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# Fern spore diversity and abundance in Australia during the Cretaceous

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## Abstract

Changes in the Cretaceous fern flora of Australia were analysed by compiling data from the palynological literature. A decline in the relative diversity and abundance of free-sporing plants during the Late Cretaceous was concurrent with a rise in angiosperms, while the relative contribution of gymnosperms was unchanged. Ferns and lycophytes were the major contributors to the free-sporing plant pattern and declined markedly from higher Early Cretaceous levels; bryophyte relative diversity peaks in the mid-Cretaceous. The fern families Schizaeaceae, Osmundaceae and Cyatheaceae/Dicksoniaceae decline only marginally, with most of the decline seen in 'miscellaneous ferns' (mostly comprising fern spores of unknown affinity). In contrast to the overall fern trend, the relative diversity of Gleicheniaceae increased significantly in the mid-Cretaceous. The decline in fern relative abundance, which is gradual throughout the entire Cretaceous, is equally complex. By far the largest contributor to this decline is Osmundaceae. Cyatheaceae/Dicksoniaceae and Gleicheniaceae increase in relative abundance in the mid-Cretaceous, but decline in the Late Cretaceous. Matoniaceae/Dipteridaceae maintain very low and stable levels of relative diversity and abundance throughout the Cretaceous. There is no evidence that polypodiaceous ferns *sensu lato* underwent any significant radiation concomitant with the angiosperm radiation in the Late Cretaceous. Trends observed in the relative diversity and abundance show that patterns occurring at high taxonomic levels (e.g. all ferns) are not consistent at lower levels (e.g. families). The Australian and North American diversity data for free-sporing plants, gymnosperms and angiosperms are broadly similar. However, Schizaeaceae and Gleicheniaceae display different trends during the mid-Cretaceous, increasing in diversity in the Australian palynofloras, but decreasing in North America. © 2002 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

Ferns were an important component of floras

during the Early and mid-Mesozoic (Triassic, Jurassic and earliest Cretaceous) comprising the understorey in forests and forming expansive fern prairies (Crane, 1987). In contrast, most modern vegetation types are dominated by angiosperms in terms of both biomass and number of species, while ferns are of minor importance. The

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transition from gymnosperm- and pteridophyte-dominated floras to angiosperm-dominated floras represents the most important vegetational change of the past 200 Myr.

Macrofossil evidence points to a highly diverse Cretaceous fern flora in the Northern Hemisphere; during the mid-Cretaceous there were more than 100 pteridophyte genera (mostly ferns), but this diversity declined to 50 genera by the end of the Cretaceous (Lidgard and Crane, 1988; Crane and Lidgard, 1989). Diversity studies of North American Cretaceous macrofloras and palynofloras show that, relative to other plant groups, pteridophytes underwent a larger decline in diversity, which is paralleled by a comparable rise in angiosperm diversity (Lidgard and Crane, 1990; Lupia et al., 1999). This reciprocal pattern is also evident in the relative abundance of spores versus angiosperm pollen; however, the drop in spore abundance is less pronounced than that of diversity (Lupia et al., 1999).

Studies of Cretaceous macrofloras from Australia (Douglas, 1973; Drinnan and Chambers, 1986; McLoughlin et al., 1995; McLoughlin, 1996), Antarctica (Jefferson, 1982; Cantrill, 1995, 1997, 1998), New Zealand (Arber, 1917) and South America (Archangelsky, 1967; Herbst, 1962, 1967, 1971) have documented a diverse array of ferns in the Southern Hemisphere from this period. However, the only quantitative analyses of Gondwana Cretaceous floristic change during the Cretaceous are a small-scale study of 14 macrofloras in Gondwana (Drinnan and Crane, 1990) and three bore cores from Northern Gondwana (Schrack and Nesterova, 1993). These preliminary data show a marked decline in fern relative and absolute diversity through the Cretaceous. Palynological investigation of smaller regions within Gondwana, for example Antarctica (Dettmann and Thompson, 1987; Askin, 1988a,b 1990), also suggests a decline in the importance of ferns during the Cretaceous.

Palynological studies of Australian Cretaceous vegetational change have been undertaken only within selected basins (Dettmann, 1963; Burger, 1980; Morgan, 1980; Backhouse, 1988). These studies have focussed on individual stratigraphic units, single exploratory well sections, single ba-

sins or certain regions and some have provided preliminary evidence for the decline in fern diversity and abundance in Australia during the Cretaceous comparable to that evident in North America. Several studies of Australian Cretaceous fern spores have focussed on evolutionary and biogeographic relationships of selected families such as Pteridaceae (Filatoff and Price, 1988; Dettmann and Clifford, 1992), Schizaeaceae (Dettmann and Clifford, 1991, 1992) and Lophosoriaceae (Dettmann, 1986). However, these studies have not provided a broad synthesis of the changing diversity and abundance of ferns and other components of the Cretaceous palynofloras.

This study utilises the extensive, existing palynofloral record to analyse changes in the Australian vegetation during the Cretaceous and, specifically, focuses on the patterns of fern diversity and abundance during this time. Trends in diversity and abundance are contrasted and are discussed in relation to the other components of the palynofloras; the results are compared with North American Cretaceous palynofloras.

## 2. Methods and sources of data

### 2.1. Methodology

Data obtained from palynological literature were compiled to provide measures of diversity and abundance during the Cretaceous. The taxonomic diversity of a flora is derived from lists of species recorded in a sample. This study utilises two measures for diversity: 'absolute diversity' and 'relative diversity'. Absolute diversity (absolute within-flora diversity) is equal to the number of species recorded in a sample; relative diversity (relative within-flora diversity) corresponds to the percentage of species from one plant group compared to all groups in a sample. The measure 'relative abundance' (relative within-flora abundance) is based on counts of pollen or spores belonging to one plant group, expressed as a percentage of the total number of palynomorphs in a sample.

All of the data were entered into the relational 'Palynology database' created by one of us (R.L.) in the program Helix Express 5.0.1<sup>®</sup>. There were

137 palynological literature sources, 25 from published reports and 112 from unpublished reports (Appendix 1). Most of these unpublished reports were produced by various Australian State Geological Surveys from petroleum exploration reports. Each sample taken within a core was regarded as an assemblage and, therefore, representative of one parent flora. In total, there were 1267 samples with diversity data and 141 samples with abundance data. Samples in this study were defined and screened according to the criteria set by Lupia et al. (1999). These are: (1) lists of palynomorphs from samples must be complete because diversity and abundance are being measured as relative values within a flora; (2) samples must be prepared from one source rock and taken from one area, as preparations combined from various sources and over large sections do not represent a single flora; and (3) samples must contain at least 10 species to remove the large effects that one or two species can have on percentage values and ensure that samples have been thoroughly investigated and described. A minimum of 10 species was chosen because Lupia et al. (1999) demonstrated that samples with a minimum number of 10 species showed the same changes in magnitude, direction and apparent timing of the angiosperm diversification as samples with a minimum of 20 species. For diversity data, taxonomic recognition to the species level was required. However, because abundance data were analysed to the family

level, taxonomic resolution was only required to the genus level. An additional criterion for abundance analysis was that at least 50 palynomorphs were counted in a sample; raising the minimum count would have reduced the already small number of samples for which abundance data are available. Counts of 50–300 are usually adequate to obtain a reliable measure of relative abundance for the more significant elements within a sample (Moore et al., 1991). Literature that did not meet these criteria was excluded from this study.

The age of each sample was accepted from the original paper if the age was based on the Australian Mesozoic palynobiostratigraphic zonation of Helby et al. (1987) or if the scheme utilised was incorporated into that of Helby et al. (1987). Ages assigned to assemblages using other biostratigraphic zonations were re-assessed using the scheme of Helby et al. (1987). An absolute age was assigned to each assemblage by using the mid-point of the assemblage's biozone or chronostratigraphic stage (e.g. Albian 112–97 Ma: mid-point = 104.5 Ma). Ages were defined according to the time scale of Harland et al. (1990).

Taxonomic affinities of palynomorphs were obtained from various literature sources including the catalogue of in situ pollen and spores compiled by Balme (1995). Species determinations were accepted from the original report, but synonymies were adjusted according to the most recent and formally described taxonomic changes. Paly-

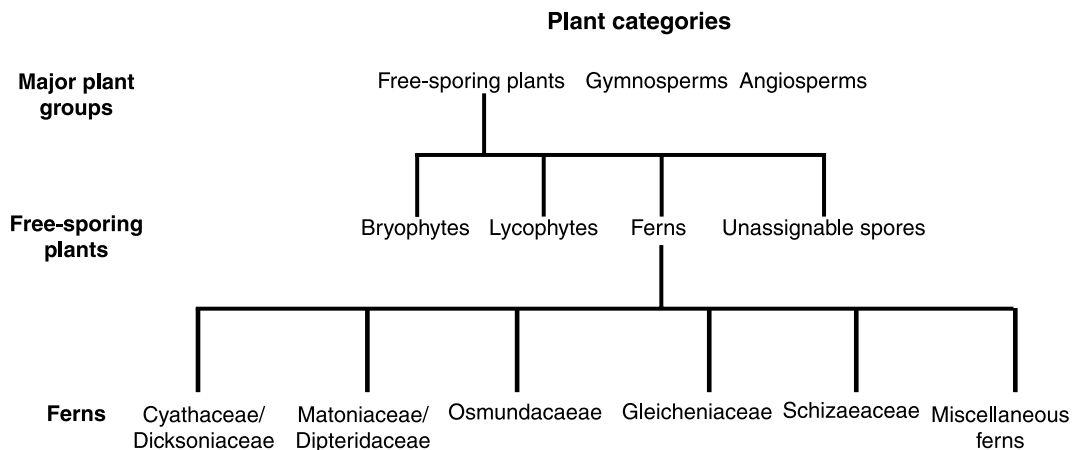


Fig. 1. Categories of the plant groups investigated.

nomorphs were assigned to one of three major categories: free-sporing plants, gymnosperms and angiosperms (Fig. 1). Spores were then further separated into bryophytes, lycophytes, ferns and unassigned spores; the final category incorporates all spores that could not be assigned to either of the three former groups. Fern spores were subsequently ascribed to a family or family group: Cyatheaceae/Dicksoniaceae, Osmundaceae, Matoniaceae/Dipteridaceae, Gleicheniaceae and Schizaeaceae. Preliminary examination of spore lists showed that, when family affinities are known, most fern spores were ascribed to one of these ‘Mesozoic’ families. Fern spores that could be ascribed to more than one family, belong to other families (e.g. Marsileaceae) or cannot be reliably attributed to these families were recorded as ‘mis-

cellaneous ferns’, and the majority of miscellaneous fern spores fell into the latter category. Data on megaspores, dinoflagellates, aquatic cysts, fungal spores and fauna were not included in this study.

The database incorporates ca. 30 000 records of spores and pollen. These data were compiled and simple moving averages were computed to summarise major trends through time. Window sizes of  $\pm 15$ ,  $\pm 10$  and  $\pm 7.5$  Myr were selected and these values are incorporated into the moving average calculation by using the window size to define which adjacent data will be included in calculations for the interval under investigation. Moving average analysis provides a mathematical basis for downweighting data that may otherwise skew the results, but it has a negative effect of

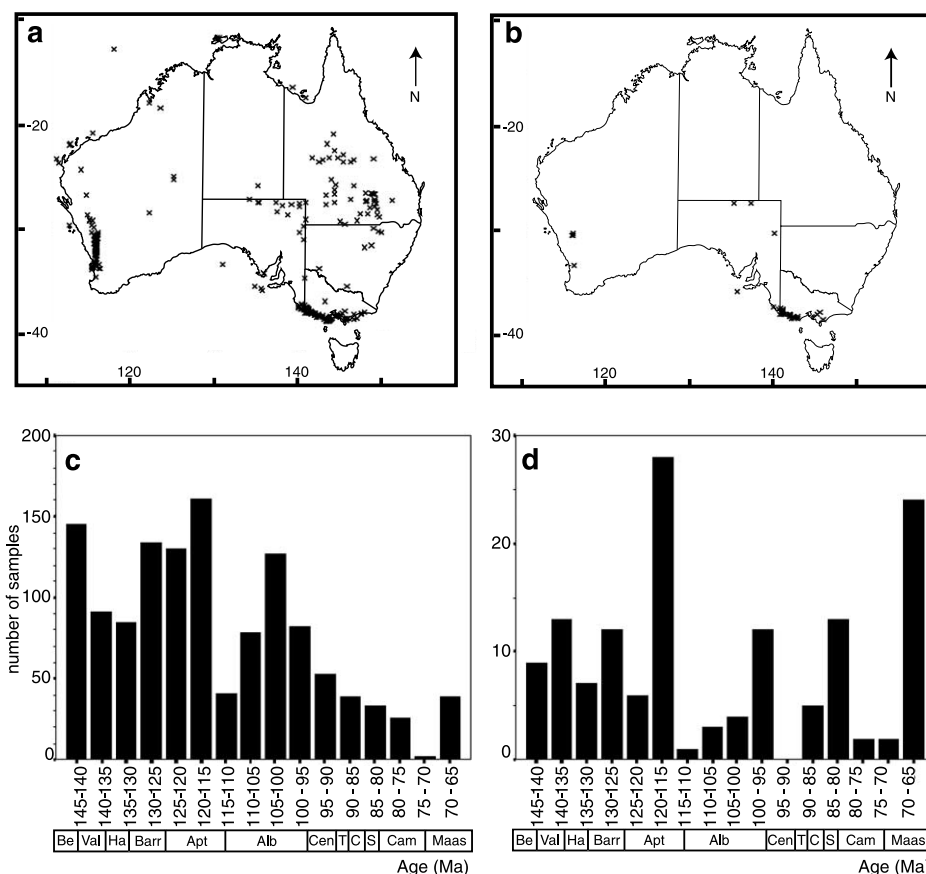


Fig. 2. Distribution of palynological samples used in this study. (a) Geographic distribution of diversity samples. (b) Geographic distribution of abundance samples. (c) Temporal distribution of diversity samples within each 5-Myr interval during the Cretaceous. (d) Temporal distribution of abundance samples within each 5-Myr interval during the Cretaceous.

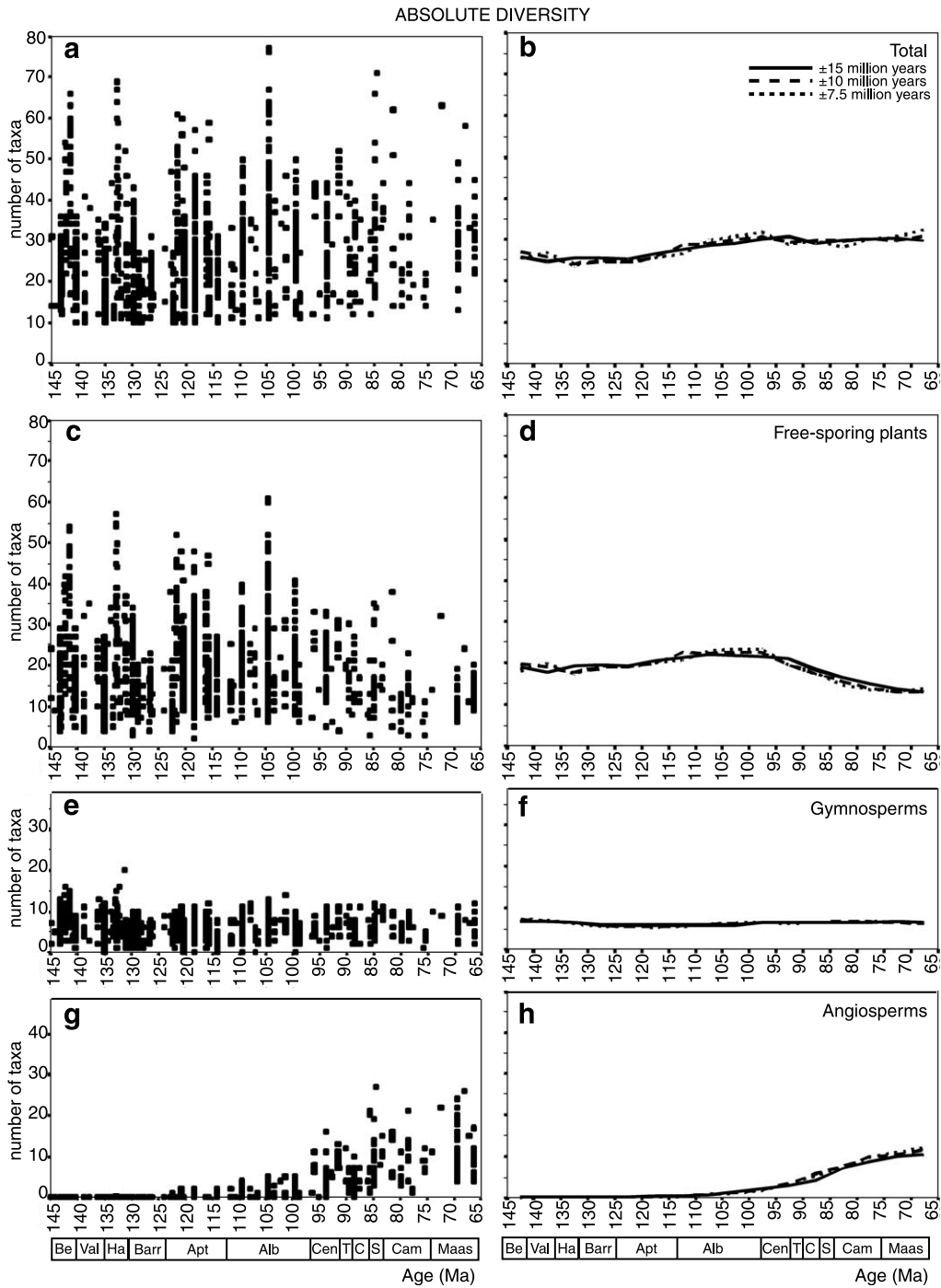


Fig. 3. Absolute diversity: scatterplots and moving average analyses for all pollen and spores and the major plant groups during the Cretaceous. (a, b) All pollen and spores. (c, d) Free-sporing plants. (e, f) Gymnosperms. (g, h) Angiosperms. Be – Berriasian, Val – Valanginian, Ha – Hauterivian, Barr – Barremian, Apt – Aptian, Alb – Albian, Cen – Cenomanian, T – Turonian, C – Conacian, S – Santonian, Cam – Campanian, Maas – Maastrichtian.

blurring rapid changes if the window is too large. Moving average values were imported into SPSS® (Statistical Package for the Social Sciences) and plotted.

## 2.2. Data distribution

Samples yielding data on the diversity of palynomorphs are widely distributed across Australia, although there are several areas with a high concentration of samples (Fig. 2a). These heavily sampled areas, the Perth, Surat, Otway and Gippsland basins, correspond to regions that have high hydrocarbon potential. By comparison, fewer samples provide data on the abundance of palynomorphs because many Australian palynological studies have been undertaken only for biostratigraphic rather than floristic analyses (Fig. 2b).

In order to examine the distribution of the data, the Cretaceous was divided into 16 intervals each spanning 5 Myr (Fig. 2c,d). Samples yielding diversity data are available for all intervals, but the majority of samples are of Early Cretaceous age (145–97 Ma); this reflects the greater hydrocarbon potential and wider distribution of sediments of this age (Fig. 2c). In the smaller abundance dataset many intervals are represented by fewer than 10 samples and some intervals lack data (Fig. 2d). Some intervals have a disproportionately large number of samples because they incorporate the mid-point of a geological stage, and or biozone (Maastrichtian 74–65 Ma, equivalent to the *Tricolpites longues* Zone of Helby et al., 1987, mid-point 69.5 Ma).

Analysis of Early Cretaceous data from southeastern Australia revealed the same patterns as Early Cretaceous data for the whole of Australia. This suggests that the Late Cretaceous data (which are only available from southeastern Australia) will also be representative of the Australia-wide pattern from this period. Diversity analysis of the subset of samples containing abundance data reveals similar patterns to the entire dataset. This allows at least a general comparison of the diversity and abundance trends, despite the discrepancy in the size of the underlying datasets.

## 3. Results

### 3.1. Absolute diversity

Average absolute diversity of the palynofloras rises gradually from 25 to 30 species during the Cretaceous (Fig. 3a,b). The absolute species diversity of free-sporing plants declines in the Late Cretaceous from 20 to 10 species (Fig. 3c,d). Gymnosperms do not show any substantial change in absolute diversity (Fig. 3e,f). The first notable appearance of angiosperms occurred during the Albian and by the Maastrichtian there is an average of 10 angiosperm species per palynoflora (Fig. 3g,h).

### 3.2. Relative diversity

#### 3.2.1. Major palynomorph categories

Free-sporing plants display a significant decline in relative diversity, falling from 70% in the Early Cretaceous to 45% in the Late Cretaceous, but similar to absolute diversity there is a slight increase from the Neocomian to the Albian that precedes the decline (Fig. 4a,b). In comparison to the decline of free-sporing plants, there is a much smaller decline in gymnosperm relative diversity from 30% to 20% through the Cretaceous (Fig. 4c,d). The rise in angiosperm diversity begins in the Albian and reaches 35% relative diversity at the end of the Cretaceous (Fig. 4e,f).

#### 3.2.2. Free-sporing plants

Separation of the free-sporing plants into ferns, lycophytes, bryophytes, and unassigned spores, allows further resolution of the decline of free-sporing plants (Fig. 5). Bryophytes display low relative diversity of 7% near the beginning and end of the Cretaceous, but have higher levels of diversity (15%) during the mid-Cretaceous (Fig. 5a,b). The large drop in free-sporing plant relative diversity is attributable to a reduction in both the lycophytes (Fig. 5c,d) and ferns (Fig. 5e,f). Lycophyte relative diversity falls from 20% to 5%. The relative diversity of ferns rises from 36% to 40% in the Early Cretaceous and their decline begins in the Cenomanian. This decline is rather pronounced and relative diversity falls to 20% by

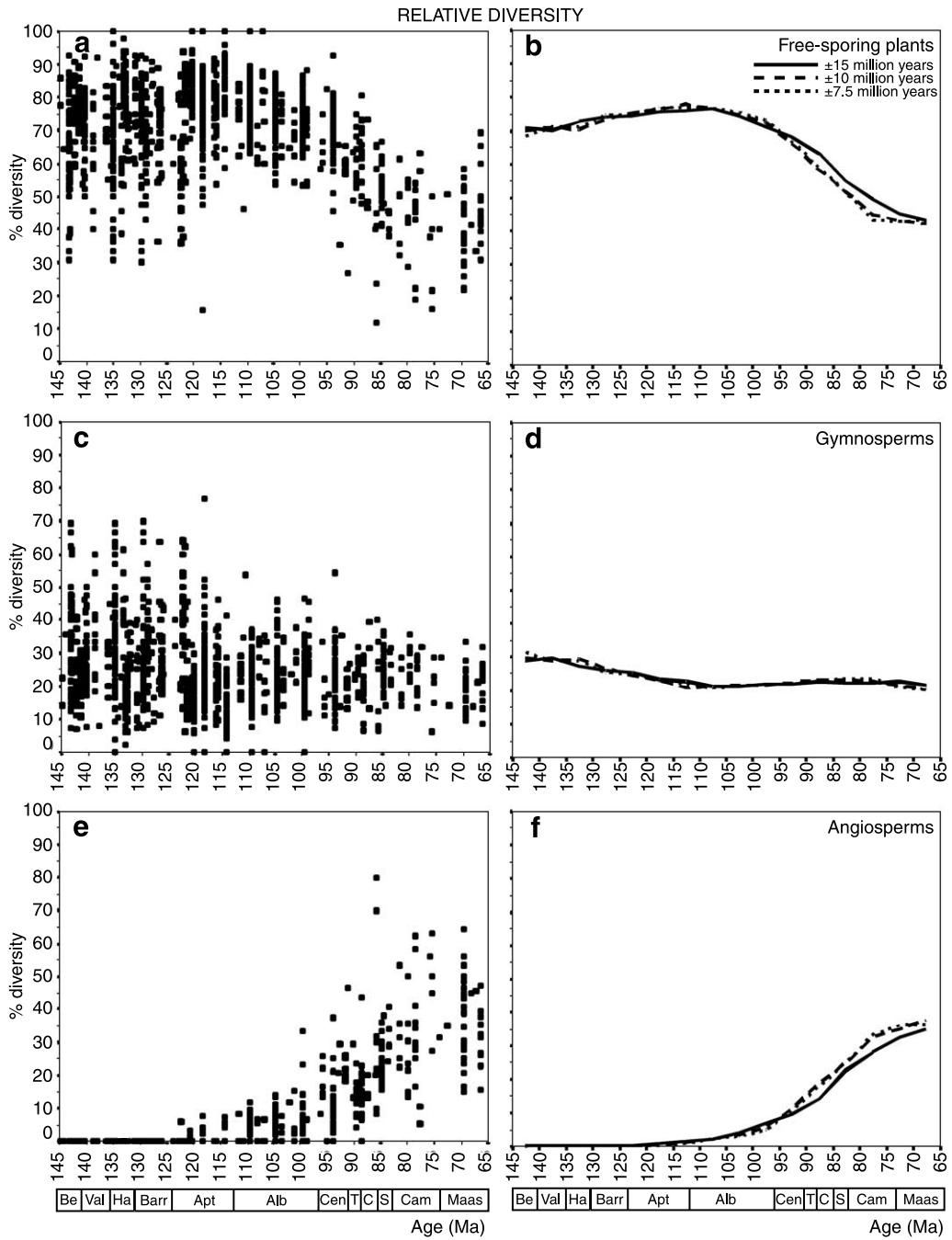


Fig. 4. Relative diversity: scatterplots and moving average analyses for the major palynomorph categories during the Cretaceous. (a, b) Free-sporing plants. (c, d) Gymnosperms. (e, f) Angiosperms. Stage abbreviations as for Fig. 3.

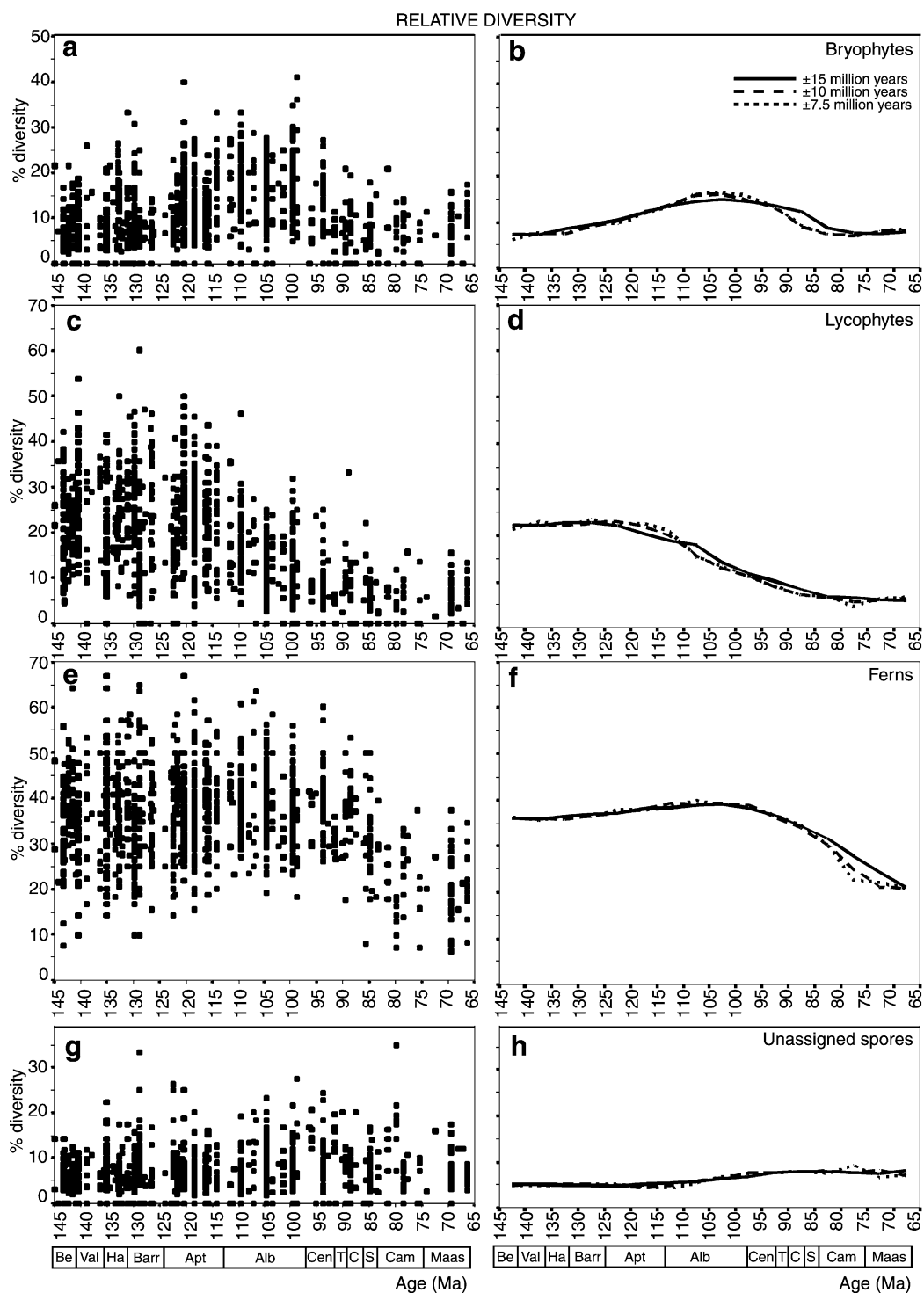


Fig. 5. Relative diversity: scatterplots and moving average analyses for free-sporing plant groups during the Cretaceous. (a, b) Bryophytes. (c, d) Lycophytes. (e, f) Ferns. (g, h) Unassigned spores. Stage abbreviations as for Fig. 3.





the end of the Cretaceous. The fall in relative diversity of lycophytes is similar in magnitude to the fern decline with both falling 15%, but the decline of the former group began earlier (in the Aptian) and resulted in a 75% reduction in initial values compared to a 50% reduction in ferns. Unassigned spores show only a very small rise from 5% diversity in the Early Cretaceous to 7% relative diversity during the Late Cretaceous (Fig. 5g,h); this 2% increase does not offset the decrease recorded in the other groups of free-sporing plants.

### 3.2.3. Fern families

The families Cyatheaceae/Dicksoniaceae (Fig. 6a,b), Matoniaceae/Dipteridaceae (Fig. 6c,d) and Osmundaceae (Fig. 6e,f) show only slight declines of less than a few percent. The pronounced decline in the diversity of ferns during the Late Cretaceous (Fig. 5f) was due to a decline in the miscellaneous ferns, (Fig. 6k,l) and to a lesser extent the Schizaeaceae (Fig. 6g,h). These miscellaneous fern spores initially had a high relative diversity, representing up to 15% of floras in the Early Cretaceous, but began to decline in the Albian and eventually fell to 5% relative diversity by the end of the Cretaceous. Relative diversity of Schizaeaceae rose gradually during the Early and mid-Cretaceous from 5% to 10%, but then declined in the Late Cretaceous to less than 2% (Fig. 6g,h). This 5% rise of Schizaeaceae accounts for the rise of 5% in ferns (Fig. 5f). Gleicheniaceae exhibits a contrasting trend to all other fern groups, increasing from 4% relative diversity in the Early Cretaceous to 10% in the Late Cretaceous (Fig. 6i,j).

## 3.3. Relative abundance

### 3.3.1. Major palynomorph categories

The largest decline in relative abundance is recorded for free-sporing plants (Fig. 7a,b). In the earliest Cretaceous, free-sporing plants underwent

a minor decline in relative abundance from approximately 60% to 55%. From the mid-Albian to mid-Cenomanian there was a major decline to 30% relative abundance and they remained at that level for the rest of the Cretaceous (Fig. 7a,b). The relative abundance of gymnosperms was more or less stable at values of 35% until the mid-Cretaceous (Fig. 7c,d). Angiosperms are first apparent in the moving averages between the mid-Albian to mid-Cenomanian and show an almost linear increase in relative abundance, reaching 35% relative abundance in the Maastrichtian (Fig. 7e,f).

### 3.3.2. Free-sporing plants

Bryophytes show no overall change with 5% relative abundance at the beginning and end of the Cretaceous, however, there is a peak in relative abundance of 10–20% during the mid-Cretaceous (Fig. 8a,b). Lycophytes fall from 15% to 5% throughout the Cretaceous (Fig. 8c,d) while ferns display the largest decline in abundance from 45% to 20% (Fig. 8e,f). Unassigned spores account for a few percent and therefore have little influence on the pattern of assignable taxa (Fig. 8g,h).

### 3.3.3. Fern families

Cyatheaceae/Dicksoniaceae increased in relative abundance from 16% to 22% in the Early Cretaceous, but a decline to 10% relative abundance occurred in the Late Cretaceous (Fig. 9a,b). Less than 5% relative abundance is recorded for miscellaneous ferns (Fig. 9k,l), Matoniaceae/Dipteridaceae (Fig. 9c,d) and Schizaeaceae (Fig. 9g,h), and there is little change in the abundance of these ferns during the Cretaceous. Osmundaceous spores declined from 25% to less than 5% relative abundance during the Early and mid-Cretaceous (Fig. 9e,f). In contrast, gleicheniaceae spores maintained consistently low (less than 2%) abundance for the first 20 Myr of the Cretaceous, increased to 7% relative abundance during the Aptian, then declined slightly between the Albian

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Fig. 6. Relative diversity: scatterplots and moving average analyses for fern groups during the Cretaceous. (a, b) Cyatheaceae/Dicksoniaceae. (c, d) Matoniaceae/Dipteridaceae. (e, f) Osmundaceae. (g, h) Gleicheniaceae. (i, j) Schizaeaceae. (k, l) Miscellaneous ferns. Stage abbreviations as for Fig. 3.

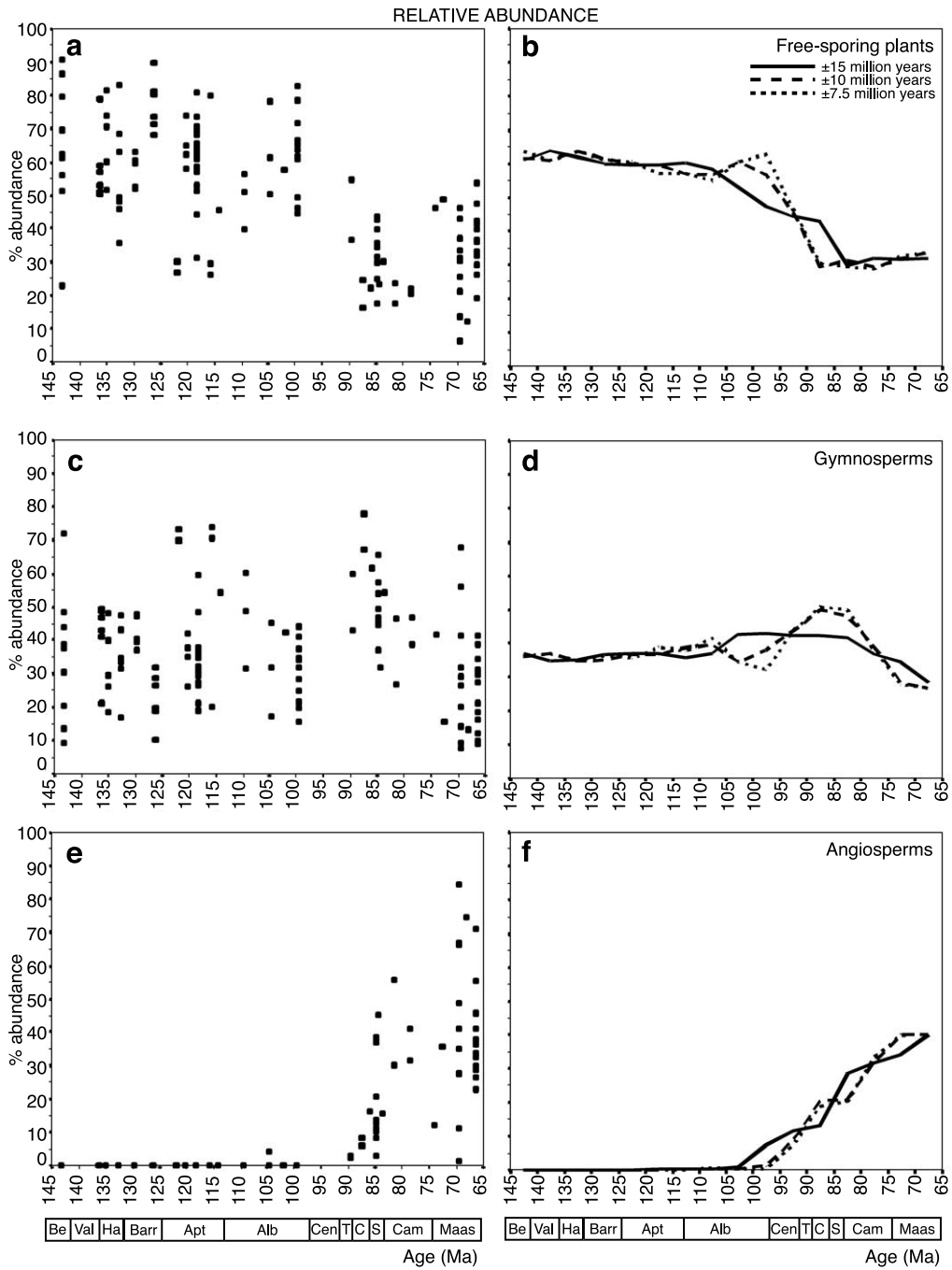


Fig. 7. Relative abundance: scatterplots and moving average analyses for the major palynomorph categories during the Cretaceous. (a, b) Free-sporing plants. (c, d) Gymnosperms. (e, f) Angiosperms. Stage abbreviations as for Fig. 3.

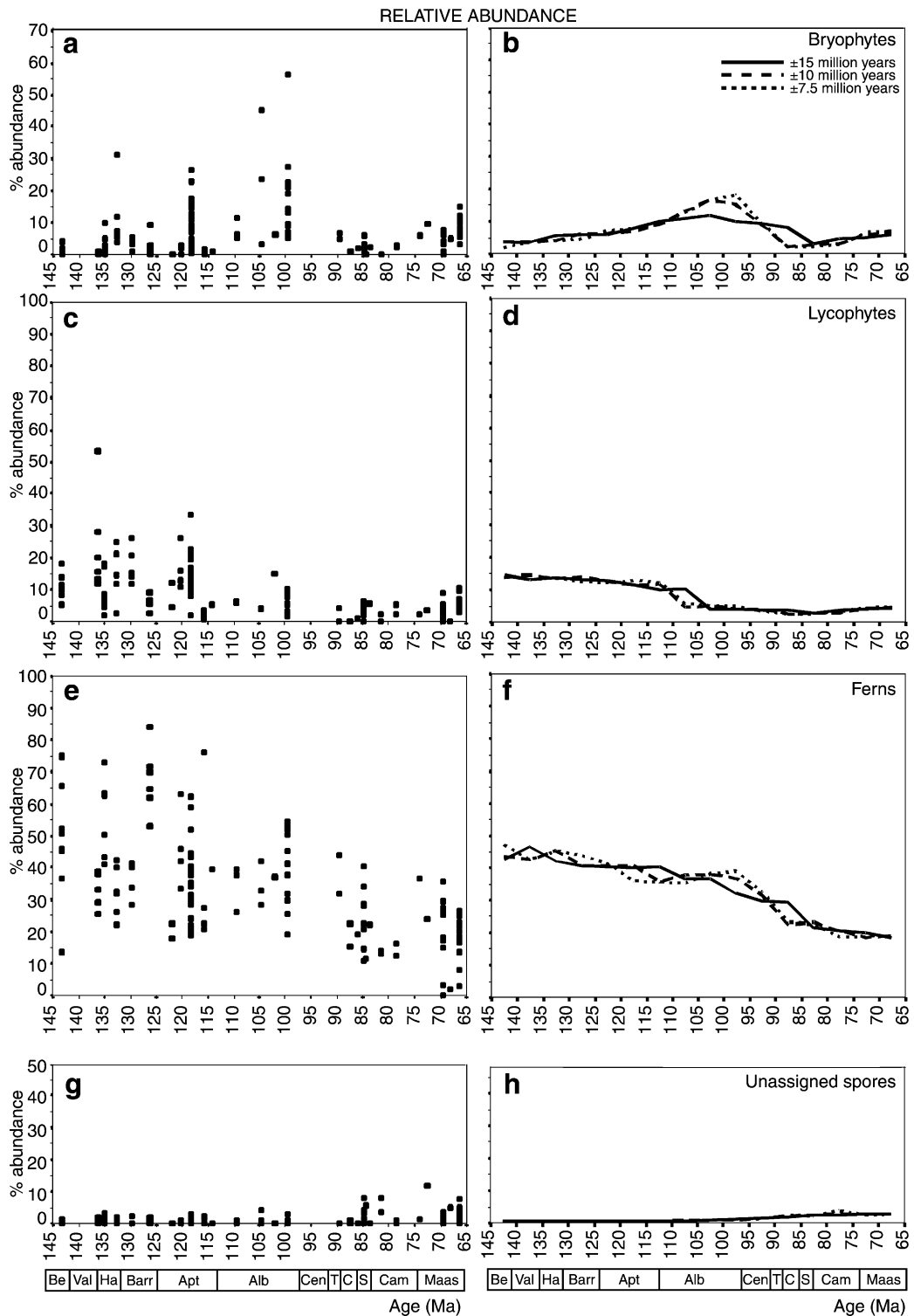


Fig. 8. Relative abundance: scatterplots and moving average analyses for free-sporing plant groups during the Cretaceous. (a, b) Bryophytes. (c, d) Lycophytes. (e, f) Ferns. (g, h) Unassigned spores. Stage abbreviations as for Fig. 3.

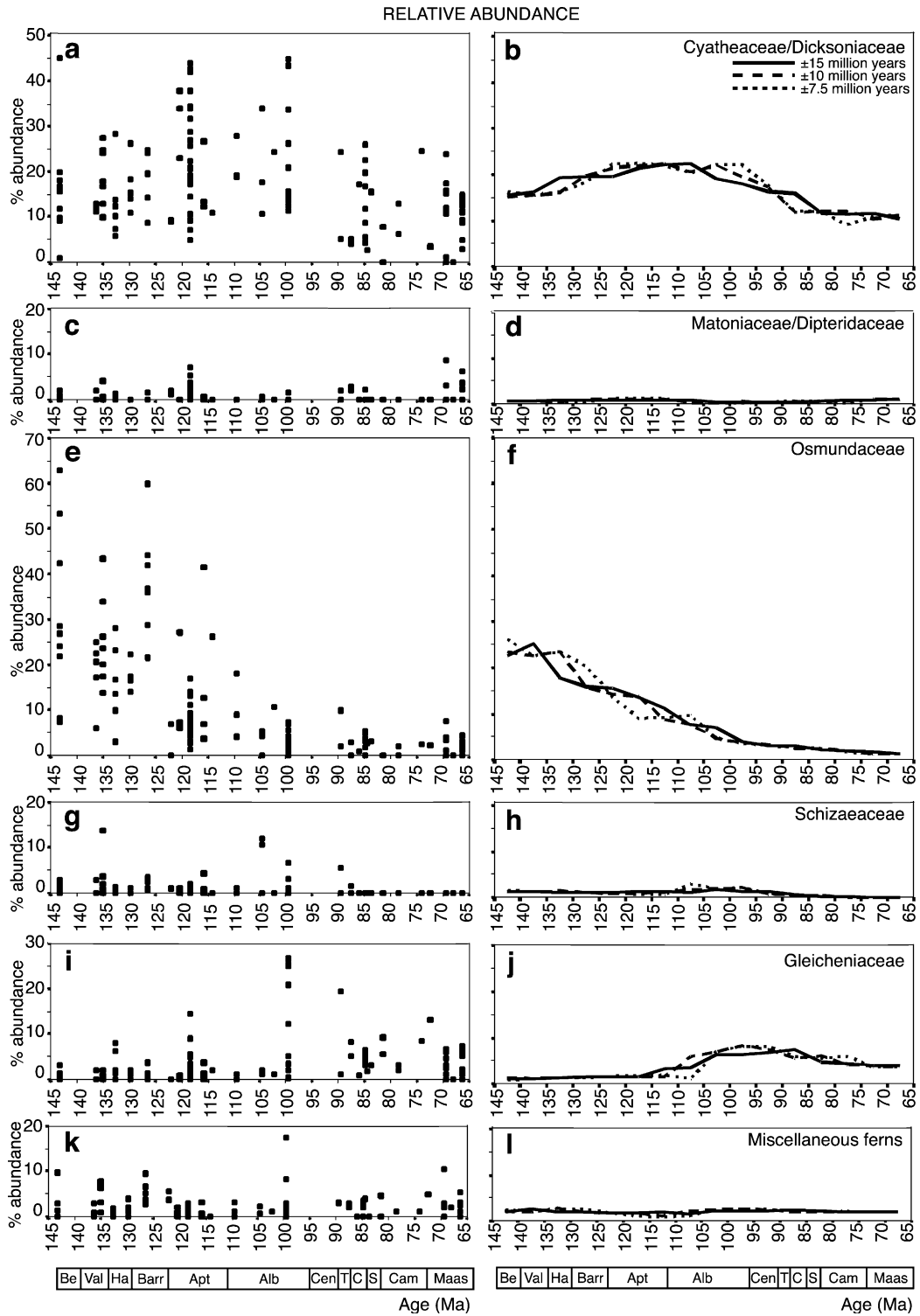


Fig. 9 (Caption overleaf).

and Maastrichtian to 4% relative abundance (Fig. 9i,j).

#### 4. Discussion

##### 4.1. Use of palynofloras to study floristic change

Palynomorphs are a valuable source of data because they are decay-resistant, produced in copious quantities, widely dispersed and can be recovered from most terrestrial and nearshore marine sediments. Although there is a bias in the over-representation of palynomorphs from floodplain, lacustrine, or deltaic habitats, this bias is probably smaller than the bias towards lowland palaeoenvironments for macro- and mesofossils. Other representation biases, such as differential preservation of palynomorphs, and recognition biases were fully addressed by Lupia et al. (1999).

The history of past vegetation is preserved as palynofossils (pollen and spores) and macrofossils (e.g. leaves, stems, fruits and roots). Palynofloral and macrofloral remains are subject to different biological and taphonomic biases and represent independent sets of data that relate to the same vegetation. Investigation of Cretaceous floristic change in North America using both the palynofloras and macrofloras has shown that the two records are broadly congruent (Lidgard and Crane, 1990). The main difference between the trends of the two fossil records was a more gradual increase in angiosperm relative diversity in the palynofloras compared to macrofloras. Most importantly, changes in the diversity of palynomorphs and macrofossils displayed similarity in both patterns and magnitude, which suggests that either one of these datasets alone will yield a reliable and robust result. In this study palynological data were used to assess the floristic changes of ferns.

Within Australia there are numerous palynological studies of bore cores and exposed sedi-

ments (137 literature reports comprising 1267 individual samples with palynofloristic data were examined in this study). This provides a vast dataset for thorough investigation of the biogeographic and temporal patterns of floristic representation and diversity in the past. By comparison, there is a much smaller Cretaceous macrofossil record for Australia as many assemblages remain undocumented or incompletely described; in fact less than 10 Cretaceous macrofloras have been reported in detail.

##### 4.2. Absolute diversity and relative diversity

Diversity can be measured as either absolute diversity or relative diversity. The use of absolute diversity poses difficulties in determining whether trends are the result of floristic change or differences in the number of taxa per sample. Relative diversity circumvents this problem by standardising the totals of all assemblages to the same scale (i.e. 100%), thus trends are examined by assessing the changes in the contribution of each group over time. In this analysis the average total number of species per flora increases by five species, angiosperms increase from zero to approximately 10 species and free-sporing plants show a real decline in species numbers by ca. 10 species (Fig. 3). Therefore, the decline observed in the relative diversity of non-angiosperm groups does not appear to be entirely a statistical consequence of increasing angiosperm diversity. Relative diversity has been employed in this study as it provides a greater degree of consistency between assemblages and is less affected by differences in palynomorph recovery (e.g. absolute diversity can be compromised by differential palynological yields and sedimentological biases rather than real floristic changes). Furthermore, relative diversity is the measure used in most previous studies and allows direct comparison of the patterns in this study to the results of Lidgard and Crane (1988) and Lupia et al. (1999).

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Fig. 9. Relative abundance: scatterplots and moving average analyses for fern groups during the Cretaceous. (a, b) Cyatheaceae/Dicksoniaceae. (c, d) Matoniaceae/Dipteridaceae. (e, f) Osmundaceae. (g, h) Gleicheniaceae. (i, j) Schizaeaceae. (k, l) Miscellaneous ferns. Stage abbreviations as for Fig. 3.

Table 1  
Values of relative diversity and relative abundance for all plant groups examined

|                           | Relative diversity (%) |                |                 | Relative abundance (%) |                |                 |
|---------------------------|------------------------|----------------|-----------------|------------------------|----------------|-----------------|
|                           | Early Cretaceous       | mid-Cretaceous | Late Cretaceous | Early Cretaceous       | mid-Cretaceous | Late Cretaceous |
| Free-sporing plants       | 70.3                   | 72.5           | 42.1            | 61.8                   | 56.6           | 33.4            |
| Gymnosperms               | 29.7                   | 21.7           | 20.3            | 36.0                   | 38.0           | 26.6            |
| Angiosperms               | 0                      | 5.8            | 37.6            | 0                      | 1.2            | 39.9            |
| Bryophytes                | 7.2                    | 14.8           | 8.1             | 3.8                    | 15.2           | 6.9             |
| Lycophytes                | 21.9                   | 11.2           | 6.3             | 14.0                   | 4.2            | 4.6             |
| Ferns                     | 36.2                   | 39.0           | 20.9            | 43.4                   | 36.7           | 19.2            |
| Unassigned spores         | 4.9                    | 7.6            | 6.9             | 0.6                    | 0.7            | 2.7             |
| Cyatheaceae/Dicksoniaceae | 8.2                    | 8.1            | 6.2             | 15.3                   | 19.5           | 11.1            |
| Osmundaceae               | 4.8                    | 4.0            | 2.5             | 23.3                   | 3.7            | 1.4             |
| Matoniaceae/Dipteridaceae | 2.4                    | 0.8            | 1.2             | 0.5                    | 0.5            | 1.1             |
| Schizaeaceae              | 5.4                    | 9.2            | 1.0             | 1.3                    | 2.1            | 0               |
| Gleicheniaceae            | 3.1                    | 5.4            | 6.6             | 1.2                    | 8.3            | 3.7             |
| Miscellaneous ferns       | 12.4                   | 11.4           | 3.7             | 2.1                    | 2.7            | 2.0             |

Ages for the Early Cretaceous are 142 Ma, mid-Cretaceous 97 Ma, and Late Cretaceous 67 Ma. Values are taken from moving average window  $\pm 10$  Myr. These percentages do not have any statistical reality and are presented as a summary of the trends.

Comparison of the absolute versus relative diversity of free-sporing plants shows that the Late Cretaceous decline in free-sporing plant absolute diversity (Fig. 3d) is smaller than the drop in relative diversity (Fig. 4b). Gymnosperm absolute diversity (Fig. 3f) and relative diversity (Fig. 4d) trends are closely comparable and both indicate only slight declines throughout the Cretaceous. The increase in angiosperms appears to be less pronounced when examined as absolute diversity (Fig. 3h) compared to relative diversity (Fig. 4f). This is probably because the decrease in free-sporing plant absolute diversity compounds the increase in angiosperm diversity, when the groups are scaled relative to each other.

#### 4.3. Relative diversity and relative abundance

Free-sporing plant relative diversity (Fig. 4b) and relative abundance (Fig. 7b) trends are very similar (Table 1): both indicate a high importance (i.e. the proportion that the group contributes to a flora) of free-sporing plants (ca. 70%) at the beginning of the Cretaceous and that there was a decline of 30% in the mid-Cretaceous (at ca. 105–95 Ma). Relative diversity and relative abundance trends for gymnosperms show small declines (less than 10%) through the Cretaceous

(Table 1). Angiosperm relative diversity and relative abundance increased rapidly in the Late Albian and reached similar magnitudes (ca. 35–40%) by the end of the Cretaceous (Table 1). Relative abundance of angiosperms increased at an almost linear rate while relative diversity rose less rapidly through the mid-Cretaceous.

Relative diversity and relative abundance trends are also similar for the separate free-sporing plant groups. There are corresponding mid-Cretaceous rises in the relative diversity and relative abundance of bryophytes (Figs. 5b and 8b), and matching declines in the relative diversity and relative abundance of lycophytes (Figs. 5d and 8d) and ferns (Figs. 5f and 8f) through the Cretaceous. A slight rise in unassigned spores (Figs. 5h and 8h) in the Late Cretaceous is recorded in both datasets. Relative importance of the free-sporing plant groups is also consistent between the two measurements with ferns being the most common component, followed by lycophytes, bryophytes and miscellaneous spores (Table 1).

For particular fern families, however, trends in relative abundance and relative diversity are not so concordant. The Early Cretaceous increase in the relative diversity of ferns (Fig. 5f) is due to the increase in Schizaeaceae and the subsequent large decline of ferns (Fig. 5f) can mainly be attributed

to a decrease in the miscellaneous ferns (Fig. 6l) and Schizaeaceae (Fig. 6h). However, the drop in relative abundance of ferns is largely due to the decline of a single family, Osmundaceae (Fig. 9f). Comparison of abundance and diversity for ferns shows matching patterns for Matoniaceae/Dipteridaceae and Gleicheniaceae, but all other fern groups have dissimilar diversity and abundance values.

The decrease in the relative diversity of miscellaneous ferns could partly be due to a 'modernisation' of form, such that spores in the Late Cretaceous are easier to assign to one of the other fern groups compared to spores of the Early Cretaceous. In contrast, the relative abundance of miscellaneous ferns is relatively low and does not exhibit a decrease in the Late Cretaceous.

These differences in fern family diversity and abundance may be due to biases in the recognition of spores. For example, distinctly shaped and large spores such as those belonging to the genus *Cyathidites* (Cyatheaceae/Dicksoniaceae) are easily recognised, and therefore well represented in the abundance data, but their lack of ornamentation, and hence taxonomically distinguishing features, results in 'low' diversity. The converse may occur for distinctly sculptured spores, such as striately ornamented spores of which many are probably schizaeaceous. This ornamentation is easily recognised and distinguished, therefore the morphological features of these spores are the basis for greater systematic investigation and separation but may occur at naturally low abundance levels. This suggests that at low taxonomic levels (i.e. at the species level), spore identification may be subject to recognition biases that could result in disparities between the abundance and diversity data, but at higher levels (i.e. orders) recognition biases have probably not a major influence on the data.

#### 4.4. 'Radiation' of the 'polypodiaceous' ferns

Most extant ferns, in terms of diversity and abundance, belong to the recently evolved 'modern' ferns, Polypodiaceae sensu Engler and Diels (1936). Many workers have argued that there was a radiation of these polypodiaceous ferns in re-

sponse to newly established niches created by the evolution of the angiosperms (Lovis, 1977; Crane, 1987; Tidwell and Ash, 1994). However, our analysis offers little evidence to support a major radiation of Polypodiaceae in the Cretaceous. The diversity and abundance of miscellaneous ferns (presumably incorporating most Polypodiaceae) do not show any increases through the Late Cretaceous (Figs. 6l and 9l; Table 1). There is a slight increase in unassigned spores and it is possible that these spores may be derived from polypodiaceous ferns but there is no firm evidence to support this interpretation. Further investigation of the affinities of these spores and examination of the Paleogene spore record may help to elucidate polypodiaceous diversification in Australia.

#### 4.5. Possible causes for the trends

There is evidence for mid-Cretaceous environmental change and disturbance beginning in the Albian in Australia (Frakes, 1999). Land area fragmentation, more extensive coastal environments, globally elevated temperatures, and rifting of Australia from Antarctica and New Zealand may correspond to high disturbance levels in the Australian region. Rises in the relative diversity and abundance of Gleicheniaceae, Schizaeaceae, and bryophytes and the beginning of the angiosperm expansion also occur at the beginning of the Albian and may be related to these changes. Some modern members of the Schizaeaceae and especially Gleicheniaceae are known to proliferate in disturbed environments and bryophytes are ready colonisers of bare ground. However, inferring ecological conditions from trends in diversity and abundance based on ecological characteristics of modern taxa may be unreliable because extant members of these families occupy diverse habitats and their environmental tolerances may differ markedly from extinct representatives. Some authors have attributed the declines in some plant groups, including ferns, to competitive exclusion caused by angiosperms (Retallack and Dilcher, 1981). The data in this study show a temporal relationship between the increase in angiosperms and decline of other groups, which is consistent



with the causal hypothesis of angiosperm competition with other plant groups.

#### 4.6. Comparison of patterns between Australia and North America

This study is the first analysis of long-term Cretaceous vegetation change associated with angiosperm evolution in the Southern Hemisphere. This study utilises 1267 samples for the study of diversity and 141 samples for the study of abundance, whereas Lupia et al. (1999) obtained 922 diversity samples and 359 abundance samples from North America. The methodology has been adopted from the investigation by Lupia et al. (1999) and the magnitudes of the Australian and the North American studies are comparable. North America is the only region for which similar aged palynofloras have been examined on the same scale and with the same methodology, therefore the only region for which direct comparisons are possible. Any differences in the results and trends from this study and that of Lupia et al. (1999) are likely to reflect floristic patterns rather than analytical differences.

##### 4.6.1. Diversity

Angiosperm diversification trends are similar in both Australia and North America. There is a gradual initial angiosperm increase, followed by a sharp increase in the mid-Cretaceous and, in the last 20 Myr of the Cretaceous, the relative diversity reaches around 40%. The patterns and timing of decreasing relative diversity in free-sporing plants are also similar. In Australian palynofloras, free-sporing plant relative diversity decreased from 70% in the earliest Cretaceous to 40% in the latest Cretaceous, while relative diversity in North America fell from 60% to 40%. Gymnosperms experienced a moderate decrease in relative diversity in Australian palynofloras from 30% at the beginning of the Cretaceous to 20% at the end of the period. North American gymnosperm relative diversity fell from 40% to 20% over the same interval.

##### 4.6.2. Abundance

In the North American analysis, sampling was

not uniform across palaeolatitudes through the Cretaceous. In that analysis, samples with abundance data are sparse above 42°N prior to the Cenomanian. Therefore comparisons will be made with samples from below 42°N in North America. The pattern of decline of free-sporing plant relative abundance is similar with a decline from 40% to 20% in North America and 60% to 30% in Australia. In the low latitude North American palynofloras, gymnosperms exhibit no consistent trend but there is a slight decline in abundance from 60% to 50% similar to the decline in the Australian palynofloras from 35% to 25% relative diversity. In Australia free-sporing plants have the greatest relative abundance values whereas gymnosperms are most abundant in North American palynofloras. Angiosperms appear in the moving average plots during the Albian in the Australian and Antarctic palynofloras and during the Aptian in North America. Despite this diachroneity, relative abundance of angiosperm values reach similar levels by the end of the Cretaceous in all regions.

##### 4.6.3. Fern families

Most other analyses of palynofloral change in the Cretaceous have focussed on angiosperm diversification and proliferation and there has been little investigation of the fern spore record; consequently there are few studies for comparison. Crane and Lidgard (1990) presented diversity and geographic trends of schizaeaceous and gleicheniaceus spores and found evidence for their reduced importance during the mid-Cretaceous in North America especially in the mid-palaeolatitudes (20°N to 20°S). However, our study shows that schizaeaceous and gleicheniaceus spores increased in relative diversity and abundance in Australia to beyond the mid-Cretaceous, with a subsequent decline in only Schizaeaceae. This indicates that regional factors, such as local environmental conditions and disturbances, may have had an important influence on the changes in the fern floras through the Cretaceous. The North American trends for Gleicheniaceae and Schizaeaceae were presented according to palaeolatitude (Crane and Lidgard, 1990) but as Australian floristic patterns have not been examined geo-

graphically, detailed comparisons cannot yet be made.

Crane and Lidgard (1990) noted that the decline of Schizaeaceae and Gleicheniaceae was consistent with the hypothesis that the decline of 'Mesozoic' families led to their eventual replacement by the derived 'polypodiaceous' fern groups. However, they did not examine the spore record for further evidence to support this hypothesis. Some results presented here provide partial support for a decline in some 'Mesozoic' fern families (Osmundaceae, Cyatheaceae/Dicksoniaceae, and Schizaeaceae), but other data contradict this hypothesis and show that there was a rise in one 'Mesozoic' fern family (Gleicheniaceae) and that some groups showed little change (Matoniaceae/Dipteridaceae). There is certainly no evidence for a radiation of polypodiaceous ferns in the Australian Cretaceous.

## 5. Conclusions

During the Cretaceous there was a large decline in free-sporing plant relative diversity and abundance compared to that of gymnosperms during the rise of angiosperms. However, more detailed analysis of the data reveals that some free-sporing groups (bryophytes) temporarily proliferated during the early phases of angiosperm evolution but eventually declined in relative diversity and abundance. Reductions of other free-sporing plants (ferns and lycophytes) began in the Late Cretaceous and the very small increase of unassigned spores in the Late Cretaceous does not offset the declines in other groups. Examination of the ferns shows that the pattern of the fern decline is not consistent within its component families and that relative diversity and abundance patterns for these families also differ. The trend in fern diversity is mainly due to the patterns of two groups, whereas the trend in fern abundance is due to one group. There is a decline in the relative diversity of miscellaneous ferns and Schizaeaceae, while relative diversity of Osmundaceae, Matoniaceae/Dipteridaceae and Cyatheaceae/Dicksoniaceae did not change. There is mid-Cretaceous rise in the relative diversity of the Schizaeaceae and Gleiche-

niaceae, which has been noted in previous palynological studies (Dettmann and Playford, 1969) and is confirmed quantitatively. During the Late Cretaceous the relative abundance of Gleicheniaceae increased, while Cyatheaceae/Dicksoniaceae declined. Throughout the Cretaceous the relative abundance of Osmundaceae steadily declined, while Matoniaceae/Dipteridaceae and miscellaneous fern abundance values did not change. The decline in the relative diversity and the steady relative abundance values for miscellaneous ferns suggest that a polypodiaceous fern radiation did not occur in Australia during the Cretaceous.

Comparison of the patterns, timing and magnitude of changes in the Northern and Southern Hemisphere suggests that there are broad similarities in the relative diversity and abundance trends of major plant groups in these regions. Free-sporing plants exhibit high diversity levels but the diversity of this group falls sharply during the Cretaceous, co-inciding with angiosperm diversification. Abundance of free-sporing plants is greater in Australia while gymnosperms were the more common element in the abundance of North American palynoflora. The greatest decline in abundance in the North American and Australian palynofloras is recorded for free-sporing plants and smaller declines are observed in the gymnosperms. Investigation of palaeolatitudinal differences in the palynofloras will further elucidate geographical patterns in the palaeofloras and enable closer comparison to the North American floristic patterns.

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## Appendix 1

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