

TROPICAL FLORAS OF THE LATE PENNSYLVANIAN–EARLY PERMIAN TRANSITION: CARRIZO ARROYO IN CONTEXT

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Abstract—The flora of Carrizo Arroyo is typical of a seasonally moisture-limited environment. Dominant elements were conifers, callipterids and the pteridosperm *Sphenopteridium*, all plants usually associated with indicators of seasonal moisture regimes. More generally, the Virgilian-Wolfcampian transition was a time of change from dominance of the tropical landscape by floras rich in tree ferns, pteridosperms, and lycopsids, to one dominated by conifers, peltasperms, and cycadophytes. The two types of floras do appear to have overlapped, but possibly in a manner reflective of local landscape heterogeneity. At Carrizo Arroyo for example, the wetland elements are rare and fragmentary, indicating local transport, most likely from wet microhabitats proximate to the site of deposition. Local environmental heterogeneity appears to have been part of larger scale heterogeneity in the region, probably reflective of climatic and edaphic differences in this tectonically active area.

INTRODUCTION

The transition from the Pennsylvanian to the Permian took place near the end of a long period of globally cool climates marked by glacial activity and attendant glacio-eustatic sea-level fluctuations (Rees et al., 2002). The timing of the final collapse of the southern hemisphere ice sheets is still debated but probably occurred during the Early Permian, perhaps near the boundary of the Asselian and Sakmarian (Wolfcampian), marking the early stages of the change to a warm Earth (Visser, 1997; Wopfner and Casshyap, 1997). During this change in global albedo, climatic fluctuations in the tropics were significant and accompanied by regional climatic variation, especially in rainfall. Peat/coal deposits at low latitudes were diminishing, paleosol evidence suggests increasing warmth and xeric conditions, and xeric floras can be found intercalated with floras typical of very wet conditions, even at the scale of individual outcrops (Kerp and Fichter, 1985; Broutin et al., 1990; DiMichele and Aronson, 1992).

During this time, the tropics were a continuous landmass straddling the equator from East to West. The proto-Tethys ocean was forming in the east, providing a moisture source that kept part of the eastern tropics very wet. In these areas, tropical rainforest vegetation similar to that of Pennsylvanian coal floras continued to thrive well into the Permian (Rees, 2002) and forms the basis of the so-called Cathaysian flora. The opposite extreme was found in the western tropics, where aridity increased but fluctuated with wetter periods, and became ever more prominent during the Late Pennsylvanian and Permian. Floras rich in conifers, peltasperms, and other seed plants began to appear at the same time as species that had dominated Pennsylvanian wetlands declined.

The flora of Carrizo Arroyo (Ash and Tidwell, 1982; Tidwell et al., 1999) is typical of the xeric floras that began to appear at this time in the western tropics. Such floras were dominated by seed plants, although they include a small admixture of plants characteristic of wetter environments. In this review, we will examine the composition of this flora and compare it to approximately contemporaneous floras from other parts of the tropical belt.

TROPICAL FLORAS OF THE PENNSYLVANIAN-PERMIAN TRANSITION

At least two distinct biomes existed in the tropical regions as early as the Middle Pennsylvanian. One, characteristic of mires,

swamps, and wet floodbasins, was dominated by spore-producing plants and primitive seed plants, and makes up the bulk of the Pennsylvanian-aged plant-fossil record. The other, drawn from moisture-limited environments, was dominated by evolutionarily derived seed plants, with conifers as a signature component due to their resistance to transport and decay. The earliest report of putative megafossil conifer remains in tropical deposits places them in the early Middle Pennsylvanian. Scott (1974) reported leaves preserved as charcoal, possibly washed into a lowland swamp deposit and Galtier et al. (1992) report fossil wood with conifer-like anatomy. Younger, but still Middle Pennsylvanian, occurrences are all small fragments preserved as charcoal from areas adjacent to tectonically active uplands (Lyons and Darrah, 1989). From these scraps we can infer that the xeric biome was “out there” but not reaching down into the basins, where complete preservation was more likely. Palynology is another source of evidence indicating the early existence of conifer-rich floras. The prepollen genus *Potonieisporites* has been reported as early as the Namurian (Clayton, 1966) and occurs in some abundance in upper Westphalian C (Middle Pennsylvanian equivalent) of Europe (Bless et al., 1977) an interval that also includes redbeds (Remy, 1964). By Late Pennsylvanian times, isolated occurrences of conifer-rich floras had begun to appear more regularly, which led Cridland and Morris (1963) to propose that an “upland” flora existed contemporaneously with the lowland swamp floras.

THE LATE PENNSYLVANIAN WETLAND FLORA

Wetland floras throughout most of the central and western tropics had undergone a dramatic reconstitution at or near the boundary between the Middle and Late Pennsylvanian (Westphalian-Stephanian boundary). This was a time of both global changes in climate and considerable tectonic activity in the tropics, which may have combined to affect both local and regional microclimates and depositional environments. Climatic changes have been implicated in extinctions at a broad scale, probably induced by a short pulse of global warming and drying (Phillips and Peppers, 1984; Cecil, 1990; Frakes et al., 1992). In Europe, floristic changes correlate with the disappearance of paralic basins, affecting both depositional regimes and the proximity of vegetation to marine sources of atmospheric moisture (Kerp, 1996, 2000; Cleal and Thomas, 1999). The result of these extrinsic environmental changes was the extirpation of most of the dominant trees of Middle Pennsylvanian wetlands (Phillips et al., 1974; Pfefferkorn and Thomson, 1982; Phillips and Peppers, 1984; Phillips et al., 1985). Gone, in particular, were several important genera of tree lycopsids, including

Lepidodendron, *Lepidophloios*, and *Paralycopodites*, which had been major contributors to peat-forming mires. Although less obvious because the generic-level lineages persisted, this extinction also eliminated from the wetlands most of the species of marattialean tree ferns and medullosan seed ferns (pteridosperms) that were common in Middle Pennsylvanian mires and clastic wetlands. The resulting wetland vegetation was dominated by a new suite of tree ferns and pteridosperms, with smaller amounts of sigillarian lycopsids (Willard and Phillips, 1993; Pryor, 1993).

The wetland flora is known from two major depositional environmental suites, peat-forming mires ("coal swamps") and clastic floodbasin deposits of various kinds (swamps, lakes, channel deposits: e.g., Scott, 1977, 1978; Gastaldo, 1987). The floras from these environments are preserved differently. Coal floras are known principally from coal-balls, which preserve plants anatomically, and pollen and spores, which capture a great range of taxonomic diversity but reveal little about the biology of the parent plants (DiMichele and Phillips, 1994; Phillips and DiMichele, 1999). Clastic floodbasin floras are known from compression and impression fossils (collectively, "adpressions" – Shute and Cleal, 1986), which preserve the gross morphology of the original plants, including the occasional whole plant, and often, through cuticular analysis, many details of leaf and stem surfaces useful in taxonomic and ecological analysis (Kerp, 1990). The floras of these two environments are distinct in terms of species composition, dominant kinds of plants, and total diversity. The distinction was much greater before the Middle-Late Pennsylvanian extinctions. Afterward, tree ferns were abundant in all wetland habitats, and pteridosperms in most, greatly homogenizing the floristic differences between coal and clastic floras (Gastaldo et al., 1995).

Within coal basins, the clastic floras often occur immediately above the coal beds, and are referred to as "roof shale" floras (Gastaldo et al., 1995). The biogeographic distribution of clastic floras vs. coal floras suggests that they may have grown under subtly different climatic conditions. Coal beds likely accumulated under conditions of high, year-round, rainfall, an inference based on the distribution of modern tropical thick peats (Ziegler, 1990). In contrast, many clastic floras probably represent vegetation from environments with some seasonality of rainfall, perhaps even a distinct dry season. Clastic adpression floras of similar taxonomic composition occur throughout the tropical belt, from New Mexico to China, in some cases where there is no notable coal in the geological section. Thus, the geographic range of these adpression-bearing deposits is greater than that of the coal beds. The plants found in these clastic deposits, whereas similar to those of coal beds, and no doubt tied to wet climates, could tolerate conditions somewhat drier, at least seasonally, than could the dominant elements of peat-forming habitats.

THE EARLY PERMIAN FLORA FROM SEASONALLY DRY ENVIRONMENTS

The Early Permian was a time of considerable floristic change in tropical latitudes. Major changes in the distribution of rainfall occurred with the end of the southern hemisphere glaciation, brought on by alteration of the width and fluctuation intensity of the atmospheric intertropical convergence zone. Following these events, the Permian settled into a pattern of latitudinal zonation much like that of the modern world (Ziegler, 1990), with changes in vegetation at any one locus primarily resulting from shifts in continental position beneath relatively stable latitudinal climate zones (Ziegler et al., 1997). In the western tropics, there is evidence of several biomes from increasingly remote and xeric areas (DiMichele et al., 2001), the more unusual of them appearing late in the Early Permian, following a long period of gradual compositional change in a relatively cohesive seasonally dry biome. Terminological designation of such floras is ambiguous. They are often referred to as "upland floras" when found in Pennsylvanian rocks

from paleotropical latitudes because they contain elements clearly distinct from the more typical coal and coal-roof-shale floras. Pfefferkorn (1980) suggested the term "extrabasinal lowland floras," recognizing that such floras existed in lowland basins but generally in areas where preservation was unlikely. Mapes and Gastaldo (1987) included such xeromorphic floras under the category of "non-peat accumulating." And Lyons and Darrah (1989) showed that allochthonous elements of these floras could be transported from true uplands adjacent to basinal areas. By the Permian, such floras rich in xeromorphic plants were the dominant elements in true lowland, basinal environments (DiMichele et al., 2001). In order to avoid a landscape positional designation, we will refer to these floras as "the seasonally dry biome," reflecting the conditions under which they were dominant.

Near the Pennsylvanian-Permian transition, seed plants dominate the seasonally dry biome. Most abundant in these low diversity floras are several genera of conifers, a number of callipterids, some of which, such as *Autunia*, have been linked to the peltasperms, the pteridosperm *Odontopteris*, and cordaite foliage. In North America, but evidently not in Europe, the seed plant *Sphenopteridium* is an important and often dominant element in seasonally dry floras (Mamay, 1992). A small sampling of taxa typical of the wetland biome continue to occur within these floras, but sporadically and generally in low abundance. Included are the sphenopsid foliage *Asterophyllites*, and *Annularia*, tree-fern foliage *Pecopteris*, the pteridosperm *Neuropteris*, and ground cover ferns and sphenopsids, including *Dicksonites* and *Sphenophyllum*.

Later in the Early Permian, by the Artinskian (Leonardian) the wetland elements become increasingly sporadic, and very rare when they do occur, with notable exceptions. Beds dominated by *Pecopteris* are known from several times and places in Texas, for example (Mamay, 1968), and calamites, although probably not of the kind typical of Pennsylvanian wetlands, dominate rarely and very locally, apparently along stream margins. Many new taxa of seed-producing plants begin to appear in these younger floras, including the cycad-like *Taeniopteris*, the possible noeggerathialean *Russelites*, numerous taxa possibly related to the peltasperms, including *Supaia* (Wang, 1997), *Glenopteris*, *Protoblechnum*, *Comia*, and *Compsopteris*, the gigantopterids *Gigantopteridium*, *Cathaysiopteris*, *Zeilleropteris*, *Evolsonia*, and *Delnortea*, and a greater variety of conifers.

PENNSYLVANIAN-PERMIAN TRANSITIONAL FLORAS

Floras from the Late Pennsylvanian or Early Permian are dominated, for the most part, by plants with either a wetland or seasonally dry environmental signature. That is, there are few reported floras where dominance is shared, distributed evenly among taxa otherwise typical of assemblages from wetland or seasonally dry environments. There are exceptions, however, which indicate that at times and places the floras were growing either intermixed or in close proximity on an edaphically heterogeneous surface, close to the site of preservation.

A good example of such a flora is that of the early Wolfcampian age "Sanzenbacher" locality in north-central Texas, which is dominated by *Autunia* and *Sphenopteridium*, and includes the conifer *Walchia*, cordaite leaves, and rare *Russelites*, all from the typically seasonally dry flora. Occurring as part of this assemblage, however, are many elements of the wetland flora, including *Neuropteris auriculata*, *Asterophyllites equisetiformis*, *Annularia carinata*, *Sphenophyllum oblongifolium*, *Dicksonites plucknetii*, *Sphenopteris bronii*, and three forms of *Pecopteris*. None of these latter species are dominant, but they do occur frequently as part of the sample collection.

An analysis of floras from the Virgilian-Wolfcampian transition in North Central Texas illustrates this floristic separation. Figure 1 is an ordination in which each point represents a flora, characterized quantitatively. Points labeled "o" are of Virgilian age and represent almost entirely wetlands floodplain environments, marked by the occurrence

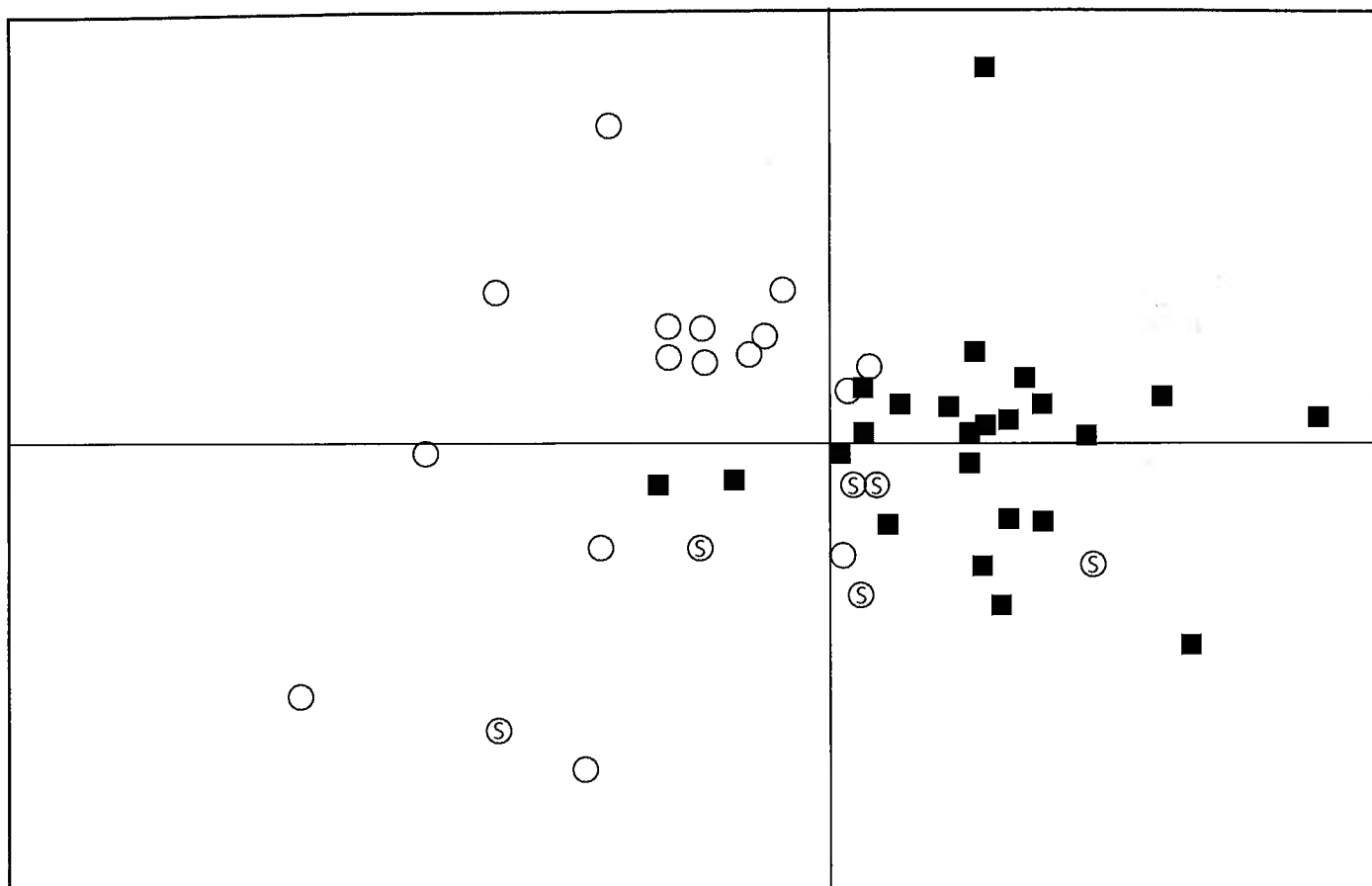


Figure 1. Ordination of 46 Virgilian and Wolfcampian age fossil plant assemblages from north-central Texas. Virgilian wetland assemblages are represented by open circles; Wolfcampian seasonally dry assemblages are represented by filled squares; Virgilian seasonally dry floras rich in the plant *Sphenopteridium* are represented by the symbol open circles with an 'S' inside. Points that plot close to each other have similar quantitative floristic composition. For the most part, the wetland and seasonally-dry floras are distinct. Virgilian seasonally-dry floras, which occur in kaolinitic mudstones intercalated on outcrop with shales bearing wetland floras, are compositionally more similar to Wolfcampian seasonally-dry floras than to coeval Virgilian wetland floras.

of organic shales, often confined to abandoned channels. Black squares are from the Wolfcampian and represent mostly assemblages from channel-fill environments lacking in significant organic accumulations. Points labeled "s" are of Virgilian age, but represent beds bearing a conifer and *Sphenopteridium*-rich flora that occurs intercalated within the Virgilian organic-rich outcrops, generally in thin, cm-thick beds of kaolinite that line the bases of channel fills. Analyses of paleosols from these intervals (Neil Tabor, personal communication) indicate that the overall transition is accompanied by a change from very wet to seasonally dry conditions. Although the distinction between Wolfcampian and Virgilian floras is not complete, they are largely separate, reflecting different dominance patterns. Note that the Virgilian-age conifer-*Sphenopteridium* beds occur in closest association with the Wolfcampian assemblages. This general pattern is similar to that found by DiMichele and Aronson (1992) among assemblages drawn from a larger geographic scale.

In comparison to the North American floras, German Rotliegendes floras are of low diversity and include several kinds of distinct assemblages (Kerp and Fichter, 1985). The most common assemblage consists of tree fern foliage, sphenopsids, and ground cover ferns, typical of the Carboniferous. Typical, but not as common as the Carboniferous-type assemblages, are those dominated by conifers with ginkgophytes and callipterids as additional elements. Another is dominated largely by callipterids. In most cases, conifers occur only in minor quantities and are clearly washed into assemblages. At several localities these different assemblages are found to occur in distinct horizons; only rarely are the assemblages intermixed. In such situa-

tions it can be demonstrated that the different assemblages occupied different habitats. Descriptions of these floras can be found in Kerp (1988, 1996, 2000), and Kerp and Fichter (1985). A similar separation of dominance patterns in different habitats was reported by Broutin et al. (1990) for the European Permo-Carboniferous, and parallels patterns seen in coeval American floras.

THE CARRIZO ARROYO FLORA

The Carrizo Arroyo flora consists of three separate plant-bearing beds, as reported in the literature. The most completely studied flora, from Unit 10 of Kues and Kietzke (1976), which is Unit 35/NMMNH locality 3437 of Lucas and Krainer (2002), has been reported and illustrated by Tidwell et al. (1999) and Ash and Tidwell (1982). An upper flora has been collected from what may be Unit 21 of Kues and Kietzke (1976), Unit 46/NMMNH locality 3431 of Lucas and Krainer (2002). Elements of this flora have been reported by Knaus and Lucas (2001, this volume). Low in the section, Kues and Kietzke (1976) report a third, low diversity flora from the top of their Unit 6, designated Unit 23/NMMNH locality 3428 of Lucas and Krainer (2002), which lies immediately below a thin coal bed.

Tidwell et al. (1999) do not provide a quantitative analysis of the KK Unit 10/LK Unit 35 flora. From descriptions in their paper, we infer that the following plants were abundant in the assemblage: the conifer *Walchia pinniformis*, the callipterid peltasperms *Autunia conferta* and *Rhachiphyllum schenkii*, the pteridosperm *Sphenopteridium manzanitanum*, and, to a lesser extent, pteridosperm foliage identified as *Neuropteris scheuchzeri* (this neuropterid foliage

lacks some critical aspects of *N. scheuchzeri* and may be *Odontopteris lingulata*). These dominant elements are all components of floras from seasonally dry environments, and probably represent that biome.

The flora also includes a number of rare elements. Those that can be identified with the greatest confidence include an *Annularia* that is probably *A. carinata* (reported as *A. stellata* and *A. sphenophylloides*, a co-occurrence that suggests the highly variable *A. carinata*, Kerp, 1984), a few fragmentary specimens of *Charliea manzanitana*, a single specimen of *Phasmatozycas*, fragmentary pteridosperm-like foliage attributed to *Neuropteris pseudoblissii*, *Mixoneura* sp., rare conifer remains of *Walchia schneideri*, an unusual conifer attributed to *Ernestiodendron* (but lacking in some key features of that genus), the calamite foliage *Annularia* sp. (due to the fragmentary nature of the material, previous identifications as *Asterophyllites grandis* and *A. charaeformis* cannot be confirmed). Also, a specimen attributed to *Lepidophloios* is doubtful. Thus, among the less common elements of the flora are species characteristic of the wetland biota, making Carrizo Arroyo a parallel to the Sanzenbacher flora of Texas, mentioned above.

Palynological analysis of the Unit 10/CA 27a flora (Traverse and Ash, 1999) indicates dominance by pollen types typical of cordaites and primitive conifers (*Potonieisporites* and *Florinites*), with a small admixture of what Traverse and Ash call "pteridosperms or precursors of various Mesozoic gymnosperms." They believe the overall aspect of this flora to be "Early Permian." As with the macrofossils, however, attribution of floras from the Pennsylvanian-Permian transition to specific time intervals is confounded by strong ecological overprinting on the distribution of major clades.

DISCUSSION

The Carrizo Arroyo flora is similar to those from moisture-limited environments found in rocks of the Virgilian-Wolfcampian transition in north-central Texas, which, in turn, are similar to some floras from the German Rotliegendes of the same age. Intense sampling of the main plant-bearing beds at Carrizo Arroyo (KK Unit 10/LK Unit 35) has revealed many minor taxa that would not have been discovered by a cursory sampling. Most of the typically "Virgilian" elements are among these minor taxa. The dominant elements, those that would have been recovered during reconnaissance sampling of the site, are typically Wolfcampian and characteristic of seasonal moisture limitation.

As an abandoned channel depositional setting, the presence of "wetland" plants as a minor component of the vegetation suggests stream bank microhabitats, or small areas of persistently wet substrates on the adjacent floodplain. The generally fragmentary nature of these plants, as reported in the literature (Tidwell et al. 1999), indicates transport to

the site of deposition, though such transport was probably quite local. Alternatively, the "wetland" and "seasonally dry" floras could record different prevailing climatic conditions, which would require that they be temporally distinct. Subsampling of the outcrop would be needed to determine if the largely "wetland" and "seasonally dry" floristic elements were spatially separated, that is, confined to different beds within the larger outcrop. If this were the case, it would imply the capture of some climatic variability within the outcrop.

If Carrizo Arroyo is indeed of Virgilian rather than Wolfcampian age, it would represent a somewhat precocious occurrence of the seasonally dry flora, paralleling that of the older Kinney Quarry locality, also from New Mexico (Mamay and Mapes, 1992; Willard, 1992), the Garnett site in Kansas (Winston, 1983) or the similarly aged Hamilton Quarry flora from Kansas (Mapes and Rothwell, 1988; Rothwell and Mapes, 1988). Carrizo Arroyo does appear, however, to occur very close to the Virgilian-Wolfcampian transition. New Mexico at this time consisted of depositional basins flanked by tectonically active uplands from which abundant sediment was being shed. Both typically Virgilian and typically Wolfcampian floras occur elsewhere in the region at about the same time as the Carrizo Arroyo flora was being deposited, although exact correlations are not possible. This pattern suggests that local microclimates were being created by and interacting with regional patterns of tectonism, and resulting position of marine moisture sources, leading to considerable terrestrial landscape heterogeneity throughout the region.

In such a setting, two distinct species pools could have broadly coexisted and been mutually overlapping. Overlapping, however, may need to be qualified to mean more "intercalated" instead of "integrated," reflective of varying degrees of microhabitat development regionally. Detailed layer-by-layer collecting of sites such as Carrizo Arroyo may reveal such distinctions more clearly. However, this may remain quite speculative if patterns of distribution cannot be teased out of the taphonomy of the depositional environments. Our speculations about Carrizo Arroyo are based on the different nature of the preservation of dominant, "Wolfcampian" elements and rare "Virgilian" elements, and on the regional co-occurrence or intercalation of assemblages dominated by wetland plants or by plants characteristic of seasonally dry habitats. These patterns are uncommon within older or younger sequences of plant-rich beds, or in basins more centrally located within stable (even if stably fluctuating) climate zones.

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