

## ECOLOGICAL STABILITY DURING THE LATE PALEOZOIC COLD INTERVAL

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ECOSYSTEM STABILITY and taxonomic stasis are the opposite aspect in the history of life from ecosystem perturbation and reorganization, or extinction and origination. Naturally, change is more exciting than stasis, and change also is more useful in many ways as, for instance, in the development of biostratigraphic frameworks. Paleontological preference for geologically rapid change has gone so far that a fast evolving group of organisms has been used to create an orthostratigraphy (Ortochronologie of Schindewolf, 1950), which is claimed to be the "real" biostratigraphy. By implication, all other taxonomic groups are relegated to a secondary status of merely delivering "parasstratigraphies," which may be useful (locally or regionally), but are not the "real thing." Ammonites, conodonts, foraminifera, and a few other taxa hold the distinction of being the "chosen" taxa, and it should be self-evident that only marine organisms qualify for this role. On the other hand, organisms on land always have been known to demonstrate coarser stratigraphic resolution. By implication, they might be more prone to ecosystem and taxonomic stasis over the long run. This, in itself, is an important observation.

The purpose of this contribution is to provide an overview of ecosystem and taxonomic stasis as recorded by plant macrofossils of the Late Paleozoic. The emphasis will be on the Carboniferous (Late Mississippian/Pennsylvanian). Rather than relying on the term stasis, which implies that essentially there is no perceptible change, we would like to stress the concept of ecosystem stability. Hence, the focus of the discussion is on ecosystems that expand or

## TAPHONOMIC FRAMEWORK OF CARBONIFEROUS MEGAFLORAS

Extensive coastal plains developed along the Late Paleozoic Euramerican continental margins and on the cratons during the interglacial High Stand Systems Tract as sediment was transported basinward, covering open marine, epicontinental, and/or nearshore marine deposits (Gastaldo et al., 1993; Demko and Gastaldo, 1996). This, coupled with sea-level fall associated with the amassing of continental ice in Gondwana (Wanless and Shepard, 1936; Vevers and Powell, 1987), resulted in widespread fluvial and estuarine wetlands in which forested vegetation became established during subsequent glacial times. Where clay mineralogies retarded percolation of groundwater, physico-chemical conditions developed in perched water tables that promoted peat mire accumulation (Gastaldo and Staub, 1997). On the other hand, where fine-grained siliciclastic environments allowed for percolation of groundwater, negating stalling of the water table, clastic swamps (Gastaldo, 1987) developed.

Peat, by definition, is the accumulation of plant biomass in the absence (or near absence) of a siliciclastic component. Peat can accumulate either in groundwater-fed depressional lows (theotrophic conditions) or above the ground surface in rain-fed, geographically extensive and thick mires

derived from coastal plain ecosystems in the majority of instances (for exceptions see Gastaldo et al., 1995). Hence, the provenance of the plants preserved within the adpression floras found intercalated between coal beds was local (parautochthonous; *sensu* Behrensmeyer and Hook, 1992).

Due to the fact that: (1) perennialized plant megafossils and, for that matter, compressed palyanomorphs within coals represent the vegetation responsible for the accumulation; and (2) adpression floras recovered from fine-grained siliciclastics deposited between coal beds of a genetic sequence are indicative of the regional coastal plain flora, comparison of biota from identical depositional settings (isotaphonomy; Behrensmeyer et al., *in press*) over a stratigraphic sequence allows for direct comparison of ecosystems through long intervals of deep time.

## PLANT MACROFOSSIL BIOSTRATIGRAPHY

Biostratigraphic applications using plant macrofossils of the Late Carboniferous coal-bearing strata were a major breakthrough that occurred in several northern hemisphere industrialized countries that relied on this fossil-fuel energy resource (only one citation is provided per country where many others should be listed): North America (White, 1900), France, (Zeller, 1879), Germany (Cremier, 1893), England (Kidston, 1893), Netherlands (Jongmans, 1915), and Russia (Zalassky, 1928). The coal mining industry benefited enormously from this new methodology, and coal-seam correlation became possible on a regional and continental scale for the first time. The recognition that nearly identical macrofloras could be identified confidently from a variety of neighboring countries led to international correlations, first worked out at the Heerlen Congresses (since 1927; now the International Congress on the Carboniferous-Permian; the XIV<sup>th</sup> held in Canada, 1999). The resulting stratigraphic scheme for the terrestrial strata of the Late Carboniferous, Euramerican

(ombrotrophic; McCabe, 1984; Hazeldine, 1989). Depending upon the rate of decay at the peat surface and the rate of accumulation, various more resistant aerial vegetative and reproductive, and subterranean plant parts may be preserved relatively unaltered (except for subsequent compression). Additionally, under unique taphonomic circumstances, delicate and easily decayed aerial plant parts may be preserved exquisitely (Gastaldo and Staub, 1999). When subsidence of mires is accompanied by subsequent marine transgression and marine waters are piped locally into the peat, calcium carbonate (e.g., Phillips et al., 1976) or siderite (e.g., Winston and Phillips, 1991) may precipitate within cellular voids of the plant parts, preserving them as concretions (or coal balls; Scott and Rex, 1985). Elsewhere, dolomite or silica may be the mineralogical agents responsible for perennialization of peat. Hence, in the majority of instances (for a possible allochthonous Carboniferous peat deposit see Yocheison and Mamay, 1962), plants recovered from coal ball assemblages are the autochthonous (*in situ*) components of the original peat mire ecosystem. Adpressions (Shute and Cleal, 1987) recovered from terrestrial or estuarine shale/siltstone directly above a coal seam (roof-shale floras) can represent one of several possible taphonomic scenarios depending upon the processes responsible for burial (Gastaldo et al., 1995). With respect to the peat, the overlying clastic material can be deposited in a continuous transition, after a short temporal break (discontinuity), or after a significant hiatus in time. Hence, in some instances the adpression floras are genetically related to the underlying coal bed and represent the final phases of peat accumulation (e.g., Scott, 1978; DiMichele and Demaris, 1987; Gastaldo et al., 1991) or thanatocoenoses of peat swamp forest (e.g., Demko and Gastaldo, 1992). In other instances, these assemblages bear little or no genetic resemblance to the underlying coal bed (e.g., Peppers and Pfefferkorn, 1970; Baird et al., 1985). Regardless of whether or not the roof-shale flora is genetically related to the underlying peat, the plants preserved in these assemblages also were

		A	B	C		
STEPHANIAN C	301 ± 2.0 Ma (Rasbury et al., 1998); 297 Ma (Menning et al., 1997)	STEPHANIAN C	STEPHANIAN B	STEPHANIAN A		
		CANTABRIAN	WESTPHALIAN D	WESTPHALIAN C <sup>2</sup>		
		WESTPHALIAN B <sup>2</sup>	WESTPHALIAN B <sup>1</sup>	NAMURIAN C <sup>1</sup>		
		WESTPHALIAN A <sup>2</sup>	Mid-Carboniferous Boundary	NAMURIAN A <sup>1</sup>		
		Alportian (H2)				
		Chokierian (H1)				
		Arnsbergian (E2)				
		Pendleian (E1)				
		327 Ma (Smith & Read, 2000)				
		STEPHANIAN C	301 ± 2.0 Ma (Rasbury et al., 1998); 297 Ma (Menning et al., 1997)	STEPHANIAN C	STEPHANIAN B	STEPHANIAN A
		Stephanian B	Stephanian B	Barruileian	Cantabrian	Westphalian D
		Stephanian A	Stephanian A	Bolsovian	Duckmantian	Langsettian
		CANTABRIAN	CANTABRIAN	Yeadonian (G1)	Marsdenian (R2)	Kinderscoutian (R1)
WESTPHALIAN D	WESTPHALIAN D	Alportian (H2)				
WESTPHALIAN C <sup>2</sup>	WESTPHALIAN C <sup>2</sup>					
WESTPHALIAN B <sup>2</sup>	WESTPHALIAN B <sup>2</sup>					
WESTPHALIAN A <sup>2</sup>	WESTPHALIAN A <sup>2</sup>					
NAMURIAN C <sup>1</sup>	NAMURIAN C <sup>1</sup>					
NAMURIAN B <sup>1</sup>	NAMURIAN B <sup>1</sup>					
NAMURIAN A <sup>1</sup>	NAMURIAN A <sup>1</sup>					

FIGURE 1.—“Traditional” (A) and current (C) stages of the Late Carboniferous. The “traditional” stages of the Namurian (marked 1) are still useful in discussing entirely terrestrial sequences; stages marked “2” have been renamed formally. Ages in Ma BP are provided for the Viséan-Namurian boundary, the Mid-Carboniferous boundary, and the Stephanian C - Permian boundary.

tropical realm has existed for more than 75 years, and is still being revised and improved. However, a few "imitations" of the system have not changed, and these provide insights into the question of ecosystem stability.

The biostratigraphic framework of the Euramerican realm consists of 11 stages (formerly 10; Fig. 1). Relatively few isotopic age dates have been obtained from the Carboniferous strata (primarily volcanic ashfall beds, or tonsteins when intercalated in a coal) relative to the siliclastic components of the genetic sequences (Gastaldo et al., 1993; Menning et al., 1997, *in press*). Hence, the duration of all stages cannot be determined as yet with absolute confidence, although it is possible to provide some estimates for particular intervals. The Namurian A in the Ostrava-Karvina basin, the Czech Republic which spans the latest Mississippian (Pendelian and Armsbergian) and earliest Pennsylvanian (Chokierian and Alportian) has a youngest radiometric age date of 320 Ma from a tonstein in the Gabeler coal, which is the last genetic sequence prior to the Mid-Carboniferous boundary, manifested as a basin-wide erosional unconformity (Dopita et al., 1987; Petr Martinec, *pers. comm.*, 9/98). Ar-Ar dates obtained from sandines (within altered volcanic ash - tonsteins) in the subjacent Poruba Member (Gabriely coal 365) have been reported at  $319.5 \pm 2.4$  (Hess and Lippolt, 1985); based upon investigations in this basin (Gastaldo et al., 1998), the Gabriely coal is 8 genetic cycles beneath the Gabeler. The basin-wide erosional unconformity represents the interval during the Mid-Carboniferous lowstand resulting from the onset of extensive glaciation (Frakes et al., 1992). There is a statistically significant systematic difference recorded in the megaflooras of the basin on either side of this boundary (Gastaldo et al., 1998; see below). Recently, Smith and Read (2000) have proposed that the onset of major glaciation was prior to the Namurian, in the late Viséan. They use a date of 327 Ma for the Viséan-Namurian boundary. Hence, the duration of the Namurian A is at least 7 Ma, with 1 Ma recorded in the Chokierian (H1) and Alportian (H2)

estimated to have been  $143 \pm 64$  ka (2 s). The entire length of the Late Carboniferous (Pennsylvanian) is approximately 22 Ma according to Menning et al. (1997; 319 - 297 Ma; Fig. 2) or 18 Ma using the Early-Late Carboniferous estimate of Menning et al. (1997, *in press*) and the Carboniferous-Permian estimate of Rasbury et al. (1998; 319-301). Thus, on average, the stages younger than the Namurian A each have a mean duration of only 2 Ma or less. For a long time, the stages were considered the same as the biostratigraphic units. That is, stage boundaries were assigned based upon changes in assemblage zones within the terrestrial flora. The subdivision of stages was possible in a few cases within a single basin (e.g., Wagner, 1971), but these intervals could not be extended elsewhere with confidence, indicating that regional paleogeography, basinal history, local facies, and/or taphonomic history were responsible. Several generations of paleobotanists tried to improve upon this system, but have found limits. Refinements came through the recognition of the mid-Westphalian D boundary (Pfefferkorn and Thomson, 1982), and even more through the use of modern biostratigraphic principles and compilation of an extensive data set from a large area by Wagner (1984). However, the duration of biostratigraphically discernible intervals remained in the range of one-to-two million years.

These results, alone, having been compiled by a larger number of scientists from many nations over the past century, demonstrate that the tropical

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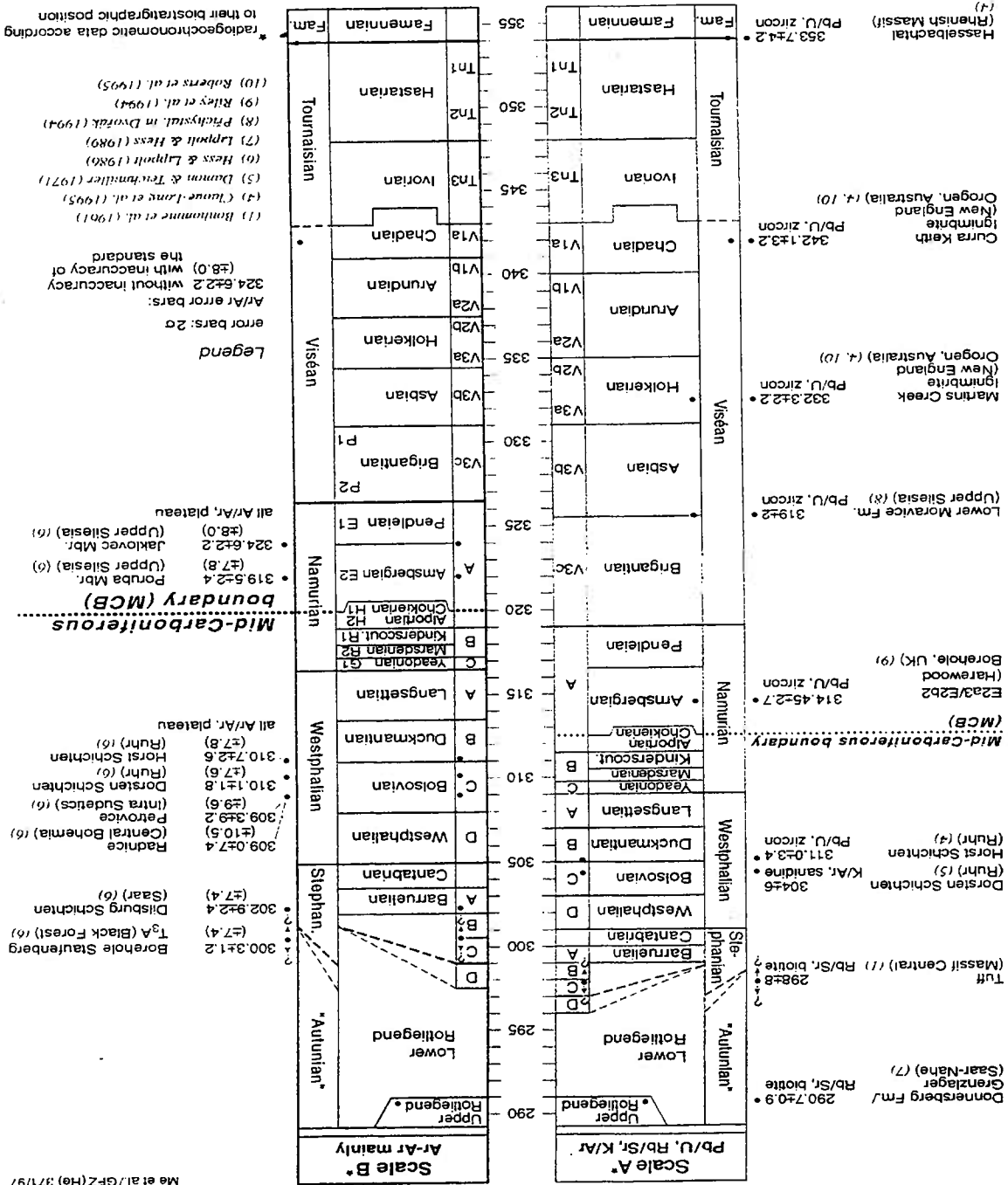


FIGURE 2.—Numerical ages for the Carboniferous showing a systematic difference depending upon the radiometric methodology utilized (Mening et al., 1997, in press). Scale A shows minimum ages; scale B shows maximum ages.

("Ober-schlesisches Becken"). This basin experienced rapid subsidence during the Namurian (Pešek, 1994; Kotas, 1995) with deposition occurring in broad plain, coastal plain, and marginal marine/open marine settings (Ostrava Fm. in the Czech Republic). The mid-Carboniferous boundary is expressed as a basin-wide erosional unconformity that occurs in the Upper Namurian A. When sedimentation resumes, the depositional settings are continental and have been termed "limnic" or "intermontane" (Havlena, 1961; Karvina Fm. in the Czech Republic). The approximate thickness of sediment in the Ostrava-Karvina basin is more than 5200 m and dwarfs the thickness of the Late Carboniferous in Illinois. The plant macrofossils were studied initially beginning in the 19<sup>th</sup> Century, but the most intensive phase of investigation began after 1945 with a concerted government effort of coal exploitation to fuel much of the industry of the two countries. Fossils and data were collected underground and from an intensive drilling program that amounted over the decades to hundreds of kilometers of continuous drill-core section due to the complex structural nature of the sequence! For example, beginning in the 1950s Czechoslovakia drilled up to 30 km of continuous drill core per year, with drilling that continued unabated until the demise of the East Bloc system. During the past decade, yearly drilling still has been impressive with approximately 15 km of drill core extracted and analyzed per year. Hence, the stratigraphic control on the drill-core data and fossiliferous beds is excellent, and the data points close to each other in the sections. Data have been published, in part, and include generalized range charts for the Czech (Purkynova, 1970, 1990) and Polish (Kotasowa and Migier, 1995) sides.

Beginning in 1995, the stratigraphic cyclicity and a-diversity of each cycle identified in the Ostrava-Karvina Basin were assessed (Gastaldo, 1996; Gastaldo et al., 1998). The Ostrava Fm. (Namurian A) is characterized by pebbly fine- to medium-grained sandstones, siltstones, mudstones, and thick economic coals (unlike time-equivalent strata in the U.S.), packaged in a genetically similar

terrestrial floras of the Late Carboniferous remained rather stable over long intervals of time. This stability is due to: (1) the re-assembly of wetland ecosystems (peat and non-peat accumulating mires) after disturbance (e.g., DiMichele and Phillips, 1996a, 1996b; DiMichele et al., 1996); (2) the longevity of individual taxa; and (3) the fact that large-scale species turnover (extinction, origination, extirpation and migration; Laveine, 1993) is concentrated at particular stratigraphic intervals. It would be possible to divide the Late Carboniferous into much shorter intervals if extinctions and originations of all plant species were distributed randomly through time. However, the fossil record indicates that many extinctions and originations occur during critical, very short stratigraphic intervals. As a consequence, these intervals have been chosen as stratigraphic boundaries and the pattern of stability and rapid changeover is observed.

**TROPICAL ECOSYSTEM  
STABILITY FOLLOWING  
INITIAL GLACIATION: AN  
EXAMPLE FROM THE  
OSTRAVA-KARVINA BASIN,  
CZECH REPUBLIC**

There are a large number of coal fields in Europe in which paleobotanical data have been collected with care for decades to a century. Each basin has a particular stratigraphic interval that is complete, or nearly complete, because the section is thick, contains numerous minable coals, and coincides with the highest subsidence rate in the basin. Hence, the biostratigraphic framework for the Euramerican realm was initially developed based upon these coal-bearing intervals.

One basin that straddles the Czech-Polish border is remarkable because it encompasses about 7,000 km<sup>2</sup> of area. On the Czech side it is known as the Ostrava-Karvina Basin ("Ostrau-Karwiner Becken" in older German literature); on the Polish side it is known as the Upper Silesian Basin

Ravinement of these coastal plain deposits terminated the cycle. Based upon analysis of an idealized stratigraphic sequence, fifty five (55) genetic cycles have been identified in the Ostrava Formation (some of which have multiple, stacked marine zones; this differs from estimates based on the work of Rehor and Rehorova [1972] that there are 80 marine zones grouped into 21 marine horizons). Using the estimate of 7 Ma presented above for the duration of the Namurian A, each cycle represents 127,273 ka (less than the duration estimated for the Late Viséan by Smith and Read [2000] - 333 ka; more similar to the Upper Pennsylvanian - Lower Permian interval estimated by Rasbury et al. [1998] - 143 ± 64 ka). Two hundred and thirty five (235) megafacial taxa have been reported from the Ostrava-Karvina Basin. Following the evaluation of 216 drill-core reports (28% available records), a first approximation of biostratigraphic ranges of 92% of the flora (217 taxa; 60 of which are known from a single locality or designated as *sp. nov.*) have been identified. Correlation matrices were calculated

in a manner to other age-equivalent paralic strata (Gastaldo et al., 1993; the stratigraphic pattern within genetic sequences differs from traditional 'cyclothems'; Wanless and Weller, 1932; Fig. 3). Genetic packages in the Ostrava Formation begin with a ravinement surface (Liu and Gastaldo, 1992a) that is overlain by open marine and/or estuarine strata in which abundant megafacial elements are preserved near the base in a condensed section. Fine-grained nearshore marine sediments overlie the invertebrate zones that coarsen to pebbly conglomerates and sandstones of a braided plain and fluvial character. Leached paleosols with sigmoidal horizons are found above these fluvial deposits; paludification of these incipient soils (Gastaldo and Staub, 1995) resulted in peat accumulation. Peat swamps were extensive, although most were breached by either overbank flood deposits and/or estuarine deposits, resulting in splits and multiple benches intercalated with fossiliferous siltstone and mudstone. The genetic cycles in the Ostrava-Karvina basin are similar to those reported by Demko and Gastaldo (1992; 1996) for the Black Warrior Basin (see below).

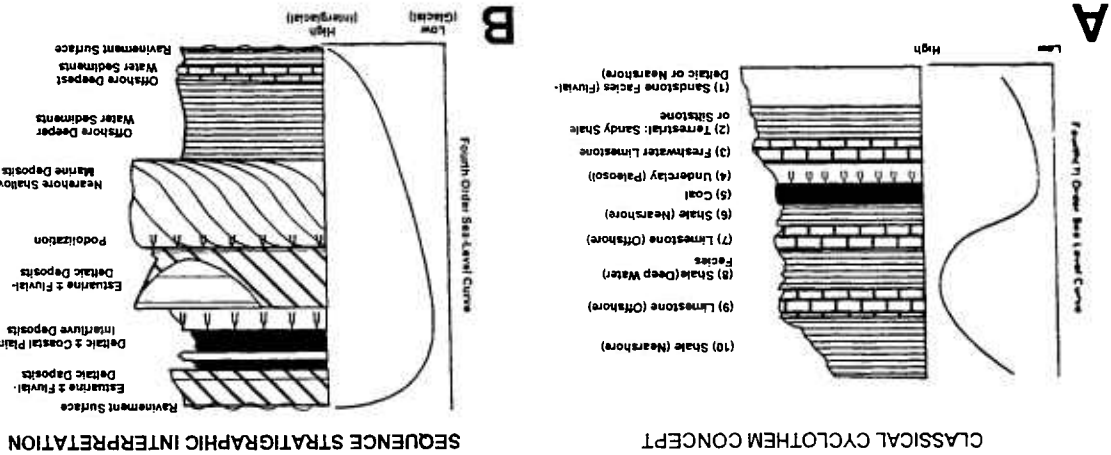


FIGURE 3.—A comparison between the classical, textbook cyclothem (A; Wanless and Weller, 1932) that can still be found in many references and interpretation within a sequence-stratigraphic context (B; Gastaldo et al., 1993). Note that each sequence is the result of a fourth-order sea-level oscillation, and that the sea-level curves for each interpretation differ dramatically.

apart from the intervals above and below. Although there are many long-ranging taxa in this basin (e.g., some of the lycopsid trees), there appears to be a perturbation threshold at which point replacement within the ecosystem results in the establishment of a new floral assemblage that remains persistent for many cycles.

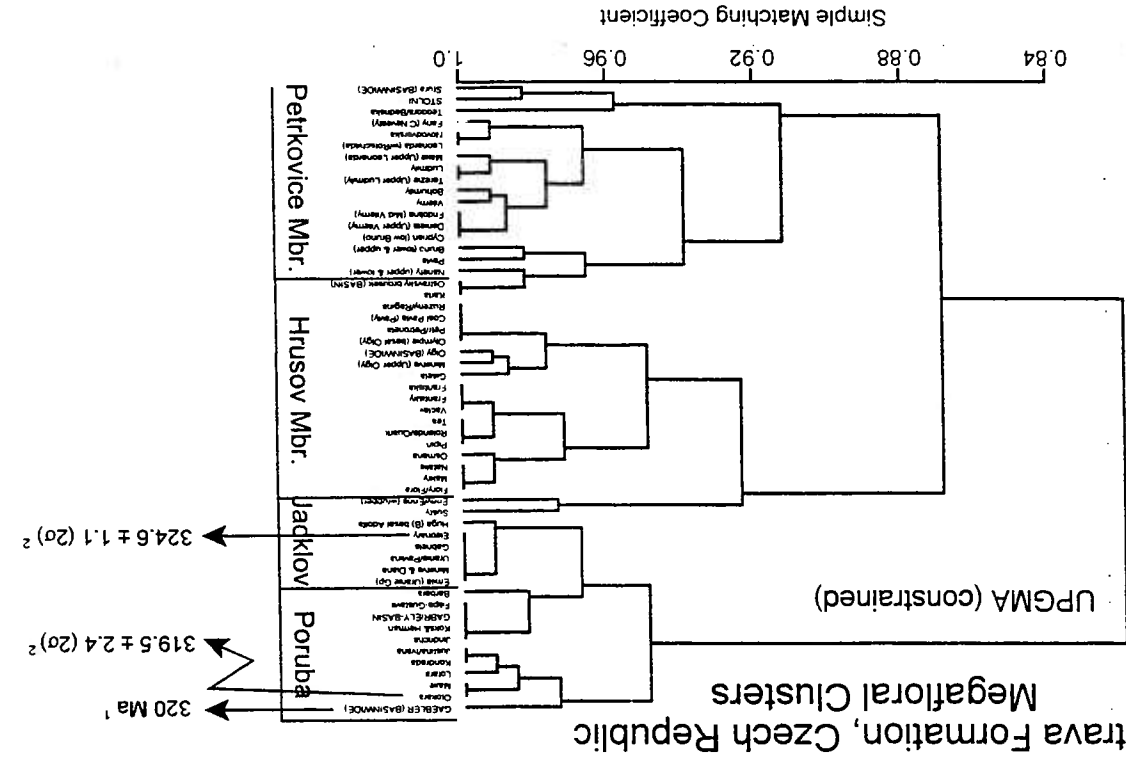
**ECOSYSTEM STABILITY  
DURING A GLACIAL  
MAXIMUM: AN EXAMPLE  
FROM THE BLACK WARRIOR  
BASIN, ALABAMA**

There is a sparse stratigraphic record of lowermost Namurian strata in North America, owing to the fact that most of the sediments are

based upon presence/absence of taxa in each genetic cycle, the results of which were subjected to constrained UPGMA cluster analysis (Fig. 4). Results of the cluster analyses parallel many, but not all, traditional stratigraphic subdivisions of the Ostrava Formation.

When the stratigraphic range charts for all observed taxa are compared with cluster analysis results, it becomes apparent that there are at least four (4) megafloral assemblages that retain their identity at high levels of similarity (>90%; Fig. 4). In this basin, ecosystems retain their systematic identity for durations of ~360 ka (basal Petkovice Mbr - these floras retain Early Carboniferous elements), 2.0 Ma (Petkovice to basal Hrusov Mbr.), 2.2 Ma (Hrusov Mbr.), and 2.2 Ma (Jaklovek Mbr.). Two cycles at the top of the base of the Jaklovek Mbr—the Enna and Susy—cluster

FIGURE 4.—Results of constrained cluster analysis using a simple matching coefficient and MVSP v. 3.1g (unweighted, pair-group average) of the macrofloras from the Namurian of the Ostrava-Karvina Basin in the Czech Republic.





deposition. However, it was not until recently that investigators acknowledged the importance of allogenic depositional cyclicity in these strata (e.g., Gastaldo et al., 1993; Pashin, 1994; Demko and Gastaldo, 1996). Following the lead of Liu and Gastaldo (1992a), Pashin (1994, 1998) defined 13 regionally extensive, flooding-surface-bounded depositional cycles between the base of the Potsville and the top of the Brookwood coal zone. Although considerable geochronologic uncertainty exists, these cycles appear to be the products of glacial-eustatic forcing associated with Milankovitch orbital eccentricity.

The Pennsylvanian megafloora throughout the Black Warrior Basin consists of a low diversity assemblage comprised of three general biostratigraphic groupings (Gillespie and Reams, 1995): (1) taxa with very long stratigraphic ranges (extending past the Langsettian), (2) endemics (e.g., Gastaldo and Boertma, 1983; Gastaldo, 1988), and (3) species that are common to both North America and western Europe coalfields of equivalent age. Nearly all taxa preserved within the lowest recognized coal zone (Black Creek; Pryor and Gastaldo, 2000) also are found in the stratigraphically highest coal zones (Brookwood). Although Lyons et al. (1985) used the presence of a single species to suggest that the Black Warrior Basin section extends into the Bolsovian (Wesphalian C), the remainder of the flora consists of typical elements of the Langsettian (Wesphalian A); the presence of a pteridospermous liana – *Lyginopteris hoeninghausii* – in the Brookwood coal supports the traditional assignment of the vegetation to the Langsettian (Wesphalian A). Additionally, the inability to biostratigraphically separate the coal groups using palynological data has resulted in the assignment of the entire sequence to the Wesphalian A (Eble and Gillespie, 1989).

The absence of datable tonsteins in the Langsettian precludes an estimate of an overall duration with absolute certainty. Hence, there are two ways in which duration can be estimated. The time scale proposed by Menning et al. (1997, in *press*) has the Langsettian beginning at 316.5 Ma

either in the deep subsurface or were eroded during the Mid-Carboniferous glacial lowstand (Fraakes et al., 1992). There are a few exceptions. For example, Gillespie and Pfefferkorn (1979) dated the late Mississippian strata on the Virginia-West Virginia border as Namurian A; Gillespie and Reams (1985) also assign a flora collected approximately 100 m above the base of the Parkwood Formation of the Black Warrior Basin to the Namurian A. Although Gondwanan deglaciation and flooding of Euramerica resulted in a sparse Upper Namurian record, the subsequent Langsettian (equivalent Westphalian A [Europe] and Morrowan [U.S.]) is comprised of a well-developed thick sequence in the developing Black Warrior foreland basin known as the Potsville Formation (Pashin, 1994).

Paleogeographic reconstructions indicate that the Black Warrior basin migrated through the southern tradewind belt into the equatorial rainy belt during the Carboniferous (Golonka et al., 1994). This migration is reflected in the transition from a thick carbonate succession containing red, vertic paleosols to a siliciclastic-dominated succession containing coal and underclay (Pashin, 1994). This transition indicates a change from a semi-humid or semi-arid climate to the ever-wet equatorial climate that prevailed in eastern North America during the Early Pennsylvanian (Cecil, 1990). Potsville strata are locally in contact with Mississippian strata (Henry et al., 1985), but in most of the basin the sub-Absaroka boundary is developed within the Pennsylvanian System and has minimal time value and minimal paleotopographic relief (Thomas, 1988). The sub-Absaroka sequence boundary marks a significant tectonic reorganization of the main Black Warrior basin in which an Appalachian subsidence center was superimposed on the older Ouachita foreland basin, but it was not until deposition of the Mary Lee coal zone that the Appalachian orogen began supplying a significant quantity of coarse-grained sediment (Liu and Gastaldo, 1992b; Pashin, 1999). McCalley (1900) recognized the clustering of coal beds into discrete zones, and Butts (1926) recognized evidence for repeated marine transgressions and regressions during Potsville

the otherhand, assuming a long-term Milankovitch eccentricity cycle duration of 125 ka/cycle for each of the regionally extensive depositional cycles, the duration of the 13 coal zones would be 1.63 Ma; the remaining 1.37 Ma attributed to the Langsettian could accommodate the remaining Lower Pennsylvanian strata in the Coosa and Cahaba coal fields. Hence, the wetlands that colonized the coastal-deltaic peat and clastic regimes of the Black Warrior Basin demonstrate stability throughout the Pottsville Formation, and represent ecosystem stability of at least 1.6 Ma in duration.

### ECOSYSTEM STABILITY TOWARDS THE END OF A COAL INTERVAL: INTERGLACIAL- GLACIAL CYCLES IN ILLINOIS

The Carbondale Formation in the Illinois Basin contains the largest number of thick and widespread mineable coals in that basin. There are eleven well-defined couplets of a thick and/or widespread coal each of which is overlain by a marine limestone (Fig. 5). The thick and widespread coal beds indicate that this is the most completely preserved part of the Pennsylvanian section in Illinois. The Carbondale Formation is Westphalian D in age, although Wagner and Lyons (1997) have postulated, by implication, that the interval is Cantabrian. This difference in interpretation of stratigraphic position does not influence the conclusions presented herein.

The limestone/coal couplets represent interglacial and glacial cycles of the Late Carboniferous cold interval prior to the first major deglaciation (Frakes et al., 1992; Gastaldo et al., 1996). Each marine limestone represents an interglacial (i.e., sea-level highstand) that is characterized by a wet-dry tropical climate interpreted as having experienced a long dry season (Cecil, 1990). Each coal or group of coals (depending upon regionally restricted coal splits) represents a glacial cycle (i.e., sea-level lowstand) during which time a tropical ever-wet climate prevailed (Cecil, 1990). DiMichèle et al. (1996) and DiMichèle and Phillips (1996a, b) analyzed cycles would represent no more than 231 ka. On then each of the regionally extensive depositional of Lower Pennsylvanian strata in the United States, Cahaba coal fields contain the thickest successions which it doesn't because the adjacent Coosa and Early Pennsylvanian in the southern Appalachians, in the Black Warrior Basin represents the entire and ending at 313.5 Ma. If the Pottsville sequence in the Westphalian D sequence in the Illinois Basin.

FIGURE 5.—The stratigraphic sequence of the Westphalian D sequence in the Illinois Basin.

11	Darville Coal	
	Galum Limestone	
10	Allenby-Baker Coal	
	Bankston Fork Ls	
9	Anvil Rock Coal	
	Conant Limestone	
8	Jamestown Coal	
	Breton Limestone	
7	Herrin (No. 6) Coal	
	unnamed Limestone	
6	Spring Lake Coal	
	St. David Limestone	
5	Springfield Coal	
	Hanover Limestone	
4	Sumnum Coal	
	unnamed Limestone	
3	Kerton Creek Roodhouse Coal	
	unnamed Limestone	
2	Surant-Lowell Coal	
	Oakgrove Limestone	
1	Colchester Coal	

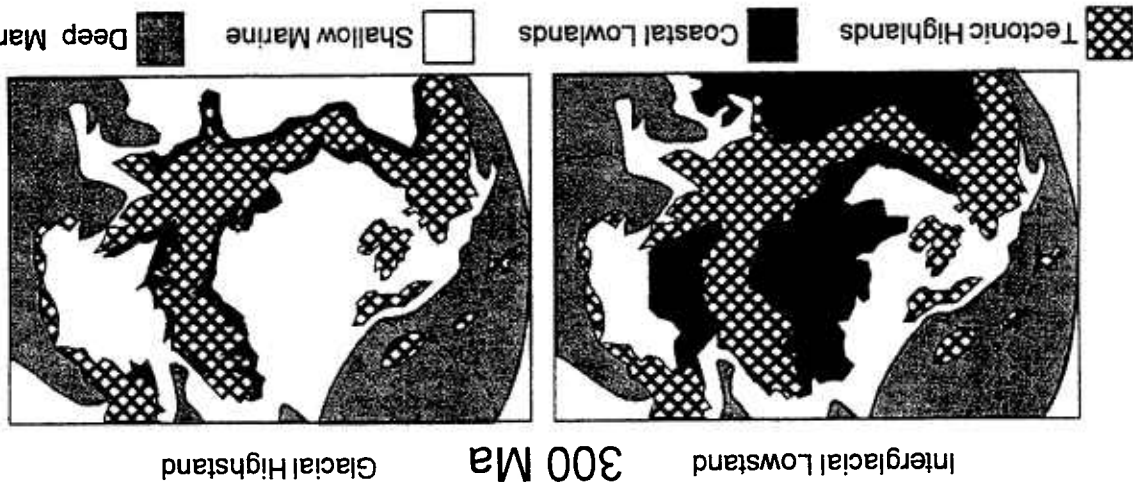


FIGURE 6.—Paleogeographic maps of the Late Carboniferous depicting the position of glacial and interglacial shorelines within the mid-continent. In the mid-continent of North America, glacial lowstands resulted in the extension of peat-accumulating coastal plain environments from the Appalachian front as far west as Kansas (e.g., Cecil and Edgar, 1994); glacial highstands resulted in shoreline progradation inland towards the Appalachian structural front.

The floral development within this interval. They used two independent data sets—permineralized floras recovered from coal balls exploited from the coal seams, representing the peat-forming vegetation, and the adpression floras from roof-shales, representing either the terminal peat swamp or non-peat vegetation that grew in clastic, alluvial soils (Gastaldo et al., 1995). DiMichele et al. (1996) found that the flora was different below the base of the Carbondale Formation and also in the lowermost part of the overlying Modesto Formation. However, within the Carbondale Formation, itself, there was nearly no change in the taxonomic composition of the fossil floras. In addition, the same plant communities were observed again and again in stratigraphically successive peat and clastic swamps. To realize the significance of this unexpected result, inspection of a paleogeographic map of North America during the Late Carboniferous is educational (Fig. 6). During interglacials, large parts of the continent were flooded by marine waters and lowland communities were extirpated. These plants apparently survived in newly established wetlands (refugia) at the margin of the epicontinental sea. When the progradation of the coastline occurred during the regressive phase, the plants extended their geographic range (migrated) back into the reestablished physico-chemical conditions of the marginal marine and coastal wetlands resulting from coastal plain expansion over large parts of the continent. The plant communities that resulted were a reassembly of those that had existed previously (DiMichele and Phillips, 1996a, 1996b; DiMichele et al., 1996). Hence, the fossil record shows stability through at least eleven interglacial-glacial cycles not only in the systematic composition of the floras, but also in the ecological associations of wetland plants on a continental scale. Both the plants and the wetland ecosystems of which they were a part not only survived the large scale environmental shifts, but also survived the climatic changes from ever-wet to wet-dry seasonality. The time spans involved

were fourth-order cycles, with a time span of approximately 1 to 1.5 Ma for the entire time interval represented by the Carbondale Formation.

## CONCLUSIONS

The Late Paleozoic cold interval beginning in the Late Mississippian (Late Viséan) and extending into the Late Pennsylvanian (Westphalian D) is an interval in deep time for which we have the best record of tropical vegetation of any long-term data set in Earth history. This includes our currently

persisting cold interval that began in the mid-Cenozoic. In the case of the Late Carboniferous, the record of these isotaphonomic tropical ecosystems was derived originally to assist in the prediction and exploitation of northern hemisphere fossil-fuel resources. The tropical record of the Tertiary remains in the present-day tropics, and only recently investigations have been undertaken to decipher ecosystem history in this setting.

While largely collected as the data base for the terrestrial biostratigraphic resolution and coal-seam correlation of coal-bearing sequences, the megafloral records can be used to interpret paleoecological and paleoclimatological patterns. One pattern that emerges from these data throughout the Carboniferous cold interval (Namurian-Westphalian D; 26 Ma duration) is that of wetland ecosystem and systematic stability. This stability is not stasis; rather, it is a dynamic response based on the survival of species following extirpation from broad coastal plain and lowland settings during interglacials, and re-assembly of

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