The Pennsylvanian-Permian Vegetational Transition: A Terrestrial Analogue to the Onshore-Offshore Hypothesis

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THE PENNSYLVANIAN-PERMIAN VEGETATIONAL TRANSITION: A TERRESTRIAL ANALOGUE TO THE ONSHORE-OFFSHORE HYPOTHESIS

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Abstract.—An analysis of 68 floras from the Pennsylvanian and Early Permian of Euramerica reveals distinct patterns of environmental distribution. Wetland assemblages are the most commonly encountered floras from the Early and Middle Pennsylvanian. Floras from drier habitats characterize the Permian. Both wetland and dry-site floras occur in the Late Pennsylvanian, but floristic overlap is minimal, which implies strong environmental controls on the distributions of the component species. Drier habitats appear to be the sites of first appearance of orders that become prominent during the Late Permian and Mesozoic. Higher taxa originated in physically heterogeneous, drier habitats, which were geographically marginal throughout most of the Pennsylvanian. They then moved into the lowlands during periods of climatic drying in the Permian, replacing older wetland vegetation. This pattern is analogous to the marine onshore-offshore pattern of origination and migration. The derivation of Mesozoic wetland clades from the Permian dry-lowland vegetation completes the parallel. The similarities of the marine and terrestrial patterns suggest that the combination of evolutionary opportunity, created by physical heterogeneity of the environment, and migrational opportunity, created by changing extrinsic conditions, may be underlying factors that transcend the specifics of organism and environment.

Key words.—Macroevolution, onshore-offshore hypothesis, paleoecology, Pennsylvanian, Permian, upland flora.

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Botanists have long regarded semixeric to xeric habitats as sites favoring the survival of morphological novelties (Stebbins, 1952; Axelrod, 1972). In contrast, swamps and associated wetlands have been characterized as refugia where archaic taxa and communities survive for long periods of geologic time (Knoll, 1985; DiMichele et al., 1987). The persistence of archaic species and communities in the wet lowlands is a generalization drawn from the vast majority of paleobotanical data (for Paleozoic data see Davies, 1929; Oshurkova, 1974, 1978; Havlena, 1970; Phillips et al., 1985). On the other hand, the inference of evolutionary innovation in extrabasinal, peripheral, or upland areas (Mapes and Gastaldo, 1987, discuss terminology) developed primarily as an explanation for the absence of expected intermediate forms linking the higher taxa found in lowland floras (e.g., Arnold, 1947; Axelrod, 1967; Stidd, 1980).

The earliest evidence of most major vascular plant groups (orders approximately) suggests that they originated or diversified in habitats that were periodically moisture-stressed and often peripheral to major basinal wetlands. For many groups this evidence is relatively recent and continues to accrue. The best documented Paleozoic examples are the conifers (Scott and Chaloner, 1983; Lyons and Darrah, 1989), early filicalean ferns (Scott and Galtier, 1985), cycads (Mamay, 1976, 1990; Leary, 1990), peltasperms (Kerp, 1988*a*), and gigantopterids (Mamay, 1986, 1988). Others that also appear to fit the pattern include the cordaitalean gymnosperms (Chaloner, 1958), the Ginkgoales (Mamay, 1981), the Noeggerathiales (Leary and Pfefferkorn, 1977), and glossopterids (Retallack and Dilcher, 1981). Early seed plants, although they may have originated in Late Devonian wetlands (Gillespie et al., 1981), radiated subsequently in more xeric habitats (Rothwell and Scheckler, 1988; Bateman and Rothwell, 1990; Retallack and Dilcher, 1988). A variety of enigmatic forms, including genera with uncertain affinities also occur first in what appear to be moisture-stressed habitats of the Early Permian (*Glenopteris*: Sellards, 1908; *Yakia*: White, 1929; *Russelites*: Mamay, 1968; *Wattia*: Mamay, 1967; callipterid complex: Kerp, 1988*b*; Kerp and Haubold, 1988).

In this paper we examine the Pennsylvanian-Permian vegetational transition as a possible analogue of the marine onshore-offshore hypothesis. Many of the genera, families and orders that originated in moisture-limited habitats during the late Paleozoic were part of a vegetation that replaced the archaic wetland floras of the Carboniferous tropics as the lowlands dried out. The new taxa, inhabitants of the new seasonally dry lowlands, became the ancestors of the dominant early Mesozoic wetland vegetation. This pattern of lineage and community replacement may be a terrestrial parallel to the "onshore-offshore" patterns detected in the Phanerozoic marine record. Major morphological innovations in benthic invertebrates first appeared in physically heterogeneous, disturbed nearshore environments and then expanded offshore into more stable deep-water environments (Jablonski et al., 1983; Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985; Bottjer and Jablonski, 1988; Jablonski and Bottjer, 1990; Sepkoski, 1991). Despite possible differences in factors mediating the habitat shifts, the similarities between the marine and terrestrial patterns are striking. Both patterns may reflect a fundamental relationship between evolution and environment.

DATA AND ANALYSIS

Floristic Data

Floras were compiled from 68 North American and European localities, part of a continuous tropical landmass during the late Paleozoic (Ziegler, 1990). The floras range in age from Early Pennsylvanian to Late Permian. A "flora" in the sense used here is a collection made from a single depositional environment at a single site. A site can vary from a meter square prospect pit to the roof shale of a coal exposed in one strip mine. Floras from depositional environments suggesting a high potential for allochthonous origin were excluded from consideration due to potential mixing of vegetational types from edaphically distinct parts of the landscape. Temporal heterogeneity and mixing of distinct vegetational types therefore are reduced as much as possible (see Scheihing and Pfefferkorn, 1980, for discussion). Floral lists representative of a formation, of a heterogeneous assemblage of lithologies, or characteristic of a time unit were rejected from the data base because the degree of species cooccurrence could not be assessed reliably.

Eighty taxa, identified to genus, or in some cases to generic groups such as "walchians," were included in the data base. Although using genera reduces ecological precision, it avoids the inconsistencies in many species-level taxonomies, and provides a conservative estimate of distributional patterns.

Environmental Data

The habitat from which a fossil plant assemblage was drawn can be described in a variety of ways, often in great detail. For the purpose of this analysis we were concerned with just two attributes: local moisture limitation and physical location relative to basinal lowlands. Unfortunately there are significant terminological difficulties associated with the description of these features, resulting in part from their being confounded (e.g., all lowlands are wet, all uplands are dry). Such problems are discussed and partially clarified by Havlena (1970) and Mapes and Gastaldo (1987), but considerable confusion remains.

We have avoided the term "stress" due to the ambiguity of its usage (see DiMichele et al., 1987). Swamps, for example, are highly "stressful" in the sense of their edaphics; physico-chemical properties of the substrate exclude nearly all plants and create a sharp, nongradational boundary with surrounding habitats (heavy metal-rich substrates have the same properties, see Bradshaw and McNeilly, 1981 and references therein). Seasonally dry habitats also are "stressful," but in a different sense. A gradient exists from habitats or microhabitats with constantly available moisture to those that are moisture "stressed." The evolutionary response of plants to edaphic stress is quite different from their response to moisture limitation. Swamps, for example, are not centers of evolutionary innovation. Over geological time they tend to accumulate species that can tolerate such conditions, and preserve species associations for long periods of time (Knoll, 1985; DiMichele et al., 1987). Swamps contrast markedly with moisture-limited regions, in which high local habitat heterogeneity leads to local floristic variation and significant evolutionary opportunity (Axelrod, 1972; Stebbins, 1952).

Nearly all the assemblages we analyzed qualify as lowland in the sense that they are from depositional basins, probably within 100 km of contemporaneous marine conditions. Noteworthy exceptions are some Lower Pennsylvanian floras studied by Leary (1981) and Leary and Pfefferkorn (1977), which appear to be extrabasinal, but still from lowland settings (Pfefferkorn, 1980). Evidence of true upland floras is indirect; Middle Pennsylvanian conifers, for example, occur as highly fragmentary and often fusinized (burned to charcoal) remains in lowland habitats proximal to contemporaneous, tectonically active, uplifted areas (Scott and Chaloner, 1983). North American conifers display a similar pattern of occurrence in the Late Pennsylvanian (Lyons and Darrah, 1989). Overall, however, the actual evidence of upland floras, which may have existed as early as the Lower Carboniferous in volcanogenic terrains (Scott and Galtier, 1985; Bateman and Rothwell, 1990; Rex and Scott, 1987), is too scattered and fragmentary in the Pennsylvanian and Early Permian to be of value in a quantitative analysis. Where Early and Middle Pennsylvanian plants can be identified in environments that suggest moisture-limitation (paleosols that formed under dry, seasonal climates, for example), they belong to the same groups that dominate dry habitats in lowlands during the Late Pennsylvanian and Early Permian.

Moisture availability was the major physical difference detectable among the floras we analyzed. In some instances it was possible to infer distinct seasonality in moisture regime, and it is probably through an increase in seasonality that progressively drier climates affected regional vegetation in Euramerica (Cecil, 1990). However, in most instances seasonality is demonstrated less easily than overall moisture limitation from rainfall and runoff, or limitation by soil drainage (Phillips and Peppers, 1984; Winston, 1990). For example, the Roaring Creek and Cuticle Coal floras of Indiana are associated closely with coals in a near-coastal environment and clearly formed under humid, wet conditions, but contemporaneous channel deposits suggest seasonal variations in discharge (Kvale and Eggert, 1988; Fishbaugh et al., 1989). At the opposite extreme, the Hermit Shale flora of Arizona also appears to have experienced seasonal fluctuations in stream flow, but superimposed on a much more arid climate, suggested by molds of salt crystals, alternation of mudcracked rocks and plant-bearing siltstones, and a strongly xeromorphic flora (White, 1929). Because these kinds of inferences are exceptional, we have not focused on the details of seasonality.

The following physical criteria were used to determine the local moisture conditions of fossil habitats. Wetland paleoenvironments were considered to be those associated with coals, either as roof shales or underclays, or as coming from coal-bearing sequences, where high moisture availability and limited seasonality are strongly suggested. Well-drained to "dry" paleoenvironments included those a) that are associated with indicators of a dry season (e.g., molds of salt crystals, mudcracks, red coloration); b) with sedimentological evidence that stream discharge was seasonal; c) that did not occur in association with coals; and/or d) bearing evidence of local relief sufficient to create areas with well-drained soil conditions. The inferred moisture regimes were partially corroborated when the morphological characteristics of the floras (particularly the proportion of xeromorphic species in the flora, an ataxonomic property) were harmonious with the inference.

Virtually all the Lower and Middle Pennsylvanian floras appear to be from very wet to mostly wet habitats. Such wetlands are not restricted to swamps, and include a broad range of poorly drained floodplains, levees, and coastal deposits such as lagoons. In contrast, the Permian deposits analyzed here all appear to be from seasonally dry habitats. The range of variation in the Permian is much greater than that of the Early and Middle Pennsylvanian. Stratigraphic overlap of wet and dry floras occurs in the Late Pennsylvanian (see Appendix 3).

Analysis

Most statistical analyses were performed with Systat, version 4.1 (Wilkinson, 1988). The discriminant function analysis was per-

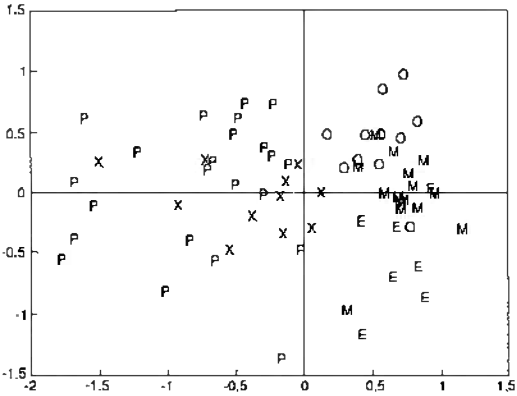

FIG. 1. Ordination of 68 Pennsylvanian and Early Permian fossil plant assemblages based on 80 genera or groups of related genera (e.g., conifers). P, Permian dry lowlands; M, Middle Pennsylvanian wetlands; E, Early Pennsylvanian wetlands. Late Pennsylvanian assemblages are divided into those from coal-bearing wetlands (O), and those from dry or seasonally dry habitats (X). Late Pennsylvanian assemblages segregate entirely by habitat-type, presaging the drying of Euramerica during the Early Permian.

formed with SPSSPC+, Advanced Statistics Version 1 (Norusis, 1986).

Runs tests were performed on the distribution of each taxon across its stratigraphic range (as that range is expressed in our data set) to test for deviation from a random dispersal of occurrences within that range; the runs test identified taxa with occurrences clustered at several consecutive sampling localities. We were concerned with identifying frequently occurring taxa with primarily Permian or Pennsylvanian "runs" in their distributions.

The relationship of floras, based on their taxonomic composition, was examined with nonmetric multidimensional scaling ordination (NMDS) in two dimensions, using the Jaccard coefficient as a measure of similarity (Kenkel and Orloci, 1986; Jackson et al., 1989). The Jaccard coefficient considers only positive matches (Archer and Maples, 1987). It slightly underestimates similarity in a presence-absence matrix with as many zeros as ours, but in a consistent manner (Maples and Archer, 1988).

Separate matrices of Jaccard coefficients also were calculated for wet site and dry site assemblages. Statistics calculated from these matrices include mean, standard deviation, median, and coefficient of variation for each of the two groups of sites. These statistics are the basis for assessing relative dispersion among the sites from each type of habitat.

The results of the ordination were evaluated further with a discriminant function analysis in which Permian and Early/Middle Pennsylvanian assemblages were treated as separate groups of knowns on which a discriminant function was based; Late Pennsylvanian assemblages were classified as unknowns on the basis of this discriminant function. Predictor variables (species) for the discriminant function were chosen in a step-wise manner. The effectiveness of variables in group separation was measured in separate analyses with Wilks' Lambda and with Mahalanobis' Distance, which yielded similar results; the results reported here are from the Wilk's Lambda analysis. Thirty-one variables (species) were dropped from the analysis because they proved to be linear combinations of other variables (their inclusion would prevent a unique solution to the discriminant analysis). The objective of this analysis was to establish the degree of confidence that could be placed in the ordination, in which habitat type (dry versus wet) appears to have exerted a greater influence on taxonomic composition of Late Pennsylvanian (Stephanian) floras than stratigraphic position (see Results).

RESULTS

The NMDS ordination (Fig. 1) summarizes the relative taxonomic similarities of the floras. There are two major groups. The first consists of Permian (P) assemblages and those Late Pennsylvanian (X) assemblages from dry habitats. The second consists of Middle (M) and Early Pennsylvanian (E) assemblages and those Late Pennsylvanian (O) assemblages from wet habitats. An apparent stratigraphic pattern in the distribution of assemblages, seen along the first axis, appears to be a reflection of the temporal wet-to-dry trend in the Euramerican tropical lowlands, based on analysis of the available sedimentological data for each flora, and on general analysis of late Paleozoic climate trends (Ziegler, 1990; Cecil, 1990). Appendix 3 summarizes the environmental indicators for Late Pennsylvanian assemblages.

The wet habitat–dry habitat distinction is

TABLE 1. Distribution and analysis of Jaccard coefficients used in calculation of Figure 1.

Habitat	N	Min	Max	Mean	SD	Median	Coefficient of variation
DRY	560	0.00	0.67	0.24	0.14	0.20	0.58
WET	560	0.00	0.78	0.30	0.14	0.29	0.47

confirmed by the discriminant analysis. All 22 of the Upper Pennsylvanian assemblages were classified correctly, that is in accordance with their position in the ordination.

Analysis of the original Jaccard coefficient matrix reveals higher average similarity, and a lower coefficient of variation among the lowland, wetland assemblages than among those from drier habitats of the Permian and Late Pennsylvanian (Table 1). This result suggests that wetland assemblages have a lower dispersion than dry habitat assemblages. The stratigraphic distribution of those taxa with significant runs tests (Table 2) illustrates that wetland and dryland sites have distinct compositional patterns, despite some overlap.

Taken together, the patterns emphasize the coherence and distinctiveness of the plant associations from wetlands and drier habitats. The greater dissimilarity among dry-habitat assemblages is expected from analyses of modern environments; a greater range of habit types is included within the dry-habitat rubric, and dry habitats are characterized by greater local habitat heterogeneity, greater opportunity for isolation, and perhaps more opportunity for evolutionary divergence (Axelrod, 1967, 1972; del Moral et al., 1985; Mason, 1946; Stebbins, 1952).

Floras from Late Pennsylvanian and Permian dry habitats also contain more uncommon genera than do floras from wetlands. Most of these are members of seed-plant clades with distinctive architectures, recognized as orders that became abundant during the Permian or in the Mesozoic. Included are the Cycadales, Gigantopteridales, Peltaspermales, Ginkgoales, and a number of taxa with unclear affinities. Most are unknown from Upper Pennsylvanian wetland assemblages. They appear to have been more narrowly limited ecologically during the Paleozoic than later.

The first axis of the ordination clearly distinguishes Permian from Middle and Early Pennsylvanian tropical floras. This apparent signal of geological age is probably an environmental signal, as indicated by the divided affinities of Late Pennsylvanian floras. Indicators of physical conditions, in particular the moisture deficit of the landscape, strongly suggest increasing moisture limitation from the Middle Pennsylvanian to the Early Permian in tropical Euramerica, probably as a consequence of changing continental configurations and the degree of polar glaciation (Phillips and Peppers, 1984; Ziegler, 1990; citations in Appendix 2 for primary data). The patterns of floristic relationship, demonstrated in Figure 1 and in the results of the subsequent discriminant analysis, indicate that the "Permian" lowland vegetation existed, as a unit, in the drier, marginal areas during the Late Pennsylvanian, if not earlier (Scott and Chaloner, 1983; McComas, 1988; Broutin et al., 1990). The uncommon, distinctive Late Pennsylvanian floras from drier habitats (Table 2; Appendices 1, 2, and 3) contain several of the important basinal lineages of the Permian and Mesozoic, specifically Cycadales (*Spermopteris* at Baldwin and Garnett; *Plagiozamites* at Kinney; *Charliea* at Kinney), Coniferales (at all dry sites), possible Ginkgoales (*Dicranophyllum* at Kinney), and members of the callipterid complex (at all dry sites except Kinney, McCoy and 7-11). Despite their temporal cooccurrence, dry-habitat floras are taxonomically and distributionally distinct from wetland assemblages throughout the Pennsylvanian.

DISCUSSION

The Onshore-Offshore Analogy

In 1983, Jablonski and others suggested that major morphological innovations in benthic invertebrates appeared in near-shore environments and then expanded across the shelf, based on patterns in Cambro-Ordo-

TABLE 2. Stratigraphic distribution of taxa used in analyses. Number of sites in each time interval is listed in parentheses. An asterisk in the last column denotes a taxon with significant ($P < 0.5$, two-tailed) runs in its distribution.

Taxon	Permian (23)	Dry Stephanian (11)	Wet Stephanian (11)	Westphalian	Runs
Spermopteris	2	2	0	0	
Gigantopteridium	4	0	0	0	*
Gigantonoclea	2	0	0	0	
Zeilleropteris	1	0	0	0	
Cathaysiopteris	2	0	0	0	
Delnortea	1	0	0	0	
Evolsonia	2	0	0	0	*
Phasmatocycas	6	0	0	0	*
Archaeocycas	1	0	0	0	
Cycadospadix	1	0	0	0	
"cycad"	1	0	0	0	
Charliea	0	1	0	0	
Podozamites	0	1	0	0	
Russelites	2	0	0	0	
Sandrewia	3	0	0	0	
Wattia	3	0	0	0	*
Tinsleya	1	0	0	0	
Yakia	2	0	0	0	
Glenopteris	3	0	0	0	*
Supaia	4	0	0	0	*
Padgettia	1	0	0	0	
Plagiozamites	0	1	0	0	
Taeniopteris	14	4	0	1	*
Walchians	8	11	0	0	*
Brachyphyllum	3	0	0	0	
Cordaites	10	7	4	15	
Callipteridium	1	0	3	2	
Callipteris s.l.	15	8	0	0	*
Neuropteris	5	8	7	22	*
Odontopteris	9	7	4	1	
Sphenopteris	4	6	3	14	*
Dicranophyllum	0	1	0	0	
Discinites	3	0	0	0	*
Daubreeia	1	1	0	0	
Pecopteris	11	5	10	14	
Ptychocarpus	0	1	5	4	*
Fascipteris	1	0	0	0	
Qasimia	1	0	0	0	
Senftenbergia	0	0	0	3	
Oligocarpia	0	0	3	2	
Dicksonites	0	0	4	2	*
Protoblechnum	1	0	0	0	
Cladophlebis	1	0	0	0	
Danaeites	0	1	1	1	
Calamites	8	8	10	20	*
Sphenophyllum	9	2	8	15	*
Lobatannularia	1	0	0	0	
Sigillaria	4	6	3	11	
Lepidodendron	0	0	1	13	*
Lepidophloios	0	0	0	7	*
Bothrodendron	0	0	0	2	
Ulodendron	0	0	0	1	
Asolanus	0	0	0	3	
Callistophyton	0	1	0	0	
Alethopteris	0	2	3	16	*
Eusphenopteris	1	0	3	9	
Neuralethopteris	0	0	0	2	*
Adiantites	0	0	0	2	
Linopteris	0	0	1	7	

TABLE 2. Continued.

Taxon	Permian (23)	Dry Stephanian (11)	Wet Stephanian (11)	Westphalian	Runs
Reticulopteris	0	0	0	1	
Lescuropteris	0	0	0	1	
Mariopteris	0	0	0	16	*
Eremopteris	0	0	0	3	*
Alloiopteris	0	1	0	5	
Pseudomariopteris	0	0	3	0	
Karinopteris	0	0	0	2	*
Desmopteris	0	0	0	1	
Palmatopteris	0	0	0	3	
Brongniartites	1	0	0	0	
Schizopteris	1	1	0	0	
Nemejcopteris	0	2	4	0	
Megalopteris	0	0	0	2	
Rhodea	0	0	0	1	
Neriopteris	0	0	0	1	
Archaeopteridium	0	0	0	1	
Tingia	0	0	0	1	
Crossopteris	0	0	0	1	
Noeggerathia	0	0	0	1	
Sphenopteridium	0	0	0	1	
Zygopteris	0	0	0	1	

vician and Cretaceous fossils. Older forms, and hence the communities they comprised, were progressively displaced offshore. There, more archaic species, communities, and community dynamics persisted. The onshore-offshore hypothesis embraces more than the origin of new morphologies; it places them within a specific ecological context. The pattern of evolutionary innovation in onshore habitats and conservatism in offshore settings has since been generalized to most marine ecosystems of the Phanerozoic (Jablonski and Bottjer, 1983; Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985; Bretsky and Klofak, 1985; Bottjer and Jablonski, 1988), including the Recent (Aronson, 1990). The causes of this pattern may reside in the greater levels of disturbance and abiotic stress in near-shore environments, creating opportunites for the survival of new body plans (Bottjer and Jablonski, 1988, and Jablonski and Bottjer, 1990, offer a number of alternative driving mechanisms).

A similar pattern appears to be widespread in vascular plants: groups that ultimately became numerically abundant in lowland basinal habitats, where conditions for preservation were most favorable, are most often recognized first in settings suggesting periodic moisture limitation, or, occasionally, as fragmented, allochthonous debris transported to basinal wetlands from surrounding areas. The fossil record provides rare glimpses of such floras before they became permanently established in lowland regions. They were contemporaneous with the older lowland floras, but occupied habitats physically removed from basinal settings.

Terminological difficulties encountered in describing these edaphically distinct terrestrial areas create conceptual difficulties. Mapes and Gastaldo (1987) list a myriad of terms that confuse distinctions between and among peat swamps and clastic swamps, lowlands and uplands, wetlands and well-drained areas, and basinal and extrabasinal areas. The most fundamental of these distinctions, in our opinion, is that between wetlands, including their characteristic swamps, and drier habitats, where plants are subject to periodic moisture deficits, particularly under seasonal rainfall regimes. This is a contrast between mesic settings (the wetlands), which are relatively homogeneous, and moisture-limited environments, which are physically heterogeneous (Havlena, 1970). It is easy to relate and describe the characteristics of the wetlands, but difficult to do so for the drier environments. Hence the terminological problems.

The terrestrial analogues of offshore settings are poorly drained wetland areas with abundant moisture availability that are rarely, if ever, exposed to drought. They are often seen in the fossil record as coastal deltaic, coal-bearing rock sequences. These environments tend to have ecologically persistent floras and communities, particularly in the Paleozoic (DiMichele and Phillips, 1990). Wetland habitats harbor long-ranging lineages of phenetically similar species and, most importantly, rarely have been areas of origin for higher taxa (Knoll, 1984, 1985; DiMichele et al., 1987). The analogues of onshore environments are water-limited habitats that are, in general, seasonally dry and often well-drained. They include both basinal centers of sediment accumulation and extrabasinal areas that only rarely and fortuitously preserve plant fossils. It is these environments that fostered the origin of most ordinal-level taxa of seed plants and ferns; the poor stratigraphic record of such habitats, at least during the wetter periods of tropical history, makes assessment of species turnover and community persistence difficult. Late Paleozoic clades centered in wetlands, such as sphenopsids and lycopsids (see Bateman et al., 1992), show lower morphological disparity than lineages centered in the drier Paleozoic habitats, such as ferns and seed plants (Crane, 1985; Doyle and Donoghue, 1986; Rothwell, 1987), possibly reflecting differences in opportunities for divergence.

The selective effect of moisture limitation at any one time is completely dependent on the physiological and structural capabilities of the plants *existing at that time.* Any truly terrestrial environment may have been a moisture-stressed "upland" for early land plants (Beerbower, 1985). Successive lineages of plants evolved increased tolerance to drought through the Phanerozoic. In effect, the adaptive frontier has been pushed back through time. Today, there is a much greater range of vegetation separating the most evolutionarily conservative basinal wetlands from the areas of greatest innovation in globally dispersed and highly heterogeneous moisture-limited areas. We speculate that the physical length of the gradient was much shorter in the Paleozoic, given the more limited spectrum of plant taxa and biologies.

Comparison of Terrestrial and Marine Dynamics

Vegetational changes in the late Paleozoic tropics can be summarized broadly as follows. Many of the plant lineages that came to dominate Permian and early Mesozoic floras first appeared in extrabasinal, dry to seasonally dry environments. The increase in regional aridity, such as that proposed for the Permian of the southwestern United States, is associated with marked increases in 1) the number of regional community types (Read and Mamay, 1964); 2) floristic variation among localities within any one community type; and 3) the appearance of many new morphologies. In rare cases (recently discovered in north-central Texas and not included in this data base) where organic-rich deposits occur in earliest Permian rocks, they retain a "Pennsylvanian" aspect: dominance by pteridosperm taxa typical of wetland basinal habitats. A similar pattern occurs in Europe and is discussed by Broutin et al. (1990). Conifer-rich floras from dry habitats of Late Pennsylvanian or Early Permian age usually contain only small numbers and few species from wetland-centered lineages, such as sphenopterids and certain pecopterids. Figure 2 illustrates the increased abundance of dry-site habitats and plants in the basinal lowlands through time.

Although the Pennsylvanian-Permian strata record only a small segment of the history of plant evolution, it is a particularly important segment because during this time seed-plant dominated, Mesozoic-style ecosystems evolved. The first appearance of conifers, cycads, ginkgoaleans and the callipterids in Late Pennsylvanian dry environments, and the later appearance of peltasperms, additional conifer genera, and enigmatic groups such as gigantopterids and *Wattia,* in dry habitats of the Early Permian stand in marked contrast to evolutionary dynamics in the wet lowlands of the Early and Middle Pennsylvanian. The time interval may be short, but the pattern is remarkably clear.

Peripheral, moisture-stressed environ-

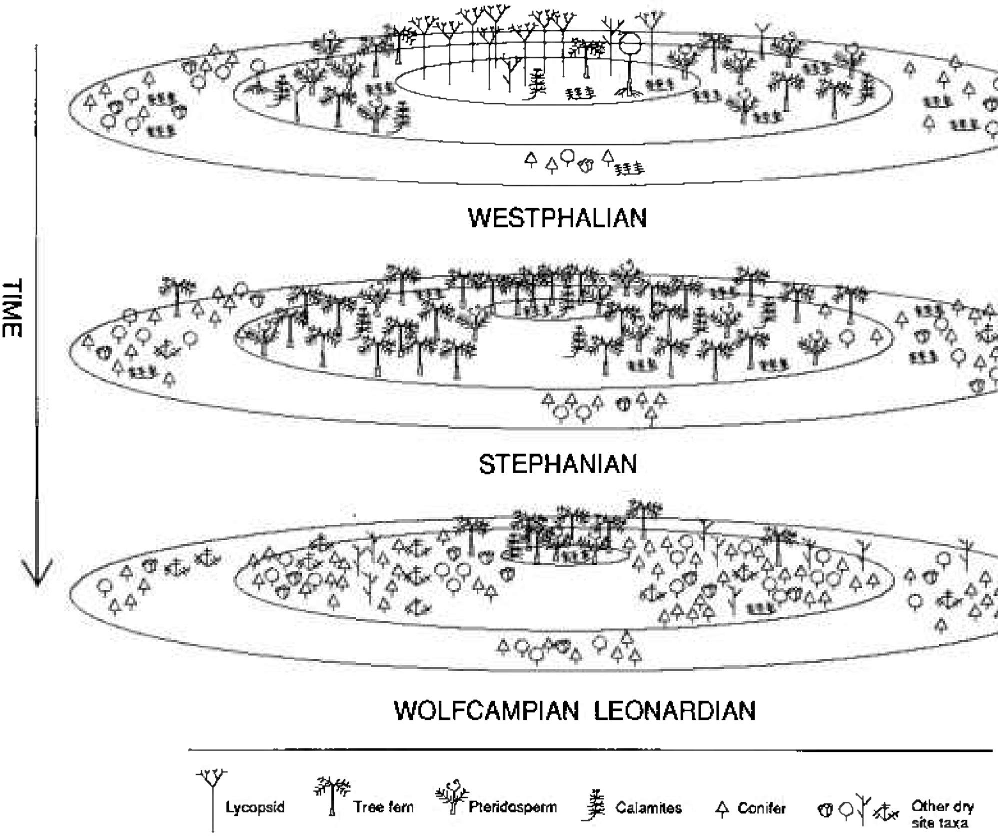

FIG. 2. Diagramatic representation of changes in the composition of basinal lowlands and surrounding uplands during the Pennsylvanian-Permian transition. The innermost circle represents the wettest basinal environments, dominated by lycopsids in the Westphalian (Early and Middle Pennsylvanian), and tree ferns and pteridosperms thereafter, into the earliest Permian (Wolfcampian-Leonardian). The area occupied by these kinds of habitats declined on average throughout this period. The middle circle represents basinal, nonswamp habitats, which were progressively more affected by seasonal dryness into the Permian; tree ferns and pteridosperms dominated these environments until the Permian, when the flora from the uplands began to move strongly into the basinal lowlands. The outer circle represents the uplands and extrabasinal lowlands, rarely sampled in the fossil record. This flora appears occasionally in the lowlands during the Stephanian (Late Pennsylvanian), probably during times of increased seasonality in moisture availability. It comes to prominence in the lowlands in the Early Permian.

ments that foster the origin of higher taxa share attributes with marine nearshore environments (cf. Jablonski and Bottjer, 1990). In moisture-limited areas the physical variability of the landscape (i.e., topography, soil, and exposure) is greater than that of wet areas, increasing local and regional variation in site quality (Stebbins, 1952; Axelrod, 1967, 1972). Such habitat heterogeneity fragments populations and therefore provides the biological framework for isolation and rapid evolution (Wright, 1982*a*, 1982*b*). Physically heterogeneous landscapes also offer greater potential for a population to encounter an "empty niche," an area of little or no competition where a population, even one poorly fit to local physical conditions, would be able to survive until stabilized by intrapopulational selection (Axelrod, 1967; Valentine, 1980; del Moral et al., 1985). In addition, xeric or semixeric habitats can appear in any climatic zone and draw much of their flora from the local vegetation on more mesic sites. This further promotes unique evolutionary events in isolated regions.

The taxa that originated in peripheral, drier habitats in the late Paleozoic tend to be subgroups of seed plants. The life histories of seed plants suggest a priori greater extinction resistance than most groups of lower vascular plants (ferns, lycopsids and sphenopsids). This prediction is confirmed by the nearly continuous expansion of seed-plant diversity during the post-Paleozoic, at the expense of lower vascular plants (Niklas et al., 1985). Thus, as in the marine record, more demanding physical environments may foster the survival of extinction-resistant clades during early stages of diversification (Jablonski and Bottjer, 1990; Sepkoski, 1991).

The evolution of major architectural innovations (the traditional grounds for recognition of new higher taxa) in dry, physically heterogeneous areas, peripheral to basinal wetlands, is only half the analogy to the onshore-offshore marine pattern. The other half is the movement of species from marginal areas into basinal lowlands, and their rise to ecological dominance there. Jablonski and Bottjer (1990) discounted extrinsic environmental factors as causes of the marine onshore–offshore pattern, and Sepkoski (1991) argued on theoretical grounds that intrinsic evolutionary processes alone could explain the pattern. However, Bretsky and Klofak (1985) documented onshore-offshore movement in an epicontinental sea contingent on changing sea level.

Physical factors appear to have been the driving force in the late Paleozoic terrestrial-plant shift as well. Marginal taxa expanded into basinal habitats in association with climatic change: increased seasonality of moisture availability in the Euramerican tropical lowlands during the late Paleozoic (Knoll, 1984; Parrish et al., 1986; Ziegler, 1990). When more favorable conditions returned to the Euramerican tropical lowlands in the Mesozoic, species of higher taxa that originated in marginal environments were the ones present in the lowlands to generate the new wetland and swamp lineages. For example, Triassic and Early Jurassic coal-bearing rock sequences include conifers, peltasperms, taeniopterid cycadeoids, cycads, and other groups of gymnosperms either belonging to or derived from lineages established in the lowlands during the Permian. They are mixed with survivors of Carboniferous wetland groups such as sphenopsids and ferns (Harris, 1926, 1931–1937; Hope and Patterson, 1969; Delevoryas and Hope, 1976, 1978, 1981; Upchurch and Doyle, 1981).

The terrestrial pattern described here differs in several important ways from the pattern in the marine realm, as documented most recently by Jablonski and Bottjer (1990). The plant record does not show individualistic expansion of clades from peripheral, dry environments into the wet lowlands. Some taxa, such as conifers, appear to have moved into the lowlands sooner and in greater numbers than many of the broad-leaved species; however, the priority of conifers may be biased taphonomically by the high preservational potential of decay-resistant conifer foliage. In general, our data and the data discussed by Broutin et al. (1990) suggest that communities from drier habitats behaved as units in replacing communities from wetter environments. This whole-community movement does not appear to be the general condition in the marine environment (Bretsky and Klofak, 1985; Bottjer and Jablonski, 1988).

The spatial relationship of marginal, well-drained, relatively dry areas to basinal wetland areas also differs in a significant way from the relationship of marine onshore to offshore habitats. Because successive plant lineages were more tolerant of moisture limitation, the terrestrial "onshore" cannot be defined relative to fixed physical reference points in the sense that the marine onshore is defined by the continental margins and coastlines. The abiotic attributes of the nearshore marine are fixed, in contrast to the terrestrial environment. The terrestrial lowlands, the "offshore" analogue, are located in coastal areas, near sea level. The "onshore" analogues represent a heterogeneous association of spatially disjunct and edaphically dissimilar areas. These may vary from lowland basins in areas with limited or highly seasonal rainfall, to true uplands distant from areas of major alluvial sedimentation.

Despite some differences, the general pattern of "onshore" origin, and "offshore" migration of taxa and the communities they comprise remains a striking parallel between the marine and terrestrial biospheres. The terrestrial biosphere was, and may still be, a more "open" system than the marine biosphere. Onshore-offshore marine environments were occupied even in the Cambrian, though by very different organisms and with a different community structure than today (Bambach, 1985; Sepkoski and Miller, 1985). Opportunities for colonization of entirely unoccupied habitats and resources were much more limited than in the terrestrial realm. Modern terrestrial environments may offer the opportunity for large-scale radiations in desert and polar regions.

Proximal Causes of the Pennsylvanian-Permian Vegetational Transition

Was this floristic change a displacement or replacement? There has been a growing acceptance in paleobotany that plants are fundamentally more "extinction resistant" than animals, owing to their construction and life history (Knoll, 1984; Traverse, 1988). There are no reported examples of global floristic extinction, and supposedly no subsequent massive ecological voids into which new or surviving taxa could initiate radiations. Consequently, competition has been invoked as the driving force in most plant evolution (Knoll, 1984). In contrast, opportunity has been implicated as a major driving force in animal evolutionary radiations (Benton, 1987; Jablonski, 1986; Jablonski and Bottjer, 1990; Valentine, 1980).

Ecological analysis of the Pennsylvanian-Permian floristic change strongly suggests that it was not *primarily* competitive. Rather, the drier habitat flora that characterized the Permian came to dominate the lowlands as seasonal dryness developed there. The wetland flora, so characteristic of the Pennsylvanian coal-bearing sequences, contracted markedly. The spatial disjunction of the two floras, despite their temporal overlap in the Late Pennsylvanian, implies replacement rather than displacement. Local competition undoubtedly occurred, perhaps even as the coup de grâce to small wetland plant populations living under suboptimal conditions (see discussion of "vegetational inertia" by Cole, 1985).

The nature of the Pennsylvanian-Permian vegetational change was addressed broadly by White (1933), Florin (1963), Remy (1975), and Havlena (1970) prior to our analysis. Knoll (1984) described it explicitly as "replacement." He excluded the "Paleophytic-Mesophytic" transition from the strictly competitive mode of floristic change he envisioned for most of the history of land plants. The underlying causes of the late Paleozoic vegetational transition, specifically climatic change and associated ecological disruption, occurred at other times during the Phanerozoic as well. It is likely that more detailed analysis of the plant fossil record will reveal additional instances in which radiations or extinctions were caused by changing physical conditions rather than by the superior biologies of the survivors (Valentine et al., 1991).

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APPENDIX 1

Taxa Occurring at Sample Localities

1 = taxon present; 0 = taxon absent.

Taxa in order by columns: *Spermopteris, Gigantopteridium, Gigantonoclea, Zeilleropteris, Cathaysiopteris, Delnortea, Evolsonia, Phasmatocycas, Archaeocycas, Cycadospadix,* "cycad," *Charliea, Podozamites, Russelites, Sandrewia, Wattia, Tinsleya, Yakia, Glenopteris, Supaia, Padgettia, Plagiozamites, Taeniopteris,* Walchians, *Brachyphyllum,* Cordaites, *Callipteridium, Callipteris* s.l., *Neuropteris, Odontopteris, Sphenopteris, Dicranophyllum, Discinites, Daubreeia, Pecopteris, Ptychocarpus, Fascipteris, Qasimia, Senftenbergia, Oligocarpia, Dicksonites, Protoblechnum, Cladophlebis, Danaeites,* Calamites, *Sphenophyllum, Lobatannularia, Sigillaria, Lepidodendron, Lepidophloios, Bothrodendron, Ulodendron, Asolanus, Callistophyton, Alethopteris, Eusphenopteris, Neuralethopteris, Adiantites, Linopteris, Reticulopteris, Lescuropteris, Mariopteris, Eremopteris, Alloiopteris, Pseudomariopteris, Karinopteris, Desmopteris, Palmatopteris, Brongniartites, Schizopteris, Nemejcopteris, Megalopteris, Rhodea, Neriopteris, Archaeopteridium, Tingia, Crossopteris, Noeggerathia, Sphenopteridium, Zygopteris.*

Floras in order by rows: Middle Khuff, Del Norte, Stamford, Lawn, Eddy/Enid, Lake Kemp 2, Lake Kemp 1, Hermit Shale, Emily Irish, Fulda, Perry, Banner, Carlton, Unayzah, Upper Abo, Canoncito de la Uva, Cutler, Reece, Washington, Spanish Queen, Padgett, Geraldine, Red Tanks, Fairplay 1, Fairplay 2, Moab, Promontory Butte, Cueli, Cooper, Voyles 1989-11, Hamilton, San Tirso, Puertollano 1656, Puertollano 3611, Swissvale, Henarejos 3093, Kinney, Baldwin, Garnett, McCoy, No Business Creek, Barruelo 384, Barruelo 118, E and B Coal Company, 7-11, Upper Freeport, Mazon Creek, Galesburg, Westphalian D, Chinook, Murphysboro, Tijeras Canyon, Secor Coal, Rowe Coal, Stanley Cemetary, Cuticle Coal, Roaring Creek, Tarter Coal, Westphalian C, Sandia Formation, Jellico, Drury Shale, Fountain Formation, Evans Peak, Arkansas River, Forkston Coal, Manning Canyon, Wyoming Hill.

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APPENDIX 2

Floras Analyzed and Sources of Data

Floras:

- Middle Khuff, Saudi Arabia: Hill and El-Khayal, 1983
- Del Norte, TX: Mamay et al., 1984; Mamay et al., 1988
- Stamford, TX: Mamay, 1976; Mamay, 1989
- Lawn, TX: Mamay, 1976; Mamay, 1975; Mamay, 1986; Mamay, 1988
- Eddy/Enid, OK: White, 1912
- Lake Kemp 2, TX: Mamay, 1967; Mamay, 1986; Mamay, 1988
- Lake Kemp 1, TX: Mamay, 1966
- Hermit Shale, AZ: White, 1929

Emily Irish, TX: Mamay, 1954; Mamay, 1968; Mamay, 1975; Mamay, 1976; Mamay, 1988
Fulda, TX: Mamay, 1954; Mamay, 1976
Perry, OK: Mamay, 1976
Banner, KS: White, 1912; Mamay, 1975; Mamay, 1976; Gillespie and Pfefferkorn, 1986
Carlton, KS: White, 1912
Unayzah, Saudi Arabia: El-Khayal et al., 1980; El-Khayal and Wagner, 1985; Hill et al., 1985
Upper Abo, NM: Ash and Tidwell, 1982
Canoncito de la Uva, NM: Hunt, 1983
Cutler, UT: Mamay and Breed, 1970
Reece, KS: White, 1912
Washington, KS: White, 1912
Spanish Queen, NM: Ash and Tidwell, 1982
Padgett, TX: Mamay, 1960
Geraldine, TX: Sander, 1987
Red Tanks, NM: Ash and Tidwell, 1982
Fairplay 1, CO: White, 1912
Fairplay 2, CO: White, 1912
Moab, UT: Tidwell, 1988
Promontory Butte, AZ: Canright and Blazey, 1974
Cueli, Spain: Wagner and Martinez Garcia, 1982
Cooper, TX: USNM Collections
Voyles 1989-11, TX: USNM Collections
Hamilton, KS: Mapes and Rothwell, 1988; Rothwell and Mapes, 1988; Leisman et al., 1988
San Tirso, Spain: Wagner and Martinez Garcia, 1982
Puertollano 1656, Spain: Wagner, 1985
Puertollano 3611, Spain: Wagner, 1985
Swissvale, CO: White, 1912
Henarejos 3093, Spain: Wagner et al., 1985
Kinney, NM: Mamay, 1981; Ash and Tidwell, 1982; Mamay and Mapes, 1992
Baldwin, KS: Cridland and Morris, 1963
Garnett, KS: Winston, 1983
McCoy, CO: Read, 1947
No Business Creek, IL: USNM collections
Barruelo 384, Spain: Wagner and Winkler Prins, 1985
Barruelo 118, Spain: Wagner and Winkler Prins, 1985
E and B Coal Company, IL: USNM Collections
7-11, OH: McComas, 1988
Upper Freeport, OH: McComas, 1988
Mazon Creek, IL: Pfefferkorn, 1979
Galesburg, IL: Pfefferkorn, 1979
Westphalian D, Germany: Pfefferkorn, 1979
Chinook, IN: DiMichele and Dolph, 1981
Murphysboro, IL: Read, 1947
Tijeras Canyon, NM: Ash and Tidwell, 1982
Secor Coal, OK: USNM Collections
Rowe Coal, MO: Basson, 1968
Stanley Cemetary, IN: Wood, 1963
Cuticle coal, IN: DiMichele and Dolph, 1981; DiMichele, 1982; DiMichele et al., 1984
Roaring Creek, IN: DiMichele and Dolph, 1981; DiMichele, 1982
Tarter Coal, IL: Hess et al., 1990; USNM Collections
Westphalian C, Germany: Pfefferkorn, 1979
Sandia Fm, NM: Ash and Tidwell, 1982
Jellico, KY: Spurgeon and Jennings, 1985
Drury Shale, IL: Read, 1947
Fountain Fm, CO: Jennings, 1980
Evans Peak, CO: Read, 1934
Arkansas River, CO: Arnold, 1941
Forkston Coal, PA: Read, 1946
Manning Canyon, UT: Tidwell, 1967; Leary and Pfefferkorn, 1977
Wyoming Hill, IA: Leary, 1981

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APPENDIX 3

Physical Indicators of Environmental Conditions for Late Pennsylvanian Floras

Fairplay 2, Colorado (upper beds): DRY-Buff and dark gray shales within a redbeds sequence. No coal. (Christopher Durden, Texas Memorial Museum, pers. comm., 1991)[1]

Fairplay 1, Colorado (lower beds): DRY-Sequence of limestones, including evidence of exposure, such as dessication cracks. No coal. (Christopher Durden, Texas Memorial Museum, pers. comm., 1991)[1]

Moab, Utah: WET-Fluvial-deltaic sediments including coaly shales and sandstones, suggesting locally wet flood-basin conditions. (Tidwell, 1988)

Promontory Butte, Arizona: DRY-Top of channel fill sequence above organic shale and below calcareous mudstone (soil?) and redbeds, including limestones. (Canright and Blazey, 1974)

Cueli, Spain: DRY-Possibly contains some allothonous elements. Fine to medium sandstone with mud partings above a sequence of red beds and caliches. No coal. (Wagner and Martinez Garcia, 1982)

Cooper, Texas: WET-Organic shale/coal within channel fill. Underclay and associated soils are non-calcareous and evidence locally wet climate and high water table. (R. W. Hook and W. A. DiMichele field obs.; M. Joeckel, University of Iowa, pers. comm., 1991)

Voyles, 1989-11, Texas: WET-Organic shale/coal within channel fill. Underclay and associated soils are noncalcareous and evidence locally wet climate and high water table. (R. W. Hook and W. A. DiMichele field obs.; M. Joeckel, University of Iowa, pers. comm., 1991)

Hamilton Quarry, Kansas: DRY-High relief local landscape in near coastal setting, suggesting well drained conditions. Channel fill without evidence of coaly, organic-rich deposits. (Rothwell and Mapes, 1988)

San Tirso, Spain: WET-Dark gray shales and sandstones intercallated with pyroclastics. Evidence is nondiagnostic but interpretation as "humid" was based on morphology of plants by Wagner and Martinez Garcia (1982).

Puertollano 1656, Spain: WET-Gray shale and sandstone between coal beds. (Wagner, 1985)

Puertollano 3611, Spain: WET-Lacustrine sequence including numerous organic deposits and clastic-rich coals. (Wagner, 1985)

Swissvale, Colorado: DRY-Redbeds sequence including numerous limestones. No coal. (White, 1912)

Henarejos 3093, Spain: WET-Fluvial-deltaic sequence of coals, limestones and organic shales. (Wagner et al., 1985)

Kinney Quarry, New Mexico: DRY-Buff to gray mudstones and siltstones associated with brackish to marine animals, suggesting a coastal lagoon. No coal. (Zidek, 1992)

Baldwin, Kansas: DRY-Possibly contains some allochthonous elements. Cross-bedded sandstone and shale. No associated coals. Possibly a mixture of proximal and distal floodplain elements on poorly drained and well drained soils. (Cridland and Morris, 1963)

Garnett, Kansas: DRY-Mudflat deposits in the mouth of an estuarine channel cut into limestone bedrock. Local relief. No coal. (Reisz et al., 1982)

McCoy, Colorado: DRY-Non-coal bearing clastic sequence. (Read, 1947)

No Business Creek, Illinois: WET-Coal underclay and roof shale. (W. A. DiMichele, field obs.)

Barruelo 384 and 118, Spain: WET-Deltaic sequence that includes numerous thin coals. (Wagner and Winkler Prins, 1985)

E and B Coal Company, Illinois: WET-Coal roof shale. (W. A. DiMichele, field obs.).

7-11 Mine, Ohio: DRY-Complex exposure. Channel fill above "caliche-like" zones suggesting exposure and deep weathering. Overall within a coal-bearing sequence, but not a roof shale or in direct association with coals. (McComas, 1988)

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[1] The age of these deposits is probably Permian, but because of uncertainty they were included in the analysis as potentially Stephanian.