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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.

Keywords: Nomenclature, NPP, taxonomy, NPP-types

1. Introduction

Once non-pollen palynomorphs (NPPs) are extracted from rock, sediment, or peat (see 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 micropaleontology, 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-taxa (Reinsch 1881; H. Potonié 1893) and back several times.

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 paleopalynologists and actuopalynologists; 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 (Pyrozinski and Weresub 1979).

In the earliest days of palynology, a schism developed between those favoring classification based on morphological properties entirely separate from taxonomic relationships (H. Potonié 1893; R. Potonié 1931; Ibrahim 1933; Iverson and Troels-Smith 1950; Thompson and Pflug 1953; Elsik 1992; Traverse 1996), 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 favor. 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 assigned to modern taxa (Traverse 1996); this approach has permitted them to become very robust paleoecologic and paleoclimatic proxies. In deep time studies, a unique taxonomic approach, wholly divorced from modern taxonomic names, has been adopted with the aim of providing taxonomic stability (Traverse 1957) and in recognition that in many cases, it was not possible to assign fossil taxa to modern families, as comparable modern forms either don't exist (the lineage is extinct), had yet to be found, the fossils are too fragmentary to gauge their systematic relationships, or the systematic position of corelative modern taxa is unknown (Wijayawardene et al. 2020). In the past 25 years, the latter three of these situations have begun to change. With the advent of phylogenetic systematics (Zuckerkandl and Pauling, 1965; Hennig, 1966) and the emergence of robust molecular clock methods calibrated to a much-expanded fossil record (Forest 2009), it became apparent that many extant taxa range well into the geological record. Likewise, with improved communication among scientists facilitated by the digital age and online fossil and extant taxonomic databases, it has become easier than ever to access obscure publications and identify previously unknown taxa. Non-pollen palynomorphs, especially fungi and arthropods, *do* often occur in fragmentary form, providing few pieces of information with which to determine the affiliation of the taxa. Further conflating the taxonomic issues with NPP groups 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 paleoecologic) confusion (Bianchinotti *et al.* 2020; Seifert *et al.* 2017; Traverse 1996).

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.

2. 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 (Ellegaard *et al*. 2018; Head *et al.* 2016).

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 2018). Early modern mycologists identified fungal species using several systems (see 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 (Crous *et al.* 2015; Seifert *et al.* 2011). Early in the 20th 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.* 2015). This system was adopted by some palaeomycologists in middle of the 20th century (Bradley 1967; Wolf 1966a-b, 1967a-d, 1968), 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, 1976a-b, Elsik 1996, among others; Jansonius 1976; Jansonius and Hills 1976; Kalgutkar 1985; Kalgutkar and Sweet 1988; Kalgutkar and McIntyre 1991; Kalgutkar and Jansonius 2000; Wijayawardene *et al.* 2020). The morpho-taxonomic approaches took two major forms: 1) use of the Sarccado system (Kalgutkar and Jansonius 2000) and use of the van der Hammen System (van der Hammen 1954, 1955; Elsik 1996; Kalgutkar and Jansonius 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 (Kendrick 1971; Ellis 1971, 1976; 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 (Spatafora *et al.* 2017; Lücking et al. 2020). However, 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; Bellemain *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 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 (Kalgutkar 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-taxa became increasingly common, especially for Miocene and older fungi (Elsik 1992; Kalgutkar and Jansonius 2000). Simultaneously, the recognition of fungal and other NPPs in sediments from the European Quaternary by Bas van Geel (Hooghiemstra 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 Hove and Hendrickse 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 paleoecologists 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 Aptroot 2001). 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 paleoecological indicators (Miola 2012). Therefore, it has become common for a single fungus to have multiple means of identification: a name formed using morphological principles (Kalgutkar and Jansonius, 2000; Pirozynski and Weresub, 1979) 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 un-matched anamorphs and teleomorphs to be recognized as different phases of a single fungus' life cycle. A movement arose in the late 20th century that proposed the "One Fungus, One Name" philosophy (Wingfield *et al.* 2011), which became cannon in 2011 when it was incorporated into the Melbourne Code (McNeill *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; McNeill *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-taxa and modern taxa competing for priority (McNeill *et al.* 2012; Hawksworth *et al.* 2016; Shumilovskikh *et al*. 2017; Nuñez Otaño *et al*. 2017; Turland *et al.* 2018; Pound *et al.* 2019; May *et al.* 2019). Therefore, the erection of form-taxa is to be avoided wherever possible and use of IAs is recommended to avoid nomenclatural and systematic chaos.

3. 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 18th century, excepting fossils governed by the ICN, which date to the late 19th 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. 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 Lentin and Williams Index of Fossil Dinoflagellates (Fensome *et al*. 2019), Guiry (2013) for the Conjugatophyceae (=Zygnematophyceae), and many others.

4. How to name NPPs?

In many ways, identifying NPPs is becoming nearly as straight-forward 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 IA's, 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 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.

4.1 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 Vris 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 unidentified 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 IA's 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 IA's are readily searchable and to avoid the problem of multiple IA's 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 IA's lack sufficient distinguishing characters to be formally named – care must be taken to avoid naming these clearly non-diagnostic fragmentary remains.

4.2 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 remarkably spore character-conservative Xylariaceae, 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.

4.2.1 Erecting a new taxon using the ICZN

The ICZN (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 (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 Figure 1-A).

4.2.2 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 (Figure 1-B), 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 1-B, 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 (www.mycobank.org), Index Fungorum (http://www.indexfungorum.org/names/IndexFungorumRegister.htm), and Fungal Names(http://124.16.146.175:58080/fungalname/fungalname.html). 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. (*in review*).

4.3 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 section 4.2, above).

4.4 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 paleoecosystem, 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 paleoecological 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).

4.5 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 catalog. 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 re-named at that point. Twenty years later, with much better access to fungal taxonomic works, this housekeeping has begun (Musotto *et al.* 2012, 2013, 2017, Martínez *et al*. 2016; Shumilovskikh *et al.* 2017; Nuñez Otaño *et al.* 2017; O'Keefe 2017; Strulliu-Derrien *et al.* 2018; Bianchinotti *et al.* 2020 among others) (see 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., *in review*).

5. Conclusions

Thus, in 100 years NPP nomenclature has come full circle: once again, close collaborations are called for between paleontologists and neontologists with expertise in morphological character states bridging the gap between biology and paleontology 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 (Strullu-Derrien *et al.* 2018; Taylor *et al.* 2015). We must all learn to speak the same nomenclatural language.

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8. Figure Caption

Figure 1. A side-by side comparison of basic taxonomic treatment using the ICZN (A) and the ICN (B). 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).

9. Tables

Table 1. NPP types and the Code of Nomenclature that governs their naming.

Non-Pollen Palynomorph Type	Nomenclatural Code[1]
Achritarcha	ICN
Arthropoda - Oribatida, Insecta, Cladocera, Copepods, etc.	ICZN
Bacterial Cysts	ICNP
Bryophytes, Pteridophytes, and similar plant spores	ICN
Chlorphyta - Shaeropleales, Trebouxiales, Oedogoniales & Prasinophyceae	ICN
Chrysophyceae	ICN
Ciliate Cysts - Tintinnids, etc.	ICZN
Cyanobacteria	ICN
Dinoflagelata	ICN
Foraminifera (linings)	ICZN
Freshwater sponges	ICZN
Fungi	Section F of the ICN
Helminth eggs	ICZN
Loricate Euglenophyta	ICN
Rhabdocoela	ICZN
Rotifers	ICZN
Scolecodonts	ICZN
Streptophyta - Zygnemataceae & Desmidiales	ICN
Tardigrades	ICZN
Testate amoebae	ICZN
Vascular plant remains - epidermal cells and hairs, stomata, bark and xylem remains	ICN
Other organismal remains	varies
Textile Fibers	n/a

[1] 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)

Table 2. Listing of NPP databases useful when completing nomenclatural work.

Identification Site	URL	Description
Non-Pollen Palynomorphs Project	http://nonpollenpalynomorphs.tsu.ru/	This is a compilation of photomicrographs of NPPs organized by Identifying Acronyms 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 http://www.indexfungorum.org/ http://124.16.146.175:58080/fungalname/fungalname.html	These are the three approved repositories for fungal taxa and serves as resource for determining taxonomic lineages, locating type specimens, and tracing

		nomenclatural history.
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.
Microworld: world of amoeboid organisms	https://www.arcella.nl/	This site presents a visual digital identification keys to modern Amoebozoa, Rhizaria, Stramenopiles, Discoba, Nucletmycea, 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.

A

Phylum Rotifera Cuvier, 1817
Class Eurotatoria De Ridder, 1957
Subclass Monogononta Plate, 1889
Superorder Gnesiotrocha Kutikova, 1970
Order Flosculariaceae Harring, 1913
Family Flosculariidae Ehrenberg, 1838
Genus *Limnias* Schrank, 1803

***Limnias exemplius* sp. n.** (for species nova or n.sp. for new species)
http://zoobank.org/restofyourURLhere (if requested by the publishing journal)

Material examined. *Holotype*. A brief description of the sample, including it identifying slide or specimen number and where it is housed goes here. Any paratypes you choose to erect also go here, with the italicized boldface heading ***Paratype***, as does the total number of specimens examined.
Etymology. Explain how you came up with the species name here; in this case, it means example, as we're providing an example, and ends in "us" as *Limnias*, which is masculine.
Type locality. Write where it was found, including the latitude & longitude and depth below surface, if known. Give environment or rock type, if known, and the date it was collected, if known.
Diagnosis. This is a very brief description of your specimen highlighting its unique features, and typically incudes reference to any figures you are including, although be aware that figures ***cannot*** be type material; they are merely representations of the actual materials.
Description. This is the detailed description of your taxon and includes measurements of the taxon. The level of detail should be sufficient that any expert in the field will understand it.
Remarks and comparisons. This section contains a detailed comparison to similar taxa both in the genus and outside of the genus. It also contains any other information that may be of use to other researchers, such as likely life habit, ecology, distribution, etc.

B

Kingdom Fungi
Phylum ASCOMYCOTA
Class SORDARIOMYCETES
Family Chaetosphaeriaceae
Genus *Chaetosphaeria*

Chaetosphaeria exemplii sp. nov. (for species nova)
MycoBank MB XXXXXXX (if needed); Plate #, figures #-##

Holotype. Specimen #; Location of the specimen (both on the slide and where the slide is housed. Paratypes, if erected, are done the same way with the boldface heading **Paratype.** on a new line.
Etymology. Explain how you came up with species name here; in this case it means example, and has a feminine ending because *Chaetosphaeria*, which ends in "a," is feminine.
Location. This is the type locality, and should include latitude and longitude, if possible, as well as depth below surface (if a core) or height in an exposure, Formation names, etc., as appropriate.
Description. This is a detailed description of your taxon , including what characters make it novel and measurements of and numbers of the specimens used to arrive at a diagnosis. It must contain sufficient detail that an expert in the field can understand it.
Remarks and comparisons. This section contains a detailed comparison to similar taxa both in the genus and outside of the genus. It also contains any other information that may be of use to other researchers, such as likely life habit, ecology, distribution, etc.

Figure 1