



ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 180 (2002) 129–146

PALAEO

www.elsevier.com/locate/palaeo

Population-based analysis and graphic interpretation of fossil palynomorph records from Palynodata: taxonomic and biostratigraphic implications

James M. White^{a,*}, Chris M. Jessop^b

^a *Natural Resources Canada, Geological Survey of Canada, Calgary, 3303 33rd St. NW, Calgary, AB, Canada T2L 2A7*

^b *Jessop Scientific Software, 31 Range Gardens NW, Calgary, AB, Canada T3G 2H1*

Received 19 February 2001; received in revised form 31 July 2001; accepted 11 October 2001

Abstract

Palynodata is a comprehensive database of the occurrences of pre-Quaternary palynomorphs, encompassing over 20 000 publications. Taxa are assumed to have distributions in time and space which are localized to a region around a central point, and, in the idealized case, can be visualized as a bell-shaped curve. A palynological study can be imagined as drawing a sample from each taxon's time/space distribution. The probability of recording any taxon is partly a function of its abundance at the sampled point in the distribution. A comprehensive database such as Palynodata should allow approximation of the underlying population distribution of the taxon. Retrievals show that useful information is recovered from Palynodata, although there are errors and inadequacies in the database, of which the chief is the generalized study locality record. A computer program, Palynoplot, produces graphic plots of retrievals from Palynodata, allowing improved recognition of the patterns and problems in the database. Images of the database may have future applications for palynological taxonomy, paleoclimatology, paleoecology, modelling of palynomorph distributions, and possibly plate tectonic reconstruction. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Palynodata; databases; palynology; palynomorphs; biostratigraphy; paleontology

1. Introduction

During the last two and a half centuries, the geological and paleontological insights of many workers, such as Smith, Cuvier, Lyell, Deshayes, d'Orbigny and Opper (Mallory and Johnson, 1992), have shown that, through geological time, a characteristic pattern for a species is origination,

rise to abundance, and decline to extinction. In the 18th century, the modern systematic classification of plants was pioneered by Linnaeus (Steere, 1992) and his system was subsequently applied broadly by natural historians during the great age of exploration. More than two centuries of global collection and systematic classification have shown that plants have geographically definable distributions at species, genus and family level (e.g. Heywood, 1978; Hora, 1980). From Lyell's uniformitarian principle (Mallory and Johnson, 1992), we expect these patterns to hold for fossil plants, and detailed syntheses have dem-

* Corresponding author. Fax: +1-403-292-7085.

E-mail addresses: jwhite@nrcan.gc.ca (J.M. White), jscisof@cadvision.com (C.M. Jessop).

onstrated such paleobiogeographic patterns (e.g. Herngreen and Chlonova, 1981; Herngreen et al., 1996; Srivastava, 1994). Here we discuss development of a method for rapidly depicting the chronological and paleogeographic patterns of fossil pollen, spores, dinoflagellates and acritarchs (collectively known as palynomorphs) using graphic presentations of a palynological database.

Palynomorphs are plant fossils, widely disseminated in sedimentary rocks. The utility of palynomorphs as biostratigraphic tools has resulted in a wealth of literature that has been captured in Palynodata¹. This palynological database houses a digital record of occurrences of 112 000 formal and informal palynomorph taxa from about 20 000 published works, representing nearly 1000 general localities around the globe (Fig. 1). Palynodata Inc. has built this impressive database of fossil palynomorph occurrences since the inception of the project by Gerhard Kremp in 1966. The project has been supported by a consortium of oil companies and scientific institutions (see discussion in Lentin et al., 1996), including the Geological Survey of Canada, which has been a member of the Palynodata consortium since 1974. Palynodata is now maintained by PalyEast for the Palynodata consortium (K. Piel, personal communication, 2000). The recent availability of compact disks and powerful personal computers permits convenient dissemination of the Palynodata database.

To date, the Palynodata database has been used

¹ PALYNODATA, Inc. provides licences to the datafile of palynological literature begun by Gerhard Kremp in 1968, along with annual updates (400–800 documents). The main components of the data are the stratigraphic and geographic occurrences of over 12 000 generic and suprageneric entities and 86 000 formal species, or nearly 112 000 including informal species, from more than 20 000 publications. Also included are the reference information for each document and, when provided by the author, taxonomic information, subspecies and lithostratigraphic data. This information comprises well over one million records. The database is now maintained by Palyeast, Halifax, NS, Canada. There is a fee for the licences. Anyone wishing details on licensing and obtaining the datafile should contact Kenneth M. Piel, 53 Eton Street, Springfield, MA 01108-2838, USA; tel.: +1-413-746-6931, fax: +1-413-746-9311, E-mail: kenpiel@mmel.com (K. Piel, personal communication, 19 October 2000).

largely as a comprehensive source of literature references, synonymies and ages for palynomorphs, instrumental for developing such reference works as *Acritarchs and fossil prasinophytes: an index to genera, species and infraspecific taxa* (Fensome et al., 1990) and for studies of diversity and radiation (MacRae et al., 1996). Depending on the search, Palynodata output can number hundreds to thousands of records. It is difficult to comprehend patterns in long lists of occurrences.

We propose a new model for understanding the nature of the database and show the potential for graphic display and analysis of the data. This allows rapid data interpretation and shows that Palynodata can be an unparalleled source of insights into biostratigraphic and paleogeographic patterns (White, 2000a,b). In the future, it may even elucidate patterns in fields as diverse as paleoclimatology and plate tectonics because climate and tectonics are both recognized as important variables in determining biogeographic patterns (e.g. Srivastava, 1994; White et al., 1997, 1999).

2. Model

Biostratigraphers are often frustrated that indicator species may not occur where they are expected, even within their known biostratigraphic and paleogeographic ranges. Paleoenvironment, paleoclimate and randomness can legitimately be invoked as explanations, but the underlying population distributions must also be considered.

Applying the insights of pioneer paleontologists and biogeographers, we can imagine the ideal distribution of a fossil population as shown in Fig. 2. For any taxon, its joint stratigraphic and paleogeographic distributions can be visualized as a joint probability density function similar to a bell-shaped distribution, where x and y axes represent space and time, and z represents abundance of a taxon. A palynological study is essentially a sample drawn from that underlying distribution. At the center of the distribution, where the taxon is most abundant, it is much more likely to be encountered than at the margins of the distribution. Thus, each palynological study is effectively

FOSSIL LOCATIONS FROM PALYNODATA, V. 5

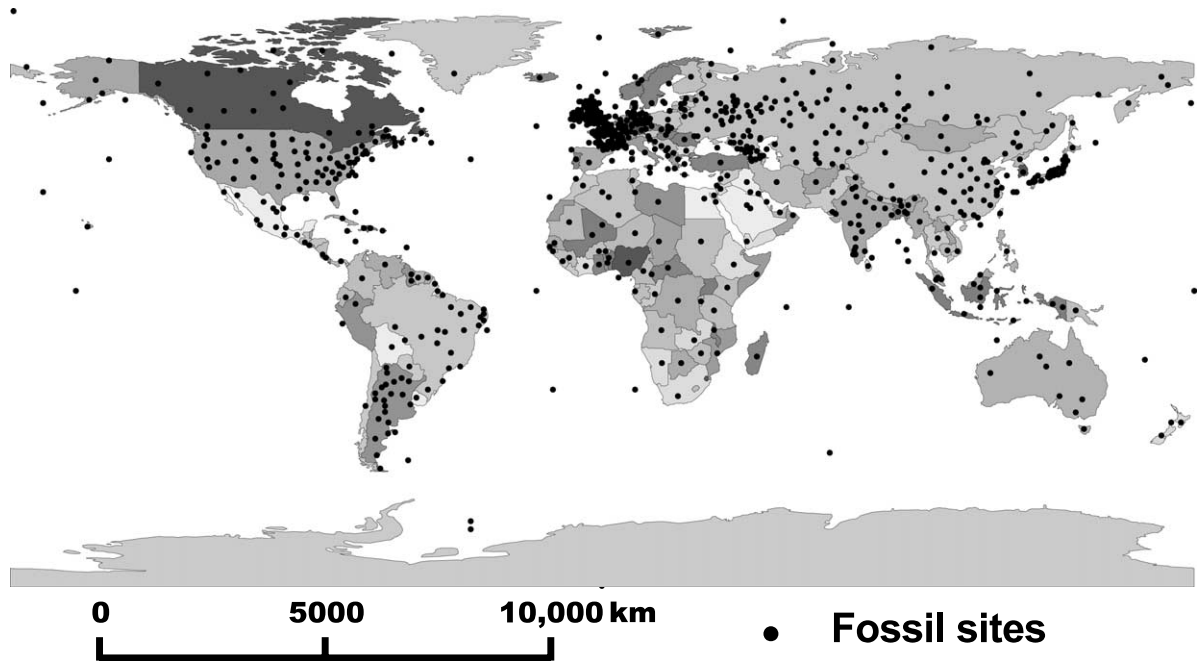


Fig. 1. The global distribution of 975 general palynological study localities recorded in Palynodata v.5.0, using geographic coordinates from the provisional locality file.

a probe of the shape of that distribution. A retrieval from a comprehensive database, such as Palynodata, should allow an approximation of the distribution of a taxon in time and space. Using the binning and plotting techniques described here and implemented by an in-house computer program, Palynoplot² (written in Perl), Palynodata retrievals can be viewed graphically. This allows rapid recognition of the main features of distributions. Graphic representations should have shapes that we would expect to be unimodal unless other factors, such as paleoclimate, intra-specific competition, or taxonomy, affect the shape of the distributions.

There are flaws in the input data and we discuss them below. Despite those flaws, we contend that

² In previous oral presentations and abstracts (White 2000a,b) the name 'Palyplot' was used. We have changed the name of our software to 'Palynoplot' to avoid confusion with palynological software released in the early 1990s by C. Chumbley.

retrievals from Palynodata can be useful approximations of the underlying distributions of fossil taxa, when interpreted with several caveats. Graphical presentation of retrievals, by the method shown here, can help to identify data flaws.

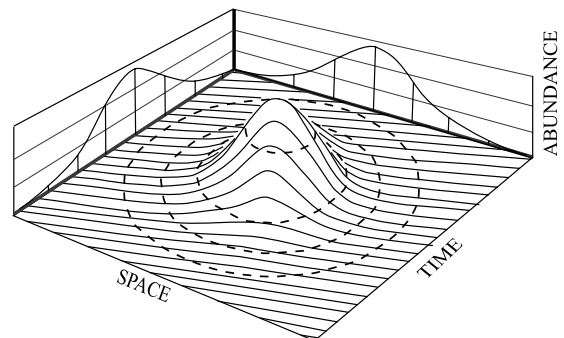


Fig. 2. For any taxon, its ideal distribution can be visualized as a bell-shaped dome, where x represents space, y time, and z represents abundance in the landscape. Thus a probe at the center of its distribution would be more likely to encounter a given fossil than a probe at the margins of its distribution.

We present this technique by describing the relationship between the underlying distribution of the fossils (c in the notation below) and their retrieval through Palynodata (c'), for which the formal mathematical description follows under 2.2. Mathematical description and 2.3. Binning options and selections. Intuitive explanations are given for the variables, under 2.1. Explanation of variables and a verbal description of the technique is found under 3. Practical method and caveats.

2.1. Explanation of variables

- T is a set of geological times
 L is a set of geological positions
 $c(t,l)$ is a fine-grained (high-resolution) distribution of a fossil in time and space, and expresses its occurrence as presence/absence at any point in time/space (the domain); geographic coordinates of a fossil are reduced to only one variable, ' l ' (see discussion of w , below)
 $\rho(t,l)$ is the density of the distribution c in time/space. Density is the number of occurrences in a unit volume
 \mathcal{R}^3 represents a three-dimensional real space (time–space (representing time, latitude, longitude))
 w is a weighting kernel (function) which allows the density to be derived from the distribution. In effect, w defines the bin size. w can be used to reduce the domain from \mathcal{R}^3 to \mathcal{R}^2 , in effect by summing over all longitudes for each latitudinal band. In practice, w can be allowed to vary slowly with the central position in question (t,l), thus we can write $w(t,t',l,l')$ as $w_{t,l}(t-t',l-l')$ or $w_j(t_j-l_j, l_j-l)$
 c' is the distribution of Palynodata records in the same way that c is the distribution of the taxon. c' has less detail than c . Each record has a non-infinitesimal width in c' . Whereas in the c distribution a fossil is a point, in c' each record has a time range and a position range, e.g. the Barremian in Alberta.
 $\chi(t,l)$ is the density function of the Palynodata records, produced by summing over c' . χ is the product of ρ and q , which is an interest factor (below)
 q is a measure of the relative interest in a location, e.g. more palynologists have studied Europe than Africa, and so χ will be much higher in the European cells than the African cells. Interest may be driven by the presence of hydrocarbons, or an abundance of graduate students. q may or may not be independent of the taxon under consideration
 j is an index of the node on the grid used to represent real space

ρ and χ are followed (below) by standard equa-

tions which convert occurrence functions to density functions by dividing the sum of records in any bin by the bin size.

2.2. Mathematical description

If we define T and L to be the (closed) sets of geological times and of geological positions then an element $(t,l) \in \mathcal{R}^3$ where $t \in T$ and $l \in L$. Typically we may choose the representation of l to be a latitude–longitude pair. A specific taxon, or collection of taxa, can be described using the existence function $c(t,l)$. c is a fine-grained function that has the form of a Dirac-delta function with a finite value where a taxon exists in the geological record and a value of zero where that taxon is absent. Being fine-grained, it has a structure, large variations and possibly a lack of smoothness, that is evident only on very small scales.

However, we may want to consider a smooth density function:

$$\rho(t,l) = \frac{\int_{L,T} c(t',l') w(t-t',l-l') dt' dl'}{\int_{L,T} w(t-t',l-l') dt' dl'} \quad (1)$$

where $w(t,l)$ has sufficient smoothness and locality, but has wide locality compared to the graininess of c . Here smoothness is measured by the number of derivatives that have no jumps. Locality is a measure of the size of the domain (region) which is not zero. w can also be used to reduce the domain from \mathcal{R}^3 to \mathcal{R}^2 , because we expect the distribution of a taxon to vary strongly with latitude, but only weakly with longitude. Unlike c , ρ is continuous and smooth.

We can also consider the set of Palynodata database records for a taxon as an existence function c' . If each entry is a point in \mathcal{R}^3 (or \mathcal{R}^2) then it too looks like a sum of Dirac-delta functions. However, each record spans a temporal range (period, epoch, age) and a geographical range ('Europe', 'Brazil'). Whether we represent each geographical name as a position, or a complete two-dimensional range, we can build a density function of studies:

$$\chi(t, l) = \frac{\int_{L,T} c'(t', l') w'(t-t', l-l') dt' dl'}{\int_{L,T} w'(t-t', l-l') dt' dl'} \quad (2)$$

with the same requirements on w' as held for w .

In the naive case that each specimen were studied separately then $\chi = \rho$, i.e. the density of specimens is equal to the density of papers. However, if the number of studies per specimen were consistent, (e.g. if there were one study for each billion specimens) then $\chi \propto \rho$. This, however, is not the case. Different parts of the world have different coverage. If, for example, western Europe has many palynologists we can expect much study of the region and many papers covering it. Thus, we introduce a function $q(t, l)$ that is a measure of the relative interest in a given location. q is some form of relative density, and hence is dimensionless. Strictly, q may depend on the taxon in question, but for now we will assume q to be independent of taxa. Now:

$$\chi(t, l) = \rho(t, l) * q(t, l) \quad (3)$$

In principle we can recover ρ if we know q . We are unlikely to ever have an absolute scale for q , so the best we can do is recover the shape of ρ .

We cannot handle a continuous domain in a computer program but must represent it by a set of discrete points. Thus any function $f(t, l)$ must be represented by a set of discrete points $f(t_j, l_j)$. The simplest approach is to create a set of bins that cover the domain, in which we build the density. That is:

$$\rho(t_j, l_j) = \frac{\int_{L,T} c(t', l') w_j(t_j-t', l_j-l') dt' dl'}{\int_{L,T} w_j(t_j-t', l_j-l') dt' dl'} \quad (4)$$

and likewise for χ . The width and separation of the peaks in the existence functions set limits on the span of w . w must be sufficiently broad compared to the granularity of c . Since each locality is

converted to a point position, the geographical size of the bins is restricted.

Boundary effects must be considered when building our density function. If a database entry overlaps a bin, then the fractional coverage must be taken into account. Also, all the final counts must be normalized by the bin sizes.

2.3. Binning options and selections

Palynoplot provides a number of options when integrating the equations to produce the density functions. Moreover, the user must select a number of points in (L, T) to build the discrete representation. For each of these points, the corresponding w_j is a square function, the operation consists of placing and counting the occurrences in the corresponding 'bins'.

The user may prefer to examine the raw counts by choosing not to weight the bins by dividing by their size:

$$\int_{L,T} w_j(t_j-t', l_j-l') dt' dl' \quad (5)$$

This can be achieved by adding to each bin an increment that is independent of the amount of coverage of the bin. This approach may be considered to be overly sensitive to tiny fractional coverage, and therefore the user can ask that a count only be increased if the bin is more than half covered by a record.

However, if the density function χ is desired, then it is important to perform the integrals properly. Thus, if a bin is partially covered, the accumulation to that bin will be proportional to the coverage. Also, in this case the final accumulations (integration) must be divided by the bin sizes. The basic program gives a density in time or time–latitude space. If true two-dimensional spatial density is desired the user can divide the results by the relative length of each latitude strip ($len = \cos(lat)$ for narrow strips).

Finally, the user can specify that each paper has the same integrated contribution to the distribution, or the same local density. We refer to this

option as ‘inverse weighting’ (see 3.2.1. Plot types and examples). This may be important if some papers cover a large temporal range and some a small range, but all report the same number of specimens.

The selection of the size of the bins is very important. The ‘binning’ inherent in using a geological period/epoch/age name may produce widening of the correct distribution. This would occur if a Cretaceous age were recorded for a taxon which occurs only in the Albian. However, the time-period name is not collapsed to a central point by Palynoplot, and so that actual choice of temporal boundaries will not cause further changes to the distribution. Thus, choosing small temporal widths for the bins only causes greater computation times, whereas large temporal widths will result in excessive loss in resolution. We typically choose 2-Myr intervals as a good compromise between underlying geochronological resolution and computational speed.

The same is not true of the spatial bin sizes. Because each position is collapsed to a point, there is a graininess to *c'* inherent in the spatial direction that does not exist in the temporal direction. If the bins are very small, then that graininess will be resolved. This is less important in such areas as Europe and Japan where the sample sites are very specific and distinct, but in places like southern Africa or western Canada, this graininess is noticeable. Therefore the bins should have a latitudinal size large enough so that this graininess is not resolved (i.e. the fluctuations are averaged). In the northern areas 2° latitude is reasonable, but in the southern and equatorial latitudes 5° starts to resolve the graininess of *c'*. Bin widths of 10° latitude are sufficiently wide to eliminate all the graininess.

3. Practical method and caveats

3.1. *Palynodata* retrievals

Palynodata software allows searches of records for individual species (formal or informal) or for genera. The search results consist of the source reference number, quality of assignment (e.g.

‘cf.’), older and younger ages assigned to the taxon, and general locality. These data may be saved as a spreadsheet or text file. When a taxon search is begun in Palynodata, orthographic variations of the name are listed. One can accept none, any, or all of the variations listed by Palynodata, but the search results are altered accordingly. Input for Palynoplot is the search retrieval list from Palynodata (the *c'* distribution), saved as a text file. The input data are binned and plotted by Palynoplot. Palynoplot can export the binned data to text files for further analysis and plotting and sophisticated algorithms can be processed in Palynoplot.

One problem with Palynodata search results is that some sources are primary references, original studies which provide new information, whereas other entries are secondary studies. The latter summarize the primary studies, effectively replicating the input data but adding no new information. Ideally, the secondary studies should be filtered out, but that would require a review of all of the input literature. (This might have been a problem for dinoflagellates, for which the Lentin and Williams catalogues (e.g. Williams et al., 1998) produce many secondary citations, but those references have no locality data, and so are ignored by Palynoplot.) We assume that the secondary studies are less numerous than the primary, but recognize that their presence will, to some extent, change the shape of the resulting plots. Secondary studies integrate other literature, and probably report longer age ranges for taxa. Thus, inverse weighting may reduce the significance of secondary studies in the plotted distributions.

Records without ages or geographic records are discarded from the plot. Records with ‘cf.’ qualifiers are included in examples below, but can be filtered from the input file. Occasionally Palynodata retrieval lists yield replicate entries. Palynoplot filters out identical replicates.

We discuss and illustrate the technique with examples of pollen and spores. The locality information in Palynodata is much richer and more precise for continental than for marine studies, permitting a more elaborate presentation of the technique.

3.2. *Palynoplot plot options*

3.2.1. *Plot types and examples*

Palynoplot makes three types of plots, each with interpretational advantages. The three plot types and the inverse weighting option are illustrated using retrievals of the species *Clavatipollenites hughesii* Couper 1958 (Fig. 3), and of the genus *Clavatipollenites* (Fig. 4). Retrievals of the species *Cicatricosisporites australiensis* (Cookson) Potonié 1956 (Fig. 5) and the genus *Cicatricosisporites* (Fig. 6) also illustrate the plotting options. Notice curve shapes and scale differences when comparing figures.

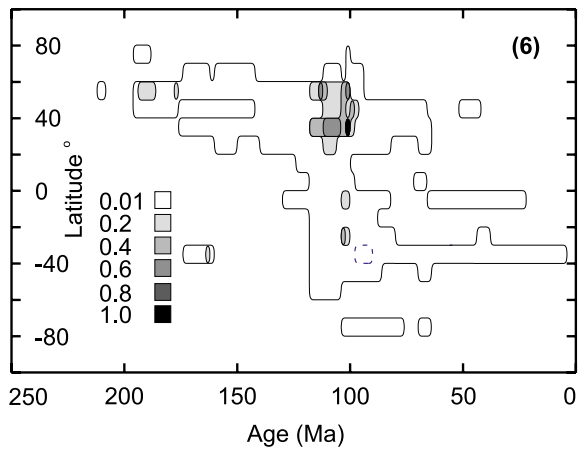
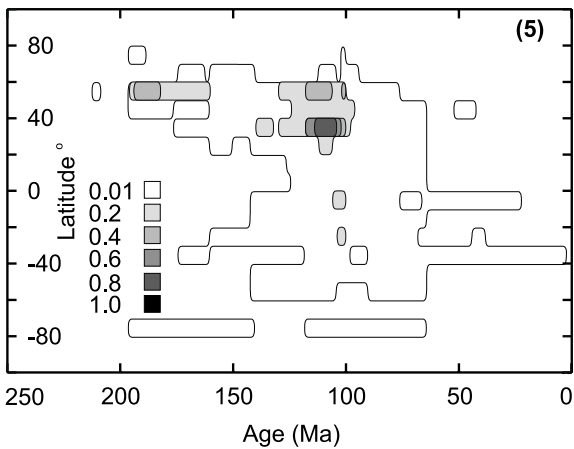
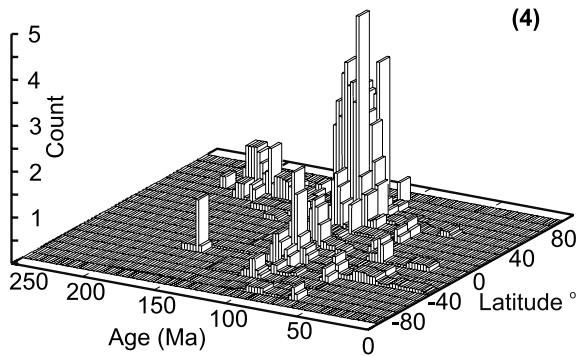
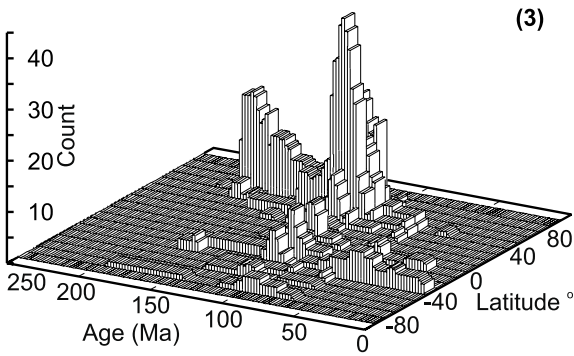
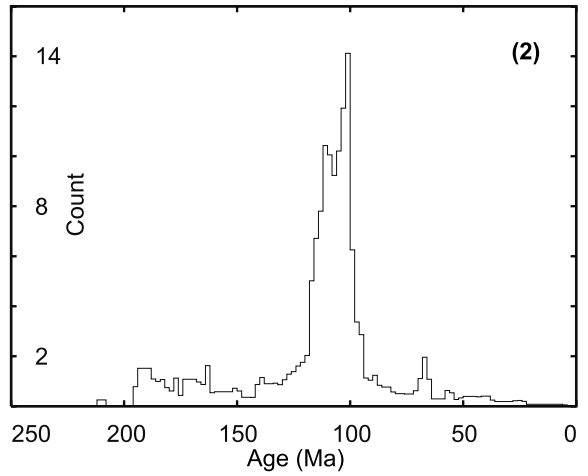
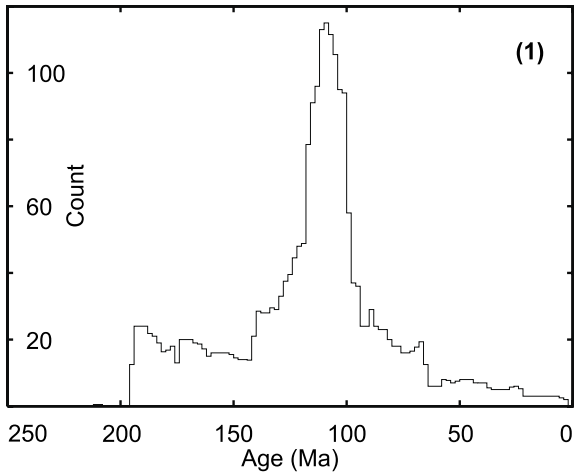
Time plots of a retrieval of *Clavatipollenites hughesii* Couper 1958, an important Early Cretaceous angiosperm pollen (e.g. Fig. 3.1, 3.2), depict the sum of all the records along an equally divided numeric time axis (*T*), using the time scale incorporated in Palynodata (see 3.3. Time domain (*T*)). The Palynodata (v.5.0) retrieval yielded a total of 321 records, including orthographic variations. If we accept the argument that density of citations allows one to estimate the underlying population distribution, *C. hughesii* clearly is at greatest abundance in the early and mid Cretaceous. Its range through to the Quaternary, at declining abundance, is reasonable considering the affinity of the taxon to the modern Chloranthaceae (Walker and Walker, 1986). Fig. 3.2 shows an inversely weighted distribution (see 3.2.2. Inverse weighting) of *C. hughesii*. The general shape of the curve remains the same, although plotted on a different scale, but the interval of greatest abundance is narrower and largely restricted to the mid-Cretaceous. The Late Triassic to Jurassic occurrences of the taxon are puzzling, and are discussed below (3.7.1. Taxonomic error).

Time–latitude plots (e.g. Fig. 3.3, 3.4) draw on a provisional locality file (see 3.4. Latitude domain (*L*)) to subdivide the time bins into latitudinal bands (*L*), and present the data as a three-dimensional surface plot. The plot gives a striking view of the distribution, viewed from the ‘south-east’, and is an excellent method of making an initial inspection of a distribution. However, the

abundance peaks hide some of the data to the ‘northwest’, and it is also difficult to precisely locate any particular time/latitude bin. The time–latitude plots elucidated the Jurassic occurrences of *Clavatipollenites hughesii*, showing that there is a distinct cluster of Jurassic occurrences of *C. hughesii* in northern high latitudes. This suggests a taxonomic problem, which is considered further in 3.7.2. Mistakes.

A complementary depiction of time–latitude plot is a contoured plot (e.g. Fig. 3.5, 3.6), which shows the complete ‘footprint’ of a taxon and on which it is easy to identify bins. It is harder to recognize abundance patterns on contoured plots, but Palynodata allows the user to control the contour interval to emphasize features of interest. Contoured plots also reveal distribution patterns which are biologically impossible. For example, the unweighted distribution of *Clavatipollenites hughesii* (Fig. 3.5) reveals a ‘horseshoe’-shaped distribution, with the earliest occurrences found at high latitudes in both hemispheres, without an intervening connection. An investigation of this pattern would need to consider taxonomy (discussed in 3.7. Taxonomy), but also whether the apparent absence of low-latitude records is due to factors such as paleogeography, the distribution of studies, or climate. Contoured plots also assist in modeling the distributions of taxa. Fig. 3.5, 3.6 show that *C. hughesii* would probably be present in a sedimentary basin at about 60°N (modern latitude) between about 140 and 120 Ma, even though it has not been recorded in Palynodata, v.5.0.

The presentation of contoured plots in this manuscript (Figs. 3.5, 3.6, 4.3, 5.5, 5.6 and 6.3) has been simplified by representing the data in each as a proportion of their peak values. This changes the scale but retains the shape of each distribution, and allows one standard legend for all figures. Each contoured plot, representing the same raw numeric scale as the equivalent time–latitude plot, would require a different contour legend. This is awkward for publication, but otherwise not a problem. The smallest proportion contoured is 0.01, depicting the basic ‘footprint’ of the taxon.



250	200			150			100	50	0	
L	E	M	L	E	M	L	E	L	Paleogene	Neog.
Perm.	Triassic			Jurassic			Cretaceous		Tertiary	

Fig. 3. Age and modern latitudinal distributions of records of *Clavatipollenites hughesii* Couper 1958 from Palynodata, v.5.0, including orthographic variations. The data are allocated to bins of 2 Myr duration, based on the timescale incorporated into Palynodata. Fractional overlap of bins makes a decimal contribution to the bin. The counts (z axis) are counts of citations, for this and subsequent figures. (1) *Clavatipollenites hughesii*, time plot. The distribution of *C. hughesii* plotted through time. Note the suggestion of bimodality in the time plot between 200 and 100 Ma. (2) *Clavatipollenites hughesii*, time plot, inverse weighting. This is the 3.1 plot, but with ‘inverse weighting’ of the input age determinations. Bimodality is still evident in the curve. (3) *Clavatipollenites hughesii*, time–latitude plot. Records of *C. hughesii* plotted by time and modern latitude of the study locality, using the provisional locality file. The bimodality suggested in 3.1 and 3.2 is shown to be due to studies in the Late Triassic–Jurassic in the high latitudes of the northern hemisphere, and would lead one to first investigate the consistency of the taxonomy. This plot gives a strong visual impression of the distribution, but it is difficult to trace and identify individual bins. (4) *Clavatipollenites hughesii*, time–latitude plot, inverse weighting. This is as 3.3, with inverse weighting applied; the same patterns are evident. (5) *Clavatipollenites hughesii*, contoured time–latitude plot. This is the same plot as 3.3, but contoured. The contoured intervals are constructed as a proportion of the peak values, changing the scale but not the shape of the distribution, and allowing one scale to serve for all contoured plots. Although the contoured plot has less visual impact than the time–latitude plot, bins are easy to identify and outliers are easily seen in this type of projection, as well as patterns of distribution which appear biologically impossible. Here, the ‘horseshoe’ distribution in the Late Triassic–Jurassic, with the earliest occurrences found at high latitudes in both hemispheres, without an intervening connection, is biologically impossible. Contoured plots allow modeling of distributions in unexplored basins. (6) *Clavatipollenites hughesii* contoured time–latitude plot, inversely weighted. This is 3.4 contoured, or 3.5, inversely weighted.

For comparison with *Clavatipollenites hughesii*, the distribution of the genus *Clavatipollenites* is depicted in Fig. 4. Palynodata v.5.0 listed 982 entries for the genus *Clavatipollenites* (including the orthographic variation, *Clavipollenites*). Paleozoic records of the genus *Clavatipollenites* are assumed to be coding errors, and these outliers are not plotted. Fig. 4.1, 4.2, 4.3 are comparable to Fig. 3.1, 3.3, 3.5, respectively. The genus plots are similar in many features to those of *C. hughesii*, in part because it is a significant component of these plots, but also because it is the same lineage. Fig. 4 plots yield larger values, longer ranges, greater occupation of the time/latitude domain, and a reduced significance of the Late Triassic to Jurassic occurrences with respect to the whole genus distribution. Thus, comparison of genus and species plots can reveal different features of the distributions.

Many input factors effect the shape of the c' distributions represented by these three types of plots, and thus affect the extent to which one can recognize the c (‘real’) distribution of a species. These are discussed below.

3.2.2. Inverse weighting

By inverse weighting, each publication has a total weight of 1 which is allocated to bins. Thus, a publication giving an age which spans five bins contributes 0.2 to each bin, but a pub-

lication which gives an age range covering 20 bins contributes only 0.05 to each bin. Thus, less precise age determinations are underweighted, and distributions are narrower than in non-weighted plots (compare unweighted Fig. 3.1, 3.3, 3.5 with inversely weighted Fig. 3.2, 3.4, 3.6). However, this tool is a two-edged sword. Although it reduces the significance of very general age determinations, it would also reduce the weight assigned to an important, long section that spanned many geological Ages.

3.3. Time domain (T)

There is a comprehensive Phanerozoic time scale in Palynodata, based on van Eysinga’s (1978) chronology, incorporating internationally and provincially recognized chronological divisions. This scale is used in binning the palynologists’ Epoch/Age determinations to numerically defined age bins. A different time scale could be used, but could make a minor change in the shape of the plots, to the extent that the age determinations were changed.

The time scale incorporated in Palynodata sometimes departs from formally accepted chronostratigraphic units, in favor of practical usage of the scale. For instance, the Palynodata scale recognizes subdivision of the Cretaceous into early, middle and late, with division points in

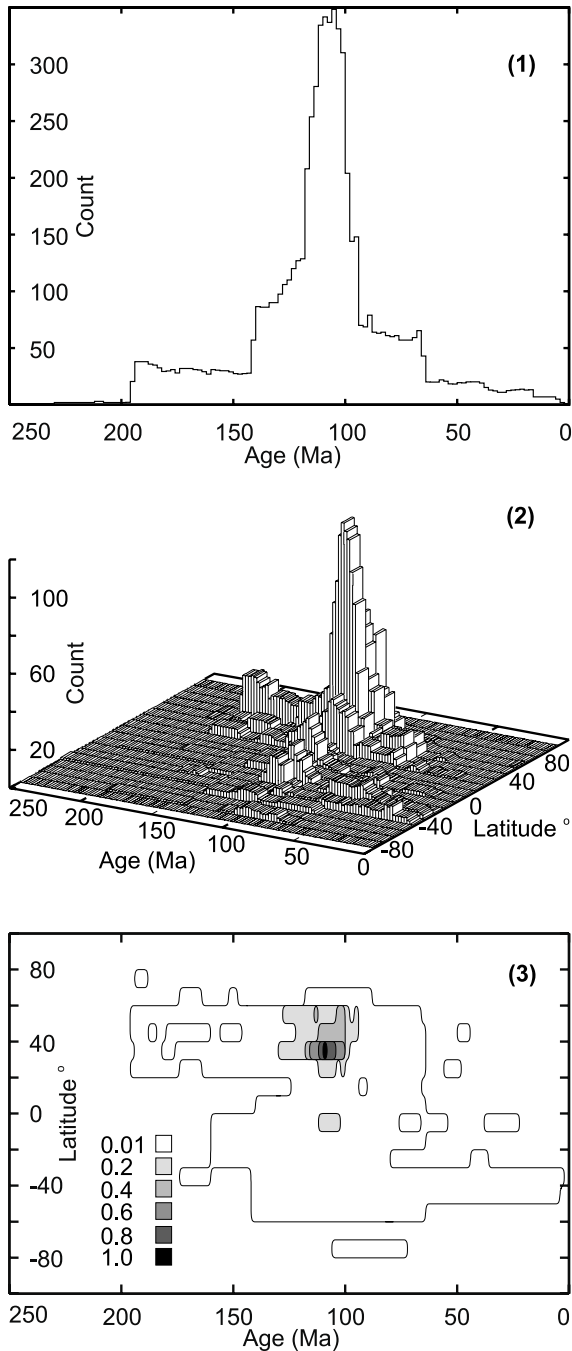


Fig. 4. The genus *Clavatipollenites* is presented for comparison with *Clavatipollenites hughesii*. The inversely weighted figures have not been plotted, for brevity. The plots are similar in many features to those of *C. hughesii* because it is a significant component of these plots. See the time scale on Fig. 3 or 5. (1) *Clavatipollenites* time plot. This plot is similar to Fig. 3.1, with a difference in the count on the y axis. There is a suggestion of bimodality, contributed probably by the distribution of *C. hughesii*. (2) *Clavatipollenites* time–latitude plot. Compare with Fig. 3.3. (3) *Clavatipollenites* time–latitude contoured plot. Compare with Fig. 3.5.

mation, as opposed to recording it only as ‘Cretaceous’. However, formal time scales (e.g. van Eysinga, 1978; Palmer, 1983; Haq and van Eysinga, 1987; Okultich, 1995; Gradstein and Ogg, 1996) recognize only the Early and Late Cretaceous. On the Palynodata time scale, the Albian, Aptian and part of the Barremian are not included in the ‘Early Cretaceous’, contrary to published time scales. Hence, an age determination of ‘Early Cretaceous’, which was intended in the formal sense of a time scale, would be recognized erroneously as spanning a shorter time interval than the author intended. There is no method of correcting the data short of reviewing the publications which make up each age determination. Also, there is no ‘right’ and ‘wrong’ resolution to this sort of formal versus informal age determination problem. There are advantages and disadvantages to both. However, it must be recognized that the time scale incorporated in Palynodata has an effect on the shape and inflection points of the curves plotted by Palynoplot.

3.4. Latitude domain (*L*)

Latitude/longitude coordinates are required for depiction of studies in space (*L*). We have created a provisional file of modern geographic coordinates for the 975 localities recorded in Palynodata v.5.0 (Fig. 1), working within the precision of the Palynodata locality information. Palynodata usually records study localities by political units, but sometimes by general geographic localities, such as ‘Pacific Northwest’, or ‘Atlantic Ocean’. Precise latitude and longitude coordinates for studies were not recorded in Palynodata, and may not

the mid-Barremian and mid-Turonian. A palynologist might well give an age of ‘middle Cretaceous’ to a sample, and no doubt the time scale in Palynodata was adapted to record that infor-

have been included in the source publications. A provisional geographic coordinates file for study localities has been developed, accurate insofar as we can make it without becoming mired in precisely locating coordinates for over 20 000 pieces of literature. This provisional file has been used to explore the information potential in Palynodata.

Although considered provisional, much effort was expended in generating and proofing the locality coordinate file over the course of a year. For the provisional file, latitudes and longitudes were assigned to the midpoint of Palynodata localities, primarily using the index of the Oxford Essential World Atlas (1998), supplemented by the *Britannica World Atlas* (Cole, 1967), the on-line Getty Thesaurus of Geographic Names (unpublished) and the on-line Alexandria Digital Library Gazetteer Server (unpublished). If coordinates could not be found for a locality, estimates of a location were made from the Oxford Essential World Atlas (1998). For some localities in the former Soviet Union and in China it was particularly difficult to derive geographic coordinates, and we have drawn heavily on the international knowledge of colleagues within the Geological Survey of Canada, Calgary, although we retain responsibility for the errors which are likely in the locality file.

Inaccuracy in locality coordinates may not have a significant effect on the results. Fossils occur at points (study sites) in the geological record, but in life, the plants grew over broad regions, so approximation of localities does not necessarily misrepresent the underlying geographic distributions. Given a latitude inaccuracy of less than 10° for a study location, it would still fall in the correct latitude band, or would falsely augment counts in adjacent latitude bands. This would not significantly affect conclusions. However, a mistake in the sign of a latitude/longitude coordinate might produce an outlier in another hemisphere.

Latitude, rather than longitude, is expected to be the more significant variable in determining the distribution of palynomorphs because it is a rough proxy for climatic temperature. Plate reconstructions (Eldridge et al., 1999) suggest that modern latitude is a general approximation for paleolatitude from the Cenozoic back through

the Mesozoic, with exceptions, and with decreasing accuracy with increasing time before present. The use of modern latitude is not ideal, but practical at this stage of development of the data presentation.

An improved locality file is a significant undertaking for future development of the technique. Locality mistakes may be more critical for planned future work involving the rotation of fossils into paleopositions to derive paleogeographic ranges.

3.5. *Latitudinal and longitudinal study site distribution (q)*

The high density of recorded study localities in northern mid-latitudes (Fig. 1) probably indicates a higher number of palynological studies in that band, representing an interest factor (q). Europe, the classic home of geology and paleontology, with a dense population, is especially heavily studied, disproportionately weighting northern mid-latitude bins. This weighting is visible in time–latitude or contoured plots and is present, but not depicted, in time-only plots. A consequence of high study density in northern mid-latitudes is high definition of patterns for those latitudes.

The distribution of localities in part reflects the relatively fine political subdivision of land in Europe as compared with newer and larger political units in the Americas and Africa, a product of improvement in communication in the 19th and 20th centuries, and the enlargement of political entities. It may also reflect sensitivity of data recorders of European–North American culture to their own political entities, whereas other entities may be used more generally.

It may be possible in the future to correct partially for the density of studies in northern Europe by constructing a parent distribution from a large number of taxa as a representative of q , and then use that distribution to detrend the density distribution. Also, a precise locality file might allow correction for this weighting. However, study density is so high in Europe, and sparse in other areas, including Canada, that it might not even then be possible to generate meaningful compar-

isons of occurrence/unit area amongst the different regions.

An additional consideration in the differential representation of latitudinal bands is that there is an inverse relationship between latitude and surface area on the globe; 10° bands at high latitude have smaller surface area than those at lower latitude, so that high-latitude bins have higher ground density than appears on the plots. This can be addressed within Palynoplot by dividing the density bins by the cosine of the latitude (see 2.3. Binning options and selections). Palynoplot output is a Mercator-type representation of latitude.

The longitudinal distribution of study sites is biased towards Europe. Thus, European chronostratigraphic standards are reflected disproportionately in the time scale. This may be an advantage in correlating to the European standards. In understanding the temperature tolerance of fossils, the longitudinal distribution of study sites is probably less significant a factor than latitude, because latitude is a better proxy for temperature.

The lack of more precise locality records is one of the chief impediments to making conclusions about the *c* distribution from the *c'* distribution recorded in Palynodata because we cannot plot or manipulate precise information about records versus surface area. An alternative way of representing the abundance change of a palynomorph through latitude would be a fully quantitative palynological database, permitting Quaternary-style isopoll maps at a given time slice. The nature of biostratigraphy and the database accumulated over the past 32 years means that Quaternary-style representations will not be realized in the near or intermediate future. The only practical approach is that followed here, to approximate palynomorph distributions from the records in Palynodata.

3.6. Chronological study density (*q*)

Economic considerations encouraged intensive study of some Systems, e.g. the Jurassic. This focus has an effect on the height of the histograms in any System, and may affect the appearance of their central distribution and variation. Ideally, this uneven study density through time could be addressed with a comprehensive assessment of the density of studies per time interval in the database. Until addressed, the impact of this question on results can be assessed practically. Search results themselves show changes in the distributions of taxa through time, thus indicating that the change in species distributions through time is a more important factor than the chronological distribution of studies. Within the Cretaceous System, a comparison of the distribution of *Clavati-pollenites hughesii* (Fig. 3) with *Cicatricosisporites australiensis* (Fig. 5) shows that the curves are governed primarily by the distribution of the taxa, rather than by the distribution of the studies.

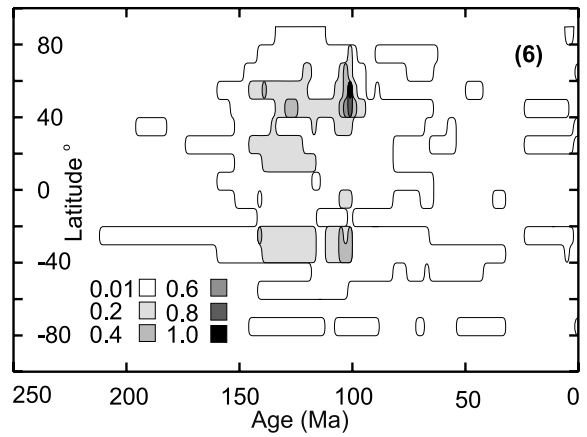
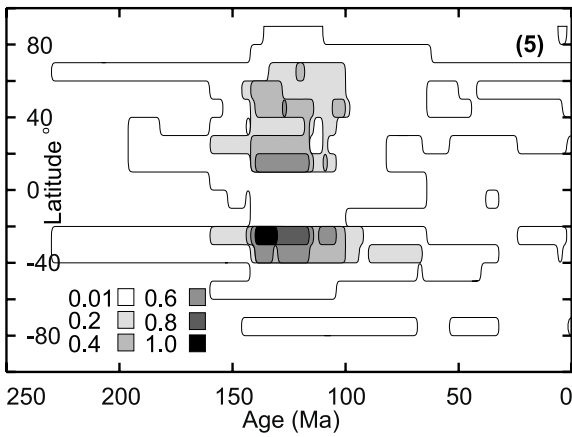
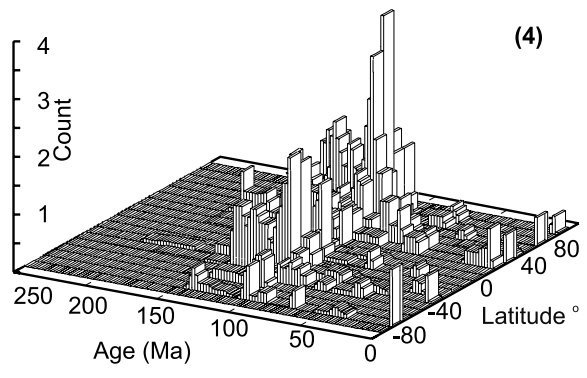
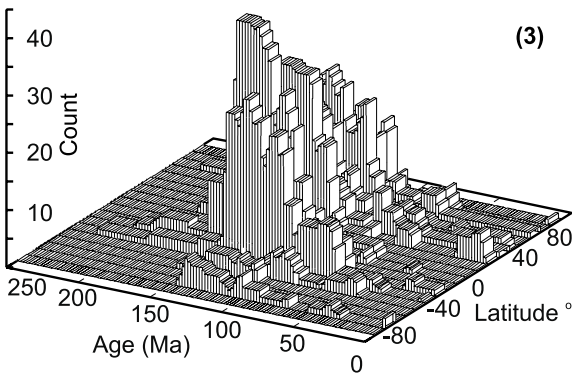
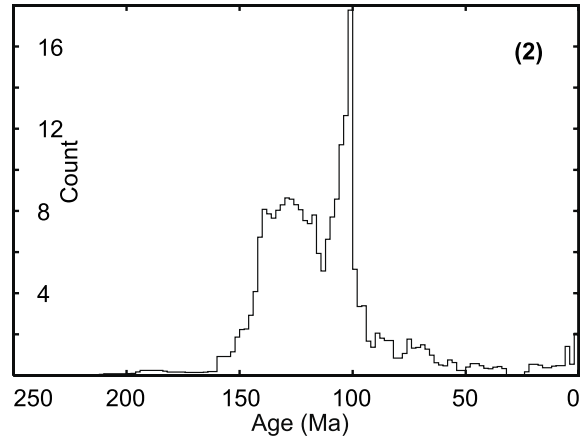
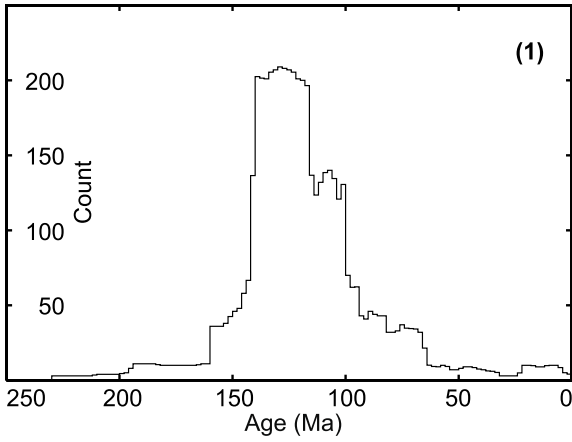
3.7. Taxonomy

Aspects of taxonomy are central concerns in paleontology. We use taxonomic ‘error’ as unavoidable uncertainty in taxonomy, whereas ‘mistakes’ are inevitably clerical mishaps, such as mistyped species lists in manuscripts or in the entry of records to Palynodata. In addition, species are often reassigned to a different genus by a later study, complicating record keeping.

3.7.1. Taxonomic error

A prime goal and hurdle in paleontology is the definition and meaningful classification of a species – the basic analytic unit. The difficulty of achieving this goal can overwhelm other aspects of the discipline. Paleontologists, being intimately

Fig. 5. Distribution of the common Cretaceous spore, *Cicatricosisporites australiensis* (Cookson) Potonié 1956 and orthographic variations. The graphs follow the same pattern as in Fig. 3.1–3.6, which may be consulted for more detailed explanations of the techniques. (1) *Cicatricosisporites australiensis*, time plot. (2) *Cicatricosisporites australiensis*, time plot, inverse weighting. (3) *Cicatricosisporites australiensis*, time–latitude plot. (4) *Cicatricosisporites australiensis*, time–latitude plot, inverse weighting. (5) *Cicatricosisporites australiensis*, contoured plot. (6) *Cicatricosisporites australiensis*, contoured plot, inverse weighting.



250	200			150			100	50	0	
L	E	M	L	E	M	L	E	L	Paleogene	Neog.
Perm.	Triassic			Jurassic			Cretaceous		Tertiary	

familiar with the taxonomic process and its ambiguities, instantly identify differences in taxonomy as a critical impediment to recognition of the true underlying distribution of any ‘natural’ species. Nonetheless, the rules and process of paleontology are designed to minimize taxonomic errors. Holotypes of species are designated, the specimens curated in known institutions, pictures of the type material are published and original descriptions and illustrations are generally carefully consulted by other workers. Paleontologists’ offices are full of publications – inadequate taxonomy is a serious professional criticism.

The techniques presented here are based on the assumption that, on average, palynologists do their work carefully, within the limits of nomenclatural and chronological systems. That this assumption is reasonably well-founded is demonstrated by the degree to which distributions of species and genera (Figs. 3–6) fit theoretical distributions (Fig. 2). Good examples are shown by the distributions of *Cicatricosisporites australiensis* (Fig. 5.1, 5.3, 5.5) and the genus *Cicatricosisporites* (Fig. 6.1, 6.2, 6.3) which we have illustrated by time, time–latitude and contoured figures. (The inversely weighted distribution (Fig. 5.2, 5.4, 5.6) has a much lower count and a notably ‘spikier’ plot. This feature of inverse weighting requires further investigation.)

The Palynodata v.5.0 search for *Cicatricosisporites australiensis* yielded 512 entries, (including 13 records of *Mihrio(i)sporites*) and the search for *Cicatricosisporites* yielded 6623 records (including 29 records of *Mohrio(i)sporites*). Figs. 5.1, 5.2 and 6.1 approximate a bell-shaped distribution, and show the relative smoothness of large n samples. Fig. 6.1 shows many of the recognized features of the genus *Cicatricosisporites*, and adds some insights. One might question the taxonomy of pre-Late Jurassic occurrences, but *Cicatricosisporites* abundance increases in the Late Jurassic, and then markedly increases in the Early Cretaceous. The mid-Cretaceous decline might be due to competition with angiosperms. Supporting this is an independent observation by Lidgard and Crane (1990), who describe a decline in diversity of free sporing plants beginning in the Barremian–Aptian, contemporaneous with a marked

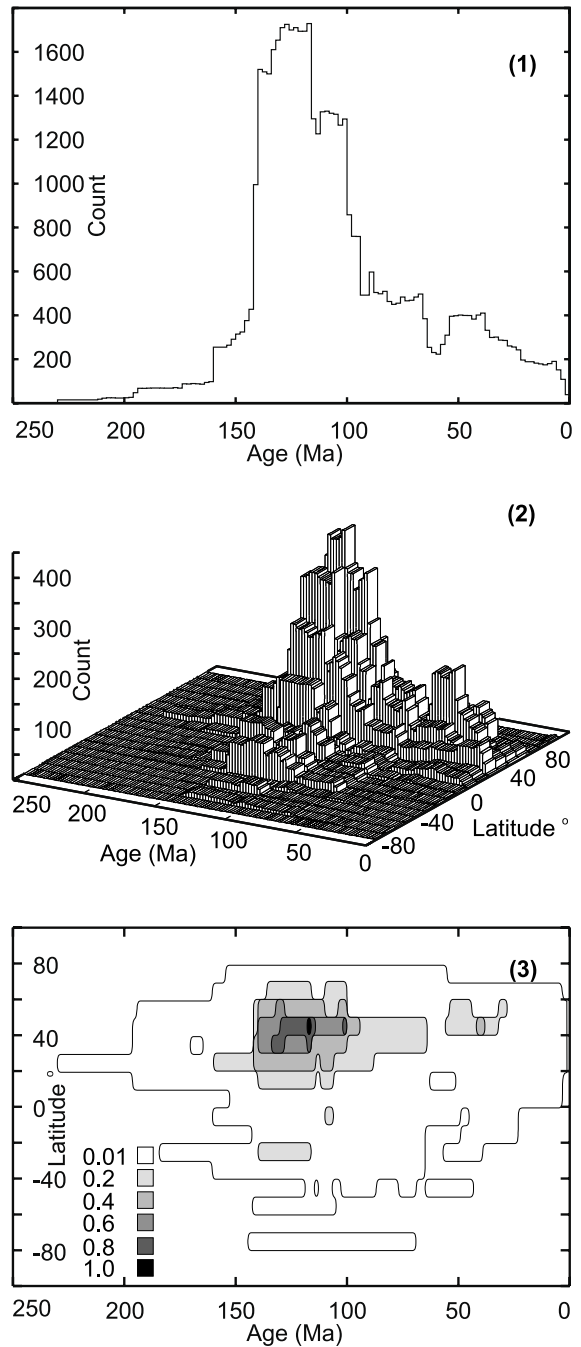


Fig. 6. The genus *Cicatricosisporites*. See the time scale on Fig. 3 or 5. (1) *Cicatricosisporites*, time plot. (2) *Cicatricosisporites*, time–latitude plot. (3) *Cicatricosisporites*, contoured plot.

increase in angiosperm diversity. A decline in *Cicatricosisporites* abundance occurs at the Cretaceous–Tertiary boundary, but then abundance recovers somewhat in the warm Eocene, a reasonable occurrence pattern for a tropical and subtropical family. This Eocene recovery is not a feature of the *C. australiensis* record (Fig. 5.1), and must be due to other species of *Cicatricosisporites*. The *Cicatricosisporites* distribution continues to the Quaternary, which is to be expected because the tropical Schizaeaceae contains modern representatives of the genus *Cicatricosisporites* (see Tryon and Lugardon, 1991). One may parenthetically note that the *Cicatricosisporites* curve is the skewed to the right (Fig. 6.1), a feature commonly found in distributions, and which might be attributed to some combination of geological recycling or relict species.

Some fossils are distinctive, but many are not. The distinctive taxa are likely to be consistently identified, and the non-distinctive taxa are likely to have greater error of identification and variation in taxonomic usage. The expertise of the worker is vital in making astute retrievals from Palynodata, in recognizing historic changes in taxonomy and possible variations in identification, and in selecting ‘good’ species.

Formal taxonomic publication is laborious, but for this paleontology might even be partially fortunate, because a more limited number of illustrated references tends to standardize taxonomic usage. On the other hand, it also encourages informal designation to handle the new fossils which may be encountered in a study (Palynodata includes about 26 000 informal species). If a species is informally designated in a study (e.g. ‘*Cicatricosisporites* sp. A’), the species record in Palynodata is not comparable between authors, but the record of the genus is comparable and useful information.

There is both natural variation in the form of a species, and variation among palynologists in the identification criteria used for a species. These sources of variation are interacting error factors. Pre-Quaternary palynologists usually consult holotype illustrations and descriptions to guide their identifications. Holotypes embody the central concept of a species, rather than the range of

variation around the holotype, and result in less formal emphasis on variability than on central tendency in form. On the other hand, Quaternary palynologists generally base identifications on reference collections of modern pollen prepared from herbarium specimens. The known source species, and the abundance of pollen on reference slides allow Quaternarists to be more certain in assessing the range of variation of pollen from the same species, genus or family. Recognition of both the central morphological concept and natural variation is necessary for sound taxonomy. A statement about central tendency and variation, essentially parallel to that made above concerning species, can be made concerning practising palynologists and their concepts of a species, which is based on individual research experience. One might think that variation in identification criteria among palynologists and morphological variation within species are compounding errors, resulting in a database ranging from imprecise to chaotic. However, it may be that variation in taxonomic usage around the central concept partially mimics the range of variation of the taxon. An analogy is found in Quaternary palynology in Maher’s (1981) demonstration that the standard deviation of interacting variables in concentration measurements is smaller than one would expect, considering the standard deviations of the individual variables.

In spite of the best efforts of palynologists, it is true that different names may be used for the same species concept, or that different species concepts may be used for the same name. An appropriate example is *Clavatipollenites hughesii*, normally considered to be an angiospermous biostratigraphic marker for the late Neocomian (Barremian). The time distribution plots (Fig. 3.1, 3.2) of *C. hughesii* suggest a bimodal distribution. Time–latitude and contoured plots, both depicted by unweighted (Fig. 3.3, 3.5) and inversely weighted (Fig. 3.4, 3.6) techniques, reveal significant Late Triassic to Jurassic, northern high-latitude occurrences of *C. hughesii*. This distribution would lead one to first investigate the consistency of the taxonomy. In fact, the cluster of early occurrences of *Clavatipollenites* are likely *C. hughesii* sensu Schulz as illustrated by Koppelhus and

Nielsen (1994) and discussed by Batten and Dutta (1997), who attribute *C. hughesii* sensu Schulz to cycadalean rather than angiospermous plants. Thus the plotting techniques described here can help to reveal these taxonomic problems.

3.7.2. Mistakes

Clerical mistakes may appear as outliers. Fig. 6.3 shows records of the genus *Cicatricosisporites* extending to 230 Ma. A Triassic occurrence of *Cicatricosisporites* is entered from Evans (1966). The Evans (1966) offprint in the Imperial Oil Collection (now at Geological Survey of Canada, Calgary) is printed on a 25.5×11-inch page, and the right and left leaves fold into the center to form a standard sized reprint. However, folding the right leaf inwards causes taxa which are in fact listed on a page under a 'Jurassic' heading, to appear to be listed under a 'Triassic' heading. This appears to explain the Triassic record of *Cicatricosisporites* in Palynodata. Given an adequate library (Palynodata encompasses over 20 000 documents), many of these these mistakes could be tracked down, but it would be very laborious. For most biostratigraphy, it is probably safe to disregard records which are very distant or disjunct from the core of a taxon's distribution. In an evolutionary study of a taxon, such records would need to be verified because they might be critical early or late appearances. Mistakes appearing within the core of the distribution will not be detectable, and only constitute a problem if they comprise a significant proportion of the data.

3.7.3. Taxonomic reassignment

If a species has been reassigned to a new genus at some time, searching Palynodata for only the new genus/species name is equivalent to beginning again, with new literature, to sample the underlying distribution c in order to produce the c' representation. Even though it is not incorrect to search for only the new name, it discards some pre-existing data. One could also search Palynodata for the old genus/species name and include it in the search results, as input for Palynoplot. Comparison of the distributions for both names could be a useful adjunct to formal taxon-

omy, if enough data were accumulated to yield non-noisy distributions.

The search for natural evolutionary groupings is a classic, central theme of paleontology, and in practice results in reassignment of species to new genera. Insightfully and thoroughly done, such work makes a great contribution. However, taxonomic answers are often not clearcut or universally agreed upon, and the result can be a plethora of names for the same concept. From a database perspective, reassignment of species makes data retrieval more difficult and error-prone. Future workers should weigh the benefits of proposing a more ideal, evolutionary-oriented nomenclature against the complications that result for data retrieval.

4. Summary

The techniques that we have described here produce graphic plots of the data in Palynodata, and these images aid in comprehending the information in retrieval lists. Nonetheless, the expertise of the palynologist is vital in making useful retrievals from Palynodata.

Plots of Palynodata help to identify errors and mistakes in the data, which may appear as outliers, and may be easily detected on Palynoplot graphs. Outliers may result from clerical mistakes or mis-identifications, but may also be important and legitimate early or last appearances, or paleogeographic range extensions. Plots of Palynodata lead to rapid formulation of useful questions at taxonomic, evolutionary, biogeographic, and paleoclimatic levels. Patterns of distribution which are biologically difficult to explain (e.g. the horse-shoe distributions of *Clavatipollenites hughesii*) are easily seen on a contoured plot and may yield useful insights into the species itself, or into the process of palynology.

Skepticism is appropriate in evaluating the Palynodata records, the Palynoplot graphs, and the many potential complications in interpretation. However, it is important to qualify one's skepticism. In fact, palynology is a powerful discipline which could not have made past achievements if meticulous publication, careful identifica-

tion and accurate record-keeping had not been the norm. We believe that Palynodata captures a largely useful body of literature and images of retrievals allow improved insight into the underlying distributions of the fossils. Applying the techniques described here to retrievals from Palynodata can enhance biostratigraphic palynology and expand palynology's input to geological and paleobiological research.

5. Future

Automated graphic presentation of retrievals from Palynodata can be applied to palynological inference in several areas.

- *Taxonomy*. The distributions are the inferences of palynologists about the stratigraphic range of a taxon, an integration of both the true stratigraphic range of a taxon and the interpretative filter applied by palynologists. Thus, changes in shape of the distributions immediately lead to questions which bear on the underlying taxonomy. In refining taxonomy, population distributions can support morphological arguments in questions of synonymy or separation.

- *Paleoclimate*. The modern latitude of study sites is a reasonable proxy for paleolatitude in Cretaceous and younger rocks. Paleolatitude is the first proxy for climatic paleotemperature, so the climatic affinities of taxa may be detected, and changes in distributions may represent climatic events.

- *Modeling*. Possibly, one could predict the biostratigraphy for an unknown frontier region, or help to reconstruct the vegetation of an paleo-landscape.

- *Paleogeography and tectonics*. In the future, palynological data may contribute to paleoplate reconstructions by plotting the results of Palynodata queries at paleopositions on paleogeographic maps.

A significant improvement in resolution could be made with a more precise file of modern latitudes and longitudes for palynological studies. Considering the number of items of literature encompassed by Palynodata, this would be a long-term project.

To be useful, a fossil taxon needs a rich record and consistent taxonomy. Many of the species recorded in Palynodata have been shown to be valuable tools. The techniques described here should help in refining and establishing the value of palynomorphs for biostratigraphic, paleoclimatic and paleogeographic analyses.

Acknowledgements

We would like to acknowledge the assistance of many people who have contributed to the development of the technique presented here. K. Piel, President of Palynodata, and B. Parsons, of Palyeast, generously answered many questions. D. Rose, B. MacMillan, P. Tzeng helped download and manipulate Palynodata files before they were available on CD. L. Bowyer, P. Davenport, E. Hau, G. Lai, D. Rose and L. McCartney assisted in compiling a provisional locality coordinate file. A. Duk-Rodkin, O. Rodkin, Z. Chen, H. Gao, G. Khidrova and J. Utting assisted in identifying localities. B. Davies and M. Hills-Urbat provided graphic support. We thank H.J.B. Birks, A. Beaudoin, D. Issler, R. Fensome, A. Sweet and P. Zippi for helpful critical comments. We would also like to recognize the foresight and effort of Gerhard Kremp, founder of the Kremp Palynological Computer Research Project that ultimately became Palynodata, the contributions of individuals who have served on the Kremp Steering Committees and on the Palynodata Boards of Directors, those who have maintained Palynodata through the last 33 years, and the support of the corporate sponsors, without whom Palynodata could not have continued. GSC Contribution No. 2000249.

References

- Alexandria Digital Library Gazetteer Server. Unpublished (<http://fat-albert.alexandria.ucsb.edu:8827/gazetteer/>), 2000.
- Batten, D.J., Dutta, R.J., 1997. Ultrastructure of exine of gymnospermous pollen grains from Jurassic and basal Cretaceous deposits in Northwest Europe and implications for botanical relationships. *Rev. Palaeobot. Palynol.* 99, 25–54.

- Cole, R.M. (Ed.), 1967. *Britannica World Atlas*. Encyclopaedia Britannica, Toronto, ON, 367 pp.
- Eldridge, J., Walsh, D.B., Scotese, C.R., 1999. *Plate Tracker for Windows*, version 2.0. PALEOMAP Project, Arlington, TX.
- Evans, P.R., 1966. Mesozoic stratigraphic palynology in Australia. *Aust. Oil Gas J.* 12, 58–63.
- Fensome, R.A., Williams, G.L., Barss, M.S., Freeman, J.M., Hill, J.M., 1990. Acritarchs and fossil prasinophytes: and index to genera, species and infraspecific taxa. American Association of Stratigraphic Palynologists Contribution Series Number 25. American Association of Stratigraphic Palynologists Foundation.
- Getty Thesaurus of Geographic Names. Unpublished (<http://www.getty.edu/research/tools/vocabulary/tgn/index.html>), 2000.
- Gradstein, F.M., Ogg, J.G., 1996. A Phanerozoic time scale. *Episodes* 19, 3–5.
- Haq, B.U., van Eysinga, F.W.B., 1987. *Geological Time Table*, 4th edn. Elsevier Science, Amsterdam.
- Herngreen, G.F.W., Chlonova, A.F., 1981. Cretaceous microfloral provinces. *Pollen Spores* XXIII, 441–555.
- Herngreen, G.F.W., Kedves, M., Rovnina, L.V., Smirnova, S.B., 1996. Cretaceous palynofloral provinces: a review. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology, Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, Vol. 3, pp. 1157–1188.
- Heywood, V.H. (Ed.), 1978. *Flowering Plants of the World*. Mayflower Books, New York, 336 pp.
- Hora, B. (Ed.), 1980. *The Oxford Encyclopedia of Trees of the World*. Equinox, Oxford, 288 pp.
- Koppellus, E.B., Nielsen, L.H., 1994. Palynostratigraphy and palaeoenvironments of the Lower to Middle Jurassic Bagå Formation of Bornholm, Denmark. *Palynology* 18, 139–194.
- Lentin, J.K., Davis, O.K., Muncey, T.S., Piel, K.M., 1996. Personal computers in palynology. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology, Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, Vol. 3, pp. 961–984.
- Lidgard, S., Crane, P.R., 1990. Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Paleobiology* 16, 77–93.
- MacRae, R.A., Fensome, R.A., Williams, G.L., 1996. Fossil dinoflagellate diversity, originations, and extinctions and their significance. *Can. J. Bot.* 74, 1687–1694.
- Maher, L.J., Jr., 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Rev. Palaeobot. Palynol.* 32, 153–191.
- Mallory, V.S., Johnson, G.D., 1992. Early views and discoveries. *The New Encyclopedia Britannica*, 15th edn. Volume 19. Encyclopaedia Britannica, London, pp. 748–752.
- Okulitch, A.V., 1995. *Geological Time Scale 1995*. Geological Survey of Canada, Open file 3040 (National Earth Science Series, Geological Atlas) Ottawa, ON.
- Oxford Essential World Atlas, 1998. Oxford University Press, New York, 176 pp.
- Palmer, A.R., 1983. The decade of North American geology 1983 geologic time scale. *Geology* 11, 503–504.
- Srivastava, S.K., 1994. Evolution of Cretaceous phytogeographic provinces, continents and climates. *Rev. Palaeobot. Palynol.* 82, 197–224.
- Steere, W.C., 1992. *Botany. The New Encyclopedia Britannica*, 15th edn. Volume 14. Encyclopaedia Britannica, London, pp. 992–995.
- Tryon, A.F., Lugardon, B., 1991. *Spores of the Pteridophyta*. Springer-Verlag, New York, 648 pp.
- van Eysinga, F.W.B., 1978. *Geological Time Table*. 3rd edn. Elsevier Scientific, Amsterdam.
- Walker, J.W., Walker, A.G., 1986. Ultrastructure of Early Cretaceous angiosperm pollen and its evolutionary implications. In: Blackmore, S., Ferguson, I.K. (Eds.), *Pollen and Spores: Form and Function*. Academic Press, London, pp. 203–217.
- White, J.M., 2000a. An automated, population-based analysis and graphic interpretation of stratigraphic and paleogeographic distributions and taxonomy of fossil palynomorphs. Oral paper and Abstract no. 713, GeoCanada2000, May 29–June 2, 2000, Calgary, Canada.
- White, J.M., 2000b. The Late Jurassic-Early Cretaceous Creticosporites: Palyplot images of data retrievals from Palynodata. Abstract and oral presentation at Geological Society of America, Session T115, *Frontiers in the Palynological Sciences II* (American Association of Stratigraphic Palynologists). Geological Society of America Annual Meeting, Summit 2000, Reno, Nevada, November 13–16. Geological Society of America Abstracts with Programs, 32, Abstract No. 51062.
- White, J.M., Ager, T.A., Adam, D.P., Leopold, E.B., Liu, G., Jetté, H., Schweger, C.E., 1997. An 18 million year record of vegetation and climate change in northwestern Canada and Alaska: tectonic and global climatic correlates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 130, 293–306.
- White, J.M., Ager, T.A., Adam, D.P., Leopold, E.B., Liu, G., Jetté, H., Schweger, C.E., 1999. Neogene and Quaternary quantitative palynostratigraphy and paleoclimatology from sections in Yukon and adjacent Northwest Territories and Alaska. *Geol. Surv. Can. Bull.* 543, 30 pp.
- Williams, G.L., Lentin, J. K., Fensome, R.A., 1998. *The Lentin and Williams index of fossil dinoflagellates*; 1998 edition. American Association of Stratigraphic Palynologists, Contributions Series 34, 817 pp.