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Pollen and spores: Microscopic keys to understanding the earth's biodiversity

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Abstract. The most distinctive feature of planet Earth is that, unlike any other world in this solar system, it is rich in biodiversity. Our own species, which evolved as part of the biosphere that sustains us, has the intelligence and curiosity to explore the world around us and to understand its complexity. Given the environmental challenges that lie ahead we have much to learn by exploring all aspects of biodiversity. One astonishingly informative field of investigation is palynology, the study of the pollen grains and spores of plants. These microscopic, self-contained biological units are surrounded by chemically resistant cell walls with distinctive structures and symmetry. They can provide insights into such fundamental questions as how and when plants first colonised the land or how the earth's vegetation has developed through geological time and on finer time scales. They provide phylogenetic evidence important in plant systematics and model systems for understanding plant development at the cellular level. This short voyage through the microscopic world of pollen grains and spores is a personal account of the interest and importance of these microscopic keys to understanding the earth's biodiversity.

Key words: biodiversity, palynology, vegetation history, climate change, phylogenetics.

This paper was presented as a plenary lecture intended to introduce the topic palynology at the 2005 International Botanical Congress in Vienna. In this published version it takes the form of an essay which explores the world of pollen grains and spores from the personal perspective of someone who has been fascinated by palynology since the early 1970's. It attempts the over-ambitious task of linking the diversity of the microscopic world of palynology, the focus of my research for over thirty years, to the diversity of life on Earth at a time of unparalleled changes in the global environment. A simpler objective of the paper is to sketch out for the non-specialist some of the principal reasons why the pollen grains and spores of land plants are intrinsically interesting. Several classic books, including those of Wodehouse (1935), Faegri and Iversen (1950), Erdtman (1952), Kremp (1968) and Moore et al. (1991), have done this far more effectively than is possible in a short article. Likewise, several authors have written papers that address the history of palynology and its application to disciplines such as systematic biology (see, for example, Blackmore 2000, Ferguson 2000). To present this short contribution without illustration is a serious omission for a science that is so visual. However, rather than present a necessarily small selection of images I encourage readers unfamiliar with palynology to be inspired by the illustrations in the accompanying articles.

The intrinsic interest of pollen grains and spores derives from a number of distinctive attributes that these independent microscopic plants have in common. These special attributes give the science of palynology the ability to provide significant insights into our understanding of the biodiversity of the extraordinary planet on which we live and how it has changed through geological time.

The presence of life is, as far as we know, a unique and distinctive characteristic of planet Earth. Yet life is not merely present here, it exists in astonishing diversity and abundance (Wilson 1992). The Global Biodiversity Assessment (Heywood and Watson 1995) summarises and synthesises the most comprehensive efforts made to estimate the richness of life in Earth in terms of species level biodiversity. It suggests that about 1.7 million species have so far been described out of an estimated total of 13 million species (for a discussion about such estimates, see Stork 1997, May 1988). From this estimate alone it is clear that our knowledge of the biosphere is still very far from complete despite centuries of exploration and documentation. Our ignorance of the world in which we live is a severe handicap when it comes to dealing with the major environmental challenges facing us in the world today. This stark fact has been recognised in scientific manifestos such as Systematics Agenda 2000 (Anonymous 1994) and in numerous books (see, for example, Diamond 2005; Wilson 2002) and articles (including commentaries of my own, Blackmore (1996, 2002).

Removing our ignorance of the world around us is the goal of fundamental science. Palynology makes an important contribution to that goal. Although the objects of study are microscopic, the issues that palynology can illuminate are large and profound. To illustrate this I will briefly discuss three important questions relating to the biodiversity of our planet. Firstly, when and how did plant life move on to land to create terrestrial ecosystems? Secondly, how have terrestrial ecosystems changed through time to create the vegetation we know today? Thirdly, how has plant life evolved and diversified through time? It is not my intention in this short paper to review the current state of knowledge pertaining to these three questions but rather to illustrate the point that palynology provides ways of answering such questions.

Before addressing these three topics, I will summarise the properties of pollen grains and spores that make them so informative and the historical contributions of three particular scientists who laid the foundations for modern palynology by exploiting these properties.

Why are pollen grains and spores so informative?

The first and most important attribute of pollen grains and spores that makes them informative in so many branches of palynology is the simple fact that they vary in form. This variation is heritable and shows a high level of consistency within a taxon (although, interestingly, a wide range forms can sometimes be encountered at low levels of abundance within a single species, see Pozhidaev 1998). The discovery of this property of pollen grains was made by the British botanist, Nehemiah Grew, in his remarkable book "The Anatomy of Plants" published in 1682. This was a work of great and much wider scientific importance because it described the basis of sexual reproduction in plants for the first time. In comparison to this profoundly important discovery the slight differences in size and shape of the pollen grains or "spermatic globules", as Grew called them, was scarcely remarked upon. Nevertheless, 1682 can be seen as the year in which palynology (as it later became known after being named by Hyde and Adams in 1944) was "discovered".

It took more than a century before the inherent variability of pollen grains came to be exploited scientifically. In 1810, Robert Brown, who had been the botanist on Matthew Flinder's voyage to Australia from 1801 to 1805, made the following observation about the family Proteaceae. “The figure of the Pollen has been attended by a few theoretical, but hardly any practical botanists; yet I am inclined to think, not only from its consideration in this family , but in many others, that it may be consulted with advantage in fixing our notions of the limits of genera” (Brown 1811). Brown noticed that most genera of Proteaceae had triangular pollen grains, whereas a few were spherical and others oblong and bilaterally symmetrical. This was the first example of the form of pollen grains influencing the classification of plants. Subsequently there have been many other examples at a variety of taxonomic levels, a fact perhaps best exemplified by the prolific work and publications of Gunnar Erdtman (Erdtman 1943, 1952, 1957, 1969; Erdtman et al. 1961). The distinction of the highest hierarchical level at which palynological characters have proved important in the recognition of monophyletic groups is probably the definition of the “tricolpate clade” of higher dicotyledons (Doyle and Hotton 1991).

The second important attribute of pollen grains and spores is their resistant outer wall, or exine, which is composed of sporopollenin, a material unrivalled in nature for its resistance to chemical attack. It is, for the most part, this special cell wall that provides the distinctive and characteristic features of pollen grains and spores. Consequently the classic textbooks on palynology contain extensive terminology for describing the surface ornamentation and the cross sectional structure of the exine (for a synthesis, see Punt et al. 1994). This resistance to chemical attack means that exines of pollen grains and spores preserve readily, for example, on a herbarium sheet or in a peat bog. The standard method of preparation by means of acetolysis (Erdtman 1960) involves boiling samples in a mixture of acetic anhydride and concentrated sulphuric acid. This removes all but the highly resistant sporopollenin component of the pollen grain or spore wall and provides an ideal method of preparing reference slides for comparative purposes because it allows the subjects to be viewed in a consistent and repeatable state. Because sporopollenin is so resistant to chemical attack and cannot easily be broken down into its components (Brooks et al. 1971) its precise composition remains elusive despite decades of interest and investigation using a wide variety of approaches (see, for example, Rittscher and Wiermann 1988, Hemsley et al. 1996).

The large numbers in which pollen grains and spores are produced by plants, especially by anemophilous plants, is the third important attribute. A study by Molina et al. (1996) showed ranges of pollen production for individual trees, in the species studied, from just over 1,000 million grains in *Juglans regia* and to more than 500,000 million in *Quercus rotundifolia*. Whilst entomophilous plants produce significantly less pollen per individual it is evident that pollen grains and spores are produced and released into the environment in vast quantities. It is this, together with the other two factors that is exploited in the field of pollen analysis which came just over a century after Brown’s pioneering work in plant classification. In 1917, Lennart von Post, from Sweden, proposed the principles of pollen analysis, setting out how the analysis of the proportions of kinds of pollen preserved in sediments could be interpreted as a “signal” of the vegetation present at the time and place where the sediment was deposited. Pollen analysis is now the largest branch of palynology, in terms of the numbers of practitioners worldwide, and is often used alongside other forms of palaeoecological evidence. A continuing topic of great debate since von Post launched the subject of pollen analysis has been how to translate the proportions of different pollen grains and spores extracted from sediments into an accurate reconstruction of the vegetation that gave rise to them (see, for example, Anderson 1973; Odgaard 1999).

In summary, the diversity of form encountered in pollen grains and spores, their abundance and their capacity for preservation in the fossil record combine to make them highly informative about many aspects of the history of life on Earth. This will now be briefly explored in relation to three topics introduced above.

When and how did plant life move onto land?

The biological conquest of the land was one of the most important chapters in the history of the Earth, marking the extension of the biosphere from the oceans, where life began, onto land and ultimately into the air. It was described by Bateman et al. (1998) as "the terrestrial equivalent of the much-debated Cambrian "explosion" of marine faunas". It might seem surprising to those uninitiated into the science of palynology, but much of the information we have about this great evolutionary leap derives from studies of the fossilised spores of the earliest land plants (for an excellent review, see Wellman and Gray 2000). Perhaps it is less surprising that palynology can inform our understanding of the earliest land plants when one considers that the possession of sporopollenin walls has in itself been considered a key adaptation for life on land, enabling the spores to resist desiccation and perhaps also the effects of ultra violet light (Chaloner 1970, 1976). Sporopollenin is present in some of the algae most closely related to land plants and although in algae it does not form wall layers around cells that are the product of meiosis, as spores are, its presence has been seen as a preadaptation for terrestrial conditions (Blackmore and Barnes 1987).

From the fossil record of dispersed spores it is known that land plants have existed since the Llanvirn (Mid-Ordovician) whereas their megafossil record begins some 40 MY later in the Wenlock (Late Silurian) (Wellman and Gray 2000). The phylogenetic affinities of these earliest land plants can also be determined by reference to their spores (Edwards et al. 2002) which are comparable to those of extant liverworts. Electron microscopy of ultra-thin sections shows that the spore walls show an identical lamellate ultrastructure to that of liverwort spores (Wellman et al. 2003). The developmental mechanism by which bryophytes build up their sporopollenin walls on "white line centred lamellae" arising from the plasma-membrane is similar to the mode of sporopollenin deposition in algae (Blackmore and Barnes 1987) and was considered by Blackmore (1990) to be the plesiomorphic mode of sporopollenin deposition.

As the fossil record becomes richer and megafossils become increasingly abundant a fuller understanding of the early stages of life on land become clear. Our understanding of what Dianne Edwards has aptly and evocatively called the "Lilliputian" world (Edwards 1996) becomes more complete as the foundations of terrestrial ecosystems fall into place. Spores are part of the earliest story of biotic interactions on land, the beginnings of the complex and highly interconnected web of life which we are still exploring and trying to understand today. By the Early Devonian, spores were already an important source of nutrition for terrestrial arthropods (Labandeira 1998) establishing the interactions between plants and animals which have been elaborated in so many ways during the course of subsequent evolution and the diversification of plant and animal biodiversity.

A further consequence of the richer fossil record has been that specialists in the field of early land plant evolution could relate what were previously only known as dispersed spores with the plants that produced them. For example, Wellman et al. (2003) was not only able to associate dispersed spores of *Apiculiretusispora plicata* with sporangia of *Rhynia gwynne-vaughanii* but also to recognise spores in different stages of maturation.

Thus, although there were no human witnesses to the early stages of colonisation of the land it is surprising how much we can learn from spores about the beginnings of the complex terrestrial ecosystems in which our own species later evolved. We ourselves are now part of the web of life and the activities of our species have shaped the biosphere for millennia. This too we can understand through palynology. As Carol Furness (pers. comm.)

points out, there is an irony to the fact that palynology has been a vital tool in the exploration for petroleum reserves by oil industry geologists. Thus the major commercial application of palynology has both underpinned our modern, industrial society and contributed to carbon dioxide emissions and global warming.

How have terrestrial ecosystems changed through time to create the vegetation we know today?

Living, as we do, in a period of unprecedented (at least, during the existence of our species) environmental change there are many reasons to be interested in the past as a way of understanding and anticipating what might happen in the future. Until time travel becomes feasible, palynology provides the best "time machine" we have. The ideas that Von Post introduced have matured into a sophisticated science that enables us to reconstruct the composition of past vegetation within the constraints of being able to identify pollen grains and spores. Pollen and spore identification is possible, in a general way, using the pollen and spore classes of Faegri and Iversen (1950) and to a more precise level by using more detailed keys (such as Moore et al. 1991) or those found in specialist Pollen Floras. Pollen Floras are the counterpart to plant identification manuals based on macro-morphological characters. For many regions their availability is currently limited and this remains the primary constraint on how accurately dispersed pollen grains and spores can be identified. In a history that parallels the documentation of whole plants, the first pollen Floras focussed on European plants (Erdtman et al. 1961, Punt and Clarke 1974) but examples now exist for countries around the world including Taiwan (Huang 1972), Qatar (El Ghazaly 1991) and China (Wang et al. 1995).

General accounts of the techniques needed to collect sediment samples in the field, extract the preserved pollen grains and spores and to reconstruct pollen diagrams from preserved pollen spectra are described in several textbooks (including Faegri and Iversen 1950 and Moore et al. 1991). An extensive literature exists on the interpretation of pollen diagrams and what this tells us about regional palaeoecology (see, for example, Goodwin 1975, Birks and Birks 1980). Such is the level of information available for some geographical regions, notably northern Europe which has been the subject of many studies, that detailed maps can be drawn showing the past and present distribution of plant species (Huntley and Birks 1983). The influence of our own species, which replies upon the exploitation of plants for food, fuel and fodder for livestock can readily be detected in Quaternary pollen diagrams. The appearance of pollen from crop plants, "weedy" species associated with cultivation and the clearance of forest can all be easily detected and interpreted as the hand of man shaping the landscape around him (see, for example, Behre 1986). Despite this knowledge, there seems to be an innate human tendency to imagine that large parts of the world are more or less natural except where we have converted the pre-existing vegetation into cultivated field systems or urban landscapes. A better perspective, because it might make us feel more responsibly engaged with the planet, would to be recognise that since the earliest evolution of our ancestors, our species has been shaping the world around us, sometimes through the most subtle manipulation of the elements of biodiversity (Blackmore 2001, Blackmore and Paterson 2005). Seen on the longer timescale that palynology can provide, the rise and fall of human civilisations can be put in perspective as the example of the Chinese Loess Plateau shows (An et al. 2004).

Whilst we can read our own history in pollen diagrams, preserved pollen grains and spores have long been recognised to be important indicators of past climatic conditions. Initially the interpretation of climate from palynological evidence related to particular species taken to be indicators of certain prevailing conditions (see for example, Iversen 1944). More sophisticated approaches have since developed based on modelling correlations between plant distribution and climatic conditions (Huntley 1993). These work well for the Quaternary, when it can reasonably assumed that the pollen and spores encountered represent the species that occur today and that their requirements and preferences for growth have not changed. Large scale, regional analyses have been developed following the introduction of the concept of "pollen biomes" by Prentice et al. (1996). Pollen grains and macrofossils are assigned to "plant functional types" and these can be attributed to the biomes with which they have the highest affinity. A distinct advantage of the method is that it can interpret pollen spectra, combinations of pollen types, that are not present in modern vegetation types. The approach has been applied on a regional level, for example in China (Yu et al. 1998) to integrate the results from large numbers of separate individual studies. Further back in geological time, for example in the Tertiary, methodologies such as the "coexistence method" of Mosbrugger and Utescher (1997) use databases of more than 800 Tertiary plant taxa, their nearest living relatives and the climatic requirements of those relatives.

Frequently, evidence from pollen analysis is coupled with other sources of palaeoecological information to build up a detailed understanding of changing vegetation and climate through time. Not only does this give us valuable insights into the past but it is also increasingly being used to anticipate the changes that can be expected in a greenhouse world. Of course, changing climate also has direct effects on the seasonal release of pollen grains, providing a short-term means of observing and monitoring climate change (see, for example, Newnham 1999).

How has plant life evolved and diversified through time?

Besides elucidating the pattern of important past changes in the vegetation and climate of the biosphere, palynology provides important insights into the phylogenetic pattern of evolution of plants through time. A large body of literature has built up on the contribution of palynology to phylogenetic systematics. The classic textbook of Erdtman (1952) provides the widest sample of angiosperm diversity in a single volume. Important papers on palynology and angiosperm phylogeny include those of Van Campo (1976) and Walker and Doyle (1975). A succession of proceedings from specialised conferences has enriched the literature: Ferguson and Muller (1976); Blackmore and Ferguson (1986), Hesse and Ehrendorfer (1990), Blackmore and Barnes (1991), Harley et al. (2000) and the present volume. Although much remains to be done, a significant proportion of all land plants have now been investigated in terms of their pollen and spore morphology and its phylogenetic significance.

Furthermore, a large number of developmental studies have contributed to an understanding of the origins of the characteristic morphological features of pollen grains and spores. This makes it possible to develop predictive developmental models that explain the origin of features such as pollen dispersal in permanent tetrads (Blackmore and Crane 1988). Characters such as aperture numbers and symmetry, that Robert Brown had observed in the Proteaceae in 1811 can potentially be understood in terms of their development. The bilaterally symmetrical diporate pollen of *Dryandra*, for example, forms as a result of successive meiotic division in which a dyad wall develops between the first and second nuclear divisions of meiosis (Blackmore and Thiele 1988). In most members of the Proteaceae, including the triporate *Grevillea*, meiosis is simultaneous so that both nuclear divisions are completed before the cytoplasm is partitioned into four daughter cells and there is no dyad stage (Blackmore and Barnes 1995). As early as 1935, Wodehouse had appreciated the power of ontogeny to analyse and explain features such as the overall symmetry and polarity of pollen grains. However, because he only distinguished between two modes of meiotic division he considered that there were too many exceptions for a general relationship between meiosis and aperture number to be established. In fact such a relationship does exist but several other variables in the process of meiosis are also involved including not just the relative timing of cytoplasmic partitioning but also the mode of wall formation (whether by centripetal furrowing or centrifugal cell plates) and whether or not there is an interaction between the microtubules of the spindle to form "supplementary" spindles (Blackmore and Crane 1995). Interestingly, meiosis in the anthers of Proteaceae is very unusual in that the partitioning of the cytoplasm between daughter cells is by centrifugal cell plates and not by constriction furrows as in the majority of higher dicots. When meiosis is simultaneous this gives rise to tetrads arranged according to what Erdtman (1969) called "Garside's Rule" in which the apertures develop in groups of three at four points in the tetrad system. The places where these apertures form correspond to the last points of shared connection between the cytoplasm of the four daughter cells. In diporate pollen of *Dryandra* the apertures also form at the last points of connection between the cytoplasm of daughter cells but the formation of the cell wall at the start of the dyad stage restricts the number of points of contact to just eight per tetrad. Erdtman (1969) contrasted the Garside's Rule tetrads of triaperturate Proteaceae pollen with those of most higher dicots which follow "Fischer's Rule" in having tetrads formed by simultaneous cytokinesis with the apertures forming in pairs at six points within the tetrad. What remains unknown is whether any other higher dicot families share the distinctive pattern of cytokinesis found in Proteaceae or whether it is an autapomorphy of the family.

Although the processes underlying pollen and spore symmetry and aperture formation are now quite well understood much less is known about the patterning of the pollen wall itself. What is clear, however, is that once again developmental insights are likely to provide the route to understanding the processes involved in generating characteristic patterns of pollen or spore wall structure and ornamentation. In recent years, the importance of self-assembly during pollen and spore wall formation has been recognised (van Uffelen 1991; Hemsley et al. 2000; Gabarayeva and Hemsley, in press; Hemsley and Gabarayeva, this volume). This new insight enables us to begin to understand the development of the extraordinarily diverse and seemingly endless variety of surface patterns encountered in pollen grains and spores. The patterning, it is becoming clear, originates during development in response to the subtle variations of the conditions within the plasmamembrane glycocalyx. What is not yet clear is whether these variations are precisely determined at a genetic level or not.

Conclusions

I have sketched out the ways in which palynology can provide insights into biodiversity, addressing questions ranging from the origins of terrestrial ecosystems, through to vegetation history, climate change and phylogenetics. Pollen grains and spores do provide keys to understanding such fundamentally important questions but much more remains to be done. Documenting the diversity of pollen and spore morphology remains a highly important task not just because it adds to phylogenetic studies but because it also contributes to more precision in the identification of dispersed pollen grains and spores. This in turn can contribute to improvements in our ability to reconstruct past vegetation and interpret climate change. If contemplating the microcosm of palynology helps to open our eyes to the world around us, even if at the purely aesthetic level (Kesseler and Harley 2004), and guides our actions towards more responsible ways of interacting with the biosphere then it is much more than a narrow, reductionist field of biology. The case of the people of Easter Island who destroyed the finite natural resources of their island world was revealed through palynology (Flenley and King 1984). That example and others inspired Jared Diamond (2005) to set out twelve sets of problems which must be overcome if we humans are to secure a sustainable future for the benefit of future generations. Perhaps it is not so strange that a better sense of our place in the universe can come from looking into the microscopic world of pollen grains and spores.

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References

An C., Feng Z., Tang L. (2004) Environmental change and cultural response between 8000 and 4000 cal. Yr BP in the western Loess Plateau, northwest China. J. Quat. Sci. 19: 529–535.

Andersen S. T. (1973) The differential pollen productivity of trees and its significance for the interpretation of a pollen diagram from a forested region. In: Birks H. J. B., West R. G. (eds.) Quaternary Plant Ecology. The 14th Symposium of the British Ecological Society, University of Cambridge, 28–20 March 1972. Blackwell Scientific Publishers, Oxford, pp. 109–105.

Anonymous (1994) Systematics Agenda 2000. American Society of Plant Taxonomists, Society of Systematic Biologists, Willi Hennig Society and Association of Systematics Collections, New York.

Bateman R. M., Crane P. R., DiMichelle W. A., Kenrick P. R., Rowe N. P., Speck T., Stein W. E. (1998) Early evolution of land plants: phylogeny, physiology and ecology of the primary terrestrial radiation. Annual Rev. Ecol. Syst. 29: 263–292.

Behre K.-E. (1986) Anthropogenic indicators in pollen diagrams. A. A. Balkema, Rotterdam.

Birks H. J. B., Birks H. H. (1980) Quaternary Palaeoecology. Edward Arnold, London.

Blackmore S. (1996) Knowing the Earth's biodiversity: challenges for the infrastructure of systematic biology. Science 274: 63–64.

Blackmore S. (1990) Sporoderm homologies and morphogenesis in land plants, with a discussion of *Echinops sphaerocephala* (Compositae). Pl. Syst. Evol. (Suppl. 5): 112.

Blackmore S. (2000) The palynological compass: the contribution of palynology to systematics. In: Nordenstam B., El Ghazaly G., Kassas M. (eds.) Plant systematics for the 21st century. Portland Press, London, pp. 161–177.

Blackmore S. (2001) All the world's a garden. Horticulturist 10: 13–16.

Blackmore S. (2002) Biodiversity update: progress in taxonomy. Science 298: 365.

Blackmore S., Barnes S. H. (1987) Embryophyte spore walls: origin, development and homologies. Cladistics 3: 185–195.

Blackmore S., Barnes S. H. (1991) (eds.) Pollen and spores: patterns of diversification. Systematics Association Special Volume Series, Oxford University Press.

Blackmore S., Barnes S. H. (1995) Garside's rule and the microspore tetrads of *Grevillea rosmarinifolia* A. Cunn. and *Dryandra polycephala* Benth. (Proteaceae). Rev. Palaeobot. Palynol. 85: 111–121.

Blackmore S., Crane P. R. (1988) Systematic implications of pollen and spore ontogeny. In: Humphries C. J. (ed.) Ontogeny and systematics. Columbia University Press, New York, pp. 83–115.

Blackmore S., Ferguson I. K. (1986) (eds.) Pollen and spores: form and function. Academic Press, London.

Blackmore S., Paterson D. S. (2005) Gardening the Earth – the contribution of botanic gardens to plant conservation and habitat restoration. In: Leadley E., Jury S. L. (eds.) Taxonomy and plant conservation. Cambridge University Press, pp. 266–273.

Blackmore S., Thiele K. (1988) Successive cytokinesis during microsporogenesis in the Proteaceae. Pollination '88: 47–49, University of Melbourne.

Brooks J., Grant P. R., Muir M., Van Gijzel P., Shaw G. (1971) Sporopollenin. Academic Press, London, New York.

Brown R. (1811) On the Proteaceae of Jussieu. Trans. Linn. Soc. Lond. 18: 36–64.

Chaloner W. G. (1970) The rise of the first land plants. Biol. Rev. 45: 353–377.

Chaloner W. G. (1976) The evolution of adaptive features in fossil exines. In: Ferguson I. K., Muller J. (eds.) The evolutionary significance of the exine. Academic Press, London, pp. 1–14.

Diamond J. (2005) Collapse: how societies choose to fail or survive. Penguin, London.

Doyle J. A., Hotton C. L. (1991) Diversification of early angiosperm pollen in a cladistic context. In: Blackmore S., Barnes S. H. (eds.) Pollen and spores: patterns of diversification. Clarendon Press, Oxford, pp. 69–195.

Edwards D. (1996) New insights into early land ecosystems: a glimpse of a Lilliputian world. Rev. Palaeobot. Palynol. 90: 159–174.

Edwards D., Duckett J. G., Richardson J. B. (2002) Hepatic characters in the earliest land plants. Nature 374: 635–636.

El Ghazaly G. A. (1991) Pollen flora of Qatar. University of Qatar.

Erdtman G. (1943) An introduction to pollen analysis. Waltham, Mass.

Erdtman G. (1952) Pollen morphology and plant taxonomy. Angiosperms. Almqvist and Wiksell, Stockholm.

Erdtman G. (1957) Pollen and spore morphology. Plant taxonomy. Gymnospermae, pteridophyta, bryophyta. Almquist and Wiksell, Stockholm.

Erdtman G. (1960) The acetolysis method, a revised description. Svensk Bot. Tidskr. 54: 561–564.

Erdtman G. (1969) Handbook of palynology - an introduction to the study of pollen grains and spores. Munksgaard, Copenhagen.

Erdtman G., Berglund B., Praglowski J. (1961) An introduction to a Scandinavian pollen flora. Almqvist and Wiksell, Stockholm.

Faegri K., Iversen J. (1950) Textbook of modern pollen analysis. Munksgaard. Copenhagen.

Ferguson I. K. (2000) Pollen-morphological data in systematics and evolution: past, present and future. In: Nordenstam B., El Ghazaly G., Kassas M. (eds.) Plant systematics for the 21st century. Portland Press, London, pp. 179–192.

Ferguson I. K., Muller J. (1976) (eds.) The evolutionary significance of the exine. Academic Press, London New York.

Flenley J. R., King S. M. (1984) Late Quaternary pollen records from Easter Island. Nature 307: 47–50.

Gabarayeva N. I., Hemsley A. R. (2006) Merging Concepts: the role of self-assembly in the development of pollen wall structure. Rev. Palaeob. Palynol. (in press).

Goodwin H. (1975) The history of the British flora, 2nd edn. Cambridge University Press, Cambridge.

Grew N. (1682) The anatomy of plants. Rawlins, London.

Harley M. M., Morton C. M., Blackmore S. (2000) (eds.) Pollen and spores: morphology and biology. Royal Botanic Gardens, Kew.

Hemsley A. R., Collinson M. E., Vicent B., Griffiths P. C., Jenkins P. D. (2000) Self-assembly of colloidal units in exine development. In: Harley M. M., Morton C. M., Blackmore S. (eds.) Pollen and spores: morphology and biology. Royal Botanic Gardens, Kew, pp. 31–44.

Hemsley A. R., Gabarayeva N. I. (2006) Exine development: the importance of looking through a colloid chemistry "window". Pl. Syst. Evol. (this issue).

Hemsley A. R., Scott A. C., Barrie P. J., Chaloner W. G. (1996). Studies of fossil and modern spore wall biomolecules using ^{13}C solid state NMR. Ann. Bot. 78: 83–94.

Hesse M., Ehrendorfer F. (1990) Morphology, development and systematic relevance of pollen and spores. Pl. Syst. Evol. Supplement 5.

Heywood V. H., Watson R. T. (1995) (eds.) Global biodiversity assessment. Cambridge University Press, Cambridge.

Huang T. C. (1972) The pollen flora of Taiwan. National Taiwan University, Taipei.

Huntley B. (1993) The use of climatic response surfaces to reconstruct palaeoclimate from Quaternary pollen and plant macrofossil data. Phil. Trans. Roy. Soc. London, B. 341: 215–223.

Huntley B., Birks H. J. B. (1983) An atlas of past and present pollen maps for Europe. 0 – 13,000 years ago. Cambridge University Press.

Hyde H. A., Adams D. A. (1944) The right word. Pollen Science Circular 8: 6.

Iversen J. (1944) *Viscum*, *Hedera* and *Ilex* as climate indicators. A contribution to the study of the Post-Glacial temperature and climate. Geol. fören. Stockh. förh. 66: 463–483.

Kesseler R., Harley M. (2004) Pollen. The hidden sexuality of flowers. Papadakis Publisher, London.

Kremp G. O. W. (1968) Morphologic encyclopedia of palynology. 2nd edn. Univ. Arizona Press, Tucson.

Labandeira C. C. (1998) Early history of arthropod and vascular plant associations. Ann. Rev. Earth Planet. Sci. 26: 329–377.

May R. M. (1988) How many species are there on Earth. Science 241: 1441–1449.

Molina R. T., Rodriguez A. M., Palacios I. S., Lopez F. G. (1996) Pollen production in anemophilous trees. Grana 35: 38–46.

Moore P. D., Webb J. A., Collinson M. (1991) Pollen analysis. Blackwell, London.

Mosbrugger V., Utescher T. (1997) The coexistence approach – a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using fossil plants. Palaeogeography, Palaeoclimatology, Palaeoecology 134: 61–86.

Newnham R. M. (1999) Monitoring biogeographical responses to climate change: the potential role of aeropalynology. Aerobiologia 15: 87–94.

Odgaard B. V. (1999) Fossil pollen as a record of past biodiversity. J. Biogeogr. 26: 7–17.

Pozhidaev A. E. (1998) Hypothetical way of pollen aperture patterning. I. Formation of 3-colpate patterns and endoaperture geometry. Rev. Palaeobot. Palynol. 104: 67–83.

Prentice C., Guiot J., Huntley B., Jolly D., Cheddadi R. (1996) Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. Climate Dynamics 12: 185–193.

Punt W., Clarke G. C. S. (1974) The Northwest European pollen flora. Elsevier, Amsterdam.

Punt W., Blackmore S., Nilsson S., Le Thomas A. (1994) Glossary of pollen and spore terminology. LPP Contribution Series 1, LPP Foundation, Utrecht.

Rittscher M., Wiermann R. (1988) Studies on sporopollenin biosynthesis in *Tulipa* anthers. II. Incorporation of precursors and degradation of the radiolabelled polymer. Sexual Plant Reproduction 1: 132–139.

Stork N. E. (1997) Measuring global biodiversity and its decline. In: Reaka-Kudla M., Wilson D. E., Wilson E. O. (eds.) Biodiversity II. Joseph Henry Press, Washington, DC, pp. 41–68.

Van Campo M. (1976) Patterns of pollen morphological variation within taxa. In: Ferguson I. K., Muller J. (eds.) The evolutionary significance of the exine. Academic Press, London, pp. 125–135.

Van Uffelen G. A. (1991) The control of spore wall formation. In: Blackmore S., Barnes S. H. (eds.) Pollen and spores: patterns of diversification. Clarendon Press, Oxford, pp. 89–102.

Von Post L. (1917) Om skogstradpollen i sydsvenska tormfmosselagerfolker. Geol. fören. Stockh. förh. 38: 384–394.

Walker J. W., Doyle J. A. (1975) The bases of angiosperm phylogeny: palynology. Ann. Missouri. Bot. Gard. 62: 644–723.

Wang F., Chien N., Zhang Y., Yang H. (1995) Pollen flora of China. Science Press, Beijing.

Wellman C. H., Gray J. (2000) The microfossil record of early land plants. Phil. Trans. Roy. Soc. 355: 717–732.

Wellman C. H., Osterloff P. L., Mohiuddin U. (2003) Fragments of the earliest land plants. Nature 425: 282–285.

Wilson E. O. (1992) The diversity of life. Penguin, London.

Wilson E. O. (2002) The future of life. Alfred A. Knopf, New York.

Wodehouse R. P. (1935) Pollen grains. Their structure, identification and significance in science and medicine. 1st edn. McGraw-Hill, London.

Yu G., Prentice C., Harrison S. P., Sun X. (1998) Pollen-based biome reconstructions for China at 0 and 6000 years. J. Biogeogr. 25: 1055–1069.

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