Taxonomy and nomenclature in palaeopalynology: basic principles, current challenges and future perspectives

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ABSTRACT

Effective communication of taxonomic concepts is crucial to meaningful application in all biological sciences, and thus the development and following of best practices in taxonomy and the formulation of clear and practical rules of nomenclature underpin a wide range of scientific studies. The *International Code of Nomenclature for algae, fungi and plants* (the *Code*), currently the *Shenzhen Code* of 2018, provides these rules. Although early versions of the *Code* were designed mainly with extant plants in mind, the *Code* has been increasingly used for fossil plants and, in recent decades, for organic-walled microfossils, the study of which is called palaeopalynology, or simply palynology. However, rules embodied in the *Code* do not fully reflect the needs and practices of this discipline; and taxonomic practices between fossil applications, especially in palynology, have tended to diverge from practices for extant plants. Differences in these rules and practices present specific challenges. We therefore review the *Shenzhen Code* as it applies to palynology, clarifying procedures and recommending approaches based on best practices, for example, in the designation and use of nomenclatural types. The application of nomenclatural types leads to taxonomic stability and precise communication, and lost or degraded types are therefore problematic because they remove the basis for understanding a taxon. Such problems are addressed using examples from the older European literature in which type specimens are missing or degraded. A review of the three most important conventions for presenting palynological taxonomic information, synonymies, diagnoses/descriptions and illustrations, concludes with recommendations of best practices. Palynology continues to play an important role in biostratigraphy, basin analysis, and evolutionary studies, and is contributing increasingly to our understanding of past climates and ocean systems. To contribute with full potential to such applied studies, consistent communication of taxonomic concepts, founded upon clear rules of nomenclature, is essential.

KEYWORDS Shenzhen Code, synonymy, types, typification, curation, diagnosis, best practice

1. Introduction

Taxonomy is the backbone of palaeopalynology, as with other biological studies. Whether in biostratigraphical or palaeoenvironmental applications, the classification and consistent identification and differentiation of taxa is crucial. Palaeopalynology (hereafter palynology for simplicity) is the study of fossil palynomorphs, which include acritarchs, chitinozoans, dinoflagellate cysts, microforaminiferal linings, pollen, prasinophyte phycomata, scolecodonts, spores and other microscopic organic-walled remains preserved in the fossil record and produced by plants, algae, protists, fungi, or invertebrates (Williams et al. 2018). Taxonomy provides a means to classify the biological diversity we observe, and it is supported by nomenclature, which provides us with naming protocols (Turland et al. 2018) to ensure consistent and effective scientific communication. Taxonomy and nomenclature are distinct but intertwined pursuits, and a mastery of both, together with a clear understanding of their distinction, is fundamental to meaningful application of palynology to biostratigraphic, palaeoenvironmental and other analyses.

Since what might be termed the "golden age" of palynotaxonomy in the 1960s and 1970s, when research palynologists were widely employed by oil companies to help understand stratigraphy related to petroleum systems, corporate support has declined. However, palynological studies remain vital in solving stratigraphical and palaeoenvironmental problems related to sedimentary basins, especially in correlating between marine and non-marine strata and in subsurface studies where macrofossils are rarely encountered. Palynology is also proving of indispensable value in elucidating evolutionary patterns, reconstructing past climates, and contributing to marine and nonmarine (pre-) Quaternary paleoenvironmental analyses.

Taxonomic research in marine palynology has benefited from generally well-curated type material and the existence of compendia and databases, and a periodically updated compilation of genera and species, the *Lentin and Williams Index of Fossil Dinoflagellates* (the latest edition being Fensome et al. 2019). By contrast, the taxonomy and nomenclature of terrestrially derived palynomorphs has been the subject of few contemporary analytical compendia and databasesilations and thus faces increasing difficulties. The best known examples are the *Catalog of Fossil Spores and Pollen*, which was discontinued in 1985 (Traverse et al. 1970; Traverse 2007; Riding et al. 2016, p. vi), and the catalogue of genera by Jansonius and Hills (1976 and subsequent updates). The complexity of spore and pollen taxonomy partly reflects the enormous diversity of plants, with closely related species sometimes producing indistinguishable spores or pollen. For this reason, pollen studies in the Quaternary and Neogene, and even in the Palaeogene, increasingly identify palynomorphs only to the generic level, assigning specimens to extant genera wherever possible. This is aided by reference collections of modern pollen and allows assemblages to be interpreted palaeoenvironmentally and climatically, based on the known ecological ranges of extant taxa. Moreover, this approach circumvents the confusion surrounding many fossil-defined taxa. However, there is an inevitable loss of taxonomic information, especially for Palaeogene and older material, as many pollen and spores cannot be assigned to extant taxa at lower ranks. The hybrid nomenclature that can develop in the application of names based on modern taxa and fossil-based names may also lead to confusion and loss of clarity.

In older parts of the fossil record, certainly in Cretaceous and older strata, the use of fossil-based names for spores and pollen is the only practical option, but increasingly this has exposed serious difficulties. The search for type material of fossil-based pollen and spores has revealed that many specimens have been misplaced or lost, due to changes in the hosting institution, social instability (e.g. World War II), the shift from analogue to digital records, or simply the ravages of time. Other problems include the designation of different names to seemingly identical taxa at different geological times (*Deltoidospora* vs. *Cyathidites* for example); also in some instances the same taxa have been described multiple times in different languages and regions of the world with different names and different types, or occasionally even using the same type. Compounding this problem is that much of the relevant literature is not easily discoverable, accessible or legible. The result is taxonomic confusion and consequent inaccuracies, for example leading to distorted estimates of diversity. Practitioners had been concerned about these burgeoning issues since the 1960s but schemes proposed to constrain the problems operating essentially outside of the *Code* (e.g., Hughes, 1989) were largely not taken up because they are impractical.

When revising the taxonomy of a particular palynomorph taxon, several laborious and frustrating challenges can arise. Some of these difficulties are inherent in palynology, with its microscopic specimens and the rigours of processing and curation. Specimens may degrade over time, and this has resulted in the loss of, or severe damage to, many type specimens. Other challenges are connected to the ways in which palynological data have been presented and communicated in the past, creating conventions that sometimes strongly contrast with those of palaeobotany and botany. This becomes apparent, for example, when comparing author guidelines on preparing synonymies in palynological, palaeobotanical and botanical journals, e.g. *Taxon* distinguishes between homo- and heterotypic synonyms while *Palaeontographica Abteilung B* does not. These differences promote confusion and hinder synergies among these intertwined disciplines. To help overcome these difficulties, we present a concise guide to the relevant nomenclatural rules and discuss some taxonomic and nomenclatural problems that can arise when attempting revisions. We then propose guidelines for best practices in taxonomy and nomenclature as they relate to palynology.

2. A brief guide to nomenclature relevant to taxonomy in palynology

The *International Code of Nomenclature for algae, fungi, and plants* (hereafter the *Code*) (Turland et al. 2018) is the governing set of nomenclatural rules. The *Code* comprises six fundamental Principles (Division I), followed by more detailed Articles (Art.; i.e. rule), and Notes and Recommendations (Rec.) in Division II. Examples (Ex.) are provided to illustrate the application of Articles. Also in Division II is Chapter F which contains rules specific to fungi including fossil fungal spores and other fungal remains as might be found in palynological preparations. The *Code* also contains a glossary that gives useful explanations of basic concepts, but as with the recommendations given in the *Code*, the glossary is not intended to be binding.

As a quasi-legal document it can be daunting to new users. *The Code Decoded* (Turland 2019), now in its second edition, was therefore written as a user-friendly guide, and much of the following information is derived from it. We additionally recommend Fensome et al. (2019) for a more palynologically, and especially dinoflagellate-oriented, introduction. Also, specific questions are addressed in the "how to" guides on the website of the International Association for Plant Taxonomy (IAPT; https://www.iaptglobal.org/index-of-nomenclatural-how-to-pages).

2.1. The Shenzhen Code, retroactivity and applicability

Although taxonomy and nomenclature are fundamentally linked, it is critical to understand the difference between them. Taxonomy is the system that circumscribes and classifies the organisms it deals with and answers the question "What is it?". It is a continuously evolving, dynamic discipline that, while evidence-based, is subject to change as ideas and opinions evolve. Nomenclature involves the protocols surrounding the naming of taxa; it addresses the question "What must we call it?". Nomenclature is guided by a written set of rules, currently the ***Shenzhen Code*** (Turland et al. 2018, online via the website of the IAPT; https://doi.org/10.12705/Code.2018). Although resembling codified law, these rules are not "legally" binding, but rely on discipline-wide adherence because standardisation facilitates communication and failure to adhere can result in contributions not being used, followed or recognised by scientific peers.

The *Code* is revised every six years at the Nomenclature Section of the International Botanical Congress. Since 2018, Chapter F, which applies only to fungi, including fossil fungi, is revised every four years at the International Mycological Congress. The location of each Botanical Congress gives each edition of the *Code* the name by which it becomes informally known, the most recent being known as the *Shenzhen Code* based on the meeting at that Chinese city in 2017. Since the first edition in 1867 (*Lois de la Nomenclature Botanique*; Candolle 1867), the *Code* has evolved over seventeen editions, with additions, deletions and alterations in each. Due to the fundamental principle of retroactivity (Principle VI), the provisions of the current edition are treated as if they had always existed in the *Code.* The nomenclatural starting point is 31 December 1820 and retroactivity dates back to this point, unless starting or ending dates are specified (Art.13.1(f)), an important rule that has been overlooked occasionally in the past. When facing a nomenclatural question today, it is irrelevant what version of the *Code* was in effect at the time the problem arose. The situation must be evaluated according to the current edition of the *Code* and all proposed changes to the *Code* are carefully evaluated to assess the potential for unintended negative consequences.

The need for good taxonomic and nomenclatural practices applies equally to fossils as to extant organisms, although special concerns arise because remains usually consist of dispersed parts of plants or life-history stages such as fossilisable cysts. Although palaeobotany and palynology have sometimes used specialised taxonomic concepts (e.g., morphotaxa, see below) when affinities are uncertain, fossils are explicitly included in the *Code* according to Art. 1.2. Each taxon bearing a name based on a fossil type is a fossil-taxon (always hyphenated with the specific rank, e.g. fossil-species, fossil-genus). The *Code* specifies that a fossil-taxon can constitute a part of the parent organism, or a single stage in a life-history, or in one or more preservational states. The most commonly used palynomorphs, i.e. acritarchs, dinoflagellate cysts, fungal remains including spores, and plant pollen and spores, are covered by the *Code* because they represent life-history stages of algae, fungi and plants, or are believed to do so. (Chitinozoans, although palynomorphs of undetermined origin, are generally named under zoological nomenclature; see for example Butcher 2012). The term "algae" is used here because it is used extensively in the *Code*. The term algae was applied historically to plant-like single-celled organisms, and the term protozoans for animal-like single-celled organisms – essentially relating to autotrophic and heterotrophic habits respectively. In modern biology such a division is recognised as untenable: for example, the dinoflagellates include both autotrophs and heterotrophs. So the word "protist" has come to encompass both algae and protozoans in the broader biological context. Such considerations have some nomenclatural relevance: for example, dinoflagellates were commonly named under zoological nomenclatural rules prior to the 1960s, but nowadays the convention is for dinoflagellates, fossil and living, to be named under "botanical" nomenclature, as is the case for palynomorphs in general.

Before the *Melbourne Code* (McNeill et al. 2012) came into effect, palaeobotanical and palynological literature often included the term "morphotaxon", which was defined as a fossil consisting of only the one part, life-history stage, or preservational state represented by its nomenclatural type. In deciding priority, the names of morphotaxa competed only with other names based on a fossil type representing the same part, life-history stage, or preservational state. However, it was felt that nomenclatural rules were interfering with what should have been entirely taxonomic decisions (Cleal and Thomas 2010). The Melbourne Congress in 2011 therefore decided to replace morphotaxa with the new "fossil-taxon" concept (Turland 2019). For practical purposes it involves the same elements (i.e. part, stage or state), but allows a circumscription that is not limited to that one part, stage or state. Following the *Melbourne Code*, a fossil-taxon can include different parts (e.g. pollen and flowers from the same parent organism); but, depending on the author's taxonomic decision, it is not obliged to. The change allowed for increased taxonomic flexibility. Because a fossil-taxon may extend to the present day, it could include extant representatives, and the term "extant taxon" is therefore ambiguous. The *Code* accordingly distinguishes between a fossil-taxon, whose name is based on a fossil type, and a non-fossil taxon, whose name is based on an extant type.

Taxonomy aims to develop a natural classification that reflects evolution insofar as possible. Key to such a successful taxonomic scheme therefore is recognising which morphological features are important at which taxonomic level and applying this hierarchy consistently. For example, in angiosperms, flower structure is more important than leaf shape at higher taxonomic ranks. As noted above, it is often easy to associate fossil Cenozoic pollen taxa with non-fossil suprageneric taxa, (families and orders for example) that are governed by the *Code*. Because of the difficulty in determining the botanical relationships of older pollen, and of spores more generally, informal artificial suprageneric naming systems developed, and these are beyond the jurisdiction of the *Code*. The most common informal morphology-based suprageneric system used for older dispersed terrestrial palynomorphs is that of "*turmae*" (Potonié 1956; Dettmann 1963). This approach was referred to as "morphographic" by Potonié

(1960, 1973). The system, first applied in Potonié and Kremp (1954), was continued in a series of publications referring to the *Sporae dispersae* (Potonié 1956, 1958, 1960, 1966, 1970). The system was further developed by Dettmann (1963) and more recently by Burger (1994). Many palynologists argue that this approach is appropriate since botanical affinities of earlier taxa are often ambiguous, with one fossil-taxon (morphotype) being produced in many different natural lineages. A similar "morphographic", or phenetic, approach is used for acritarchs (Strother 1996), for which by definition few clues exist to their phylogenetic relationships.

The turma system places an emphasis on morphological features arbitrarily, and sometimes this leads to a clearly unnatural taxonomy. For example, at the suprageneric level, the turma system emphasises the pattern of wall thickness in the amb of trilete spores. Thus, the presence or absence of interradial crassitudes, however subtle, has been treated as an important criterion also at the generic level, and authors have tended to describe and delineate genera and species so that they readily fit into this system. Such features may indeed be taxonomically important in some groups of spores, but commonly other morphological features appear to be of greater importance in assessing natural relationships. For example, *Staplinisporites caminus* (Balme 1957) Pocock 1962 has been used to encompass forms without interradial equatorial crassitudes. Dettmann (1963) allocated almost identical forms, but with interradial equatorial thickenings, to *Coronatispora valdensis* (Couper 1958) Dettmann 1963. The morphologies of *Staplinisporites caminus* and *Coronatisporites valdensis* are otherwise practically identical. It is clear from overall morphology that *Coronatisporites valdensis* and *Staplinisporites caminus* are more closely related (arguably even conspecific) than are *Coronatisporites valdensis* and *Coronatisporites perforata Dettmann*, 1963, the type of *Coronatisporites*. Some argue that using a more natural classification scheme, even if leaving many open categories, leads to more meaningful applied interpretations, for example of palaeoenvironments and palaeoclimate (e.g. Galloway et al. 2013).

2.2. Finding the correct name

A common reason for referring to the *Code* is to determine the "correct" name from a suite of competing names for a taxon or to decide how to name a new taxon (e.g. sp. nov., gen. nov.) or a new combination (e.g. comb. nov., stat. nov.). When intending to publish such a **nomenclatural novelty**, one should keep the following rules in mind (important technical terms in bold).

A fundamental principle is that an organism at the rank of family or below can bear only one **correct name** (Principle IV), except for fossils, where different parts/life-history stages/preservational states of the parent organism can each have one correct name (Art. 11.1). An example of the latter is *Sigillaria*, the name for fossil bark of arborescent lycopods that is used concurrently with many other generic names for other parts and preservational states of the same parent organism, such as *Lycospora* for the spores found in the strobili (Art. 11 Ex. 1 in the *Code*, Forey et al. 2004; Taylor et al. 2009). But how do we determine the correct name, and how do we refer to those names that are not correct?

The label (i.e. name or designation) for each (fossil-)taxon has a **status** (Art. 6): it can be **effectively published, validly published, legitimate** and **correct** (Figure 1, also see checklist with more detailed requirements in Figure 2), four steps that are outlined in the four sections below. The status is determined by the criteria this label fulfils on its way to becoming the correct name. Until this label is validly published, it is not even referred to as a "**name**" but only as a "**designation**."

(1) Any material (i.e. text, illustrations etc.) must be **effectively published** to have any status under the *Code* (Art. 6.1). This means that prior to 1 January 2012 it had to be distributed in print to the general public (via a minimum of two scientific institutions with accessible libraries, although distribution to ten or more institutions is recommended; Art. 29.1, Rec. 30A). Many theses for scientific degrees published from 1953 onward generally do not count for effective publication, unless evidence exists that the author or publisher (e.g. provision of an International Standard Book Number or ISBN) considered it to be effectively published (Art. 30.9). However, with the revolutionary onset of online electronic publication, electronic material published on or after 1 January 2012 in Portable Document Format (PDF) in an online publication with an ISSN or ISBN is also effectively published (Art. 29.1), as first allowed by the *Melbourne Code* (McNeill et al. 2012). Announcing a nomenclatural novelty at a public meeting, e.g. verbally or on-screen in a presentation, does not constitute effective publication. However, effective publication can be accomplished through a conference proceedings volume.

(2) To be considered a "name" under the *Code*, a designation has to be **validly published**. This means it has to be published in accordance with the rules specified in Art. 6.2. Many of these requirements are tied to certain starting dates for particular rules. For

an overview of these requirements, see the checklist in Figure 2. A commonly discussed aspect challenging validity is the requirement for a description OR a diagnosis as indicated in Art. 38.1(a) and 38.2 (for a discussion about the distinction between description and diagnosis, see subsection 5.3). If the publication of a new name lacks a description or diagnosis, it is not validly published and therefore remains a designation only (although sometimes referred to as a "naked name" = *nomen nudum*). Note however, that for monotypic genera, it is sufficient to give a description or diagnosis for only one of the two ranks, i.e. at the rank of the genus or the species (Art. 38.5 and 38.6), although this may not be the best approach in developing taxonomic concepts.

One sometimes comes across such citations as *Areoligera medusettiformis* Wetzel 1933 ex Lejeune-Carpentier 1938. The "**ex**" means "…from, according to…" and is used to connect two author citations, where the latter author validly published a name that was proposed by the former author who had not validly published it (Fensome et al. 2019). This applies to many palynological works from the 1930s and 1940s, when later publications formalised earlier proposals for names in use but which at the time did not fulfil all the rules – often a diagnosis or description was missing. Citing the name of the example above as *Areoligera medusettiformis* Lejeune-Carpentier 1938 would be acceptable, because the designation when introduced by Wetzel (1933) had no official status until it was validly published by Lejeune-Carpentier (1938); but it is less courteous and informative than the full citation (Fensome et al. 2019).

The author validly publishing a name, for example by providing a description in the case of a new species or a basionym in the case of a new combination, does not need to indicate that they are doing so; they may even be validating a name unwittingly. This was the case with the dinoflagellate cyst name *Andreedinium elongatum* (Beju 1971) Feist-Burkhardt 1990; Feist-Burkhardt (1990) inadvertently fulfilled all requirements for the new combination while assuming it had already been done by "Feist-Burkhardt and Monteil (1990)" a prospective article that was not actually published.

(3) Once a name is effectively and validly published, the next consideration is whether it is **legitimate** or illegitimate. To be legitimate it must not be a later homonym (i.e. its spelling must not be identical to a name that was validly published earlier; Art. 53 and

54), and it must not be nomenclaturally superfluous when published (i.e. the author must not circumscribe the taxon such that it includes the type of a name that should have been used instead; Art. 52) (Figure 2). If a name is illegitimate, it can only become legitimate through conservation, protection or sanctioning, which can occur even if it lacks priority (see below). An example involving both legitimacy and superfluity is that of the dinoflagellate cyst names *Albertia*, *Alterbia* and *Alterbidinium* (Fensome et al. 2019). *Albertia* Vozzhennikova, 1967, is a junior homonym of *Albertia* Schimper, 1837 and therefore an illegitimate name. Lentin and Williams (1976) thus proposed to replace it with the new name *Alterbia*, but while doing so inadvertently included the types of the earlier generic names *Senegalinium* Jain and Millepied 1973 and *Andalusiella* Riegel 1974. Following Article 52.1, therefore, *Alterbia* was a superfluous, and hence illegitimate, name. Consequently, Lentin and Williams (1985) proposed a second new name for *Albertia* Vozzhennikova, *Alterbidinium*, this time excluding the types of *Andalusiella* and *Senegalinium* and therefore achieving legitimacy. The use of the term superfluous in the nomenclatural sense should not be confused with a taxonomic situation where an author subjectively determines that two or more names are synonymous and hence is obliged to use the senior of the synonyms.

(4) The last hurdle for a name to be considered correct is for it to have historical priority (Principle III, Art. 11). If there are multiple names to choose from, then it is the first effectively and validly published, legitimate name that must be used. It is important to note that names of fossil-taxa compete only with names based on fossil types (Art. 11.7). The names of organisms based on non-fossil types have priority over names based on fossil types (Art. 11.8), although this rule has been misunderstood, as discussed by Ellegaard et al. (2018).

For example, in the case of dinoflagellates, only one stage in their life history is usually fossilisable, and that is its resting cyst. Just because a named fossil dinoflagellate cyst may resemble the cyst of a named non-fossil dinoflagellate, that does not necessarily make them synonymous (in a heterotypic sense). They are conceptually different entities, one based on the cyst alone (the fossil) and the other (at least theoretically) on the entire life history (the living organism) (Head et al. 2016). The *Code* in fact offers a choice for dealing with fossil dinoflagellate cysts: to refer them to their fossil-typified name, or to their non-fossil-typified name (Head et al. 2016). For example, the dinoflagellate cyst *Tuberculodinium vancampoae* (Rossignol 1962) Wall 1967 is typified by a fossil specimen from the subsurface Quaternary of the Mediterranean and has a fossil record extending back to the Oligocene. The distinctive morphotype it represents has since been found to be a stage in the life history of the non-fossil species *Pyrophacus steinii* (Schiller 1935) Wall & Dale 1971. The cysts can therefore be referred to as *Tuberculodinium vancampoae* or as the cysts of *Pyrophacus steinii* depending on preference and context. This is allowed under the *Code* (Art. 1.2, 11.1, 11.7 and 11.8) and is an example of **dual nomenclature** as practiced extensively in late Cenozoic dinoflagellate cyst studies (Head et al. 2016).

Recall that it is also possible for fossil taxa to have more than one correct name for different parts or life-history stages AND preservational states. For the purpose of determining priority, it is important that names based on fossil types and names based on non-fossil types are dealt with seperately, and it is the author's taxonomic judgement that decides which circumscription is used.

The word "correct" requires some additional discussion as it has taxonomic as well as nomenclatural implications. If an author considers two legitimate names based on different types to be synonymous (**heterotypic synonyms**), then the correct name is the senior name of the two heterotypic synonyms. Those taxa determined to be taxonomic synonyms are based on the taxonomic judgement of the author. In contrast, **homotypic synonyms** are names based on the same type and therefore require no taxonomic judgement. In some ways it may be better to think of legitimate names (i.e. those names that are effectively published, validly published and not illegitimate) as being available to be considered correct.

When seeking the earliest effectively and validly published legitimate name, new challenges have been introduced by the recent introduction and acceptance of online publications as a mechanism for effective publication. Riding et al. (2019) have pointed out how difficult it can be to ascertain the date of online publications with the availability of "early access" articles and slightly different versions placed online at different times, ending with a publication sometimes with differing final pagination and usually assignment to a specific volume and issue. The crux of this discussion is the phrasing of the *Code* in Art 30.2, which rules "An electronic publication is not effectively published if there is evidence within or associated with the publication that its content is merely preliminary and was, or is to be, replaced by content that the publisher considers final, in which case only the version with that final content is effectively published." Art. 30.3 further specifies that "content" excludes volume, issue, article and page numbers. This implies that electronic publication can be effectively published, even if it is evident that volume, issue, article and page numbers are not final, so long as there is no indication that other content is preliminary or to be replaced later. Currently the *Code* does not explicitly mention the typesetting. One could argue that, if nothing else of the actual text changes except the layout, the typesetting too could be excluded from the content. Yet, Art. 30.3 currently specifies that "content" includes "that which is visible on the page" which would reasonably include typesetting as well. At the moment, the *Code* recommends (Rec. 30A.1) that preliminary and final versions should be indicated differently, and that the phrase "Version of Record" should only be used for a final version with content that will not change (except for page, issue and similar numbers), but this is no assurance that this is followed in regular practice. Where the Version of Record is not indicated by a publisher, corrected page proofs can reasonably be assumed to represent the final version for nomenclatural purposes. The subject of when a pre-press article is a Version of Record is still an actively debated topic in the nomenclatural community and exemplifies the constant evolution of the *Code* from one edition to the next. Therefore, the reader should be alert to future developments as the details pertaining to electronic publishing are worked out.

A related complexity involves the year assigned to cited taxonomic literature, where the Version of Record (without volume or issue numbers and final pagination) may have been published near the end of one year and the final version (with full final bibliographic details) the following year. The year attached to the taxon name will then be earlier than the year finally assigned to the literature in which it was published, and the pagination may have changed also. Riding et al. (2019) proposed a solution where a reference would be cited with the date of the Version of Record but followed by the pagination and other details of the final version, and with a parenthetical note after the reference giving the year of final publication. The presence or absence of a printed version is not at issue here: the real issue is the assignation of articles to volumes with continuous pagination, and should be resolved with journals in future publishing stand-alone articles with unique article numbers and their own permanent pagination. Whether an article is digital, printed, or both is irrelevant.

2.3. Typification – categories of types

One of the key tools in nomenclature is the designation and use of types. The **nomenclatural type**, often simply referred to as the "type", is the specimen (or illustration, but not for fossils – see below) that determines the application of the name of a taxon, and to which the name is permanently attached (Art. 7.2). It thereby serves as a reference that must be consulted to check and compare with any other specimens attributed to the taxon under that name. Although ideally representative, the type of a name does not necessarily reflect the most typical example of the taxon to which the name applies. There are many different categories of types, depending on who designates them, when they are designated, and what material they are designated from; an overview is given in Figure 3. A fossil type must be a specimen (Art. 8.5), not an illustration. The latter is permitted for non-fossil taxa and routinely used for certain single-celled algal groups where actual specimens can be difficult to preserve and curate. For palynology, therefore, the type of a fossil-taxon always has to be an actual palynomorph (traditionally a single "grain" but see discussion below), usually preserved as a "permanent" mount on a microscope slide. The word permanent is placed in quotation marks because microscope slides are notoriously susceptible to degradation – one of the most significant sources of problems for palynological nomenclature (see below).

If the author who first describes a taxon designates a single type specimen for the name of the taxon, this is the **holotype** (Art. 9.1) (Figure 3.A). All other specimen(s) of the same taxon cited in the **protologue** (everything associated with a name at its valid publication, such as description, diagnosis, illustrations, synonymy, discussion, comments etc.; Art. 6.13 footnote), are **paratypes** (Art. 9.7). The terms holotype or paratype apply even if they were not actually used in the protologue, which is commonly the case in older literature. Some authors explicitly designate paratypes, but formally all specimens other than the holotype encompassed in the protologue are paratypes, so designated or not.

Types are associated not only with species names, but also with names of all ranks below and up to and including family (Art. 7.1). The *Code* uses the term "typus" or "type" for names regardless of rank (see also Art. 10 Note 1). Terms such as "genotype" (Potonié 1956; Mädler 1963; Takahashi and Jux 1986), "generotype" (Potonié 1966, 1970; Bóna 1969; Krutzsch 1971), "generitype" (Jarvis 2007) or "type species" (Couper 1958; Pocock and Jansonius 1961; Jansonius and Hills 1976) for the type of a genus, still often incorrectly used, are confusing and should be avoided. The term "type species" is problematic as it confuses the notion that whereas names have types, and a type belongs to a taxon, taxa (e.g., genera, species) do not have types. The type of a genus name (Art. 10.2) is the type specimen (holotype) of one of the species included in the genus, not the species itself. That specimen is thus the type of both the genus name and the species name (Art. 10.1). Moreover, the type of the genus name remains constant, even if the species name that applied to the type specimen when the genus name was established is later synonymised with an earlier species name. Emphasising that the type of the genus is a specimen, not a species may sound like an esoteric technicality, but in groups where the taxonomy is complicated and has been revised by later authors, the distinction can be important. In such situations, reference to a "type species" can be especially confusing. In citing the type of a genus name it is preferable to use the term "Type" followed by the correct name of the species for the type specimen, or preferably by reference to the type specimen. In cases where the correct name of the species differs from the original name that was used when the genus name was established, both names should be cited.

Sometimes, however, things go wrong, especially in older cases from times when nomenclatural rules were less clear or developed than they are now. For example, the author of a name might have neglected to designate a holotype (Figure 3.B), or designated more than one specimen (Figure 3.C). From 1958 on such missteps would have rendered the name not validly published. But prior to 1958, if no holotype was designated, all cited specimens are **syntypes** (Art. 9.6) and by definition no paratypes exist. If more than one specimen was designated as the holotype, they are treated as syntypes, even if paratypes might also exist (Figure 3).

If a later author wishes to rectify the lack of a designated holotype, or replace a type that was "lost or destroyed" (Art. 9.3), their options depend on whether or not **original material** (Art. 9.4) still exists (Figure 3.E, F). What can and cannot be considered as original material is not trivial and is further discussed in Section 3.3. If original material exists, one can designate a **lectotype** from the original material (Art. 9.3); if no original material exists one can designate a **neotype** from any other material (Art. 9.8), though ideally from comparable material.

Art. 43.2 stipulates that, as of 1 January 1912, a name of a new fossil-taxon at genus or lower rank published on or after this date is not validly published unless it is accompanied by an illustration or figure (or reference to such) showing the essential characters. A problem arose in older palynological literature in which some authors designated a holotype but did not indicate directly or indirectly (e.g. through specimen numbers) which of their illustrations was of that type. Hence, Art. 43.3 stipulates that as of 1 January 2001, to be validly published a name of a new fossil-species or infraspecific fossil-taxon must have at least one of the validating illustrations identified as representing the type specimen (for discussion and examples, see Fensome et al. 1998). And Art. 9.15 states that when, prior to 1 January 2001, in the protologue of a name of a new fossil-taxon at the rank of species or below, a type specimen is indicated but not identified, a lectotype must be designated from among the specimens illustrated in the protologue. However, that choice would be superseded if it is shown that the (intended) original type specimen corresponds to another illustration in the protologue.

A special role exists for epitypes, and the term can be a source of confusion. Whereas all other types for names of fossil taxa at the rank of species or below must be a specimen, an epitype *can* be an illustration (Art. 8.5). But epitypes are only interpretative types that help disambiguate a situation where the holotype, lectotype or neotype is "demonstrably ambiguous and cannot be critically identified for the purposes of the precise application of the name to a taxon" (Art. 9.9). Epitypes thus do not stand alone but are an adjunct to one of the other type categories – holotype, lectotype or neotype. Consequently, the epitype loses its standing if the type it supports is "lost, destroyed, or superseded" (Art. 9 Note 8).

Holotypes, syntypes, lectotypes, neotypes and epitypes can theoretically be more than one entity (i.e. isotypes, isolectotypes, etc.) (Art. 9.4 footnote, Art. 9.5) (Figure 3 in grey). Whether this is actually applicable in palynology is discussed in the next section.

3. Challenges in applying the *Code* to palynology

In earlier times, Robert Potonié, Alfred Traverse and other advocates strove tirelessly to mould the *Code* so that it accommodated the special needs of palynology. In the spirit of continuing that tradition, we hope to inspire a discipline-wide conversation leading to refinements in the Code in order to make it a better tool for the discipline.

Like other quasi-legal codices, the Code has to be phrased broadly enough to cover a vast number of situations, and it needs to be precise enough to remain clear in meaning. Because the *Code* is written to accommodate several disciplines and sub-disciplines, it has to be written in a relatively abstract fashion while still covering particular situations that could apply widely. Compared to botany, out of which the *Code* largely grew, palaeobotany and palynology can be challenging to accommodate under the *Code* due to the nature of the material and complexities of their taxonomy.

So far, the general rules as reviewed above are relatively straightforward but, just as with real law, the *Code* uses several terms and phrasings that are potentially ambiguous and open to misinterpretation. The process of subsuming a real-life situation under the rules in broader society becomes one of the sole tasks of an entire profession (lawyers). As scientists, we apply nomenclatural rules more as a side issue. But as in law, it is important to provide interpretations of the rules in less straightforward cases, thus providing guidance and "precedents" in the application of the rules. In this section, we focus on some problematic terms and their meaning in a palynological context.

3.1. The terms specimen, gathering and admixture

For fossil-taxa the type of a name at the rank of a species or below must be a **specimen** (illustrations are explicitly excluded; Art. 8.5). Note that for this discussion we are ignoring epitypes, which have very limited utility in palaeobotany and palynology. What then is a specimen? Art. 8.2 states that "for the purpose of typification a specimen is a gathering, or part of a gathering, of a single species, disregarding admixtures". And the footnote to Art. 8.2 further explains that "the term "gathering' is used for a collection presumed to be of a single taxon made by the same collector(s) at the same time from a single locality". Therefore, the definition of "specimen" is dependent on the meaning of the term "**gathering**", and both terms are important because together they define what can serve as type material, what sort of type material we are dealing with (isotypes versus paratypes) or what counts as original material for the purpose of lecto- and neotypification. The problem in using these terms stems from the fact that the definition of gathering is based on standard botanical and mycological collecting practices and does not take into consideration the very different aspects of palaeobotanical and palynological sampling protocols. As a consequence, palynological samples are not easily understood in the framework of "gathering" and "specimen". This is also true to some extent for macrofossils where multiple fossil organs are preserved on a single slab of rock.

In palynology the equivalent to the gathering is a sample of sediment/rock collected in a bag or other container. Samples are taken from an outcrop or core of rock or sediment, a collection of ditch-cuttings representing a specific drilled interval, or from surface sediment (Figure 4). In an outcrop or core where there is stratification, a sample is taken, usually from as thin a layer as necessary or possible from a single stratum or lamination. For ditch cuttings, the same general principle applies, but the sample is actually a mixture of fragments usually less than a few millimetres in length representing a drilled interval of perhaps several tens of metres, with multiple beds undifferentiable and represented by one sample, and with potential contamination from the core wall higher in the well. In all three cases, but especially so for ditch cuttings, applying the definition "at the same time from a single locality" is commonly problematic: multiple times and several palaeoenvironments may be conflated in such samples. In addition, even before the preservation and fossilisation process, the transportation of whole or partial organisms as sedimentary particles from where they lived to where they were finally deposited means that elements in a single collection of fossils probably originated from many different times and locations. Bioturbation, which is often pervasive in aquatic sediments, causes further mixing of specimens between layers (Kristensen et al. 2012). These factors are inherent in most geological samples but have similarities with those of non-fossil microscopic organisms governed by the *Code*, including algae and diatoms, which might originate from different places (compare Art. 8 Ex. 2).

In palynology, samples comprising specimens from a single taxon are exceedingly rare. Unless a palynological sample is taken from a spore- or pollen-producing organ of a fossil plant, we must assume that it contains a mixture of taxa. Currently **admixture** is not formally defined in the *Code*, but the glossary explains that it is "something mixed in, especially a minor ingredient". It further explains that admixture is used to refer to components of a gathering that represent a taxon (or taxa) other than that (or those) intended by the collector and, because the admixture is disregarded, does not prevent the gathering, or part thereof, from being a type specimen (Art. 8.2). So, according to the last part of this informal definition, and disregarding the temporal and geographical conflation to which palynological samples are necessarily subject, one might be able to regard a palynological sample as, or at least compare it to, a gathering and treat the other taxa that are found in the sample as an admixture (Figure 4).

If we accept this, or at least regard the palynological rock/sediment sample as homologous to the gathering, what is the **specimen**? Usually in palynology, only a subsample of the originally collected sample is processed, the remainder being stored. Once the subsample has been chemically digested with acids, all that is left is an organic residue, which is then used for making strew mounts on slides (Figure 4). Often not all the residue is used, with the surplus being stored for possible later use. The residue is then a subsample of the gathering and is split between one or more microscope slides and the stored surplus (Figure 4). Each microscope slide often contains hundreds or thousands of palynomorphs. So what then is the specimen? Art. 8.3 states that "a specimen may be mounted as more than one preparation, as long as the parts are clearly labelled as being part of that same specimen, or bear a single, original label in common". The latter half of the sentence also makes use of the term "specimen", creating a circular argument, which is unhelpful when it seems to mean an individual. Art. 8.2, states that a specimen "may consist of a single organism, parts of one or several organisms, or of multiple small organisms". What then is the specimen in this context? Is it (1) one individual palynomorph indicated by an England Finder (Graticules Ltd. 1962) reference or equivalent reference or coordinate, or is it (2) one individual slide (or multiple slides and stored residue arising from the same residue preparation) with multiple palynomorphs given the allowance for "multiple small organisms" in Art. 8.2?

In non-fossil vascular plants, the specimen is most commonly the (entire) individual herbarium sheet. For example, when several individuals of the newly described taxon *Trifolium phitosianum* Greuter et al. (Böhling et al. 2000), representing part of the single gathering *Böhling 8299*, are mounted on the same herbarium sheet (Figure 5.B), they represent the same "specimen". Using this as an analogue for palynomorphs would make an entire microscope slide the "specimen" as in interpretation (2): one slide or multiple slides from the same residue. However, this interpretation would not be consistent with common curation practices in palynology. In some rare palynological preparations, single grains are mounted on a grid providing a raster with coordinates (Figure 5.A.a). The most common palynological preparation is a strew mount representing a subsample of the organic residue, which in turn is usually a subsample of the gathering (Figures 4, 5.A.b). For such preparations the England Finder can provide reference locations. Only occasionally are palynomorphs mounted as single-grain slides (Figure 5.A.c). Mesh or strew mount slides often hold multiple types (e.g. four on Figure 5.A.a and three on Figure 5.A.b), each of which is recorded with an inventory number from a type-catalogue.

According to this common practice, only one palynomorph is the type specimen, thus following interpretation (1): in this case the holotype is the one palynomorph identified by a unique reference or coordinates. All other palynomorphs on the same slide cited in the protologue are paratypes, and all other uncited palynomorphs on the same slide complying with the circumscription of the taxon but not explicitly cited in the protologue comprise other parts of the original material (i.e. they are uncited specimens). Although this is not a direct parallel with botanical practices, this interpretation (an individual palynomorph with a specified location representing the specimen) seems to be the necessary approach for palynology, respecting universal usage by palynologists. Any other approach would cause chaos and be ignored by practitioners.

Unfortunately, the *Code* is not entirely clear in its definitions of specimen, gathering and admixture in regard to palynology. As discussed above, we need to make particular broad interpretations fit the definition of a gathering (which under current phrasing is a precondition to defining a specimen) to palynology and to have material that can serve as types for fossil-taxa. For future editions of the *Code* it would benefit palynology to adjust the definition of gathering, specimen, admixture or a combination thereof.

3.2. Duplicates

The concept of **duplicates** is another aspect of the *Code* that has little utility in palynology. The *Code* defines a duplicate as “part of a single gathering of a single species or infraspecific taxon” (Art. 8.3 footnote). The concept can be further illustrated by the following botanical example in the *Code* (Art. 8 Ex. 8). “The holotype specimen ... is mounted on a single herbarium sheet in F [Chicago]. A fragment was removed from the specimen subsequent to its designation as holotype and is now conserved in LL [Austin]. The fragment is mounted on a herbarium sheet along with a photograph of the holotype and is labelled ‘fragment of type!’. The fragment is no longer part of the holotype specimen because it is not permanently conserved in the same herbarium as the holotype. It is a duplicate, i.e. an isotype.” In contrast to the situation for macroscopic specimens of algae, fungi and plants, it seems highly unlikely to have duplicates for microfossils including palynomorphs or even macrofossils at large, based on our concept for a specimen, as discussed above. For example, part and counterpart of a compression or impression macrofossil are parts of the same single specimen and not duplicates. Similarly, microfossils such as a dinoflagellate cyst broken in two parts should also be treated as two parts of a single specimen (compare also Art. 8 Ex. 5, 6, 7 and 9). Although there might be some arcane examples of potential fragments of an individual, arguably for example individual grains from a spore or pollen tetrad, duplicates are generally not available in palynology and palaeobotany, and consequently isotypes can seldom be used.

3.3. Original material

Understanding what conforms to the definition of "original material" determines the scope of action possible in later designations of a type, either when the original author did not designate a holotype, or if the holotype is "lost or destroyed" (Art. 9.3). If original material is available, it should be used in designating the lectotype; if there is no original material left, a neotype can be designated. The definition of original material therefore is important because it determines what is available as potential lectotype candidates. Art. 9.4 gives four categories of potential original material (those parts that delimit original material available to palynology are in bold type):

> (a) **those specimens** and illustrations (both unpublished and published prior to publication of the protologue) **that the author associated with the taxon,** and that were available to the author prior to, or at the time of, preparation of the description, diagnosis, or illustration with analysis (Art. 38.7 and 38.8), validating the name;
>
> (b) any illustrations published as part of the protologue;
>
> (c) **the holotype and those specimens which**, even if not seen by the author of the description or diagnosis validating the name, **were indicated as types (syntypes or paratypes)** of the name at its valid publication; and
>
> (d) the isotypes or isosyntypes of the name irrespective of whether such specimens were seen by either the author of the validating description or diagnosis or the author of the name (but see Art. 7.8, 7.9, and F.3.9).

Given that isotypes and isosyntypes (i.e. duplicates) generally do not exist for palynology and palaeobotany, clause (d) can generally be disregarded. The availability of the holotype, syntypes and paratypes as original material (clause c) is obvious. Clause (a) and especially clause (b) are problematic for palaeobotany and palynology in their mention of illustrations: currently, the definition of original material includes specimens and illustrations, but Art. 8.5 of the *Code* expressly bans illustrations from serving as types for names of fossil taxa, except for epitypes (Gravendyck et al. 2020b). In those cases where no original material exists except for illustrations, we face a paradox. We cannot designate a neotype because we still have the illustrations as original material, even though illustrations are not eligible to serve as a type for fossil taxa. Section 4 below illustrates how common this problem might be. Gravendyck et al. (2020b) proposed amendments to Art. 9.4 to exclude illustrations from original material for names of fossil-taxa in the next edition of the *Code*. Unless this proposal is accepted at the next International Botanical Congress, all neotypifications made despite the existence of illustrations will remain ineffective.

Beyond the material already discussed, what other material is available for lectotypification? Apart from clause (c), clause (a) is the only one left that applies to palynology, and the crucial part of the sentence is "those specimens … that the author associated with the taxon, and that were available to the author … validating the name". This should apply to all residues and surplus slides from which the author described the taxon. Due to the particular preparation practices in palynology of subsampling (Figure 4), all other slides and residues from which the taxon was described by the author should be eligible as original material. Any of the palynomorphs in this material that are consistent with the circumscription of the fossil-taxon in question could then serve as a potential new type specimen, i.e. a lectotype.

4. Challenges while working with type material

4.1. Type material "lost" or "destroyed"

If no holotype was designated for a taxon, one can designate a lecto- or neotype. The same can be done if the holotype is no longer available, having been "lost" or "destroyed" (Art. 9.3 and Art. 9.11). Although both states result in the specimen being "not available", a "lost" specimen can be potentially recovered, whereas a destroyed specimen cannot. When working with older material, situations involving "lost" or "destroyed" types arise regularly, as illustrated by the following case studies.

4.1.1 Case 1: microscope slide not retrievable

Due to the transfer of collections without proper documentation, such as after the retirement or death of authors or following destructive events such as war and fire, it can become impossible to relocate collections or parts of collections.

Example 1. Although most of the microscope slides used by Thiergart (1949) can be relocated, those from his Hohenwestedt locality have not been found. The two syntypes for *Sporites saturni* Thiergart 1949 (≡ *Aratrisporites saturni*; Figures 6.A.a, b) and the holotype of *Pollenites pseudoalatus* Thiergart 1949 (≡ *Ovalipollis pseudoalatus*; Figure 6.A.c) must be considered ***lost***. Both species are typical fossil-taxa from the Keuper (Middle–Upper Triassic), and the latter species has a much-disputed circumscription (Schuurman 1976). Without the holotype and lack of other associated “original material”, only neotypes can fill in for lost holotypes and syntypes.

Example 2. A similar case involves *Patinasporites iustus* Klaus 1960 and *Ellipsovelatisporites plicatus* Klaus 1960 (Figure 6.A.d). Most of the material used by Klaus (1960) is in good condition, which is especially surprising because Klaus used a mounting technique that produced very fragile slides. For his single-grain preparations, he mounted the palynomorphs between two coverslips held together by a “pouch” made of paper/lino and a layer of stable plastic of the size of a standard microscope slide with a hole punched in the middle (Fig. 6.A.d). The double coverslip is inserted between the paper/lino and the plastic. In these slides the palynomorph can be easily seen from both sides, but the disadvantage is that the coverslip is easily movable (Figure 6.A.e top) with a high risk of it falling out (Figure 7.A.d). This precarious situation led to a series of later remounts, probably by curators, in order to conserve and secure the material (Figure 6.A.e bottom). For the holotypes of *Patinasporites iustus* and *Ellipsovelatisporites plicatus* the “pouch” itself is still present, but the double coverslip that should contain the specimens is missing. Remounts such as that shown in Figure 6.A.e could not be found. Therefore, the types have to be considered as ***lost***. With no other material available from the protologue, nothing is left from which to designate lectotypes, so designation of neotypes is required.

Example 3: The material used by Reissinger (1950) provides a rather unusual case of lost material, or perhaps even “destroyed” material. In the introduction to his work, Reissinger (1950) explained that the material on which his new descriptions were based was destroyed in the bombing of Munich on 12 July 1944. In the later pages of his publication, he reminisced on the insights one might get if the material were still available. Since the author himself attested to the destruction of the material, this is a compelling case of irreversible damage, indeed of ***destroyed*** type material. Although it appears strange to describe new taxa based on material that was already destroyed, this was nomenclaturally acceptable at that time as it was not unusual to publish a new name without designating a holotype. However, one has the impression from the author's introduction and notes that he felt obliged to explain why he was not designating types, even though it was not necessary under the rules.

4.1.2 Case 2: microscope slide retrievable, but specimen not relocatable

After the euphoria of finally finding a slide that should hold a type specimen, hopes can still be dashed when failing to relocate the type specimen on that slide.

Example 1. In the case of *Paracirculina maljavkinae* Klaus 1960, one of us (JG) retrieved a slide labelled as containing the type specimen. It is a remount of one of Klaus's fragile mounts described above. In most cases of this kind of preparation, she found the remounted slide with the original but empty pouch on top (Figure 6.B.a). But for *Paracirculina malkjavkinae* there was only the remounted slide (Figure 6.B.b). Unfortunately, the type specimen itself could not be relocated: the slide appeared to be empty. When making remounts, the two coverslips would have had to have been prised apart, and in this case we must assume that the type specimen was lost in this process – perhaps by accidently mounting the empty cover slip from the double mount instead of the one bearing the type. Because the possibility of future rediscovery cannot be excluded, this case involves a ***lost*** specimen rather than a destroyed specimen, even though a slide labelled as bearing the holotype still exists.

Example 2. In other cases, one might still have the original slide (Figure 6.C.a), but despite an exhaustive search the type specimens originally illustrated (Figure 6.C.b) cannot be located. An example is the case of *Pollenites macroserratus* forma *keuperianus* Thiergart 1949 and *Pollenites serratus* forma *helmstedtensis* Thiergart 1949. Desiccation of the glycerine jelly has partially aggregated material on the slides that bear the remaining syntypes for these names (Figure 6.C.c). This clumping can make the type specimens irretrievable or unrecognisable. Since future relocation cannot be entirely excluded, the type specimens can be considered presumed ***lost***.

4.2. Type material "lost"/ "destroyed" or merely ambiguous – a grey zone

Sometimes the type material is in poor condition due to progressive degradation, a recurrent problem in palynology and often linked to the mounting medium. Poor preservation can make recognition of characteristics or overall identification of a specimen so ambiguous that it becomes difficult to decide whether the type specimen is "lost"/ "destroyed" or merely ambiguous. In the latter case, the situation can be so awkward that it would be easier if the type specimen were not available at all.

If, for example, a holotype is not the ideal representative of the taxon and, if it "cannot be critically identified for purposes of the precise application of the name to a taxon" (Art. 9.9), one can designate an epitype, an interpretative type, to help resolve the taxonomic ambiguity. It is questionable whether the wording of Art. 9.9 allows the designation of an epitype even in cases where the preservation of the type has become compromised and causes the ambiguity, as elaborated below.

The following case studies illustrate challenges that occur when attempting to relocate and re-identify type material that has been subject to gradual degradation. In all these cases, it is difficult to evaluate the status of the material and determine how to move forward.

4.2.1 Case 3: microscope slide retrieved but material has moved

Different kinds of mounts and storage conditions lead to striking differences in preservational quality. Glycerine jelly, a mixture of gelatin, glycerine (glycerol), water, and preservative, is a commonly used mounting medium for palynological preparations. It can desiccate over time if too much water or too little glycerine had been used when making it. The desiccation process does not progress uniformly, and in extreme cases the organic material can move or deform or become obscured, masking the basic characteristics of a specimen even if it can be relocated.

For example, in many of Thiergart's (1949) slides, the glycerine jelly has desiccated in such a way as to clump the organic material (Figure 6.C.c). The suspected holotype of *Sporites interscriptus* (≡ *Zebrasporites interscriptus*) (Figure 6.C.b) is now covered with organic material, obscuring crucial characteristics such as the outline and nature of the zona (Figure 6.C.d). This problem adds to the already unfavourable light-refracting effects resulting from the loss of glycerine jelly surrounding the specimen. Unfortunately, in the original illustration of the type, part of the background surrounding the holotype was cut away (Figure 6.C.b). The material near the right-margin of the original photograph, especially the pointed and sharp-edged element, could be the same as the element visible in light brown covering at the lower right-corner of the suspected holotype (Figure 6.C.d). Fortunately, in most studied cases from Thiergart and other authors, material was found in exactly the same place and orientation as in the original photograph.

Although not common, material that has moved was found in other collections, too. An example involves the type specimen of *Ovalipollis rarus* Klaus 1960 (Figure 6.C.e–g). However, in this case the organic material may have moved as a result of remounting rather than desiccation.

The question remains as to whether the holotype in such cases should be considered “lost”/ “destroyed” or merely ambiguous. This will ultimately depend on the particular case and the author’s judgment. For the example of *Sporites interscriptus* (≡ *Zebrasporites interscriptus*), it is tempting to consider the type “destroyed”. It is not preserved well enough to be informative or to disambiguate the application of the name. If an epitype were designated on the basis that the holotype exists but is ambiguous, its standing would depend on the agreement of subsequent authors. Any later author could make an equally good argument that the holotype is irretrievably obscure and should be considered “destroyed” – meaning that the epitype has no standing (Art. 9 Note 8), thus allowing for the designation of a lectotype or neotype that could more clearly support nomenclatural stability.

4.2.2 Case 4: relocation and visible characteristics are ambiguous

Problems become compounded if the process of desiccation and/or preservation has altered material to such an extent that it has become impossible to unambiguously recognise particular specimens, including types. Such a situation arises for example in the case of the holotype of *Zebrasporites laevigatus* Schulz 1967 (Figure 6.D.a–d). The slide that contains this and other type specimens is in poor condition: the cover slip is broken and the palynomorphs are no longer embedded in the mounting medium, making it very hard to discern their characteristics. It is not clear which of at least two specimens represents the holotype designated by Schulz. It could be either the specimen shown in Figure 6.D.d or that in Figure 6.D.e. One helpful characteristic could be the outline, but because Schulz cut around the specimens in his photographs and pasted them on a template (Supplement 1), it is unclear whether the outline now seen on the slide is that evident from the original photograph. Any potential remains of extraneous organic material that could help to relocate the specimen were also removed from Schulz's photograph. Moreover, the poor preservation also obscures the crucial characteristics, reducing the informative value that the type could have had. In this case it would have been helpful to see whether the spore possesses a margo (i.e. a thickened border to the laesurae; Punt et al. 2007), the absence of which would distinguish the species from *Zebrasporites sinelineatus* Bóna 1966. The nature of the distal ornamentation, which crucially would distinguish *Zebrasporites laevigatus* from *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960 (Figure 6.C.a–d), is also not visible. The interspecific and/or intraspecific variation of *Zebrasporites interscriptus* and *Zebrasporites laevigatus* has caused much discussion and has stratigraphic implications in the Upper Triassic and Lower Jurassic (Zhang and Grant-Mackie 2001; De Jersey and McKellar 2013). The particularly poor preservation of the holotypes of both names is singularly unhelpful in resolving this taxonomic issue.

The present case therefore combines two problems: the type cannot be relocated beyond reasonable doubt (especially since England Finder references are not available) and, even if correctly located, the crucial distinguishing characteristics are barely visible. Thus we can make the case that the type is lost if it cannot be identified to a particular specimens; or "presumed destroyed" due to poor preservation in the event that someone claimed to be able to relocate the specimen. To resolve the problem, the designation of a lectotype or neotype is necessary in either case.

4.2.3 Case 5: preservation too poor to be informative

Also causing ambiguity are cases in which the state of preservation is poor, but still permits the relocation and reidentification of the type specimen. Although they represent less severe alterations than those detailed above, they may nonetheless be problematic (Figure 7).

For example, due to a distinctive secondary fold, the only remaining syntype of *Pollenites reclusus* Thiergart 1949 (≡ *Classopollis reclusus*), which was designated as lectotype by Mädler, can be relocated beyond doubt, even though some siliceous material, not present originally, has moved into the vicinity of the specimen (Figure 6.E.a–d). Unfortunately, the specimen is poorly preserved and, without the embedding glycerine jelly, the nature of its species-defining sub-rimulate ornamentation cannot be verified. This circumstance was discussed by Pocock and Jansonius (1961) who considered the type specimen to be unhelpful in differentiating *Pollenites recluses* from *Pollenites torosus* Reissinger 1950 and *Classopollis* *classoides* Pflug 1950; the type specimens of all three names could be conspecific. If so, then the name *Pollenites reclusus* would have priority. But in view of the preservation of the lectotype of *Pollenites reclusus*, a decision might never be possible, unless a new type could be designated. Such a step could help to resolve the taxonomic relationships among the more than 100 formal and 30 informal species of *Classopollis* described in the literature.

Many similar examples can be found to illustrate the dilemma we face when the available type material is so ambiguous and unhelpful that it would perhaps be easier, taxonomically and nomenclaturally, if the material did not exist. This realisation can have a paralysing effect because there seems to be no way out, with the lectotype still physically available but technically useless. In the event that the type "cannot be critically identified for purposes of the precise application of the name to a taxon" (Art. 9.9), one available option is to designate an epitype. However, it remains uncertain whether Art. 9.9 is intended to cover cases of secondary ambiguity arising from degrading preservation of the slide, rather than the primary ambiguity of the type, e.g. by lacking any relevant feature. We believe that Art. 9.9 should be interpreted to allow designation of an epitype in such cases where the type specimen may or may not be informative, but its utility is precluded by deterioration of the embedding medium in which it is preserved.

It is important to remember though that an epitype loses its standing when the type it supports is "lost", "destroyed" or "superseded" (Art. 9 Note 8). The difference between whether a specimen is considered "ambiguous" or "destroyed" can be subtle and debatable. For the case discussed above we believe that designation of an epitype would be an appropriate remedy, but we also caution that the nomenclatural utility of an epitype may be doubtful if the lectotype is so poorly preserved that it can be asserted to be effectively "destroyed". In such a case it would be best to designate a lectotype or a neotype. It depends on the individual case in question and a decision by the author(s) as to the best resolution of the problem. In the end, it is in the interest of all to update and revise the taxonomic system as the basis of all subsequent palynological studies. Such decisions are necessary to solve problems and move ahead because without them future taxonomic work on the group can be muddled and the effective applied use of the taxa impeded.

With respect to degraded microscope slides, it should be noted that the rehydration of glycerine jelly is possible with certain solutions (see for example Hartkopf-Fröder 2018). This improves the preservation of specimens at least temporarily, perhaps long enough to take a better photograph or to make stacks of images of different focal planes, if possible with a combination of bright field, and phase or differential interference contrast illumination. But rehydration methods are relatively invasive, and many collections do not permit them. They may further damage or flush out the palynomorphs in question, especially those lying at the edge of the slide, and they may introduce contamination and cause fungal growth. In addition, even if one has the opportunity to try to rehydrate a specimen, there are few protocols to do so efficiently. Because this is a matter of concern to many curators, we can only encourage communication of effective methods and treatments and exchange information on optimal storage conditions and other helpful curation practices.

For situations like Case 5, we suggest that the current condition of the original type material should be illustrated. Further treatment then depends on taxonomic judgment as to how to evaluate different preservational states of types as laid out above. Thereby we can contribute to the continuity of our discipline and inform future taxonomic decisions.

4.2.4 Other options for action with poorly preserved type material

In cases where a nomenclatural situation cannot be resolved, it may be necessary to abandon the name rather than to try saving it. For example, when the type material is so poorly preserved that one cannot be sure whether a potential epitype, lectotype or neotype is conspecific to the taxon of interest, other solutions are possible. If we are dealing with a fossil-taxon in which the circumscription is ambiguous, and poor preservation of the type specimen(s) makes application of the name impossible, it might be best not to use the name at all.

The most decisive way to prevent the use of a name is to propose it for rejection (Art. 56). This is only possible, however, if the name to be rejected would otherwise cause a disadvantageous nomenclatural change (Art. 56.1), i.e. only if it threatens another name (Turland 2019). Moreover, rejection is a lengthy process (see Art. 56.2 and Turland 2019), requiring a formal, published proposal, committee discussions, and a vote at the Nomenclature Section of the International Botanical Congress held every six years. If the proposal is approved and the name is rejected, this is a formal decision that must be followed like all other rules of the *Code*. Related to rejection is the act of conservation, an example of which is the conservation of the genus name for the commonly recorded Mesozoic gymnosperm pollen *Classopollis* Pflug 1953. For more than 50 years, controversy prevailed as to whether *Corollina*

Malyavkina 1949*, Circulina* Malyavkina 1949 and *Classopollis* were synonymous (e.g. Pocock and Jansonius 1961). The main problem was that Malyavkina (1949) had provided only simple line drawings of the types of her two generic names. Many authors thought it reasonable that the types of the three genera were closely similar if not congeneric, but others considered Malyavkina's drawing inadequate to confirm this (Pocock and Jansonius 1961; Traverse 2004). To finally put an end to the taxonomically destabilising debate, Traverse (2004) proposed the conservation of *Classopollis* (the type of which was supposedly unambiguous – but see the discussion of *Classopollis reclusus* above). Traverse's proposal was accepted and *Classopollis* is now conserved against *Corollina* and *Circulina*. However, note that the last two names could still be used if they are shown not to be congeneric with *Classopollis*.

Most of the problems with types detailed above are predominantly nomenclatural in nature, and many consume much time and intellectual energy, without any guarantee of a clear or satisfactory solution. Improvements might be implemented through advocacy of changes to the *Code* or by proposing conservation/rejection of specific taxonomic names. Taxonomy and nomenclature are active modern fields of science so the need for revisions to the *Code* is inevitable and the rules of nomenclature are constantly being refined. The process requires nomenclatural expertise and deliberations of committees and ultimately approval at an International Botanical Congress. Sometimes for more intractable nomenclatural problems, authors have resorted to informal taxonomic solutions. Examples are found in the overview of fossil dinoflagellate taxonomy by Stover and Evitt (1978), two leaders in the field at the time. They reviewed each genus of fossil organic-walled dinoflagellate cyst then known and listed species under the categories (where appropriate) "type species", "other accepted species", "provisionally accepted species" and "problematical species". It is worth citing some of those authors' rationale for the two categories of equivocal species (Stover and Evitt 1978, p. 5):

> Provisionally Accepted Species indicates that some question about generic assignment exists ... . The generic assignment of Problematical Species is even less secure. These are species which, from available information, cannot be assigned with even the level of confidence suggested by provisional acceptance and probably do not belong to the genus under which they are listed. But since we are unable to propose a significantly more acceptable generic assignment, we retain such species under the genus of last assignment. ... . In general, we recommend that the names

> of problematical species be applied to type specimens only, unless there is substantial justification for doing otherwise.

Their aim was to provide expert taxonomic guidance on the use of names. Such practices, including "recommendations" to restrict some names to the type specimen because its status (as in many of the cases above) or morphological interpretation is highly problematic, have been followed in the Lentin and Williams indexes of fossil dinoflagellates (e.g. Williams et al. 2017). Stover and Evitt (1978) specifically stated that their taxonomic decisions were open to verifications and clearly promoted adherence to the *Code*. Such organising works are a significant reason why fossil dinoflagellates have been an ongoing success in Mesozoic and Cenozoic stratigraphical applications.

4.3. When preservational changes to palynomorphs in collections affect identifications

The body colour of palynomorphs in aqueous residues or on microscope slides steadily diminishes over time. This phenomenon is analogous to the gradual fading of photographs and transparencies. Like these photographic materials, the fading of palynomorph body colour is only discernible over several decades. However, relatively recent (i.e. Neogene and Quaternary) and highly thermally altered palynomorphs apparently do not exhibit this fading, in contrast to well-preserved Mesozoic material, which is highly susceptible to it.

This situation may make affected palynomorphs more difficult to photograph but does not normally hinder identifications. One notable exception, is the Jurassic dinoflagellate cyst *Tabulodinium senarium* Dodekova 1990, which ranges from the Callovian to the early Oxfordian (Riding et al. 2010, fig. 10). This is a cavate pareodinioid genus with an ovoidal cyst body, a prominent apical horn, a thin periphragm and dark, dense areolate ornamentation confined to the penitabular areas on the endophragm. The latter feature means that the tabulation is clearly indicated by the ornament-free, narrow pandasutural bands (Riding and Helby 2001, figs 14–16). It is clear that the dark penitabular ornamentation, and the thin periphragm, are somewhat labile. If the material is subjected to oxidising conditions in the laboratory, the ornamentation on the endophragm is selectively destroyed and the periphragm gradually loses its integrity. This loss of ornamentation and periphragm also occurs on microscope slides. For example, Riding and Helby (2001) noted that specimens of *Tabulodinium senarium* from slides produced in early 1979 had fully altered/faded by 1999.

Material prepared in 1992, however, was still pristine in 1999. This selective degradation of a dinoflagellate cyst, although interesting in itself, has a taxonomic dimension. Fresh, unaltered/unfaded material with the intact penitabular ornament and a distinct periphragm are easily recognisable as *Tabulodinium senarium* (Figure 6.F.a, 6.F.c, 6.F.e Riding and Helby 2001, figs 15; 16E, I, M). By contrast, specimens that have lost their ornamentation and periphragm would be identified as species of *Pareodinia* (Figure 6.F.b, 6.F.d, 6.F.f; Riding and Helby 2001, figs 16F–H, J–L, N–P).

If one is studying material within the stratigraphical range of a species susceptible to partial degradation and/or fading, such as *Tabulodinium senarium*, attention should be paid to any taxa that might have been “derived” from the original species. In this particular case, all specimens of *Pareodinia* should be examined at high magnification to check for aspects such as “ghosts” of the dark penitabular ornamentation typical of *Tabulodinium senarium*.

5. Challenges arising from conventions and future perspectives and recommendations on best practices

Apart from the inherent challenges of nomenclature and taxonomy in palynology that are particularly connected to the relatively poor preservation of type material, challenges arise when using existing literature or when publishing new material.

5.1. Typification

Palynology has limitations (e.g. no isotypes) and inherent problems (e.g. progressive degradation) associated with organic-walled microfossils. To minimise these issues when designating types, several factors should be considered. Old collections especially have been shown to be prone to loss or destruction, and hence it may be desirable to distribute holotypes and paratypes among different institutions and locations. In the past, this was not always possible. For example in the former East Germany (German Democratic Republic – GDR), geological information was treated as a state secret, and therefore it would have been inconceivable for palynological samples from the collection of Eberhard Schulz, for example, to have been stored outside the GDR or even the hosting institute (Gravendyck et al. 2020a). Storing type material in various different locations is still not always possible due to the proprietary rights of the funding source and institutional policies, but it should be considered whenever possible. The increasingly international and cooperative projects today increase possibilities for such distributions. This practice would reduce the risk of simultaneously losing all type material in one unfortunate event and would expose the material to different storage conditions, thereby spreading the risk of deterioration to varying degrees. It also makes the types more widely available for study.

Palynology uses various mounting media based on natural substances such as Canada balsam and glycerine jelly, or synthetic resins (e.g. Elvacite®, Entellan® and Eukitt™). All these have advantages and disadvantages regarding durability, fluorescence, refractive index, and remounting (Neuhaus et al. 2017; Riding 2021). Given that techniques in microscopy are increasingly diversifying, it might be worth considering adapting our typification practices to take this into account. An inherent limitation of mounted specimens is that they cannot be studied with microscope techniques that require the unembedded specimen (i.e. SEM and TEM). Additionally, for light microscopy, mounting media based on natural resins are strongly autofluorescent and, therefore, unsuitable for fluorescence microscopy (Neuhaus et al. 2017). Canada balsam is very long lasting and the oldest and best-preserved specimens investigated for this paper were mounted in it. Some sources claim it to be stable for over 100 years, but it is somewhat difficult to work with, the yellowing and potential colour alteration of the specimen over time are disadvantageous, and its refractive index may be suboptimal (Traverse 2007; Neuhaus et al. 2017). By contrast, glycerine jelly is very quick and easy to handle, but requires careful formulation because too much water or too little glycerine can result in slides drying out in less than 20 years, even when sealed properly (Woessner 2005; Traverse 2007; Neuhaus et al. 2017). Furthermore, the hygroscopic nature of glycerine jelly may lead to the alteration of palynomorph size (e.g. Praglowski 1970; Sluyter 1997; Meltsov et al. 2008). Many synthetic resins are suitable for fluorescence microscopy, dry quickly and are easy to handle, but usually at the cost of reduced longevity (Neuhaus et al. 2017). The disadvantage with many of these mounting media is that they dry the residue onto the coverslip which causes thin-walled specimens to collapse and flatten, a particular problem for late Cenozoic dinoflagellate cyst assemblages. Glycerine jelly does not collapse thin-walled specimens and along with its favourable refractive index is the preferred mounting medium for these preparations. The often-reported propensity for glycerine jelly slides to dry out is reduced considerably if sufficient glycerine jelly is used during slide making, and the problems resulting from overly thick slides is obviated by following the method outlined by Evitt (1984).

Depending on the microscopy techniques used in documenting a new fossil-taxon, and other factors including the availability of sample material and abundance and physical properties of the new fossil-taxon, it might therefore be desirable to use different mounting media for the type material. The holotype can then be designated from a slide with a more durable medium, and paratypes designated from other mounts to make use of the combination of advantages and disadvantages of, for example, handling, availability, and simultaneously spreading the risk of degradation while still facilitating fluorescence microscopy. Ideally, the type material would be supplemented by a subsample of the original residue and of the original rock or sediment, to facilitate later studies that require special mounting methods as needed for example in SEM studies.

5.2. Synonymies

A common feature of taxonomic publications is the **synonymy** (here treated as a list of synonyms). This list should comprise names that apply to the same taxon – i.e. synonyms. Following the *Code* (Art. 14.4), synonyms can be of two types (Figure 8), homotypic and heterotypic. **Homotypic synonyms**, also called **nomenclatural synonyms**, have the same nomenclatural type. Because they have the same type, they are synonyms as a matter of fact, not taxonomic judgement, and are indicated with an identity sign (≡). **Heterotypic synonyms**, also called **taxonomic synonyms**, have different types, but are considered to apply to the same taxon, based on taxonomic decisions. They are indicated with an equality sign (=). For clarity, we recommend use of the terms homotypic and heterotypic rather than nomenclatural and taxonomic.

Although many journal guidelines stipulate nomenclature that strictly adheres to the requirements of the *Code* (see *Palaeontographica, Abteilung B*'s Guide for Authors – https://www.schweizerbart.de/journals/palb/instructions), the guidelines for synonymy lists, although not uniform, generally do *not* follow the recommendations of the *Code*. Rather, these guidelines allow a listing of records into which the true synonymy has been blended, following a presentation style that has evolved over many years in palynology and palaeobotany. These formats that are common in palynology and palaeobotany do not clearly distinguish between homotypic and heterotypic synonyms or use their respective signs, for example (Figure 9 left), although it would be best practice to use such signs. Also uncommon is citation of the type for each listed name. Doing so would save later authors time and effort in researching the taxonomic history of a correct name and its synonyms, and would quickly allow discrimination between those synonyms that are undisputed because they are based on the same type (i.e. homotypic synonyms), and those subject to evolving taxonomic opinion.

Matters are further complicated in palynological and palaeobotanical taxonomy by inclusion in the synonymies of names that have been misapplied (i.e. when the type of the name does not belong to the taxon to which the name is applied, such as misidentifications by post-protologue authors) and usages of the correct name (therefore not actually a synonym) in post-protologue publications. Misapplied names and post-protologue usage of correct names should not be comingled with actual synonyms (see Rec. 50D.1). A true synonym list should therefore contain only homotypic and heterotypic synonyms. Lists of misapplications and of later usage of correct names can nevertheless be very informative (although increasingly lengthy), because they give the author’s opinion on former misapplications of names (compare for example lists in Filatoff and Price, 1988, and Achilles, 1981) and can be used to provide a succinct record of earlier reports of a taxon. They are therefore useful as long as they are kept separate from the true synonymy.

The typical format in which palynological and palaeobotanical taxonomy and nomenclature is presented differs from standard formats used in botany. Differences in the conventions used for synonymies and their formatting can be easily minimised by adjusting palynological conventions, bringing the two fields closer together, and thereby improving interdisciplinarity and synergy. Small adjustments to current palynological conventions for synonymies would improve the organisation of the information presented, and move current practice closer to the recommendations of the *Code* (Figure 9 right).

We recommend that **true synonymies** be clearly divided from lists of post-protologue usages of names (i.e. “**other records**”) and of misapplications (i.e. “**misapplication list**”), and all three kinds of lists should be encouraged for their informative value. Ideally, the synonymy can give a brief overview of the taxonomic history of a name. Using the appropriate signs (“≡” and “=“) can further aid concise presentation of the necessary information. The “other records” and “misapplication lists” can provide more specialist knowledge and can aid those checking or revising the taxon in question, rather than searching for (only) a general historical overview of the name in question. If space in the main article is limited, these lists could be placed in the supplementary material.

In Figure 9, we give an example of what such a revised synonymy and other lists could look like, but emphasise that this is only one of many conceivable versions that can be customised by journals to suit their guidelines. Whatever the final layout, it would be highly desirable to provide a clearer distinction between homotypic and heterotypic synonyms, as it is conventional in botanical literature and in the Appendices of the *Code*, and a separation of the true synonymy from the other listings.

5.3. Description versus diagnosis

5.3.1 Distinction

As discussed above, one of the prerequisites for valid publication is that a newly described taxon must have a **description** or a **diagnosis**, or make reference to an effectively published description or diagnosis (Art. 38.1a). The problem is that the two terms are not always used consistently, and very commonly a description is labelled as a “diagnosis”. For the purpose of the *Code* the semantics are irrelevant so long as either of the two (or both) is provided to permit valid publication. For the purpose of taxonomy however, diagnoses are generally more helpful than descriptions, because descriptions involve a cataloguing of a taxon’s features, whereas a diagnosis makes a statement about the features that distinguish the taxon from other taxa (Art. 38.2, Turland 2019). A good diagnosis is therefore an answer to the question “Why is this taxon unique?” or “How does this taxon differ from all other taxa?” A diagnosis can more critically assign a certain morphospace to a taxon, differentiating it from other taxa, even if they and the particular morphospace that they inhabit has not been described yet.

It is noteworthy that from the Paris *Code* (Lanjouw et al. 1956) until the Montreal *Code* (Lanjouw et al. 1961), a provision existed stipulating that the description of a monotypic genus of fossil plants had to be accompanied by an indication how it differed from other genera (Art. PB. 6 in the Paris *Code*, Art. 42 in the Montreal *Code*). This caused discussion among authors as to whether or not a name without such a diagnosis additional to the description was validly published. This was the case for *Limbosporites lundbladiae* Nilsson 1958 (Potonié 1960, 1970; de Jersey and Raine 1990), an important Rhaetian marker that was published as a monotypic genus without mention of such discriminating features. Accordingly, until 1966 the name was not validly published but when the Edinburgh *Code* (Lanjouw et al. 1966) eliminated this precondition, it had to be considered validly published (Potonié 1960, 1970; de Jersey and

Raine 1990). Due to the retroactivity of the *Code* (Principle VI), we treat the current edition of the *Code*, and in this case the absence of such requirement, as if it had always been so. It does show, however, that distinctive criteria named in a diagnosis were sufficiently appreciated that they were once part of the *Code*. Future authors are therefore strongly urged to develop diagnoses in addition to a detailed description. Some would argue that the ability to write a meaningful diagnosis demonstrates an author's understanding of the taxonomic group involved.

5.3.2 What makes a good diagnosis?

So, what makes a good diagnosis? It could be as simple as the following diagnosis for the dinoflagellate cyst subfamily Cribroperidinioideae (Fensome et al. 1993, p. 88):

> Gonyaulacaceans in which there is an L-type ventral organization, dextral torsion and six Kofoid precingular plates.

Of the three subfamilies of the family Gonyaulacaceae defined/known at the time, this diagnosis clearly separated the Cribroperidinioideae from the other two. A diagnosis emphasises the morphological features appropriate and useful for a taxon of the relevant rank and phylogeny. A feature such as granulate surface ornamentation is commonly used as a diagnostic feature at species level and appears to have developed multiple times among the Gonyaulacaceae, in all subfamilies. So, it would *not* be helpful or appropriate to diagnose the subfamily as follows:

> Gonyaulacaceans in which there is an L-type ventral organization, dextral torsion and six Kofoid precingular plates. Surface ornament granulate, rugulate or reticulate.

Not only would this addition be of limited use, but would mean that a new diagnosis would be required if a verrucate form was found, a relatively trivial feature compared to the truly diagnostic criteria.

If the diagnosis is for a taxon placed within a group of taxa of the same rank that are quite subtly differentiated, the diagnosis may need to be relatively long. For example, a group of mid-Cretaceous to Palaeogene dinoflagellate cysts includes the genera *Alterbidinium*, *Cerodinium*, *Chatangiella, Diconodinium*, *Isabelidinium* and *Spinidinium*. These are all in the dinoflagellate family Peridiniaceae, implying a certain arrangement of their tabulation pattern, and the subfamily Deflandreoideae, implying an excystment opening involving a mid-dorsal intercalary plate (2a). The genera are separated from one another by an array of features. These include the shape of the 2a plate, whether or not it remains attached to the cysts during excystment, the expression of the cingulum (an equatorial groove for the transverse flagellum on the motile cell, commonly reflected on the surface of the cyst), whether or not the cyst wall has spines, and to some degree cyst shape. Therefore, for example, the emended generic diagnosis by Fensome et al. (2016, p. 24) for *Alterbidinium* is relatively long:

> Peridiniacean (deflandreoid) cysts that are proximate and peridinioid, usually elongate, in outline. The antapical horns are always asymmetrically arranged, the left horn being larger. Bicavate. The pericyst surface is generally atabulate, smooth, or with low ornament; the cingulum is commonly indicated, if only marginally. The periarchaeopyle is intercalary or combination intercalary–precingular; always involving an iso- to stenodeltaform hexa plate 2a and commonly plate 4″, the operculum remaining attached posteriorly; archaeopyle I2a @ or ($I_{2a}P_{4'}$)@.

Although somewhat convoluted, the emended diagnosis attempts to be efficient in not mentioning features that are not useful in distinguishing this genus. By indicating that the taxon is peridiniacean and deflandreoidian, features important at higher hierarchical levels do not have to be detailed in the diagnosis. Such details can be expressed in a separate description if desired.

Thus a good diagnosis captures the conceptual "essence" of a taxon, and provides a useful and efficient device for researchers seeking to discriminate between taxa. However, it is also helpful for a diagnosis to include sufficient detail that in the event of changes at higher taxonomic level the original diagnosis will not require emending. Moreover, a good species diagnosis does not merely distinguish the new species from those already described for a particular genus: it will also distinguish it from species that we might anticipate being discovered in the future. Implementing foresight becomes especially important when diagnosing the species of a new monospecific genus. Hence, the species diagnosis should be sufficiently narrow compared with that of the genus to allow new species to be added in the future. We therefore need to be creative in deciding what details to include in a diagnosis. A good diagnosis also demonstrates that authors have clear concepts of the taxa they are defining.

5.4. Illustrations

The case studies highlighted in Section 4 above describe several situations in which it is difficult to relocate type material. This is particularly true in works that do not use England Finder references but, even if they are used, remounting or movement and deformation as a result of desiccation can prevent relocation of type specimens. Surrounding organic material, especially phytoclasts and other palynomorphs can help relocate a specimen. Unfortunately, such surrounding material is sometimes removed in the process of making illustrations, including those for the protologue. Until the digital age, photographs out physically and pasted on a template (Figures 7.D.b, c, supplement 1). Nowadays, using graphic design software, the cropping of images to provide a clean background can be accomplished digitally. The advantage of this practice is the production of aesthetically pleasing plates and efficient use of space. The disadvantage, especially in the case of type material, is the removal of context information that can be crucial in relocating a type specimen. Cropping around images can also potentially remove a feature considered extraneous but which in fact is part of the specimen. This practice should therefore be discouraged. For a more elaborate history of microscopy and illustration techniques, developments and recommendations, see Riding and Head (2018).

While the digital age has heralded numerous advances in image capture and processing, caution should be used especially when depicting type material. The new freedom to place additional images in data repositories and journal supplements should be used more widely to (re)document type material. For example, high-end digital cameras have piezoelectrical cooling and acquire a series of images rapidly at the same focal plan that are then merged to yield a single noise-reduced, high-resolution image. Such images are superior to the view seen when looking through the microscope at high magnification. Stacked digital images taken at progressively increasing focal depth through a palynomorph can simulate the act of focusing through that specimen. Confocal laser scanning microscopy similarly captures the three-dimensionality of palynomorphs and the resulting images can be rotated through 360° or indeed processed to obtain virtual cross-sections through the palynomorph (e.g. Soliman et al. 2009; Gavrilova et al. 2018). These various methods of imaging would immortalise the original preservational state of a type that might be otherwise altered as discussed in section 4.2. Such imagery can be made widely accessible, and while still subject to problems of digital preservation, is very likely more durable than the relatively short life-span of many rapidly desiccating microscope slides. Although not eligible as type material, such documentation can help future interpretations of deteriorating type material, and thereby avoid the situation experienced with very old literature containing poor photographs. More importantly, excellent illustrations of type material transcend even excellent descriptions and ideally make it unnecessary ever to inspect the actual material.

5.5. Curation

Natural history museums have limited resources, and an advantage of palynological material is that it demands relatively little space. However, this also makes it more vulnerable to mishandling, neglect, poor preservation and deterioration, factors not as readily visible as, for example, larger palaeobotanical material. Due to the poorly documented fate of some collections, it can be difficult to find and obtain access to material despite the enormous effort of the curators to make their collections more available.

While collections holding botanical herbarium specimens have well-established lending and registry systems, permitting exchange and access to scientists globally, we do not have the same elaborate options available for palynological collections. The problem is exacerbated by the fact that most museums do not have the high-performance microscopes and camera systems needed for the examination of these collections onsite. Loans are usually the only option.

For a series of taxonomic revisions, we consulted several collections, asking them to loan type material in order to newly document it and make comparisons. Such loans were generally not permitted internationally, and it was only in 2020 due to the Covid-19 pandemic that exceptional permissions were granted to mitigate personal restrictions, including travel. It shows, however, that greater international exchange may be possible in the future. As with any collection, material is only valuable if it is used. Of course, a great deal of care must be taken in preserving precious type material, but how far should this be taken? What if it is never consulted as a result of (over)protective measures? Indeed, the rather flexible lending system in practice for herbarium sheets always poses the risk of material getting “lost” or “destroyed”, as in the infamous case of 230-year-old type material being destroyed by customs officials in Australia in 2017 when sent from France for academic study (Straight 2017; O’Malley 2018). But the risks are balanced by the broader possibilities of exchange and scientific study of type specimens before their condition has deteriorated.

Several strategies could help improve this situation and make old and new type material more available to the public. (1) Scientists could deposit their type specimens in more than one institution for example (e.g. holotype in one, paratypes in one or more others). This would spread the risk and make material available for consultation in more than one place. (2) Institutions could register themselves in the Index Herbariorum (http://sweetgum.nybg.org/science/ih/), a database for botanical, mycological and phycological collections. This would make collections, especially those often stored in geological surveys and smaller universities that are not yet registered, more visible for all (palaeo)botanical workers; it would provide each collection with an official abbreviation. These abbreviations, called herbarium codes, are universally accepted in botanical literature and save considerable time and space when citing locations and collections. (However, this would not replace the need to cite the full name of the repository at least once in a taxonomic publication.) (3) Institutions could consider revising their current lending regulations. Many large university and museum collections have established systems already and it would be worth considering how such existing networks could be extended and connected. This would make working with collections more accessible to palynologists and, given experiences during the Covid-19 pandemic, the option might be considered more readily than before. (4) We encourage scientists to work with collection materials. This validates the efforts invested in collections to preserve and curate the material available. The sooner we work with old type material, the higher the chances that we can still use what information value is left in them. Whether we work with material from collections as curators or researchers or both, this research is a necessary step in revising the inherited body of palynological literature, and it helps us update the foundation on which all our palynological studies and subsequent interpretations are based.

Finally, we strongly encourage authors not to use private/corporate collections (such as those within oil companies) as repositories for types. These collections often have relatively short lives. There are several instances of the contents of entire palynology laboratories, including the slide collections, being discarded to landfill *en masse*. One such instance took place in Scotland, UK during the early 1990s. Similarly, we do not recommend the personal collections of palynologists being used as formal repositories.

6. Summary and Conclusions

Many aspects of biological sciences are underpinned by taxon names, and so it is a clear but often overlooked fact that poor practices in taxonomy (the identification and classification of taxa) and nomenclature (the naming of taxa) will have a deleterious impact on a broad range of disciplines and applications. Modern practices in the taxonomy and nomenclature of plants, algae and fungi have largely developed to serve classical botany. This is especially true of nomenclatural rules, now governed by the *Shenzhen Code* (Turland et al. 2018), although the treatment of fossils under the *Code* has evolved and improved in recent decades. However, some aspects of the taxonomy and nomenclature of fossil plants remain problematic, especially for plant microfossils – including organic-walled microfossils (palynomorphs studied by palynologists). In this paper we outline some of these problems and suggest best practices and possible solutions (see summary in Table 1). While our focus is on palynology, some of the issues raised will have a broader resonance within palaeobotany in general and even botany.

While promoting the value of taxonomy and nomenclature, we acknowledge that the rules and practices are complex and daunting to many, and that certain aspects of the *Code* can be difficult to apply to palynology. Moreover, changes to rules and practices sometimes lead to seemingly intractable problems, which are not always immediately evident. These issues need to be identified and addressed as the ultimate aim is to refine tools (taxonomy and nomenclature) pivotal for many applications of palynology.

In this paper we have therefore highlighted various aspects of the *Code* that are difficult to apply in palynology and which will lead to more refinements in the *Code* and taxonomic practices (see Table 1). Most notably, we have discussed and illustrated problems arising when working with original and type material and made recommendations on how to evaluate such situations and progress from them. The delicate nature and vulnerability of material underscores the great care required in preparing samples for longevity as well as optimal study, and the importance of carefully designating and illustrating type specimens.

Other challenges arise from conventions, especially in the publishing process. Our recommendations for best practices in regard to synonymies, descriptions and diagnoses, and curation (see Table 1) can bring differing publishing conventions between botany and palaeobotany closer together, and potential changes to the *Code* could improve applicability in a palynological context. If we face these challenges and adjust our practices accordingly, we ensure a healthy future for palynology and its applicability to broader scientific problems. We also encourage publishers, editors and authors to accommodate practices that better facilitate taxonomic studies, and authors to more effectively use, organise and update our inherited body of taxonomic literature.

Today, palaeopalynology continues to play an important role in biostratigraphical and palaeoenvironmental studies integral to understanding the origin and evolution of sedimentary basins and is increasingly applicable to studies of climate change, evolution, mass extinctions, palaeoceanography and palaeogeography. To contribute meaningfully and with full potential to such studies, we need consistent identifications of taxa and communication of taxonomic concepts, which in turn requires best practices in taxonomy and nomenclature. We offer this paper to promote within palynology a better understanding of the principles, rules and practices of nomenclature and taxonomy and to promote an active discussion of these within the discipline.

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Figure Captions

Figure 1. Status descriptions and flow chart for designations and names under the *Shenzhen Code*.

Figure 2. Checklist to determine the nomenclaturally correct name for fossils according to the *Shenzhen Code*. The list gives the requirements for names of fossil-genera and fossil-species; except where the *Code* gives a specific starting date, the requirements always apply and have retroactive effect, meaning that they apply also to names that were published at a time when a different edition of the *Code* was in effect.

Figure 3. Different kinds of nomenclatural types according to the *Shenzhen Code*. Note that duplicates in palynology generally do not exist. Therefore isotypes (indicated in grey) are generally not available in palynology.

Figure 4. Overview of sampling and slide preparation in palynology. Nomenclatural terminology indicated in bold.

Figure 5. Comparison of palynological slides and a herbarium sheet of a vascular plant specimen. **A.** three kinds of palynological slide preparations from Mädler (1964) – **A.a.** Palynomorphs are placed in a raster of A–K and 1–10; the slide contains the type specimens for four names. **A.b.** Three holotype specimens are designated from a mixed mount; one of them could be relocated and is marked by four surrounding dots. **A.c.** Holotype of *Striatella seebergensis* Mädler 1964 mounted as single grain preparation. Location is indicated with two surrounding dots. Note that the slides are smaller than the standard size, which is apparent through comparison with an England Finder in A.c. **B**. Holotype of *Trifolium phitosianum* Greuter et al. 2000 (Fabaceae), *Böhling 8299* (B 10 0001518; https://herbarium.bgbm.org/object/B100001518), reproduced from Curators Herbarium B (2000+).

Figure 6. Illustrations for Case studies 1–5. Case 1. A.a. and **A.b.** Lost syntypes *Sporites saturni* Thiergart 1949; **A.c.** Holotype of *Pollenites pseudoalatus* Thiergart 1949; **A.d.** Special "pouch" preparations made by Wilhelm Klaus with missing double cover slip (left) and moved cover slip (top right) and remounted cover slip (bottom right). **Case 2. B.a.** Empty pouch for holotype of *Aratrisporite scabratus* Klaus 1960 with remounted slide underneath; **B.b.** Remounted cover slip for the holotype of *Paracirculina maljavkina* Klaus 1960; the palynomorph representing the holotype (**B.c.**) could not be found on the slide and is considered "lost". **Case 3. C.a.** The only remaining slides from Thiergart (1949) for the "Helmstedt" location, one of which should contain the holotype of **C.b.** *Sporites interscriptus* Thiergart 1949; **C.c.** Overview impression of the slide; the drying glycerine jelly seems to have moved and clumped the material together; **C.d.** After scanning of both slides, this specimen comes closest to the holotype depicted in C.b; **C.e.** Remounted slide of the holotype of *Ovalipollis rarus* Klaus 1960; **C.f.** Reprint of the original photograph of the holotype of *Ovalipollis rarus* Klaus 1960; **C.g.** Relocated type specimen; the view is partially obstructed by phytoclasts that have moved, probably as a result of the remounting process. **Case 4. D.a.** Slide holding several types (inventory numbers indicated with x) for Schulz (1967); **D.b** and **D.c.** Reprint of the original photograph of the holotype of *Zebrasporites laevigatus* Schulz 1967; **D.d** and **D.e.** Two palynomorphs, both of which could represent the holotype of *Zebrasporites laevigatus*. **Case 5. E.a.** Slide holding the holotype of *Pollenites reclusus* Thiergart 1949; **E.b.** Overview of the slide with granular remains of glycerine jelly mixed with silicates and organic material, holotype indicated with a triangle; **E.c.** Reprint of the original photograph of the holotype of *Pollenites reclusus* Thiergart 1949; **E.d.** Current condition of the holotype of *Pollenites reclusus*. **F**. Specimens of *Tabulodinium senarium* Dodekova 1990 from Riding and Helby (2001). **F.a., F.c., F.e**. Specimens photographed in 1980s; **F.b., F.d., F.f.** The same specimens photographed in 2000. **Scale** in overviews = 200 µm, scale for individual palynomorphs = 10 µm. A.a–c., C.b. and E.c. reprinted from Thiergart (1949) with kind permission of Schweizerbart Science Publishers (www.schweizerbart.de/journals/palb). A.a–c. and B.c. reprinted from Klaus (1960) with kind permission of the Geological Survey of Austria. D.b. and D.c. reprinted from Schulz (1967) with kind permission of Walter de Gruyter GmbH. F.a-f. reprinted from with kind permission of the Association of Australasian Palaeontologists.

Figure 7. The “lost and destroyed” grey zone of uncertainty as opposed to merely ambiguous material. In cases of ambiguous material (left) an epitype can be designated to resolve the problem. Decreasing preservation of palynological type material (left to right) has different implications for the types available to us; which are discussed in case studies 1–5. Types indicated with an asterisk (*) are not always available for fossils at the moment.

Figure 8. Information box: Homotypic synonyms vs. heterotypic synonyms.

Figure 9. Traditional “synonymy” list and recommended synonym and listing of records. An all-encompassing “synonymy” as often found in the palynological literature (**left**), and the same information presented in a format that complies with the *Code*’s recommended format of a synonymy while retaining all helpful additional information (**right**). This example is modified from Riding (1994). The recommended format on the right distinguishes publications that validate taxonomic names that are relevant to the accepted name of the taxon being treated from other publications that are not directly relevant to the nomenclatural history, such as publications that report the occurrence of the taxon but that do not have any nomenclatural significance, and publications that have been judged to have incorrectly identified a fossil as the taxon in question. Information denoted in grey are optional, but best practice would be to include them.

Supplement 1. Template for Plates with analogue images from Schulz inheritance.