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Geological Society, London, Special Publications

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DOI: https://doi.org/10.1144/SP511-2021-83

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Received 27 April 2021
Accepted 13 May 2021

Why a new volume on Non-Pollen Palynomorphs?

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1. Introduction

Why a new volume on Non-Pollen Palynomorphs? Quite simply put because there isn't one. Most especially not one that bridges the gaps between the use of NPPs in Quaternary and pre-Quaternary studies.

Non-pollen palynomorphs (NPPs) are an increasingly important part of archaeological, palaeoecological, palaeoclimatic, and biostratigraphic studies throughout the geological and archaeological record. While recognised in the fossil record for nearly two centuries, it is only in the past 75 years that marine dinoflagellate cysts have become robust biostratigraphic and palaeoecological proxies throughout the rock record, as have other marine NPPs such as Acritarchs, Prasinophytes, Chitinozoa, and Scolecodonts. Application of terrestrial NPP groups, especially in deep time, has been sporadic at best, although archaeologists, and Quaternary geologists and palaeoecologists have made significant strides in the past 30 years, thanks in a very large part to the work of Bas van Geel (Figure 1; 1978, 1979, 1998, 2001) and his students and colleagues (van Geel and van der Hammen 1978; van Geel *et al*. 1994, 1996, 2011; van Geel and Grenfell 1996; van Hoeve and Hendrickse 1998; van Geel and Aptroot 2006, among many others). This early work catalysed Russian Quaternary paleoecologists (Kats *et al.* 1977). A similar effort, focused on fungi only, was seen among Canadian, Indian, and American deep-time geologists (Figure 2). However, as the focus of groups led by Jansonius (1962, 1976); Elsik (1968, 1970, 1976a&b, 1992, 1996; Elsik and Jansonius 1974), Kalgutkar (1985; Kalgutkar and Sweet 1988; Kalgutkar and McIntyre 1991; Kalgutkar and Jansonius 2000), and Saxena (1991, 2006, 2019) was largely biostratigraphic, and the majority of these scientists were not at universities, their work was not as widely adopted. Of note, both recent schools of NPP study appear to have been catalysed, at least in part, by the work of Graham (1962), who in turn had studied works stretching as far back as

1850, and Frey (1964). Recent advances in palynological processing (see Pound *et al*. 2021, this volume), changes in approach to nomenclature (see O'Keefe *et al*. 2021, this volume), especially for fossil fungi, and collaborations with mycologists (see Nuñez Otaño *et al*. 2021, this volume) and protistologists (see Andrews *et al.* 2021, this volume) have allowed the recognition of many NPPs deeper in the rock record. Indeed, some of the earliest recorded forms of life are NPPs – acid-resistant carbonaceous spheres in Archean rocks (Javeaux et al. 2010; Agic *et al*. 2021, this volume).

2. Early History of Palynology and NPP Studies

The name "non-pollen palynomorph", in many ways, is based on the assumption that pollen are most important for palynological, especially palaeoecologic, studies. This is a uniquely Quaternary viewpoint. Indeed, while pollen was described by Malphigi and Grew in 1675-1682 (Malpighi 1675, 1679; Grew 1682), what we now call NPPs began to be described very soon thereafter (Figure 3), beginning with pteridophyte and fungal spores by Tournefort in the 1690s and Geoffroy in the early 1700s (Geoffroy 1714; Stroup, 1990; Bernasconi and Taiz 2006) and dinoflagellates in the mid-1700s (Baker, 1753; Rochon et al. 2013). The first fossil pollen were described from thin-sections of coal in 1833 by Witham (1833), although they were initially described as resin vessels. The first undisputed fossil pollen were described and illustrated by line drawings in 1836 by Göppert as part of a study of fossil plants; dinoflagellate cysts and acritarchs were described near-simultaneously by Ehrenberg (Figure 4a; Ehrenberg 1837; Sarjeant 2002; Traverse 2007); these studies culminated with the publication of *Mikrogeologie* in 1854 (Ehrenberg 1854). Fossil microfungi were first described in 1848 (Figure 4b; Berkeley 1848; Taylor et al. 2015), and their study progressed to parallel that of fossil pollen through the early 1900s. The late 1840s and early 1850s were an era of discovery; in addition to those named above, many other NPPs were identified for the first time, largely through the efforts of microscopy clubs, such as that in Clapham, UK (Sarjeant 1991): foraminiferal linings and *Botryococcus* algae were both described in 1849; prasinophytes were described in 1852; and scolecodonts in 1854 (Sarjeant 2002). In the early years, emphasis was on documenting ***all*** the microscopic taxa recovered in the course of a study, whether it be from a modern lake or bog or from Pleistocene peats or from Carboniferous coals. This trend continued through the earliest part of the 1900s as additional NPPs, including testate amoebae, spermatophores of copepods, and Rhabdocoelan oocytes (Rudolph 1917), were described in Quaternary bogs and peats. While changes were in the air, discovery continued, with heliozoans, *Macrobiotus* sp. eggs, and chytrids on pollen walls being described in the late 1920s (Hesmer 1929) and chitinozoans in 1931 (Figure 4c; Eisenack 1931; Sarjeant 2002).

Quaternary palaeoecology began to blossom in the 1890s and early 1900s in Sweden, Denmark, Finland, and Germany with the recognition that different layers of sediment from bogs preserved different quantities and assemblages of palynomorphs (Weber 1893, 1896; Sarauw 1897; Lagerheim 1895; Lindberg 1900; Witte 1905; Holst 1908). With the publication of Von Post's 1916 and 1918 papers, Quaternary palaeoecology, firmly tied to the pollen record, was born, and solidified through the work of his colleagues and students, most notably Erdtman (1925, Sarjeant (2002) and Traverse (2007). Despite this emphasis on pollen, studies of NPPs occurring in palynology slides continued, albeit sporadically, until renewed interest in them began in the 1960s.

Palaeopalynology had begun to diverge from actuopalynology at about the same time as Quaternary palaeoecology developed, beginning with adoption of the artificial nomenclatural scheme originally proposed by Reinsch, Bennie and Kidston in the 1880s, first used by H. Potonié in the 1890s, and subsequently by palaeobotanists, especially Bartlett, in the 1920s (Sarjeant 2002; Bartlett 1929a,b; Bennie and Kidston 1886; see O'Keefe *et al*. 2021, this volume), and continuing with the recognition that palynomorphs could be useful in correlating coal seams beginning in 1918 (Thiessen 1918, 1920; Thiessen and Staud 1923). This realization, which came into its own in England and Germany from cross-fertilization due to visits in the mid-1920s from both Thiessen, to Sheffield and many other places (Lyons and Teichmüller 1995), and Erdtman, to various universities, including Leeds, where he worked closely with the botany and palynology group led by Burrell (Cross and Kosanke 1995; Marshall, 2005). This knowledge was carried to the United States by both Erdtman himself and a young student named L.R. Wilson, who happened to be studying at the University of Leeds with Burrell immediately following Erdtman's visit (Cross and Kosanke 1999). While trained as an actuopalynologist, L.R. Wilson turned his attention to palaeopalynology beginning with a 1937 study of palynomorphs from a coal seam in Iowa (Wilson and Brokaw 1937), and collaborated with J.M. Schopf, who has himself begun to study palynomorphs in 1936, eventually producing a seminal work on Carboniferous spores in the Illinois Basin (Schopf *et al*. 1944). By 1944, however, palynostratigraphy had become the major emphasis in deep-time palynology (Wilson, 1944). Interestingly, the development of palaeopalynology in Britain also began at Leeds around the same time, when A. Raistrick was a student and young researcher there. Raistrick began publishing palynological studies in the 1930s, and like Wilson, began with actuopalynological studies of peat before progressing to studies of Carboniferous spores (Raistrick & Woodhead 1930; Raistrick 1933 a&b, 1934 a&B, 1935, 1936, 1937, 1938, 1939; Marshall, 2005). Raistrick, along with his collaborator Kathleen Blackburn, continued work on palynology ranging from Quaternary to Carboniferous studies after his move to Newcastle; a key addition in terms of NPP research was their confirmation that the Carboniferous algae noted by Thiessen many years earlier were indeed *Botryococcus*, and indistinguishable from their modern counterparts (Marshall, 2005). Again, during the same period in the mid-1920s, I. Cookson was in residence in Britain, first at Imperial College London, then at the University of Manchester (Dettmann, 1993; Riding and Dettmann 2013); it is likely that she, too, was catalysed by lectures from Erdtman and Thiessen, although her interest in fossil plants and fungi was already developing: Cookson was trained as a modern botanist and mycologist in Australia, but turned her attention to palaeobotany and palaeomycology while in the UK; this collaboration produced many notable works, most importantly her seminal paper on Cenozoic fungi (1947). Near-simultaneously, in Germany, R. Potonié, beginning with his 1931 papers (Potonié 1931a-c), demonstrated the utility of palynostratigraphy and correlation in Paleogene coal-bearing sediments; these studies used the system of form-nomenclature propounded by Bartlett, which rapidly became entrenched in palaeopalynology – thus, not only were actuopalynologists and deep-time palynologists going in different directions, from the 1930s onward, they were speaking separate languages (see O'Keefe *et al.* 2021, this volume), and much of the early cross-fertilization of ideas began to wane.

Elsewhere in the world, studies of pre-Quaternary NPPs, primarily spores, acritarchs, chitinozoans, dinoflagellate cysts, and prasinophytes, began in earnest in the lead-up to World War II (Sarjeant 2002). In Russia, much of this early work was led by S. Naumova (1939) and A.A. Liuber (1938), with an emphasis on late Paleozoic spores and pre-pollen. In India, pioneering work by Virkki (1937), a student of Birbal Sahni on Permian floras set the stage for an explosion of palaeopalynological studies in that country. Dinoflagellate cyst studies experienced a renaissance in the 1930s, beginning with the work of O. Wetzel (1932, 1933a&b), G. Deflandre (1935, 1936, 1937), M. Lejeune (1936), and A. Eisenack (1931, 1935, 1936a,b), and H. Lewis (1940), and early explorations of their utility as biostratigraphic indicators by Shell Oil (Sarjeant 2002), although WWII put a hiatus on much progress. It was not until the nestor of dinoflagellate studies, W. Evitt turned his attention to their biology and geology in the late 1950s that their study blossomed into the robust community it is today (Riding & Lucas-Clarke 2016). His work catalysed fellow dinoflagellate workers Downie, Gocht, Hughes, Rossignol, Sarjeant, Vozzhennikova, Wetzel, among others (Sarjeant 2002), and led to the establishment of two major centres of fossil dinoflagellate research: 1) Stanford University in the United States and 2) The University of Sheffield in the United Kingdom. Downie's research group at Sheffield was instrumental in advancing acritarch research following WWII, as were Naumova in Moscow and Timofeyev in Leningrad, and many others in mainland Europe. Prasinophyte research did not make many advances until the post-war era, when some 14 genera were named in the period from 1952-1967 (Sarjeant 2002; Guy-Ohlson 1996). It was also in this period that the origin of Scolecodonts was realised after Lange (1947, 1949) and Kozlowski (1956) presented articulated jaws from the Devonian of Brazil and Ordovician of Poland, respectively, and further study in Poland led to Kielan-Jaworowska's (1966) seminal work on the preliminary phylogeny of this group. However, much of this phylogeny is now obsolete and the phylogeny and classification of scolecodonts is part and parcel of the study of fossil annelids (Parry *et al*. 2019), as is the study of clitellate cocoons, although these cocoons are of limited taxonomic value in and of themselves. Studies of Chitinozoa, too, blossomed in the post-war period, and continue to be robust biostratigraphic markers throughout their range, although their affinity remains unknown, although the consensus is that they are the remains of an extinct organism (Liang *et al*. 2019). By the late 1960s and early 1970s, study of NPPs, in both geological and Quaternary contexts was coming into its own, and, through the early 2000s, has become increasingly important in palaeoecological studies.

3. Evolutionary History of NPPs

For much of the fossil record, it is NPPs that are dominant, and their diversification parallels the development of multicellular life and land plants (Table 1, Figure 5). Beginning with the simple spherical carbonaceous forms noted by Javeaux *et al.* (2010), both marine and terrestrial NPPs, including acritarchs, monolete and trilete plant spores, have been keys to understanding the oxygenation of Earth's atmosphere (Agic & Cohen 2021, this volume), rise of multicellular life in the oceans (Agic & Cohen 2021, this volume), and the invasion of land (Wellman & Ball 2021, this volume). Indeed, Precambrian through Paleozoic biostratigraphic studies rely on NPPs, including acritarchs, chitinozoans, and precursors to dinoflagellates (Molyneux *et al.* 2013; Servais *et al.* 2013; Knoll *et al.* 2007; Huntley *et al.* 2006), as do Mesozoic and Cenozoic studies of marine sediments (Hubbard *et al.* 1994; Penaud *et al.* 2018). Thus, the evolutionary history of NPP groups is the evolutionary history of the earliest life, and a vibrant record of its diversification and preservation in the rock record.

4. An Overview of this Book

To date, no compendium addressing NPPs and their utilities from modern to ancient applications exists. This book endeavours to fill the gap by providing 12 review papers on the use and identification of non-pollen palynomorphs. It is arranged in three sections. The first contains three background chapters: an overview of what organismal remains are considered NPPs (Shumilovskikh *et al.* 2021), how processing impacts the NPP spectrum obtained by the researcher (Pound *et al.* 2021), and a historical overview of nomenclature and recommendations for naming NPPs moving forward (O'Keefe *et al.* 2021). These chapters provide necessary background for current and student NPP researchers and context for interpreting what is known about NPP occurrence and utility as proxies. The second contains an overview of the major groups of NPPs: fungi (Nuñez Otaño *et al.* 2021); freshwater remains including dinoflagellates, tintinnids, euglenids, arcellinids, rotifers thecae and eggs, flatworm egg cases, nematode eggs, and the remains of cladocerans & diptera (McCarthy *et al.*, 2021); testate amoebae (Andrews *et al.* 2021); marine remains including dinoflagellates, acritarchs, tintinnids, ostracod and foraminiferal linings, copepods, and worm remains (Mudie *et al.* 2021). These chapters provide in-depth overviews of the major NPP groups in the context of their occurrence (terrestrial or marine). They are invaluable resources for understanding the intricacies of each taxon as a proxy and interpreting their distribution in rocks and sediments. The third section provides reviews of state of the art of application of NPPs to a variety of problems: interpreting human impact on the environment (Gauthier & Jouffroy-Bapicot 2021); using coprophilous fungal spores to study megaherbivores (van Asperen *et al*. 2021; examining NPP distribution in marine settings across a major hyperthermal event (Denison 2021); tracing the origin and distribution of early land plants (Wellman & Ball 2021); and tracing the origin of early life and eukaryotes (Agic & Cohen 2021).

5. Acknowledgements

Development of this book was not without its unforeseen challenges. The COVID-19 pandemic struck just as papers were being finalised for submission, significantly slowing the process as several co-authors and their families battled for their health and sanity during repeated global, regional, and local shut-downs as well as a transition to primarily online course delivery and/or working remotely. We thank our many contributors, reviewers, production staff, and families for their patience and support during the lengthy process.

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Table Captions.

Table 1: Geological age ranges of major groups of non-pollen palynomorphs.

Figure Captions.

Figure 1: Bas van Geel. Photograph courtesy of Encarni Montoya.

Figure 2: Early American and Indian mycopalynologists. A) Jan Jansonius, B) Ramakant M. Kalgutkar, C) William C. Elsik. Photographs A and B courtesy of AASP-The Palynological Society; used with permission; Photograph C courtesy of Vaughn M. Bryant, Jr.

Figure 3: A timeline of NPP discoveries. Dinoflagellate and Acritarch images from Ehrenberg (1837); the dinoflagellate preserves the unusual orientation chosen by Ehrenberg. Microfungi image by R. Kalgutkar in Kalgutkar and Jansonius (2000); used with permission of the AASP Foundation. Heliozoan image by Jablot via Wikipedia (image is in the public domain). All other palynomorph images adapted from the authors' collections.

Figure 4: Discoverers and Describers of early NPPs: A) Christian Gottfried Ehrenberg (1795-1876); B) Rev. Miles Joseph Berkeley MA FLS (1803-1889); C) Alfred Eisenack (1891-1982). Painting of Ehrenberg by Eduard Radke courtesy of Wikipedia; Photograph of Berkeley by Maull & Polybank, courtesy of the Wellcome Collection, Attribution 4.0 International (CC BY 4.0); Photograph of Alfred Eisenack by Werner Wetzel (Tübingen) from Gocht & Sarjeant (1983); used with permission of *Micropaleontology*.

Figure 5: Origin and geological age ranges of major groups of NPPs.

Non-Pollen Palynomorph Type	Range in Millions of Years Ago (MA)	References
Bacterial Cysts	3200 - Recent	Agic et al. 2021 (this volume)
Cyanobacteria	2017 - Recent	Hodgskiss et al. 2019
Achritarcha	1650 - Recent	Agic et al. 2021 (this volume)
Fungi	1230 - Recent	Loron et al. 2019
Chlorphyta	1000 - Recent	Tang et al. 2020
Arthropoda	541 - Recent	Betts et al. 2014
Foraminifera (linings)	540 - Recent	Pawlowski et al. 2003
Scolecodonts	497 - Recent	Szaniawski 1996
Helminth eggs	485 - Recent	De Baets et al. 2020 preprint
Chitinozoa	480 - 359	Servais et al. (2013); Miller (1996)
Non-reproductive vascular plant remains	460 - Recent	Retallack et al. 2020
Monolete and Trilete plant spores	460 - Recent	Retallack et al. 2020
Testate amoebae	407 - Recent	Strullu-Derrien et al. 2019
Streptophyta	407 - Recent	Head 1992, van Geel & Grenfell 1996, Wellman et al. 2019
Freshwater sponges	304 - Recent	Schindler et al. 2008
Dinoflagellata	247.2 - Recent	Janouškovec et al. 2016
Tintinnids	201.3 - Recent	Lipps et al. 2013
Tardigrades	145 - Recent	Guidetti & Bertolani, 2018
Loricate Euglenophyta	145 - Recent	Ascaso et al. 2005
Chrysophyceae	112 - Recent	Kristiansen and Škaloud 2016
Rotifers	40 - Recent	Waggoner & Poinar 1993
Rhabdocoela	37.2 - Recent	Poinar 2004 Baltic Amber
Textile Fibers	0.34 - Recent	Kvavadze et al. 2009

Table 1

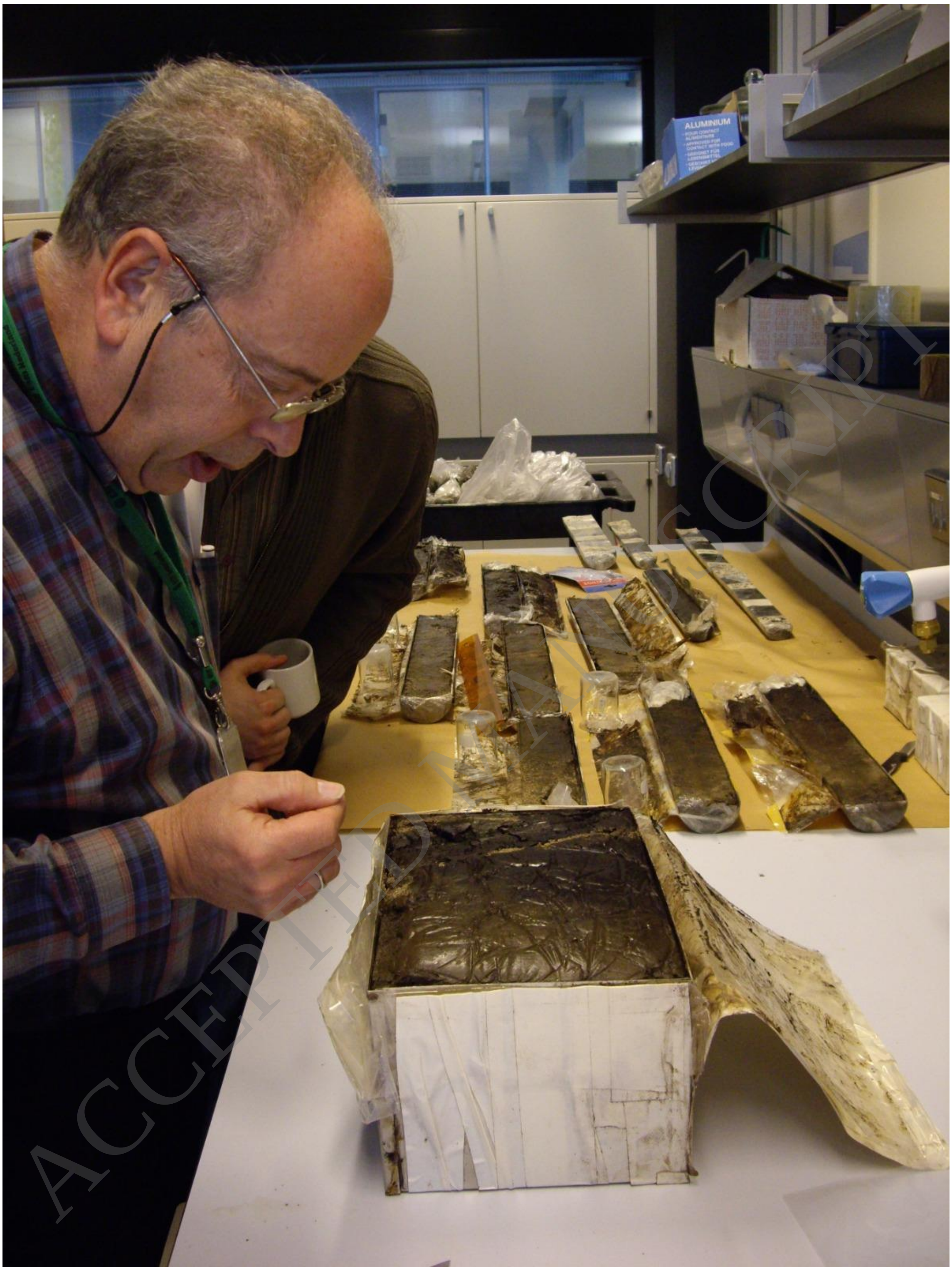

Figure 1

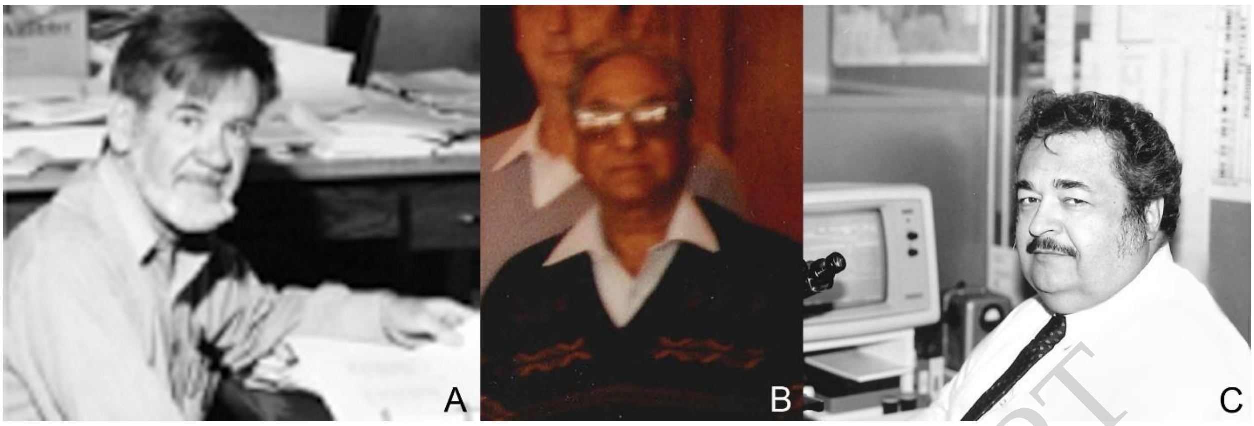

Figure 2

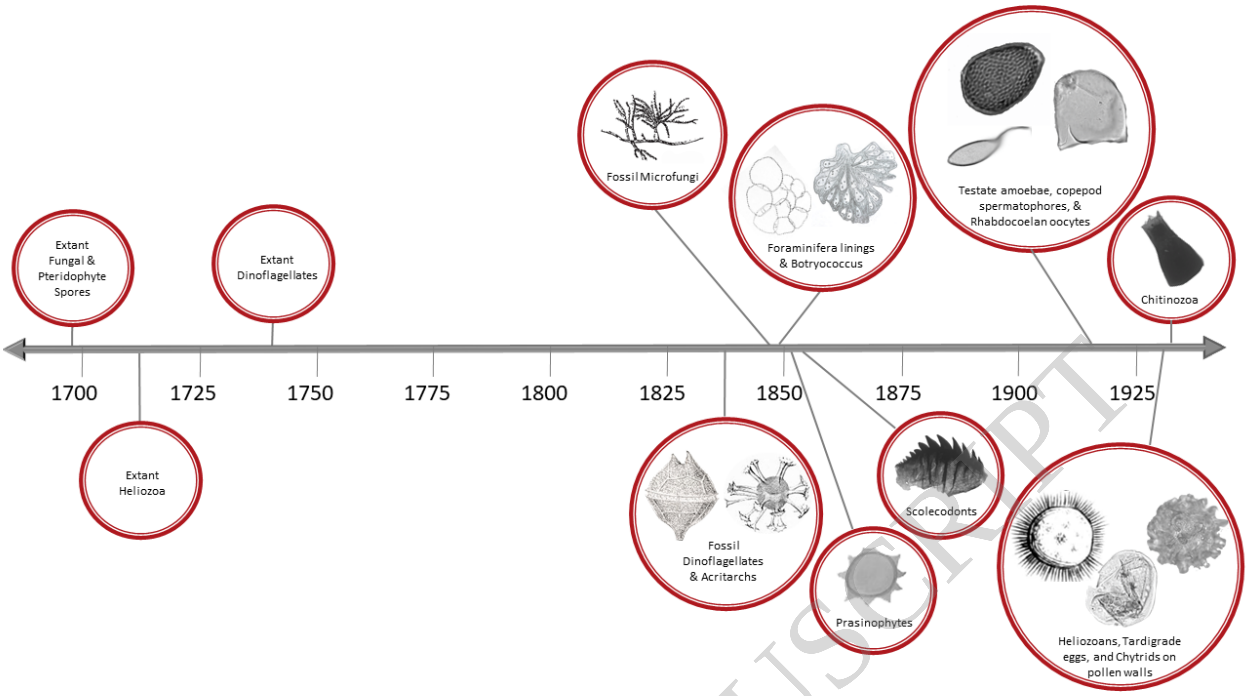
Fossil Microfungi
Foraminifera linings & Botryococcus
Testate amoebae, copepod spermatophores, & Rhabdocoelan oocytes
Chitinozoa
Extant Fungal & Pteridophyte Spores
Extant Dinoflagellates
1700
1725
1750
1775
1800
1825
1850
1875
1900
1925
Extant Heliozoa
Fossil Dinoflagellates & Acritarchs
Scolecodonts
Prasinophytes
Heliozoans, Tardigrade eggs, and Chytrids on pollen walls

Figure 3

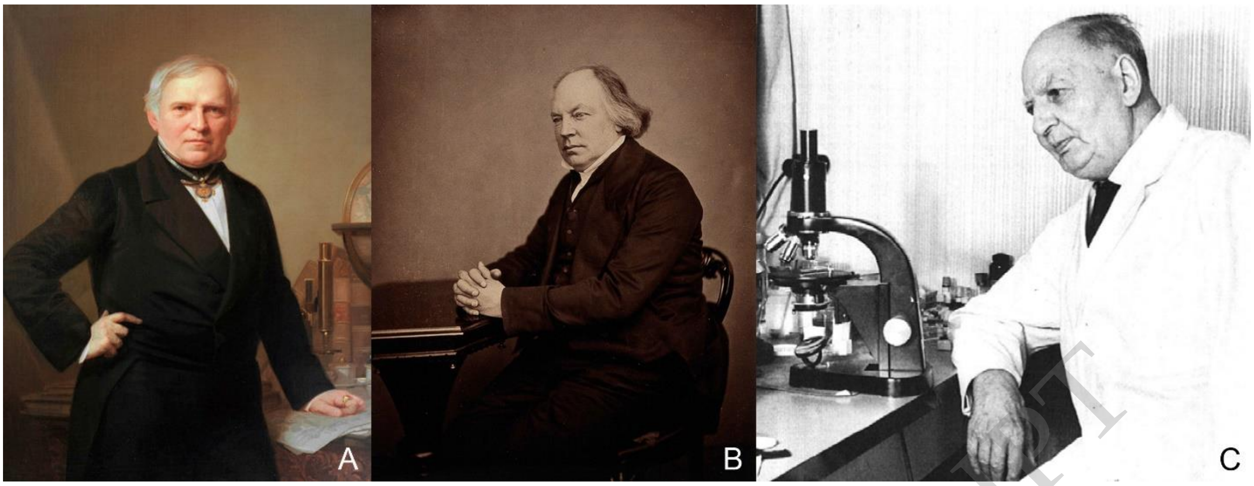

Figure 4

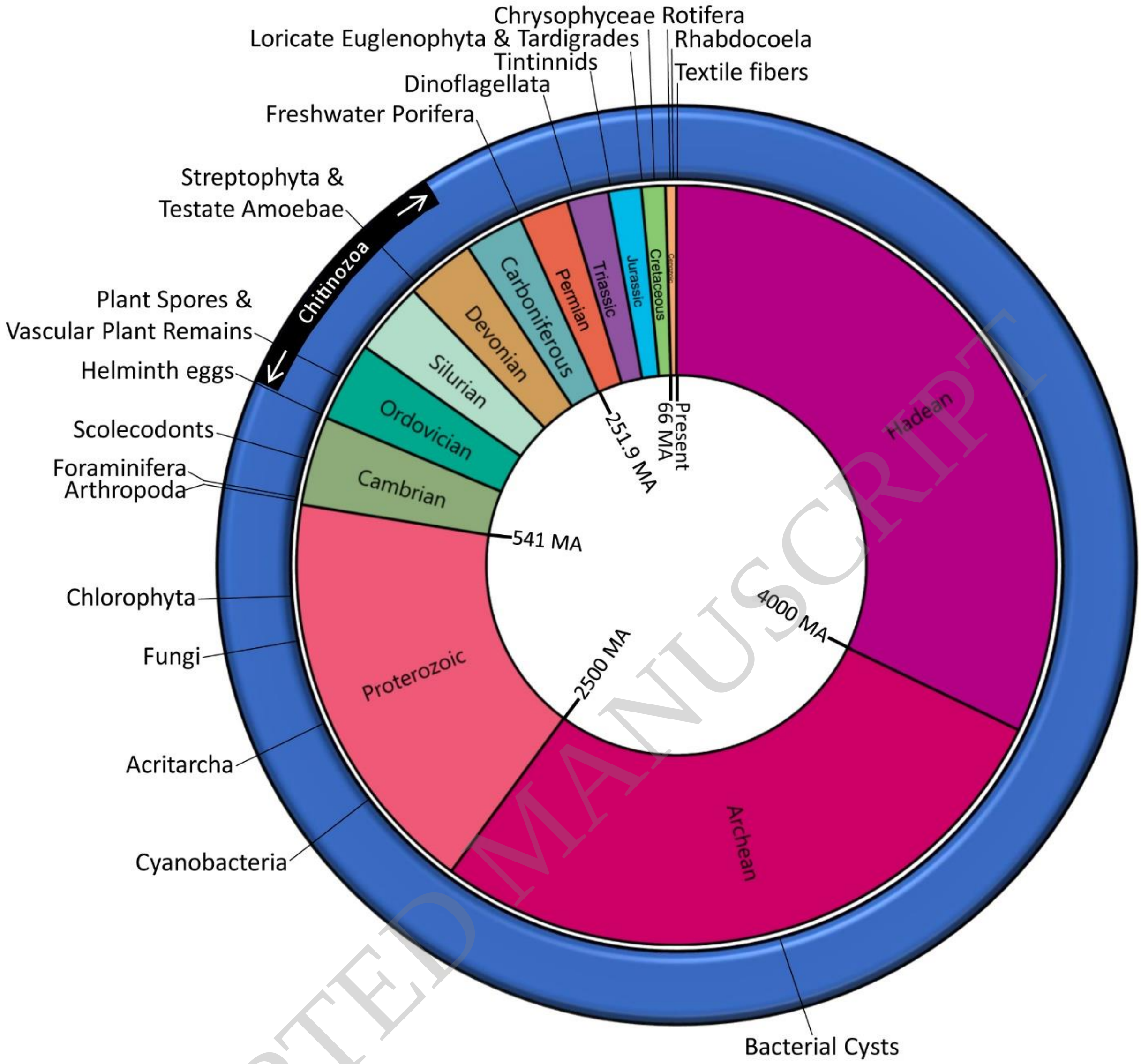
Chrysophyceae
Rotifera
Loricate Euglenophyta
& Tardigrades
Rhabdocoela
Tintinnids
Textile fibers
Dinoflagellata
Freshwater Porifera
Streptophyta &
Testate Amoebae
Chitinozoa
Plant Spores &
Vascular Plant Remains
Helminth eggs
Scolecodonts
Foraminifera
Arthropoda
Chlorophyta
Fungi
Acritarcha
Cyanobacteria
Bacterial Cysts
Hadean
Archean
Proterozoic
Cambrian
Ordovician
Silurian
Devonian
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Present
66 MA
251.9 MA
541 MA
2500 MA
4000 MA

Figure 5