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Approaches to pollen taxonomic harmonisation in Quaternary palynology

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ABSTRACT

Pollen taxonomic harmonisation involves the standardisation of the nomenclature of pollen and fern spores with similar morphotypes at the determination level that is common to all grains or spores with that morphotype within the pollen sequence(s) of interest. Such harmonisation is required prior to subsequent investigations such as numerical analysis, comparing, mapping, synthesis, and environmental reconstruction involving several pollen sequences. Here we present two approaches to harmonisation. These are a 'top-down' and a 'bottom-up' approach. The bottom-up approach is preferred. It is based on the concept of the regional pollen flora for the sequence(s) in the spatial area(s) of study. We present bottom-up harmonisation tables for the continental or subcontinental scales developed for the Humans on Planet Earth (HOPE) project. The tables are for North America, Latin America, Europe, Asia (three parts), and Indo-Pacific. These harmonisations are project-specific and sequence-specific, relating to the geographical area and to the sequences in the area under consideration, both of which are linked to the research questions being addressed. A new bottom-up harmonisation with a consistent taxonomic level and nomenclature is needed when additional sequences or areas are added. However, the HOPE tables can serve as a starting point for further research involving multi-sequence analyses or syntheses.

1. Introduction

Quaternary pollen analysis demands careful and critical identification of pollen and spores from ferns and fern allies (hereafter 'pollen') and meticulous counting. The taxonomic level of the identifications should be to the lowest (= finest) level possible so as to achieve the maximum amount of botanical and ecological information from such analyses (see, for example, Adeleye et al., 2023; Andersen, 1961; Birks, 1973, 1976; Cushing, 1963; Iversen, 1954). The ever-improving quality and availability of high-quality optical equipment, the assembly of large and representative modern pollen-reference collections, and advances in pollen morphology (e.g., Beug, 2004; Punt et al., 1976-2009) make possible the determination of some pollen types that were considered indistinguishable a few decades ago. In view of these developments, it is essential to have consistent and unambiguous identification and nomenclature of the fossil pollen recorded at different depths in the stratigraphical pollen sequence(s) (hereafter 'sequence(s)') of interest. To achieve this, taxonomic and nomenclatural harmonisation of pollen names is essential.

The importance of harmonisation and of standardising harmonisation protocols and nomenclature is also recognised in neo-ecological research (Grenié et al., 2023), analytical palaeobiology (sensu Dillon et al., 2023) involving both deep-time and Quaternary-time palaeobiology including Quaternary pollen analysis (Brown et al., 2023; König et al., 2019; Nieto-Lugilde et al., 2021; Rapacciuolo and Blois, 2019), Quaternary macrofossil analysis (e.g., de Vareilles et al., 2023), Quaternary palaeolimnology (e.g., Duda et al., 2023; Heiri et al., 2011; Munro et al., 1990), and Quaternary palaeozoology (e.g., Brown et al.,

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2023).

In Quaternary pollen analysis, the same pollen-morphological entity may have been given different names and be at different taxonomic levels in different pollen-identification manuals (compare Fægri and Iversen, 1950, 1964; Fægri et al., 1989; Beug, 2004; Punt et al., 1976-2009). The names for modern pollen-reference material of the same plant taxon may vary between laboratories or change over time as the name of the parent taxon, especially at the family, sub-family, tribe, or genus level, may change due to plant systematic revisions, resulting in different pollen nomenclatures between analysts, between laboratories, and between publications. An additional cause of variation in nomenclature is differences in how analysts make their determinations. The reasons for such differences can be the different qualities and availability of microscopes, the use of different optical systems, the availability and extent of modern reference material, the availability of the relevant pollen-morphological literature, and the research question(s) being addressed. When comparing pollen-analytical data from different analysts and laboratories, there is the need for rigorous pollen nomenclatural and taxonomic harmonisation (hereafter 'harmonisation') to amalgamate synonyms and to assign all determinations of a particular pollen morphotype to the same taxonomic level that should be at the finest possible taxonomic level within the data (Brown et al., 2023; Flantua et al., 2023). Prior to discussing harmonisation, we outline pollen identification protocols and basic nomenclatural conventions.

2. Pollen identification and nomenclatural conventions

Identification of fossil pollen is most rigorously done by comparing the fossil grain of interest with modern pollen-reference material prepared in a similar way to the fossil pollen. The modern reference material should encompass the likely regional pollen flora for the sequences (s) under study. This pollen flora is usually defined on the basis of modern plant geography such as the present occurrences of plant taxa in the area of interest, sometimes with additional knowledge (or assumptions) about past distributions. The concept of a regional pollen flora is, in practice, an abstraction as it contains the local, extra-local, and regional pollen-dispersal components (sensu Janssen, 1973). Sometimes it can also contain some extra-regional pollen (sensu Janssen, 1973). As Cushing (1963 p.15) warns [that as] "some pollen can be transported considerable distances from its source, there exists a finite probability that pollen of any plant in the world can be encountered during pollen analysis".

All identified pollen should be named in a consistent manner that indicates the degree of certainty of the determination so that equal weight in interpretation or harmonisation is not given to both certain (i. e. beyond all reasonable doubt for the geographical area of study) and doubtful determinations. The recommended conventions given below build on the systems presented by Cushing (1963 pp. 14–16), Birks (1973 pp. 225–226), and Birks and Birks (1980 p. 24). The use of a consistent nomenclatural convention greatly aids harmonisation if new sequences are considered and provides a sound basis for comparisons within and between study areas. These conventions are as follows.

- 1. Family determination certain; sub-families, tribes, genera, subgenera, species or types, undetermined or indeterminable (e.g., Poaceae)
- 2. Sub-family determination certain; tribes, genera, sub-genera, species or types undetermined or indeterminable (e.g., Asteroideae)
- 3. Tribe determination certain; genera, sub-genera, species or types undetermined or indeterminable (e.g., Callitricheae)
- 4. Genus determination certain; species or types undetermined or indeterminable (e.g., *Plantago*)
- 5. Sub-genus determination certain; species or types undetermined or indeterminable (e.g., *Pinus* sub-genus *Strobus*)

- 6. Species determination certain. No other species with similar pollen morphology present in the regional pollen flora (e.g., *Plantago lanceolata*)
- 7. Genus determination certain; species determination less certain because of poor preservation, inadequate reference material, or close morphological similarity of the fossil pollen with the pollen morphology of other taxa present in the regional pollen flora (e. g., *Plantago* cf. *P. lanceolata*)
- 8. Only one fossil pollen-morphological type present but two plant taxa in the regional pollen flora are considered probable alternatives; further distinctions are not possible based on fossil pollen morphology alone (e.g., *Plantago lanceolata/P. maritima*)
- 9. One fossil pollen-morphological type present but three or more taxa in the regional pollen flora are considered possible alternatives; further distinctions are not possible based on fossil pollen morphology alone. The taxonomic composition of the pollenmorphological type should be stated (e.g., *Plantago*-type)
- 10. Family determination certain, some pollen morphological types distinguished and recorded separately, and the remaining pollen types in the family are grouped here. This fossil category represents fossil pollen that were not or could not be separated below family level (e.g., Rosaceae undifferentiated (undiff.))
- 11. Sub-family determination certain, some pollen-morphological types distinguished and recorded separately, and the remaining pollen types in the sub-family are grouped here. This fossil category represents fossil pollen that were not or could not be separated below sub-family level (e.g., Asteroideae undiff.)
- 12. Tribe determination certain, some pollen-morphological types distinguished and recorded separately, and the remaining pollen types in the tribe are grouped here. This fossil category represents fossil pollen that were not or could not be separated below tribe level (e.g., Callitricheae undiff.)
- 13. Genus determination certain, some pollen-morphological types distinguished and recorded separately, and the remaining pollen types in the genus are grouped here. This fossil category represents fossils that were not or could not be separated below genus level (e.g., *Plantago* undiff.)
- 14. Sub-genus determination certain, some pollen morphological types distinguished and recorded separately, and the remaining pollen types in the sub-genus are grouped here. This fossil category represents fossil pollen that were not or could not be separated below sub-genus level (e.g., *Pinus* sub-genus *Strobus* undiff.)

3. Pollen taxonomic harmonisation – Top-down and bottom-up approaches

There are several instances where harmonisation is essential. For example, an analyst may count part of a sequence in one year and return to fill in detail a year or two later. A pollen-morphological type may be assigned different names in the years between the analyses due to increased analytical experience, and/or access to more modern reference material and/or new relevant literature.

Similarly, two or more analysts may study the same stratigraphic sequence(s). Leaving aside the critical question of analytical quality control between the analysts' pollen counts, different names may be assigned to the same pollen-morphological type by the analysts. To achieve nomenclatural consistency, pollen taxonomic names must be harmonised in such situations when there is more than one analyst.

The need for harmonisation becomes increasingly important when pollen-analytical data from many sequences in a geographical area are combined, synthesised, and compared. The extent of the geographical area may range from a single valley (e.g., Birks, 2007) to a large island (e.g., Birks, 1973), a landform unit (e.g., Walker, 1966), a state (e.g., Cushing, 1963), part of a country (e.g., Connor, 2011; Tonkov, 2021; Woodbridge et al., 2023), an entire country (e.g., Fredskild, 1973), a biome or a major climate zone (e.g., Cruz-Silva et al., 2023; Liu et al.,

Table 1

Summary of the harmonisation tables (archived on)	ig Share) that were develo	ped for the seven harmonisation reg	ions used in HOPE.
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Region	No. sequences	No. unharmonised taxa	No. harmonised taxa	Harmoniser
North America	986	1318	281	HJBB
Europe	1025	2057	280	TG, VAF, HJBB
Asia (main)	139	1596	317	KPB, HJBB
Asia (Siberia)	192	526	148	KPB, HJBB
Asia (Levant)	34	651	233	KPB, HJBB
Latin America	262	5399	1423	HH, SGAF, HJBB
Indo-Pacific	152	1640	871	AH, SGH

HJBB = HJB Birks; TG = T Giesecke et al. (2019); VAF = VA Felde; KPB = KP Bhatta; HH = H Hooghiemstra; SGAF = SGA Flantua; AH = A Herbert; SGH = SG Haberle.

2020; Liu et al., 2023), part of a continent (e.g., Cao et al., 2013; Cao et al., 2020; Seddon et al., 2015), an entire continent (e.g., Giesecke et al., 2019; Githumbi et al., 2022; Huntley, 1990; Huntley and Birks, 1983; Mottl et al., 2021; Phelps et al., 2020; Trondman et al., 2015; Williams and Shuman, 2008), a hemisphere (Cao et al., 2019), or the Earth (Herzschuh et al., 2021; Herzschuh et al., 2022). Harmonisation seeks to find a pollen taxonomic level to which all the pollen of a particular plant taxon (or taxa) have been consistently determined in all the sequences within the geographical area of study and to give an unambiguous and appropriate name to that morphotype (Flantua et al., 2023).

There are two contrasting approaches to harmonisation – the 'topdown' approach of Herzschuh et al. (2021, 2022) and the 'bottom-up' approach illustrated by the pollen harmonisation tables outlined in this paper and available from the Fig Share link (see Data Availability).

The 'top-down' approach presented by Herzschuh et al. (2021, 2022) is created at the global scale, It uses 2831 pollen sequences as the basis for harmonisation, consisting of 1075 sequences from Europe, 1032 from North America, 488 from Asia, 150 from Latin America, 54 from Africa, and 32 from the Indo-Pacific region. These 2831 sequences contain 10,110 pollen taxon names. These names are initially screened to remove synonyms prior to harmonisation. The harmonisation criteria applied are: (i) pollen of all woody taxa and of major herbaceous taxa (e. g., *Artemisia, Rumex, Thalictrum*) are harmonised to genus level, and (ii) pollen of other herbaceous taxa (e.g., Poaceae, Cyperaceae, Fabaceae, Apiaceae) are harmonised to family level (see Herzschuh et al., 2021, 2022 for further details). As the starting point is 2831 sequences from six continents, it can be viewed as a top-down procedure that reduces 10,110 unharmonised taxon names to 1002 harmonised taxon names.

After this harmonisation, Li et al. (2022) use a consistent age-depth procedure to derive harmonised chronologies for these 2831 sequences. Many of the top-down harmonised pollen sequences form the basis for climate (2594 sequences) and biome (1887 sequences) reconstructions for the Northern Hemisphere (Cao et al., 2019; Herzschuh et al., 2023a; Herzschuh et al., 2023b; Herzschuh et al., 2023c - see also Chevalier et al., 2023).

An alternative approach ('bottom-up') is achieved by first defining the likely regional pollen source-area and flora for the geographical area under study based on the present-day flora and plant geography and, if known, possible past history (harmonisation region, sensu Flantua et al., 2023). Knowledge of the pollen morphology and nomenclature of all the plant taxa in the regional flora is required so that morphologically similar fossil pollen that have been identified and named in different sequences within the harmonisation region can be assigned to the finest pollen taxonomic level that is consistently distinguished within all the sequences in the region of study and then given an appropriate and unambiguous name. Taxon names at the species level (e.g., Plantago lanceolata) may have to be assigned to a coarser pollen taxonomical level (e.g., Plantago lanceolata-type, Plantago, or Plantago-type) as additional sequences and their taxa are added. This means losing some taxonomic detail and thus potential botanical and ecological insights. Monospecific taxa with distinctive pollen morphology (e.g., Zea mays) remain at the specific level, in contrast to the harmonisation in the top-down approach where Zea mays is grouped with all other Poaceae.

Different hierarchical levels can be distinguished in the bottom-up approach within a study area such as Europe. For example, Giesecke et al. (2019) discuss three harmonisation levels (H_0 , H_1 , H_2). Level H_0 represents the currently accepted most detailed level of pollen identification based on the relevant literature, extensive reference collections, and expert knowledge and contains about 1200 taxon names. Based on this H_0 taxonomy, Giesecke et al. (2019) present two coarser hierarchical levels (H_1 , H_2) reflecting different levels of taxonomic precision. Level H_1 (860 taxa) combines morphologically similar pollen types that can only be separated using extensive modern reference collections and requiring considerable palynological expertise. This often results in identification of pollen taxa at the species, species-group, genus, or subgenus taxonomic level. Level H_2 contains 310 pollen taxa with distinctive and readily identifiable features. These taxa mainly belong to plant genera, sub-genera, groups of genera, or families (Giesecke et al., 2019).

4. Examples of pollen harmonisation tables

As examples of harmonisation tables, we present pollen harmonisation tables constructed using the bottom-up approach to harmonise fossil pollen records in the HOPE (Humans On Planet Earth) project (https://www.uib.no/rg/EECRG/107501/hope) (Table 1 and Fig Share archive; see Data availability).

Initially, fossil pollen data were downloaded from the Neotoma Paleoecology Database (Williams et al., 2018; www.neotomadb.org) or from the Pangaea archive (Data Publisher for Earth and Environmental Science, www.pangaea.de), or were provided by individual researchers (Bhatta et al., 2023). The world was divided into seven harmonisation regions (see the Shapefile delimiting these regions archived on Fig Share; see Data availability) covering all continents except Africa and Antarctica. Harmonisation tables were developed for each region using the bottom-up approach. Several data-quality or data-type criteria (e.g., depositional environment, chronological controls) were applied to these data following the guide to processing pollen data for broad-scale analysis (see fig. 1 in Flantua et al., 2023). The main criteria applied were (i) only data-sets from certain sediment depositional environments were included (see Table S3 in Bhatta et al., 2023); (ii) only pollen of terrestrial tree, shrub, dwarf-shrub, herb, palm, succulent, and mangrove taxa were included, (iii) only data-sets with five or more levels were included; and (iv) only data-sets with more than two acceptable chronology control points were included (see Table S2 in Bhatta et al., 2023).

The seven tables are summarised in Table 1 and are archived on Fig Share (see Data availability). For each table, the number of pollen sequences used in the harmonisation, the number of unharmonised pollen taxa, the number of harmonised taxa, and the initials of the person/ people responsible for the harmonisation for the particular region are given.

In all the harmonisation tables archived on Fig Share except Europe, column 1 contains the unharmonised raw pollen taxon names in the original data from that geographical region, column 2 gives the raw taxon names modified into a form readable by the FOSSILPOL workflow (Flantua et al., 2023), and column 3 contains the harmonised taxon names for all regions except Europe. In the European table, column 3

contains the harmonised names (741 taxa) at the finer H_1 taxonomic level (MHVar.1) of Giesecke et al. (2019), and column 4 lists the H_2 harmonisation (280 taxa) (MHVar.2) level of Giesecke et al. (2019) updated and slightly modified by VAF and HJBB. In all HOPE data analyses for Europe, the harmonisation from column 4 was always used.

By looking at the raw unharmonised pollen taxon names and the harmonised pollen taxon names in the Fig Share tables, an interested reader can readily see what harmonisations were made and which and how many unharmonised taxon names were included in a particular harmonised taxon.

5. Discussion and conclusions

Despite the inevitable loss of taxonomic detail and hence botanical and ecological information due to harmonisation, such harmonisation whether it be top-down or bottom-up is essential to achieve a critical and consistent pollen taxonomy and nomenclature for the comparison and analyses of the stratigraphical sequences used in synthetic studies. At a broad scale of analysis, this is adequate, even though some taxonomic and ecological detail at individual sites may be lost.

Harmonisation is conventionally done for a specific region to address particular research questions (e.g., Birks, 1973; Birks, 2007; Giesecke et al., 2019; Huntley, 1990; Huntley and Birks, 1983; Liu et al., 2023; Mottl et al., 2021; Phelps et al., 2020; Walker, 1966). These questions define the spatial and temporal domains of study and thus the harmonisation region. Harmonisation based on the bottom-up approach described above is spatially specific and hence project-specific. It is also important to note that such a bottom-up harmonisation table constructed for a specific area and based on all appropriate pollen sequences in that area may not necessarily be identical to a harmonisation table for the same area but based on, say, only 50% of the sequences in the area. Bottom-up harmonisation tables are thus not only area-specific but are also sequence-specific. These harmonisation tables cannot thus be directly transferred to a different project but they may serve as a starting point for creating a table relevant to that project and the sequences in hand. Flantua et al. (2023) emphasise that "it is advisable to work with an expert familiar with the modern and fossil pollen flora of the spatiotemporal domain of interest in order to create a reliable project-specific table of harmonized taxa".

It is therefore necessary to create new tables for different projects, each with their specific spatial and temporal domains as the bottom-up harmonisation procedure is based solely on which pollen sequences are included and their pollen composition to be harmonised which, in turn, depends on the research question(s) being addressed (e.g., comparing rates of palynological change in Scandinavia with rates of palynological change in the European Mediterranean). The locations of the sequences define the harmonisation region of the underlying regional pollen flora and the nomenclature of all the pollen taxa in the individual sequences selected from that geographical area provide the basic material for critical bottom-up taxonomic and nomenclatural harmonisation.

The problem of sequence-specificity inherent in the bottom-up approach is largely avoided in the top-down harmonisation procedure of Herzschuh et al. (2021, 2022) as it is based on harmonised pollen taxon names for 2831 sequences from six continents at the genus or family level. The harmonised names are 'fixed' in contrast to the bottomup approach where the harmonised names depend solely on the sequences included for a particular study. Inevitably in the top-down approach using only genera and families for the taxonomic levels adopted, loss of taxonomic detail occurs, particularly in herbaceous taxa (e.g., Poaceae, Saxifragaceae, Gentianaceae, Plantaginaceae, Scrophulariaceae). In the HOPE bottom-up approach some harmonisations remain at the species level (e.g., Zea mays, Secale cereale) in contrast to the top-down approach where these cereals are amalgamated with other Poaceae pollen. There may also be a loss of taxonomic detail for some major arboreal taxa (e.g., Pinus, Quercus) in the top-down approach. In the bottom-up approach, pollen of taxa consistently distinguished at the

Table 2

Strengths and weaknesses of the top-down and bottom-up approaches to pollen taxonomic harmonisation.

	Top-down	Bottom-up
Taxonomic level of harmonisation	Genus or family	From family to species
Spatial scale used in the harmonisation	Global	Continental to single valley
Sequence specific?	No	Yes
Area specific?	No	Yes
Level of expert knowledge required to develop	High	Very high
Level of expert knowledge required to apply	Low	High
Appropriate spatial scale for use	Mainly global, hemispherical, continental, or national	Continental to single valley

sub-genus level (e.g., sub-genus *Pinus* (diploxylon pines) and sub-genus *Strobus* (haploxylon pines); sub-genus *Quercus* (deciduous oaks) and subgenus *Cerris* (evergreen oaks)) are harmonised below the genus level, whereas in the top-down approach they are automatically harmonised at the genus level. In harmonising the 2057 unharmonised pollen taxa in the European HOPE data, the bottom-up approach yields a total of 280 harmonised taxa (Table 1) whereas the top-down approach results in 208 harmonised taxa. This is a reduction of 26% compared to the bottom-up harmonisation. A reduction in the number of harmonised taxa (22%) similarly occurs when the North American HOPE data are harmonised using the top-down approach compared to the bottom-up harmonisation summarised in Table 1.

The strengths and weaknesses of these two approaches are summarised in Table 2.

It is important to emphasise that all harmonisation tables relate directly to pollen and spores and not to plants or vegetation (De Klerk and Joosten, 2007). To link pollen and plants, the plant data need to be converted into pollen taxa to create a 'common currency' (sensu Flantua et al., 2023) or taxonomic equivalents ('species equivalents' sensu Brown et al., 2023) between pollen and plants that are required to permit comparison of the two. For example, Birks (1973) compared modern surface-pollen data with the composition of contemporary vegetation from which the pollen samples were collected by grouping the taxa in the vegetation into their corresponding pollen taxa (see also Blaus et al., 2020).

In conclusion, careful and rigorous pollen taxonomic harmonisation is an essential step to ensure a consistent and unambiguous taxonomy and nomenclature of the fossil pollen recorded in all the stratigraphical sequences under study prior to any synthetic analyses of combined pollen data-sets. It can be achieved using either the top-down or bottomup approach. Which to use depends on the research questions being asked, which in turn define the relevant taxonomic detail and spatial scale. The tables provided in Fig Share serve as a starting point for future palaeoecological or biogeographical studies, which may require a bottom-up harmonisation approach to ensure consistent comparisons between sequences at different locations.

Author contributions

HJBB wrote the first draft and all authors commented on the various versions of the text.

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Declaration of Competing Interest

The authors have no conflicts of interest to declare.

Data availability

The harmonisation tables and shapefile are given in Fig Share doi: 10.6084/m9.figshare.24088194.

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