



## Past and future species definitions for *Bacteria* and *Archaea*



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### ABSTRACT

Species is the basic unit of biological diversity. However, among the different microbiological disciplines there is an important degree of disagreement as to what this unit may be. In this minireview, we argue that the main point of disagreement is the definition (i.e. the way species are circumscribed by means of observable characters) rather than the concept (i.e. the idea of what a species may be as a unit of biodiversity, the meaning of the patterns of recurrence observed in nature, and the why of their existence). Taxonomists have defined species by means of genetic and expressed characters that ensure the members of the unit are monophyletic, and exhibit a large degree of genomic and phenotypic coherence. The new technologies allowing high-throughput data acquisition are expected to improve future classifications significantly and will lead to database-based taxonomy centered on portable and interactive data. Future species descriptions of *Bacteria* and *Archaea* should include a high quality genome sequence of at least the type strain as an obligatory requirement, just as today an almost full-length 16S rRNA gene sequence must be provided. Serious efforts are needed in order to re-evaluate the major guidelines for standard descriptions.

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### Introduction

Species is the basic unit of biological diversity. However, microbiologists' perceptions of what a species is differ significantly, not least for semantic reasons [44]. Taxonomists, ecologists and evolutionary biologists interpret species differently and necessarily within the framework of their needs and the tools they use for identification. In this context, it is important to recall that the concept of species is different from the species definition, which is the way species are described [48]. On the other hand, the concept of species is the idea and the theoretical framework that explains what the unit can be. This idea should be as universal as possible in order to embrace all living beings. The concept explains what experts consider a species to be as a unit of biodiversity, the meaning of the patterns of recurrence observed in nature, and the why of their existence [21].

Given the relevance of the unit for different disciplines, several concepts have been proposed. These range from understanding species as ecotype lineages that are bound to periodic selection by means of evolutionary and environmental constraints [9], to more

abstract concepts, such as the method-free species that provides scientists with the freedom to decide on the methods, thresholds and criteria for circumscribing their units [1]. The latter considers species as “metapopulation lineages” evolving separately from other such entities, that “occupy an adaptive zone minimally different from any other lineage in its range”, and that “do not have to be phenotypically distinguishable, or diagnosable, or monophyletic, or reproductively isolated or ecologically divergent to be species” [1]. However, if there are no measurable phenotypic, genealogical or ecological parameters, species identification will be difficult, and it will not be possible to classify species in a universal system. The capabilities of circumscribing species depend on the measurable parameters [48]. For example, in ecology, where discrimination has hitherto mostly been carried out by means of 16S rRNA gene variation, a relaxed and more flexible circumscription might be sufficient [40], whereas among evolutionary microbiologists able to discriminate closely related lineages with distinct evolutionary fate, ecotypes would be more suitable units of diversity [28]. One way or another, what is used in taxonomy stays within these two extremes.

Contrary to other opinions [11–13], we believe that a satisfactory universal and pragmatic formulation of the species concept for *Bacteria* and *Archaea* can be achieved based on the current knowledge of taxonomic and technological developments. Actually, this

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belief is reinforced by the fact that recent (meta-)genomic studies provide strong evidence that discrete populations thrive in natural environments [5,29]. These populations are reminiscent of species circumscribed for cultured prokaryotes when the common taxonomic (i.e. genetic) thresholds are applied.

We previously proposed a phylo-phenetic species concept in which a species was “a monophyletic and genomically coherent cluster of individual organisms that show a high degree of overall similarity with respect to many independent characteristics and is diagnosable by a discriminative phenotypic property” [49]. This was subsequently reformulated as “a category that circumscribes a (preferably) genomically coherent group of individual isolates/strains sharing a high degree of similarity in (many) independent features, comparatively tested under highly standardized conditions” [53]. Here, the wording is specifically tailored for strains isolated in the laboratory, and reflects Rule 18a of the International Code of Nomenclature of Bacteria that only the names of cultured prokaryotes can be validly published [32]. As a consequence, this concept cannot be universally applied to all Bacteria and Archaea, since only a minor fraction of all microbial species thriving in the biosphere have so far been cultured and classified [68].

Based on recent technological advances in high-throughput methods, it is now possible to circumscribe biological units based on their genealogic, genomic and phenotypic coherence at relatively low cost, and most of these methods can even be applied to uncultured organisms. Therefore, we now suggest using a concept in which a species is “a category that circumscribes monophyletic, and genomically and phenotypically coherent populations of individuals that can be clearly discriminated from other such entities by means of standardized parameters”. Such parameters should be based on genetic and phenotypic data, retrievable by methods allowing the generation of interactive databases, which permit computerized comparisons using generally used bioinformatics tools. We believe that this concept embraces evolutionary units of different size (i.e. the extent of genetic and phenotypic diversity is allowed to vary within itself) depending on the thresholds used, which are covered by the definition (i.e. the way we recognize the units by means of observable characters). We are aware that distinct disciplines in microbiology are provided with different tools for recognizing microbial populations and, depending on their resolution, the definitions may not be equivalent [48]. Monophyly is an absolute premise that guarantees that the organisms embraced by the concept have a common evolutionary history. The genomic coherence modulates the circumscription of the unit by means of understanding to which extent the amount and identity of shared genes guarantees the observation of an unequivocal phenotype that serves as a diagnostic tool for identification purposes. Finally, phenotypic coherence should demonstrate that the organisms belonging to the same taxon share physiological, structural and even ecological properties that justify considering a single taxonomic unit. The phenotype can either be predicted from the inference of the genome sequences, or from the determination of the largest set of characters possible (metabolic, chemical, morphological, and even ecological), which would tend to minimize the relevance of singular changes caused by horizontal gene transfer. We believe that the “species problem” in microbiology is caused rather by differences in the species definition than by a failure in the conceptual basis.

The definition is the way we circumscribe the unit, which is the compilation of different parameters (e.g. genomic, phenotypic) that allow its unequivocal identification. However, these parameters vary depending on the organisms under study. What is valid for animals may not be applicable to prokaryotes, as they exhibit completely different characters, evolutionary fate and ecological constraints. The simple morphological characters of

microorganisms together with their expected vast diversity have promoted the development of methodologies that go far beyond the description of the phenotype. The taxonomy of prokaryotes has benefited enormously from the technological advances in molecular biology and analytical chemistry [49]. Therefore, in the following, we briefly recall the past before reviewing recent advances towards a more solid definition of bacterial and archaeal species, and finally suggest additional data that should be obligatory for future descriptions.

## The past

The first descriptions of bacterial species were made based on phenotypic traits that led to fuzzy classifications [49]. Then an important breakthrough occurred in the 1960s when methodological developments permitted genome comparisons, which were initially by means of mol% G + C content and DNA-DNA hybridization (DDH). The integration of the genomic data into the species descriptions had an important influence on the definition and shaped the current view of taxonomic classifications [48]. Potentially, the most important finding of this period was when scientists observed that phenotypically coherent microorganisms could be regarded as a single species if they shared high DDH values, in general above 70%. This cutoff value was later recommended by an ad hoc committee as an approximate threshold for circumscribing species genomically, which especially reinforced that only the complete DNA sequence should be the reference standard for determining phylogeny and, therefore, taxonomy [60]. As a result, in many cases, the approximate value of 70% DDH was taken strictly as a “gold standard” for circumscribing species, which in some cases forced the division of sets of isolates that could objectively represent single species [49]. The second breakthrough in the 1970s was genealogical reconstruction based on the ribosomal RNA genes, in particular 16S rRNA [63], which became the standard for reconstructing genealogies and the backbone for a new prokaryotic taxonomy [33]. Since then, a 16S rRNA-directed classification of prokaryotes has been superimposed on the hierarchical framework provided by the rules of nomenclature [16]. This second breakthrough was responsible for the arithmetical increase of new descriptions [55], but it also resulted in a flood of species descriptions based on single strains with a 16S rRNA gene having a similarity of <98.6% compared to the validly named species [15]. However, Single Strain Species Descriptions (SSSDs) neglect the strain diversity within a species, resulting in incomplete descriptions, even though the single strain may have been studied with a detailed polyphasic approach [18].

## The present

Currently, there is general agreement that circumscriptions of species for taxonomic purposes (i.e. the definition) must be founded on a wide set of parameters that guarantee the understanding of their uniqueness. This is referred to as the “polyphasic approach” which aims at obtaining a consensus classification by integrating different kinds of data into a classification of minimal contradictions [18]. For an accurate classification of a species, three major premises should be fulfilled: (i) monophyly, (ii) genomic coherence, and (iii) phenotypic coherence.

### Monophyly

In general, the demonstration that the members of a new species all belong to one monophyletic lineage has been performed by means of phylogenetic inferences based on housekeeping genes, in particular by comparative sequence analysis of the 16S rRNA

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