



## Options and considerations for validation of prokaryotic names under the SeqCode

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### ARTICLE INFO

#### Keywords:

Novel species  
Nomenclature  
ICNP  
Candidatus  
SeqCode  
Genome Taxonomy Database

### ABSTRACT

Stable taxon names for *Bacteria* and *Archaea* are essential for capturing and documenting prokaryotic diversity. They are also crucial for scientific communication, effective accumulation of biological data related to the taxon names and for developing a comprehensive understanding of prokaryotic evolution. However, after more than a hundred years, taxonomists have succeeded in valid publication of only around 30 000 species names, based mostly on pure cultures under the International Code of Nomenclature of Prokaryotes (ICNP), out of the millions estimated to reside in the biosphere. The vast majority of prokaryotic species have not been cultured and are becoming increasingly known to us via culture-independent sequence-based approaches. Until recently, such taxa could only be addressed nomenclaturally via provisional names such as *Candidatus* or alphanumeric identifiers. Here, we present options and considerations to facilitate validation of names for these taxa using the recently established *Code of Nomenclature of Prokaryotes Described from Sequence Data* (SeqCode). Community engagement and participation of relevant taxon specialists are critical and encouraged for the success of endeavours to formally name the uncultured majority.

### Diversity of *Bacteria* and *Archaea* and the valid publication of taxonomic names

The number of bacterial and archaeal species has long been debated and estimates ranging between several million to  $10^{12}$  species have been suggested (Dykhuisen, 2005; Locey and Lennon, 2016; Schloss et al., 2016). These estimations are hampered by the preferential focus on clinically and economically relevant microorganisms and niches, while microbes in other environments have not been sufficiently surveyed, if at all (Vitorino and Bessa, 2018). No matter how large the number, over the past hundred years only a fraction of the species diversity has been formally captured, with only around 30 000 species names considered to be validly published under the International Code of Nomenclature of Prokaryotes (ICNP) (Oren et al., 2023), as indicated on the List of Prokaryotic Names with Standing in Nomenclature (LPSN; accessed 20 May 2024) (Parte et al., 2020). By contrast, the Genome Taxonomy Database (GTDB) (Parks et al., 2022) has reported > 113 000 bacterial and archaeal species as of April 2024 (Release 09-RS220). This database

includes publicly available genomic data obtained from isolates, metagenome-assembled genomes (MAGs) and single amplified genomes (SAGs). This discrepancy between the number of species with validly published names and GTDB-delineated species, most of which are unnamed, is compounded by the discordance between the ICNP's rules and the current approaches to species descriptions.

Despite effective publication of species descriptions and names, validation of the names under the ICNP is often precluded. According to the ICNP rules (Oren et al., 2023), each species name should be correctly formed, all the culture collection information provided and accompanied by a clear description or protologue included as part of the original publication (although names published in online supplementary material are excluded). Since 2001 when Rule 30(3b) was revised, it is also compulsory that the type strain should be available without any restriction as an axenic and viable culture in two culture collections in different countries (De Vos and Truper, 2000). Not meeting these requirements are the main reasons why names are often not validly published after effective publication (Oren et al., 2018). For taxonomists in

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<https://doi.org/10.1016/j.syapm.2024.126554>

Received 20 July 2024; Received in revised form 12 September 2024; Accepted 13 September 2024

Available online 19 September 2024

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countries such as India, South Africa and Brazil, deposition of type strains in international collections is a major problem as the access regulations linked to the protection of biological material in these countries place restrictions on sharing the cultures (Tindall, 2020; Da Silva et al., 2023; van Lill et al., 2024). For uncultured taxa known mainly from their genetic sequences, the ICNP suggests that the provisional status of *Candidatus* (Oren, 2021; Arahal et al., 2024) be used when naming these organisms. However, numerous researchers have expressed dissatisfaction with the current status of *Candidatus* names, mostly around the lack of standing in nomenclature and therefore priority and lack of formal regulations (Konstantinidis et al., 2017; Murray et al., 2020).

Another hurdle to the formal naming of new species is that descriptions based on single isolates are strongly discouraged. Avoidance of this taxonomic practice is seen as a way to optimise efforts and resources required for the review and publication of descriptions (Trujillo and Oren, 2018). This perspective is unlikely to have major implications in fields such as clinical microbiology and plant pathology, as most serious pathogens have been described and new or emerging pathogens are treated with urgency, and multiple clinical isolates are typically available. However, it could impact systematics research by delaying publication of novel species for which only one representative is available. Providing all species, even those based on single representatives, with a validly published name has great value as it contributes to our growing formal recognition of prokaryotic diversity, especially those from distinct environments and niches.

Increases in the rate at which new species are described and the accompanying advances in our understanding of microbial diversity and evolution are dependent on nomenclatural regulations resulting in stable taxon names embedded in a robust taxonomic framework. A fitting step in this direction would be to overcome the current obstacles in describing and naming the diversity of species already known from previous research. A workable solution is to use the recently established *Code of Nomenclature of Prokaryotes Described from Sequence Data* (also known as SeqCode) (Hedlund et al., 2022) as it uses whole genome sequence as nomenclatural type for naming taxa that cannot attain standing under the ICNP (Whitman, 2016; Rossello-Mora et al., 2020; Palmer et al., 2022; Jiménez and Rosado, 2024). The availability of stable names would accordingly enable researchers to link the current information captured in scientific literature and databases to these microbes (Hugenholtz et al., 2021). It will also allow the linking of new studies on the distribution, ecology and biology to new and existing taxon names. Community-wide adoption of such a cumulative approach would undoubtedly lead to the development of relevant species descriptions, resulting in a better synergy between microbial taxonomy and ecology (Godfray et al., 2004).

The SeqCode is fully compatible with the polyphasic taxonomic approach, which now typically includes the use of whole genome sequence information (Chun et al., 2018; Riesco and Trujillo, 2024). Genome data have become invaluable for taxonomic revisions and updates (Chan et al., 2012; Hahnke et al., 2016; Sangal et al., 2016; Hördt et al., 2020) and for species delineation via various Overall Genome Relatedness Indices (OGRI) (Rosselló-Móra and Amann, 2015). Among these, average nucleotide identity (ANI) and digital DNA-DNA hybridization (dDDH) present primary criteria for circumscribing species (Konstantinidis and Tiedje, 2005; Meier-Kolthoff et al., 2014), although detailed descriptions are still mostly based on the comparison of a range of additional genotypic, phenotypic and chemotaxonomic properties determined for a set of closely related isolates (Tindall et al., 2010). The need for capturing phenotypic data is, however, increasingly being questioned given their limited taxonomic value and the wide availability of whole genome sequences (Sutcliffe et al., 2012; Vandamme and Peeters, 2014; Sutcliffe, 2015). Prokaryotic taxonomy has thus shifted its focus from requiring that taxa are phenotypically distinguishable (as defined in the taxon's description) to the use of whole genome information for identification or diagnosis *sensu* Rheindt et al. (2023).

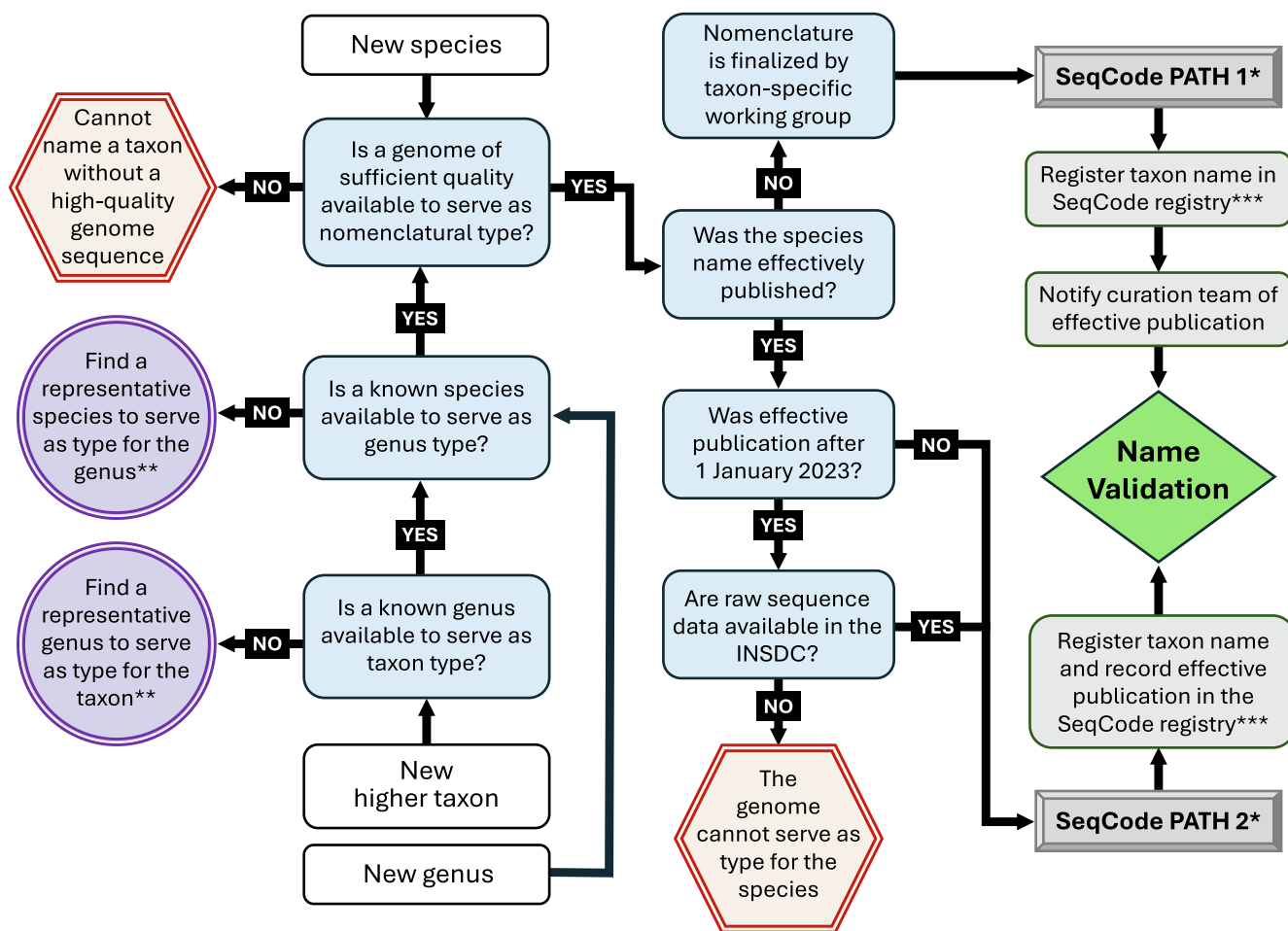
Although the SeqCode provides a viable solution for the stable and well-regulated naming of taxa for which no validly published names exist, it is also important to look at the alternative options. In this paper we first consider the *Candidatus* status as an option for naming taxa whose names cannot be validly published under the current rules of the ICNP (Oren, 2021; Pallen 2021), followed by an overview of the rules of nomenclature and data quality requirements of the SeqCode. We then propose different approaches (Fig. 1) to facilitate validation of names of effectively published and *Candidatus* taxa via the SeqCode, as well as for dealing with the multitude of nameless taxa recognised in databases such as the GTDB where they only received provisional alphanumeric identifiers. We believe that community engagement is critical to this process and encourage the participation of relevant taxon specialists and the broader research community.

### Unresolved issues around the *Candidatus* status

The debate over the use of sequence data as nomenclatural types for uncultured and fastidious taxa started about a decade ago (Hedlund et al., 2015; Whitman, 2015; Whitman, 2016; Konstantinidis et al., 2017) culminating in the SeqCode (Hedlund et al., 2022). Prior to this, the provisional status *Candidatus* was the only option for naming such taxa, although naming *Candidatus* taxa is at present unregulated, with names having no standing in nomenclature (Oren, 2021; Pallen, 2021). The latest development is a proposal by Arahal et al. (2024) to formally integrate the naming of *Candidatus* taxa into the ICNP as an alternative to the SeqCode, which partially addresses the shortcomings of *Candidatus* status. This is an explicit acknowledgement that it would be beneficial to regulate the nomenclature of the uncultured majority of prokaryotes whose names cannot be validly published under the ICNP.

The new section 10 proposed by Arahal et al. (2024) will have several implications. It aims to address issues such as creation of homonyms (the same name is given to two or more different taxa) and the priority among *Candidatus* names that are considered to be synonyms (same taxon has different names). It also introduces measures to protect species names by means of the requirement to reuse a "pro-validly published and pro-legitimate [*Candidatus*] name" (Proposed Rule 72), which is presented as a major step towards creating "the best of both worlds". Based on the proposal, the names of *Candidatus* species should be retained when a conspecific strain is cultivated and is used to validate the species name. However, *Candidatus* names still cannot be validly published, lack standing in nomenclature and therefore do not provide protection for higher taxa as any cultured isolate with a validly published name belonging to a different genus but to the same higher taxon as the *Candidatus* taxon, will have priority (Whitman and Venter, 2024). An example that foreshadows the destabilizing effect of such a taxonomic practice is the replacement of the phylum name *Candidatus* Eremiobacterota (Ji et al., 2021) with *Vulcanimicrobiota* (Yabe et al., 2023).

Two of the most prominent and useful aspects of the SeqCode were not incorporated in the Arahal et al. (2024) proposal. The first pertains to data quality requirements for the DNA sequences when used as nomenclature types such as those required under the SeqCode. Based on proposed ICNP Rule 69(1), apart from mixed cultures or preserved specimens (which are preferred, and for which quality considerations are also missing), sequence data could be used but the quality thereof is not specified. For genomes there are no specifications in terms of the acceptable completeness or contamination. The type material could even consist of the sequence of a single gene (Arahal et al., 2024), which in many cases would not provide sufficient taxonomic resolution for delineating novel species. Single genes are often only useful for demonstrating the novelty of deep-branching taxa (Bartos et al., 2024). The second aspect of the SeqCode not considered by Arahal et al. (2024) is the use of an online registry, which is especially useful when dealing with the current estimate of around 90,000 unnamed species according to the GTDB taxonomy (Release 09-RS220). Instead, their proposal to amend the ICNP still appears to rely upon the existing complex, labour-



**Fig. 1.** Decision tree for validating the names of taxa with effectively published names, Candidatus taxa and taxa without scientific names using the rules of the SeqCode.\* The use of Path 1 and 2 is explained in detail in Hedlund et al., 2022.\*\* The current genome is unsuitable to serve as nomenclatural type and an alternative genome or another species should be obtained to serve as type for the genus (and higher taxa).\*\* Registry will initiate the necessary curation by performing nomenclature and genome quality checks.

intensive, systems for generating Validation Lists.

We propose that the SeqCode remains the best option for naming prokaryotic taxa whose names cannot be validly published under the ICNP. Rather than introducing yet another complicated set of rules that would not settle the issues related to the *Candidatus* status in nomenclature, a more elegant and scientifically justifiable approach would be for the ICNP to recognize names validly published under the SeqCode. There is a precedence for this as the ICNP already recognizes names of cyanobacteria that are validly published under a different nomenclatural code, the *International Code of Nomenclature for algae, fungi and plants*. The implementation of this decision only requires the emendation a single General Consideration and three Rules of the ICNP. A similar recognition of names validly published under the SeqCode would truly be an example of the “best of both worlds” and would represent an important step towards reconciliation of the two codes.

### SeqCode: Rules and requirements

An important motivation for the development of the SeqCode was to ensure the stability and regulation of taxon names that cannot be validly published under the ICNP (Whitman et al., 2022). Providing such names with standing in nomenclature will minimise the creation of synonyms (Hugenholtz et al., 2021) and enhance scientific communication (Konstantinidis et al., 2017), as well as resolve the chaotic situation where higher taxa are not linked to specific type material (Chuvochina et al., 2019; Oren and Göker, 2023). In addition, the SeqCode

governance structures promote greater community participation compared to ICSP governance (Sutcliffe et al., 2024).

The SeqCode rules for naming a species or higher taxon are similar to those of the ICNP (Whitman et al., 2022). The main differences are the use of high-quality genome sequences as type material (see below), application of priority and the process of name validation by the SeqCode. The process of registration and validation of names has been extensively modernised. There is no longer a requirement for names to be included in an official validation list published in a single scientific journal, but instead the SeqCode has an electronic equivalent called Register Lists. This allows for a semi-automated process of reviewing proposed names both ahead or post publication, which is fully transparent and documented (Whitman et al., 2024). The use of FAIR (Findable, Accessible, Interoperable and Reusable) data principles enable Registry users to explore and analyse SeqCode data, and developers to build and implement tools for integrating the SeqCode Registry with other prominent data repositories and platforms such as the GTDB and the Microbial Genomes Atlas (MiGA) (Rodriguez-R et al., 2020; Parks et al., 2022).

The quality requirements for genome sequences used as nomenclatural types apply to species descriptions based on MAGs, SAGs and individual isolates (Hedlund et al., 2022). The minimal standards for the genomic data required by the SeqCode are based on the requirements of the Genomic Standards Consortium, an international community-driven entity (Field et al., 2008; Bowers et al., 2017). Type genome sequences should be > 90 % complete, contain < 5 % contamination, and in the

case of individual isolates, have a read coverage of  $\geq 10X$ . As of 1 January 2023, the raw data for type genomes of taxa named after this date must also be available in one of the International Nucleotide Sequence Database Collaboration (INSDC) databases. In addition to these minimal requirements, genome data should ideally further fulfil several recommendations related to issues such as genome integrity, number of canonical amino acids with encoded tRNA elements and the presence and length of 16S rRNA gene sequences. Also, while there is no requirement in the SeqCode for strain deposition as strains are treated as additional reference material, researchers are encouraged to deposit strains whose genomes were designated as type material in international culture collections.

As of June 2024, the names of 517 taxa including 219 bacterial and 77 archaeal species have been validly published under the SeqCode. To stabilize the names of higher taxa in the GTDB, names of 49 taxa delineated in GTDB at the ranks of phylum, class, order and family, as well as names of 23 genera (and their type species) associated with these higher taxa have been validly published (Chuvochina et al., 2023). The SeqCode has also been used to validate the name of an isolate, *Salinibacter pepae*, because its maintenance and, as a result, deposition in culture collections proved to be problematic (Viver et al., 2023). The SeqCode also provides the opportunity to validly publish the names of taxa based on the genomes of isolates from countries where permission for sharing of cultures (but not Digital Sequence Information) is required according to the national benefit sharing regulations linked to the Nagoya Protocol (Da Silva et al., 2023). A recent example of this is the naming of several *Mesorhizobium* species from South Africa that would otherwise not have gained standing in nomenclature under the ICNP (van Lill et al., 2024).

The SeqCode is specifically developed to complement the ICNP and it recognises names that are validly published under the ICNP (Hedlund et al., 2022; Jiménez and Rosado, 2024). This arrangement serves to minimise the occurrence of synonyms and allows for the possible future merger of the two codes (Hedlund et al., 2022). As of 1 January 2023, names under the two codes are competing for priority when applied to the same taxon. Currently the ICNP does not reciprocate recognition of names validated under the SeqCode, and the International Committee on the Systematics of Prokaryotes (ICSP) does not endorse the SeqCode itself (Göker et al., 2023). As stated by proponents of both Codes (Arabal et al., 2024; Jiménez and Rosado, 2024; Whitman and Venter, 2024), such discord may cause significant confusion when different nomenclatural types and/or names are proposed for the same taxon. Accordingly, several authors have given preference to naming taxa under the ICNP when an isolate meets all relevant requirements and can be used as the nomenclature type, while the naming of other taxa not meeting the ICNP requirements is proposed under the SeqCode (Chuvochina et al., 2023; Viver et al., 2023).

#### Valid publication of names of effectively published taxa and *Candidatus* taxa, and naming of known but unnamed taxa under the SeqCode

The nearly 90 000 species that have been delineated in the GTDB, but for which no validly published name exists, fall into two distinct groups. The first group consists of taxa whose names are effectively published in the literature based on isolates or other evidence including genomes (i.e., *Candidatus* taxa), but their names are not validly published under the ICNP. The second group is essentially nameless and consists of taxa that have been delineated in the literature or based on the GTDB framework but have not been named in any publication and are only linked to alphanumeric identifiers. Currently, the majority of known bacterial and archaeal species delineated in GTDB fall in the second category (Parks et al., 2022).

#### Taxa with effectively published names and *Candidatus* taxa

Taxa named in effective publications (Oren et al., 2018) are either represented by isolates or sequence data and have been given a conventional Latin name or a *Candidatus* name (Oren, 2021). Some of these names cannot be considered to be validly published as they are not compliant with ICNP Rules 25a and/or 27 (e.g. missing formal protologues; protologues published in Supplementary material). To deal with these taxa under the SeqCode, provision has been made for formally naming them by following Path 2 (Fig. 1), as outlined by Hedlund et al. (Hedlund et al., 2022). The only requirement for names published prior to 1 January 2023, is that a genome of sufficient quality is available for serving as nomenclature type. For names published after 1 January 2023, the raw sequence data in addition to a genome of sufficient quality is required for validation. Validation of a name following Path 2 could be done by the original authors of the publication [seqco.de/r:wmpix60f – the genus *Sulfuritelmatomonas* and its type species *S. gaucii* (Hausmann et al., 2018)] or on their behalf [seqco.de/r:f-kh4ko6 – *Enterovibrio baiacui* (Azevedo et al., 2020)] as the SeqCode Registry links the name with the associated publication.

Not all *Candidatus* taxa linked to species that have been described based on unique 16S rRNA gene sequences alone, or poor-quality genomes, will gain standing in nomenclature under the SeqCode. Only high-quality, whole genome sequences are acceptable as type material. These species and taxa linked to them can only be formally named once they meet the requirements of either the ICNP or the SeqCode.

#### Known species and higher taxa without scientific names

Unique but unnamed taxa for which high-quality genome sequences are available, are often reported in the literature. For example, comparative genomics revealed that the *Pseudomonas stutzeri* complex may contain as many as 27 novel *Pseudomonas* species (Li et al., 2022). However, by far the biggest source of such taxa is the GTDB, where species are delineated using ANI and relative evolutionary divergence are used for higher taxa (Parks et al., 2018; Parks et al., 2020). Of the 96,258 species with placeholder names in GTDB, 12,251 (12.7 %) species are linked to genomes obtained from isolates, while the remaining 87.3 % are linked only to MAGs recovered from a wide range of environments (GTDB Release 09-RS220). In cases where the strains are not available in public culture collections (Greenlon et al., 2019), it is difficult to trace, and almost impossible to describe and name under the ICNP.

In our opinion, these known but unnamed taxa are excellent candidates for naming under Path 1 of the SeqCode (Fig. 1), especially when it involves relevant taxon specialists. In spite of this potentially being a prolonged process, it has been applied with success. The recent description and naming of 15 new *Pantoea* species captured in the GTDB was a collective effort of taxonomists and researchers working with this genus in different parts of the globe (Crosby et al., 2023). Another example of such community involvement is the international collaborative effort to name 18 *Enterococcus* species under the SeqCode (Schwartzman et al., 2024). Although it is possible to name species at a large scale (Pallen et al., 2022), without community participation and involvement, the proposed names are unlikely to be widely accepted.

#### The way forward

We believe that community participation and involvement are crucial components of stable nomenclatural frameworks. Therefore, to involve specialised taxonomists and the broader research community alike, we suggest the formation of taxon-specific working groups, similar to the ICSP Subcommittees, to assist with naming of relevant taxa. Guidance for the formation of such Working Groups is already provided for by Article 13 of the SeqCode statutes (Sutcliffe et al., 2024). Such groups could contribute to providing stable names by advising on the

current state of classification and naming of higher taxa and their associated type genera and species within a specific lineage. For the naming of species, we envision that the working groups establish contact with the original researchers who isolated strains and/or sequenced the genomes targeted as possible type material. It will also assist with tracing isolates where possible and any relevant metadata. Although this approach would represent a slower and more *ad hoc* process, it would contribute to a more meaningful and stable nomenclature for future use. An excellent example of community involvement in major taxonomic changes is the splitting of *Lactobacillus* into 23 different genera (Zheng et al., 2020), which only took effect after extensive consultation among researchers and with relevant stakeholder communities (Pot et al., 2019; Qiao et al., 2022). This approach likely also allays the typical negative sentiments from user communities when faced with taxonomic revisions and name changes (Tortoli et al., 2019).

We strongly believe that naming taxa under the SeqCode as outlined above will be of great benefit to the wider community of microbiologists, particularly microbial ecologists. It will enhance our efforts in capturing and documenting prokaryotic diversity, facilitate scientific communication, create stable nomenclature, assist with the accumulation of biological data related to prokaryotic species and allow for a more comprehensive approach towards studying the evolution of *Bacteria* and *Archaea*.

### CRedit authorship contribution statement

**Stephanus N. Venter:** Writing – review & editing, Writing – original draft, Conceptualization. **Luis M. Rodriguez-R:** Writing – review & editing, Conceptualization. **Maria Chuvochina:** Writing – review & editing, Conceptualization. **Marika Palmer:** Writing – review & editing, Conceptualization. **Philip Hugenholtz:** Writing – review & editing, Conceptualization. **Emma T. Steenkamp:** Writing – review & editing, Writing – original draft, Conceptualization.

### Data availability

Data will be made available on request.

### Acknowledgements

We thank Pierre-Alain Chaumueil for assistance with data retrieval from the GTDB statistics for release 09-RS220.MC and PH were supported by an Australian Research Council Discovery Project (DP220100900) and UQ Strategic Funding.

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