PART I **The setting of the problem**

1 Outline history of investigations

1.1 *The general purpose of study*

Angiosperms are the perceived group of living plants dominating most land areas of the present world in an astonishing variety of form and function. Their total number of species at more than 250 000 easily exceeds the numbers from all other groups of plants taken together. They naturally figure in most studies by botanists, and they form the basis of most pharmacology, horticulture and agriculture; their conservation and successful exploitation closely affected the fortunes and future of humanity, and of all other animals. In the geologic past, angiosperms clearly dominated all the lands in Cenozoic and Late Cretaceous time covering the last 100 million years, with presumably a similar influence over the land animals concerned. Geologists attempting to unravel the past conditions of land life on earth, employ studies of stratigraphy, paleogeography, paleoecology, and paleoclimatology, which are all greatly dependent in this era on plant fossil evidence provided from angiosperms. It is therefore logical for all the scientists involved in these studies to attempt to understand, to classify and to predict the properties of these universal living plants and the preceding fossils, by elucidating their evolutionary history; this investigation has, however, proved to be unexpectedly difficult.

1.2 *The object of search*

A definition of an angiosperm is an elusive target; the sum of characters of 250 000 living species cannot be otherwise and in practice there are no characters that are present in all of the extant species. The difficulty of definition could reflect a proposition that the living angiosperms are not a natural group but represent a level of development now attained by land plants with seeds. In practice, paleobotanists have stayed primarily with the characters that face them in fossils: (a) reticulate venation in the leaf (including the monocotyledon pattern), (b) columellate–tectate pollen, and (c) wood that includes vessels. A glimpse of an occasional more elaborate character, as in a flower, amounted to a bonus. Until late in the twentieth century supposedly critical characters for identifying angiosperms have often been seen rather negatively as very rare successes or as frequent failures to rise above gymnosperm level, the latter being defined more easily (than an angiosperm) from a relatively small number of living plants.

1.3 *The nineteenth century*

Plant fossils were widely and successfully studied through the nineteenth century, both in Europe and a little later in North America, where with few exceptions pure exploration continued until the end of the century. Relatively familiar-looking angiospermous leaves were common in Tertiary rocks, but in Europe these were separated stratigraphically from all Mesozoic and earlier rocks by the widespread White Chalk marine succession (barren of such fossils) so that no relevant evidence of fossil sequence was available for this critical Cretaceous period of the early development of angiospermous plants. At the time there was so much else to examine in paleobotany that little comment was made on this difficulty. In the first half of the nineteenth century perhaps more attention was paid to animal fossils that were often more complete and thus easier to interpret. Significant work on plants was largely concerned with the unusually well-preserved material from Carboniferous rocks and from adjacent Late Paleozoic strata. In mid-century, Charles Darwin (1859) remarked in a letter on the 'mystery' of the origins of angiosperms, but did not follow it up himself; others were probably more exercised by the principal elements of his work and did not at the time appear to have genuinely or directly accepted the challenge of this particular 'mystery'.

Very large numbers of observations of angiospermous fossils were made by Oswald Heer of Zurich (1809–1883) especially at Oeningen (1876) and elsewhere in Switzerland but also with collections from all over the then known geologic world. He apparently believed in a kind of creationist punctuated equilibrium and was not an admirer of the work of Darwin. Baron von Ettingshausen of Vienna also recorded angiospermous leaf fossils from all over Europe, and was an enthusiastic follower of Darwin, but his work was criticised as inadequately researched by Schenk (Professor of Palaeophytology at Leipzig 1868–1891), and subsequently by many others. The first complete textbook on fossil plants was attempted (1868–1874) by Schimper in Paris, and was eventually completed by Schenk, who exerted great influence on the subject and who insisted that a sound knowledge of systematic botany was essential. This dictum appears to have carried enough weight to have resulted in virtually all late nineteenth century paleobotanical practitioners being botanists. A consequence of this was that angiospermous fossils became neglected again because most botanists regarded leaf fossils as of no use to a botanical systematist. This is reflected in typical textbooks of fossil plants at this time. Solms-Laubach (1887; 1891 in English translation) gave only six individual index mentions and no chapter to angiosperms in a 400 page book. Zeiller (1900) devoted fifty pages to angiosperms, but very few leaves were illustrated and those were attributed to von

Ettingshausen; Zeiller did, however, pick up some monocotyledonous fossils and particularly palms from Late Cretaceous and Eocene strata. No attention was paid to possible origins of this vast group of angiosperms that dominate the Holocene floras.

This state of appreciation persisted into the first quarter of the twentieth century, when great advances were being made with Paleozoic plants and even to some extent with Jurassic plants by Nathorst and others. It presumably formed the background to the important attempts by Arber and Parkin (1907) and by Wettstein (1907) to visualise angiosperm ancestors on a purely theoretical basis. Seward's *Fossil plants* (1898–1919) in four volumes ceased after describing fossil coniferophytes; interestingly Seward did not attempt to cover fossil angiosperms in his other authoritative works, although a field trip in West Greenland (Seward 1926) did result in a geographic theory of origin of the angiosperms in the Arctic region. Many geologic observations since his time have tended through improved dating to invalidate this suggestion.

1.4 The early twentieth century

The transition to the twentieth century was gradual in paleobotany, with the science dominated by Zeiller (France), Kidston (UK), Nathorst (Sweden) and Seward (UK). In America, Wieland researched cycads and cycadeoids and Berry the description of the Potomac floras of Maryland, although the stratigraphic position of most American early Cretaceous rocks remained imprecise. In Russia, Zalessky and subsequently Krychtofovich were naturally concerned with exploration in that vast territory. The students of Seward, particularly Hamshaw Thomas (1925) using cuticles in the description of the new Caytoniales, and Sahni (1948), who ultimately described the *Pentoxylon* group from India, sought information on angiosperm ancestors.

These palaeobotanists were all botanically trained and one acceptable conclusion may be the repetition of Schenk's earlier dictum that a clear knowledge of, or at least an adequate feeling for, systematic botany is indispensable in this search, although now must be added the qualification that it should be accompanied by great restraint in applying such knowledge beyond the 'time' field in which it is based. A second conclusion or warning might well be that frustration and disappointment are likely in the absence of an equally sensitive appreciation of time-scale and stratigraphic succession in relation to the distribution of fossil discoveries.

1.5 Routine search and some despair

The twentieth century, however, was soon to witness a significant paleobotanical failure, which had the effect indirectly of discouraging attention to the angiosperm origin and various other problems. The failure was in data handling of the very large quantities of well-preserved and varied fossil plant materials of the Carboniferous Coal Measures, which were seen not to be providing the promised stratigraphic control that geologists expected of these valuable resources. With hindsight, the failure can be seen to have been due to very weak taxonomy unduly influenced by overbearing traditional nomenclature; the effect was creeping and was entirely international through the work of many diligent paleobotanists including Kidston (UK), Jongmans (Holland), Gothan (Germany), Bertrand (France), Crookall (UK), Dix (UK) and Remy (Germany). The disastrous result was that geologists working on the Carboniferous Coal Measures turned away for stratigraphic delimitation to the far less character-bearing non-marine lamellibranchs (bivalve molluscs), with which in the end they achieved very little more, while all fossil plants were completely left aside. This had happened in Britain by the time of 1939–1945 war, but the problem was earlier evident in the extraordinary wasted opportunity of David Davies (1929) in which great effort was expended on a huge collection of plants from one South Wales colliery without any profitable outcome, evidently because ideas were lacking. The whole of paleontology for geologists became almost completely centred on animal fossils for a generation.

Perhaps Hamshaw Thomas became discouraged after perceptively erecting both the Caytoniales and the Corystospermales but not being adequately acknowledged for his success with the problems of these fossils; again with hindsight, he was in effect defeated by the dogma of a monophyletic origin for the angiosperms. Subsequent prominent Mesozoic workers such as Florin (Sweden), T. M. Harris (UK) and Kräusel (Germany) all dealt with fossil gymnosperms, but this was almost certainly to develop to the full the study of cuticles, which in this Mesozoic group were both thick and very durable and therefore newly useful as evidence of characters. Angiosperms were studied at this time but quite separately and essentially from a Cenozoic point of view by, among others, Chandler (UK) and Chaney (USA). Other well-known paleobotanists including Hoeg (Norway), Arnold, Andrews and Banks (all USA) and Leclerq (Belgium) were primarily concerned with the Devonian early plant life. Right through until about 1960, the only further angiosperm origin activity was a scatter of poorly substantiated claims based on individual characters of fossils and often on single specimens (for details, see Hughes 1976, chapter 13).

1.6 The advent of palynology

Although pre-Quaternary paleopalynology was born from German brown coal (Cenozoic) and then from Carboniferous studies and some early Soviet work in the thirties, most interest was generated by Schopf *et al.* (1944), in a simplified and well-illustrated manual on palynomorphs of the North American Pennsylvanian Coal Measures. The fifties decade was a period of organisation led by Thiergart, Pflug and Robert Potonié (all Germany), Naumova (USSR), Dijkstra (Holland), Couper (New Zealand) and others; the classifications of palynomorphs, although necessary, became over elaborate and to some extent have since inhibited the general reconnaissance exploration of the sixties and later. Not until the mid-seventies, however, was paleopalynologic study applied directly to the angiosperm origin problem; general Phanerozoic (Phanerophytic) exploration had until then provided adequate general incentive for study.

1.7 The current background

Thus, until the last quarter of the twentieth century, there had been no significant new area of progress with fossils of possible angiosperm ancestors since the work of Hamshaw Thomas. Throughout the century, however, there had been great activity in the classification of living angiosperms including the work of Engler and Prantl (1897–1915), Wettstein (1901), Bessey (1915), Hutchinson (1964), Cronquist (1968), Takhtajan (1969 translation), Thorne (1976) and Cuerrier *et al.* (1992). Naturally because of the relative vacuum in studies of fossils, botanists interpreted phylogenies from consideration of these bountiful sources alone. Although such interpretations may have appeared promising for a while, it is now clear that they cannot replace the study of the fossil record in its relevant entirety and also clear that they have frequently misled scientists into work on diversionary topics.

Cambridge University Press
0521675545 - The Enigma of Angiosperm Origins
Norman F. Hughes
Excerpt
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2 Current contributions on origin

2.1 Trying all approaches

In the last fifteen years there has been more sustained interest in the angiosperm origin problem than ever before. Many paleobotanists and botanists have contributed either directly or in passing, and there have been many more suggested solutions, the majority based on observations of Cretaceous pre-Aptian fossils, at least in the first instance. The several recent general textbooks of paleobotany (Taylor 1981, Stewart 1983, Thomas and Spicer 1986, Meyen 1987, Taylor and Taylor 1993, Stewart and Rothwell 1993) comment on some of these suggestions but mostly follow tradition and devote surprisingly little space to either the development or the subsequent evolution of angiosperms. The exceptions are those of Thomas and Spicer (1986), who allotted nearly a third of their space to a balanced criticism and some useful suggestions, and Taylor and Taylor (1993), who updated all recent discoveries. A personal selection of major contributors to the solution of the problem is offered below, primarily to illustrate the diverse nature of the continuing difficulties; apologies are certainly due to any whose ideas have been unintentionally distorted, unduly abbreviated, or worse still omitted; obviously many more have thought about the problem.

2.2 Detailed development of comparative morphology

Among the more theoretical investigations was that of Kenneth R. Sporne (1915–1989), who very thoroughly compiled (Sporne 1980, also 1974 and earlier) comparative morphology characters for all extant angiosperm families into his 'Advancement Index' in which a low percentage score was considered to indicate primitive taxa. Monocotyledons had to be handled separately under different characters (see Sporne 1974), and a strangely assorted set including Liliaceae and Orchidaceae showed low (primitive) values, while palms, grasses and many water plants showed high values; no recognisable pattern emerged. Among dicotyledons, Magnoliaceae showed a low value of 25%, several Hamamelid families 33% (Sporne 1980), and also some Euphorbiaceae, but the pattern otherwise was of relatively high values and curiously the Chloranthaceae, so much favoured in various other schemes (see below), had an index of over 60%. Some of these values were varied by Chapman (1987*a*), who re-examined the statistical basis, and attempted some calculation of 'Evolutionary Distance'

(ED). Sporne himself did the original extensive compiling work with several updates but chose not to speculate; 'it is prudent to go no further than knowledge will allow' (Sporne 1974, p. 184), although his sympathy appeared to lie with Bessey (1915), with Takhtajan (1969) and with Cronquist (1968).

2.3 Application of various evolutionary theories

Sergei V. Meyen (1936–1987), well known for his encyclopaedic work on Permian and other earlier fossil plants, has suggested that a bennettitalean ancestry for angiosperms could appear more botanically probable if allowance were made for gamoheterotropy, the transfer of characters in evolution from one sex to another (Meyen 1988). In detail he proposed the origin of the angiosperm gynoecium from the bennettitalean microporophyll structure as support for similarities already observed in wood, stomatal structure and pollen. Sadly, this paper was posthumously published and Meyen was not able to develop the idea further, particularly in relation to the foliage of the two groups.

William C. Burger provided a brief study of the success of angiosperms in their very great variety (Burger 1981*a*), followed by a lively revival (Burger 1981*b*) of an old hypothesis that monocotyledons arose first; although he does not discuss reproductive structures as such, this revival includes the slight possibility of monocotyledon origin even from eusporangiate pteridophytes. He refers in passing to Triassic *Sanmiguelia*, but this was prior to the publication by Cornet (1986). The introduction of his paper (Burger 1981*b*, pp. 189–90) eloquently presses the case for an alternative theoretical framework for the origin of angiosperms to avoid circularity of argument inherent in matching data to a single overriding hypothesis such as a monophyletic origin from gymnosperms through dicotyledons to monocotyledons.

A. D. J. Meeuse announced himself as a dissident (Meeuse 1990 and earlier) and his non-acceptance of what he referred to as traditional foliar carpel theory led to his Anthocorm Theory (Meeuse 1981, p. 434) of a central axis becoming a group of bracteated gonoclads. Unfortunately for the author he had developed the theory through various improvements and amendments over twenty years in a long succession of earlier papers, which he subsequently considered with some truth to have confused his readers. Additionally, although he did not himself work with fossils, Meeuse (1979) assessed with very great enthusiasm all the Mesozoic literature and fairly concluded that fixed attitudes in particular to a monophyletic origin of all angiosperms were responsible for the marked lack of progress and to human-imposed barriers of distinction between 'gymnosperms' and 'angiosperms'. Although many botanists may not appreciate his ideas, his stirring contribution has provided very important diversity of approach.

David L. Dilcher, although his better-known contributions are to new Cenomanian plants from the Dakota Formation, provided (Dilcher 1979) an encouraging and stimulating discussion of some of the angiosperm origin problems.

While firmly highlighting the fossil record, he described the long established 'primitive angiosperm' concept as biased and thus unhelpful. On the interpretative side he suggested that the small flowers in such groups as the Hamamelidales should be considered as initially simple rather than as 'reduced' flowers, again supporting a straightforward uncomplicated approach.

2.4 Relatively remote pre-Jurassic fossil evidence

Working with Early Carboniferous pteridosperms, Albert G. Long (1977) followed botanical tradition in regarding the angiosperm origin problem as essentially concerned with the carpel, enclosed ovules, and the evident difference of inner from outer integument. He was comparing the excellently preserved Lower Carboniferous *Eurystoma*, which he had found and developed, with an idealised 'central' angiosperm. This evidence should certainly be added to that from other very early pre-Cretaceous records, but it carries on its own no special conviction.

Working in the fifties in the Herbarium of the Royal Botanic Gardens, Kew, on floral evolution, Ronald Melville (1903–1985) developed his theory of angiosperm origin through the 'gonophyll' rather than through some kind of carpel, which he rightly insisted had not been demonstrated in any pre-Cretaceous fossil. Melville (1962, 1983) sensed the importance of *Glossopteris*; he was particularly interested in the then-supposed bisexual nature of the fructifications of these fossils which were being described essentially for the first time (Plumstead 1952). His enthusiasm appeared to lead him to describe the anastomosing leaf venation pattern of *Glossopteris* as discernible in many angiosperm petal and leaf details, and to depend on descriptions of *Glossopteris* fructifications made for the most part from very difficult impression fossils without cuticle or even carbon (see also Retallack and Dilcher 1981*a*). Once again it must be said that these suggestions should certainly be listed, but that this very early evidence alone is not convincing. It should also be recorded that Melville (1983), in defending his proposal, was obliged to admit that all *Glossopteris* fructifications then known were unisexual, and that is still the position (Taylor and Taylor 1993). Additionally in explaining the time gap of appropriate fossils by invoking Earth Magnetic Reversal to account for the 'sudden' destruction of the *Glossopteris* flora and replacement by the *Dicroidium* flora, and by invoking upland survival (unobserved) through the Jurassic, his hypotheses became more and more elaborate and unlikely. The original morphologic point, however, should stand in the record as a possibility.

After greatly expanding the knowledge of *Sanmiguelia* (Cornet 1986), a unique Late Triassic plant first discovered in Arizona thirty years earlier, Cornet (1989*b*) has described a large new palynomorph assemblage from the Late Triassic beds of the Richmond Rift Basin, Virginia. In both cases he has enthusiastically introduced evidence for Triassic angiosperms. The megafossil reproductive organs of *Sanmiguelia* are unlike those of any other described plant, angiosperm or gymnosperm. From Virginia 2% of the dispersed pollen, among predominantly normal late Triassic forms, includes eleven new species of angiosperm-like reticulate-columellates in a new group of 'Crinopolles'; these new species broadly resemble Cretaceous *Liliacidites* but they are of considerably larger dimensions. Although many workers will await some connecting fossil records from Jurassic rocks (see Cornet and Habib 1992), all this new evidence clearly requires assimilation into those theories that at present include first effective radiation in early Cretaceous time.

2.5 Cryptic upland vegetation

Writing from south-western Australia, which has a startlingly rich extant flora of angiosperm endemics, J. S. Beard (1989) challenged Retallack (1977), who was also followed by White (1986), over his belief in extensive Mesozoic upland vegetation; Beard found no evidence of plants living far from water, evidence that might have been provided by adequate descriptions of the nature of fossil soils of the period, if they had been found. He further pointed out that rafted logs of trees are not evidence for upland forests; they are most likely to represent river-bank vegetation ripped away by floods, as upland tree casualties do not on average travel far. For other reasons he also suggested that it was the angiosperm radiation itself that first began to clothe the non-aggradational land, and that perhaps not immediately in Cretaceous time.

As author of an influential overview of the whole group of flowering plants Armen Takhtajan (1969 and earlier *in litt.*) appreciated the lack of progress either through comparative morphology or fossils and so attempted to apply the theory of neoteny (Takhtajan 1976 and earlier) borrowed from a previous generation of zoologists and animal geneticists. He envisaged this throughout the vascular plants and particularly in the derivation of Magnoliophyta from gymnosperms, and Liliopsida (monocotyledons) from Magnoliopsida (dicotyledons). He described the effect in detail, particularly in the case of the apparently reduced form of both male and female gametophytes. The logic continued to the point of concluding that 'neotenous forms arise under some kind of environmental stress', and that in the case of early flowering plants it probably consisted of 'moderate drought on rocky mountain slopes in an area under monsoon climate'. This amounts again to the cryptic evolution in upland areas, an overelaborate proposition that most geologists find little reason to support.

2.6 General study of gymnospermous fossils

Tom M. Harris (1903–1983) was a great investigator of Mesozoic plant fossils both in the field and in the laboratory, (e.g. Harris 1961, 1964, 1969, 1979;

Harris *et al.* 1974) and he eschewed speculation in his penetrating descriptions of many 'unexpected kinds of plants, each a problem in itself' (Chaloner 1985). He was directly involved (Thomas and Harris 1960) in the elucidation of *Caytonia*, and therefore automatically drawn into the angiosperm origin problem (Andrews 1980). Despite his curious reluctance to countenance any new taxa for fossils (Harris 1976), his records of Mesozoic seed-plants remain the best available in very many groups and consequently most relevant hypotheses will come to be tested against his knowledge and expertise.

2.7 Earliest angiospermous megafossils

The diverse nature of Mesozoic seed-plants has frequently been emphasised by descriptions of new discoveries from Asia published in Russian and frequently also very lucidly in English by Valentin A. Krassilov (1977, 1982*a*, *b*, 1984, 1987, 1990, 1991). He maintains a healthy scepticism about most dogma, both botanical and geologic, and particularly supports a polyphyletic origin (Krassilov 1990). Like others from the USSR he preferred the era-scale geologic time division Mesophyticum from approximately mid-Permian to mid-Cretaceous periods (see Chapter 14) as being more naturally relevant to events on land, but this useful Russian device has not been followed elsewhere; this may be because the general trend to greater precision causes geologic periods rather than eras to be more often used as time divisions except in very sweeping reconnaissance. Relatively new observations on interaction between plants and insects are recorded from early Cretaceous rocks of Mongolia (Krassilov and Sukatcheva 1979) and Transbaikalia (Krassilov and Rasnitzyn 1982), and comments on vegetation changes and extinction of dinosaurs (Krassilov 1981). All these papers are attractive for a wealth of new ideas and asides, sometimes heretical and frequently not developed to the full. He has also brought together in a book a great deal about the paleobiological events of the Cretaceous period (Krassilov 1985).

Subsequent to his collaboration with Doyle, Leo J. Hickey has published articles on the major features of angiospermous leaf architecture in the fossil record (Hickey 1978, Hickey in Metcalfe and Chalk 1979) and particularly of their origin in mid-Cretaceous floras. Others have subsequently built further on this information in the continuing struggle to relate Cretaceous vegetation and climate (Upchurch and Wolfe 1987). Also relating to probably mid-Cretaceous paleoecological conditions for early angiosperms are two papers (Hickey and Doyle 1977, Hickey 1984), of more geologic discussion.

2.8 Earliest obviously angiospermous pollen

In addition to being the first (Brenner 1963) to describe fully an important pollen-bearing succession of Mid-Cretaceous age in Maryland, Gilbert J. Brenner (1976) was also the first to relate occurrences in different Cretaceous provinces