Nomenclature: how do we designate NPP taxa?

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Abstract: Identification and naming of fossil and subfossil organisms are not easy tasks. We are in the midst of a paradigm shift in how NPP taxa are named, driven in large part by (1) molecular clock taxonomic efforts in the past 25 years and (2) greater connectivity among scientific communities. Concurrent with this is the understanding that sometimes a name is not necessary, and identifying acronyms, pending further taxonomic work, or where fragmentary or synapomorphic remains cannot be assigned to their original taxon, are sufficient. The overarching goal of the paradigm shift is to maintain stability of the code and avoid increasing the number of names that refer to single taxa. The history and current state of nomenclature for non-pollen palynomorphs groups, highlighting recent developments with dinoflagellates and fungi, is given, and recommendations for a unified approach to NPP nomenclature through geological time are made.

Once non-pollen palynomorphs (NPPs) are extracted from rock, sediment, or peat (see Pound et al. 2021, Chapter 3, this volume), the next step is nomenclatural: how do we designate NPP taxa? The most desirable approach to naming any fossil, including NPPs, is to follow modern taxonomic schemes whenever possible (van Geel and Aptroot 2006). This is not a new idea. Throughout the history of palynology and micropalaeontology and, by extension, NPP studies, attitudes have swung from the use of modern names for fossil taxa where possible (Ehrenberg 1854) to the use of form-taxon where possible (van Geel and Aptroot 2006). This is not a new idea. Throughout the history of palynology and micropalaeontology and, by extension, NPP studies, attitudes have swung from the use of modern names for fossil taxa where possible (van Geel and Aptroot 2006). This is not a new idea. Throughout the history of palynology and micropalaeontology and, by extension, NPP studies, attitudes have swung from the use of modern names for fossil taxa where possible (van Geel and Aptroot 2006).

Taxonomic nomenclature is, at its heart, simply assigning names to organisms to provide a common means of reference when discussing said organism. It should not be confused with phylogenetic classification, although the two are often closely linked. By convention, organisms treated under the International Code of Zoological Nomenclature (ICZN) and International Code of Nomenclature for Algae, Fungi, and Plants (ICN) are assigned Linnean binomials (Pirozynski and Weresub 1979). Within the codes, the rules for naming are clear – a name is a name, whether it refers to a fossil or a modern taxon, a whole organism or a fragment. However, it is outside of the code, within the specialist palynological community, that the methods are less clear, and very different approaches to naming are taken, depending upon how geologically old the palynomorph in question is and which nomenclatural philosophy the palynologist espouses. It is this question of how, and when, do we apply a name to NPPs that is the focus of this chapter.

The answer to this conundrum is inextricably linked to three phenomena: (1) the history of nomenclatural practice among palaeopalynologists and actupalynologists; (2) the history of nomenclatural practice among modern specialist groups, especially mycologists; and (3) our ability as palynologists to recognize the vast array of organisms we might encounter in the course of our studies. As an overarching goal of this book is to increase our ability to recognize the fossilized organisms we are encountering, this phenomenon will not be treated further here, other than to say that we should be cognizant that modern taxa are often erected using fragmentary material, and thus fragmented fossils are as worthy of taxonomic treatment as whole organisms (Pirozynski and Weresub 1979).

In the earliest days of palynology, a schism developed between those favouring classification based on morphological properties entirely separate from taxonomic relationships (Potońi 1893, 1931; Ibrahim...
and those who classify and name new taxa based on their relationships to extant organisms (Meschinelli 1892, 1902; Cookson 1947; Erdtman 1948; Wolf 1966a, b, 1967a, d, 1968; Bradley 1967). Hybrid systems, like that of van der Hammen (1958), exist but are generally not in favour. Therefore, from the very beginning of NPP studies, there have been two approaches: (1) artificial classification systems with no connection to modern taxon names; and (2) application of family, genus, and sometimes species names of extant organisms to fossil organisms. That this schism occurs along a Neogene–Recent line is not surprising—we speak two different nomenclatural languages. In Holocene and Quaternary studies, palynomorphs in general are more frequently treated under the ICN only is that some NPPs occur as dispersed propagules representing different phases of life, or modern and fossilized forms, and thus may have multiple names under the ICN for a single organism (Penaud et al. 2018; Turland et al. 2018). In some cases, it is not only impossible, but irresponsible, to assign a name, as insufficient distinguishing character states exist, and assigning a name, however validly, leads to taxonomic (and often palaeoecological) confusion (Traverse 1996; Seifert 2017; Bianchinotti et al. 2020).

In many cases, judgement calls must also be made as to the origin of the NPPs, as this impacts which nomenclatural schemes and philosophies are applied, i.e. which Code is used. Here we examine challenges encountered when naming NPPs using the lenses of fungal and dinoflagellate nomenclature, as the paradigm shift underway in those groups is mirrored in many other groups.

**Nomenclatural challenges**

The problems with nomenclature in general are mirrored by the problems encountered among the fungi and the dinoflagellates. Historically, the dinoflagellates have been treated using two different codes of nomenclature (Ellegaard et al. 2018), whereby the motile, heterotrophic phase is treated using the ICZN, but the encysted phase (which is the form typically found as fossils) is treated using the ICN; as extant heterotrophic and encysted forms are recognized as representatives of single organisms, they are listed as synonymous (Ellegaard et al. 2018). Recent molecular work and detailed observations of dinoflagellate life cycle phases has exposed multiple problems with this system, first in that several fossil forms have been shown to be the encysted phase of extant motile forms with previously unknown encysted forms, and second in that some forms named as fossil cysts can also be found as modern cysts (Ellegaard et al. 2018). Reconciliation of the two systems of nomenclature is both desirable and difficult, but the current trend is to follow the ICN for fossil cysts, which may retain their names where they are not equated with modern cysts (Head et al. 2016; Ellegaard et al. 2018).

The problem is magnified for the fungi as until recently, pleomorphic fungi had separate names for the teleomorph and anamorph reproductive phases; likewise, many fungi are described only from fragmentary material (Pirozynski and Weresub 1979); and worse, what we know about modern fungal taxa is the tip of a very large iceberg as literally millions of fungi have yet to be identified and named (Hawksworth and Lücking 2017). Early modern mycologists identified fungal species using several systems (see Nuñez Otaño et al. 2021, Chapter 5, this volume); the most frequently applied was the morpho-taxonomic Saccardo System. This system established a rigid hierarchy of morphological characters based on spore producing structures, pigmentation, and spore morphology (Seifert et al. 2011; Crous et al. 2015). Early in the twentieth century, the axiom ‘ontogeny recapitulates phylogeny’ began to be applied in fungal taxonomy and, for example, conidial ontogeny was used as a primary character for sorting anamorphic fungi (Vuillemin 1910a, b, 1911; Mason 1933; Hughes 1953; Crous et al. 1993; Iversen and Troels-Smith 1950; Thomson and Pfug 1953; Elsik 1992; Traverse 1996), and those...
et al. 2015). This system was adopted by some palaeomycologists in the middle of the twentieth century (Wolf 1966a, b, 1967a–d, 1968; Bradley 1967), while others continued to apply morpho-taxonomic approaches along the same lines as those used for pollen, because it is rare to find conidia in varying stages of development attached to conidiophores, etc. (Elsik 1968, 1969, 1970, 1976, 1980a, b, 1996, among others; Jansonius 1976; Jansonius and Hills 1976; Kalgotkar 1985; Kalgotkar and Sweet 1988; Kalgotkar and McIntyre 1991; Kalgotkar and Jansonius 2000; Wijayawardene et al. 2020). The morpho-taxonomic approaches took two major forms: (1) use of the Saccardo System (Kalgotkar and Jansonius 2000) and use of the van der Hammen System (van der Hammen 1954, 1956; Elsik 1996; Kalgutkar 2000). Since then, systems based on both ontogenic concepts and morpho-taxonomic systems were applied, primarily to fossil, rather than extant fungi, while morpho-taxonomic approaches have given way to combined (polyphasic) approaches for extant fungi (Ellis 1971, 1976; Kendrick 1971; Kendrick and Carmichael 1973; Carmichael et al. 1980; Seifert et al. 2011; Simões et al. 2013; Crous et al. 2015; Lücking et al. 2020). This disjunct in approaches has been largely driven by the vast datasets generated by, and increased utility and efficiency of, molecular taxonomy and somewhat greater availability of whole-fungus specimens to the neontologist. Extant fungal taxonomy is in a state of constant and drastic change based on results of molecular genetic studies, which have revolutionized our understanding of both fungal lineages and likely evolutionary rates (Statafora et al. 2017; Lücking et al. 2020). These methods can be applied to fossilized fungal remains only very rarely, and not at all to specimens older than the latest Miocene (Allentoft et al. 2012; Bellmain et al. 2013). Even before the development of this disjunct, challenges existed in establishing necessary collaborations between modern mycologists and those working on fossilized materials.

Nomenclature of fungal NPPs has had a cyclical century-long history. In the early years following recognition of fossil fungi, the philosophy was, as with most other fossil forms, that taxa should be assigned to extant families and genera, where possible, using the same morphological characters used by modern mycologists (Kalgotkar and Jansonius 2000). The difficulties presented by this approach were manifold, not least of which was that many taxa could not be readily assigned to modern groups as mycology was, itself, in its infancy. For this reason, and mirroring the practices of deep-time palynologists, the use of form-taxon became increasingly common, especially for Miocene and older fungi (Elsik 1992; Kalgotkar and Jansonius 2000). Simultaneously, the recognition of fungal and other NPPs in sediments from the European Quaternary by Bas van Geel (Hooghienstra 2012) led to the development of identifying acronyms (IA), also referred to as ‘NPP-types,’ ‘lab codes,’ or ‘van Geel types’ to designate NPPs pending correlation with modern taxa (van Hoeve and Hendrikse 1998; Miola 2012). This approach was preferred to erection of form-genera and the risk of producing taxonomic chaos, the likes of which exists for many deep-time fossil palynomorphs, and has achieved near-total buy-in among Quaternary palaeoecologists for treatment of NPPs. This was coupled with a push for increased collaboration between palaeo- and neontologists with the goal of assigning these forms to their proper taxonomic group (van Geel and Aptom 2006). This push for collaborations proved especially difficult, as during the same period, modern taxonomic practices, especially among mycologists, moved away from morphological approaches and into molecular approaches, thus fewer and fewer modern mycologists had the requisite knowledge, and IAs became the de facto identifier of choice to avoid taxonomic instability and to promote the use of NPPs as palaeoecological indicators (Miola 2012). Therefore, it has become common for a single fungus to have multiple means of identification: a name formed using morphological principles (Pirozynski and Weresub 1979; Kalgotkar and Jansonius 2000) for its Miocene and older fossils (although some taxa named this way range into the Recent!), an IA for its Quaternary fossils, and one or more names for its modern form, as many fungi have still have different names for the teleomorphic and anamorphic states, though this is being rapidly rectified by modern fungal taxonomists.

The use of dual nomenclature among modern fungi became viewed as increasingly problematic as improved culture practices and molecular genetics permitted previously unmatched anamorphs and teleomorphs to be recognized as different phases of a single fungus’ life cycle. A movement arose in the late twentieth century that proposed the ‘One Fungus, One Name’ philosophy (Wingfield et al. 2011), which became canon in 2011 when it was incorporated into the Melbourne Code (Neill et al. 2012). The implications of incorporation of this philosophy into the ICN were stark: one name for each fungal organism, whether it be living or fossil; all protections for multiple names for dispersed parts of single fungal organisms were removed, permitting significant simplification of fungal taxonomy and clarifying relationships between anamorphs and teleomorphs (Hawksworth 2011; Neill et al. 2012; Crous et al. 2015; Wijayawardene et al. 2020). For most NPPs treated under the ICN, fossil names only compete with fossil names of the same rank for priority (article 11.7), unless treated as synonymous with modern taxa (article 11.8) (Turland
et al. 2018). However, adoption of ‘one fungus one name’ and the current Section F (San Juan), which supersedes the remainder of the code for fungal taxonomy whether intended or not, has resulted in fungal form-taxon and modern taxa competing for priority (McNeill et al. 2012; Hawksworth et al. 2016; Nuñez Otaño et al. 2017; Shumilovskikh et al. 2017; Turland et al. 2018; May et al. 2019; Pound et al. 2019). Therefore, the erection of form-taxon is to be avoided wherever possible and use of IAs is recommended to avoid nomenclatural and systematic chaos.

Which code?

Beyond the challenges posed by nomenclature, simply naming a NPP can be challenging, as how you name it depends upon what it is, or you think it is (Table 1). The majority of NPPs— including plant spores; algae; fungi and fungus-like organisms such as slime moulds and oomycetes; Cyanobacteria; and most photosynthetic protists and their non-photosynthetic allies with the notable exception of Microsporidia — fall under the International Code of Nomenclature for algae, fungi, and plants (ICN; Shenzhen Code) (Turland et al. 2018). Metazoa, Microsporidia (even though they are closely related to fungi, either as a basal branch or possibly a sister taxon), and some protists are named using the International Code of Zoological Nomenclature (ICZN; The Code) (Ride et al. 1999), while bacterial cysts, a rare component of NPP assemblages, are named using the International Code of Nomenclature of Prokaryotes (ICNP; Parker et al. 2019). In 2005, the International Society of Protistologists adopted a new system of nomenclature for all extant protists, utilizing the existing genus–species names, but organized phylogenetically (Adl et al. 2005, 2007, 2012, 2019). At present, this system is only used for extant protozoans, while the ICZN, ICN, and ICNP are used for fossil organisms.

Each code is updated as deemed necessary by its governing body; for example, the ICN is typically updated at each meeting of the International Botanical Congress and referred to by the name of the city hosting the congress (i.e. as of this writing, the current ICN is known as the Shenzhen Code); the ICZN and ICNP are updated less frequently. Until 1975, organisms currently covered by the ICNP were covered by the precursor to the ICN, the International Code of Botanical Nomenclature (ICBN). Of note, from 2018, matters impacting only fungal nomenclature are to be decided not at the International Botanical Congresses, rather at the International Mycological Congresses, and rules specific to fungi, which supersede earlier provisions in the code, are present in a separate section of the ICN, Section F (Hawksworth et al. 2017; May et al. 2019).

Regardless of the specific guidelines contained in each of the codes of nomenclature, the goal is the same — to provide guidance in naming new organisms and revising existing extant and fossil and non-fossil taxa— toward an overarching goal of maintaining the stability of taxonomic names. There the similarities end. Each of the codes has a different starting date (the date from which the code takes effect), generally in the first quarter of the eighteenth century, excepting fossils governed by the ICN, which date to the late nineteenth century, and the ICNP, which dates to 1980. There are somewhat differing nomenclatural goals, as well. For example, the ICZN is most concerned with naming organisms between and including the ranks of superfamily and subspecies, while the ICN is concerned primarily with families and below. Even within each code, there are variations in ‘expectations’ for naming organisms.

| Table 1. NPP types and the code of nomenclature that governs their naming |
|-----------------------------|-------------|
| Non-pollen palynomorph type | Nomenclatural Code* |
| Achritarcha                | ICN         |
| Arthropoda – Oribatida, Insecta, Cladocera, Copepods, etc. | ICZN |
| Bacterial cysts            | ICNP        |
| Bryophytes, Pteridophytes, and similar plant spores | ICN |
| Chlorophyta – Shaeropaleas, Trebouxiales, Oedogoniales & Prasinophyceae | ICN |
| Chrysophyceae              | ICN         |
| Ciliate cysts – Tintinnids, etc. | ICZN |
| Cyanobacteria              | ICN         |
| Dinoflagellata             | ICN         |
| Foraminifera (linings)     | ICZN        |
| Freshwater sponges         | ICZN        |
| Fungi                       | Section F of the ICN |
| Helminth eggs              | ICZN        |
| Loricate Euglenophyta      | ICN         |
| Rhabdocoela                | ICZN        |
| Rotifers                   | ICZN        |
| Scolocodonts               | ICZN        |
| Streptophyta – Zygnemataceae & Desmidae | ICN |
| Tardigrades                | ICZN        |
| Testate amoebae            | ICZN        |
| Vascular plant remains – epidermal cells and hairs, stomata, bark and xylem remains | ICN |
| Other organisinal remains  | varies      |
| Textile fibres             | n/a         |

*Nomenclatural Code Abbreviations: International Code of Nomenclature for algae, fungi, and plants (ICN); International Code of Nomenclature of Prokaryotes (ICNP); International Code of Zoological Nomenclature (ICZN).*
There are numerous guides to using the codes that explain the processes more fully, including Turland (2019) for the ICN and Thompson (2003) for the ICZN. Additional guides exist for specific taxa, including Spies and Sæther (2004) for chironomids, Kosakyan et al. (2016) for testate amoebae, the Lentini and Williams Index of Fossil Dinoflagellates (Fensome et al. 2019), Guiry (2013) for the Conjugatophyceae (=Zygematophyceae), and many others.

How to name NPPs?

In many ways, identifying NPPs is becoming nearly as straightforward as identifying pollen, even when access to type collections is challenging and reference collections are scarce, thanks in large part to a series of digital resources that aggregate published IAs and taxonomic treatment of NPPs (Table 2). However, the vast majority of these identifications are made using IAs, rather than taxonomic names. NPP aggregating websites have become invaluable, as it is as undesirable to have multiple IAs to refer to a single NPP type as it is to have multiple taxonomic names for the same NPP type. Above and beyond the sites, identification keys published for each group as noted in Chapter 2 (Shumilovskikh et al. 2021) are also invaluable. Once the available resources have been consulted and it is established that the NPP in question is not previously named or given an IA, there are two options for giving it a designation: (1) apply a new IA and supply a detailed description, including measurements and photographs of the NPP, in your publication; or (2) give it a new taxonomic name. New names follow two patterns: (1) if it is clearly assignable to an extant genus or family but not identical to any extant taxon within that genus or family, a new taxon may be erected; or (2) if it is deep-time fossil form that is not clearly assignable to an extant genus or family, a fossil name may be produced, following the guidelines for fossils given in the relevant code.

Applying an IA

The method for crafting IAs for NPPs were described in detail by Miola (2012) and will be summarized here only briefly. IAs for NPPs are not binomial taxonomic identifiers, and do not have designated type specimens, rather they are constructed by a lab acronym, a dash, and a number. In some cases, a letter may follow the number, indicating a possible taxonomic relationship or similar morphology between non-identical taxa. The acronym is typically two or three letters and refers to the laboratory in which the slides are archived, not necessarily the scientist conducting the analysis. For example, Hdv, is the acronym for the Hugo de Vries Laboratory, where slides containing NPPs identified by Bas van Geel are housed (Miola 2012). Prior to 2012, greater variation in acronyms existed, with some referring to study sites or to the type of NPP (macrofossil or microfossil) encountered. Miola’s (2012) suggested simplification of this system has become standard practice. The number is ideally sequential, with the first unidentifed taxon noted in a given lab being numbered 1, the tenth 10, and so on. Not all of these numbers may be published (Miola 2012), as they may be identified prior to publication, and thus the taxonomic name is used, but should be recorded in the home laboratory. Beyond the IA itself, any publication identifying a NPP in this manner should note the wider identification category for the taxon in question (see Table 1). This is followed by a description, which should contain sufficient morphological detail that it could be used by any future researcher to identify the same taxon in their samples, i.e. it should be virtually the same as in a formal taxonomic description, and the specimen should be figured with sufficient high-quality photographs that all diagnostic features are apparent to the reader. These IAs should not only be published as part of the study in which they were encountered, but also submitted to one or both of the existing online NPP databases (Table 2), so that new IAs are readily searchable and to avoid the problem of multiple IAs for the same NPP. While these databases are presently stable, the NPP community must continue to support them and develop a plan for their continuance or incorporation into a well-funded databasing system. The overarching goal is, eventually, to match each NPP denoted initially by an IA to an existing genus, and, where possible, species, or, if experts agree, to erect a new species, or possibly, genus. The a priori assumption is that the vast majority of Quaternary NPPs represent extant taxa and require no new taxonomic treatment beyond a short note demonstrating that, for example, Hdv-364 is Thecaphora sp. That said, many deep-time NPPs represent extinct taxa (incertae sedis) and will require careful taxonomic treatment and some NPP IAs lack sufficient distinguishing characters to be formally named – care must be taken to avoid naming these clearly non-diagnostic fragmentary remains.

Erecting a new taxon

It is strongly recommended that you work closely with a modern taxonomist specializing in the group to which your new taxon belongs during the validation process, and that only very distinctive NPPs with multiple representative examples be erected as new taxa. In some cases, it is better to say, for example, that you have a Hypoxylon-type, rather than denoting a new species for this member of the
| Identification site                                      | URL                                      | Description                                                                                                                                                                                                 |
|----------------------------------------------------------|------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Non-Pollen Palynomorphs Project                          | http://nonpollenpalynomorphs.tsu.ru/    | This is a compilation of photomicrographs of NPPs organized by identifying acronyms (IAs) as defined by Miola (2012) with associated occurrence and taxonomic information, where known. The full image gallery is only accessible via secure log-in, available at no cost to contributors to the project and is designed to reduce duplication in assigning IAs and also to correlate IAs with otogenic names as they become available. A key feature of this project is the ability to search the database using the NPP characters of Coles (1990). |
| Non-Pollen Palynomorphs Database                         | https://www.wikis.uni-kiel.de/non_pollen_palynomorphs/doku.php/home | This is a compilation of NPPs found primarily in archaeological studies completed by the authors and correlated to images in other publications and taxonomic names.                                                                                       |
| The Kalgutkar and Jansonius Database of Fossil Fungi     | https://advance.science.sfu.ca/fungi/fossils/Kalgutkar_and_Jansonius/ | This is a compilation of scans of the information contained in the Kalgutkar and Jansonius card file of fossil fungi as well as line drawings of the fungi. Fungal palynomorphs covered by the database range from Paleozoic to Holocene. |
| CyberTruffle                                             | http://www.cybertruffle.org.uk/eng/index.htm | The Cypertruffle server is an aggregator of information about fungi that contains four main databases: Cyberliber (digital library for mycology), Cybernome (nomenclature and taxonomy), Robigalia (fungal distributions in space and time), and Valhalla (biographies of past mycologists); as well as links to numerous other mycological resources. |
| MycoBank, Index Fungorum, & Fungal Names                  | http://mycobank.org                      | These are the three approved repositories for fungal taxa and serve as a resource for determining taxonomic lineages, locating type specimens, and tracing nomenclatural history.                                                                                     |
| MycoBank, Index Fungorum, & Fungal Names                  | http://www.indexfungorum.org/            |                                                                                                                                                                                                             |
| MycoBank, Index Fungorum, & Fungal Names                  | http://www.fungalinfo.net/               |                                                                                                                                                                                                             |
| MyCoPortal                                               | https://mycoportal.org/portal/           | The Mycology Collections Portal contains identification keys, nomenclatural information, distribution data, etc. for North America and for worldwide microfungi.                                                                                       |
| Fungal Planet                                            | https://www.fungalplanet.org/            | This online peer-reviewed project provides a platform for rapid publication of new fungal taxa, complete with high-quality illustrations.                                                                 |
| Fungal Genera                                            | https://fungalgenera.org/                | This site provides a rapid means of locating key papers on individual fungal genera as well as determining taxonomic lineages.                                                                                      |
| MycoCosm                                                 | https://mycocosm.jgi.doe.gov/mycocosm/home | This site provides access to fungal genomic information. Importantly, given its phylogenetic organization, provides clues about where fungal fossil characters would have most parsimoniously evolved.                                              |
| PhycoCosm                                                | https://phycocosm.jgi.doe.gov/phycocosm/home | This site provides access to algal genomic information. Importantly, given its phylogenetic organization, provides clues about where algal fossil characters would have most parsimoniously evolved.                    |
| ISTAR Identification Keys and Illustrated Monographs     | http://istar.wikidot.com/id-keys         | The International Society for Testate Amoeba Research hosts a series of identification keys and illustrated monographs for modern testate amoebae.                                                                |

(Continued)
remarkably spore character-conservative Xylaria- ceae, or to use an existing deep-time name, especially for extinct taxa. If you and your collaborators do decide to erect new taxa, there are some basic rules to follow, and they vary depending upon which code applies to the organism. The majority of the differences outlined in Traverse (1996) still stand as of this (2021) writing. A key similarity is the use of Latin binomials to designate genera and species, with the gender of the genus dictating the ending of the species epithet. At present, the ICNP focuses on use of DNA sequence data, thus is unlikely to be applicable to fossil taxa.

**Erecting a new taxon using the ICZN.** The ICZN (http://www.iczn.org) contains very few explicit rules in terms of formatting and formulating new taxonomic entries, save that the new taxon be registered in Zoobank (http://www.zoobank.org); and validly published in a work (journal, book, etc.) meant to constitute a public and permanent scientific record. In general, when establishing a new species name, the entry should begin with a listing of the higher taxa to which the new taxon belongs. This listing should be followed by the genus name, material or specimens examined (which includes the holotype and any other types you choose to erect), type locality, etymology of the name, the distinguishing characters, a detailed description, and the distribution (see Fig. 1a).

**Erecting a new taxon using the ICN.** The ICN (https://www.iapt-taxon.org/nomen/main.php) contains more stringent guidelines in terms of formatting new taxonomic entries (Fig. 1b), but has fewer categories of information required, with levels of information lumped together. At its most basic level, a binomial Latin name, a diagnosis of the taxon, and publication in a resource with an ISBN or ISSN are all that is required for valid publication; in practice, taxa are rarely considered validly published if they do not contain at least the information outlined in Figure 1b, however, many fungi are validly published in ISSN-bearing databases with a minimum of information. Of note, Latin genders can be complicated in the ICN (Manara 1991), as some taxa, most notably trees, are treated as a single gender regardless of the gender of the genus. In the case of fungi, like animalia, their taxonomic descriptions must be entered into a database, and the names approved prior to publication. Currently approved databases under San Juan Section F (May et al. 2019) are: MycoBank (http://www.mycobank.org), Index Fungorum (http://www.indexfungorum.org/)

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**Table 2. Continued.**

| Identification site | URL | Description |
|---------------------|-----|-------------|
| Microworld: world of amoeboid organisms | https://www.arcella.nl/ | This site presents a visual digital identification key to modern Amoebozoa, Rhizaria, Stramenopiles, Discoba, Nucleotmycea, and Heliozoa. |
| Digital Image Collection of Desmids | http://www.digicodes.info/index.html | This site presents digital photographs, primarily light micrographs, of modern Desmids. Each image refers the reader to the original taxonomic description. |
| AlgaeBase | https://www.algaebase.org/ | This site provides taxonomic, nomenclatural, and global distribution information about algae. |
| Modern Dinocyst Key | https://www.marum.de/Karin-Zonneveld/dinocystkey.html | This site presents digital photographs of the single grain type collection at MARUM organized via an interactive identification key. |
| Dinoflaj3 | http://dinoflaj.smu.ca/dinoflaj3/index.php/Main_Page | This site is the digital version of the Lentin and Williams Dinoflagellate Index and presents hyperlinked taxonomic information for fossil dinoflagellates. |
| International Plant Name Index | https://www.ipni.org/ | This site serves as a resource for determining taxonomic lineages, locating type specimens, and tracing nomenclatural history of plants, including spore-producing plants considered to be NPPs. |
| Taxonomy Project | https://www.ncbi.nlm.nih.gov/taxonomy/ | This international aggregator of genetic sequence data from worldwide databases is organized phylogenetically, permitting close relatives and most parsimonious evolutionary placement of fossil NPP taxon characters to be identified. |
Fig. 1. A side-by-side comparison of basic taxonomic treatment using (a) the ICZN and (b) the ICN. Example (a) uses a fictitious Rotifer species within an actual Rotifer genus (see Meksuwan et al. 2018). Example (b) uses a fictitious Fungal species within an actual Fungal genus (see Pound et al. 2019).
names/IndexFungorumRegister.htm), and Fungal Names (http://www.fungalinfo.net/). The database entries contain the name and diagnosis, at a minimum. MycoBank encourages the deposit of significantly more information, including the description, where and when (geologically) a fungus is found, and images of the taxon. The registration process permits many orthographic errors to be rectified prior to publication. Valid publication under the aegis of the ICN requires publication as paper copy or PDF in a journal, book, or other form having an ISSN or ISBN that is generally available to the public or scientific institutions with library access to the public. A detailed description of the process and current challenges associated with use of the ICN for palynology can be found in Gravendyck et al. (2021).

Assigning a taxonomic name to an IA

The overarching goal is to have taxonomic names associated with as many NPP IAs as possible. Collaborations with experts in each organism under consideration are key to this task. When an identification is made, publication of a short paper or communication making the correlation and sending this paper to one of the two NPP databases (Table 2) is sufficient if the taxonomic name is applied directly. Where a new species of a known genus is erected, or a new genus of a known family, the rules of the appropriate Code must be followed (see the section ‘Erecting a new taxon’).

Citing taxonomic names of NPPs in publications

Using taxonomic names, rather than IAs permits the ecological tolerances of the extant taxon to be used seamlessly to interpret the palaeoecosystem, rather than using correlations with pollen associated with the IA to make this interpretation, thus using the NPP as a direct, and therefore more robust, proxy. IAs are, however, deeply entrenched in the NPP literature. For this reason, we recommend that the IA code for NPPs with taxonomic names be placed in parenthesis following the name the first time it is used in a palaeoecological publication outside of any systematic palynology and in any table of NPP taxa contained in the paper. For example, Tetraploa aristata (HdV-89) or Helicoon pluriseptatum (HdV-30). There are some NPPs that do not have IAs, only taxonomic names; these should be referred to by their epithet alone, such as Rhexoampullifera stogieana (Pound et al. 2019).

The need for taxonomic housekeeping

Taxonomic housekeeping for NPPs falls into two broad categories, (1) maintaining a master list of NPP types, descriptions, images, and their taxonomic names; (2) resolving past taxonomic decisions for deep-time fossil fungi in light of the San Juan Section F (May et al. 2019) and future iterations of Section F. The first category is in hand, with two dedicated databases, but community support, in terms of time or funding, is vital to ensure success and continuity. It is unlikely that all NPPs will be assigned to modern taxa, therefore, the databases are and will remain the prime tool in avoiding multiple IA for single taxa.

As has been pointed out in other contexts, the chief nestor of deep-time fungal palynology, William C. Elsik, generated significant taxonomic uncertainty (Eyde 1991) and both used and taught others to use many unvalidated taxonomic names, e.g. many of the ‘in prep’ taxa in the 1992 short-course were never validated (Elsik 1992; Kalgutkar and Jansonius 2000), and type specimens for these invalid taxa were lost upon Elsik’s death. Kalgutkar and Jansonius (2000) made an immense effort to clean up some of the taxonomic uncertainty among deep-time fossil fungi in their catalogue. However valiant an effort, it did not resolve the problem of status. In 2000, the code was written such that when the name of a fossil taxon is synonymous with that of a modern taxon, the name of the modern taxon takes priority (Traverse 1996; Turland et al. 2018); many fossil taxa, especially those with ranges extending into the Quaternary and Recent, should have been synonymized and renamed at that point. Twenty years later, with much better access to fungal taxonomic works, this housekeeping has begun (Musotto et al. 2012, 2013, 2017; Martinez et al. 2016; Nuñez Otaño et al. 2017; O’Keefe 2017; Shumilovskikh et al. 2017; Strullu-Derrien et al. 2018; Bianchiniotti et al. 2020 among others) (see Nuñez Otaño et al. 2021, Chapter 5, this volume, for examples), but it still has a long way to go, and must be done under the aegis of the San Juan section F.

Similar and more complex taxonomic housekeeping is needed in many other groups of NPPs. Holotypes and members of type series needed for direct comparisons have been lost to fire, flood, and war, and there are difficulties in erecting Neotypes in some taxa due to how the various codes are written (Gravendyck et al. 2021).

Conclusions

Thus, in 100 years NPP nomenclature has come full circle: once again, close collaborations are called for between palaontologists and neontologists with expertise in morphological character states bridging the gap between biology and palaeontology in our drive to identify NPPs. Pending formal identification, identifying acronyms (IAs) following the
guidance of Miola (2012) should be used to avoid any further nomenclatural instability (Seifert 2017), and unstable deep-time NPP nomenclature should be revised to align with that of late Cenozoic workers. During this period of identification and taxonomic revision, NPP databases are of vital importance – without them it is nearly impossible to keep track of which NPPs have and have not yet been identified. Taxonomic housekeeping and re-alignment of deep-time NPP nomenclature is urgently needed because it forms the backbone for calibrating molecular clock phylogenies (Taylor et al. 2015; Strullu-Derrien et al. 2018). We must all learn to speak the same nomenclatural language.

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References
Adl, S.M., Simpson, A.G.B. et al. 2005. The new higher level classification of Protists. Journal of Eukaryotic Microbiology, 52, 399–451, https://doi.org/10.1111/j.1550-7408.2005.00053.x
Adl, S.M., Leander, B.S. et al. 2007. Diversity, nomenclature, and taxonomy of Protists. Systematic Biology, 56, 684–689, https://doi.org/10.1080/10635150701494127
Adl, S.M., Simpson, A.G. et al. 2012. The revised classification of eukaryotes. Journal of Eukaryotic Microbiology, 59, 429–493, https://doi.org/10.1111/j.1550-7408.2012.00644.x
Adl, S.M., Bass, D. et al. 2019. Revisions to the classification, nomenclature, and diversity of eukaryotes. Journal of Eukaryotic Microbiology, 66, 4–119, https://doi.org/10.1111/jem.12691
Allentoft, M.E., Collins, M. et al. 2012. The half-life of DNA in bone: measuring decay kinetics in 158 dated fossils. Proceedings of the Royal Society B, 279, 4724–4733, https://doi.org/10.1098/rspb.2012.1745
Bellemain, E., Davey, M.L. et al. 2013. Fungal palaeodiversity revealed using high-throughput metabarcoding of ancient DNA from arctic permafrost. Environmental Microbiology, 15, 1176–1189, https://doi.org/10.1111/1462-9020.12020
Bianchinotti, M.V., Martinez, M.A. and Cornou, M.E. 2020. The utility of Desmidiospora: a paradigm shift based on Paleogene fungal remains from the Ninhua Basin, Argentina. Palynology, 44, 587–596, https://doi.org/10.1080/01916122.2019.1657514
Bradley, W.H. 1967. Two aquatic fungi (Chytridiales) of Eocene age from the Green River Formation of Wyoming. American Journal of Botany, 54, 577–582, https://doi.org/10.2307/2440661
Carmichael, J.W., Kendrick, W.B., Conners, I.L. and Sigler, L. 1980. Genera of Hyphomycetes. University of Alberta Press, Calgary, Canada.
Coles, G.M. 1990. A note on the systematic recording of organic-walled microfossils (other than pollen and spores) found in archaeological and Quaternary palynological preparations. Circarea, 7, 103–111.
Cookson, I.C. 1947. Plant microfossils from the lignites of Kerguelen Archipelago, B.A.N.Z. Antarctic Research Expedition Report Series A, 2, 127–142.
Crous, P.W., Hawksworth, D.L. and Wingfield, M.J. 2015. Identifying and naming plant-pathogenic fungi: past, present, and future. Annual Reviews of Phytopathology, 53, 247–267, https://doi.org/10.1146/annurev-phyto-080614-120245
Ehrenberg, C.G. 1854. Mikrogeologie: Das Erden und Felsen schaffende Wirken des unsichtbar kleinen selbständigigen Lebens auf der Erde. Verlag von Leopold Voss, Leipzig.
Ellegaard, M., Head, M.J. and Versteegh, G.J.M. 2018. Linking biological and geological data on dinoflagellates using the genus Spiniferites as an example: the implications of species concepts, taxonomy and dual nomenclature. Palynology, 42(supp1): 221–230, https://doi.org/10.1080/01916122.2018.1465732
Ellis, M.B. 1971. Dematiaceous Hyphomycetes. Commonwealth Mycological Institute, Kew, UK.
Ellis, M.B. 1976. More dematiaceous Hyphomycetes. Commonwealth Mycological Institute, Kew, UK.
Elsik, W.C. 1968. Palynology of a Paleocene Rockdale lignite, Milam County, Texas, I. Morphology and taxonomy. Pollen et Spores, 10, 263–314, pl. 1–15.
Elsik, W.C. 1969. Late Neogene palynomorph diagrams, northern Gulf of Mexico. Transactions of the Gulf Coast Association of Geological Societies, 19, 509–528, pl. 1–5.
Elsik, W.C. 1970. Palynology of a Paleocene Rockdale lignite, Milam County, Texas, III. Errata and taxonomic revisions. Pollen et Spores, 12, 99–101.
Elsik, W.C. 1976a. Fossil fungal spores. In: Weber, D.J. and Hess, W.M. (eds) The Fungal Spore: Form and Function. John Wiley & Sons, New York, 849–862.
Elsik, W.C. 1976b. Fossil fungal spores and Cenozoic palynostratigraphy. Geoscience and Man, 15, 115–120, https://doi.org/10.1080/00721395.1976.9989779
Elsik, W.C. 1992. The Morphology, Taxonomy, Classification and Geologic Occurrence of Fungal Palynomorphs. A Shortcourse presented under the auspices
of The American Association of Stratigraphic Palynologists, Inc. Houston, TX.

Elsik, W.C. 1996. Chapter 10 – Fungi. In: Jansonius, J. and McGregor, D.C. (eds) Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Foundation, Dallas, TX, 1, 293–305.

Erdtman, G. 1948. Pollen and spore morphology. In: Erdtman, G. (ed.) Palynology: Prospects and Aspects. Svensk botanisk tidskrift, 42, 467–483.

Eyde, R.H. 1991. Nyssa-like fossil pollen: a case for stabilizing nomenclature. Taxon, 40, 75–88, https://doi.org/10.2307/1229294

Fensome, R.A., Williams, G.L. and MacRae, R.A. 2009. Calibrating the Tree of Life: fossils, fungi: impacts of decisions made in Melbourne in 1977–1992, unpaginated; introductory notes are now available online: http://contentdm.ucalgary.ca/digital/collection/p22007coll22/id/168 [last accessed 15 May 2020].

Fensome, R.A., Williams, G.L. and MacRae, R.A. 1991. The Lentin and Williams index of fossil dinoflagellates. American Association of Stratigraphic Palynologists Foundation, Dallas, TX, Contribution Series, 50.

Forest, F. 2009. Calibrating the Tree of Life: fossils, molecules and evolutionary timescales. Annals of Botany, 104, 789–794, https://doi.org/10.1093/aob/mcp192

Gravendenck, J., Fensome, R.A., Head, M.J., Herendeen, P.S., Riding, J.B., Bachelier, J.B. and Turland, N.J. 2021. Taxonomy and nomenclature in palaeopalynology: basic principles, current challenges and future perspectives. Palynology, https://doi.org/10.1080/01916122.2021.1918279.

Guiry, M.D. 2013. Taxonomy and nomenclature of the Conjugatophyceae (=Zygnematophyceae). Algae, 28, 1–29, https://doi.org/10.4490/algaea.2013.28.1.001

Hawksworth, D.L. 2011. A new dawn for the naming of fungi: impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. MycoKeys, 1, 7–20, https://doi.org/10.3897/mycokeys.1.2062

Hawksworth, D.L. and Lücking, R. 2017. Fungal Diversity Revisited: 2.2 to 3.8 Million Species. In: Heitman, J., Howlett, B.J., Crous, P.W., Stukkenbrock, E.H., James, T.Y. and Gow, N.A.R. The Fungal Kingdom, https://doi.org/10.1128/9781555819583.ch4

Hawksworth, D.L., van Geel, B. and Wiltshire, P.E.J. 2016. The enigma of the Diporothea polynormorph. Review of Palaeobotany and Palynology, 235, 94–98, https://doi.org/10.1016/j.revpalbo.2016.09.010

Hawksworth, D.L., May, T.W. and Redhead, S.A. 2017. Fungal nomenclature evolving: changes adopted by the 19th International Botanical Congress in Shenzhen 2017, and procedures for the Fungal Nomenclature Session at the 11th International Mycological Congress in Puerto Rico 2018. IMA Fungus, 8, 211–218, https://doi.org/10.5598/imafungus.2017.08.02.01

Head, M.J., Fensome, R.A., Herendeen, P.S. and Skog, J.E. 2016. (315–319) Proposals to amend article 11.8 and its Examples to remove ambiguity in the sanctioning of dual nomenclature for dinoflagellates, and an emendation of Article 11.7, Example 29. Taxon, 65, 902–903, https://doi.org/10.12705/654.34

Hennig, W. 1966. Phylogenetisches System: University of Illinios Press, Urbana, IL.

Hooghiemstra, H. 2012. Non-pollen palynomorphs: From unknown curiosities to informative fossils. Celebrating the scientific career of Bas van Geel. Review of Palaeobotany and Palynology, 186, 2–4, https://doi.org/10.1016/j.revpalbo.2012.07.015

Hughes, S.J. 1953. Conidiophores, conidia, and classification. Canadian Journal of Botany, 31, 577–659, https://doi.org/10.1139/h53-046

Ibrahim, A.C. 1933. Sporeformen des Aegirhorizontes des Ruhrreviers. Publication of 1932 Doctoral Dissertation from the Technische Hochschule Berlin, Konrad Triltsch, Würzburg/Berlin, Germany.

Iversen, J. and Troels-Smith, J. 1950. Pollenmorfologiske Nitio- nen und Typen. Danmarks Geologiske Undersøgelse. 4. Rieke, Forelsbligne meddelelser og mindre afhandlinger, 3, 1–52.

Jansonius, J. 1976. Paleogene fungal spores and fruiting bodies of the Canadian Arctic. Geoscience and Man, 15, 129–132, https://doi.org/10.1080/00721395.1976.9989782

Jansonius, J. and Hills, L.V. 1976. Genera file of fossil spores and pollen. Department of Geology and Geophysics, University of Calgary, Alberta, Special Publication with 11 supplements (1977–1992), unpaginated; introductory notes are now available online: http://contentdm.ucalgary.ca/digital/collection/p22007coll22/id/168 [last accessed 15 May 2020].

Kalugutka, R.M. 1985. Fossil fungal fructifications from Bonnet Plume Formation, Yukon Territory. Geological Survey of Canada Paper, 85–1B, 259–268.

Kalugutka, R.M. and Jansonius, J. 2000. Synopsis of fossil fungal spores, mycelia and fructifications. American Association of Stratigraphic Palynologists Foundation Contributions Series, 39.

Kalugutka, R.M. and McIntyre, D.J. 1991. Holocarpous fungi and Early Eocene pollen, Eureka Sound Group, Axel Heiberg Island, Northwest Territories. Canadian Journal of Earth Sciences, 28, 364–371, https://doi.org/10.1139/e91-033

Kalugutka, R.M. and Sweet, A.R. 1988. Morphology, taxonomy and phylogeny of the fossil fungal genus Pesavis from northwestern Canada. Bulletin of the Geological Survey of Canada, 379, 117–133.

Kendrick, B. (ed.) 1971. Taxonomy of Fungi Imperfecti: Proceedings of the First International Specialists’ Workshop Conference on Criteria and Terminology in the Classification of Fungi Imperfecti, Kananskis, Alberta, Canada. University of Toronto Press, Toronto.

Kendrick, W.B. and Carmichael, J.W. 1973. Hyphomycetes. In: Ainsworth, G.C., Sparrow, F.K. and Sussman, A.A. (eds) The Fungi, An Advanced Treatise, 4A. Academic Press, New York, 323–509.

Kosakyan, A., Gomaa, F., Lara, E. and Lahr, D.J.G. 2016. Fossil fungi: impacts of decisions made in Melbourne in 1977–1992, unpaginated; introductory notes are now available online: http://contentdm.ucalgary.ca/digital/collection/p22007coll22/id/168 [last accessed 15 May 2020].

Lücking, R., Aime, M.C. et al. 2020. Unambiguous identification of fungi: where do we stand and how accurate and precise is fungal DNA barcoding? IMA Fungus, 11, 14, https://doi.org/10.1186/s43008-020-00033-z

Manara, B. 1991. Some guidelines on the use of gender in generic names and species epithets. Taxon, 40, 301–308, https://doi.org/10.2307/1222983

Martinez, M.A., Bianchiniotti, M.V., Saxena, R.K., Cornou, M.E. and Quattrichio, M.E. 2016. Fungal spores from the Palaeogene El Foyel Group of Nirihau Basin,

Nomenclature and NPP taxa
van der Hammen, T. 1954. Principios para la nomenclatura palinológica sistemática. Boletín Geologico, Bogotá, 2, 4–24.

Simões, M.F., Pereira, L., Santos, C. and Lima, N. 2013. Polymorphic identification and preservation of fungal diversity: concepts and applications. In: Malik, A., Grohmann, E. and Alves, M. (eds) Management of Microbial Resources in the Environment. Springer Science + Business Media, Dordrecht, 91–117.

Spies, M. and Sæther, O.A. 2004. Notes and Recommendations on Taxonomy and Nomenclature of Chironomidae (Diptera). Zootaxa 752, Magnolia Press, Auckland, New Zealand.

Statafora, J.W., Aime, M.C., Grigoriev, I.V., Martin, F., Stajich, J.E. and Blackwell, M. 2017. The fungal tree of life: from molecular systematics to genome-scale phylogenies. Microbiology Spectrum, 5, FUNK-0053-2016, https://doi.org/10.1128/microbiolspec.FUNK-0053-2016

Strullu-Derrien, C., Selosse, M.-A., Kenrick, P. and Martin, F.M. 2018. The origin and evolution of mycorrhizal symbioses: from palaeomycology to phylogenomics. New Phytologist, 220, 1012–1030, https://doi.org/10.1111/nph.15076

Taylor, T.N., Krings, M. and Taylor, E.L. 2015. Fossil Fungi. Academic Press, Elsevier, Amsterdam.

Thomson, F.C. 2003. Nomenclature and classification, principles of. In: Resh, V.H. and Carde, R.T. (eds) Encyclopedia of Insects. Academic Press, San Diego, 798–807.

Thomson, P.W. and Pflug, H. 1953. Pollen und Sporen des mitteleuropäischen Tertiärs. Palaeontographica Abteilung B. Paläophytologie, 94, 1–138.

Traverse, A. 1957. The nomenclatural problem of plant microfossil species belonging to extant genera. Micro-paleontology, 3, 255–258, https://doi.org/10.2307/1484110

Traverse, A. 1996. Chapter 2. Nomenclature and Taxonomy, Dallas, TX, International Code of Nomenclature for Algae, Fungi, and Plants, 2nd edn. Pensoft, Sofia, Bulgaria.

Turland, N., Wiersema, J.H. et al. (eds) 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code), adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten, https://doi.org/10.12705/Code.2018

van der Hammen, T. 1956. Nomenclatura palinológica sistemática/A palynological systematic nomenclature. Boletín Geologico, Bogotá, 4, 26–101.

van der Hammen, T. 1958. Recommendations and proposals for palynological systematic nomenclature. Taxon, 7, 273–274, https://doi.org/10.2307/1217639

van Geel, B. and Aptroot, A. 2006. Fossil ascomycetes in Quaternary deposits. Nova Hedwigia, 82, 313–329, https://doi.org/10.1127/0029-5035/2006/0082-0313

van Hoeve, M.L. and Hendrikse, M. (eds) 1998. A Study of Non-pollen Objects in Pollen Slides. The Types as Described by Dr. Bas van Geel and Colleagues. Laboratory of Palynology and Paleobotany, Utrecht.

Vuillemin, P. 1910a. Matériaux pour une classification rationelle des Fungi Imperfecti. Comptes rendus de l’Académie des Sciences Paris, 150, 882–884.

Vuillemin, P. 1910b. Les Conidiosporés. Bulletin de la Société des Sciences de Nancy, Serie 3, 11, 129–172.

Vuillemin, P. 1911. Les Aleuriosporés. Bulletin de la Société des Sciences de Nancy, Serie 3, 12, 151–175.

Wijayawardene, N.N., Hyde, K.D. 2020. Outline of fungi and fungus-like organisms. Mycosphere, 11, 1060–1456, https://doi.org/10.5943/mycosphere/11/1/8

Wingfield, M.J., De Beer, Z.W., Slippers, B., Wingfield, B.D., Groenewald, J.Z., Lombard, L. and Crous, P.W. 2011. One fungus, one name promotes progressive plant pathology. Molecular Plant Pathology, 13, 604–613, https://doi.org/10.1111/j.1364-3703.2011.00768.x

Wolf, F.A. 1966a. Fungus spores in East African lake sediments. Bulletin of the Torrey Botanical Club, 93, 104–113, https://doi.org/10.2307/2483751

Wolf, F.A. 1966b. Fungus spores in East African lake sediments, II. Journal of the Elisha Mitchell Scientific Society, 82, 57–61.

Wolf, F.A. 1967a. Fungus spores in East African lake sediments. IV. Bulletin of the Torrey Botanical Club, 94, 31–34, https://doi.org/10.2307/2483599

Wolf, F.A. 1967b. Fungus spores in East African lake sediments. V. Mycologia, 59, 397–404.

Wolf, F.A. 1967c. Fungus spores in East African lake sediments. VI. Journal of the Elisha Mitchell Scientific Society, 83, 113–117.

Wolf, F.A. 1967d. Fungus spores in East African lake sediments. VII. Bulletin of the Torrey Botanical Club, 94, 480–486, https://doi.org/10.2307/2483565

Wijayawardene, N.N., Hyde, K.D. 2018. Outline of fungi and fungus-like organisms. Mycosphere, 11, 1060–1456, https://doi.org/10.5943/mycosphere/11/1/8

Zuckerkandl, E. and Pauling, L. 1965. Molecules as documents of evolutionary history. Journal of Molecular Biology, 8, 357–366.