

## Paleobotany: some aspects of non-flowering and flowering plant evolution

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### Summary

Dilcher, D. L.: Paleobotany: some aspects of non-flowering and flowering plant evolution. – Taxon 50: 697–711. 2001. – ISSN 0040-0262.

When an examination of some aspects of the evolution of vascular land plants is made across broad sweeps of Paleozoic, Mesozoic and Tertiary time, three basic patterns occur in unrelated groups in vascular land plant evolution: independent evolution of similar morphologies, nearly contemporaneous evolution of similar structures and strategies, and repeated evolution of similar features or strategies at different times. Examples are given in non-flowering plants and also in the evolution of angiosperms. A database is presented to illustrate the presence of angiosperms in the Jurassic/Lower Cretaceous fossil record and the diversity and abundance of organs recovered from these early angiosperms. These data are presented as working documents with the anticipation that they may grow into a major database for interested scholars world-wide.

**Keywords:** angiosperm evolution, Cretaceous, fossil angiosperms, Mesozoic, paleobotany, plant evolution.

### Introduction

Paleobotany has always been an important part of plant systematics. Our understanding of the fundamental relationships of major vascular land plant groups comes from the fossil record. There are a few special expressions of vascular plant evolution that I want to mention first in this paper to demonstrate the importance of knowing the history of systematic groups and the evolutionary history of traits or characters used in their classification. After these are presented, I will focus attention upon the angiosperms. Background for the information that I will discuss in the following paragraphs relating to non-flowering plants can be found in paleobotany textbooks of Taylor & Taylor (1993) and Stewart & Rothwell (1993).

### The fossil record of non-flowering plants

Lycophyta are a unique group among land plants that, because of their long and independent history, have been a distinct lineage separate from all other land plants. Their history begins in the Upper Silurian/Lower Devonian (400 plus million years bp) so that the evolution of leaves, tree habit, heterospory, seed-like reproduction, and roots have been independent of the evolution of these features in other groups of land plants. Many of these features found in lycopods evolved at nearly the same time independently in several other terrestrial groups. They often developed similar forms by using different tissues. Of particular interest in lycopod evolution is how they developed the tree habit. They used tissues derived from the outer cortex and bark rather than by thickening a central mass of tracheids and fibers, common in woody plants today. The result was tall cylinders of outer cortex and thickened bark that supported the lycopod trees of the Carboniferous. Most lycopod leaves are not

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large, complex or branching. Just as in lycopods, sporangia of many other vascular land plant taxa are also often closely associated with leaves. The sporangia frequently are borne on and sometimes enclosed by the leaves, which may be clustered into cone-like masses. These cones may resemble cones in the sphenopsids, but they were formed quite independently of any other cones or cone-like structures. From these examples we can see the potential for various vascular land plant groups, such as sphenopsids, pteridophytes, progymnosperms, and pteridosperms to develop leaves, trees, roots, cones, heterospory, and seeds or seed-like organs independently of one another. This contemporaneous evolution raises questions about the total independence of basic evolutionary trends in vascular land plant history.

Another aspect of vascular land plant evolution is that successful strategies may be reinvented *at different times* in different plant groups. The evolution of heterospory, of the tree habit, the seed habit, the association of reproductive structures with leaves, and clustering of reproductive units into cones may sometimes repeat themselves in different groups separated by many millions of years. This is seen in the evolution of heterospory in the aquatically dispersed spores of lycopods during the Devonian and by the aquatic ferns during the Cretaceous (Dilcher & al., 1992). Also, evolution toward wind dispersal of seeds or fruits is seen in some Permian plants (Dilcher & al., 1997), in the Jurassic/Cretaceous by *Welwitschia*, in the Cretaceous by conifers, and in the Tertiary by angiosperms. The vine habit has been repeatedly developed in the Carboniferous by the seed ferns, in the Mesozoic by the *Gnetales* and in the Cretaceous/Tertiary by the monocots and dicots. The clustering of reproductive organs into seed-bearing units and pollen-bearing units (only sometimes into bisexual units) has happened in the Carboniferous in *Medullosa*, and in the Mesozoic in *Gnetales*, seed ferns, *Cycadeoidea*, *Williamsonia*, *Williamsoniella* and angiosperms. Also, several of these fossil plants developed presentations of attractive colourful displays or offered rewards of pollen/nectar to encourage insect pollination.

These expressions of plant evolution in the fossil record provide new perspectives of the potential of plant evolution. Vascular land plant evolution demonstrates examples in unrelated groups of:

- **independent evolution** of similar morphologies,
- **nearly contemporaneous evolution** of similar structures and strategies,
- **repeated evolution** of similar features or strategies.

The potential of independent, contemporaneous, and repeated evolution must have become a part of the angiosperm genome as it evolved. Therefore, when we attempt to untangle the basal branches of major angiosperm clades, based upon phenotypic expressions in their early history from the fossil record, we need to consider their potential to evolve.

### The angiosperm fossil record

Angiosperm systematics is the present-day expression of our limited understanding of the products of a long evolutionary history of flowering plants. The time when angiosperms originated remains a mystery (Crane & Lidgard, 1989). We have more hope now than ever before, however, of finding the first flowers with aid of

new fossil collections (Gandolfo & al., 1998; Sun & al., 1998; Friis & al., 2001), and of understanding the time of angiosperm origins by combining fossil data with new molecular information (Sanderson & Doyle, in press). New techniques and new ways of thinking about the fossil angiosperm record (Dilcher, 2000) will produce a revolutionary challenge and lead to change in many of our long-held concepts and misconceptions about angiosperm origins and early evolution.

The evolution of angiosperms is a Mesozoic event. The time of origins, the source group for origins, and the multiple radiations, diversification and migrations around the world are all Mesozoic events. Therefore, to understand these events in angiosperm history, and thus better understand living angiosperm diversity today, we need to know as much as possible about Mesozoic plants. This is a time when ferns often dominated (Skog & Dilcher, 1994), gymnosperms and ferns modernized, aquatic ferns evolved, *Bennettitales* (*Cycadeoidales*) evolved, radiated and became extinct, and *Gnetales* evolved and radiated into diverse forms including the genera we know today. This is a time when biotic pressures were affecting the evolution of life.

#### Fossil angiosperm database

Presentation of the angiosperm fossil record here centers upon two data sets (Figs. 1, 2). Each data set represents a large amount of information that should be viewed as a working document to be taken apart, evaluated and subjected to revision. In order to keep these data current, it would be helpful if workers generating more records of fossil angiosperms would forward this information to keep the database current. Printouts will be made on request, and the entire archive soon will be available on the Internet for ease of access.

The data in Fig. 1 represent a working model of the records of fossil floras that contain angiosperms. The data are presented in a geologic time sequence beginning in the lower Mesozoic and extending until the end of the Cenomanian in the mid-Cretaceous. They represent only the time and place of megafossil floras containing angiosperms so that they can be evaluated for their age and their location (when continental drift is considered). The data collection stops at this point, because at that time so many fossils of near-modern angiosperm taxa can be found (Gandolfo & al., 1998). The purpose here is to encourage examination of floras that contain remains of angiosperms by age, from all regions of the world. We need to be critical of the age reported for each of the floras, develop a file to comment upon the evidence used to establish an age, and draw as objective conclusions about the age of the floras as possible. Another focus is to examine lines of occurrences of the earliest flowering plants and the characters they contain, which may demonstrate the evolution of the basal groups of angiosperms. We now have sufficient fossil material and the hope of collecting sufficient additional material to be able to trace diagnostic angiosperm morphological/anatomical characters back in time.

Lidgard & Crane (1990), Lupia (1999) and Lupia & al. (1999) established databases for many reports of Cretaceous angiosperm taxa. The specific question they addressed was the occurrence of angiosperm species abundance in relation to geographical distribution. They considered published reports of both

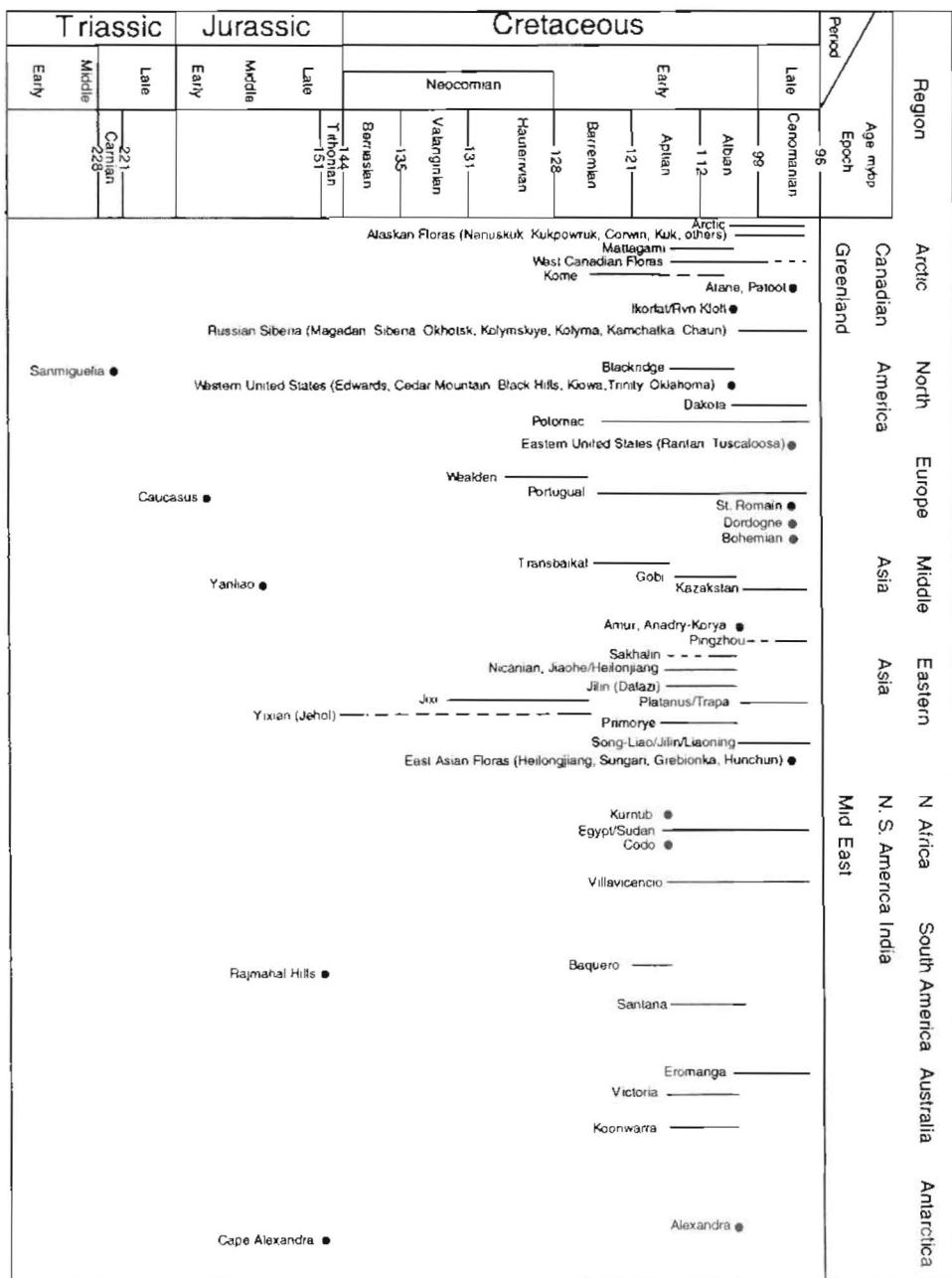


Fig. 1. Early angiosperm(ous) macro/meso fossil floras of the world. Arctic: Sweet, 1979; Alaska: Hollick, 1930; Smiley, 1966, 1969; Scott & Smiley, 1979; Spicer, 1987a, b; Mattagami: Hopkins & Sweet, 1976; West Canadian: Bell, 1956, 1965; Kome: Heer, 1874; Pedersen, 1967; Boyd, 1998; Alana/Paloot: Heer, 1874; Seward & Conway, 1935; Boyd, 1998; Ikorfat/Ravn kloft: Boyd, 1996, 1998; Russian Siberia: Samylnina, 1960, 1968a, b, 1976; Lebedev, 1974; Lebedev & Herman, 1989; Shchepetov, 1991; Vakhrameev,

1991; Shchepetov & al., 1992; Sanmiguelia: Brown, 1956; Ash, 1976; Cornet, 1986; Blackridge: Dilcher & Erickson, 1983; Western United States: Fontaine, 1889; Gress, 1922; Ball, 1937, 1939; Serlin, 1982; Thayne & al., 1983, 1985; Thayne & Tidwell, 1984; Upchurch, 1995; Dakota: Capellini & Heer, 1866; Lesquereux, 1868, 1874, 1874 [1876], 1875 [1876], 1892, 1893a, b; Newberry, 1868, 1898; Hollick, 1895, 1894; Ward, 1897, 1899; Knowlton, 1898, 1896, 1911, 1919, 1920; Berry, 1922; Schemel, 1950; Hall, 1963; Hall & Peake, 1968; Rushforth, 1971; Dilcher & al., 1976; Dilcher, 1979; Schwarzwalder & Dilcher, 1981; Retallack & Dilcher, 1981a, b; Basinger & Dilcher, 1984; Crane & Dilcher, 1984; Dilcher & Crane, 1984a, b; Dilcher & Kovach, 1986; Upchurch & Dilcher, 1990; Huang, 1992; Kvacek & Dilcher 2000; Potomac: Ward, 1888, 1895, 1905; Fontaine, 1889, 1905 [1906]; Knowlton, 1898, 1919; Berry, 1911b; Dorf, 1952; Doyle & Hickey, 1976; Hickey, 1978; Hickey & Doyle, 1977; Krassilov, 1977; Upchurch, 1984a, b; Friis & al., 1986, 1988, 1994b, 1995, 1997; Crane & al., 1986, 1989, 1993, 1994; Drinnan & al., 1990, 1991; Herendeen, 1991a, b; Pedersen & al., 1991, 1994; Upchurch & al., 1994; Crane & Herendeen, 1996; Pedersen & Friis, 1998; Tuscaloosa: Berry, 1919; Knowlton, 1919; Cahoon, 1972; Raritan: Newberry, 1886, 1895 [1896]; Berry, 1911a; Knowlton, 1919; Wealden: Hill, 1996; Portugal: Saporta, 1894; Teixeira, 1948, 1950; Vakhrameev, 1991; Friis & al., 1994a, 1997, 1999, 2001; St. Romain: Deak & Combaz, 1967; Dordogne: Colin, 1973; Bohemian: Heer, 1869; Krasser, 1869; Velenovsky, 1882, 1883, 1884, 1885, 1888; Bayer, 1900, 1921; Velenovsky & Viniklar, 1926, 1927, 1929, 1931; Paclova, 1961; Knobloch, 1978, 1979; Knobloch & Mai, 1986; Eklund & Kvacek, 1998; Kvacek, 1992; Kvacek & Dilcher 2000; Caucasus: Krassilov, 1977; Transbaikal: Vakhrameev & Kotova, 1977; Gobi: Krassilov, 1982; Kazakhstan: Vakhrameev, 1952; Samsonov, 1966; Takhtajan, 1974; Vakhrameev & Krassiov, 1979; Krassilov & al., 1983; Frumin & Friis, 1996; Yanliao: Kuang, 1990, 1996; Pingzhou: Zhou & al., 1990; Platanus: Sun Ge & al. 2000; Nicanian/Jiaohé/Heilonjiang: Krassilov, 1973, Tao & Sun, 1980; Tao & Xiong, 1986; Li & al., 1986, Sun Ge & al. 2000; East Asian: Philippov, 1979; Shuang-Xing, 1984, 2000; Amur: Koshman, 1973; Kapitsa & Ablayev, 1984; Jilin: Zhang, 1980; Tao & Zhang, 1990, 1992; Sun Ge & al., 2000; Jixi: Sun Ge & Dilcher, 1996, 1997; Sun Ge & al. 2000; Yixian: Sun Ge & al., 1998, 2000; Shun-Qing, 1999; Song-Liao: Sun Ge & al. 2000; Sakhalin: Kryshtsovitch, 1937; Krassilov, 1979; Primorye: Krassilov, 1967, 1977; Kurnub: Krassilov & Dobruskina, 1995; Egypt/Sudan: Lejal-Nicol, 1987; Codo: Duarte & Santos, 1993; Santana: Barreto & al., 2000; Villavicencio: Pons, 1988; Baquero: Romero & Archangelsky, 1986; Rajmahal Hills: Sharma, 1997; Eromanga: Pole, 1999, 2000; Victoria: Douglas, 1965, 1969; Douglas & Williams, 1982; Koonwarra: Douglas, 1963; Taylor & Hickey, 1990; Cape Alexandra: Jefferson, 1980; Alexandra: Cantrill & Nichols, 1996. These data are presented as a working document. The author welcomes revisions, corrections and new material.

palynofloras and megafossil floras. They presented approximately 50 megafossil floras between 145 to 90 million years. In Fig. 1 the records of about 75 megafossil (including mesofossils) floras are plotted, the ages ranging from 145 to 90 million years (with three exceptions). Detailed literature is given in the legend to make these data accessible and clear. In order to accommodate any methods of analysis or suggest any trends derived from these data, no floras have been omitted. While results of the database developed by Lidgard & Crane (1990), Lupia & al. (1999) and Lupia (1999) have been published, these databases apparently have not been shared or used in further analysis by the authors. I propose that we establish an open database that each investigator can access and examine. Individual parts of the data such as precise stratigraphic placement and/or age of the fossil flora can be challenged and further validated.

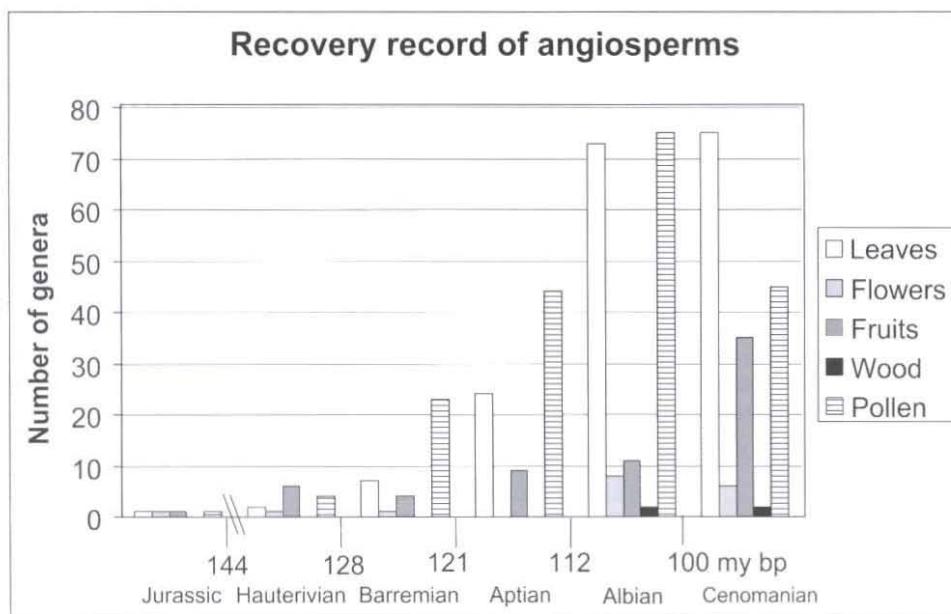


Fig. 2. World-wide reports of isolated plant organs including leaves, flowers, fruits, wood and pollen of angiospermous genera for time periods from the Upper Jurassic until the end of the Cenomanian. Berriasian and Valanginian not included. References for this figure are given in the legend of Fig. 1.

Figure 1 shows that the records of possible and probable angiosperms extend back to the Jurassic while *Sanmiguelia* remains an enigmatic fossil plant from the Triassic. A few reports are made from the Hauterivian while a few more fossil localities containing angiosperms can be found in the Barremian. Certainly this record suggests that angiosperm origins extend back into the Upper Jurassic or lowermost Cretaceous. While some diversity might be expected in floras from the Barremian, the more common records begin in the Aptian. By the time of the Aptian there are several floras around the world that contain angiosperms. These early floras need to be carefully evaluated so that as the individual elements from them are studied, we can place the characters of the plants and the potential systematic relationships into a good time series. The need for such careful evaluations is obvious when we see recent reports of early angiosperms published that give a 10 million-year range in age extending from the mid-Barremian to the mid-Aptian (Friis & al., 2001). It is a credit to the authors of this report that they gave such a range in age, being honest with their data and not taking a position by assuming only the oldest possible age. However, it is confusing to other researchers when, within the same paper, statements are made that the fossil reported represents the oldest known reproductive material of the angiosperms (assuming, then, the oldest age). The ages of the early reports listed in Fig. 1 are important so we may agree upon which angiosperm reports are older than others and which characters are the earliest known from the fossil record.

By the Aptian-Albian boundary, at about 112 million years, there are approximately 16 floras known which contain angiosperm remains. These floras extend from the Arctic, nearly to the Antarctic. The record of angiosperms around the world seems to be nearly comprehensive by the end of the Albian and early Cenomanian. During the Cenomanian, the angiosperms became dominant elements in many of the fossil floras of the world. Depending upon examination of fossil pollen/spores or megafossils (Farley & Dilcher, 1986; Skog & Dilcher, 1994), however, there is a distinct difference in the nature of dominance of angiosperms in these deposits. In general, data in Fig. 1 suggest that by the end of the Cenomanian, angiosperms are common elements in fossil floras and were dispersed to all areas of the world. For this reason I have elected not to continue tabulating data on fossil floras after this time.

The second data set (Fig. 2) presents the record of individual occurrences of angiosperms that make up the megafossil floras reported in Fig. 1 and is tied to a record of its geologic age. It is based upon 425 records (see citations in legend of Fig. 1) of individual floras and reports of fossil taxa from these floras. This should also be used as a working document and updated as new information becomes available. For example, the Raritan Flora in New Jersey is listed in Fig. 1 as Cenomanian, but I have removed the leaf data for the Raritan in Fig. 2 because we now understand it to be Turonian (Gandolfo & al., 1998).

The objective of Fig. 2 is to allow each element in the floras to be studied, challenged, and evaluated. We need to consider particular questions for each fossil: Is it an angiosperm? Has it useful characters for analysis? What are those characters? A critical evaluation of each fossil specimen should include re-examination of the specimen, evaluation of its characters, and new illustrations as needed so that researchers may put them on the World Wide Web for general examination. Fossils no longer available for study need to be discounted until new or substitute material can be found for detailed and objective critical analysis. Such revisions are now in progress with the Dakota Flora of late Albian-early Cenomanian age (Wang & Dilcher, 2000). From the work completed thus far, rather than 437 species of angiosperm leaves reported by Lesquereux (1892), there are probably about 75 species (Fig. 2). When this is plotted, it brings the Cenomanian leaf records to a level similar to leaf and pollen types reported for the Albian. This may be, however, an artifact of current sampling; as more records are recorded and evaluated, these data should change.

Figure 2 shows a slow rise of numbers of angiosperms from the Upper Jurassic or lowermost Cretaceous to the Cenomanian. This profile may change as data on nearly 140 to 150 angiosperm taxa (mentioned by Friis & al, 2001) from the Barremian/Aptian become available for evaluation. In Fig. 2 the entire record of leaves, flowers, fruits, wood and pollen is given for each time-span. These records are not broken down into further increments of time, which in the future might be desirable. If one were to plot nearly 150 angiosperm taxa for the Barremian/Aptian on Fig. 2, then the total perspective of the origins, radiations and diversity of angiosperms changes. These are the insights we hope to achieve as the record is developed and made available to a wider audience.

We have developed a group of scientists who are interested in use of the paleobotanical record, morphological data, and molecular data, to help unravel relationships of the basal lineages of angiosperms including the ANITA group (Upchurch & Dilcher, 1990; Sun & al., 1998; Friis & al., 2001). This group is called Deep Time (co-ordinators are Douglas Soltis, David Dilcher, Pamela Soltis, and Patrick Herendeen), and we hope that it will help facilitate the exchange and analysis of data such as those presented in Figs. 1 and 2.

### An overview

How does the evolution of vascular land plants, discussed earlier in this paper, relate to the evolution of the angiosperms? There were three major observations made about patterns of evolution in unrelated land plants: **independent evolution** of similar morphologies, **nearly contemporaneous evolution** and **repeated evolution** of similar features and strategies. These are the same evolutionary patterns that we can expect to see in the origin and evolution of angiosperms. When we consider the number of separate families that developed bilateral symmetry of their flowers in the late Cretaceous/early Tertiary (Dilcher, 1995, 2000), certainly independent evolution is the rule in angiosperms. This is also the case with presumed development of fleshy fruits and nuts during the Paleocene/Eocene in response to co-evolution with animals (Dilcher, 1995, 1996, 2000). These evolutionary events were nearly contemporaneous in several groups of angiosperms as each took advantage of the potential available. Finally, evolution continues to repeat itself *at different times* in angiosperms in many ways. Examples of this might include leaves being reinvented by modified branch systems after they are lost, a variety of thorns and spines originating in different flowering plants, leaves acting as accessory petals to attract insects, and inflorescences evolving at different times in different groups. Application of these three evolutionary patterns to the origin of angiosperms is beyond the scope of this paper, but suffice it to say that when applied to a carefully documented revised record, they will raise interesting questions regarding the evolution of the early angiosperms.

### Acknowledgements

Thanks are extended to Terry Lott for his help in data collection, organisation and presentation in Figs. 1 and 2 and for his help in organisation and preparation of this paper.

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