

Considerations and consequences of allowing DNA sequence data as types of fungal taxa

Juan Carlos Zamora¹, Måns Svensson¹, Roland Kirschner², Ibai Olariaga³, Svengunnar Ryman¹, Luis Alberto Parra⁴, József Geml⁵, Anna Rosling⁶, Slavomír Adamčík*, Teuvo Ahti, M. Catherine Aime, A. Martyn Ainsworth, László Albert, Edgardo Albertó, Alberto Altés García, Dmitry Ageev, Reinhard Agerer, Begonia Aguirre-Hudson, Joe Ammirati, Harry Andersson, Claudio Angelini, Vladimír Antonín, Takayuki Aoki, André Aptroot, Didier Argaud, Blanca Imelda Arguello Sosa, Arne Aronsen, Ulf Arup, Bitá Asgari, Boris Assyov, Violeta Atienza, Ditte Bandini, João Luís Baptista-Ferreira, Hans-Otto Baral, Tim Baroni, Robert Weingart Barreto, Henry Beker, Ann Bell, Jean-Michel Bellanger, Francesco Bellù, Martin Bemmann, Mika Bendiksby, Egil Bendiksen, Katriina Bendiksen, Lajos Benedek, Anna Bérešová-Guttová, Franz Berger, Reinhard Berndt, Annarosa Bernicchia, Alona Yu. Biketova, Enrico Bizio, Curtis Bjork, Teun Boekhout, David Boertmann, Tanja Böhning, Florent Boittin, Carlos G. Boluda, Menno W. Boomsliuter, Jan Borovička, Tor Erik Brandrud, Uwe Braun, Irwin Brodo, Tatiana Bulyonkova, Harold H. Burdsall Jr., Bart Buyck, Ana Rosa Burgaz, Vicent Calatayud, Philippe Callac, Emanuele Campo, Massimo Candusso, Brigitte Capoen, Joaquim Carbó, Matteo Carbone, Rafael F. Castañeda-Ruiz, Michael A. Castellano, Jie Chen, Philippe Clerc, Giovanni Consiglio, Gilles Corriol, Régis Courtécuisse, Ana Crespo, Cathy Cripps, Pedro W. Crous, Gladstone Alves da Silva, Meiriele da Silva, Marjo Dam, Nico Dam, Frank Dämmrich, Kanad Das, Linda Davies, Eske De Crop, Andre De Kesel, Ruben De Lange, Bárbara De Madrigal Bonzi, Thomas Edison E. dela Cruz, Lynn Delgat, Vincent Demoulin, Dennis E. Desjardin, Paul Diederich, Bálint Dima, Maria Martha Dios, Pradeep Kumar Divakar, Clovis Douanla-Meli, Brian Douglas, Elisandro Ricardo Drechsler-Santos, Paul S. 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Nagy, Maria Alice Neves, Tuomo Niemelä, Pier Luigi Nimis, Nicolas Niveiro, Machiel E. Noordeloos, Anders Nordin, Sara Raouia Noumeur, Yuri Novozhilov, Jorinde Nuytinck, Esteri Ohenoja, Patricia Oliveira Fiuza, Alan Orange, Alexander Ordynets, Beatriz Ortiz-Santana, Leticia Pacheco, Ferenc Pál-Fám, Melissa Palacio, Zdeněk Palice, Viktor Papp, Kadri Pärtel, Julia Pawlowska, Aurelia Paz, Ursula Peintner, Shaun Pennycook, Olinto Liparini Pereira, Pablo Pérez Daniëls, Miquel À. Pérez-De-Gregorio Capella, Carlos Manuel Pérez del Amo, Sergio Pérez Gorjón, Sergio Pérez-Ortega, Israel Pérez-Vargas, Brian A. Perry, Jens H. Petersen, Ronald H. Petersen, Donald H. Pfister, Chayanard Phukhamsakda, Marcin Piątek, Meike Piepenbring, Raquel Pino-Bodas, Juan Pablo Pinzón Esquivel, Paul Pirot, Eugene S. Popov, Orlando Popoff, María Prieto Álvaro, Christian Printzen, Nadezhda Psurtseva, Witoon Purahong, Luis Quijada, Gerhard Rambold, Natalia A. Ramírez, Huzefa Raja, Olivier Raspé, Tania Raymundo, Martina Réblová, Yury A. Rebriev, Juan de Dios Reyes García, Miguel Ángel Ribes Ripoll, Franck Richard, Mike J. Richardson, Víctor J. Rico, Gerardo Lucio Robledo, Flavia Rodrigues Barbosa, Cristina Rodriguez-Caycedo, Pamela Rodriguez-Flakus, Anna Ronikier, Luis Rubio Casas, Katerina Rusevska, Günter Saar, Irja Saar, Isabel Salcedo, Sergio M. Salcedo Martínez, Carlos A. Salvador Montoya, Santiago Sánchez-

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¹Museum of Evolution, Uppsala University, Norbyvägen 16, 75236 Uppsala, Sweden; corresponding author e-mail: jczamora@em.uu.se

²National Central University, Taoyuan City, Taiwan

³Universidad Rey Juan Carlos, 28933 Móstoles, Madrid, Spain

⁴Avenida Padre Claret 7, 5^o G, 09400 Aranda de Duero, Burgos, Spain

⁵Naturalis Biodiversity Center, Vondellaan 55, 2332AA Leiden, The Netherlands

⁶Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 75236 Uppsala, Sweden

*A first version of this text was prepared by the first eight authors and the last one. The other listed co-authors support the content, and their actual contributions varied from only support to additions that substantially improved the content. The full details of all co-authors, with their affiliations, are included in Supplementary Table 1 for reasons of clarity and space.

Abstract: Nomenclatural type definitions are one of the most important concepts in biological nomenclature. Being physical objects that can be re-studied by other researchers, types permanently link taxonomy (an artificial agreement to classify biological diversity) with nomenclature (an artificial agreement to name biological diversity). Two proposals to amend the International Code of Nomenclature for algae, fungi, and plants (ICN), allowing DNA sequences alone (of any region and extent) to serve as types of taxon names for voucherless fungi (mainly putative taxa from environmental DNA sequences), have been submitted to be voted on at the 11th International Mycological Congress (Puerto Rico, July 2018). We consider various genetic processes affecting the distribution of alleles among taxa and find that alleles may not consistently and uniquely represent the species within which they are contained. Should the proposals be accepted, the meaning of nomenclatural types would change in a fundamental way from physical objects as sources of data to the data themselves. Such changes are conducive to irreproducible science, the potential typification on artefactual data, and massive creation of names with low information content, ultimately causing nomenclatural instability and unnecessary work for future researchers that would stall future explorations of fungal diversity. We conclude that the acceptance of DNA sequences alone as types of names of taxa, under the terms used in the current proposals, is unnecessary and would not solve the problem of naming putative taxa known only from DNA sequences in a scientifically defensible way. As an alternative, we highlight the use of formulas for naming putative taxa (candidate taxa) that do not require any modification of the ICN.

Key words:

IMC11
nomenclature
speciation
taxonomy
typification
voucherless fungi

Article info: Submitted: 14 May 2018; Accepted: 21 May 2018; Published: 24 May 2018.

INTRODUCTION

Hawksworth *et al.* (2016) recently submitted a set of proposals to modify the *International Code of Nomenclature for algae, fungi, and plants* (ICN), aimed at allowing DNA sequences without vouchered specimens to serve as types for fungal taxon names. These proposals were first rejected by the Nomenclature Committee for Fungi (see Turland & Wiersema 2017) and subsequently by the XIX International Botanical Congress (IBC) in Shenzhen, China, in 2017. At the same time, a Special-purpose Committee on DNA sequences as types was proposed to explore and carefully discuss this issue, paving the way for further debate during the next IBC in Rio de Janeiro in 2023 (Turland *et al.* 2017).

However, apparently because of a perceived urgency in the establishment of a system for naming putative new taxa known only from DNA sequences, the same proposals were

recently re-published (Hawksworth *et al.* 2018) with the intent that they be discussed and voted on at the forthcoming 11th International Mycological Congress (IMC11) in Puerto Rico in July 2018. The proposals aim at allowing the formal naming of fungal taxa only known by DNA sequences (the “dark matter fungi” of Grossart *et al.* 2016), by authorizing the DNA sequence itself to be the type of a taxon name in the absence of a specimen.

The ICN attempts to create “the provision of a stable method of naming taxonomic groups, avoiding and rejecting the use of names that may cause error and ambiguity or throw science into confusion” (Preamble 1). This provision relies on the use of the nomenclatural type, “the face — the desiccated, flattened face to be sure, but still the face — that is attached to the name of a species” (Daston 2004).

In our opinion, the fungal-specific amendments proposed to the ICN by Hawksworth *et al.* (2018) should be rejected on

the grounds that they would have major negative implications for fungal nomenclature and systematics, or more specifically, violate Preamble 1, promote irreproducible science, and fundamentally change the meaning of the type concept compared to how it has been applied during the last century. An informed debate is needed to avoid any unwanted effects of a rushed decision.

THE PROPOSALS

The proposals of Hawksworth *et al.* (2018) intend to insert a single article, Art. F.4.2, through proposal (F-005), followed by three recommendations, Rec. F.4A.1-3, through proposal (F-006). As only Art. F.4.2 would be mandatory, it is crucial to evaluate proposal (F-005) in particular detail: “(F-005) Insert a new paragraph after Art. F.4.1 as follows: F.4.2. In fungi, when DNA sequence data corresponding to a new taxon have been detected, but no physical specimen has been found to serve as the type of the name of the new taxon (Art. 8.1–8.4), the type may be composed of DNA sequence data deposited in a public repository.”

The recommendations that follow suggest, in summary, that “the new taxon should be described with reference to a published phylogenetic analysis” (Rec. F.4A.1), that the new taxon “should be represented by multiple sequences obtained in independent studies” (Rec. F.4A.2), and that the sequence should derive from “the molecular regions that are appropriate for delimiting species” (Rec. F.4A.3). These are merely recommendations, however, and need not be followed (as emphasized by Turland & Wiersema 2017).

SPECIES VERSUS DNA SEQUENCES

It has been argued that “the *Code* serves only to regulate the valid publication of names, not to pass judgment on the scientific hypotheses embodied in names” (Herr *et al.* 2015). Although nomenclature can be seen as a “remarkable act of applied metaphysics” (Daston 2004), the circumscription of the taxa being named is a fundamentally scientific process. The proposal recommends that a new taxon “be described with reference to a published phylogenetic analysis” (Rec. F.4A.1 of proposal F-006). This wording implies that it is possible to first circumscribe a new taxon by phylogenetic analysis, then name the new taxon using a DNA sequence type that can be unequivocally associated with the new taxon. For the reasons outlined below, this may not readily be the case at the level of species in recombining organisms, which we suspect is where Art. F.4.2 is most frequently going to be applied.

Assuming that species are understood as somehow separately evolving units (e.g. de Queiroz 1998, 2005, 2007, Hey 2006), they can, sooner or later after formation, be detected using a variety of methods (often misleadingly termed ‘species concepts’; Hey 2006), e.g. reproductive isolation (the ‘biological species concept’), morphology, or genealogical monophyly with or without auxiliary criteria like concordance among genes (corresponding to the genetic versions of ‘phylogenetic species concept’). During a simple

divergence of one ancestral species into two daughter species, (nearly) neutral loci will inherit random samples of alleles from the ancestral species, some of which are likely to be shared across the daughter species (ancestral polymorphisms). Given time, ancestral alleles will go extinct randomly and new alleles will arise, in the most likely case causing species to appear non-monophyletic on the gene trees. Finally, species will achieve reciprocal monophyly on the gene trees. This process has been known and described in the literature for decades (e.g. Tajima 1983, Takahata & Nei 1985, Neigel & Avise 1986, Nei 1987, Pamilo & Nei 1988, Takahata 1989, Avise & Ball 1990, Hudson *et al.* 1992, Hey 1994, Harrison 1998, Avise 2000, Hudson & Coyne 2002, Rosenberg 2003, Coyne & Orr 2004, Naciri & Linder 2015) and has been elegantly explained and illustrated by, for example, Leliaert *et al.* (2014). The lag time from lineage divergence until reciprocal monophyly in neutral loci will depend on the effective population size, generation time, and population structure (Hudson 1990, Wakeley 2000) and its duration will vary stochastically between nuclear loci in recombining organisms (Hudson & Turelli 2003). Obviously, any species recognition protocol requiring reciprocal monophyly will only be able to detect the species long after they diverged (Hudson & Coyne 2002). Positive selection can substantially shorten the time it takes to remove ancestral polymorphisms and finally reach reciprocal monophyly. The proportion of the genome undergoing positive selection during and after speciation appears to be small, however, probably reaching at most a few per cent (e.g., 1.1 and 1.7 % of the genes in humans and chimpanzee, respectively; Bakewell *et al.* 2007). As an aside, the stochastic process finally leading to reciprocal monophyly in the individual genes also means that there cannot exist a universal divergence threshold for delimiting fungal (or other) species using DNA sequences, not for the very widely used internal transcribed spacer (ITS) region in fungi (e.g. Nilsson *et al.* 2008, Badotti *et al.* 2017), nor any other DNA region in any organism group (e.g. Meier *et al.* 2006 concerning metazoans).

Gene histories, a standard product in applied phylogenetics, cannot automatically be equated with the species history (e.g. Tajima 1983, Pamilo & Nei 1988, Maddison 1997, Knowles & Carstens 2007). There is no reason to think that any DNA region or any organism group is free of mechanisms that create a discordance between the gene and species histories. Such mechanisms have been found to be widespread across the tree of life (e.g. Sota & Vogler 2001, Rautenberg *et al.* 2008, Blanco-Pastor *et al.* 2012, Kutschera *et al.* 2014, Lamichhaney *et al.* 2015, Garrido *et al.* 2017, Kudryavtseva & Gladkikh 2017, Meyer *et al.* 2017, Parks *et al.* 2017, Peyrégne *et al.* 2017, Vd’áčný 2017). Incongruence between gene histories, demonstrating that at least some of them must be different from the history of the species, has indeed also been demonstrated to occur in the fungi (e.g. O’Donnell & Cigelnik 1997, Sung *et al.* 2007, Harder *et al.* 2013, Altermann *et al.* 2014, Saag *et al.* 2014, Stewart *et al.* 2014). A conflict between the gene histories and species history is not only caused by the randomness of genetic drift described above. Other mechanisms, all observed also in fungi, obscure relationships among taxa

and some (the first three) have the potential to cause non-identifiability of a single DNA sequence: the exchange of entire nuclei between heterospecific fungal syncytia, horizontal gene transfer, hybridization (sometimes followed by introgression or allopolyploidy), gene duplication (including also pseudogene and *numt* formation), and intra-individual variability in the ribosomal DNA repeat caused by limits to concerted evolution (Dean *et al.* 2005, Ruths & Nakhleh 2005, Jeffroy *et al.* 2006, Neafsey *et al.* 2010, Ellison *et al.* 2011, Lindner & Banik 2011, Roper *et al.* 2011, Hughes *et al.* 2013, Li *et al.* 2013, Lindner *et al.* 2013, Gladieux *et al.* 2014, Som 2014, Naciri & Linder 2015, Shapiro *et al.* 2016, Thiéry *et al.* 2016, Fourie *et al.* 2017, Li *et al.* 2017, Hughes *et al.* 2018, Steenkamp *et al.* 2018). Obviously, species delineations generated from a single marker cannot be evaluated using data from the same marker, because that would make the argument circular.

We conclude that a DNA sequence of an allele cannot be seen as “corresponding to” any taxon (the wording of the proposal), but represents the diversity of alleles of the gene from which it was derived. An allele cannot be expected to be unique to the species from which it was derived and we cannot know whether or not alleles are unique to a species when sequence data are only available from a single or a limited number of markers and individuals (e.g. the popular ITS barcode in fungi; Schoch *et al.* 2012, Badotti *et al.* 2017). “If species membership is contingent for organisms in general, it ought to be contingent for those chosen as the type specimens for their species” (Levine 2001). Having said that, some of these pitfalls are more easily detected and remedied when the number of markers is high and methods designed to handle them (including but not limited to versions of the ‘phylogenetic analysis’ prescribed by Rec. F.4A.1) are applied (Dupuis *et al.* 2012, Fujita *et al.* 2012).

IMPACT ON NOMENCLATORIAL TYPES (SPECIMENS VERSUS DNA SEQUENCES)

An acceptance of the proposal would fundamentally alter the meaning of nomenclatorial types. This is because instead of using a physical object as the type of a name, we would just use information from a character of the organism as the type. Indeed, the parallel to the designation of a DNA sequence as a type would be the designation of information extracted from organisms (specimens) as types, not with the designation of specimens as types. In other words, this would be akin to designating a sample of spore measurements as the type of an organism. It should be noted that the possibility to select a description as a type existed before the publication of the *Berlin Code* in 1988. However, this option was eventually rejected by the scientific community, and removed from the *Berlin Code* with this note in the Preface: “The provision that existed for a type to be a description under certain circumstances — something that many felt amounted to a repudiation of the type method — has been deleted from the *Code*” (Greuter *et al.* 1988: viii).

Names of taxa are applied to organisms, not to characters of those organisms. Therefore, a physical object should preferably serve as the type of a name, rather than the

characteristics of that object. By allowing already extracted data, such as a DNA sequence, to serve as type instead of the source of the data, new information cannot be obtained when this is required (see below). In addition, we suspect that bypassing the current concept of a type is often unnecessary, because techniques exist to visualize fungal DNA with high specificity (Baschien *et al.* 2001, Behrens *et al.* 2003, Inácio *et al.* 2003, Baschien *et al.* 2008, Vági *et al.* 2014, Spribille *et al.* 2016). Although not yet standard parts of the mycological toolbox, such techniques can with relative ease be applied to locate physical specimens even for taxa that cannot currently be cultivated.

According to the ICN, a nomenclatorial type is “that element to which the name of a taxon is permanently attached, whether as the correct name or as a synonym” (Art. 7.2). For species-level taxa and infraspecific taxa, which are the basic units in taxonomy, a type is “either a single specimen conserved in one herbarium or other collection or institution, or an illustration” (Art. 8.1). Why have researchers agreed to keep these definitions for such a long time? The answer is straightforward: because types are an almost never-ending source of information, as they can be analyzed by different people using different methods and thus provide new answers. Every time a type specimen is re-examined, there is an opportunity to extract new information, which may be useful for solving problems that are constantly arising as our knowledge increases. Most types are specimens (especially nowadays) because a specimen of any living organism is such a complex entity that it is hard to imagine us being able to extract all the possible information contained in it. These properties have already been considered in an editorial of *IMA Fungus* written by the President of the International Mycological Association (Seifert 2017). Therefore, even though the problem of non-unique characters used for diagnosis is not restricted to sequence data, the crucial distinction from morphological descriptions of biological type specimens is that having a DNA sequence as type virtually precludes the obtaining of any new information to resolve any taxonomic problems. In contrast, even illustrations, which are now accepted as types only in very specific situations (see Art. 40.5 for the current use of these) and increasingly falling into disuse, may be a source of overlooked information.

Epitype selection may be seen as a possible solution in the expected cases when the DNA sequence alone is insufficient for the precise application of the name of a taxon (Ryberg & Nilsson 2018). Epitypification was conceived as a practical solution in cases when the type of a name turns out to be ambiguous (ICN, Art. 9.8). Epitypes are frequently designated for old names, and they are not free of undesired problems affecting nomenclatorial stability (Rindi *et al.* 2017). Epitypifications have to be based on an existing type, and are often being made because our knowledge or the present technology are the limits for extracting the needed information from the type that already exists. Those limitations may be overcome by other researchers or by new technologies in the future. For DNA sequence data, the type itself would always be the limiting bottleneck, regardless of the researcher’s skills or the progress of science.

IMPACT ON NAMES OF TAXA AND FUTURE TAXONOMIC STUDIES

The main argument used by Hawksworth *et al.* (2016), to justify the urgency of allowing DNA sequences as types, is that taxa only known from DNA sequences “require scientific names in order to facilitate communication about them”. While researchers indeed need names of taxa to communicate among colleagues and with the general public, those names are linked to information that makes them useful, like biology, distribution, ecology, morphology, physiology, pathology, etc. (Crous *et al.* 2015). In other words, we are using scientific names because they are meaningful to a wide range of people.

In addition, taxonomists are aware that an increased number of validly published names will not necessarily facilitate communication. On the contrary, in the not uncommon situation in which the same taxon has been named on several occasions, much confusion may arise until the identity of those names is finally settled. Indeed, taxa based solely on DNA sequences not precisely matching any of those present in public repositories have already been described and fallen into more or less immediate synonymy, because the necessary comparisons with previously described taxa were not undertaken (Gams 2016). The proposals would promote such bad practice.

An undesired side-effect that should also be considered is that, in practice, few researchers will be devoted to re-describing (or actually describing) species that have been previously named based on just a DNA sequence. This has several causes, but among them, there is an important bias in research journals disfavoring the publication of re-descriptions of already known taxa, *versus* the description of new taxa. Another reason is time constraints, since it is not uncommon that specialists do not have the time to properly describe all of the numerous undescribed species they are aware of. This makes them focus on those that are more likely to be published as new species and not on those that have been already described, even if previous descriptions are faulty or defective. Anyhow, having numerous names only based on DNA sequences and few descriptions of the actual organisms would create an enormous number of validly published names applied to taxa for which virtually no information exists.

RELIABILITY AND EXTENT OF DATA

The proposed Art. F.4.2. effectively means that any DNA sequence of any region and extent, generated by any procedure or taken from a public repository, could serve as the type of a name of a taxon somehow indicated to be new. In practice, the sequence selected as the type could range from an oligonucleotide to the entire genome. The proposal provides very little guidance, except for the recommendations that the type sequence should be represented by “multiple sequences” and that the selected marker should be “appropriate for delimiting species” (proposed Rec. F.4A.2, F.4A.3). It is not clear what ‘multiple’ means or how a marker is established as universally ‘appropriate’. One can

infer, however, that the ‘appropriate’ marker will, in most applications, be the ITS region, which has been dubbed as the primary barcode marker in fungi (Schoch *et al.* 2012).

A major concern is the reliability of the DNA sequence data (Bridge *et al.* 2003, Nilsson *et al.* 2006). PCR or cloning errors (including the introduction of chimeras), DNA degradation, and post-processing of chromatograms, have been shown to be a source of sequence variation in at least some groups (Haas *et al.* 2011, Sandoval-Sierra *et al.* 2014, Hughes *et al.* 2015, Strid *et al.* 2015, Aas *et al.* 2017, Nilsson *et al.* 2017, Thielecke *et al.* 2017, Bieker & Martin 2018). Such DNA sequences are not real and cannot be checked or corrected without access to a physical specimen or, as a minimum, access to the raw sequence reads (Tripp & Lendemer 2014). If accepted as types, this means mycology would embrace irreproducible science.

The concerns outlined here, in combination with the risk of comparing non-orthologous sequences or incompletely concerted copies of the ribosomal DNA, are really about scientific quality and not nomenclature *per se*. However, nomenclature assumes that taxa are first delineated, then named. The proposal, if implemented, would risk opening the floodgates to poor data and questionable scientific practice being translated into formally named taxa that will throw fungal taxonomy into paralysis and disrepute.

CANDIDATE NAMES

If we really want to strive for a comprehensive code of nomenclature able to cover all living organisms, it is necessary to consider the rules of the other existing codes of nomenclature. For our purposes, these are mainly the International Code of Zoological Nomenclature (ICZN; Ride *et al.* 1999) and the International Code of Nomenclature of Prokaryotes (ICNP; Parker *et al.* 2015). Also, it is important to consider the use of nomenclature by specialists in different taxonomic groups. In general, we think it is better to strive for standardization of rules instead of sharpening the differences between Codes. The goal should be to create a solid code of nomenclature that, some day, may perhaps cover all living organisms with all their peculiarities (e.g. the BioCode initiative; Greuter *et al.* 2011, <http://www.bionomenclature.net/biocode2011.html>).

An interesting formula concerning taxa that cannot be properly described under the rules of a code of nomenclature is the use of the term “*Candidatus*”. Originally, this working term was proposed by Murray & Schleifer (1994), and soon after improved by Murray & Stackebrandt (1995) for “describing prokaryotic entities for which more than a mere sequence is available but for which characteristics required for description according to the Code are lacking”. It was proposed because, under the rules of the ICNP, a prokaryotic organism can only be validly described if the type, which in this case is a living strain, can be conserved as an axenic culture. There are of course thousands of prokaryotic taxa that are not cultivable in such a way. Many of them can, however, be studied with regard to morphology, ecology, metabolism, DNA data, etc. For fungi, having such additional information for a particular cluster of DNA sequences (never a single one), or several

DNA regions from the same organism (ultimately and ideally, a complete genome), would be essential to ensure that a true taxon is being provisionally named, and to comply with basic scientific standards.

The *Candidatus* working term has proved to be a good solution for microbiologists who want to respect the rules of the ICNP as well as to apply useful names to certain taxa. Being aware that important information (e.g. a proper living strain as type) is lacking to allow a formal description, such taxa can be validated when the requirements of the ICNP are fulfilled. The best example of how well this alternative nomenclature works is the Candidate Phyla Radiation, a huge, well-known and well-communicated group of Bacteria that was proposed based on the combined information of hundreds of genomes, obtained from single cells as well as metagenomics (Hug *et al.* 2016, Danczak *et al.* 2017).

The alternative of using preliminary names for taxa only known from DNA data has already been proposed by Öpik *et al.* (2009) as “virtual taxa”, by Taylor (2011) as “ENAS fungi”, by Kõljalg *et al.* (2013) as “species hypothesis”, and indeed also by Hibbett *et al.* (2011) as “candidate species”. We think this is an interesting idea that should be further explored and discussed in the future. Such candidate names can be re-evaluated and possibly formally described in the future when enough information has become available to provide a good taxon description (see also Seifert 2017). Finally, they could be used with some freedom, since no specific rules within the codes of nomenclature apply for invalidly published names. If a major concern about fungi only known from DNA sequences is that “they do not enter names-based taxonomic databases” (see Herr *et al.* 2015), a reasonably easy solution would be to allow the registration of candidate or putative names in those databases, in the process making it clear that those names have not yet been validly published because one or more of the requirements for valid publication are lacking (e.g. <http://www.bacterio.net/-candidatus.html> for candidate names of prokaryotic taxa).

CONCLUSIONS

We consider the proposals by Hawksworth *et al.* (2018) highly problematic for the following reasons:

- DNA sequence types will have a very low information content; subsequent extraction of additional data or verification of the already extracted data will not be possible.
- Two different taxa may share identical DNA sequences at a given locus, even for already tested barcoding markers. Conversely, not all members of a species can be assumed to share the same DNA sequence at a specific locus.
- Intraspecific (or even intraindividual) differences in the DNA sequence of a marker may be comparable to or exceed interspecific differences.
- Some DNA sequences generated through different sequencing techniques may be artifacts and consequently not represent reality. The proposal does not say anything

about data validation other than a recommendation that the DNA sequence should be represented by ‘multiple sequences’.

- The proposal promotes the mechanical production of taxon names based on minor sequence divergence, without taking any other data (such as genetic variability or already described taxa) into account. Much downstream time will have to be spent by future mycologists gathering additional information.
- As taxa with DNA sequence types accumulate, the description of a new species will be increasingly difficult without DNA sequence data. Describing new species based on the morphology of unsequenced material will in practice not be feasible if the possibility exists that this species has been described based on a DNA sequence.
- Since the proposals allow any part of the genome to be used as a DNA type, situations in which different taxa may have been described using different parts of the genome will force researchers to sequence a variety of loci to establish whether an earlier name already exists. Likewise, a single taxon may be described as novel several times using different genomic regions as type. This will be impossible to detect without a specimen from which different genomic regions can be sequenced and may contribute to the description of unnecessary new names.

FINAL REMARKS

As discussed above, there are alternative ways of communicating the existence of taxa only known from DNA data, which do not require modifications to the ICN. Instead of allowing DNA data as types for taxon names, database registration of candidate names can be used for putative new taxa, when their existence has been made plausible based on various sources of information (including but not limited to DNA sequences). A functional system for environmental sequences under the *Candidatus* or species hypotheses approach could result from a carefully selected set of requirements to ensure high-quality data and reproducibility.

We submit that proposals F-005 and F-006, for the reasons outlined here, will not solve the problems they are intended to solve, disregard knowledge acquired through decades of research in the genetics of speciation, and will instead create confusion and substantial extra work for contemporary and future mycologists. We all have the responsibility to maintain the scientific standards of reproducibility as well as to provide well-considered rules for coming generations, so they can improve on our work and take appropriate, well-informed taxonomic decisions using all available information.

ACKNOWLEDGEMENTS

We want to express our gratitude to all people who enriched both the text and our views by generously sharing their opinions and scientific experience.

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Supplementary Table 1.

Name	Affiliation
Slavomír Adamčík	Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravská cesta 9, 845 23 Bratislava, Slovakia
Teuvo Ahti	Finnish Museum of Natural History, P.O. Box 7, 00014 University of Helsinki, Finland
M. Catherine Aime	Purdue University, 915 W. State St., West Lafayette, Indiana 47907, U.S.A.
A. Martyn Ainsworth	Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom
László Albert	Hungarian Mycological Society, 1087 Könyves Kálmán krt. 40, Budapest, Hungary
Edgardo Albertó	Instituto de Investigaciones Biotecnológicas-Instituto Tecnológico de Chascomús, Universidad Nacional de San Martín-Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina
Alberto Altés García	Facultad de Biología, Ciencias Ambientales y Química, Universidad de Alcalá, 28805 Alcalá de Henares, Madrid, Spain
Dmitry Ageev	SIGNATEC Ltd., 630090, Novosibirsk, Akademgorodok (Novosibirsk Scientific Center), Inzhenernaya str., 22, Russia
Reinhard Agerer	Ludwig-Maximilians-Universität München, Menzinger Str. 67, 80638 München, Germany
Begona Aguirre-Hudson	Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom
Joe Ammirati	University of Washington, Seattle, Washington 98195-1800, U.S.A.
Harry Andersson	Eichhahnweg 29a, 38108 Braunschweig, Germany
Claudio Angelini	Jardín Botánico Nacional Dr. Rafael Ma. Moscoso, Apartado 21-9, Santo Domingo, Dominican Republic
Vladimír Antonín	Moravian Museum, Zeny trh 6, 659 37 Brno, Czech Republic
Takayuki Aoki	Genetic Resources Center, National Agriculture and Food Research Organization, 2-1-2 Kannondai, Tsukuba, Ibaraki 305-8602, Japan
André Aptroot	ABL Herbarium, G.v.d.Veenstraat 107, 3762 XK Soest, The Netherlands
Didier Argaud	40 rue du Justemont, 57290 Fameck, France
Blanca Imelda Arguello Sosa	Instituto Tecnológico de Ciudad Victoria, Tecnológico Nacional de México, Ciudad Victoria, Tamaulipas, Mexico
Arne Aronsen	Torødveien 54, 3135 Torød, Norway
Ulf Arup	Biological Museum, Lund University, Box 117, 221 00 Lund, Sweden
Bitá Asgari	Iranian Research Institute of Plant Protection, Agricultural Research, Education and Extension Organization, Tehran, Iran
Boris Assyov	Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Str., 1113 Sofia, Bulgaria
Violeta Atienza	Facultad de Ciencias Biológicas, Universitat de València, C/Dr Moliner 50, 46100, Burjasot, Valencia, Spain
Ditte Bandini	Panoramastr 47, 69257 Wiesenbach, Germany
João Luís Baptista-Ferreira	Instituto de Biosistemas e Ciências Integrativas, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal
Hans-Otto Baral	Blaihofstr. 42, 72074 Tübingen, Germany
Tim Baroni	The State University of New York, 340 Bowers Hall, P.O. Box 2000, Cortland, New York 13045, U.S.A.
Robert Weingart Barreto	Universidade Federal de Viçosa, 36570-000, Viçosa, Minas Gerais, Brazil
Henry Beker	(1) Royal Holloway, University of London, United Kingdom; (2) Botanic Garden Meise, Nieuwelaan 38, 1860 Meise, Belgium
Ann Bell	45 Gurney Road, Lower Hutt, New Zealand
Jean-Michel Bellanger	CEFE UMR5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, INSERM, 1919 Route de Mende, 34293 Montpellier Cédex 5, France
Francesco Bellù	Naturmuseum of Bolzano, CP 104, 39100, Bolzano, Italy
Martin Bemann	Kleingemünderstraße 111, 69118 Heidelberg, Germany
Mika Bendiksby	NTNU, University Museum, Norwegian University of Science and Technology, 7491 Trondheim, Norway
Egil Bendiksen	Norwegian Institute for Nature Research, Gaustadalleen 21, 0349 Oslo, Norway
Katriina Bendiksen	Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway
Lajos Benedek	Szent Istvan University, Hungary
Anna Bérešová-Guttová	Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravská cesta 9, 845 23 Bratislava, Slovakia
Franz Berger	University of Salzburg, Salzburg, Austria
Reinhard Berndt	Herbaria Z+ZT, ETH Zürich, CHN D37, Universitätstr. 16, 8092 Zürich, Switzerland
Annarosa Bernicchia	Via A. Guidotti 39, 40134 Bologna, Italy
Alona Yu. Biketova	Institute of Biochemistry, BRC-HAS, 6726 Szeged, Temesvari krt. 62, 6726 Szeged, Hungary

Enrico Bizio	Società Veneziana di Micologia, Società Veneziana di Scienze Naturali, Fontego dei Turchi, Santa Croce 1730, 30135 Venice, Italy
Curtis Bjork	UBC Herbarium, Beaty Biodiversity Museum, University of British Columbia, Canada
Teun Boekhout	(1) Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, 3508 AD, Utrecht, The Netherlands; (2) Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands
David Boertmann	Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
Tanja Böhning	AG Geobotanik Schleswig-Holstein & Hamburg, c/o University of Kiel, Olshausenstraße 75, 24098 Kiel, Germany
Florent Boittin	Ascomycete.org, 36 rue de la Garde, 69005 Lyon, France
Carlos G. Boluda	Conservatoire et Jardin botaniques de la Ville de Genève, 1292 Genève, Switzerland
Menno W. Boomsliuter	T.v.Lohuizenstraat 34, 8172xl, Vaassen, The Netherlands
Jan Borovička	Institute of Geology, Czech Academy of Sciences, Rozvojova 269, 165 00 Prague 6, Czech Republic
Tor Erik Brandrud	Norwegian Institute for Nature Research, Gaustadalleen 21, 0349 Oslo, Norway
Uwe Braun	Martin-Luther-Universität, Institut für Biologie, Bereich Geobotanik, und Botanischer Garten, Herbarium, Neuwerk 21, 06099 Halle, Germany
Irwin Brodo	Canadian Museum of Nature, 240 McLeod Street, Ottawa, Ontario, Canada
Tatiana Bulyonkova	A.P. Ershov Institute of Informatics Systems, Russian Academy of Sciences, Siberian Branch, 6 Acad. Lavrentjev pr., Novosibirsk 630090, Russia
Harold H. Burdsall Jr.	Fungal & Decay Diagnostics, LLC, 9350 Union Valley Road, Black Earth, Wisconsin 53515, U.S.A.
Bart Buyck	Muséum National d'Histoire Naturelle, CP 39, ISYEB, UMR 7205 CNRS MNHN UPMC EPHE, 12 rue Buffon, 75005 Paris, France
Ana Rosa Burgaz	Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, 28040 Madrid, Spain
Vicent Calatayud	Fundación CEAM, c/ Charles R. Darwin, 14, Parque Tecnológico, 46980 Paterna, Valencia, Spain
Philippe Callac	INRA, MycSA, CS 20032, 33882 Villenave d'Ornon, France
Emanuele Campo	Associazione Micologica Bresadola, Via Alessandro Volta 46, 38123 Trento, Italy
Massimo Candusso	Via Ottone Primo 90, 17021, Alassio, Savona, Italy
Brigitte Capoen	Queffioec, rue de Saint Gonval, 22710 Penvenan, France
Joaquim Carbó	Roser, 60, 17257 Torroella de Montgrí, Girona, Spain
Matteo Carbone	Via Don Luigi Sturzo 173 16148 Genova, Italy
Rafael F. Castañeda-Ruiz	Instituto de Investigaciones Fundamentales en Agricultura, Tropical 'Alejandro de Humboldt', OSDE, Grupo Agrícola, Calle 1 Esq. 2, Santiago de Las Vegas, C. Habana 17200, Cuba
Michael A. Castellano	USDA, Forest Service, Northern Research Station, Corvallis, Oregon 97330, U.S.A.
Jie Chen	Mae Fah Luang University, Chang Wat Chiang Rai 57100, Thailand
Philippe Clerc	Conservatoire et Jardin botaniques de la Ville de Genève, 1292 Genève, Switzerland
Giovanni Consiglio	Via C. Ronzani 61, 40033 Casalecchio Bologna, Italy
Gilles Corriol	National Botanical Conservatory for Pyrenees and Midi-Pyrénées Region of France and BBF Herbarium, Vallon de Salut. B.P. 315. 65203 Bagnères-de-Bigorre, France
Régis Courtecuisse	Université Lille, Fac. Pharma. Lille, EA4483 IMPECS, 59000 Lille, France
Ana Crespo	Facultad de Farmacia, Universidad Complutense de Madrid, 28040 Madrid, Spain
Cathy Cripps	Plant Sciences & Plant Pathology, 119 Plant Biosciences Building, Montana State University, Bozeman, Montana 59717, U.S.A.
Pedro W. Crous	Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, 3508 AD, Utrecht, The Netherlands
Gladstone Alves da Silva	Universidade Federal de Pernambuco, Centro de Biociências, Avenida da Engenharia, S/N, Cidade Universitária, Recife, Pernambuco, Brazil
Meiriele da Silva	Universidade Federal de Viçosa, 36570-000, Viçosa, Minas Gerais, Brazil
Marjo Dam	Hooischelf 13, 6581 SL Malden, The Netherlands
Nico Dam	Hooischelf 13, 6581 SL Malden, The Netherlands
Frank Dämmrich	The Bavarian Natural History Collections (SNSB Munich), Menzinger Strasse 71, 80638, München, Germany
Kanad Das	Botanical Survey of India, Cryptogamic Unit, P.O. Botanic Garden, Howrah 711103, W.B., India
Linda Davies	Centre for Environmental Policy, Imperial College London, SW7 2AZ, United Kingdom
Eske De Crop	Ghent University K.L. Ledeganckstraat 35, 9000 Ghent, Belgium
Andre De Kesel	Botanic Garden Meise, Nieuwelaan 38, 1860 Meise, Belgium
Ruben De Lange	Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium
Bárbara De Madrigal Bonzi	Instituto de Botánica del Nordeste, Universidad Nacional de Nordeste-Consejo Nacional de Investigaciones Científicas y Técnicas, Sargento Cabral 2131, CC 209, Corrientes Capital, Argentina
Thomas Edison E. dela Cruz	University of Santo Tomas, Espana 1008 Manila, Philippines

Lynn Delgat	Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium
Vincent Demoulin	Institut de Botanique, B.22, Université de Liège, 4000 Liège I, Belgium
Dennis E. Desjardin	HD Thiers Herbarium (SFSU), San Francisco State University, 1600 Holloway Ave, San Francisco, California 94132, U.S.A.
Paul Diederich	Musée national d'histoire naturelle, 25 rue Münster, 2160 Luxembourg, Luxembourg
Bálint Dima	(1) Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/c, 1117 Budapest, Hungary; (2) Viikki Plant Science Centre, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland
Maria Martha Dios	Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Catamarca, Av Belgrano 300, 4700 San Fernando del Valle de Catamarca, Argentina
Pradeep Kumar Divakar	Facultad de Farmacia, Universidad Complutense de Madrid, 28040 Madrid, Spain
Clovis Douanla-Meli	Julius Kühn-Institut, Federal Research Centre for Cultivated Plants, Institute for National and International Plant Health, Messeweg 11-12, 38104 Braunschweig, Germany
Brian Douglas	Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom
Elisandro Ricardo Drechsler-Santos	Universidade Federal de Santa Catarina, Campus Universitário Reitor João David Ferreira Lima, Trindade, Florianópolis, Santa Catarina CEP 88040-900, Brazil
Paul S. Dyer	School of Life Sciences, University of Nottingham, University Park, Nottingham NG7 2RD, United Kingdom
Ursula Eberhardt	Abt. Botanik, Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany
Damien Ertz	Botanic Garden Meise, Nieuwelaan 38, 1860 Meise, Belgium
Fernando Esteve-Raventós	Facultad de Biología, Ciencias Ambientales y Química, Universidad de Alcalá, 28805 Alcalá de Henares, Madrid, Spain
Javier Angel Etayo Salazar	Navarro Villoslada 16, 3ª dcha., 31003 Pamplona, Navarra, Spain
Vera Evenson	Sam Mitchel Herbarium of Fungi, Denver Botanic Gardens, 1007 York Street, Denver, Colorado 80206, U.S.A.
Guillaume Eyssartier	Muséum national d'histoire naturelle, Jardin des plantes, 57 rue Cuvier, 75005 Paris, France
Edit Farkas	Institute of Ecology and Botany, MTA Centre for Ecological Research, 2163 Vácrátót, Hungary
Alain Favre	Fédération Mycologique et Botanique Dauphiné Savoie, Le Prieuré, 144 Place de l'Eglise, 74320 Sevrier, France
Anna G. Fedosova	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Mario Filippa	Regione Monsarineri 36, 14041 Agliano Terme, Italy
Péter Finy	8000 Székesfehérvár, Zsombolyai u. 56, Hungary
Adam Flakus	W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Krakow, Poland
Simón Fos	Facultad de Ciencias Biológicas, Universitat de València, C/Dr Moliner 50, 46100, Burjassot, Valencia, Spain
Jacques Fournier	Las Muros, F. 09420 Rimont, France
André Fraiture	Botanic Garden Meise, Nieuwelaan 38, 1860 Meise, Belgium
Paolo Franchi	Associazione Micologica Bresadola, Via Alessandro Volta 46, 38123 Trento, Italy
Ana Esperanza Franco Molano	Escuela de Microbiología, Universidad de Antioquia, AA1226, Fundación Biodiversa Colombia, Medellín, Colombia
Gernot Friebes	Centre of Natural History, Botany & Mycology, Universalmuseum Joanneum, Weinzöttlstraße 16, 8045 Graz, Austria
Andreas Frisch	NTNU, University Museum, Norwegian University of Science and Technology, 7491 Trondheim, Norway
Alan Fryday	Michigan State University, East Lansing, Michigan 48824, U.S.A.
Giuliana Furci	The Fungi Foundation, Paseo Bulnes 79 of. 112A, Santiago, Chile
Ricardo Galán Márquez	Facultad de Biología, Ciencias Ambientales y Química, Universidad de Alcalá, 28805 Alcalá de Henares, Madrid, Spain
Matteo Garbelotto	University of California, 130 Mulford Hall #3114 Berkeley, California 94720, U.S.A.
Joaquina Maria Garcia-Martin	Real Jardín Botánico-CSIC, Plaza de Murillo 2, 28014, Madrid, Spain
Mónica A. García Otálora	Herbaria Z+ZT, ETH Zürich, CHN D37, Universitätstr. 16, 8092 Zürich, Switzerland
Dania García Sánchez	Universitat Rovira i Virgili, C/ Sant Llorenç 21, 43201 Reus, Tarragona, Spain
Alain Gardiennet	14 rue Roulette, 21260 Véronnes, France
Sigisfredo Garnica	Instituto de Bioquímica y Microbiología, Universidad Austral de Chile, Isla Teja Campus, Casilla 567, Valdivia, Chile
Isaac Garrido Benavent	Real Jardín Botánico-CSIC, Plaza de Murillo 2, 28014, Madrid, Spain
Genevieve Gates	Tasmanian Institute of Agriculture, Private Bag 54, Hobart, Tasmania 7001, Australia
Alice da Cruz Lima Gerlach	Conservatoire et Jardin Botaniques de la ville de Genève, Genève, Switzerland
Masoomeh Ghobad-Nejhad	Iranian Research Organization for Science and Technology, P.O. Box 15815-3538, Tehran 15819, Iran

Tatiana B. Gibertoni	Universidade Federal de Pernambuco, Centro de Biociências, Avenida da Engenharia, S/N, Cidade Universitária, Recife, Pernambuco, Brazil
Tine Grebenc	Slovenian Forestry Institute, Vecna pot 2, 100 Ljubljana, Slovenia
Irmgard Greilhuber	University of Vienna, Rennweg 14, 1030 Vienna, Austria
Bella Grishkan	Institute of Evolution, University of Haifa, Aba Khoushi Ave. 199, Mt. Carmel, Haifa 3498838, Israel
Johannes Z. Groenewald	Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, 3508 AD, Utrecht, The Netherlands
Martin Grube	Institute of Biology, University of Graz, Holteiasse 6, 8010 Graz, Austria
Gérald Gruhn	Office National des Forêts, 2 Avenue de Saint-Mandé, 75570 Paris Cedex 12, France
Cécile Gueidan	CSIRO - Australian National Herbarium, Clunies Ross Street, Canberra ACT 2601, Australia
Gro Gulden	Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway
Luis FP Gusmão	Universidade Estadual de Feira de Santana, Av. Transnordestina, s/n, Bairro Novo Horizonte, CEP:44036-900, Feira de Santana, Bahia, Brazil
Josef Hafellner	Institute of Biology, University of Graz, Holteiasse 6, 8010 Graz, Austria
Michel Hairaud	2 Impasse des Marronniers, 79360 Poivendre de Marigny, France
Marek Halama	Museum of Natural History, Wrocław University, ul. H. Sienkiewicza 5, 50-335 Wrocław, Poland
Nils Hallenberg	University of Gothenburg, Box 461, 40530 Göteborg, Sweden
Roy E. Halling	Institute of Systematic Botany, New York Botanical Garden, 2900 Southern Blvd, Bronx, New York 10458-5126, U.S.A.
Karen Hansen	Swedish Museum of Natural History, P.O. Box 50007, 104 05 Stockholm, Sweden
Christoffer Bugge Harder	Texas Tech University, Box 42122, Lubbock, Texas 79409, U.S.A.
Jacob Heilmann-Clausen	Natural History Museum of Denmark, Universitetsparken 15, 2100 København, Denmark
Stip Helleman	Sweelinck 78, 5831KT Boxmeer, The Netherlands
Alain Henriot	Mycological Society of France, 20 rue Rottembourg, 12th arrondissement, Paris, France
Margarita Hernandez-Restrepo	Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, 3508 AD, Utrecht, The Netherlands
Raphaël Herve	24 rue des Fougères, 86550 Mignaloux-Beauvoir, France
Caroline Hobart	84 Stafford Road, Sheffield, South Yorkshire S2 2SF, United Kingdom
Mascha Hoffmeister	Julius Kühn-Institut, Institute for Epidemiology and Pathogen Diagnostics, Braunschweig, Germany
Klaus Høiland	University of Oslo, P.O.Box 1066, Blindern, 0316 Oslo, Norway
Jan Holec	National Museum, Herbarium PRM, Cirkusová 1740, 193 00 Praha 9, Czech Republic
Håkon Holien	Faculty of Bioscience and Aquaculture, NORU University, P.O. Box 2501, 7729 Steinkjer, Norway
Karen Hughes	University of Tennessee, Knoxville, Tennessee 37996, U.S.A.
Vít Hubka	Faculty of Science, Charles University, Benátská 2, 128 01 Praha 2, Czech Republic
Seppo Huhtinen	Herbarium TUR, Biodiversity Unit, University of Turku, 20014 Turku, Finland
Boris Ivančević	Natural History Museum, Njegoševa 51, P.O. Box 401, 11000 Belgrade, Serbia
Marian Jagers	Reelaan 13, 7522 LR Enschede, The Netherlands
Walter Jaklitsch	Institute of Forest Entomology, Forest Pathology and Forest Protection, University of Natural Resources and Life Sciences Vienna, Vienna, Austria
AnnaElise Jansen	Stationsstraat 10, 6701 AM Wageningen, the Netherlands
Ruvishika S. Jayawardena	Mae Fah Luang University, Chang Wat Chiang Rai 57100, Thailand
Thomas Stjernegaard Jeppesen	Global Biodiversity Information Facility, Universitetsparken 15, 2100 København Ø, Denmark
Mikael Jeppson	Lilla Håjumsgatan 4, 46135 Trollhättan, Sweden
Peter Johnston	Manaaki Whenua Landcare Research, Private Bag 92170, Auckland 1072, New Zealand
Per Magnus Jørgensen	University of Bergen, Allégaten 41, P.O. Box 7800, 5020 Bergen, Norway
Ingvar Kärnefelt	Biological Museum, Lund University, Box 117, 221 00 Lund, Sweden
Liudmila B. Kalinina	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Gintaras Kantvilas	Tasmanian Herbarium (HO), Tasmanian Museum and Art Gallery, P.O. Box 5058, UTAS L.P.O., Sandy Bay, Tasmania 7005, Australia
Mitko Karadelev	Institute of Biology, Faculty of Natural Science and Mathematics, Ss. Cyril and Methodius University, Arhimedova 5, 1000 Skopje, Republic of Macedonia
Taiga Kasuya	Faculty of Risk and Crisis Management, Chiba Institute of Science, 3 Shiomi-cho, Choshi, Chiba 288-0025, Japan
Ivona Kautmanová	Natural History Museum, Slovak National Museum, Bratislava, Slovakia
Richard W. Kerrigan	RWK Research, Kittanning, Pennsylvania 16201, U.S.A.

Martin Kirchmair	Institut für Mikrobiologie, Universität Innsbruck, Technikerstraße 25, 6020 Innsbruck, Austria
Anna Kiyashko	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Dániel G. Knapp	Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/c, 1117 Budapest, Hungary
Henning Knudsen	Natural History Museum of Denmark, Universitetsparken 15, 2100 København, Denmark
Kerry Knudsen	Faculty of Environmental Sciences, University of Life Sciences at Prague, Prague, Czech Republic
Tommy Knutsson	Nedra Västerstad 111, 380 62 Mörbylånga, Sweden
Miroslav Kolařík	Institute of Microbiology ASCR, Videnska 1083, 142 20 Prague 4, Czech Republic
Urmas Kõljalg	Institute of Ecology and Earth Sciences, 40 Lai Street, Tartu 51005, Estonia
Alica Košuthová	Swedish Museum of Natural History, P.O. Box 50007, 104 05 Stockholm, Sweden
Attila Koszka	Faculty of Agricultural and Environmental Sciences, Kaposvar University, 7400 Kaposvar, Hungary
Heikki Kotiranta	Finnish Environment Institute, P.O. Box 140, 00251 Helsinki, Finland
Vera Kotkova	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Ondřej Koukol	Faculty of Science, Charles University, Benátská 2, 128 01 Praha 2, Czech Republic
Jiří Kout	University of West Bohemia, Faculty of Education, Klatovska 51, 306 19 Pilsen, Czech Republic
Gábor M. Kovács	Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/c, 1117 Budapest, Hungary
Martin Kříž	Faculty of Science, Charles University, Benátská 2, 128 01 Praha 2, Czech Republic
Åsa Krüys	Museum of Evolution, Uppsala University, Norbyvägen 16, 75236 Uppsala, Sweden
Viktor Kučera	Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravská cesta 9, 845 23 Bratislava, Slovakia
Linas Kudzma	37 Maple Ave. Annandale, New Jersey 08801, U.S.A.
Francisco Kuhar	Instituto Multidisciplinario de Biología Vegetal, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina
Martin Kukwa	Faculty of Biology, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland
T. K. Arun Kumar	The Zamorin's Guruvayurappan College, Kozhikode, Kerala 673014, India
Vladimír Kunca	Technical University in Zvolen, Ul. T. G. Masaryka 24, 960 53 Zvolen, Slovakia
Ivana Kušan	Ruđer Bošković Institute, Bijenička cesta 54, 10000 Zagreb, Croatia
Thomas W. Kuyper	Wageningen University & Research, Droevendaalsesteeg 4, 6708 PB Wageningen, The Netherlands
Carlos Lado	Real Jardín Botánico-CSIC, Plaza de Murillo 2, 28014, Madrid, Spain
Thomas Læssøe	Natural History Museum of Denmark, Universitetsparken 15, 2100 København, Denmark
Patrice Lainé	123 rue Saint Antoine, 75004, Paris, France
Ewald Langer	University of Kassel, Heinrich-Plett-Strasse 40, 34132 Kassel, Germany
Ellen Larsson	University of Gothenburg, Box 461, 40530 Göteborg, Sweden
Karl-Henrik Larsson	Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway
Gary Laursen	Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775-7000, U.S.A.
Christian Lechat	Ascofrance, 64 route de Chizé, 79360 Villiers en Bois, France
Serena Lee	Herbarium Singapore Botanic Gardens, National Parks Board, Singapore
James C. Lendemer	(1) Institute of Systematic Botany, New York Botanical Garden, 2900 Southern Blvd, Bronx, New York 10458-5126, U.S.A.; (2) Graduate Center, City University of New York, 365 5th Ave, New York, New York 10016, U.S.A.
Laura Levin	University of Buenos Aires, Junin 956, 1113, Buenos Aires, Argentina
Uwe Lindemann	Landesmuseum für Naturkunde, Münster, Germany
Håkan Lindström	Östansjö 150, 840 64 Kälarne, Sweden
Xingzhong Liu	Institute of Microbiology, Chinese Academy of Sciences, No 3 Park 1, Beichen West Road, Chaoyang District, Beijing 100101, China
Regulo Carlos Llerena Hernandez	Facultad de Ciencias Biológicas y Agropecuarias, Peñuela, Universidad Veracruzana, Amatlán de los Reyes, Ver., Mexico
Esteve Llop	Facultat de Biologia, Universitat de Barcelona, Av. Diagonal, 643, 08028 Barcelona, Spain
Csaba Locsmándi	Hungarian Natural History Museum, 1087 Budapest, Hungary
Deborah Jean Lodge	USDA Forest Service, NRS, P.O. Box 1377, Luquillo, Puerto Rico 00773-1377, U.S.A.
Michael Loizides	P.O. Box 58499, 3734 Limassol, Cyprus
László Lőkös	Hungarian Natural History Museum, 1087 Budapest, Hungary

Jennifer Luangsa-ard	National Center for Genetic Engineering and Biotechnology (BIOTEC), NSTDA, 113 Thailand Science Park, Phaholyothin Rd., Klong Nueng, Klong Luang, Pathum Thani 12120, Thailand
Matthias Lüderitz	AG Geobotanik Schleswig-Holstein & Hamburg, c/o University of Kiel, Olshausenstraße 75, 24098 Kiel, Germany
Thorsten Lumbsch	Field Museum, 1400 S. Lake Shore Dr., Chicago, Illinois 60605, U.S.A.
Matthias Lutz	Institute of Evolution and Ecology, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany
Dan Mahoney	Callaghan Innovation, 69 Gracefield Road, Lower Hutt 5010, New Zealand
Ekaterina Malysheva	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Vera Malysheva	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Patinjareveettil Manimohan	University of Calicut, Kerala, 673 635, India
Yasmina Marin-Felix	Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, 3508 AD, Utrecht, The Netherlands
Guilhermina Marques	Centre for the Research and Technology of Agro-Environmental and Biological Sciences, University of Trás-os-Montes and Alto Douro, Laboratory of Mycology and Soil Microbiology, 5000-801 Vila Real, Portugal
Rubén Martínez-Gil	Ascomycete.org, 36 rue de la Garde, 69005 Lyon, France
Guy Marson	Musée national d'histoire naturelle, 25 rue Münster, 2160 Luxembourg, Luxembourg
Gerardo Mata	Instituto de Ecología, A.C., Carretera antigua a Coatepec 351, El Haya, Xalapa 91070, Veracruz, Mexico
P. Brandon Matheny	University of Tennessee, Knoxville, Tennessee 37996, U.S.A.
Geir Harald Mathiassen	Tromsø University Museum, University of Tromsø - The Arctic University of Norway, 9037 Tromsø, Norway
Neven Matočec	Ruđer Bošković Institute, Bijenička cesta 54, 10000 Zagreb, Croatia
Helmut Mayrhofer	Institute of Biology, University of Graz, Holteiasse 6, 8010 Graz, Austria
Mehdi Mehrabi	Iranian Research Institute of Plant Protection, Agricultural Research, Education and Extension Organization, Tehran, Iran
Ireneia Melo	Botanical Garden, National Museum of Natural History and Science, University of Lisbon, Portugal
Armin Mešić	Ruđer Bošković Institute, Bijenička cesta 54, 10000 Zagreb, Croatia
Andrew S. Methven	Savannah State University, Savannah, Georgia 31404, U.S.A.
Otto Miettinen	Finnish Museum of Natural History, P.O. Box 7, 00014 University of Helsinki, Finland
Ana M. Millanes Romero	Universidad Rey Juan Carlos, 28933 Móstoles, Madrid, Spain
Andrew N. Miller	Illinois Natural History Survey, University of Illinois Urbana-Champaign, 1816 South Oak Street, Champaign, Illinois 61820-6970, U.S.A.
James K. Mitchell	Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A.
Roland Moberg	Museum of Evolution, Uppsala University, Norbyvägen 16, 75236 Uppsala, Sweden
Pierre-Arthur Moreau	Université Lille, Fac. Pharma. Lille, EA4483 IMPECS, 59000 Lille, France
Gabriel Moreno	Facultad de Biología, Ciencias Ambientales y Química, Universidad de Alcalá, 28805 Alcalá de Henares, Madrid, Spain
Olga Morozova	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Asunción Morte	Facultad de Biología, Universidad de Murcia, Campus de Espinardo, 30100 Murcia, Spain
Lucia Muggia	University of Trieste, via L. Giorgieri 10, 34127 Trieste, Italy
Guillermo Muñoz González	Avda Valvanera N.32, 5D, 26500 Calahorra, La Rioja, Spain
Leena Myllys	Finnish Museum of Natural History, P.O. Box 7, 00014 University of Helsinki, Finland
István Nagy	Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/c, 1117 Budapest, Hungary
László G. Nagy	Institute of Biochemistry, BRC-HAS, 6726 Szeged, Temesvari krt. 62, 6726 Szeged, Hungary
Maria Alice Neves	Universidade Federal de Santa Catarina, Campus Universitário Reitor João David Ferreira Lima, Trindade, Florianópolis, Santa Catarina CEP 88040-900, Brazil
Tuomo Niemelä	Finnish Museum of Natural History, P.O. Box 7, 00014 University of Helsinki, Finland
Pier Luigi Nimis	University of Trieste, via L. Giorgieri 10, 34127 Trieste, Italy
Nicolas Niveiro	Instituto de Botánica del Nordeste, Universidad Nacional de Nordeste-Consejo Nacional de Investigaciones Científicas y Técnicas, Sargento Cabral 2131, CC 209, Corrientes Capital, Argentina
Machiel E. Noordeloos	Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA, Leiden, The Netherlands
Anders Nordin	Museum of Evolution, Uppsala University, Norbyvägen 16, 75236 Uppsala, Sweden
Sara Raouia Noumeur	Faculty of Natural and Life Sciences, University of Batna 2, 05000 Batna, Algeria
Yuri Novozhilov	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia

Jorinde Nuytinck	Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands
Esteri Ohenoja	Botanical Museum, University of Oulu, Finland
Patricia Oliveira Fiuza	Universidade Estadual de Feira de Santana, Av. Transnordestina, s/n, Bairro Novo Horizonte, CEP:44036-900, Feira de Santana, Bahia, Brazil
Alan Orange	National Museum of Wales, Cardiff CF10 3NP, United Kingdom
Alexander Ordynets	University of Kassel, Heinrich-Plett-Strasse 40, 34132 Kassel, Germany
Beatriz Ortiz-Santana	USDA Forest Service, Northern Research Station, One Gifford Pinchot Dr, Madison, Wisconsin 53726, U.S.A.
Leticia Pacheco	Universidad Autónoma Metropolitana-Iztapalapa, Av. San Rafael Atlixco 186, Col. Vicentina, 09340 México, D. F., Mexico
Ferenc Pál-Fám	Faculty of Agricultural and Environmental Sciences, Kaposvar University, 7400 Kaposvar, Hungary
Melissa Palacio	Universidade Federal do Rio Grande do Sul, Brazil
Zdeněk Palice	Faculty of Science, Charles University, Benátská 2, 128 01 Praha 2, Czech Republic
Viktor Papp	Szent Istvan University, 1118 Budapest, Menesi st. 44, Hungary
Kadri Pärtel	Institute of Ecology and Earth Sciences, 40 Lai Street, Tartu 51005, Estonia
Julia Pawlowska	Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Żwirki i Wigury 101, 02-089 Warsaw, Poland
Aurelia Paz	Urb. La Llosa, 219, 39509 Villanueva de la Peña, Mazcuerras, Cantabria, Spain
Ursula Peintner	Institut für Mikrobiologie, Universität Innsbruck, Technikerstraße 25, 6020 Innsbruck, Austria
Shaun Pennycook	Manaaki Whenua Landcare Research, Private Bag 92170, Auckland 1072, New Zealand
Olinto Liparini Pereira	Universidade Federal de Viçosa, 36570-000, Viçosa, Minas Gerais, Brazil
Pablo Pérez Daniëls	University of Córdoba, 14071, Córdoba, Spain
Miquel À. Pérez-De-Gregorio Capella	C/ Pau Casals, 6, 1 ^a , 1 ^a , 17001, Girona, Spain
Carlos Manuel Pérez del Amo	C/ Luis de Ulloa, 1, 7 ^a I, 26004 Logroño, Navarra, Spain
Sergio Pérez Gorjón	Universidad de Salamanca, Avda. Licenciado Mendez Nieto s/n, 37007 Salamanca, Spain
Sergio Pérez-Ortega	Real Jardín Botánico-CSIC, Plaza de Murillo 2, 28014, Madrid, Spain
Israel Pérez-Vargas	Facultad de Farmacia, Universidad de La Laguna, c/ Astrofísico Sánchez s/n 38071 La Laguna, Tenerife, Canary Islands, Spain
Brian A. Perry	California State University East Bay, Hayward, California 94542, U.S.A.
Jens H. Petersen	Nøruplundvej 2, 8400 Ebeltoft, Denmark
Ronald H. Petersen	University of Tennessee, Knoxville, Tennessee 37996, U.S.A.
Donald H. Pfister	Harvard University, 22 Divinity Avenue, Cambridge MA 02138, U.S.A.
Chayanard Phukhamsakda	Mae Fah Luang University, Chang Wat Chiang Rai 57100, Thailand
Marcin Piątek	W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Krakow, Poland
Meike Piepenbring	Faculty of Biosciences, Goethe University Frankfurt am Main, Germany
Raquel Pino-Bodas	Real Jardín Botánico-CSIC, Plaza de Murillo 2, 28014, Madrid, Spain
Juan Pablo Pinzón Esquivel	Universidad Autónoma de Yucatán, Carretera Mérida-Xmatkuil Km. 15.5, Apdo. Postal: 4-116 Itzimmá, C.P: 97100, Merida, Yucatan, Mexico
Paul Pirot	Rue des Peupliers 10, 6840 Neufchâteau, Belgium
Eugene S. Popov	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Orlando Popoff	Instituto de Botánica del Nordeste, Universidad Nacional de Nordeste-Consejo Nacional de Investigaciones Científicas y Técnicas, Sargento Cabral 2131, CC 209, Corrientes Capital, Argentina
María Prieto Álvaro	Universidad Rey Juan Carlos, 28933 Móstoles, Madrid, Spain
Christian Printzen	Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Abteilung Botanik und Molekulare Evolutionsforschung, Herbarium Senckenbergianum (FR), Senckenberganlage 25, 60325 Frankfurt am Main, Germany
Nadezhda Psurtseva	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Witton Purahong	Helmholtz Centre for Environmental Research GmbH - UFZ, Theodor-Lieser-Straße 4, 06120 Halle, Germany
Luis Quijada	Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A.
Gerhard Rambold	University of Bayreuth, Universitätsstrasse 30, 95447 Bayreuth, Germany
Natalia A. Ramírez	Instituto de Botánica del Nordeste, Universidad Nacional de Nordeste-Consejo Nacional de Investigaciones Científicas y Técnicas, Sargento Cabral 2131, CC 209, Corrientes Capital, Argentina
Huzefa Raja	University of North Carolina at Greensboro, 435 Sullivan Science Building, PO Box 26170, Greensboro North Carolina 27402-6170, U.S.A.
Olivier Raspé	Botanic Garden Meise, Nieuwelaan 38, 1860 Meise, Belgium

Tania Raymundo	Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Prolongación de Carpio y Plan de Ayala s/n, Miguel Hidalgo, Santo Tomás, 11340 Ciudad de México, Mexico
Martina Réblová	Institute of Botany, Czech Academy of Sciences, Pruhonice, Czech Republic
Yury A. Rebriev	Southern Scientific Center, Russian Academy of Sciences, 41 Chehova str., Rostov-on-Don, 344006, Russia
Juan de Dios Reyes García	Paseo Virgen de Linares 6 2 D, Linares, Jaen, Spain
Miguel Ángel Ribes Ripoll	Avda. Pablo Neruda 120 F, 2ºD, 28018 Madrid, Spain
Franck Richard	CEFE UMR5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, INSERM, 1919 Route de Mende, 34293 Montpellier Cédex 5, France
Mike J. Richardson	Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, EH3 5LR, United Kingdom
Víctor J. Rico	Facultad de Farmacia, Universidad Complutense de Madrid, 28040 Madrid, Spain
Gerardo Lucio Robledo	Instituto Multidisciplinario de Biología Vegetal, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina
Flavia Rodrigues Barbosa	Universidade Federal de Mato Grosso, Av. Alexandre Ferronato, 1200, Setor Industrial, Sinop, Mato Grosso, Brazil
Cristina Rodriguez-Caycedo	UT Southwestern Medical Center, Dallas, Texas 75390, U.S.A.
Pamela Rodriguez-Flakus	W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Krakow, Poland
Anna Ronikier	W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Krakow, Poland
Luis Rubio Casas	Ul. Andrieja Sacharowa 1/1, 30-806 Kraków, Poland
Katerina Rusevska	Institute of Biology, Faculty of Natural Science and Mathematics, Ss. Cyril and Methodius University, Arhimedova 5, 1000 Skopje, Republic of Macedonia
Günter Saar	Dammenmühle 7, 77933 Lahr-Sulz, Germany
Irja Saar	Institute of Ecology and Earth Sciences, 40 Lai Street, Tartu 51005, Estonia
Isabel Salcedo	University of the Basque Country (UPV/EHU), Apdo 644, 48080 Bilbao, Spain
Sergio M. Salcedo Martínez	Facultad de Ciencias Biológicas, UANL. Ave. Pedro de Alba s/n esq. Manuel Barragán Cd. Universitaria, San Nicolás de los Garza Nuevo León, CP. 66451, Mexico
Carlos A. Salvador Montoya	Instituto de Botánica del Nordeste, Universidad Nacional de Nordeste-Consejo Nacional de Investigaciones Científicas y Técnicas, Sargento Cabral 2131, CC 209, Corrientes Capital, Argentina
Santiago Sánchez-Ramírez	University of Toronto, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada
J. Vladimir Sandoval-Sierra	Health Science Centre, University of Tennessee, U.S.A.
Sergi Santamaria	Facultat de Biociències, Edifici C, Despatx C1/331, Campus de la UAB, 08193 Bellaterra, (Cerdanyola del Vallès), Barcelona, Spain
Josiane Santana Monteiro	Botany Coordination, Museu Paraense Emílio Goeldi, 66077-830, Belém, Pará, Brazil
Hans Josef Schroers	Agricultural Institute of Slovenia, Hacquetova ulica 17, 1000 Ljubljana, Slovenia
Barbara Schulz	Institute of Microbiology, Technische Universität Braunschweig, Germany
Geert Schmidt-Stohn	Burgstr. 25, 29553 Bienenbüttel, Germany
Trond Schumacher	University of Oslo, P.O.Box 1066, Blindern, 0316 Oslo, Norway
Beatrice Senn-Irlet	RU Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstr. 111, 8903 Birmensdorf, Switzerland
Hana Ševčíková	Moravian Museum, Zeny trh 6, 659 37 Brno, Czech Republic
Oleg Shchepin	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Takashi Shirouzu	Graduate School of Bioresources, Mie University, 1577 Kurima-machiya, Tsu, Mie 514-8507, Japan
Anton Shiryayev	Institute of Plant & Animal Ecology Ural Branch of the Russian Academy of Sciences, 620144 Ekaterinburg, 8 March str., 202/3, Russia
Klaus Siepe	Geeste 133, 46342 Velen, Germany
Esteban B. Sir	Fundación Miguel Lillo, Consejo Nacional de Investigaciones Científicas y Técnicas, Miguel Lillo 251, San Miguel de Tucumán 4000, Tucumán, Argentina
Mohammad Sohrabi	Iranian Research Organization for Science and Technology, P.O. Box 33535111, Tehran, Iran
Karl Soop	Swedish Museum of Natural History, P.O. Box 50007, 104 05 Stockholm, Sweden
Viacheslav Spirin	Finnish Museum of Natural History, P.O. Box 7, 00014 University of Helsinki, Finland
Toby Spribille	University of Alberta, Edmonton, Alberta T6G 2R3, Canada
Marc Stadler	Helmholtz Centre for Infection Research, Inhoffenstrasse 7, 38124 Braunschweig, Germany
Joost Stalpers	Torenlaan 43, 3742CR Baarn, The Netherlands
Soili Stenroos	Finnish Museum of Natural History, P.O. Box 7, 00014 University of Helsinki, Finland
Ave Suija	Institute of Ecology and Earth Sciences, 40 Lai Street, Tartu 51005, Estonia

Stellan Sunhede	Hökaskog Sandbacken 1, 533 92 Lundsbrunn, Sweden
Sten Svantesson	University of Gothenburg, Box 461, 40530 Göteborg, Sweden
Sigvard Svensson	Biological Museum, Lund University, Box 117, 221 00 Lund, Sweden
Tatyana Yu. Svetasheva	(1) Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia; (2) Department of Technologies of Living Systems, Tula State Lev Tolstoy Pedagogical University, Lenin ave. 125, Tula, 300026, Russia
Krzysztof Świerkosz	Museum of Natural History, Wrocław University, ul. H. Sienkiewicza 5, 50-335 Wrocław, Poland
Heidi Tamm	Institute of Ecology and Earth Sciences, 40 Lai Street, Tartu 51005, Estonia
Hatira Taskin	Faculty of Agriculture, University of Çukurova, 01330 Adana, Turkey
Adrien Taudière	CEFE UMR5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, INSERM, 1919 Route de Mende, 34293 Montpellier Cédex 5, France
Jan-Olof Tedebrand	Sundsvall Mycological Society, Medelpad, Sweden
Raúl Tena Lahoz	C/Arreñales del Portillo B 21 1ºD, 44003 Teruel, Spain
Marina Temina	Institute of Evolution, University of Haifa, Aba Khoushi Ave. 199, Mt. Carmel, Haifa 3498838, Israel
Arne Thell	Biological Museum, Lund University, Box 117, 221 00 Lund, Sweden
Marco Thines	Faculty of Biosciences, Goethe University Frankfurt am Main, Germany
Göran Thor	Swedish University of Agricultural Sciences, P. O. Box 7044, 750 07 Uppsala, Sweden
Holger Thüs	State Museum of Natural History Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany
Leif Tibell	Evolutionary Biology Centre, Norbyvägen 18D, 75236 Uppsala, Sweden
Sanja Tibell	Evolutionary Biology Centre, Norbyvägen 18D, 75236 Uppsala, Sweden
Einar Timdal	Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway
Zdenko Tkalčec	Ruđer Bošković Institute, Bijenička cesta 54, 10000 Zagreb, Croatia
Tor Tønnsberg	University of Bergen, Allégaten 41, P.O. Box 7800, 5020 Bergen, Norway
Gérard Trichies	5, impasse des Écoles S7700 Neufchef, France
Dagmar Triebel	Botanische Staatssammlung München, Menzinger Straße 67, 80638 München, Germany
Andrei Tsurukau	(1) F. Skorina Gomel State University, Sovetskaja Str. 104, 246019 Gomel, Belarus; (2) Institute of Natural Sciences, Samara National Research University, Moskovskoye shosse 34, 443086 Samara, Russia
Rodham E. Tulloss	Herbarium Amanitarum Rooseveltensis, P. O. Box 57, Roosevelt, New Jersey 08555-0057, U.S.A.
Veera Tuovinen	University of Alberta, Edmonton, Alberta T6G 2R3, Canada
Miguel Ulloa Sosa	Universidad Nacional Autónoma de México, Tercer Circuito/Sin Número, Ciudad Universitaria, Ciudad de México, C. P. 04510, Mexico
Carlos Urcelay	Instituto Multidisciplinario de Biología Vegetal, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina
François Valade	11 rue haras, le boqueteau, 91240 Saint-Michel-sur-Orge, France
Ricardo Valenzuela Garza	Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Prolongación de Carpio y Plan de Ayala s/n, Miguel Hidalgo, Santo Tomás, 11340 Ciudad de México, Mexico
Pieter van den Boom	Arafura 16, 5691 JA Son, The Netherlands
Nicolas Van Vooren	Ascomycete.org, 36 rue de la Garde, 69005 Lyon, France
Aida M. Vasco-Palacios	Escuela de Microbiología, Universidad de Antioquia, AA1226, Fundación Biodiversa Colombia, Medellín, Colombia
Jukka Vauras	Herbarium TUR, Biodiversity Unit, University of Turku, 20014 Turku, Finland
Juan Manuel Velasco Santos	3 C/Pontevedra, 18, 1º C, 37003 Salamanca, Spain
Else Vellinga	861 Keeler Avenue, Berkeley, California 94708, U.S.A.
Annemieke Verbeken	Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium
Per Vetlesen	Norges Sopp- og Nyttevekstforbund, Schweigaards gate 34F, 0191 Oslo, Norway
Alfredo Vizzini	University of Torino, Viale P.A. Mattioli 25, 10125, Torino, Italy
Hermann Voglmayr	University of Vienna, Rennweg 14, 1030 Vienna, Austria
Sergey Volobuev	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia
Wolfgang von Brackel	Kirchenweg 2, 91341 Röttenbach, Germany
Elena Voronina	Lomonosov Moscow State University, Biology Faculty, Moscow, Russia
Grit Walther	Arvid-Harnack-Str. 4, 07743 Jena, Germany
Roy Watling	Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, EH3 5LR, United Kingdom
Evi Weber	Blaihofstr. 42, 72074 Tübingen, Germany
Mats Wedin	Swedish Museum of Natural History, P.O. Box 50007, 104 05 Stockholm, Sweden

Øyvind Weholt	Nord University, Nesna, 8700 Nesna, Norway
Martin Westberg	Museum of Evolution, Uppsala University, Norbyvägen 16, 75236 Uppsala, Sweden
Eugene Yurchenko	Polesky State University, Dnyaprouskai flatyiii str. 23, 225710, Pinsk, Belarus
Petr Zehnálek	Faculty of Science, Charles University, Benátská 2, 128 01 Praha 2, Czech Republic
Huang Zhang	Kunming University of Science & Technology, Kunming, China
Mikhail P. Zhurbenko	Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Street, St. Petersburg, 197376, Russia

The following institutions are also supporting the present text (institutional support means that committees from the mentioned

Asociación Micológica Carlos Spegazzini (Argentina)

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