

Opinion

Microbial Taxonomy Run Amok

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DNA sequencing has led to an explosion in discovery of microbial phylogenetic novelty, especially that represented by uncultivated taxa, to which the traditional system of prokaryotic taxonomy has not adapted. A lack of expansion of the International Code of Nomenclature of Prokaryotes (ICNP, 'the Code') to effectively capture this information has created a 'wild west' situation where names are published or appear in popular reference databases without further verification or validation. The rapid propagation of variant and questionable naming methods has led to widespread confusion and undermines prior accomplishments. We exemplify inconsistencies that have arisen from this practice and endanger the interoperability of scientific findings. The immediate solution to this problem is to develop and adopt universal best practices that are accepted by expert researchers, major publishers, the International Committee on Systematics of Prokaryotes (ICSP), and international microbiological societies.

DNA-Based Discovery of Microbial Phylogenetic Novelty Outpaces Traditional Prokaryotic Taxonomy

Scientific inquiry in the microbial sciences relies frequently on interpreting an enormous amount of DNA and RNA sequence information [1,2]. One of the most significant research areas that has blossomed due to next-generation sequencing technologies is the study of diverse natural microbial communities and their uncultivated taxa. Large metagenomic DNA sequence datasets can be assembled and then binned, using bioinformatic techniques, into **metagenome-assembled genomes (MAGs)** (see [Glossary](#)) [3]. Similarly, sequences obtained from **single-amplified genomes (SAGs)**, generated from microbial cells physically separated from their environment [4], can be analyzed using bioinformatic tools. A meaningful analysis of sequence datasets requires determination of the taxonomic composition of the genomes of the sample under study. To make taxonomic assignments, the analyses of these datasets either focus on a single **phylogenetic marker** (e.g., the 16S rRNA gene) or a suite of universally conserved genes with taxonomic information [5]. Curated nucleic acid **sequence databases** have been developed for this purpose – for example, the Ribosomal Database Project (RDP) [6], Greengenes [7], and SILVA for 16S rRNA genes [8], and the Genome Taxonomy Database (GTDB) [9], the EZBioCloud [10], and the National Center for Biotechnology Information (NCBI) taxonomy [11,12] for genomes, MAGs and SAGs. The RDP assignments are primarily based on the available taxonomy of 16S rRNA gene sequences representing cultured organisms following taxonomic roadmaps outlined in the 2015 edition of *Bergey's Manual of Systematics of Archaea and Bacteria* [13], and secondarily, a few well studied uncultured groups. Both the SILVA database and the GTDB include nomenclature proposed by individual researchers based on DNA sequences of uncultured as well as cultured taxa.

Traditional prokaryotic **taxonomy** relies on cultivation and in-depth characterization of **axenic cultures** in order to group them at the appropriate taxonomic rank, that is, species or genus (i.e., the **classification** component of taxonomy), followed by naming of the isolate(s) (i.e., the nomenclature component of taxonomy) according to the rules set by the **International Code**

Highlights

Traditional polyphasic taxonomy has been the gold standard for classifying microbes but modern DNA sequencing technology unravels microbial phylogenetic novelty at an unprecedented pace, to which the current framework of nomenclature (the International Code of Nomenclature of Prokaryotes –[the ICNP, 'the Code']) has not yet adapted.

Traditional and modern approaches operate in parallel and are often practiced by largely different scientific communities, resulting in redundant, often conflicting, nomenclature.

The lack of a unified nomenclature framework, which could be established under a modified Code, has led to a 'wild west' situation in which unvalidated names appear in taxonomic databases and are then adopted by researchers without the effort or background to critique them.

The current practice endangers the interoperability of scientific findings because of disagreement between taxonomic databases, inconsistencies with the peer-reviewed literature, proliferation of synonyms resulting from improper naming of taxa, and the naming of taxa with no reference in the literature at all.

The global research community is in desperate need of a unified approach, and 'chaos will reign until unity is found'.

Potential immediate solutions to the nomenclature quandary include the expansion of the Code to uncultivated and fastidious taxa, often represented only by DNA sequences, and adjustments to the process of publishing proposals for new names and name changes, for example, by creating a new process allowing the research community to critique proposals for new names and/or name changes before names that are included in a Validation List. Database curators should refrain from adopting any proposed new names or new

of Nomenclature of Prokaryotes (ICNP, 'the Code') [14,15], and description of diagnostic features (phenotypes) (i.e., the identification component of taxonomy). The **International Committee on Systematics of Prokaryotes (ICSP)**, a part of the Bacteriology and Applied Microbiology (BAM) Division of the International Union of Microbiological Societies (IUMS) (Figure 1), oversees the Code. The Code's rules include stringent guidelines for introducing new, or revising existing, **nomenclature**, which is directly connected to taxonomy since names must be consistent with taxonomic groupings. Following publication of new or revised names in any reputable scientific outlet (i.e., effective publication), the **List Editors** of the *International Journal of Systematic and Evolutionary Microbiology (IJSEM)* review new nomenclature and prepare a **Validation List** published in IJSEM every 2 months [16]. Inclusion in the Validation List validates the published names (i.e., valid publication) and gives them a 'standing in nomenclature' status [16,17]. Names that do not comply with the Code are not validated, although they could still be used by the scientific community since they are effectively published (Figure 1). Such cases, although far from ideal, are not uncommon. Validly and effectively published names are rapidly included in the **List of Prokaryotic Names with Standing in Nomenclature (LPSN; <https://lpsn.dsmz.de>)**, an independent database and valuable resource for information about nomenclature [18–20].

names overwriting existing nomenclature prior to their inclusion in the Validation List published in the *International Journal of Systematic and Evolutionary Microbiology (IJSEM)*.

Over the past three decades or so, the system of rules laid out in the Code has provided a robust nomenclature framework of isolated organisms facilitating research, communication, and policy around the globe. This traditional system is challenged to accommodate an increasing number of sequences that lack cultured representatives, and names that are coined outside the bounds of the Code [21,22]. To accommodate uncultured taxa, the provisional status **Candidatus** was introduced [23]; however, the Code does not give *Candidatus* taxa standing in the nomenclature, and *Candidatus* names can be overwritten following characterization and publication of a representative isolate. Further, formal descriptions of *Candidatus* taxa require distinctive morphological and/or phenotypic characteristics that are not available for the majority of uncultured taxa [23]. Accordingly, only about 1000 *Candidatus* taxa have been reported in the literature [24], and the current approach cannot scale with the pace that phylogenetic diversity of uncultured taxa is being revealed [21,22]. Naming **uncultured (uncultivated) taxa** is, however, justified, since the sequences belong to real organisms that must be categorized and named in order to be studied efficiently.

MAGs and 16S rRNA gene amplicons representing uncultured taxa often dominate both the diversity and abundance of microbial cells in environmental samples [1,2,25]. Furthermore, a number of organisms can be grown in the laboratory but are either fastidious, such as the highly abundant ocean microbe SAR11 [26], or depend on intricate syntrophic interactions, such as the anaerobic methanotrophs ANME-1 [27] or the specialized anaerobes that metabolize dichloromethane [28,29]. Even though these organisms are technically cultured, axenic cultures are not available for deposition in two independent culture collections, which is a prerequisite for validly naming such taxa based on the rules of the Code that anchor microbial nomenclature [14]. Recently, the ICSP voted down a proposed amendment to the Code to include genetic material from uncultured organisms or cultured organisms not available in axenic culture as type material [30]. This lack of inclusion of uncultivated taxa and fastidious growers in the Code has resulted in less centralized approaches for developing a robust nomenclature for these organisms. Proposals for applying nomenclature rules specified in the Code to uncultured organisms represented by SAGs or MAGs have been put forward [21,22,31,32], but none of them has yet been adopted, leaving current research in limbo between competing nomenclatures.

The GTDB has developed a new taxonomy based on relative evolutionary distance (RED) scores of high-quality genomes, with the main goal of establishing groupings of taxa at the same rank

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across the bacterial and archaeal domains that encompass similar intra-rank evolutionary diversity [9]. The GTDB includes names of uncultured organisms that are given, *ad hoc*, by scientists, with little, or commonly no, description of distinctive functional characteristics; that is, the nomenclature does not follow the recommendations for naming *Candidatus* taxa [23]. Further, the GTDB does not tag putative taxa with the word *Candidatus*, making it challenging to readily recognize such taxa compared with cultured taxa. The SILVA database has partially incorporated the GTDB nomenclature, especially at the higher ranks (e.g., phylum and class levels), but has included additional new taxon names, including names of taxa represented by isolates that are not found in the published literature and are therefore neither effectively nor validly published. The resulting independently generated nomenclatures for uncultured or cultured taxa do not follow the rules of the Code and increasingly impact data analysis and data interpretation of cultured organisms, for which a validly published nomenclature was already established. Consequently, confusion among researchers at a level that will damage research progress around the globe is emerging.

As a representative example, the GTDB proposes that *Shigella flexneri* is renamed as *Escherichia flexneri* because the divergence of *S. flexneri* from typical *Escherichia coli* genomes is not high enough to justify a separate genus description, a well appreciated case debated for about two decades now [33]. This change of established nomenclature will impact clinical practice and effective communication among researchers worldwide. RED scores are one aspect of taxonomic classification but should not be used as the sole criterion for (re)classification. Perhaps more importantly, name changes that affect cultured organisms like *S. flexneri* should only be made in consultation with experts, including practitioners working with these organisms. Of note, the ICSP currently has 15 Subcommittees on Taxonomy that appear to exist to provide expertise and materials towards the general acceptance of a classification; however, some of these groups have not issued reports for several years [34], and do not cover the full range of microbial diversity known to be present in nature. While it is important to make progress and amend taxa descriptions that are apparently not appropriate (such as possibly the *S. flexneri*–*E. coli* example mentioned above), such amendments should occur within a clearly defined and widely accepted framework, in consultation with the respective experts. Mechanisms that ensure that the Subcommittees on Taxonomy comprise experts in existing and emerging taxonomies are currently not transparent, and it is uncertain if the current structure allows the governing body (i.e., the ICSP) to effectively respond given the high rate at which researchers unravel microbial phylogenetic novelty. We provide selected examples of proposed name changes below, illustrating how sequence data analysis using the current database resources generates results, even for cultured representatives and organisms with validly published names, that are not supported by the published nomenclature or the scientific understanding of the biology of the organisms under study. We make specific recommendations on how to deal with such issues in the (near) future.

For taxonomic classification of datasets that comprise sequences of uncultured, or, better, **not-yet-cultured organisms**, or of organisms that can be maintained in the laboratory but for which no axenic cultures (i.e., isolates) are available, the SILVA SSU rRNA gene database 138 (released December 16, 2019) is the preferred resource for many researchers analyzing sequence data. SILVA stays at the cutting edge of the informal nomenclature and states that it is a 'comprehensive on-line resource for quality checked and aligned ribosomal RNA sequence data' (www.arb-silva.de). SILVA does include some *Candidatus* names as well. Two additional 16S rRNA gene sequence databases, Greengenes and the RDP, have been popular among many researchers. Greengenes uses nomenclature proposed from phylogenetic methods applied prior to 2013, and the RDP has not been updated since 2016, although a new release is forthcoming. Therefore, these databases do not include more recently proposed

Glossary

Axenic culture: a single, defined population growing in the absence of other organisms. Also referred to as an isolate or pure culture.

***Candidatus*:** a provisional category for the naming of not-yet-cultured taxa (i.e., not available as axenic culture) of any rank.

Classification: the hierarchical grouping of organisms based on evolutionary relationships and/or phenotypic characteristics.

International Code of Nomenclature of Prokaryotes (ICNP): referred to as 'the Code'. The definitive set of rules, principles, and recommendations for naming members of the bacteria and archaea [14].

International Committee on Systematics of Prokaryotes (ICSP): formerly the International Committee on Systematic Bacteriology (ICSB), it is the body that oversees the nomenclature of prokaryotes and supervises the publication of the ICNP. Their Judicial Commission issues opinions concerning nomenclatural matters and revisions to the Code.

International Journal of Systematic and Evolutionary Microbiology

(IJSEM): previously the *International Journal of Systematic Bacteriology*, it is the journal of record for publication of taxonomic descriptions of microbial taxa and the official publication venue of the ICSP and the Bacteriology and Applied Microbiology Division (BAM) of the International Union of Microbiological Societies (IUMS) (Figure 1).

List Editors: those who review effectively published names and decide on inclusion in a Validation List published every 2 months in IJSEM. IJSEM currently has two List Editors, who can solicit input from currently three Nomenclature Reviewers.

List of Prokaryotic Names with Standing in Nomenclature (LPSN): an independent database (<https://lpsn.dsmz.de>) that lists the names of prokaryotes (bacteria and archaea) that have been effectively or validly published, including *Candidatus* taxa.

Metagenome-assembled genome (MAG): a single-taxon genome assembly based on DNA-sequence contigs binned (or grouped together) from a metagenome. A MAG may represent the average of multiple, co-occurring subpopulations (with minor sequence variants) and thus equate to a

and/or validated names at the time of this writing and are therefore of limited utility for taxonomic analysis of environmental samples.

SILVA 138 aligns with the GTDB in reporting name changes at higher taxonomic ranks, including the complete reclassification of taxa previously associated with the class Deltaproteobacteria (Table 1) [35]. SILVA introduced this updated nomenclature in 2019, and the GTDB adopted these classification revisions in June, 2020. Of note, several of these revisions were implemented prior to any peer-reviewed publication proposing these changes, which were finally published in November 2020 [35]. This new nomenclature, included in SILVA 138 and the GTDB, deviates from established names and phenotypes in the delineation of genera, despite the fact that Deltaproteobacteria is a lineage with many cultured isolates and many validly published names. Specifically, following the established and validly published nomenclature, the order Desulfuromonadales within the Deltaproteobacteria comprises the families Desulfuromonadaceae, Pelobacteraceae, and Geobacteraceae, each comprising several well established and well studied genera such as *Geobacter* within the Geobacteraceae. Until the most recent release, GTDB conserved this existing nomenclature (i.e., family and genus names); however, it distinguished phylogenetically distinct genera of sufficient intragenus evolutionary diversity (based on RED scores) into lettered subsets (e.g., *Geobacter-A*, *Geobacter-B*, etc.). This approach was also applied to higher taxonomic ranks, and such names remained useful as they provided a means to identify taxa as evolutionarily distinct even though they shared the same genus epithet. Therefore, the approach also preserved the continuity of the LPSN. By contrast, the latest releases of the SILVA 138 database and the GTDB do not follow this logic and both have changed their previously established nomenclature, creating new genus names prior to documentation in the published literature [35]. In detail, the family Desulfuromonadaceae now comprises the genera *Desulfuromonas*, '*Candidatus* Deferrimonas', and '*Trichloromonas*' ('*Thrichloromonas*' in GTDB) (Table 1). The only place where these genus names appeared prior to November 2020 was in the SILVA 138 database (since 2019) and in the GTDB (since June 2020), so researchers had no access to any documentation explaining the alterations.

Within the new order Geobacterales, the SILVA 138 database, the GTDB, and the recent publication proposing a reclassification of the Deltaproteobacteria [35] list two families: the Geobacteraceae and the new family 'Pseudopelobacteraceae' (Table 1). Within SILVA, the family Geobacteraceae now includes the genera *Geobacter*, '*Citri fermentans*', '*Geotalea*', and '*Trichlorobacter*' (Table 1 and Figure 2). '*Citri fermentans*' provides an example of a name that should not have been proposed or/and used before its acceptance as a validly published name and was certainly never listed in public databases previously. Specifically, this genus contains the well characterized species *Geobacter bemidjensis* (proposed to be renamed to "*Citri fermentans* bemidjense"), which in 2019 was renamed *Geomonas bemidjensis* [36]. The name *Geomonas* has been validly published and appears in the LPSN, which indicates that, according to the Code, any renaming of the genus epithet of this species should not have occurred. In addition, the name '*Citri fermentans*' implies that members of this genus ferment citrate, as stated in a recent publication [35]; however, no evidence for this claim was provided, and members of the Geobacteraceae have never been shown to ferment citrate. The proposed name '*Citri fermentans*' is apparently not based on a shared physiological feature, and its use would most certainly lead to unnecessary confusion, which is in direct conflict with Principle 1 of the Code. To correct such missteps, the ICSP Judicial Committee would have to enact Rule 56a and place illegitimate names, such as '*Citri fermentans*', on the list of rejected names (*nomina rejicienda*) [14], a process that, in recent times, has often taken too long (e.g., several years). Had experts with knowledge about the Geobacteraceae been consulted during the creation of the proposed reclassification of the Deltaproteobacteria, the name '*Citri fermentans*' would have been dismissed and the official

species-level group rather than a single genetic variant – or strain – that is typically represented by a cultivated isolate.

Nomenclature: the application of a set of rules and conventions that govern the naming of organisms. For bacteria and archaea, the International Code of Nomenclature of Prokaryotes (ICNP, the Code) establishes these rules.

Not-yet-cultured organisms: a term recognizing that taxa (taxon, singular) can potentially be cultivated with sufficient understanding of organismal biology (but have not been cultivated yet).

Phylogenetic marker: a single gene (e.g., the 16S rRNA gene), or a set of conserved genes, used for taxonomic and phylogenetic profiling of a microbiome or an isolate.

Polyphasic taxonomy: a consensus approach that utilizes multiple phenotypic, morphologic, and genetic data in order to group organisms into taxa.

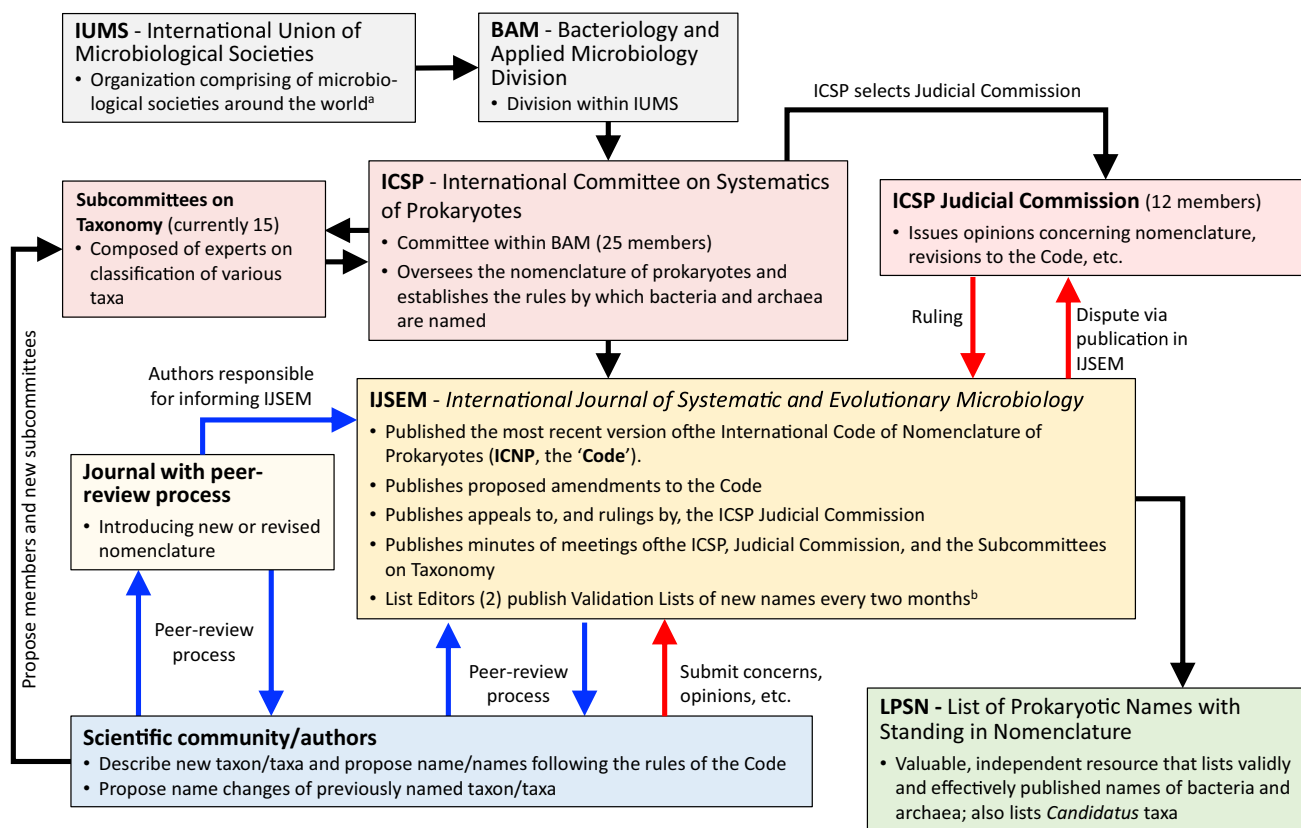
Sequence databases: repositories that store and make available digital nucleic acid and/or protein sequences. Databases differ in scope (comprehensive versus specialized), are generally interlinked, and form the basis for big-data biology.

Single-amplified genome (SAG): genome information generated from a single cell that has been lysed and its genome amplified and sequenced.

Taxonomy: a term derived from the Greek *taxis* (arrangement) and *nomia* (method); it refers to the science and practice of identifying and circumscribing, classifying, and naming microorganisms based on genomic and/or phenotypic characteristics.

Uncultured (uncultivated) taxa: real organisms, existing in nature, that have so far resisted targeted cultivation *in situ* or in the laboratory (see not-yet-cultured organisms, earlier). Note that 'unculturable taxa' is a misnomer because, if the organisms exist in nature, conditions allowing their growth exist and they can potentially be cultured.

Validation List: in order for a name to obtain standing in the nomenclature it must be included in a Validation List, which IJSEM publishes every 2 months. Names included in a Validation List are considered validly published.



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Figure 1. Overview of Governing Bodies Involved in the Taxonomy of Prokaryotes (i.e., Bacteria and Archaea), with Focus on the Nomenclature Component. The Statutes of the ICSP clarify the formation and responsibilities of subsidiaries (i.e., the Subcommittees on Taxonomy, the Judicial Commission, and the Executive Board) of the ICSP [38]. The blue arrows indicate the process for introducing new and revising existing nomenclature via input by the scientific community (i.e., the authors). The red arrows show how disputes over validly published nomenclature and requests of opinion on how to interpret and apply the Code are resolved by the Judicial Commission [14]. The LPSN (green box) is a private initiative independent of the ICSP; it provides updates of the new names published in IJSEM in electronic format and is a valuable resource for information about nomenclature. ^aIUMS (the International Union of Microbiological Societies) requires member societies to pay a fee to participate. The American Society of Microbiology, the largest microbiological society in the world, is currently not a member of IUMS. ^bInclusion in the Validation List transitions effectively published names to validly published names with standing in nomenclature [16,17].

name *Geomonas* would have been identified. Of note, only the genera *Geomonas*, *Geobacter*, and *Trichlorobacter* have validly published names, but the latter has been reclassified as *Geobacter* [37]. In addition to 'Citrifermentans', 'Geotalea' had also not appeared in the peer-reviewed literature until November 2020 [35] or in any database other than in SILVA 138 and the latest version of the GTDB, even though the name *Geobacter uraniireducens*, now proposed to belong to the genus 'Geotalea', had been validly published and is listed in the LPSN (Figure 2).

Associated with the family 'Pseudopelobacteraceae' are several validly published *Pelobacter* species, which the recently proposed nomenclature groups under the new genus '*Pseudopelobacter*' [35]. Another newly proposed genus is '*Syntrophotalea*' in the family Syntrophotaleaceae, which also comprises published *Pelobacter* species (Figure 3). Neither of these families or genera had any referenced use in the peer-reviewed literature at the time they were listed in the SILVA 138 database and the GTDB. Table 1 compares the SILVA, LPSN, and GTDB nomenclatures of the Geobacterales and Desulfuromonadales, illustrating that the SILVA database and the GTDB incorporate taxa that do not follow the validly published nomenclature and the LPSN. This issue is not

Table 1. Comparison of the Taxonomies of the Family Geobacteraceae between the SILVA SSU rRNA Gene 138 Database, the List of Prokaryotic Names with Standing in Nomenclature (LPSN), and the Genome Taxonomy Database (GTDB) (Release 04-RS89)^a

Reference Culture	Database	Phylum	Class	Order	Family	Genus
<i>Geobacter bemedjiensis</i>	SILVA	Desulfobacterota	Desulfuromonadia	Geobacterales	Geobacteraceae	Citrifermentans
	LPSN	Proteobacteria	Deltaproteobacteria	Desulfuromonadales	Geobacteraceae	Geomonas
	GTDB	Desulfobacterota	Desulfuromonadia	Geobacterales	Geobacteraceae	Citrifermentans
<i>Geobacter uraniireducens</i>	SILVA	Desulfobacterota	Desulfuromonadia	Geobacterales	Geobacteraceae	Geotalea
	LPSN	Proteobacteria	Deltaproteobacteria	Desulfuromonadales	Geobacteraceae	Geobacter
	GTDB	Desulfobacterota	Desulfuromonadia	Geobacterales	Geobacteraceae	Geotalea
<i>Geobacter lovleyi</i>	SILVA	Desulfobacterota	Desulfuromonadia	Geobacterales	Geobacteraceae	Trichlorobacter
	LPSN	Proteobacteria	Deltaproteobacteria	Desulfuromonadales	Geobacteraceae	Geobacter
	GTDB	Desulfobacterota	Desulfuromonadia	Geobacterales	Pseudopelobacteraceae	Trichlorobacter
<i>Pelobacter propionicus</i>	SILVA	Desulfobacterota	Desulfuromonadia	Geobacterales	Pseudopelobacteraceae	Pseudopelobacter
	LPSN	Proteobacteria	Deltaproteobacteria	Desulfuromonadales	Desulfuromonadaceae	Pelobacter
	GTDB	Desulfobacterota	Desulfuromonadia	Geobacterales	Pseudopelobacteraceae	Pseudopelobacter
<i>Pelobacter carbinolicus</i>	SILVA	Desulfobacterota	Desulfuromonadia	Desulfuromonadales	Syntrophotaleaceae	Syntrophotalea
	LPSN	Proteobacteria	Deltaproteobacteria	Desulfuromonadales	Desulfuromonadaceae	Pelobacter
	GTDB	Desulfobacterota	Desulfuromonadia	Desulfuromonadales	Syntrophotaleaceae	Syntrophotalea
<i>Desulfuromonas acetexigens</i>	SILVA	Desulfobacterota	Desulfuromonadia	Desulfuromonadales	Desulfuromonadaceae	Trichloromonas
	LPSN	Proteobacteria	Deltaproteobacteria	Desulfuromonadales	Desulfuromonadaceae	Desulfuromonas
	GTDB	Desulfobacterota	Desulfuromonadia	Desulfuromonadales	Trichloromonadaceae	Trichloromonas
'Cand. Desulfuromonas soudanensis'	SILVA	Desulfobacterota	Desulfuromonadia	Desulfuromonadales	Desulfuromonadaceae	'Cand. Deferrimonas'
	NCBI ^b	Proteobacteria	Deltaproteobacteria	Desulfuromonadales	Desulfuromonadaceae	Desulfuromonas
	GTDB	Desulfobacterota	Desulfuromonadia	Desulfuromonadales	Trichloromonadaceae	Deferrimonas

^aYellow-highlighted cells represent new taxonomic rank names listed in the GTDB. Green highlights indicate new family and genus designations found only in the GTDB and the SILVA 138 database lacking any reference in the peer-reviewed literature prior to November 2020. Text in red font indicates new names found only in the GTDB, or names that do not match between the SILVA database and the GTDB. Text in blue font indicates the validly published genus name *Geomonas* with no match in the GTDB or the SILVA database, and a validly published reclassification of *Geobacter bemedjiensis* [36].

^bNCBI taxonomy is used for the '*Candidatus Desulfuromonas soudanensis*' nomenclature because this culture has not been deposited in any culture collection and therefore the name has not been validly published. The SILVA database refers to this organism as '*Candidatus Deferrimonas*'.

limited to these orders, and inconsistent naming occurs in other orders and families listed in both databases.

The Code protects the nomenclature framework that has been painstakingly developed and maintained by dedicated taxonomists, including former and current IJSEM editors, and researchers around the globe, over the past decades. Deep sequencing will continue to reveal new diversity requiring a rational approach to include sequences without cultured representatives in an overarching taxonomic framework. For the foreseeable future, the discovery of new sequences will continue to outpace the traditional practice of **polyphasic taxonomy**, which generates the problem: researchers need up-to-date databases for sequence analysis, putting database curators under pressure to constantly refine and update the taxonomic framework for the classification. The current Code rules for validly publishing names for new taxa cannot accommodate this need as lengthy and labor-intensive experimental efforts are required for these publications (i.e., taxon descriptions). Roadmaps have been proposed for naming uncultivated archaea and bacteria, and these efforts highlight the need for a sensible path forward to include not-yet-cultured organisms in a taxonomic framework [21,22,31,32]. Clearly, such an effort requires consensus and buy-in from all parties, and solo efforts by individual stakeholders

		<i>Geobacter bemidjiensis</i> <i>Geobacter uraniireducens</i> <i>Geobacter lovleyi</i>	
	LPSN	SILVA	GTDB
Phylum	Proteobacteria	Desulfuromonadota	Desulfuromonadota
Class	Deltaproteobacteria	Desulfuromonadia	Desulfuromonadia
Order	Desulfuromonadales	Geobacterales	Geobacterales
Family	Geobacteraceae	Geobacteraceae	Geobacteraceae Pseudopelobacteraceae
Genus	<i>Geobacter</i> <i>Geomonas</i> ^a	'Citrifermentans' 'Geotalea' <i>Trichlorobacter</i>	'Citrifermentans' 'Geotalea' <i>Trichlorobacter</i>

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Figure 2. Illustration of Different Taxonomic Assignments of the Three Well Characterized *Geobacter* Species, *Geobacter bemidjiensis* (Red Font), *Geobacter uraniireducens* (Purple Font), and *Geobacter lovleyi* (Green Font), in the SILVA Database and the Genome Taxonomy Database (GTDB) Compared with the List of Prokaryotic Names with Standing in Nomenclature (LPSN) Taxonomy. The font color tracks the name changes in the SILVA database and the GTDB. Highlighted in yellow are the name changes of taxonomic ranks (i.e., phylum, class, and order) associated with the GTDB and the SILVA database. The GTDB places *Geobacter lovleyi* in the Pseudopelobacteraceae, a family name that has not been validly published. ^aA validly published reclassification of *Geobacter bemidjiensis* to the new genus *Geomonas* [36]. As a result, four genus names (i.e., *Geomonas*, *Trichlorobacter*, 'Citrifermentans', and 'Geotalea') are now associated with these three well known *Geobacter* species, but only two (i.e., *Geomonas* and *Trichlorobacter*) of these new genus designations have been validly published and/or listed in the LPSN.

		<i>Pelobacter propionicus</i> <i>Pelobacter carbinolicus</i>	
	LPSN	SILVA	GTDB
Phylum	Proteobacteria	Desulfuromonadota	Desulfuromonadota
Class	Deltaproteobacteria	Desulfuromonadia	Desulfuromonadia
Order	Desulfuromonadales	Geobacterales Desulfuromonadales	Geobacterales Desulfuromonadales
Family	Desulfuromonadaceae	Pseudopelobacteraceae Syntrophotaleaceae	Pseudopelobacteraceae Syntrophotaleaceae
Genus	<i>Pelobacter</i>	'Pseudopelobacter' 'Syntrophotalea'	'Pseudopelobacter' 'Syntrophotalea'

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Figure 3. Illustration of Different Taxonomic Assignments of the Two Well Characterized *Pelobacter* Species, *Pelobacter propionicus* (Red Font) and *Pelobacter carbinolicus* (Green Font), in the SILVA Database and the Genome Taxonomy Database (GTDB) Compared with the List of Prokaryotic Names with Standing in Nomenclature (LPSN) Taxonomy. The font colors track the name changes in the SILVA database and the GTDB. Highlighted in yellow are the name changes of taxonomic ranks (i.e., phylum, class, and order) associated with the GTDB and the SILVA database. Both SILVA and the GTDB used two unpublished family and genus names to accommodate *Pelobacter propionicus* and *Pelobacter carbinolicus* until the recently published proposal for reclassification [35].

cannot deliver productive solutions. Changing the established taxonomic framework must follow scientific discourse and rules, including a peer-review process that includes experts in the organisms that are being renamed. Curators of online databases are in a position of power because they control a product many researchers around the world demand for data analysis. It would be a disservice to the scientific community at large if the curators do not follow best professional practice, or otherwise risk the constructed taxonomic framework to crumble without providing the services and standardization the global scientific community is looking for. The taxonomic framework of axenic cultures has been robust and provided invaluable services to the international research community and policy makers, but it is apparent that the system has to adjust in order to continue to fulfill its purpose and stay relevant. Opportunities exist to reconcile fast-paced sequence discovery with a responsive nomenclature, and thus, taxonomic framework, and specific plans have been proposed [22].

Although it is generally accepted that adjustments need to take place in order for the existing taxonomic framework to avoid aberrations and stay current, reaching consensus among the various stakeholders has been shown to be challenging with slow progress. Considering the fast pace at which researchers discover new genetic diversity of microorganisms, speed is essential if the goal is to maintain and build a meaningful taxonomic framework. Even without consensus, and an agreed-upon framework with guidelines and rules, adherence to professional best practices can bridge this current phase of uncertainty and help coalesce the community. A number of points can help to ensure that the taxonomic framework, and especially its nomenclature component, stay relevant and can fulfill its purpose for the global research community, practitioners, and policy makers.

- Name changes should be transparent. A rationale for each proposed name change should be communicated in the peer-reviewed literature. Databases should not adopt name changes before they appear in Validation Lists published in IJSEM.
 - Names that are changed should have links (identifiers) to the previous nomenclature in the databases to allow continuity of research.
 - Name changes should take place in consultation with, or review by, recognized experts of the taxon/taxa in question. The ICSP Subcommittees on Taxonomy could play an active role in this process.
- There is legitimate tension between taxonomic descriptions of microbial taxa based on in-depth physiological, functional, and ecological characterization and those based on sequencing and genomic markers. Both approaches have unique contributions to microbial taxonomy, but integration of both worlds is challenging. One solution is to develop two different, parallel systems of taxonomic descriptions that follow different sets of rules, but this approach has the obvious drawback that different rules applied to the study of the same (or similar) organism(s) will very likely lead to confusion. Another path forward would be for the Subcommittees on Taxonomy to include experts from both camps.
- New names that have not appeared in the peer-reviewed literature (i.e., names not effectively published) should not be introduced in public databases since some of these databases are widely used for 16S rRNA gene sequence analysis. New names and name changes should only occur after effective publication, or, even better, after the new names have been included in a Validation List. It would also help to have a time period after effective publication of proposed names (i.e., following the initial appearance in the peer-reviewed literature), and before the names appear in a Validation List in IJSEM, for experts outside the realm of IJSEM editors and reviewers to be able to comment on proposed new names and, importantly, nomenclature changes. Such a mechanism would help to avoid inappropriate names such as the 'Citrifermentans'. The wide accessibility of internet resources/web servers suggests that such

efforts could be very effective, and the IJSEM could play an important role in the implementation of such a mechanism.

- The ICSP should reconsider the proposal to use gene/genome sequences as type material for the naming of prokaryotes. Modification of the Code to accommodate uncultured microorganisms, microorganisms that cannot be maintained in axenic culture in two culture collections, and MAGs and SAGs could offer a productive solution for an integrated nomenclature framework. The rules should follow previously suggested guidelines, efforts that have been advocated by a subset of current members of the ICSP [31,38,39].
 - Naming of new taxa based on polyphasic taxonomy of isolates versus sequence-only-based description (i.e., SAGs and MAGs) should be apparent, for instance, by superscript/subscript identifier letters attached to the taxonomic name, as proposed previously [21].
 - Naming based on genomic sequence analyses (i.e., MAGs or SAGs) should follow the principles of the Code. A recent computational tool provides an effective means for generating appropriate Latin names for new organisms and overcomes a common roadblock in the generation of new nomenclature [40].
 - In general, a conservative approach should be applied, and the existing nomenclature based on polyphasic taxonomy upheld to the extent possible. Of course, name changes should go forward if clear benefits to the community at large are apparent.
 - *Candidatus* names should be established for uncultured taxa based on the existing naming guidelines and then be given equal priority to validly published names of isolates. This practice will further promote the description of uncultivated taxa using the *Candidatus* approach [21,41], and hence, support a robust taxonomic framework during the current period, in which the sequence-based discovery of microbial phylogenetic novelty outpaces cultivation and polyphasic characterization. Of note, reclassification and name changes are possible should subsequent polyphasic characterization and additional phylogenetic information justify revisions [14].
- The current structure of oversight of the Code by the ICSP should be reviewed and re-evaluated. Currently, this group is comprised of a small number of scientists, several of whom are associated with culture collections. A biased representation and potential conflicts of interest may hinder progress and implementing solutions expeditiously. Expansion of this group to increase breadth and diversity of researchers with expertise in genomics, microbial ecology, and uncultivated organisms should be considered.

Although incomplete, this list can guide database curators to implement a best practice approach that should avoid 'wild west' conditions before comprehensive reform of the existing Code catalog of rules has been accomplished to accommodate the needs of modern research and taxonomy, including nomenclature. The expectation is that database curators engage in open dialog with all stakeholders to build a best practice approach that can assist the governing bodies overseeing the Code and its implementation (Figure 1) in setting up a revised and workable framework.

Concluding Remarks

The Code has provided a robust nomenclature framework for isolated organisms and has given researchers the freedom to (re-)classify and (re-)name organisms while maintaining stability of names to facilitate research, communication, and policy around the globe. This traditional system is being challenged to: (i) accommodate an increasing number of sequences that represent real organisms but lack cultured representatives, (ii) handle names that are coined outside the bounds of the Code, and (iii) manage name changes that destabilize the existing nomenclature. Curators of online taxonomic databases are in a position of power because they control a popular product many researchers around the world demand for data analysis; however, the broad dissemination

Outstanding Questions

What immediate steps can be taken to uphold the integrity of prokaryotic nomenclature?

Can stakeholders come together and establish a unified nomenclature framework in the short term?

What mechanisms exist, or should be put in place, to engage experts (i.e., researchers with documented expertise in studying the organisms under consideration) when renaming of established taxa is proposed?

What opportunities exist to sharpen the focus and increase the effectiveness of the Subcommittees on Taxonomy of the ICSP?

Are additional (control) mechanisms needed to safeguard the integrity of the process for name changes and ensure that the interests of all stakeholders are met?

Would engagement of the scientific community at large (rather than relying on small groups of experts alone) generate a nomenclature with broad acceptance? For example, proposals for new or revised nomenclature published in a taxonomic journal (e.g., IJSEM) could accept comments for a certain time period (<2 months) before names are considered for inclusion in a Validation List.

of names and classifications formed outside the bounds of the Code create a 'wild west' situation and increasingly destabilize the existing taxonomic framework. Adjustments to the current practice are urgently needed to enable databases to stay current without contributing to aberrations, and to maintain a robust and stable framework that will continue to serve all stakeholders. We suggest that future efforts coalesce around solving this problem in a timely and inclusive manner (see [Outstanding Questions](#)).

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