



Review

The changing landscape of microbial biodiversity exploration and its implications for systematics

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ABSTRACT

A vast diversity of *Bacteria* and *Archaea* exists in nature that has evaded axenic culture. Advancements in single-cell genomics, metagenomics, and molecular microbial ecology approaches provide ever-improving insight into the biology of this so-called "microbial dark matter"; however, due to the *International Code of Nomenclature of Prokaryotes*, yet-uncultivated microorganisms are not accommodated in formal taxonomy regardless of the quantity or quality of data. Meanwhile, efforts to calibrate the existing taxonomy with phylogenetic anchors and genomic data are increasingly robust. The current climate provides an exciting opportunity to leverage rapidly expanding single-cell genomics and metagenomics datasets to improve the taxonomy of *Bacteria* and *Archaea*. However, this opportunity must be weighted carefully in light of the strengths and limitations of these approaches. We propose to expand the definition of the *Candidatus* taxonomy to include taxa, from the phylum level to the species level, that are described genomically, particularly when genomic work is coupled with advanced molecular ecology approaches to probe metabolic functions in situ. This system would preserve the rigor and value of traditional microbial systematics while enabling growth of a provisional taxonomic structure to facilitate communication about "dark" lineages on the tree of life.

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Current framework for systematics and its strengths and weaknesses

Currently, editors and reviewers of manuscripts describing new taxa of *Bacteria* and *Archaea* often mandate a polyphasic study of axenic cultures, including physiological, chemotaxonomic, morphological, and genetic comparisons to existing related taxa [63]. The precise combination of experiments and the degree of dissimilarity to justify new taxa is highly taxon-dependent, drawing on historical precedent and best practices defined by the International Committee on the Systematics of Prokaryotes (ICSP) and its subcommittees. The strength of the polyphasic approach and the focus on axenic cultures is rooted in its reproducibility and the large amount of descriptive data it provides, which is an invaluable resource for the greater microbiology community, including ecologists, physiologists, molecular biologists, and clinicians.

These strengths notwithstanding, the rigor demanded by the current system combined with the difficulties in cultivating many microorganisms and a dearth in funding for these efforts limits the efficacy of the current taxonomic framework [64]. The funding climate for microbial systematics is especially poor in Europe and North America. For example, the Systematics and Biodiversity Science Cluster at the U.S. National Science Foundation, the only U.S. federal program dedicated to systematics, currently allocates only ~2% of their projects and ~2% of the program's funding to microbiology projects (Table S1). With almost no funding available, it is not surprising that the rate of new taxon descriptions from these continents has stagnated, with Asia taking over the lion's share of publications [42,61]. There are currently ~12,000 validly described species of *Bacteria* and *Archaea* [42] and it is estimated that it will take >1000 years to describe the remaining species, given the current rate of ~600–700 new species descriptions per year [42,51]. If one considers that the current taxonomic descriptions are heavily biased toward taxa that are relatively easy to cultivate [27], the prognosis is even less rosy. On the other hand, a more optimistic view is that advancements, both methodological and ideological, will continue to push biodiversity exploration and systematics forward at an ever-accelerating pace. One such

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ideological advancement could come through the development of 'minimal standards' for systematics [57,64], which would likely deprioritize extensive phenotypic and chemotaxonomic characterizations for individual species descriptions and better leverage more objective genomic criteria and other high-throughput technologies [51,57,62].

It is also useful to note that our poor understanding of microbial diversity is not only at the species level, but it also extends deep into the tree of life. Common estimates place the number of yet-uncultivated bacterial phyla at ~50–100 [3,26]; however, a recent effort using conservative criteria estimated ~1300 yet-uncultivated phylum-level clades [73]. The diversity of yet-uncultivated *Archaea* is also high.

The changing landscape of microbial biodiversity exploration

Progress exploring the microbial world outside of formal systematics has blossomed in recent years, fueled in large part by rapid advancements in DNA sequencing technology, which dropped in cost of over four orders of magnitude over the last decade [6]. Two approaches, single-cell genomics and metagenomics, provide distinct but highly complementary types of datasets (Fig. 1). Although both produce data that are inferior to full genomes from microbial isolates, they have greatly accelerated genomic exploration. For example, the Genomic Encyclopedia of *Bacteria* and *Archaea* (GEBA) project, designed to maximize genomic exploration of microbial isolates, doubled genomic novelty, as measured by phylogenetic diversity per genome [72]. Yet, the project's successor, GEBA-MDM (MDM, microbial dark matter) nearly quintupled genomic novelty by using single-cell genomics to explore habitats rich in underexplored microbial diversity [49]. The current iteration, GEBA-MDM II, inclusive of both single-cell genomics and functional exploration, promises future advancement of "microbial dark matter" biology.

Advancements have also taken place to reframe microbial systematics in the genomics age. Central to this work is the calibration of genomic comparisons to existing microbial species. This body of work has already been quite decisive, with microbial species boundaries corresponding to 95–96% average nucleotide identity (ANI), ~10 Karlin genomic signature, and 70% digital DNA–DNA hybridization [48,51,62]. With this robust calibration in hand, along with robust pipelines for phylogenomics analyses to guide higher-order taxonomy [49,72], a fantastic opportunity exists to expand

the taxonomic structure to include single-cell genomics and/or metagenomics datasets.

This expansion has already begun on an ad hoc basis but it is currently poorly coordinated with the systematics community. At this time, significant genomic data have been recovered, assembled, and annotated from >35 candidate microbial phyla, >25 of which have been given informal names in the peer-reviewed literature (Table 1). A few of these names are listed in the List of Prokaryotic Names with Standing in Nomenclature (LPSN) as *Candidatus* taxa [44]; however, most of them cannot readily be identified microscopically in their natural environment (i.e., morphologically or by fluorescence in situ hybridization) so they do not meet the current criteria for *Candidatus* status [37,38]. The future of these candidate phyla within microbial systematics is uncertain on several grounds. First, under the current system of microbial systematics, no taxonomic proposals can be accepted by the ICSP without well-described axenic cultures. Second, the *International Code of Nomenclature of Prokaryotes* does not cover taxonomy above the rank of class, so, in fact, no phylum or domain names are approved by the ICSP [16,29,59]. Instead, Bergey's Manual Trust has become the *de facto* governing body for the higher-order taxonomy. In this vein, it is useful to note that *Bergey's Manual* is not specifically endorsed by the ICSP to serve in this role, and Bergey's Manual Trust has only acted on decadal timeframes to revise phylum-level taxonomy. This may change because *Bergey's Manual of Systematics of Archaea and Bacteria* is currently moving to an online platform that provides a venue for more frequent updates. Finally, the primary literature also includes debates on whether several proposed candidate phyla deserve that rank even informally or whether they are equivalent to lower taxonomic ranks, such as classes [21,54]. This problem is particularly acute among *Archaea* [15,16,19].

Single-cell genomics and metagenomics: strengths and limitations

Single-cell genomics and metagenomics both provide data that are invaluable for biodiversity exploration. These approaches could further be leveraged to guide expansion of a provisional taxonomy; however, each approach has strengths and weaknesses that should be considered carefully (Table 2). Single-cell genomics requires the separation of individual cells from a population, cell lysis, whole genome amplification (WGA), DNA sequencing, and bioinformatics analysis. The details of different workflows for single-cell genomics

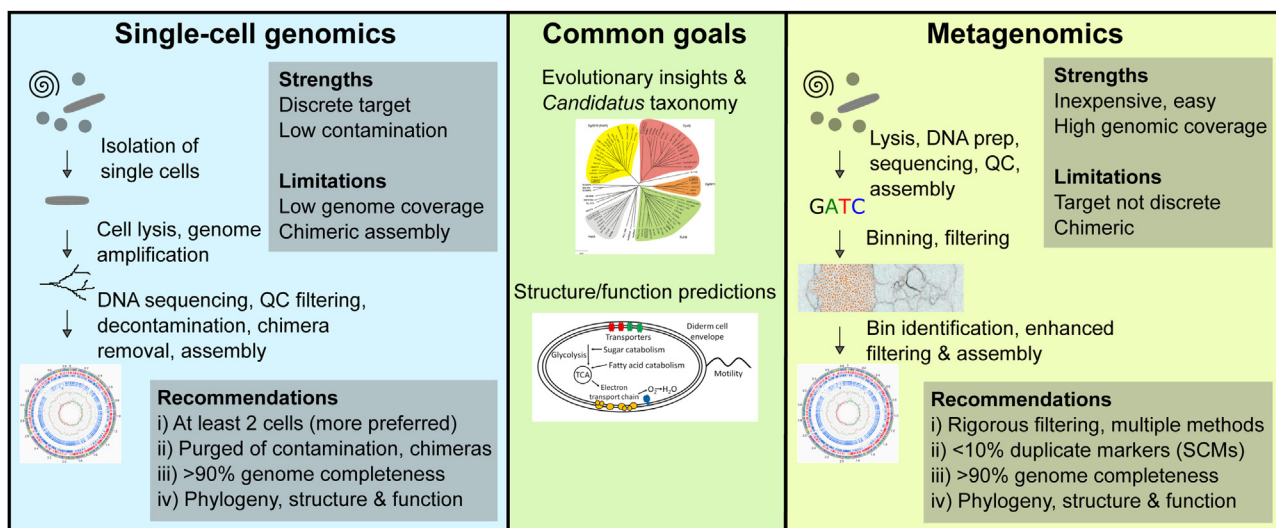


Fig. 1. Summary of workflows, strengths and limitations, and recommendations for single-cell genomics and metagenomics datasets for *Candidatus* taxonomy.

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