



## Dialogue on the nomenclature and classification of prokaryotes

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### ARTICLE INFO

#### Keywords:

Bacteriological code  
Taxonomy  
Nomenclature  
Candidatus  
Type material

### ABSTRACT

The application of next generation sequencing and molecular ecology to the systematics and taxonomy of prokaryotes offers enormous insights into prokaryotic biology. This discussion explores some major disagreements but also considers the opportunities associated with the nomenclature of the uncultured taxa, the use of genome sequences as type material, the plurality of the nomenclatural code, and the roles of an official or computer-assisted taxonomy.

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### Is naming important when defined here as providing labels for biological entities?

Whitman

When discussing the nomenclature of prokaryotes, we must first establish the role and importance of naming. In the International Code of Nomenclature for Prokaryotes (or the Code), names are more properly considered as identifiers that have a one-to-one correspondence with natural entities, and they do not have to describe the taxon or serve any other ancillary purpose beyond identification [36]. Although the Code has elaborate rules for forming names (*i.e.* they must comprise both a genus and species name and be derived from Latin in a certain way), these rules are clearly secondary and not related to the importance of names. In terms of function, the binomial nomenclature could easily be replaced by numbers, such as the LIM system [54], or by sequences of an arbitrary gene, such as the 16S rRNA gene.

Furthermore, experience in many fields of science has demonstrated that naming is essential for accurate communication. Thus, astronomers have developed a system for naming stars [23], chemists a system for naming compounds [26], and biochemists a system for naming enzymes [57]. All these fields share a common motivation, since it is simply not possible to provide precise descriptions of nature without clearly identifying the entities involved. This feature of knowledge is not discipline specific.

Prokaryotic biology has had its own experience of imprecise naming. Prior to the development of the Approved List and the modern Code [36,47], many prokaryotes had more than one name.

Prior to the 1980s, one of the major functions of Bergey's Manual was to associate the multiple names in current usage with the correct organism. For instance, in the 1948 edition of the Manual, 21 and 33 names were associated with the common bacterial species now named *Escherichia coli* and *Bacillus subtilis*, respectively [5]. This experience illustrates that without a naming system generally agreed upon by the scientists working in a specific discipline, nomenclature becomes imprecise, redundant and confusing.

Therefore, the role of naming is to provide precise labels for prokaryotes, and naming is essential to scientific communication in the field. Precise naming is also critical for creation of large databases and the large-scale analyses made possible by electronic computing. Without a single, permanent name, databases would require frequent curation, which would be increasingly difficult as the information content grows. Thus, the absence of a naming system also precludes the application of modern informatics tools.

Rosselló-Móra

Classifications appear as a need so that our minds can understand and use nature for our own purposes [21]. Anthropologists and, especially, structuralists, understand that classifications of organisms appear due to the basic need of human societies to order the biological diversity they see. Scientists construct taxonomies based on the scientific criteria they expect will reflect natural relationships. Since the human mind needs to name objects in ways that it can retain and relate to their relevant properties, I would like to distinguish between taxonomic names (since Linnaeus we have used his devised code) and identifiers (alphanumeric codes that serve as the basis for ordering entries in databases). Substituting numerical codes for names has been proposed several times in different taxonomies, such as suggested for prokaryotes by Cowan in 1965 [9], for a global taxonomical system in the late 1990s [11],

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and in a similar way but with a different basis for coding in the LIM system [54]. However, for reasons intrinsic to the human mind, numbers are not adequate for nomenclatural purposes, and such initiatives never had any success. Similarly, newly proposed codes different from the Linnaean system, such as the Phylocode [7], have been heavily criticized as not pragmatic [39]. On the other hand, numerical identifiers are of the utmost importance in a computer-based biology where taxonomy needs to adapt to such changes [41]. Genes and genomes are ordered in public digital databases using accession numbers that can be considered as the unique identifiers for each entry. Similarly, journals such as Systematic and Applied Microbiology [44] and Antonie van Leeuwenhoek [45] have for the first time implemented a computer-based database of species protologues, each having a unique Taxonumber or identifier.

Therefore, I believe that names, whether they are binomial or not, Latinized and/or Grecized or not, will remain the best solution for the nomenclature of units of diversity because of the structural requirements of our minds. However, I also believe that Taxonumbers, LIMs or any other type of alphanumeric identifier can be very important in organizing diversity. If their construction corresponds to a hierarchical structure reflecting natural relationships, then the result may have wide application. In addition, in order to avoid problems such as synonymies, which were common in the past, universal and interlinked public databases [41], being the official sources of knowledge related to taxonomic classification, will be a pragmatic solution for the future of classification and nomenclature. Small nomenclature differences, such as those proposed [16] for differentiating what has been cultured from what has never been cultured (the latter with just a superscript U for uncultured), may well be the basis for a universal classification of *Bacteria* and *Archaea*.

Whitman

The requirement for names is more fundamental than the issues related to the types of names and classification, and it should be put in a separate class of issues. Once we agree that there should be names, we can easily accommodate multiple naming systems as long as each naming system produces a unique name for each object. As you point out, multiple numerical naming systems are used in prokaryote biology alongside the Linnaean system of the Code, and each naming system might have value for a specific group of users. For instance, a numerical system might facilitate complex computational analyses of genomic sequences, whereas a Linnaean system might be useful for ordinary conversation. The problem facing microbiologists today is that the *candidatus* names for the uncultured taxa do not have equal priority with the names of organisms in culture collections. Thus, an organism that is well described and named as *candidatus* can be renamed when it is cultured, completely disregarding all previous knowledge.

### The classification of uncultured: is it worth classifying something that only exists *in silico*?

Rosselló-Móra

When preparing this very special issue of SAM and when looking for authors who would contribute their own expertise, we were concerned about whether or not classifying something that had never been brought to pure culture even made sense. It is true that current technologies allow us to sequence and extract groups of contigs from environmental DNA. However, these are usually a mosaic of genes representing multiple genomes of simultaneously co-occurring populations of the same species [16] and they reflect the local species pangenome in a unit denominated

the Metagenome Assembled Genome (MAG). Nevertheless, it is also true that such gene composites, in the absence of additional evidence such as FISH, are only *in silico* reconstructions of naturally occurring microorganisms. However, the current experience with genomics and metagenomics applied to taxonomy and ecology indicates (see above; [8,42]) that discontinuities exist in both, thus it is possible to associate MAGs with species.

To me, the question is whether or not the purpose of taxonomy should only be for the organization of what is cultivable and solely a motivation for the *in vitro* preservation of microbiological diversity. Instead, I think that taxonomy should embrace the complete biological diversity, independently of whether or not laboratory conditions can bring the organisms being classified into pure culture. Microbial ecologists, using modern, high throughput sequencing techniques, are starting to compile MAGs with qualities comparable to the genomes of cultured microorganisms. With the phenotypic inferences from genomic data, the descriptions of these uncultured microorganisms also have a high standard [16]. The future of metagenomics, together with the other different – omics, especially metaproteomics [3] combined with metabolomics [43], is to enhance the genomic and phenotypic descriptions of uncultured taxa, with standards at least as good as the current streamlined descriptions of the cultured taxa [51]. With these premises, I think that microbial ecologists have a real need to classify the diversity that they see in a more structured and stable way, using a system similar to that currently used for the cultured [16]. Actually, the current metagenome databases already possess evidence for approximately 8000 sequence-discrete natural populations, which is roughly equivalent to species at the 95% ANI (average nucleotide identity) level. This number nearly equates to the number of recognized species with validly published names [37]. The problem is that, because of the lack of a naming system, the uncultured are in nomenclatural chaos [17]. Either the problem is urgently solved or, due to current fast technological developments, an unsolvable chaos will be created by the exponentially growing capabilities for detecting uncultured environmental “species”.

Whitman

This question, which is common, also poses a false equivalency. Organisms described by their nucleic acid sequences are real biological entities, many of which are common in nature and play fundamental roles in the biogeochemistry of the Earth. To say that they exist ‘*in silico*’ attempts to trivialize the evidence without addressing the experimental basis for the observations. Instead of providing evidence that the observations are wrong, it tries to invalidate the very nature of the observation. Moreover, this criticism does not withstand close examination. There are many examples in the literature of the prokaryotes first discovered by molecular ecologists that were later brought into culture [46,50]. If we accept the premise that sequences obtained from environmental material can serve as evidence for real biological entities, the question as to whether or not specific types of sequences, such as MAGs, can serve as the type material for a species can be settled experimentally. To make the same point another way, separating the taxonomy of the cultured and uncultured prokaryotes creates a false dichotomy based mostly on an artificial and anthropogenic distinction (*i.e.* culturability). This distinction does not exist in nature, and it is confusing to incorporate it into our thinking.

It is also important to examine the rationale for the requirement that type strains be deposited with species descriptions. The use of type strains only became common in the 1980s with the creation of the Approved List. At that time, cultures were necessary in order to determine if isolates were unique. Since the ability to identify synonyms is an essential part of the Code, a recommendation for type strains was justified. When molecular methods were developed

that could serve this purpose, there was no longer a rationale for type strains for the operation of the Code. Nevertheless, at the same time as molecular methods for distinguishing strains approached maturity, the official body for nomenclature precluded their use as type material [19,27]. Perhaps this is a good example of why an official taxonomy is not a wise policy (see below).

A second issue is the purpose of taxonomy. If taxonomy is to be considered as a discipline separate from other approaches in biology, it will become marginal and uninteresting. However, if its goal is to further our understanding of prokaryotic biology in the most general sense, it becomes a valuable and vibrant area of research. Taxonomy should embrace all biological diversity. Moreover, combining the taxonomy of the cultured and uncultured is a powerful paradigm with many inherent synergies. For instance, the hypothesis that an ANI of 95% represents a species comes entirely from examination of cultures. Applying this concept to the uncultured allows the description of discrete entities or species that have not been cultured. From the other perspective, the methods used to describe the uncultured greatly enrich our knowledge of the cultured. The abundance and distribution in the environment as well as the existence of uncultured relatives is very important to the way we view the cultured organisms. For instance, we would be much less interested in *Prochlorococcus* if it was not one of the most abundant organisms on earth.

Another common concern is that uniting the taxonomy of the cultured and uncultured taxa will marginalize research focused on the isolation of novel organisms. However, I expect the effect will be the exact opposite. For instance, the *Acidobacteria* were shown to be a common and abundant group of soil bacteria in the 1990s, and these discoveries led to a number of successful efforts to isolate and characterize them [10,35,38]. If their existence had not been recognized, the importance of this group of bacteria would not have been appreciated, and they would not have been targeted for isolation. Thus, characterization of the uncultured will both focus and energize efforts to cultivate.

Rosselló-Móra

Indeed, knowledge of an interesting organism that has never been brought to pure culture encourages isolation attempts. Thus, we have isolated *Salinibacter ruber*, which we have now been studying for more than 15 years [1,2]. However, most of the organisms thriving in a given ecosystem may have very similar properties. For instance, they may be heterotrophs lacking conspicuous features that are metabolically redundant. In themselves, they may not be interesting enough to warrant isolation. Nevertheless, they deserve to be classified, and the new molecular methods constitute an excellent tool for this purpose. Moreover, an official classification is possible by using universal parameters, although not under strict inflexible boundaries and concepts. For example, while the ANI difference between closely related species was formulated using small datasets based on cultures, large-scale comparisons of over 90,000 genomes [15] reinforces the fact that there is a distinct ANI threshold between species and not a continuum. This would imply that species (or whatever we want to call this biological unit) discreteness indeed exists and can therefore be catalogued. Another goal for cultivating the organisms with well-characterized MAGs would be to reveal the functions of hypothetical proteins, which often constitute over 50% of single genomes and a large part of the species pangenome.

Whitman

I just want to make a small point about the apparent redundancy of prokaryotes. In a large part, we have very little knowledge of what prokaryotes actually do in nature, and we view their poten-

tial through the very narrow lens of what they do in the laboratory or what we can easily measure in the field. If we knew more about their lifestyles, we would likely discover that most prokaryotes possess unique and fascinating adaptations to their environments. Currently, the genome sequences provide us with the best opportunity to learn about these aspects of microorganisms.

Lastly, using genome sequences as type material avoids a number of practical problems. For example, type strains are often lost from culture collections but, since the sequence will always remain in various databases, the taxonomic consequences are minimized. In addition, some countries prohibit the export of microorganisms and DNA, although the sequence will be readily available even when exchanges of cultures are restricted.

### Genomes as type material should be compulsory or only an optional alternative to the deposit of cultures?

Rosselló-Móra

I must admit that I am normally conservative in my ideas, and when I first read your proposal for DNA to become type material [58], I thought that it would also be a good idea to require deposition of extracted DNA in culture collections or DNA banks to ensure their preservation. As I came to understand that the sequence already provides enough information for taxonomic uses, I realized that this idea was not necessary. Indeed, culture collections are extremely relevant [25], since they preserve living biological material and make the type strains universally accessible, allowing taxonomists to reproduce experimental results. However, one of the already reported concerns of such collections is the overall effort needed to maintain strain data as well as biomaterial [25]. In contrast, there is still a huge diversity of species awaiting classification [62]. Taking into account that large collections, such as the DSMZ ([www.dsmz.de](http://www.dsmz.de)), currently host about 50,000 items, the perhaps conservative estimate of  $1 \times 10^7$  species, and the requirement of the Code for two deposits for each type strain, means that 400 specialized international collections similar in size to the DSMZ would be needed only for type strains. This seems to be a Sisyphean task, which would be difficult to achieve and would require pragmatic reevaluation. For me, it is only realistic for the Judicial Commission of the International Committee on Systematics for Prokaryotes (JC-ICSP) to accept your modest proposal [59] and allow DNA sequences to serve as type material. Moreover, in my opinion, almost full genome sequences should form a compulsory part of the description of new species. While the deposition of pure cultures in international collections should be highly encouraged, it should not be compulsory. Nevertheless, I favor a compulsory deposition of genome sequences, which is very practical given that sequencing is very inexpensive on next generation sequencing (NGS) platforms. In this regard, the editors (including myself) of this journal, Systematic and Applied Microbiology, now require an almost complete genome sequence of any type strain used for a taxonomic description, and we only publish new taxa accompanied by the genome sequence.

Whitman

We must recognize that microbiology is like a big tent and species descriptions must satisfy a variety of very legitimate demands. It is unproductive to require that the species description of an obligate endosymbiont be the same as that of a freely growing heterotroph or a fastidious obligate chemolithotroph. For this reason, there should only be two universal requirements for species descriptions. First, the identification requirement of the Code must be met, and the description must enable the identification of other

members of the species and the exclusion of organisms not belonging to the species. Second, the reproducibility requirement must be met so that others have sufficient detail to repeat the work. These very general requirements would enable useful descriptions of all the prokaryotes we know about.

For many studies, the genome sequence offers so much information that it is difficult to justify not sequencing the genome of a new species. Nevertheless, I can imagine cases where it would be very difficult to sequence the genome, possibly for some obligate symbionts or extremely slowly growing bacteria, even when a species circumscription is possible. Imagine if someday a robot went to Mars and discovered prokaryotic life. It should still be possible to describe and name the organisms even without deposition in two culture collections and a nearly complete genome sequence. It is the responsibility of editors and reviewers to recognize the types of evidence appropriate for descriptions in specific situations.

While it is perfectly appropriate for journals to require or strongly encourage genome sequences, the Code should never require specific types of evidence for a description. General Consideration 4 states that the Code does not govern delimitation of taxa or determine their relationships [36]. For this reason, it cannot be used to constrain taxonomic approaches. The type of evidence considered important in taxonomy is a direct consequence of the taxonomic philosophy. For instance, a deterministic taxonomy emphasizes properties that are easily measured. The modern, consensus taxonomy is largely phylogenetic [56] and so emphasizes sequence data. However, in the future we may find that other approaches are even more successful. The Code allows names to be retained even when different taxonomic philosophies are used. This fundamental principle of the Code should not be abandoned.

### **One single taxonomy for cultured and uncultured or accept plurality? Can we have in the same nomenclature code two equivalent categories for species, one for cultured and another for uncultured?**

Rosselló-Móra

As we have already discussed, there is a problem with the Code requiring pure cultures deposited in international repositories for validly published species names. This restriction makes it impossible for ecologists and some taxonomists to formally classify microorganisms that are well characterized in nature but cannot be brought into pure culture. The *candidatus* provisional category [28,29] was devised to “unofficially” name organisms when sufficient evidence of their existence could be collected (*i.e.* rRNA gene sequence and phylogeny, microscopy evidence of their morphology, size, abundance, and some metabolic traits) when a pure culture could not be isolated. The major problem is that *candidatus* was never fully recognized by taxonomists and incorporated as a stable category within the Code. *Candidatus* names never had standing in nomenclature and lacked priority. Thus, ecologists were discouraged from describing what they could detect even though it was clearly circumscribable [16]. Technology has evolved enormously in the last two decades, and the current capabilities for characterizing uncultured taxa are nearly the same quality as for the cultured taxa, they just lack pure culture in the laboratory [16]. As we discussed above, your proposal for DNA sequences as type material [59] could solve the major problem in classifying uncultured taxa.

Given the importance of this problem, it is remarkable that there has been more than a two-year delay in the expression of an opinion by the JC-ICSP. The slow motion of the JC-ICSP contrasts with the high speed detection of genome novelty within existing metagenomes [37]. As a consequence, within a few years, the

number of high quality MAGs capable of being classified will surpass the current 16,000 species descriptions. The rapid detection of novel taxa together with the uncontrolled nomenclatural chaos of *candidatus* taxa [31] has the potential to create chaos for cataloguing the vast diversity that is being unveiled. Unless the JC-ICSP takes action soon and allows classification of the uncultured, ecologists will have to take independent actions. Thus, we proposed [16] that ecologists construct their own classification system based on a nomenclatural code that exactly mirrors the ICNP, but with DNA as type material. It would have its own judicial commission supervising the organization of the classified taxa, all under the umbrella of an international independent society (we believe that the ISME would be the most appropriate). In the face of the apparently relaxed attitude of the judicial commission of the ICSP, this would be the best way forward. While it would lead to two parallel nomenclatural systems and taxonomic pluralism [12], we hope that the two systems would converge after a given time. Although undesirable [32], pluralism already exists between the cultured prokaryotes and cyanobacteria [17] and it seems to be the only solution for avoiding the chaos foreseeable in the near future. Actually, I believe that using the ICNP nomenclatural system, but identifying what has not been cultured with a superscript U preceding the generic names, could coexist very well with the current nomenclature. As long as both ruling committees, the JC of the ICSP for the cultured and an hypothetical new committee for the uncultured, cooperate to avoid homonymies, I am sure that pluralism can be the solution in the short term.

Whitman

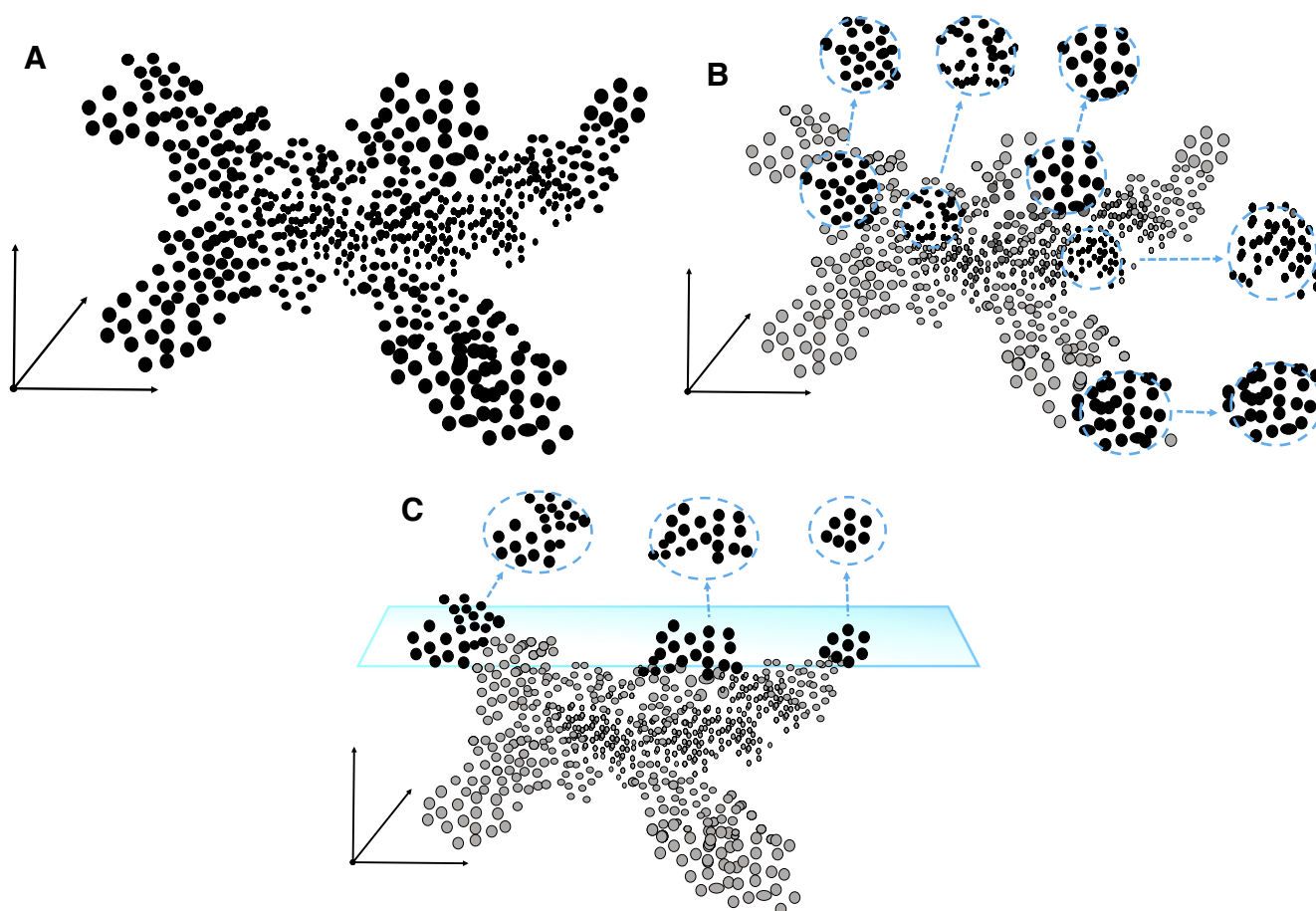
While I admit that pluralism may be the only practical solution in the short term, it should only be considered as a last resort. The nomenclature of the cyanobacteria is a good example of what happens when two nomenclatural systems become institutionalized in the literature. Decades of discussions have failed to resolve the differences between the botanical and bacteriological approaches [33]. Creation of a separate nomenclature for the uncultured taxa has the same risk.

Ironically, the 1990 Code easily included the uncultured. At that time, it was possible to validly name organisms based upon a description, and the genome sequence would certainly serve as an adequate description. The name would then have equal priority with names of cultured species. If the organism was subsequently brought into culture, Rule 18f of the Code allowed designation of a type strain by a simple emendation of the name [20]. In any case, I agree that MAGs have the potential to offer stunning insights into the nature of the prokaryotic world, and the urgency for settling the nomenclatural issues is real.

### **Why is there no official taxonomy and is it feasible to have one?**

Rosselló-Móra

I have always wondered why there is no official classification for *Bacteria* and *Archaea*, a fact that has been often indicated in the literature (*e.g.* Refs. [6,30,48]). This seems to respond to the sentiment that “*taxonomy is partly a matter of judgment and opinion, as is all science, and until new information is available, different bacteriologists may legitimately hold different views. They cannot be forced to agree to any “official classification” [48]*”. This may be directly related to the high degree of freedom that the nomenclatural codes give to taxonomists on how to circumscribe taxa (*e.g.* the ICNP; [36]). However, I would like to emphasize that in practice the taxonomic opinions are often constrained by journal



**Fig. 1.** Representation of the diversity of a population that has adapted to a range of growth conditions and lifestyles in multidimensional space. A. The genetic and functional properties of each member of the population are similar to another member of the population, although not all members of the population are similar to each other. Dimensions might include both chemical and physical factors, such as  $O_2$  partial pressure, pH, availability of organic C and temperature, or lifestyle factors, such as motility, availability of resting stages and symbioses. An irregular distribution in each dimension might result from limitations of the biochemical and physiological abilities of the population to adapt as well as compete with other populations. B. If sampling is incomplete, each sample will appear to represent a discontinuous population with approximately the same amount of diversity. Artifacts of this type could result from sampling geographically limited samples or cultivation studies with a small number of growth conditions. C. Sampling through fewer dimensions than the population exists will artificially truncate the population diversity. This artifact would be common in culturing, where only a limited number of growth conditions are examined, or in studies dealing with very similar environments. For instance, if only the pathogenic strains of a population are examined, a large non-pathogenic portion of the population may not be observed.

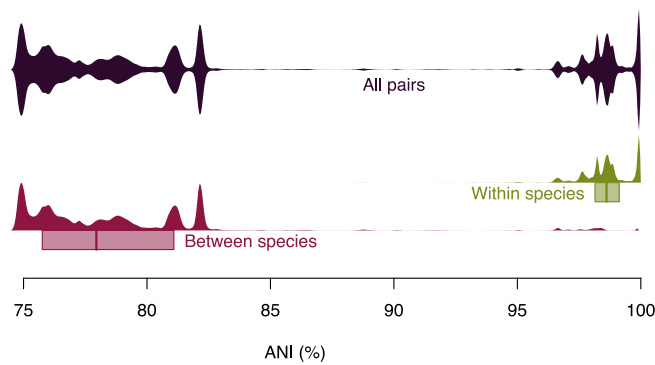
reviewers and editors, as well as recommendations made by *ad hoc* expert committees (e.g. Refs. [49,56]). Thus, behind any new species classification there is a hidden imperative from reviewers and taxonomic experts [17]. Moreover, microbial taxonomy has developed in parallel with technological advances [41] and, in general, the taxa circumscriptions have been shaped ultimately by the experimental methods available at the time. I think that it is unquestionable that genome-derived parameters, such as GC mol% content and DNA–DNA hybridization in the past and *in silico* genome to genome comparisons together with phylogenetic inferences using house-keeping genes today, have shaped the way we envisage species and higher taxa [42,62], which has relegated phenotyping to poor, often meaningless, streamlined descriptions [51].

The current accumulation of genomic data from genomic and metagenomic approaches is revealing a discreteness in the diversity of the prokaryotes [8,15,42] that seems to represent the units we call species. These observations will be even clearer as more genomes are described [15]. Thus, my question is, given the current capabilities for analyzing molecular data and bioinformatically circumscribing taxa, why not construct an official classification based on the generally accepted parameters? As we proposed for the uncultured [16], a single supervised website could harbor lists, digitalized protologues, type material (e.g. DNA sequences), and even

phenotype annotations, along with additional metadata not given in the protologues, all supervised by an official committee and supported by a worldwide recognized society such as IUMS, BISMIS or ISME. An “official” classification of cultivated and uncultivated prokaryotes appears to be a doable and highly needed endeavor.

Whitman

Let’s focus on the three aspects of the question separately. Firstly, in the modern scientific community, taxonomic practice is governed to a large degree by the consensus of the practitioners and not by an official body. The consensus operates through peer review of publications and grants, the ICSP Subcommittees on the Minimum Standards for description of specific groups, and similar informal mechanisms. Assuming that consensus is based on shared knowledge, it is of enormous benefit that ensures the quality of the data and its interpretation, and furthermore it instructs newcomers to the field on the best practices. However, the control of taxonomic practice is not absolute. For instance, even if a major journal will not publish a taxonomic description, often another journal with editors and reviewers of different opinions will. This flexibility allows new ideas to be disseminated rapidly, some of which will become the new consensus. In the



**Fig. 2.** Density plot of a pairwise fastANI comparison of 89,499 genomes, from which 806 million pairs were used. The data were calculated and kindly supplied by Konstantinos Konstantinidis and Luis Miguel Rodríguez-R, and they are an excerpt from their submitted work Jain et al. [15]. The upper plot shows the full set of pairwise comparisons, which are mirrored for aesthetic reasons. The two lower plots show the value distribution in relation to their genome's taxonomic assignment. The middle one shows the intraspecific variability and the lower one the interspecific variability. Boxplots below the density plots indicate the median (line) and inter-quartile range (IQR; in the box) for both categories. Real values were: Intraspecific, median 98.61%; IQR 98.14–99.12%. Interspecific: median 77.95%; IQR 75.76–81.09%.

1980s, 16S rRNA sequencing was introduced into the taxonomic literature in this fashion, first by publications from a relatively small number of investigators and later by becoming the consensus opinion. Currently, taxonomies based on genome sequencing, including the uncultured, are replacing the 16S rRNA sequence classifications and are becoming the new consensus. The flexibility of an ever-changing consensus allows new ideas to be introduced and examined by the wider community. Good ideas may then be widely accepted and become part of the consensus. Your idea of a supervised website combining bioinformatically circumscribed taxa with associated metadata may be one of these good ideas.

Nevertheless, it is difficult to see how an official taxonomy, presumably constructed by some official board of expert taxonomists, would improve on this informal system. We only have fragmentary glimpses of the prokaryotic world through strain isolations and by sequencing environmental DNA, as well as through the genomes of uncultured organisms, and our knowledge of prokaryotic biology remains woefully incomplete. Given the absence of knowledge, a flexible system allowing the rapid sharing of new ideas and their incorporation into a consensus would be a great advantage. An official taxonomy would only slow this process. It would also be inherently misleading and imply that more is known than really is. On the other hand, a recognized taxonomy is occasionally useful. In these cases, a number of unofficial taxonomies based on the consensus are available, such as the LPSN, Bergey's Manual, the NIH classification, and studies by individual laboratories on specific groups. When these are accompanied by full examination of the issues they can be especially valuable, providing a summary of current knowledge and a path forward in the future. In special cases, such as the designation of bioterrorism agents, *ad hoc* committees can make official taxonomic recommendations.

Secondly, even though there have been great advances in systematics in the last decade, especially with the recent revelations from phylogenomics and metagenomics, our ignorance is still profound. Even though we have some reasonable theories of prokaryotic speciation [4,13,24,34], we know little about their general applicability across the prokaryotic world. Likewise, the criteria for higher taxa are largely *ad hoc* and lacking any theoretical basis. Currently, the consensus seems to be forming higher taxa of comparable diversity or phylogenetic depth across different groups of

prokaryotes, but there are few principles guiding these decisions. Therefore, considering these areas of active research, I expect great changes will occur in the next couple of decades as more genomic and metagenomic sequences are accumulated.

Lastly, I am also skeptical about observed discontinuities in the diversity of environmental populations. While exciting, the evidence that these constitute evidence for species must be critically examined to see if they fit the criteria for species or higher level taxonomic groups. First, it is necessary to demonstrate that they are formed by some biological mechanism. Second, they must be shown to represent groups of comparable diversity. Third, it is necessary to eliminate the possibility that they are sampling artifacts. These artifacts could arise in a number of ways. For instance, we can imagine that a prokaryotic population exists in a multidimensional space comprised of dimensions representing possible growth conditions, such as temperature, salinity, pH and organic carbon availability, as well as lifestyle adaptations, such as motility, availability of resting stages and the capacity to form symbioses (Fig. 1). While each member of the population must be closely related to at least one other member, it could also be distantly related to at least some members. For example, all members might possess >99% ANI to another member, but the most diverse pairs might have <85% ANI. Such a population could possess a very irregular “shape” as the distribution in each dimension might result from limitations of the biochemical abilities of the population, as well as competition with other populations. Sampling such a population is subject to many artifacts, and it can be easily incomplete (Fig. 1B). For instance, if culturing is used, enrichment or selective media may only isolate individual strains adapted for a small portion of the multidimensional space occupied by the entire population. Likewise, metagenomic samples from similar environments can also yield similar results because they are again only sampling a portion of the entire space occupied. While these artifacts will certainly be eliminated with more sampling, this has not yet been done.

#### Rosselló-Móra

I completely agree with your view that what we culture is probably distorting our view of the real diversity in nature. However, it seems that naturally occurring communities are indeed formed by discrete units (based on whole genome sequence identities; [8]), and that the latest large-scale genome comparison analyses, with approximately 90,000 genomes and MAGs based on over 8 billion genome pairs [15], seem to reinforce the fact that discrete biological genome groups exist (Fig. 2). Such discreteness reinforces what has been inferred from DNA reassociation techniques supported by half a century of taxonomic research. This conclusion will probably be tested in the very near future as the number of MAGs increases in public repositories. If it remains true, the idea of classifying such discrete units makes sense. In addition, taxonomic classification has always evolved and been restructured according to technological developments. When 16S rRNA gene analyses revealed the polyphyletic nature of *Pseudomonas*, many members of this genus were reclassified into different genera, families, orders, and even classes. Thus, why not start from a standard, universal “official” classification based on discrete genomic groups, which are not necessarily immutable. Most taxonomists can then just follow the major guidelines drawn up by experts and *ad hoc* committees. Using criteria that are generally universally accepted by editors, reviewers and authors, taxonomists will ultimately construct a harmonized catalogue of units that we call species and generally correspond to discrete genomic groups.

## Will we be able to rely on automatic decisions taken by algorithms checking databases on what can be a species, extract the relevant diagnostic data and assign a place in the classification system?

Rosselló-Móra

One of the major drivers for speeding up the description of species, but also one of the major problems in explaining diversity, has been the single strain species descriptions (SSSDs). On the one hand, the use of the 16S rRNA gene sequence to demonstrate taxonomic novelty has been responsible for the large increase of species descriptions since the early 1990s [52]. However, on the other hand, this has promoted an explosion of species classifications based on a single isolate, with poor and streamlined descriptions [51]. The major problem I see is the fact that one species – one description – one paper is allowed [52] as a scientific goal, which promotes a moribund field with low general interest [51].

However, in the current era of high throughput database-based research, taxonomy needs to embrace the opportunities currently available [41]. Most of the molecular analyses can be bioinformatically treated in such a way that even machines could take decisions. Genomes and MAGs can be accumulated in public repositories, such as MiGA [40], where bioinformatic tools can analyze and generate virtual clouds of genomes and MAGs, similar to the gene swarming organization [22]. An ANI threshold of 94–96% could delineate species [14], and an average amino acid identity (AAI) of approximately 70% could delineate genera [18]. In addition, such pipelines can also infer metabolism and, in the future, interact with proteomic, metabolomic and other high throughput phenotypic data to reveal the uniqueness of each genome or MAG cloud. By machine learning, the observation of genomic and phenotypic discreteness will enable computers to decide what is classifiable as a new species. This information, together with an accurate digital protologue [44,45], could serve as the source for an “official” classification. Digital protologues could receive a DOI number that could replace SSSD papers. In conclusion, I can imagine a future where scientists researching in fields different from taxonomy but that detect putative novelty, submit the genomes or MAGs to specialized databases with discovery and classification capabilities. Scientists will only have to prepare a thorough digital protologue to leave their benchmark of discovery.

Whitman

The point of view regarding single strain species description depends somewhat on your area of interest. Having watched colleagues struggle for years to isolate a single strain with some interesting physiological property, I am thrilled when they describe a new species. Their description provides a roadmap for future investigations and is not the end of the story. The second aspect of requiring more than one strain to describe a species is what number of strains should be required and who decides? *E. coli* is one of the few prokaryotic species whose population structure is known. Comprising  $10^{20}$  individuals and possibly  $10^4$  clonal groups [61], it seems unrealistic to expect that its diversity will be described by a small selection of strains. Lastly, all things come with a cost. If multiple strains are required for a species description, are we willing to accept fewer descriptions? In my opinion, we must trust our colleagues to make their own decisions in this matter based on the scientific issues and their personal situations.

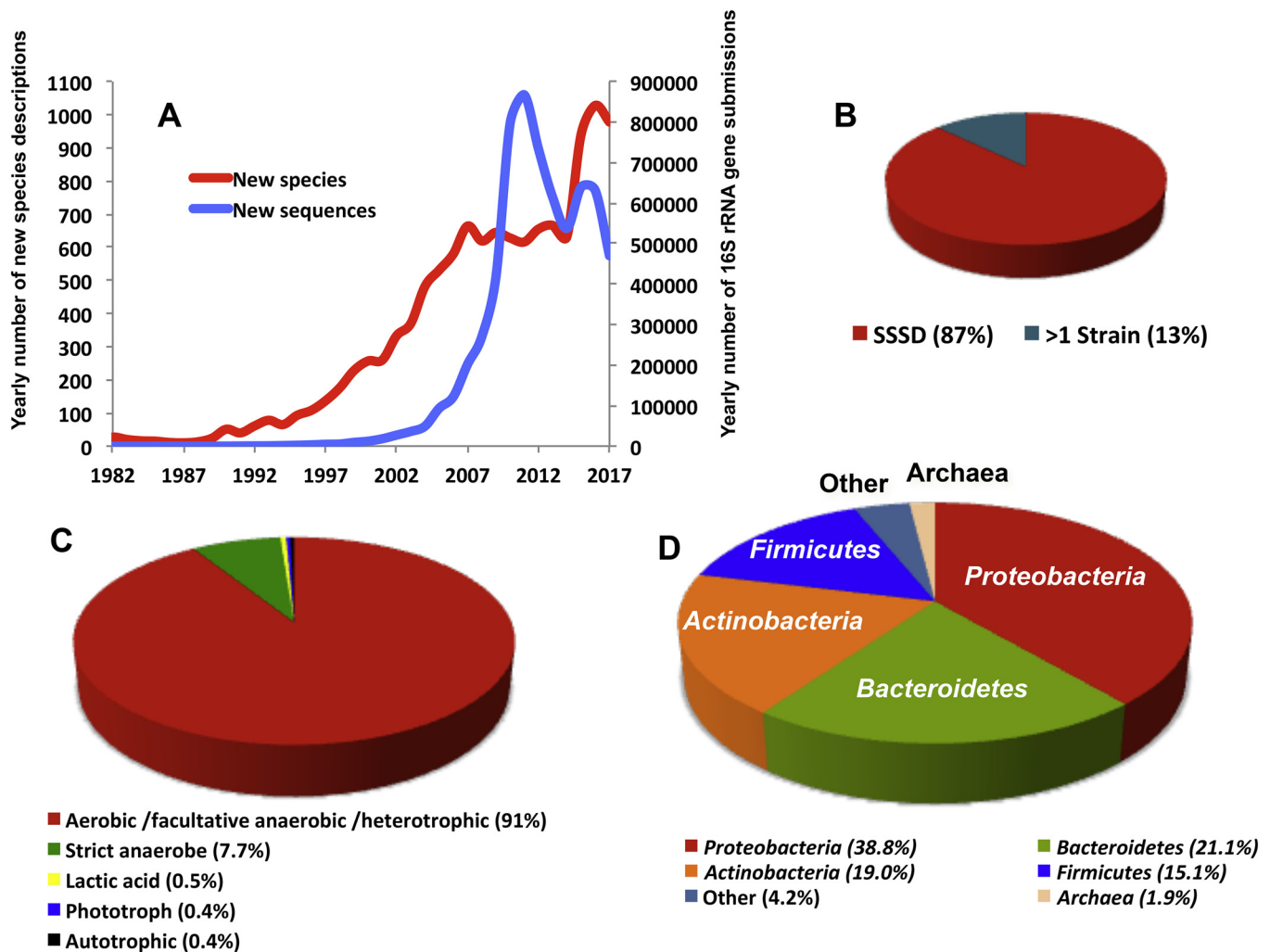
One of the reasons many single strain descriptions are so boring is that the taxonomy journals insist on a large number of chemotaxonomic characters that have no intrinsic interest. While chemotaxonomy was justifiable prior to genomics, it plays little role in modern systematics, which is based almost entirely

on sequence analyses. What then should comprise the description of a novel species? After meeting the criteria of unambiguity and reproducibility, there is no single answer. Nevertheless, we should encourage descriptions that go beyond the minimum. But to what purpose? It is unfair to require researchers to collect data for a database when their time and money could be spent solving their own problems. Instead, we should encourage descriptions that address important biological issues and the reasons for which the organism was isolated. For instance, if a new species is isolated because it stimulates plant growth or degrades some recalcitrant toxin, documentation of these properties should be in the description. In this manner, descriptions become an important research tool for the rest of biology. Importantly, researchers from outside the field of systematics are encouraged to participate rather than be excluded. Since descriptions will differ depending on the taxonomic group, comparative studies will become more difficult. However, when comparative studies beyond genome sequences are justified, resources should be sought for these studies as well.

Regarding the future of systematics, my vision is very similar to yours. I maintain that systematics is intimately entwined with the rest of biology. For the last several decades, we have been creating a description of the prokaryotic world based on three complementary approaches: genomic sequencing, systematics and metagenomics. Together, they allow a detailed description of the entirety of the prokaryotic world. First, in theory at least, the genomic sequence describes the entire potential of an organism. While translating the genome sequence into functional properties is currently difficult, improvements continue to be made. Even though the task is difficult, so far we have not discovered any theoretical reasons why this approach will fail if sufficient resources are expended. Importantly, genomes also reveal properties of great interest that are difficult to measure in the laboratory, such as the complex systems involved in symbiosis, quorum sensing, stress responses and development. Thus, they provide more insight into lifestyle than many of the growth properties typically measured. Second, it is not possible to sequence the genome of every prokaryote, and systematics allows us to infer the properties of organisms from the measured properties of their relatives. It also tells us which properties cannot be inferred and must be measured directly. Systematics is the key here, not only in providing descriptions of individuals but also in discovering the underlying principles of how to predict properties from relationships. This area is particularly exciting. While a great deal of our current research attempts to discover the phylogeny of modern organisms, it is not clear if phylogeny alone will predict most of the properties of cells. I envisage that systematics will need to integrate a variety of approaches in order to address this fundamental goal. Lastly, metagenomics tells us the distribution of prokaryotes in nature. Not only is an organism's environment fundamental to understanding how it functions, but it also informs us of its role in the world and tells us how the world works. Creation of this modern synthesis is the work of thousands of laboratories worldwide. Systematists should embrace their role.

Rosselló-Móra

I do not want to give the wrong impression by criticizing SSSDs, because I mean that, for many of the newly described organisms, the search for additional strains should not be complicated. For example, in our laboratory, we prepare large collections of isolates from a single site that are preliminarily classified by means of MALDI-TOF MS whole cell profiles [55]. For those clusters that do not match any existing profile, we sequence their 16S rRNA in order to reveal their identity and perhaps uniqueness within the classification system. Thus, our laboratory has hundreds of new species identified with more than one strain that could be classified. You



**Fig. 3.** Some metrics on the quality of the new species descriptions. A) shows the yearly increase of new 16S rRNA gene sequences deposited in public repositories with a quality above the thresholds of the SILVA database ([www.arb-silva.de](http://www.arb-silva.de)) referenced in the left Y axis labeled in blue, and the yearly increase of new species descriptions with validly published names as listed in the validation and notification lists of IJSEM. B) shows the proportion of SSSDs and species descriptions with two or more strains in the IJSEM during the period January 2016 to March 2018, and they account for almost 1,750 descriptions. C) shows the proportions of different metabolisms of the species described in the same period shown in B), which had been divided into the following subsections: heterotrophic aerobes or facultative anaerobes, strict anaerobes, lactic acid bacteria, phototrophs and lithoautotrophs. D) shows the proportion of manuscripts dealing with different phyla in the same period previously indicated.

are right that there are groups of fastidious organisms that are difficult to grow and isolate, but they may have special properties that make them appropriate for SSSDs. However, by examining all of the nearly 1750 new descriptions published in IJSEM from January 2016 to March 2018, 87% of them were based on a single strain (Fig. 3) and 91% were aerobes or facultative anaerobes with heterotrophic metabolism. Only 9% could be identified as autotrophic (litho- or photoautotrophic) and 8% were anaerobic. Moreover, 94% of the isolates were from *Proteobacteria* (39%), *Bacteroidetes* (21%), *Actinobacteria* (19%) and *Firmicutes* (15%). Only 6% corresponded to *Archaea* and several different bacterial lineages, which altogether seemed to correspond to a very large part of the uncultured diversity. So, in practice, most of the SSSDs represent organisms that are easily cultivatable with no special features that prevent isolation of additional strains.

### Can the code be modified towards a more simple reader-friendly approach?

Whitman

The Code is one of the great intellectual legacies of the first half of the twentieth century to modern bacteriologists. The General Con-

siderations and Principles elucidated in the first few pages provide a clear direction for nomenclature [36]. Moreover, it establishes priority for species and genera and a system for resolving disagreements as they occur. Importantly, it allows for the straightforward creation of hierarchical taxonomies through the use of types. For instance, in the Code, the names of higher taxa all refer to a type, for instance, the family name refers to a type genus, which refers to a type species, which refers to a type strain. Thus, each name ultimately refers to some biological entity. This feature makes forming taxonomic hierarchies straightforward.

However, when the Code was written, it was unusual to name higher taxa, and most of the Code deals with issues regarding species and genera. Perhaps, as a consequence, the rules are often either contradictory or ambiguous for higher taxa [63]. For instance, I adopt the position first explained to me by Jean Euzéby that the priority of the higher taxa should be based upon the priority of the types. In my opinion, this is the only system that will produce a stable nomenclature for the higher ranks. While there is some justification for this point of view in the Code, there are also contradictory messages as well [53,60]. Therefore, we should consider the Code as a living document and periodically rewrite it. To remain useful, the Code should be suited to our times and reflect our cur-



rent knowledge about prokaryotic biology. Moreover, the language of the Code is often complex and difficult to understand, and some consider it a better sleep aid rather than anything useful. Rewriting the Code to make it easier to read would be very worthwhile.

### Rosselló-Móra

Indeed, I raised this question because the Code is sometimes difficult to follow and, thus, to implement precisely. Only very patient and engaged taxonomists know it well and apply the rules adequately. As the editor of a journal publishing new taxa and not being primarily supervised by the IJSEM nomenclature reviewers, more often than I wished some of our manuscripts lack nomenclatural accuracy. In general, mistakes are due to wrong etymologies, but some cases have been due to a failure in the application of some code rules only really known by the true experts. While this does not abrogate my responsibility in interpreting and knowing the Code, its modernization would create an excellent tool, perhaps based on web support from a database that could help to formulate names. Besides making the effort to simplify the written text of the Code, I really think that we are in the era of informatics and, based on current text mining, database management and machine learning, an interactive and easily interpreted Code should be feasible. Such an interactive database-based code may even allow a future informatically-driven, automatic way of classifying taxa, as discussed in a previous question.

### Acknowledgements

RRM acknowledges Kostas Konstantinidis and Luis Miguel Rodríguez-R for providing Fig. 2 that was produced as an excerpt from their own results; and their whole laboratory team for their support and help in calculating the numbers provided in Fig. 3. RRM's research is funded by the Spanish Ministry of Economy projects CLG2015.66686-C3-1-P, which is also supported with European Regional Development Fund (FEDER) funds. WBW acknowledges support from the NSF Dimensions in Biodiversity grant OCE-1342694.

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