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## LEAF ARCHITECTURAL PROFILES OF ANGIOSPERM FLORAS ACROSS THE CRETACEOUS/TERTIARY BOUNDARY

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**ABSTRACT.** The Cretaceous/Tertiary boundary extinction has long been considered one of the most important identifiable events in the course of Phanerozoic evolution. At times, the dramatic evidence for this has obscured the fact that any extinction event is selective and may not affect all groups of organisms in the same way. In this paper we examine a North American plant fossil database from the Mesozoic and Cenozoic eras in order to re-evaluate the evolutionary significance of the Cretaceous/Tertiary extinction on plants. When we compare the leaf architectural profiles of fossil floras in each stage of the Cretaceous and epoch of the Cenozoic, we find that the changes in leaf architecture at the Maastrichtian/Paleocene boundary cannot be statistically distinguished from the population of changes at other boundaries. To the extent that patterns in leaf architecture reflect ecosystem structure, we can therefore conclude that despite the local species or morphotype extinctions that are known to have taken place at the boundary, the effect of the extinction on the structure of plant ecosystems was either minor or short-lived. Certainly, the extinction seems insignificant compared with the dramatic changes in leaf architecture that accompanied the rise of angiosperms in the middle Cretaceous. This analysis also provides an example of the importance of time scales in the evaluation of macro-evolutionary pattern, and shows how the use of morphological categories instead of phylogenetic groups or simple diversity measures can produce rich and ecologically informative semi-quantitative proxy measurements of plant evolutionary patterns.

### INTRODUCTION

Since 1980, when Alvarez and others proposed an extra-terrestrial impact as the extinction mechanism at the K/T boundary, questions about the significance of this extinction for plant ecosystems have remained contentious, though there seems to be little question that the K/T extinctions dramatically affected the course of terrestrial vertebrate evolution. Long before the probable cause of the extinction was determined, the faunal discontinuity at the boundary was considered so important that it was used to identify major subdivisions of geological time. The floral record, however, does not show as clear a discontinuity. Did the K/T boundary event change the course of plant evolution, or did it merely cause some local species extinctions without affecting plant evolution in any lasting way? Were the K/T extinctions more or less influential than the rise of angiosperms in the middle Cretaceous? Answers to these questions based on data sets of limited geographical and chronological extent have been numerous, but the difficulty of amassing a large set of comparable data on botanical macrofossil occurrences has restricted most data-based discussions to local dynamics and short-term effects.

In order to address these questions about the long-term effects of the K/T boundary extinction on plant evolution at a continental scale, we have examined a database of fossil leaf occurrences through the Mesozoic and Cenozoic eras from an eco-morphological perspective. That is, we have intentionally ignored the available

taxonomic information, instead examining only change in patterns of leaf architecture. This provides a more complex and ecologically informative view of change than most prior examinations of the floral record at a comparable geographical scale and temporal resolution, which have focussed on species diversity as the sole response variable.

Consensus on the floral response to the K/T boundary event has varied widely during the past twenty years: the initial reaction by one of us (LJH) in 1981 was that the North American macrobotanical record made it 'unnecessary for the paleobotanist to invoke a catastrophic or unusual mechanism to explain the observed patterns of localized extinctions' (Hickey, 1981:302). Subsequently, however, palynological data, better correlation, and more thorough sampling at good boundary sections modified this general response to the point where Johnson and Hickey (1990) discussing a composite stratigraphic section in Marmarth, North Dakota, wrote that 'results of this analysis of the terrestrial plant record are compatible with the hypothesis of a biotic crisis caused by extraterrestrial impact at the end of the Cretaceous' (Johnson and Hickey, 1990:433). The most recent discussions seem to reinforce this latter point of view; a new analysis of the Hell Creek/Fort Union boundary in North Dakota (Wilf and Johnson, 2004), which is clearly the best-studied plant macrofossil boundary section, gives a local species/morphotype extinction rate of about 57 percent, and stresses the 'sharp shift' in floristic composition at the boundary.

But the question remains: have we in the past twenty years actually modified our ideas about the plant fossil record, or have we just agreed that other evidence for the impact is conclusive and then found a correlative signal in the macrobotanical record? Note that there is a substantive difference between on the one hand identifying such a signal or even suggesting that the extinction rate at the boundary is statistically different from background, and on the other hand arguing that such extinctions played a significant role in plant evolution. So it remains an open question: were plant ecosystems doing anything substantively different in the Paleocene from what they had been doing in the Cretaceous?

Such broad questions about plant evolutionary history have been asked for over a century (see, for example, Ward, 1883–4), but our knowledge of the evolution of plant ecosystems is limited by the difficulty of collecting unbiased data on plant fossils distributed through time. Obviously any sample of past vegetation will be affected by taphonomy, by irregular sampling, by varying volumes of preserved sediment, by different intensity of research, and by differing taxonomic practices and the incomparability of modern and fossil taxa. Nevertheless, the few instances in which diachronic data on plant diversity have been assembled have given us some semi-quantitative support for assumptions about historical events like the rise of angiosperms and the K/T boundary event. In particular, the data set initially described by Knoll and others (1979) and subsequently published as species diversity curves in Niklas and others (1985) has been nearly as influential in paleobotany as the similar data on marine invertebrate diversity collected by Raup and Sepkoski (Raup, 1972; Sepkoski and others, 1981; Sepkoski, 2002) have been in invertebrate paleontology. The picture of changing plant diversity through time provided by Niklas and others (1985) has been independently substantiated in part by Lidgard and Crane (1988), but to the best of our knowledge, few subsequent attempts to elaborate on this picture have been particularly influential.

An eco-morphological approach, in which patterns of change in leaf architecture are treated as measures of ecological change, has the potential to tell a more detailed story. In this paper, we will examine the question of ecosystem continuity at the K/T boundary by looking at changes in leaf architectural profiles of fossil floras since the beginning of the Cretaceous as represented in the *Compendium Index of North American Mesozoic and Cenozoic*

*Type Fossil Plants* (henceforth *Compendium Index*), a database that is more-or-less independent of, and complementary to the diversity data of Niklas and others (1985).

This paper is not meant either as a review of literature on the K/T boundary generally, or as a justification of the ecological interpretation of leaf architectural patterns. Instead, like Raup and Sepkoski's initial work on the marine invertebrate record, it is intended to identify patterns and correlations in the known fossil record, and interpret them based on the assumption that such patterns in the fossil record have evolutionary significance.

#### DATA

The data from the *Compendium Index* that we will consider are derived from a card index at the Peabody Museum, Yale University, with entries for published descriptions of fossil plant species or morphotypes from the Mesozoic and Cenozoic Eras. Each entry consists of the published illustration and description of the fossil species and a reference to the source from which the illustration and description were obtained. A library of all cited sources is also maintained in the paleobotany collections of the Peabody Museum. The intent of the *Compendium Index* has been to provide full descriptions of all described North American fossil species, and although it is far from complete it is probably at the current time the most comprehensive single reference in North America for identification of Mesozoic and Cenozoic leaf fossils. Erling Dorf began compiling the *Compendium Index* at Princeton University in 1937 as an aid to taxonomic identification, and by 1940 he and his staff had amassed cards for some 4500 species from 126 references (Dorf, 1940). In 1984, after Dorf's death, the *Compendium Index* was transferred to Yale University where it has since been maintained and augmented at the Peabody Museum.

Currently, there are about 9800 species or morphotypes represented from 233 references, and the list continues to grow at a rate of about 25 new references per year including both current publications and gaps in the coverage of the older literature. The intent has been to enter all newly published type material as well as important emendations and range extensions of species that are already represented in the catalog (that is, additional cards are added for species that have been revised or are reported from stages, localities, or formations from which they had not previously been known). While the temporal resolution of each card depends on the publication from which it was obtained, the minimum resolution in the *Compendium Index* is to epoch in the Triassic, Jurassic, and Cenozoic, and to age in the Cretaceous. Spatial resolution also varies by source and for the most part has not yet been electronically recorded. Beginning in the 1980s, portions of the *Compendium Index* were entered into a computer database (originally dBase; the files are currently maintained in FileMaker Pro) allowing electronic manipulation of some of the data. The analyses in this paper are based on this data set, version 1.0 of which has been released on the Peabody Museum paleobotany collections website as an electronic publication (Hickey and others, 2006).

Partly because of the interests of those responsible for maintaining the *Compendium Index*, partly because identification of angiosperm leaves remains one of the most difficult and potentially rewarding pursuits for the systematic paleobotanist, there has been a distinct bias towards including leaves at the expense of other organs (there is only one category, for instance, for angiosperm wood and over fifty for angiosperm leaves). In addition, as in any taxonomic database, different researchers are predisposed to be 'splitters' or 'lumpers', thereby unnaturally proliferating or impoverishing the numbers of species recorded from a given locality. Like any record of fossil data, the *Compendium Index* is also affected by taphonomic sorting during fossilization: because the most favourable conditions for preservation (high sedimentation rates and anoxic sediments) occur in lowland floodplain facies, there is an enormous bias in the fossil record in favor of the plants that grow in those habitats. Moreover,

mechanically strong and well-vascularized leaves, such as those produced by canopy trees, preserve much better than the soft, weakly veined leaves generally produced by herbs (Behrensmeyer and Hook, 1992). Therefore the leaf fossil record is largely a record of the woody component of lowland forests, though occasional catastrophically buried floras provide a more complete picture of the vegetation at particular localities (Wing and others, 1993). Such extraordinarily well preserved floras are rare, however, so if we are interested in producing a relatively continuous picture of variation in time and space, we cannot limit our analysis to these fossil *Lagerstätten*.

Unlike the *Index of Generic Names of Fossil Plants* (Andrews, 1970) and its antecedents (Knowlton, 1919; LaMotte, 1952) which were based on the bibliographic *Compendium Index of Paleobotany* at the Smithsonian Institution, the Princeton/Yale *Compendium Index* provides an illustration and description for each fossil as well as its name and citation. Thus it can perhaps better be compared with regional monographs (Berry, 1916; Chandler, 1961–1978), illustrated museum catalogs (Steward, 1894; Stopes, 1913; Reid and Chandler 1926, 1933), or the *Traité de Paléobotanique* (Boreau, 1964–). Since the failure of the *Traité* in the 1970s, when faced with the taxonomic difficulties of the plant fossil record in general and with fossil angiosperm organs in particular (Collinson and others, 1993), the *Compendium Index* remains the best approximation of a comprehensive paleobotanical reference work analogous to the *Treatise on Invertebrate Paleontology* (Moore and others, editors, 1952–). A new resource, the Paleobiology Database (<<http://www.paleod-b.org>>), may be useful in the future, but does not now have sufficient morphological information associated with its taxon records for our purposes.

Following Raup and Sepkoski's (Raup, 1972; Sepkoski, 2002) lead in using a reference work originally intended for identification (in their case the *Treatise on Invertebrate Paleontology*) as a record of macro-evolutionary change, one might try to plot family diversities through time in the *Compendium Index* data. This, however, would prove impossible: if the *Compendium Index* were arranged taxonomically as the *Treatise* is, over half of all described species would fall into a single category—class Angiospermae, Incertae Sedis—because they cannot be firmly attributed to any modern order. Therefore, from the outset, the *Compendium Index* was organized into a set of morphological categories to facilitate identification of fossils, based on aspects of gross morphology like overall shape and pattern of venation rather than on phylogenetic principles. The current index has 118 categories, which have been designed for further subdivision as groups are studied in more detail. These *Compendium Index* Categories, or CICs, which are identified by three-digit numbers between 100 and 990 are composite categories, which were originally illustrated and described in Ash and others (1999) and are listed (in a slightly revised form) in Appendix B. CIC 111, for instance, includes all simple, unlobed, pinnately veined, elliptic, entire angiosperm leaves. The categories are based on characters like organ type (leaf, axis, reproductive structure), petiolar attachment (compound, central or marginal), primary vein course (pinnate or palmate), tooth presence, and tooth shape (serrate, dentate, or crenate). They are categories of convenience, designed for quick, simple, morphological classification using readily observed features and application to fossil plants in all degrees of preservation and to illustrations of variable quality. The theoretical issues surrounding ecological interpretation of data from such a classification system will be dealt with in detail in a future publication; in this paper we are concerned with identifying morphological patterns through time, not necessarily with relating particular morphological attributes to ecological variables. It should be remembered, however, that some of the patterns in leaf architecture that are reflected in the CICs have been shown to correlate strongly with ecological and environmental variables. The best known example of this is the correlation between the percentage of toothed leaves and cool temperatures (Bailey and Sinnott, 1915; Wolfe, 1993).

Our analyses are concerned with the recorded numbers of species (or morphotypes or operational taxonomic units) per time-division in each CIC. In some ways, this is roughly analogous to the initial, coarsely resolved data on marine invertebrate diversity collected by Raup (1972), but because the *Compendium Index* is organized by morphological category rather than by super-specific Linnaean taxa, it does not suffer from the incomparability of taxonomic ranks in different groups. That is to say, when we compare counts in two different CICs in the *Compendium Index*, we are not looking at a measure of diversity (which is sensitive to the degree of splitting or lumping that has been applied) but at the proportion of operational taxonomic units that have a particular morphology, which is comparatively insensitive to such biases. In other words, some taxonomists may be 'splitters' and others 'lumpers', but few systematically split ovate leaves and lump obovate leaves. In addition, the organization of the *Compendium Index* by morphological category instead of by higher taxon provides us with the ability to examine it for ecological rather than phylogenetic patterns.

Using the open-source application and programming language, *R* (R Development Core Team 1998–2004), we extracted and tabulated the number of described morphospecies from each time period in each CIC. At a coarse taxonomic level (for example, class), leaf shapes uniquely identify phylogenetic groups, so we can equate groups of leaf shapes with clades or Linnaean taxa (Dimichele and others, 2001). At higher taxonomic resolutions, however, this assumption breaks down. Therefore to examine patterns through time in any more detail than by class (or at best subclass), we need to think in terms of architectural groups that may share functional and morphological attributes but are not necessarily genetically related. The scripts used for extraction and tabulation and the data matrices analyzed in this paper can be downloaded from the world wide web at <[http://geology.yale.edu/~wag6/Downloads/Green\\_and\\_Hickey\\_2005\\_supplement](http://geology.yale.edu/~wag6/Downloads/Green_and_Hickey_2005_supplement)> or obtained from the authors; the latest version of the database (version 1.0) has been released as Hickey and others (2006) and can be downloaded from the world wide web at <<http://www.peabody.yale.edu/collections/pb/eCI/v1.0>>. The actual data matrices used in the following graphs (Appendix A) were extracted from this or earlier versions of the database.

Statistical manipulation at this stage has intentionally been restricted to an exploratory level because there are issues of sampling and systematic bias that must be fully discussed before applying specific confirmatory tests. While we are exploring the signal-to-noise ratio in the data and looking at first-order trends and patterns, it seems relatively unproductive to depend on techniques of variable reduction and parametric testing, though we do rely on relative correlations. It is easy to find statistically significant effects in the fossil record; harder to determine what they signify. As the data are of variable quality and unevenly distributed through time and space, we sometimes would like to draw conclusions based on very small samples, while at other times very large samples tell us nothing of biological interest. For exploratory analysis of this sort, graphical display of the data has proven to be the most effective tool (Tukey, 1977; Tufte, 2001). Despite the inevitable presence of noise in the data, the patterns we can now identify are robust enough that we are confident they will survive the cleaning up of the signal that is currently in progress.

Figure 1 shows the overall frequency distribution of species in the *Compendium Index* by CIC, which is roughly log-normal, as is expected from a set of counts. When all the entries in the *Compendium Index* are sorted by morphological category, the vector of counts obtained ranges from almost 700 taxa with simple, entire, ovate, pinnate leaves with regular secondaries (CIC 116) to only a few taxa with peltate, lobed leaves (CIC 155). This vector is shown as a profile in figure 1B, with the actual number of species in each category plotted as a vertical black bar, and in figure 1A the dotted curve is a plot of the counts on a log-log scale against a theoretical Gaussian probability distribution



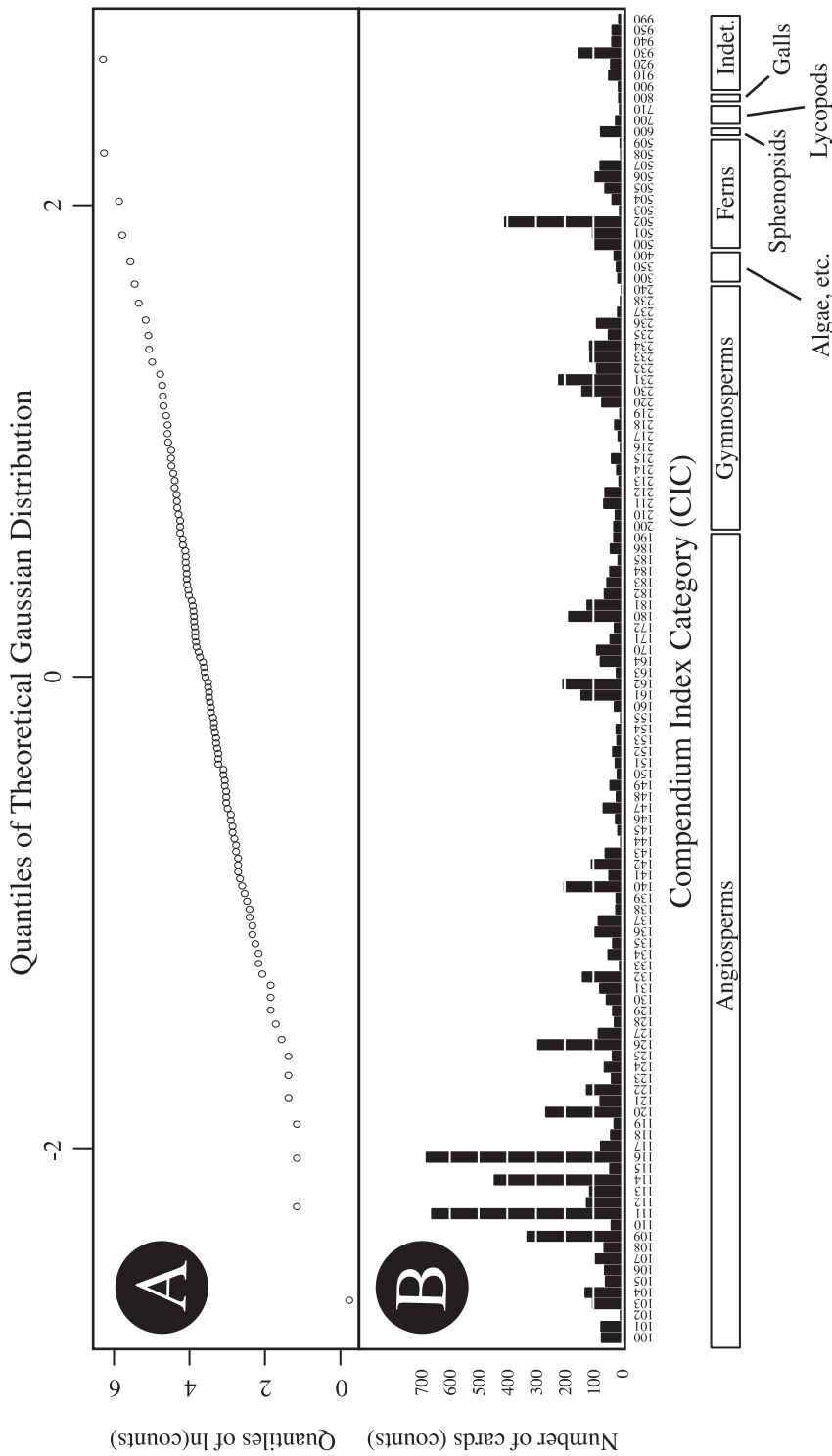


Fig. 1. (A) Log-normal quantile-quantile plot of the counts in the *Compendium Index*. This is a scatter plot of the quantiles of the log-transformed counts plotted against the corresponding quantiles of the theoretical Gaussian distribution. Therefore a straight line indicates log-normal distribution of the count statistics. (B) Bar chart showing the actual counts in each Compendium Index Category (CIC). See Appendix B for a description of the categories.

TABLE 1  
*The approximate number of floras represented in the Compendium Index in each time period*

<i>Time Period</i>	<i>Approximate Number of Floras Represented</i>	<i>Number of Floras with more than 20 species</i>
Pleistocene	1	0
Pliocene	34	3
Miocene	106	12
Oligocene	31	6
Eocene	193	10
Paleocene	106	10
Maastrichtian	65	7
Campanian	36	2
Santonian	33	1
Coniacian	7	0
Turonian	8	0
Cenomanian	26	6
Albian	50	2
Aptian	47	1
Barremian	36	0
Neocomian	7	0
Malm	6	0
Lias	7	0
Dogger	10	0
Triassic	30	0
TOTAL	839	60

function. In such a log-normal quantile-quantile plot, a variable with a perfectly log-normal distribution will be distributed along a straight diagonal line.

*Compendium Index* records include representatives of approximately 840 floras (see table 1), almost exclusively from continental North America, but with a few additions from other parts of the world. By the nature of the geographic distribution of geological strata, any one time period is likely to be represented only by a small geographic area. For instance, the Turonian stage of the Cretaceous is represented almost exclusively by floras from Greenland. The *Compendium Index* does, however, include most of the 'classic' American floras, including many of those described by Lequeraux, Berry, Knowlton, *et cetera*, so whatever biases are introduced by the patchy nature of the fossil record, the analysis of the *Compendium Index* should reflect the paleobotanical record insofar as it has been cataloged by some century and a half of investigation.

#### RESULTS

The 118 morphological categories into which the *Compendium Index* species records are sorted can also be lumped into aggregate groups which are synonymous with the higher Linnaean taxa used by Niklas and others (1985). That is, we can add together all the angiosperm counts, all the conifer counts, *et cetera*, and plot the resulting sums as mountain charts through time, as we have done in figure 2. These charts are plotted alongside a redrawn version of the plot from page 112 of Niklas and

others (1985). Note, however, that the data from Niklas and others (fig. 2A) are absolute numbers of described species in each time interval, while our data (figs. 2B and 2C) are shown as the percentage of described species (or operational taxonomic units) in each morphological category in each time interval. Our *Compendium Index* data are plotted twice: once averaged by epoch (fig. 2B) and once at the finest chronological resolution now available (fig. 2C). We are in the process of refining the chronological sampling by reference to the stratigraphic information in the *Compendium Index*. On the extreme right (fig. 2D), are shown the absolute numbers of cards in the *Compendium Index* (which are roughly proportional to the numbers of described species). At the top (fig. 2E) are estimates of modern species abundances from Raven and others (1999). The chronology used is the Geological Society of America 1999 Geological Time Scale (Palmer and Geissman, 1999) and the values are plotted at the midpoints of chronostratigraphic divisions.

Regardless of whether one examines the absolute species diversity data from Niklas and others (1985) in figure 2A, or our proportional morphological data in figure 2B, it is apparent that there is no discontinuity at the K/T boundary. The picture obtained of floral change through time is uncannily similar to that provided by plate 56 in Ward (1883–4), even to the extent of duplicating a substantial drop in angiosperm diversity in the Turonian—because sample sizes are so low, we are not confident that this represents a true signal in our data, but the discovery of the same pattern in Ward's data raises the possibility that it is real.

The *Compendium Index* data do confirm a broad picture of relative floral stability since the Campanian (logistic growth curve) that has already been proposed (Lidgard and Crane, 1988), but many of the criticisms of diversity-curve data are not applicable to our proportional morphology curves: as discussed above, incomparability of higher taxa and biases caused by differing intensities of study are automatically normalized by considering a proportional metric. Note also that in our data, in contrast to that of Niklas and others (1985), the expansion of angiosperms seems precipitous (essentially taking place from the Albian to the Santonian stages of the Cretaceous), rather than happening slowly over the course of the Late Cretaceous and Tertiary. Because proportional counts of taxa in morphological classes are likely to reveal ecological dynamics while ignoring species turnover, we can conclude that the ecological expansion of angiosperms was indeed more precipitous than their rate of speciation: that is we see the broad-leaf angiosperms appear, restructuring ecosystems in an explosive radiation, but because we are looking at morphological categories we do not then notice the continued taxonomic turnover that we know occurred during the Tertiary. To use Gould's (1991) terminology, angiosperms attained modern disparity levels by the end of the Santonian, but may have taken the rest of the Cretaceous and all of the Tertiary to attain modern diversity. Alternatively, it could be argued that there were as many species with angiosperm leaves (proportional to non-angiosperms) in, for instance, the Campanian as there were in the Miocene, but they were different species with similar leaves, and the replacement of one species by another with similar leaves is invisible in our record of eco-morphological change (figs. 2B and 2C) while it is apparent in a diversity curve (fig. 2A).

An intensification of this effect may come from the over-representation of a number of early Late Cretaceous floras by zealous splitters, but because we are dealing with proportions, this effect could only be caused by inconsistent splitting of some morphologies more than others. (Note that this sort of inconsistent splitting is possible, as when a group of people working on a particular taxonomic group evolve a different implicit notion of the amount of morphological variation allowable at a given taxonomic rank.) Reduction to proportions will minimize this error, but it will not necessarily eliminate it; therefore the resulting patterns will be most reliable when they



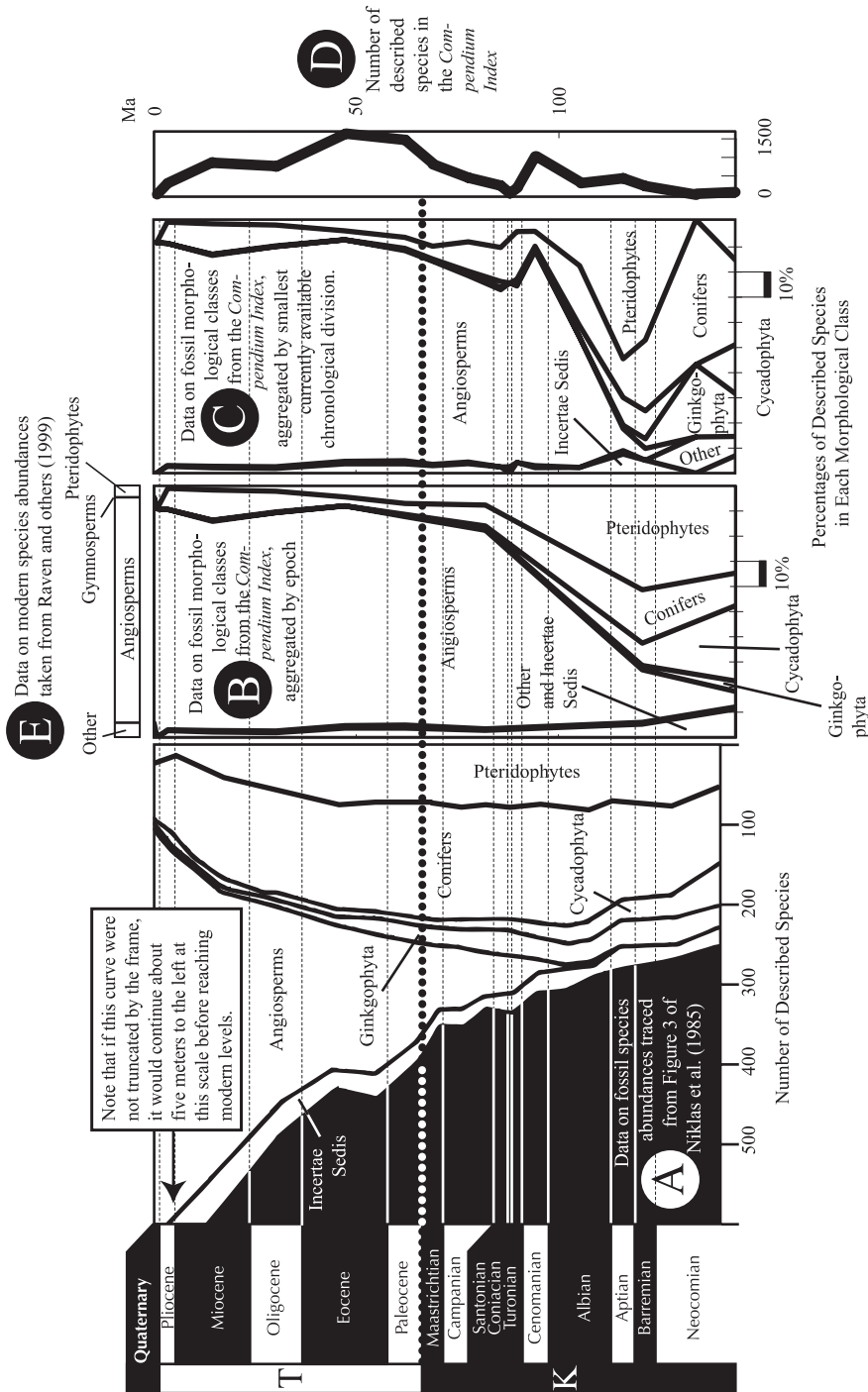


Fig. 2. (A-E) Juxtaposition of the curves from Niklas and others (1985) giving absolute species diversities through time (A) with similar mountain plots showing the numbers of entries in the *Compendium Index* (B, C) in the morphological groups corresponding to each higher Linnean taxon. Also shown are the absolute numbers of entries in the *Compendium Index* in each time division (D) and estimates of modern species diversities from Raven and others (1999) (E). Note the smoothing artifacts like the implication in 2B that there are a large number of Neocomian angiosperms: this arises from lumping all Lower Cretaceous counts together in a single chronological bin.

are based on comparison of like with like as in the case of the angiosperm subset of the *Compendium Index* analyzed below.

Associated with the rise of angiosperms were proportional decreases in the numbers of cycadophytes, ginkgophytes, and pteridophytes, while the conifers remained relatively unaffected. This agrees with the results of Lidgard and Crane (1988) and supports the contention of Taylor and Hickey (1992, 1996) that the earliest angiosperms occurred in disturbed habitats.

Figure 2 and the discussion up to this point have only dealt with the aggregate morphological categories that are equivalent to Linnaean classes. Examination of these provides an overview of plant evolution through time that does not conflict with the conclusions of Niklas and others (1985) and Lidgard and Crane (1988), but such aggregate categories give little additional information. To describe the K/T boundary dynamics in more detail, we need to examine the morphological categories individually instead of lumping them together so that they correspond to higher taxa. In the following discussion and figures 3, 4, and 5, we will look individually at the angiosperm leaf categories (CICs 100–155) in each time interval and set about quantifying the degree of discontinuity in eco-morphological dominance at the K/T boundary.

One way to do this is by producing a bivariate plot with associated correlation statistics. Figure 3 provides an example of such a plot of the counts in each CIC of the species in the *Compendium Index* for the Maastrichtian age and the Paleocene epoch, that is, the stage transition that corresponds to the K/T boundary. The CIC numerical codes and cartoons of the leaf shapes they represent are plotted alongside the points in order to show which categories are represented. The points lying above the diagonal are more abundant in Paleocene assemblages while those lying below the line are more abundant in Maastrichtian floras.

Correlations provide only a rough measure of the strength of linear association between two sets of counts. This measure is difficult to evaluate except in the context of other similar measurements, so in order to determine whether the correlation between the Maastrichtian and Paleocene is unusual, we must look at it in the context of other correlations between successive time periods.

Figure 4A shows this comparison: the solid line shows the ordinary parametric autocorrelation (Pearson's product-moment correlation,  $r$ , of each time period with its neighbors), plotted at the interval boundaries. The fine dotted line gives a 95 percent one-sided confidence interval for these correlations. We also calculated two non-parametric correlation coefficients, Spearman's  $\rho$ , and Kendall's  $\tau$ , shown by the two dashed lines. In general, these show the same patterns as the parametric correlation coefficient, their lower statistical power does not matter in this comparative context, and they depend only on the rank-order similarity of their arguments, so they are more likely to be applicable to noisy and abnormally distributed data. Quantitative similarity measures like the Horn-Morisita index, which is used in ecology to measure species abundance data, also show similar patterns but have not been plotted because it is not clear whether the rationale for using such measures applies in the case of counts in morphological categories.

Low correlations imply times of leaf architectural change; high values suggest floral continuity. The trend line has no significant slope. From the figure, it is apparent that the Maastrichtian/Paleocene boundary does not stand out as a low point, so we can conclude that it was not a time of dramatic change in leaf architecture.

In figure 4B the correlation of each time period with the present is plotted in the same way that the autocorrelations were plotted in figure 4A; again the difference between the Maastrichtian and Paleocene does not stand out (if it did it would look like the vertical riser of a step), but in this case there is a slight but significant trend, which remains even in the absence of three outlying points. This provides an empirical test of the uniformitarian assumption that modern floras provide unbiased estimators of the distribution of architec-

## Comparison of counts in each CIC

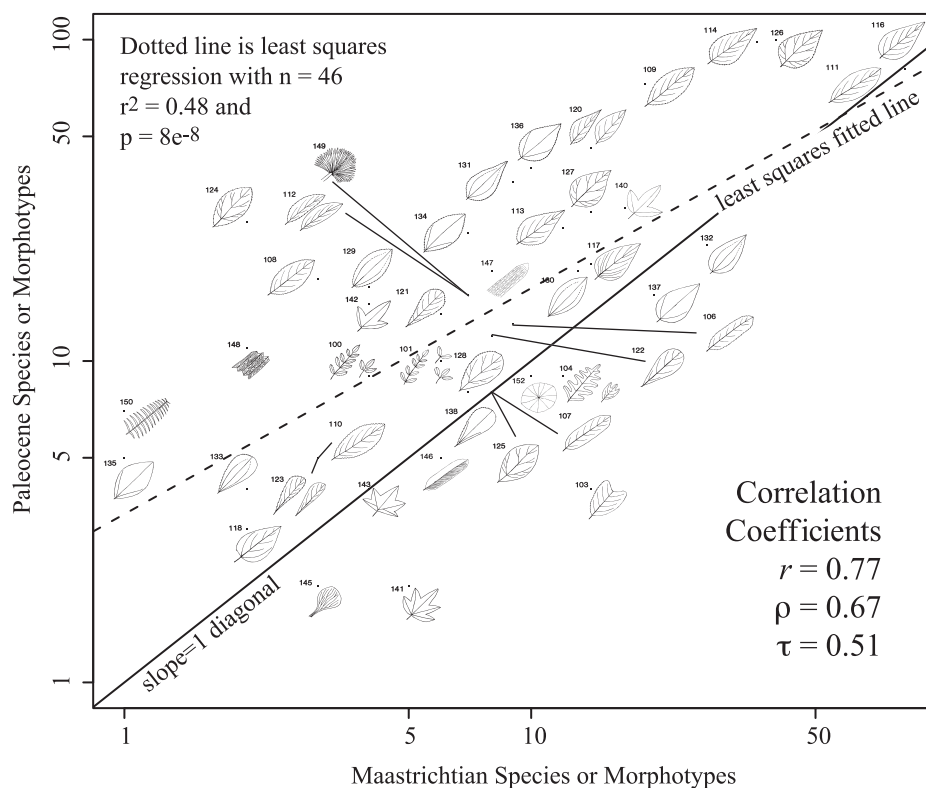


Fig. 3. Comparison of the counts of operational taxonomic units with particular leaf shapes found in Maastrichtian and Paleocene floras. In addition to the parametric correlation,  $r$  (formally, Pearson's product-moment correlation coefficient), we have calculated least squares regression statistics, Spearman's rank-order correlation coefficient,  $\rho$ , and Kendall's rank-order correlation coefficient,  $\tau$ . For further details of the algorithms used, see the help page for `cor.test()` in R Development Core Team (1998–2004), and references therein. This plot shows the type of raw data from which the correlation statistics that are discussed below were obtained.

tural characters in past floras, which underlies the practice of estimating paleotemperatures from leaf morphology (leaf physiognomy, Wolfe, 1993; 1995; Wilf, 1997). The negative trend in modern–fossil correlations from left to right contradicts this assumption.

The argument that the Maastrichtian/Paleocene (K/T) boundary does not stand out can also be made statistically explicit by plotting the empirical distributions of the correlation coefficients as histograms or smoothed densities as is done in figure 5 for all three correlation coefficients. In each case the position of the K/T boundary in the distribution is shown. For each correlation coefficient, the exact probability that the correlation at the Maastrichtian/Paleocene transition is significantly greater than the mean age transition correlation is dependent on the exact shape of the distribution, and since there are only 15 points, the shapes of the distributions are poorly constrained. Nevertheless in all three cases it is clear that the Maastrichtian/Paleocene boundary is not a low outlier.

## DISCUSSION

Both the smooth curves across the Cretaceous/Tertiary boundary in figure 2 and the similarity of the Maastrichtian and Paleocene floral profiles suggest that the K/T

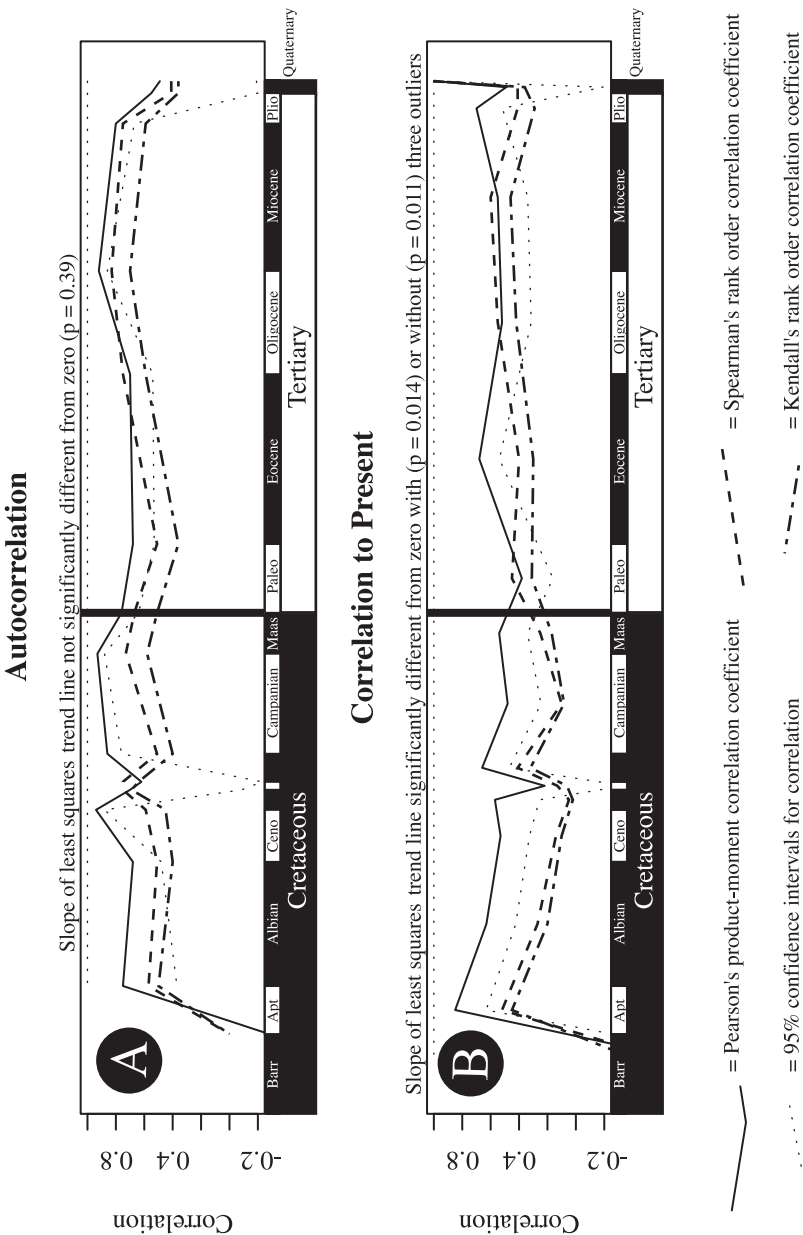


Fig. 4. Autocorrelation (A) and correlation with the present (B) of each geological time period, using all three measures of correlation. The fine dotted line gives a 95% one sided confidence interval for Pearson's correlation coefficient. Note in both cases the small-sample effect giving an anomaly in the Cretaceous.

## Distributions of Correlation Coefficients Between Adjacent Ages

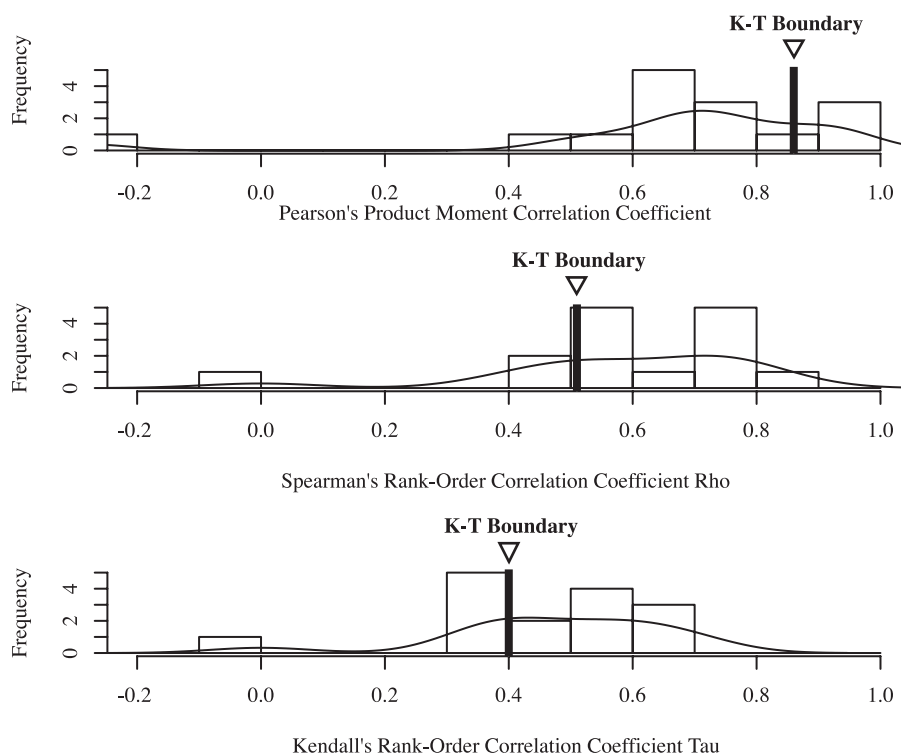


Fig. 5. Plots of the empirical distributions of the three correlation coefficients (both as histograms and as smoothed densities) make explicit what can also be seen from the previous figures: that the Maastrichtian/Paleocene (K/T) boundary is far from being a low outlier.

boundary event had little lasting effect on the evolution of angiosperm leaf architecture. Qualitative appreciation of this point initially led a number of paleobotanists to doubt the extinction mechanism proposed by Alvarez and others (1980) because of the apparent continuity of the plant fossil record examined at a resolution of geological stage (Clemens and others, 1981). Examined at an increased stratigraphic resolution, as it was by Wolfe and Upchurch (1986, 1987), Johnson and Hickey (1990), and Wilf and Johnson (2004), the K/T boundary does indeed show a concentration of last appearances, though it is still not clear that this concentration rises above a base extinction rate to a statistically significant extent. On the other hand, as we decrease the chronologic resolution, we effectively smooth the time-series with a low-pass filter. Comparing figure 2C with 2B, we have accomplished an appropriate degree of smoothing by increasing the temporal bin size, but the same results would have been achieved by a moving average filter that replaced each value by the arithmetic mean of it and its neighbors. In this case, the higher frequency dynamics that we avoid by discussing figure 2B in preference to 2C seem to be due to small-sample effects. It is common for the quality of paleontological data to be too low and irregular for routine application of statistical time series tools like autoregression and spectral analysis.

It is worth examining in some detail, however, the apparent conflict between our data, which show no significant changes at the K/T boundary and the 57 percent

extinction of morphotypes reported by Wilf and Johnson (2004). Two (non-exclusive) explanations for this difference present themselves: first of all, it could be entirely an effect of time (or space) averaging: that is, because all our Paleocene data from North America are lumped together, we miss the dramatic changes that appear in the beginning of the Paleocene because we can only see the overall epochal average. Secondly, an examination of morphological attributes (which is in this context equivalent to an examination of proportional representation in architectural categories) may reveal ecological stability while a measure of species or morphotype diversity may show population level fluctuations. As Wilf and Johnson (2004) point out, even 57 percent of morphotypes is not a particularly large extinction compared with 95 percent of marine species at the Permo-Triassic boundary or 100 percent of dinosaur species at the end of the Cretaceous.

In order to see whether these differences were a result of looking purely at continent- and epoch-scale averages, we collected the CIC attributions for 286 of the Hell Creek/Fort Union boundary section morphotypes from Johnson (ms, 1989) though we could not obtain the appropriate morphotype descriptions to recode the most recent data (Wilf and Johnson, 2004). In figure 6 we have plotted the profiles of four biozones defined by Johnson and Hickey (1990), three from the Hell Creek Formation (HC 1–3), immediately below the K/T boundary, and one from the Fort Union Formation (FU1), immediately above the boundary.

The profiles of the biozones do not seem to look radically different from each other and certainly the flora of the Fort Union biozone immediately after the K/T boundary does not seem to represent a dramatic break from the earlier Hell Creek floras. With only four points in the time series, it is difficult to test this statistically, but again correlations among the zones give a certain ability to measure similarities of the counts in each architectural category across the boundary.

Figure 7 shows pairwise plots of the counts from each of the biozones against the counts from each other zone. The correlations amongst all of them are positive, but the weakest of the correlations is indeed between FU1 and HC3. When empty and singleton categories are eliminated, the HC3:FU1 relationship loses its significance at the 5 percent level, while the other pairwise comparisons remain significant by at least some measure. Note that this is not a robust statistical result in which the HC3:FU1 comparison lacks real significance while the HC1:HC2 and HC2:HC3 retain it, but it is clear that of the correlations, the HC3:FU1 relationship is the weakest.

A final illustration of the similarity of Johnson and Hickey's biozones to each other is provided by a hierarchical cluster analysis (fig. 8). Though the particular arrangement of the floras is far from robust (experimentation has shown that it is dependent on data pre-treatment, distance metric and clustering method), the clustering of the biozones does continue to appear despite variation in clustering technique. Thus we can conclude that the leaf architectural difference between the Hell Creek and Fort Union floras is much less dramatic than most other differences between floras, fossil and modern.

So by the leaf architectural or eco-morphological measure we are using, the K/T boundary shows only a weak preeminence in a section representing about three million years. This suggests that time and space averaging alone are not enough to explain our data: even when the plant record is examined at the smallest possible temporal and spatial scale, the ecological effects of the K/T boundary were not dramatic. The K/T boundary event does seem to have been marginally the most important effect on plant ecosystems in three million years, but the evolutionary question is whether or not it had any effect that lasted on a longer time scale, and every examination of this question seems to indicate that forests responded homeostatically to the K/T boundary event.

This is comparable to results obtained by Cantrill and Poole (2005), in the southern hemisphere (Patagonia and Antarctica) where the K/T boundary is still visible in the fern spike, but minor, transient, or totally absent in the macrofloral



# CIC Profiles Boundary Section Biozones of Johnson and Hickey (1990)

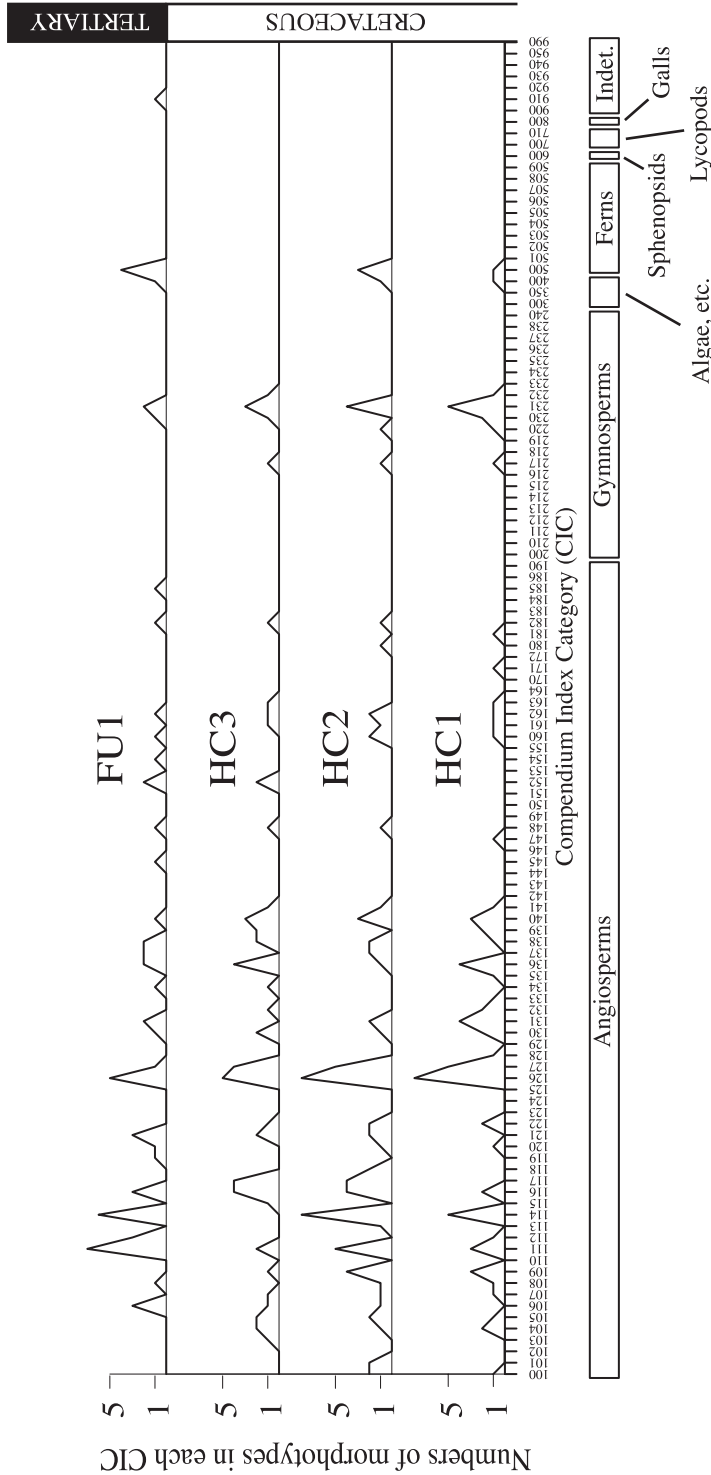


Fig. 6. Leaf architectural profiles for each of the four biozones defined by Johnson and Hickey (1980): Hell Creek 1–3 and Fort Union 1. In this representation, there seems to be no dramatic change between HC3 and FU1, as one would expect if the K/T boundary extinction had had significant ecological effects. The FU1 profile does provide a slight echo of the fern spore spike following the K/T boundary, but otherwise there is no convincing indication of a change in leaf architecture across the boundary.

## Correlations among the Boundary Section Biozones of Johnson and Hickey (1990)

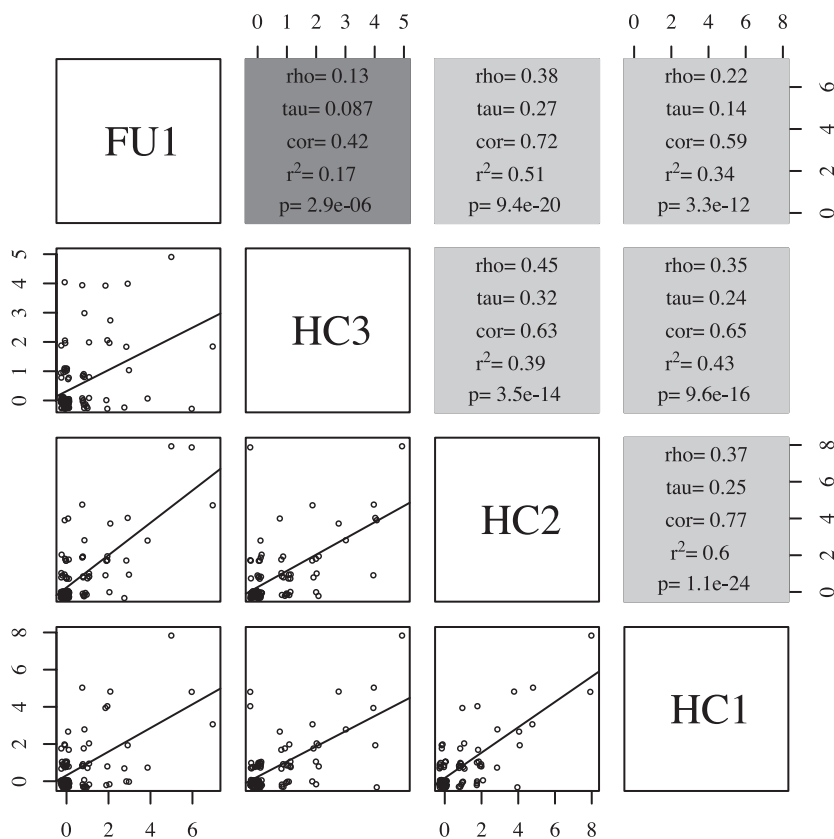


Fig. 7. Pairwise plots of the same four biozones whose profiles are shown in figure 6. Note that according to the correlation statistics, the relationship between the Fort Union flora and the floras of the three Hell Creek biozones is slightly more distant than the relationships among the Hell Creek biozones. This supports the contention of Wilf and Johnson (2004) that the K/T boundary was the most significant modification of the flora during the 2–3 million year period represented by this composite section. Note that for this plot some random noise has been added to the data so that duplicate points do not plot exactly on top of each other, and zeros are left in the data (which will naturally increase the apparent significance of the regression).

record. It is worth also comparing this result with the analysis of the same boundary section by Labandeira and others (2002), which showed a drop in the diversity and variety of insect feeding traces on leaves at the beginning of the Paleocene. Our demonstration that leaf architecture did not change substantially at the same time, supports one of Labandeira's scenarios in which the disappearance of feeding traces was caused by insect extinctions: a crash due to failure of demand rather than supply.

So in answer to the question: 'How did the K/T boundary event affect the evolution of forest ecosystems?' the response suggested by our data is 'Not fundamentally.' Whatever species extinctions occurred must have been replaced within a few million years by migration of closely related species or re-radiation into empty niches. At the scale at which we can examine it, the plant macrofossil record shows no dramatic change in ecosystem structure, though of course the possibility remains likely that even shorter term fluctuations were more dramatic. If all the forests in North America were burned over in a single summer, that would clearly count as a dramatic ecological effect, but it seems intuitively likely that such an effect would have few or no effects that

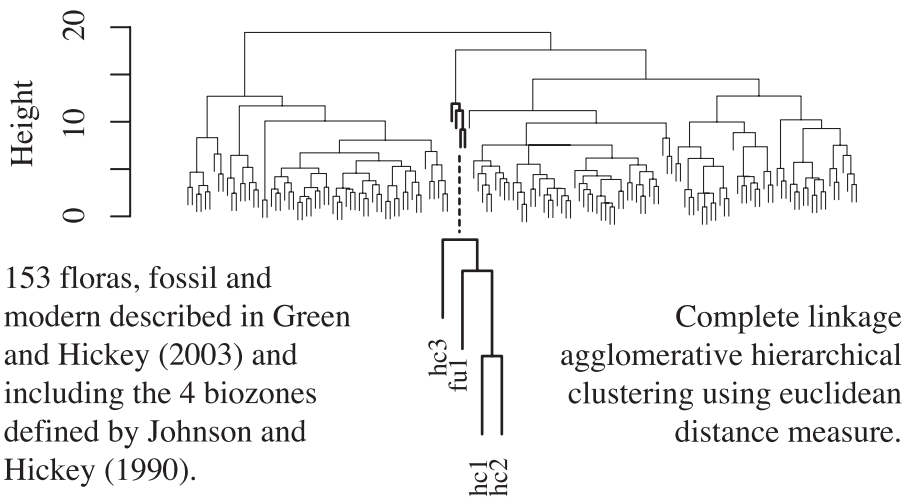


Fig. 8. Algorithmic hierarchical cluster map showing how the Hell Creek and Fort Union biozones, despite spanning the K/T boundary, are better correlated with each other than any one is with 149 other fossil and modern floras. The comparative data come from related work (see Green and Hickey, 2003). Note that the exact arrangement of floras in such a dendrogram is sensitive to distance measure, data standardization, and clustering method. The example presented here is for illustrative purposes only; it is not possible to determine from it alone that the clustering of the Hell Creek and Fort Union floras is relatively robust, which we have observed by broader experimentation.

lasted longer than the time taken for the forests to regrow. The effects of migration plus regrowth from seed banks would make any lasting change in the physiognomy of forests unlikely, and these theoretical predictions are (in general terms) substantiated by natural experiments like the catastrophic destruction of Krakatoa in 1883 (Thorn-ton, 1996). Recent treatments of the K/T boundary like Wilf and Johnson (2004), however, continue to remain focussed on the 'mass extinction' of plants at the K/T boundary. We believe that for plants the boundary event should be considered a 'mass death' not a 'mass extinction', and this raises the evolutionary question of whether plant ecosystems have ever suffered a setback comparable to animal mass extinctions.

An important caveat is that we are discussing a lack of fundamental change in a data set that captures information on the architecture of woody dicot leaves. Therefore what we are actually saying is that the leaf-litter on the forest floor in the early Cenozoic was not significantly different from the leaf-litter on the forest floor in the late Cretaceous. The spread of grasslands in the Miocene, of course, restructured terrestrial ecosystems in a way that is probably almost as dramatic as the rise of angiosperms, but notice that it is entirely invisible in our data. One reason for this invisibility is that all angiosperm leaf forms were lumped together in figure 2, so in that particular representation differences in leaf shape among angiosperms are not apparent. More important, however, is the sampling bias in the fossil record: because the fossilization potential of herbaceous plants is vanishingly small in the climatic and edaphic conditions in which grasslands occur, we expect grasslands to go essentially unrepresented in the plant macrofossil record. So we should interpret our data as a history of lowland forest ecosystems, not as a history of terrestrial environments. The rise of angiosperms and the extinction at the K/T boundary have been considered two of the most dramatic evolutionary events that restructured terrestrial ecosystems since the end of the Paleozoic. Traditional descriptions of plant evolution and an examination of figure 2 substantiate the importance of the rise of angiosperms in the middle of the Cretaceous, but the K/T boundary event seems to have had no lasting effect on leaf architecture, and therefore by analogy on the ecological structure of forests.

A final theme for discussion is the potential for generalizing the use of morphological bins rather than diversity in the production and analysis of paleontological time series. Diversity, which is peculiarly susceptible to biases due to differing taxonomic practices, has been relied upon very heavily not only by paleontologists, but also by modern ecologists who have taken it to be one of the most fundamental attributes and best scalar descriptions of an ecosystem. Nevertheless, as criticism of Raup and Sepkoski's data base (for example, Peters and Foote, 2001) and the ecological literature on the connection between diversity and stability in ecosystems (for example, Tilman, 1999) have shown, evaluating the meaning of diversity can be highly problematic. Because of the nature of macrobotanical remains and the way they can best be organized, our data set suggests a useful alternative or supplement to the diversity curve for summarizing evolutionary change: choose a set of morphological bins (or, alternatively, a set of morphological variables), split the data set into the smallest units possible (operational taxonomic units), and record their proportional representation in each morphological bin or variable. Like any proportional metric, this minimizes the effect of biases in time series data by automatically normalizing for sample size, intensity of study, interval length, *et cetera*. Moreover, it provides a multivariate data set rather than the univariate time series provided by a measurement of diversity. Since environmental variables frequently influence morphological attributes in simple, predictable ways, functional explanation is also easier than in the case of diversity, which can interact with the environment in complex ways. Most important, diversity is a single variable known to be controlled by a number of factors and it is manifestly impossible to de-convolute complex interactions of many variables from a single composite measurement. Proportions of operational taxonomic units in morphological classes provide multivariate data distributed through time, so if the difficulties of dealing with correlated, non-normal, multivariate data can be overcome, then we have a reasonable hope of being able to investigate macro-ecological change in the remote past in more detail.

#### CONCLUSIONS

At the scale and resolution of the *Compendium Index* data, we have found no indication of a change in the leaf architectural profiles between the Maastrichtian and the Paleocene comparable to the changes that we see earlier in the Cretaceous, associated with the rise of angiosperms. This lack of change at the K/T boundary highlights the influence of evolutionary innovation compared with catastrophic extinction on plant evolutionary history. Also, if we accept that there is a connection between ecosystem properties and leaf morphology, we must conclude that plant extinctions at the end of the Cretaceous, while they may have selectively eliminated certain species, do not seem to have restructured plant ecosystems in a way that was significant on an evolutionary time scale. Finally, in comparison with datasets with better stratigraphic resolution, the patterns identified show the importance of temporal scale in any discussion of macro-evolutionary dynamics and illustrate the utility of morphological categories in examining evolutionary change.

#### ACKNOWLEDGMENTS

Over the past 60 years, the *Compendium Index* has been maintained financially by Princeton University and Yale University, and practically by the work of many volunteers and museum employees including the current paleobotany collections manager at the Peabody museum, L. Klise, and many others whose names cannot be obtained. We are nevertheless grateful to them for their contributions to a multi-generational project of which we are now reaping the benefit. Thanks also to J. P. Downs, K. T. Smith, I. M. Miller, A. Seilacher, E. Vrba, S. Wing, and several anonymous reviewers for comments on earlier versions of this manuscript. Funding for this work was provided by a Yale University Fellowship and by NSF Grant DEB-0235736.

APPENDIX A  
Data Matrices

TABLE 1  
Data for figure 1

No.	CIC	Counts	No.	CIC	Counts	No.	CIC	Counts	No.	CIC	Counts
1	100	71	26	125	33	51	150	16	76	212	59
2	101	73	27	126	294	52	151	23	77	213	10
3	102	5	28	127	82	53	152	32	78	214	18
4	103	102	29	128	26	54	153	17	79	215	36
5	104	128	30	129	32	55	154	20	80	216	5
6	105	57	31	130	54	56	155	4	81	217	13
7	106	60	32	131	77	57	160	26	82	218	25
8	107	92	33	132	137	58	161	142	83	219	7
9	108	62	34	133	8	59	162	205	84	220	70
10	109	330	35	134	48	60	163	19	85	230	139
11	110	37	36	135	32	61	164	75	86	231	220
12	111	662	37	136	95	62	170	88	87	232	88
13	112	123	38	137	82	63	171	41	88	233	111
14	113	112	39	138	21	64	172	26	89	234	112
15	114	444	40	139	20	65	180	185	90	235	47
16	115	42	41	140	201	66	181	121	91	236	88
17	116	681	42	141	45	67	182	61	92	237	15
18	117	74	43	142	106	68	183	52	93	238	137
19	118	39	44	143	58	69	184	42	94	240	5
20	119	27	45	144	4	70	185	13	95	300	1
21	120	265	46	145	14	71	186	40	96	350	14
22	121	76	47	146	22	72	190	28	97	400	19
23	122	123	48	147	65	73	200	28	98	500	27
24	123	36	49	148	19	74	210	23	99	501	97
25	124	61	50	149	41	75	211	63	100	502	102

TABLE 2  
Data for figure 2

Time Interval	Pteridophytes	Conifers	Cycadophytes	Ginkgophytes	Angiosperms	Other	Incertae sedis
Recent	12020	550	100	1	235000	15100	0
Pleistocene	1	0	0	0	10	0	0
Pliocene	3	25	0	0	262	1	8
Miocene	14	102	1	3	708	5	18
Oligocene	16	62	2	0	654	5	14
Eocene	72	57	1	0	1427	16	60
Paleocene	103	64	7	6	1221	18	54
Maastrichtian	85	41	5	2	650	4	24
Campanian	40	53	4	4	336	3	17
Santonian	27	33	6	2	172	0	6
Coniacian	3	7	0	0	29	1	0
Turonian	9	36	4	1	133	0	8
Cenomanian	47	60	9	10	864	8	22
Albian	56	73	14	0	158	0	7
Aptian	241	67	48	6	38	6	33
Barremian	112	66	26	9	11	0	12
Neocomian	0	4	0	2	0	1	0
Malm	37	11	45	6	0	1	16
Dogger	8	6	18	12	0	1	0
Lias	20	16	39	1	0	0	4
Triassic	100	42	58	6	1	2	24



TABLE 3  
Data for figures 3, 4, and 5

Time Interval	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117
Recent	226	284	24	6	107	24	2	15	17	249	44	589	8	4	74	22	157	0
Pleistocene	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Pliocene	2	0	0	2	11	4	2	2	5	20	1	34	7	7	15	4	21	1
Miocene	10	3	0	2	28	7	8	5	13	76	7	60	22	7	79	7	38	1
Oligocene	24	15	1	5	27	5	10	3	7	52	3	32	13	11	74	2	30	2
Eocene	16	13	3	22	21	18	15	33	7	71	6	175	41	15	94	1	164	15
Paleocene	9	10	0	4	8	0	10	6	18	66	5	60	14	25	93	5	80	20
Maastrichtian	4	6	0	14	12	12	9	8	3	19	3	67	7	12	36	0	83	14
Campanian	1	1	0	0	3	0	1	3	4	5	2	40	0	13	19	2	62	3
Santonian	1	3	0	2	3	1	1	9	1	5	1	23	4	3	6	0	19	1
Coniacian	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	12	0
Turonian	0	1	0	3	1	5	0	7	0	2	0	23	1	2	3	0	23	4
Cenomanian	3	12	1	47	7	2	3	16	4	9	6	113	12	14	18	17	130	13
Albian	1	9	0	1	6	2	1	0	0	4	3	16	2	3	5	3	10	0
Aptian	0	0	0	0	1	1	0	0	0	1	0	14	0	0	2	0	7	0
Barremian	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0

TABLE 3  
(continued)

[illegible]



TABLE 4  
*Data for figures 6 and 7*

Biozone	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118
HC1	1	0	0	0	2	1	0	1	1	3	0	3	1	0	5	0	2	0	0
HC2	2	2	0	0	1	2	1	1	1	4	0	5	0	1	8	0	4	4	2
HC3	0	0	0	1	2	2	1	1	0	1	0	2	0	0	0	1	4	4	0
FU1	0	0	0	0	0	0	3	0	1	0	0	7	3	0	6	0	3	0	0

Biozone	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137
HC1	0	1	0	2	0	0	0	8	5	1	0	2	4	2	1	0	1	4	0
HC2	0	1	2	2	0	0	0	8	5	0	0	1	2	0	0	0	0	1	2
HC3	0	0	2	1	0	0	0	5	4	0	0	2	0	1	0	1	0	4	0
FU1	0	1	3	0	0	0	0	5	1	0	0	1	2	0	0	1	0	2	2

Biozone	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	160
HC1	1	2	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
HC2	2	0	3	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
HC3	2	2	3	1	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0
FU1	2	0	1	0	0	0	0	1	0	0	1	0	0	0	2	0	1	0	1

Biozone	161	162	163	164	170	171	172	180	181	182	183	184	185	186	190	200	210	211	212
HC1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
HC2	1	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
HC3	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
FU1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0

TABLE 4  
(continued)

Biozone	213	214	215	216	217	218	219	220	230	231	232	233	234	235	236	237	238	240	300
HC1	0	0	0	0	1	0	0	1	2	5	1	0	0	0	0	0	0	0	0
HC2	0	0	0	0	1	0	0	1	0	4	0	0	0	0	0	0	0	0	0
HC3	0	0	0	0	1	0	0	0	1	3	1	0	0	0	0	0	0	0	0
FU1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0

Biozone	350	400	500	501	502	503	504	505	506	507	508	509	600	700	710	800	900	910	920
HC1	0	1	1	0	0	1	0	0	1	2	5	1	0	0	0	0	0	0	0
HC2	0	1	0	0	0	1	0	0	1	0	4	0	0	0	0	0	0	0	0
HC3	0	0	3	0	0	1	0	0	0	1	3	1	0	0	0	0	0	0	0
FU1	0	1	4	0	0	0	0	0	0	1	2	0	0	0	0	0	0	1	0

Biozone	930	940	950	990
HC1	0	0	0	0
HC2	0	0	0	0
HC3	0	0	0	0
FU1	0	0	0	0

Note: The three-digit headings in **boldface** are codes for the Compendium Index Categories (CICs). All the plotted data is present except for the matrix used to construct the dendrogram in figure 8, which is too voluminous to print in this format. It and all the data matrices printed here can also be obtained as ASCII files from the authors or at [http://geology.yale.edu/~wag6/Downloads/Green\\_and\\_Hickey\\_2005\\_supplement](http://geology.yale.edu/~wag6/Downloads/Green_and_Hickey_2005_supplement). The electronic publication of the Compendium Index database (Hickey and others, 2006) has been an ongoing project, and it should be noted that the counts in these matrices were derived from a pre-release version of the Compendium Index (which is available at <http://www.peobody.yale.edu/collections/pb/eCI/v0.0beta>). Therefore the exact counts may differ slightly from similar compilations of data made from the version 1.0 release of the dataset. Although broad features of the data are the same in both versions, we strongly recommend use of at least the version 1.0 release for all purposes because it is cleaner (has fewer corrupt records) and is better documented.

APPENDIX B

The following dichotomous keys were produced from Ash and others (1999) and unpublished material in the paleobotany collections of the Yale Peabody Museum. For definition of terms see Ash and others (1999) and Hickey (1973). The categories for angiosperm leaves are illustrated; most of the other categories are conventional enough that they do not require illustration, as in the case of CIC 234, conifer cones. Note also that some of the categories have a systematic component (for example, ‘*conifer* cones’ explicitly excludes lycopod strobili that may be morphologically similar). As discussed in the text, this paper is concerned with pattern in the historical record, not with the theoretical issues of morphological versus phylogenetic classification, so we rely on the consistency of a pseudo-morphological *Gestalt* like ‘conifer cones’. Issues of ecological interpretation of these data will be dealt with in a future publication.

KEY 1: Presumed Plant Fossils	CIC
A. Angiosperm 1—	
B. Leaf reasonably complete	see Key 2 100–155
B. Leaf shape unusual or indeterminate	16–
C. Lamina of unusual shape	160
C. Pinnately veined or indeterminate	
D. Toothed	161
D. Entire or indeterminate	162
C. Palmately veined	
D. Toothed	163
D. Entire or indeterminate	164
B. Flower or inflorescence 17–	
C. Single flower	170
C. Catkin/ament	171
C. Head/capitulum	172
B. Fruit or infructescence 18–	
C. Single fruit, dry	
D. Indehiscent	
E. Small	180
E. Large	181
D. Dehiscent	
E. Capsule, follicle, silique	182
E. Legume, loment	183
C. Single fruit, fleshy (berry, drupe, pome)	184
C. Infructescence	185
C. Indeterminate fruiting structure	186
B. Wood/axis 19–	190
A. Gymnosperm 2—	
B. Pteridosperm (including Caytoniales)	200
B. Cycadophyte 21–	
C. Leaf	
D. Dissected	
E. Pinnules entire	210
F. Veins parallel in pinnule	
G. Pinnule 3 cm long	211
G. Pinnule 3 cm long	212
F. Veins pinnate in pinnule	213
E. Pinnules with teeth	214
D. Undissected	
E. Veins unforked	215
E. Veins forked	216
D. Indeterminate	217
C. Seed, cone, or flower	218
C. Wood or stem	219
B. Ginkgophyte 22–	220
B. Conifer 23–	



C. Foliage	
D. Scaly	230
D. Needles 3 cm long	231
D. Needles 3 cm long	232
D. Needles flattened	233
C. Reproductive structure	
D. Cone	234
D. Cone scale	235
D. Seed	236
C. Wood	237
C. Indeterminate	238
B. Gnetophyte	240
A. Alga or fungus 3—	
B. Alga	300
B. Fungus	350
A. Bryophyte 4—	400
A. Fern 5—	
B. Leaf with sterile tissue dominant	
C. Blades dissected	
D. Ultimate laminar divisions without midribs	
E. Veins open	
F. Veins forked	500
F. Veins unforked	501
E. Veins closed	
F. Veins forked	502
F. Veins unforked	503
D. Ultimate laminar divisions with midribs	504
C. Blades undissected	505
C. Indeterminate fragments	506
B. Leaf with fertile tissue dominant	507
B. Stem or rhizome	508
B. Indeterminate fragments	509
A. Sphenopsid 6—	
A. Lycopod 7—	
B. Lycopodium or Selaginella 70—	700
B. Isoetales 71—	710
A. Gall or Lesion 8—	800
A. Indeterminate 9—	
B. Stem or axis with attachments	900
B. Rhizome, root, or detached axis	910
B. Leaf	920
B. Seed	930
B. Other organ	940
B. Indeterminate; probably plant	950
B. Indeterminate; probably not plant	990

**KEY 2: Angiosperm Leaves****CIC**

C. Leaf Compound	
D. Pinnately compound	
E. Toothed	100
E. Entire	101
D. Palmately compound	102
C. Leaf simple	
D. Petiole marginally attached	

E. Veination pinnate	
F. Lobed	
G. Even number of lobes	103
G. Odd number of lobes	104
F. Unlobed	
G. Pectinal absent	
H. Shape linear	105
H. Shape oblong	
I. Toothed	106
I. Entire	107
H. Shape elliptic	
I. Symmetrical	
J. Teeth dentate	108
J. Teeth serrate	109
J. Teeth crenate	110
J. Entire	111
I. Asymmetrical	112
H. Shape ovate	
I. Symmetrical	
J. Teeth dentate	113
J. Teeth serrate	114
J. Teeth crenate	115
J. Entire	
K. Secondaries uniform	116
K. Secondaries crowded towards base	117
K. Basal secondaries lower angle	118
K. Intramarginal present	119
I. Asymmetrical	120
H. Shape obovate	
I. Symmetrical	
J. Toothed	121
J. Entire	122
I. Asymmetrical	123
G. Pectinal present	
H. Shape elliptic or oblong	
I. Toothed	124
I. Entire	125
H. Shape ovate	
I. Toothed	126
I. Entire	127
H. Shape obovate	128
E. Veination palmate	
F. Veination acrodromous	
G. Shape elliptic	
H. Toothed	129
H. Entire	130
G. Shape ovate	
H. Toothed	131
H. Entire	132
G. Shape obovate	133
F. Veination actinodromous or indeterminate	
G. Unlobed	
H. Shape elliptic	
I. Toothed	134
I. Entire	135
H. Shape ovate	
I. Toothed	136

I. Entire	137
H. Shape obovate	138
G. Lobed	
H. Paripalmately lobed	139
H. Trilobed	140
H. 5+ lobed	141
F. Veination palinactinodromous	
G. Trilobed	142
G. 5+ lobed	143
F. Veination campylodromous	144
F. Veination flabellate	145
F. Veination parallelodromous	
G. Pinnately parallelodromous	146
G. Parallel from base	147
F. Veination plicate	
G. Leaf shape uncertain	148
G. Leaf palmate	149
G. Leaf palmate	150
D. Petiole attached centrally	
E. Veination pinnate	151
E. Veination palmate	
F. Unlobed	
G. Shape orbicular	152
G. Shape ovate	
H. Toothed	153
H. Entire	154
F. Lobed	155

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