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Mesozoic gymnosperms and period classifications

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Using as an example the apparent fossil record of the Gnetales, a distinction is drawn between traditional classification methods and a new system of period classification for fossils only. This new method is expected to improve interpretations of Mesozoic gymnosperms for evolutionary and palaeoenvironmental purposes, and in particular to aid the search for origins of angiosperms among Mesozoic gymnosperms.

As a step towards understanding the evolutionary origin of angiosperm plants from gymnosperms in the Mesozoic era, it is first necessary to penetrate the fog of classification which still enshrouds the Triassic to Cretaceous gymnosperms. The usual unimaginative arrangement of these plants into pteridosperms, cycadophytes and coniferophytes derives from the traditional consideration of the very small number of living members of this large ancient group. These few living members may prove to have been efficiently classified as they stand for present-day purposes, but with under 800 living species such relative success has not been difficult to achieve. The known fossils from the whole Mesozoic era amount already to several thousands of species although in most cases they are not complete plants.

Tom M. Harris, the most successful explorer of Mesozoic gymnosperms in this century, always maintained that there was great hidden variety in most groups of Jurassic land plants although he coupled this insight with a persistent reluctance to countenance any additional names or new classification to accommodate it. Before the use of computer-aided data handling, this attitude was understandable; however, it is unfortunate that it continues now in a parallel form which is much more damaging to successful interpretation.

The whole global land area was occupied for 150 million years by these gymnosperms before they became outnumbered in Middle to Late Cretaceous time; even then the dwindling band of survivors occupied some available niches for another 100 million years down to the Holocene time with its familiar, widely scattered relicts which are certainly unrepresentative of the many

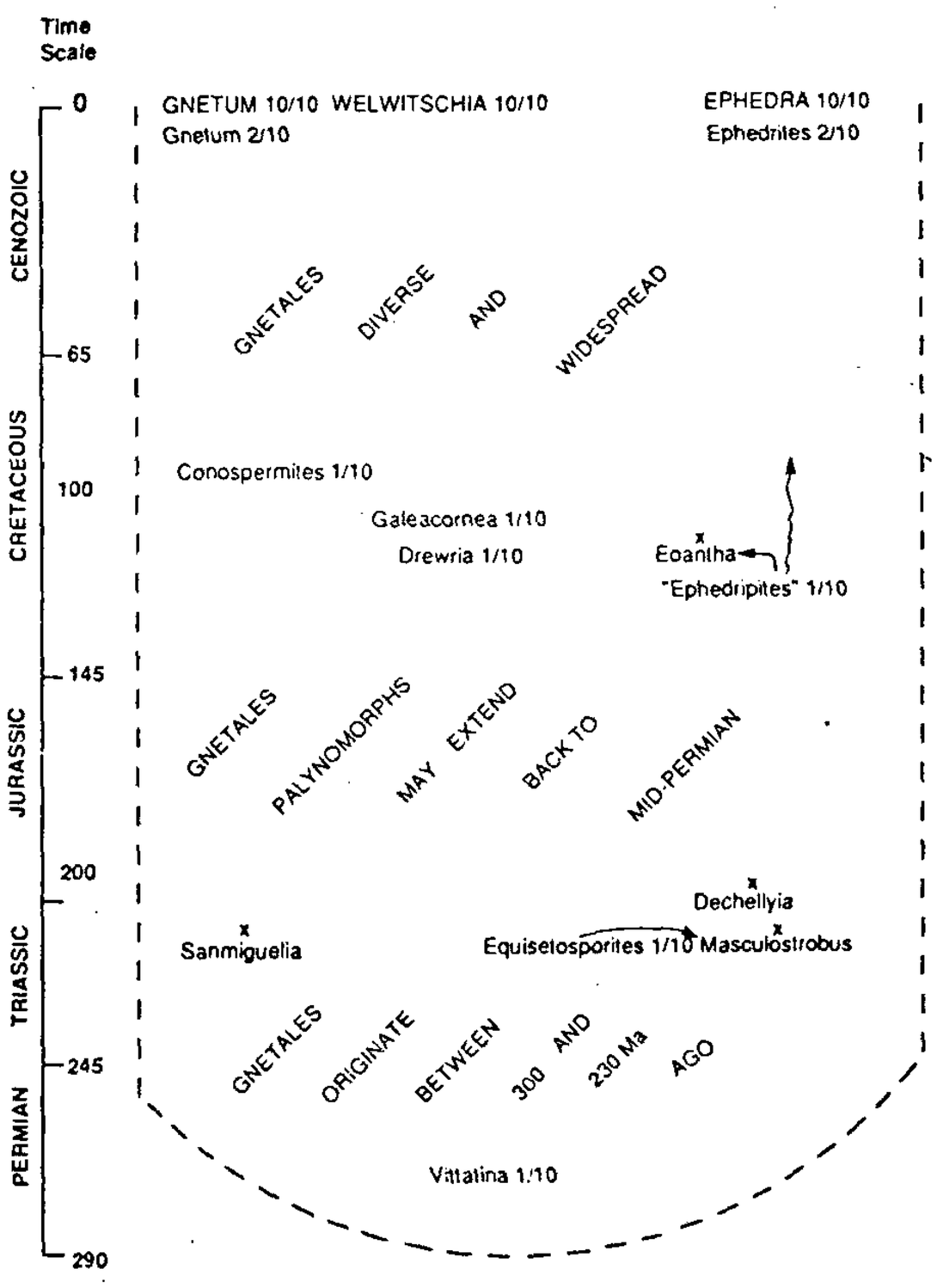

Figure 1. Supposed geological history of the group Gnetales implied in the use of the traditional Holocene-based classification as exemplified by Crane[1]. Notional scale of characters: 1/10 = one character of one living genus displayed in this fossil taxon; x = taxon normally attributed elsewhere, but included here by some authors.

taxa and habitats of the rich Mesozoic flora of the past in its prime. Perhaps, simply through custom, most authors persist in classifying all Mesozoic plants in terms of this remnant, even adding a non-contributory statistical gloss from cladistic studies. Ironically Crane[1] even quotes the warning of Arnold[2] that 'obsolete classifications retard progress'!

In order to be able to understand the evolution that has taken place in, for example, such past time as the Middle Jurassic (Bajocian to Callovian ages), it is necessary to consider what was present at the beginning and at the end of such a time slice. No knowledge solely based in other (e.g. Holocene) plants living 160 million years later can logically be of any assistance; no palaeobotanist discussing Late Carboniferous plants would even consider using Cretaceous-based information. The resulting procedure suggested by Hughes[3] is to erect period classifications which comprise data obtained only from fossils which occurred before the selected date for each classification. Use of the present-day classification would then be confined to the Holocene and Late Tertiary periods. Naturally, all earlier-period classification would be very incomplete at first, but the data available would all have direct meaning.

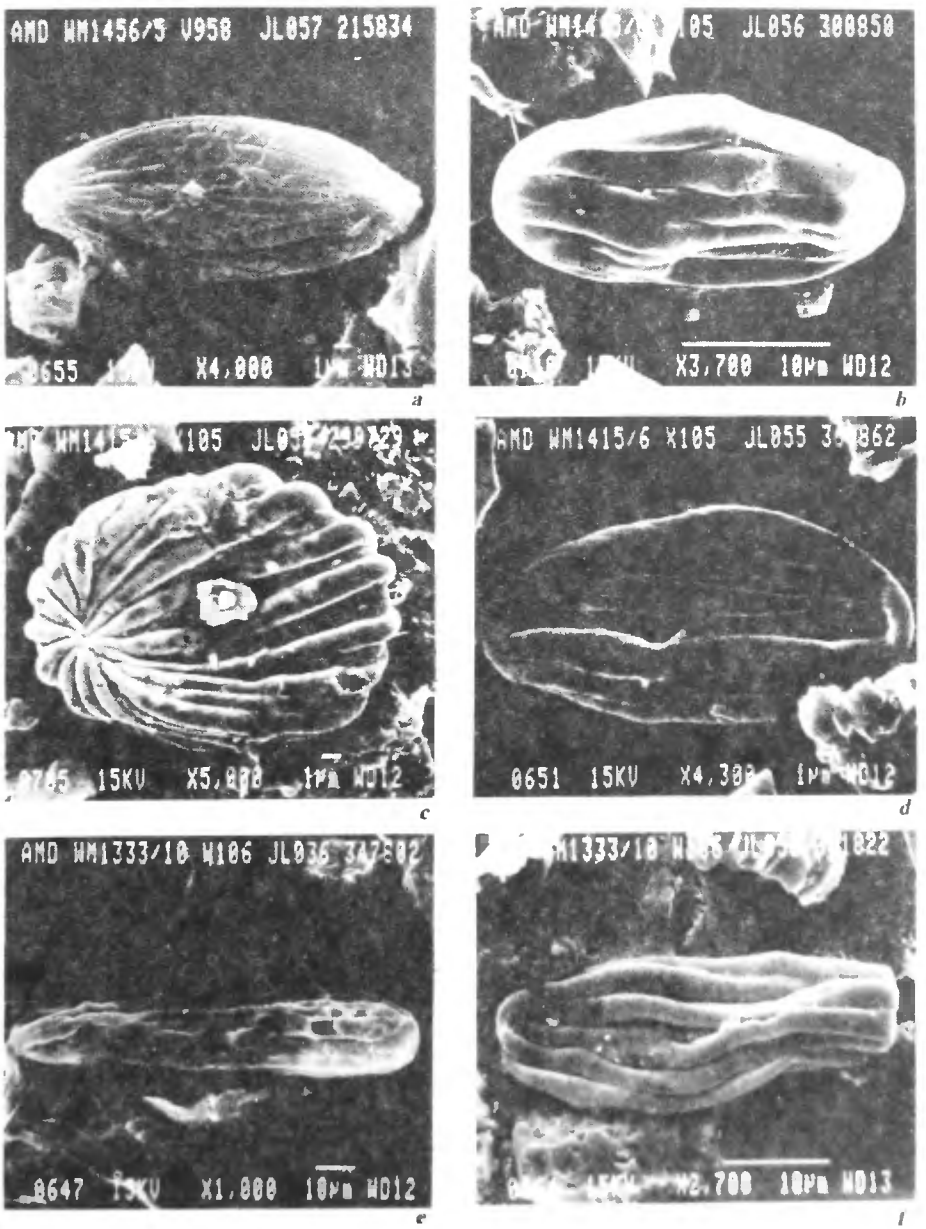

Figure 2. Polyplicate palynomorphs of Late Hauterivian to Early Barremian age from Warlingham borehole, England. *a*, Earliest recorded, WM 1456/5, length 25 μm. *b*, Few muri, WM 1415/6, length 25 μm. *c*, Wide lumina, WM 1415 6, length 35 μm. *d*, Main sulcus, numerous muri, WM 1415/6, length 27 μm. *e*, Few muri, WM 1333, 10, length 100 μm, *f*, Open-end muri, WM 1333 10, length 35 μm.

Gnetales taken in illustration

The relatively small extant group known to many as the Gnetales is taken as an example, although what is said below applies equally to the Coniferales, Cycadales and *Ginkgo*. The three extant plants *Gnetum*, *Welwitschia* and *Ephedra* are well-enough known although their homogeneity as a group is less certain.

Megafossil remains of leaves and shoots for two of the genera (Figure 1) have long been known from Tertiary strata[4], but these fossils are individually unimpressive. Palynologists working on Permian and Mesozoic rocks have enthusiastically labelled various polyplicate pollen as evidence of occurrence of *Ephedra* and *Welwitschia*, leading to the confident positive statements on the past history of the group shown in Figure 1. Interestingly, *Gnetum* pollen which at the present day is very small ($< 20\ \mu m$) and devoid of simple identification features, has not been claimed to be present in the Mesozoic. The pollen discoveries have led to certain unusual Late Triassic megafossils such as *Sanmiguelia* and *Dechellyia* being listed as possible Gnetalean plants, but without much conviction; polyplicate *Equisetosporites* has even been found *in situ* in a *Masculostrobus* cone species, but other species of this genus have normally been associated with conifer-like foliage. Thus the supposed Triassic and earlier occurrences of Gnetales do not really indicate the presence of the group Gnetales; they are at best uncertain and are better left unattributed where they do not cause confusion.

Early Cretaceous palynofossils

While studying the very small tectate monosulcate angiospermid pollen[5] of Hauterivian–Barremian–Aptian time in southern England, a range of kinds of (also) small polyplicate grains of '*Ephedripites*' were observed in many of the same samples. These polyplicates even entered the succession in Late Hauterivian time almost coevally with the first angiospermids. Six contrasting palynomorphs (Figure 2) of this general type have been recorded from all the successions involved in the angiosperm search[5,6], but for convenience the specimens illustrated here come from the Warlingham borehole, just south of London, from samples WM 1456/5 to WM 1333/10 extending up into Early Barremian time (the sample numbers were originally depths in feet as the borehole was made in 1954; the depth range is about 40 m). As with the Triassic palynofossils mentioned above, the variety of these Cretaceous polyplicates extends beyond the scope of morphology of living species of *Ephedra*. There are two significant megafossils, of which the first is *Drewria* described by Crane and Upchurch[7] from the Potomac Group of the eastern USA; this has associated pollen from the same bed (but not *in situ* pollen) said to resemble pollen of *Welwitschia*. The plant is well described and reasonably well preserved, but the implied affinity is weak and fortunately the name is neutral. The second megafossil is *Eoantha zherikhinii* described by Krassilo[8] from Early Cretaceous rocks near Lake Baikal and this is a small fertile structure with '*Ephedripites*' pollen actually found in the micropyles of its ovules. In this case the author does not claim any resemblance to the Gnetales or to any other living plant, but describes the fossil as a flower, hence the name. Any likeness therefore to the extant group Gnetales resides simply in the general polyplicate character borne by the pollen.

Period classification

Because of the misleading palaeodistribution data deriving from over-optimistic use of traditional botanical classification based in the Holocene floras, both for evolutionary and for palaeoenvironmental studies, it is suggested[3] that fossils should be classified only with other fossil material collected up to but not later than a selected time-scale point (Figure 3). This should

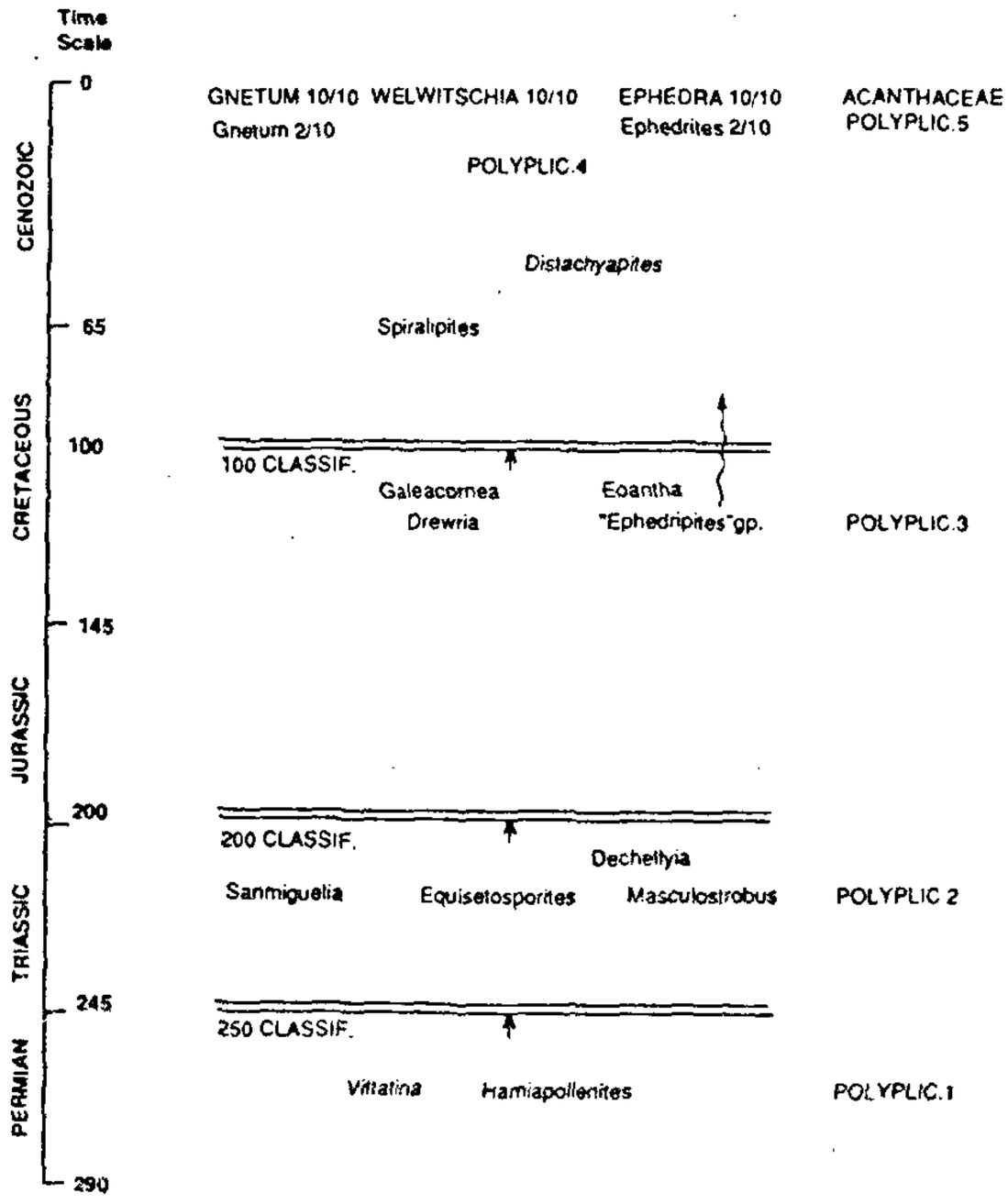

Figure 3. Diagram to illustrate the effect of employing 'period' classifications. The five polyplicate occurrences are considered separately, and their attributions can only be discussed in terms of those megafossils known in each case from the same 'period' classification. Evolutionary or euphylogenetic connections between them can only be postulated with a chain of appropriate fossil occurrences.

completely eliminate irrelevant data (however complete) taken from times long after the occurrence date of fossils under consideration.

In the current simple example, the five polyplicate pollen occurrences would be left separately in different period classifications (Figure 3) until the megafossil affinities were greatly strengthened or until a chain of appropriate fossil pollen occurrences could be shown to connect in close detail two successive polyplicate waves.

Summary

Plants with supposed gnetalean affinity form a small relatively straightforward case, but the same logic applied to the much larger Coniferales as a whole would have the beneficial effect of removing all conifer families from pre-Middle Cretaceous (100 Ma) consideration, and perhaps of removing the Cheirolepidiaceae from conifer association altogether. When the majority of living gymnosperms are conifers, and the major part of the Mesozoic gymnosperm flora has to be viewed with the same blinkered approach, it is not surprising that tracing angiosperm origin in the Mesozoic has become so unrewarding. At the distance of over forty years, Birbal Sahni and his contemporaries appear not to have been inhibited by such narrow concepts of evolutionary connections; they made correspondingly more progress.

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