater. J. Environ. Sci. 147: 310–321.
65. Zhao, L., Yan, J., Luo, L., Zhang, H., Shi, J., and Wang, D. 2022. Effects of different fertilization methods on soil microbial community and diversity and crop yield in a sweet potato field.
66. Zhao, L., Yan, J., Luo, L., Zhang, H., Shi, J., and Wang, D. 2022. Effects of different fertilization methods on soil microbial community and diversity and crop yield in a sweet potato field.
67. Zhong, Y.W., Zhou, P., Cheng, H., Zhou, Y.D., Pan, J., Xu, L., Li, M., Tao, C.H., Wu, Y.H., and Xu, X.W. 2022. Metagenomic features characterized with microbial iron oxidoreduction and mineral interaction in southwest Indian ridge. Microbiol. Spectr. 10(6): e00614-22.
68. Zhu, Y., Wang, H., Li, J., Wang, Z., and Wang, Y. 2024. Metabolic profiles and microbial synergy mechanism of anammox biomass enrichment and membrane fouling alleviation in the anammox dynamic membrane bioreactor. Environ. Sci. Technol. 58(14): 6284–6295.

69. Zinke, L.A., Glombitza, C., Bird, J.T., Røy, H., Jørgensen, B.B., Lloyd, K.G., Amend, J.P., and Reese, B.K. 2019. Microbial organic matter degradation potential in Baltic Sea sediments is influenced by depositional conditions and in situ geochemistry. *Appl. Environ. Microbiol.* 85(4): e02164-18.

Chapter 4: Conclusion

This thesis addressed two major gaps in our understanding of the bacterial phylum "*Zixibacterota*": the absence of a taxonomic framework and the limited knowledge of metabolic diversity across the lineage. Together, the data compiled in this work provide both a stable taxonomic foundation and a broad view of the ecological and metabolic diversity of the phylum.

"*Zixibacterota*" is a deeply branching and globally distributed bacterial lineage known almost exclusively from metagenome-derived genomes. Since its initial discovery as the "RBG-1" lineage in Colorado River aquifer sediments, members of the phylum have been detected in a wide range of aquatic, terrestrial, and subsurface environments (Castelle et al., 2013). Despite this broad distribution, the lineage lacked nomenclatural standing and remained taxonomically unresolved. This reflected a broader challenge in microbial systematics, where most uncultivated prokaryotic diversity falls outside the scope of traditional nomenclatural frameworks (Palmer et al., 2022).

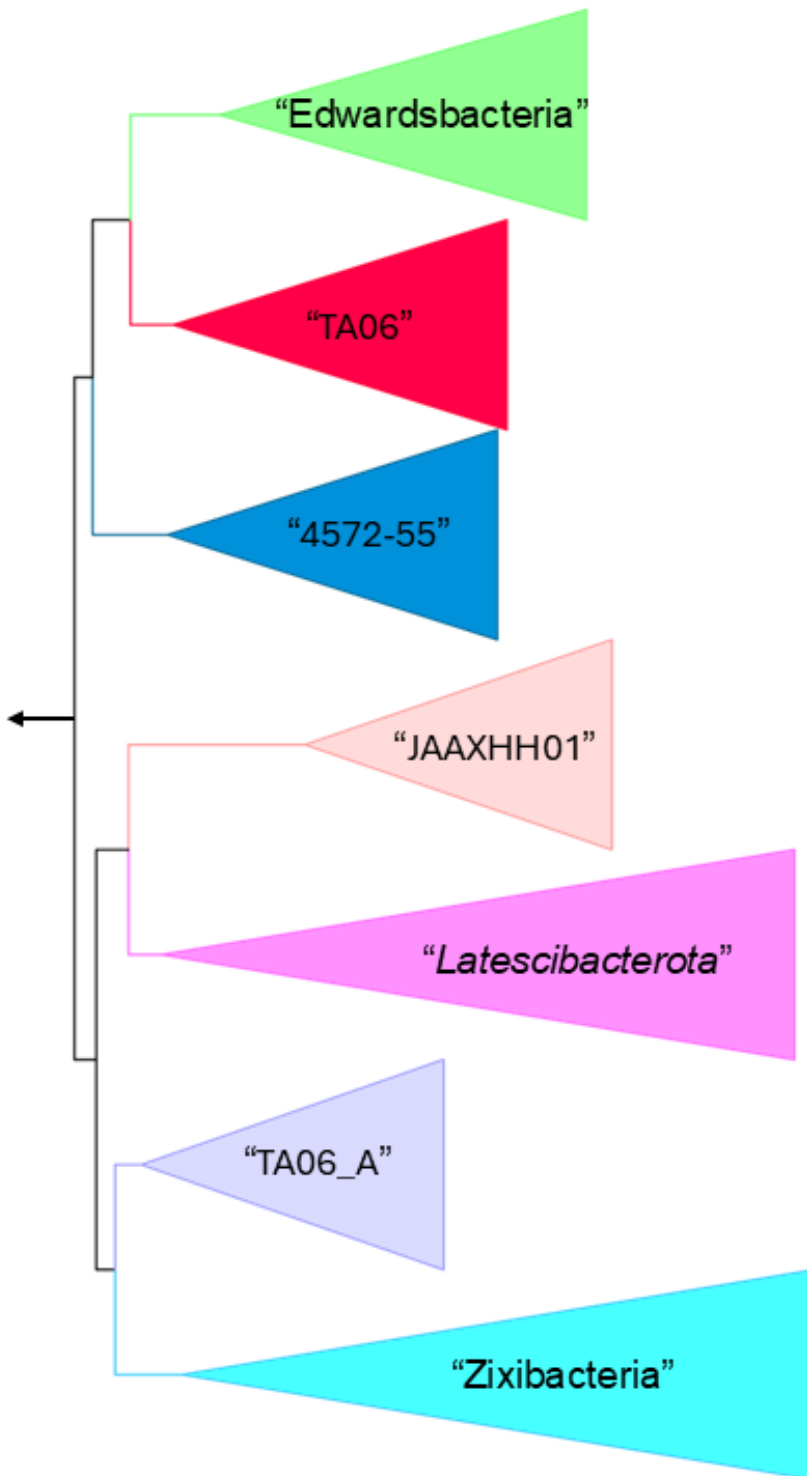
The research component of this thesis addressed this challenge by establishing the first genome-based taxonomy for "*Zixibacterota*". Phylogenomic analyses based on three complementary bacterial marker sets consistently recovered the phylum as a monophyletic lineage. The resulting classification includes 1 class, 10 Orders, 21 families, 109 genera, and 210 species. Names are proposed for the phylum and its major subordinate taxa, providing the first stable and citable nomenclature for this lineage.

Comparative genomic analyses further revealed that "*Zixibacterota*" possess a conserved physiological core alongside extensive metabolic diversification. Most genomes encoded a diderm cell envelope, heterotrophic oxidative metabolism, and a core respiratory component, suggesting these traits represent the ancestral physiological framework of the phylum. In contrast, traits such as terminal oxidase repertoires, Alternative Complex III distribution, sulfate reduction, iron redox potential, hydrogen metabolism, and polysaccharide degradation capacities exhibited strong phylogenetic structuring. These patterns indicate that diversification within the phylum has occurred through repeated adaptation to distinct ecological niches.

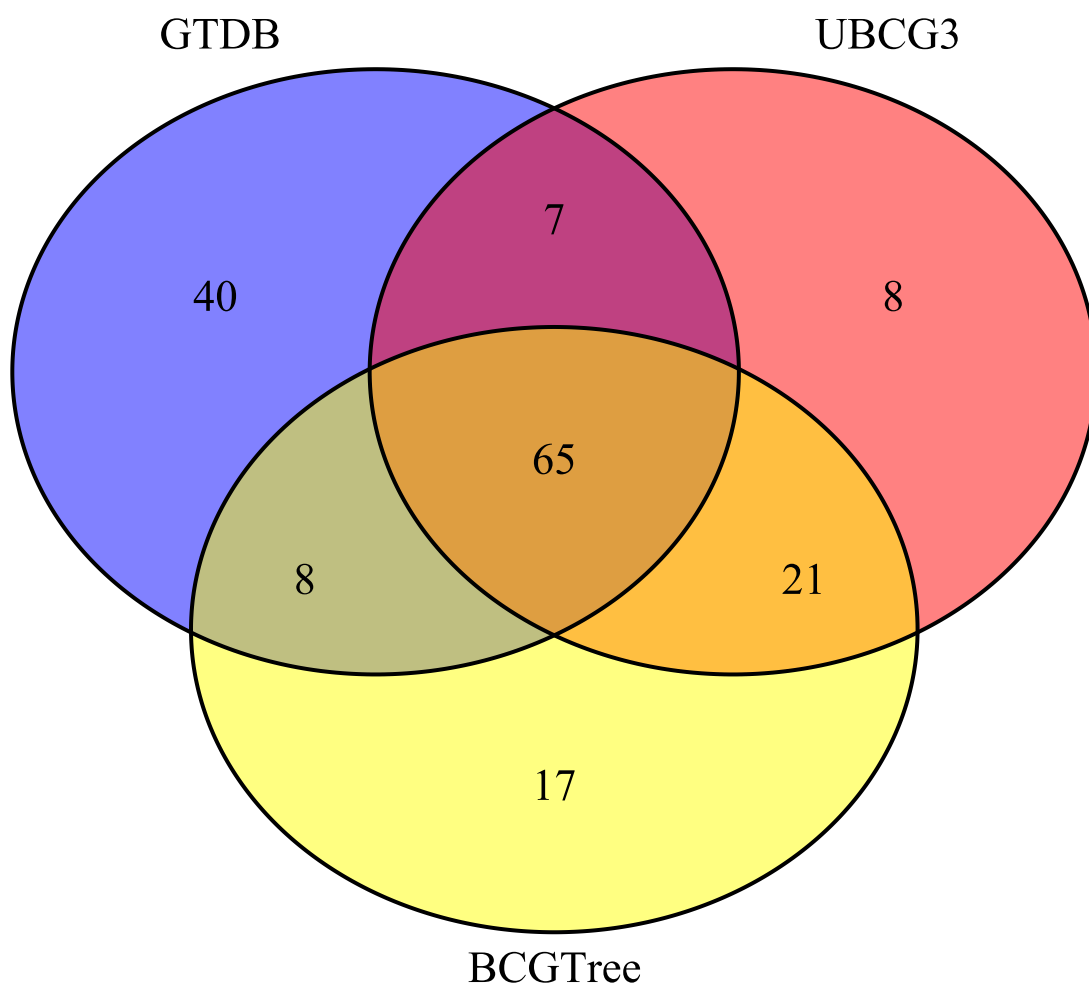
Although this study substantially expands our understanding of "*Zixibacterota*", several questions remain. Functional predictions, including those related to ACIII-aa₃ respiratory coupling, Cyc2-associated iron redox processes, and syntrophic alcohol metabolism, require experimental validation. Additional high-quality genomes and cultivation efforts will further refine our understanding of metabolic evolution within the phylum and help resolve the ecological roles of individual lineages.

Overall, this thesis demonstrates how genome-resolved approaches combined with sequence-based nomenclature can accelerate the characterization of previously inaccessible microbial diversity. The results show that "*Zixibacterota*" are not a metabolically generalised group, but rather a diverse radiation that has adapted to a wide range of chemically distinct environments. The taxonomic and metabolic framework established here provides a foundation for future studies of the ecology, evolution, and biogeochemical significance of this previously understudied bacterial phylum.

Appendix I: Supplementary Figures



Supplementary figure 1. Phylogenetic placement of “*Zixibacterota*” and closely related outgroup phyla inferred using the GTDB-Tk *classify* workflow.

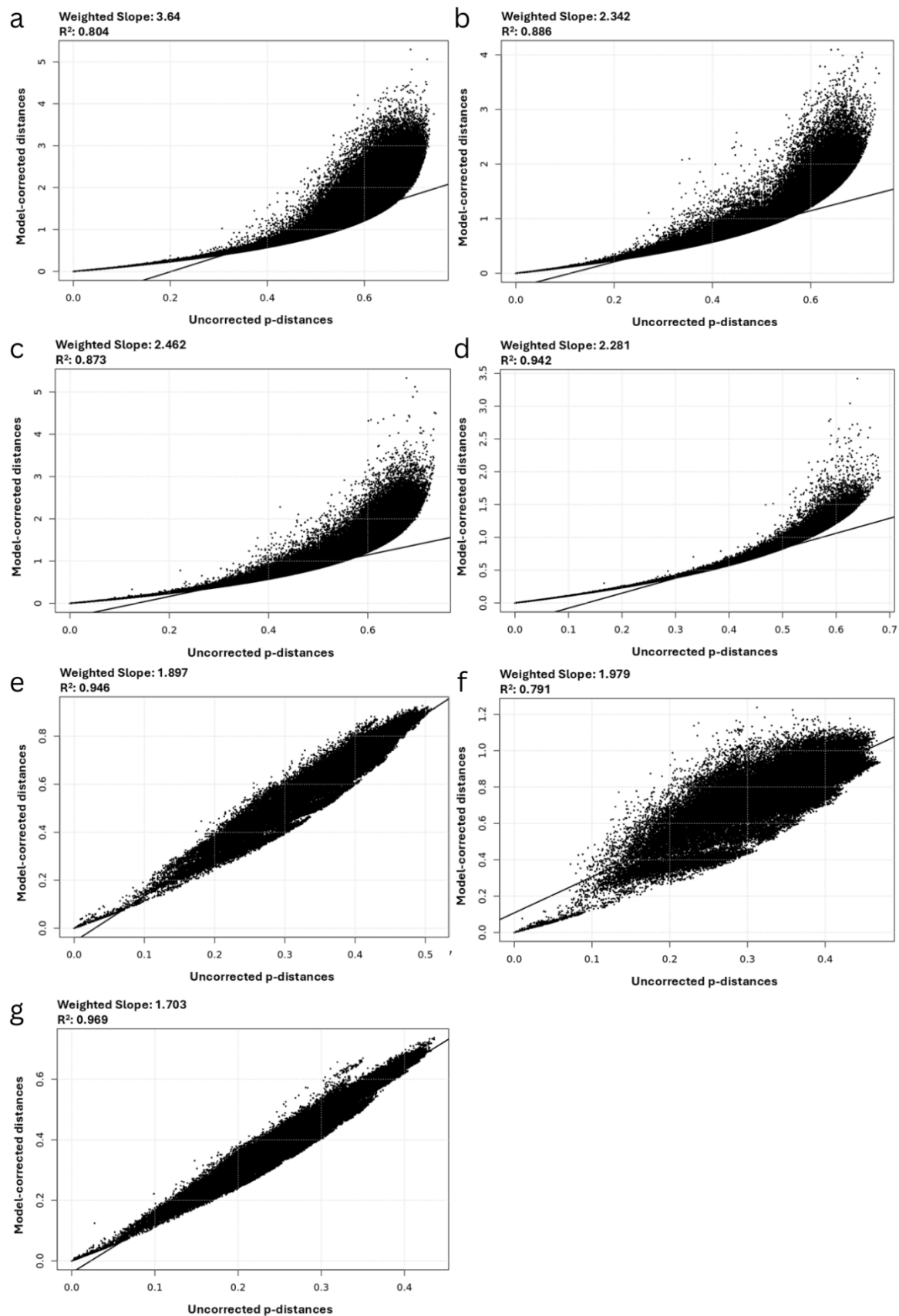


Supplementary figure 2. Venn diagram illustrating the overlap and uniqueness of marker genes among the GTDB-Tk, UBCG3, and BcgTree marker sets.

Tree scale: 1



Supplementary figure 3. Maximum-likelihood phylogeny of 16S rRNA gene sequences from the phylum "*Zixibacterota*" and closely related bacterial phyla. The tree was reconstructed from aligned 16S rRNA gene sequences to examine the phylogenetic placement of "*Zixibacterota*". Branch lengths are proportional to the estimated number of substitutions per site.



Supplementary figure 4. Substitution saturation plots. Saturation analyses of the UBCG3 nucleotide dataset showing third (a), second (b), and first (c) codon positions, along with the combined dataset using length-weighted regression (d). Uncorrected p-distances are shown on the x-axis and TN93 model-corrected distances on the y-axis. The slopes of the linear regression lines are 3.640, 2.342, 2.462, and 2.281 with corresponding R^2 values of 0.804, 0.886, 0.873, and 0.942, respectively. Saturation plots for the UBCG3-AA (e), GTDB-AA bac120 (f), and BCGTree-AA (g) amino acid datasets are also shown. Uncorrected p-distances are plotted on the x-axis and model-corrected distances (using partition-specific substitution models) on the y-axis. The slopes of the regression lines are 1.897, 1.979, and 1.703 with corresponding R^2 values of 0.946, 0.791, and 0.969, respectively.