Flöznah and Flözfern Assemblages: Potential Predictors of Late Carboniferous Biome Replacement?

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ABSTRACT.—Megafloras preserved within the intermontane basins of the Czech Republic provide an excellent opportunity to evaluate whether Late Carboniferous biome replacement parallels, presages, or postdates that documented within coastal lowland settings. Two principal assemblages, Flöznah and Flözfern, first identified by Havlena, are preserved in association with wetland soils (inceptisols/entisols and histosols) and fluviolacustrine deposits, respectively. A distinct cyclical arrangement exists with regard to these depositional sequences. It is proposed that the alternation between peat-accumulation and coarse-clastic fluviatile deposition in these Namurian–Westphalian rocks reflects paleoclimate shifts related to fluctuations in Mid- to Late Carboniferous continental glaciation. In turn, Flöznah and Flözfern assemblages reflect what appears to be wholescale biome turnover in response to these climate shifts. Based upon available published data, though, it is impossible to determine if there is actual replacement of vegetational elements when there is this dramatic change in depositional style. The exact timing of when the first megafloral elements in Flöznah assemblages appear that predict future biome replacement in the Stephanian also is unclear due to the lack of taphonomic data on exactly where Flöznah and Flözfern assemblages are found in the rock record.

INTRODUCTION

Vegetational trends throughout the Late Carboniferous provide evidence of plant responses to changing global climatic conditions from an icehouse to a greenhouse environment (Gastaldo et al. 1995a, 1996). It is generally accepted that maximum polar glaciation occurred during the Westphalian and Early Permian (Crowley and Baum 1991, 1992; Frakes et al. 1992), with a warmer intervening Stephanian (Dorofyeva and others 1982). This trend is reflected in the Westphalian–Stephanian Euramerican lowland stratigraphies where coal resource distributional patterns (Phillips and Peppers 1984) and megafloral assemblages (Lyons and Darrah 1989; DiMichele and Aronson 1992) indicate a change from ever-wet to drier and seasonal climates. Variations in plant assemblages throughout the Stephanian appear to reflect pulse-like oscillations between overall wetter and drier periods. Gradually, beginning in the Late Stephanian and continuing into the Permian, there appears to be a secular shift towards drier climates in the tropical lowlands (Cecil 1990; DiMichele and Aronson 1992; Zhou and Raymond 1995; Kerp 1996). Similar, but speculative, trends have been implied for interpreted biomes, based upon palynological data, preserved within intermontane basins of Pennsylvanian-Permian age (Alpern 1970; Broutin et al. 1986, 1990).

There is little doubt that climate changes that occurred during the Late Carboniferous, in response to both glaciation and the assembly of Pangaea, disrupted the organization of the well-established and relatively well-partitioned terrestrial vegetation (Gastaldo et al. 1995a, 1996). Late Carboniferous biomes were composed of dominants derived from at least four vascular plant clades, with major lineages evolutionarily and ecologically centered in different parts of the landscape. Rhizomorphic lycopsids dominated wetlands; sphenopsids colonized aggradational streamside, limnic, and wetland settings; ferns succeeded in disturbed areas of all major ecosystems; and gymnosperms dominated a broad array of *terra firma* habitats (Galtier and Scott 1985; DiMichele and Hook 1992). This archaic landscape ultimately collapsed under increasing climatic stress, either due to global perturbation (Wagner 1993) or regional tectonism (Kerp 1996). This collapse and replacement, though, does not appear to be traumatic.

Late Paleophytic floral collapse and replacement appear to have occurred in a step-wise pattern both within and between biomes. Replacement of vegetational elements within biomes is well documented in both peat-accumulating floras (Phillips et al. 1985; Peppers 1985) and clastic substrate communities (Pfefferkorn and Thompson 1982) of coastal lowland settings in the latest Westphalian through early Stephanian. Here, floristic

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turnover is first evident in taphofloras derived from mineral-substrate communities. This turnover is followed subsequently by a homologous change in the peat-accumulating swamps. Eventually there is a radical replacement of biomes, with the "mesophytic" biome completely replacing the "paleophytic." In this new world order, gymnosperms play a significantly increased role in the landscape, while there is a concomitant reduction in the ecological roles of the other clades (Knoll and Niklas 1987; Broutin et al. 1990; DiMichele and Aronson 1992; Kerp 1996). The overall pattern of turnover and replacement appears to be similar in continental interiors, but it is unclear whether or not vegetational response in these settings precedes, parallels, or lags behind the trends documented in coastal lowlands.

Details of biome reorganization and biome replacement in continental interiors is unclear for many reasons. Originally, megafloras collected from within intermontane basins were used to develop biozonations for continental interiors (Jongmans and Pruvost 1950; Wagner 1984; Wagner and Winkler-Prins 1991, 1993). Revisions to these biostratigraphies have come from palynological data primarily derived from drill cores (e.g., Doubinger and Bouroz 1984). Depending upon the disposition of the investigator, biozone assemblages have been viewed as representative of either local or regional vegetation. Disparities between basins had been relegated to problems in lithostratigraphic correlation rather than considering them a reflection of changes in local and/or regional phytological contribution. Although this view has begun to change recently with the application of paleobiogeographic techniques to these data (Broutin et al. 1990; Laveine 1993), depositional and taphonomic data are, for the most part, lacking for these assemblages. Without the data of megafloral context, interpretations for most of these assemblages must be viewed as speculative (Gastaldo et al. 1995b).

The character of megafloral and microfloral assemblages is dependent upon the environment in which the assemblage is preserved. Until recently, plant-fossil assemblages were viewed as providing an accurate, high-fidelity record of local and regional vegetation. Actuopaleontological investigations have demonstrated that a wide variety of taphonomic factors act as filters between the biosphere and lithosphere (e.g., Gastaldo 1988; Spicer 1989; Burnham 1993). Plant biomass is subjected to a complex of interrelated processes (Gastaldo 1994). None of these mechanisms is divorced from the life strategy of individual taxa, the environments and ecological associations in which the plants originally lived, the original biochemical constituents of the plants themselves, and the nature of the depositional regimes into which they may be placed (Gastaldo 1992). Additionally, large-scale geological processes operating regionally (intrabasinal) and/or globally (interbasinal) play a role not only in the composition of the original community and all the above factors, but also with regard to the lithostratigraphic character of the geologic record. All these factors ultimately affect the recoverable plant assemblages from which interpretations are constructed.

The fact that a relationship existed between a particular megafloral assemblage and specific lithology was recognized in Carboniferous strata early by Gothan and Gimm (1930), with later verification by others (e.g., Daber 1957; Drägert 1964; Fissunenko 1965). A similar pattern was recognized by Havlena (1961) working in the Namurian A–B of the Czech Republic. Although taphonomic and depositional factors were not considered, the overall character of the Czech Republic assemblages was used to delimit biomes that formed the basis for interpreting ecological features of the intermontane landscape (Havlena 1975). Changes in vegetation were ascribed to changes in environmental (edaphic?) parameters due to changes in the rate of basinal subsidence or lithofacies (Havlena 1982). It is these relationships that provide data that can be used to evaluate the timing of biome replacement and turnover within Late Carboniferous continental interiors which, in turn, may reflect ecological response to climate oscillation.

CONCEPT OF FLÖZNAH AND FLÖZFERN ASSEMBLAGES

Havlena (1961) noted the recurrence of two distinctive megafloral associations in drill cores of Namurian age. One association characterized by lycopsids (*Lepidodendron obovatum*) and calamites (*Mesocalamites*) was preserved above coal seams and was termed Flöznah. This assemblage was believed to be autochthonous and interpreted to represent contribution from a hygrophytic community. Assemblages preserved between coal seams, termed Flözfern, were characterized by pteridosperms and ferns (e.g., *Rhodea moravic, Sphenopteridium bifidum, Sphenocylopteridium bertrandii*). These assemblages were thought to be allochthonous and were interpreted to represent elements contributed from a more mesophytic community. The Flözfern concept was later subdivided into two separate assemblages (Havlena 1971, 1975) based upon the supposition that different plants were derived originally from different growth sites within the basin. Both assemblages were interpreted to be extrabasinal (*sensu* Havlena 1971; Pfefferkorn 1980) in origin and, hence, allochthonous. One assemblage, termed the extra-basin mesophilous flora (=denudo-mesophilous), mimicked the composition of the previously described Flözfern assemblages. The second assemblage, termed extra-basin xerophilous flora (=denudo-xerophilous), included interpreted mesophytic (*Subsigillaria, Odontopteris*) and xerophytic (*Walchia*) elements. It must be noted that the data used to delimit these assemblages are limited because the vast majority was derived from drill core (see Havlena 1971).

At the time that these concepts were proposed, all peat accumulation was believed to have occurred in topogenous bogs (rheotropic *sensu* Moore 1987). Therefore, the Flöznah assemblages preserved in the peat-clastic transition (roof-shale floras) were believed to represent the final stages of hydrosere development. The establishment of a clastic swamp (*sensu* Gastaldo 1987) or wetland community generally followed the depressional infilling. Both the peat-swamp (coal) and Flöznah assemblages reflect the archaic palaeophytic biome, well adapted to ever-wet climatic conditions (DiMichele and Hook 1992). Havlena (1975) later referred these assemblages to the basin floral facies which he equated to the coal-forming flora.

Whether or not Flöznah floras represent a transition from peat swamp to clastic swamp or two distinct and separate wetland communities, separated by a temporal hiatus, cannot be determined without taphonomic data and an understanding of the development of these intermontane histosols. The presence of a macroflora overlying a coal does not necessarily imply, in and of itself, any genetic relationship with the peat-mire vegetation (Gastaldo et al. 1995b). In some instances these assemblages are genetically related to the underlying coal bed and represent the final phases of peat accumulation (e.g., Scott 1978; DiMichele and Demaris 1987) or thanatocoenoses of peat-swamp forests (e.g., Demko and Gastaldo 1992). In other instances, these assemblages bear little or no genetic relationship to the underlying coal (e.g., Peppers and Pfefferkorn 1970; Baird et al. 1985). These fossils may represent parautochthonous assemblages of subsequent communities or allochthonous elements originating from any one of a number of communities in which the parent plants grew.

Flözfern assemblages, on the other hand, are acknowledged as being composed of allochthonous (?parautochthonous) phytoclasts. These interseam assemblages are preserved exclusively in clastic settings within a variety of depositional environments, and may have been comprised of mesophytic or xerophytic elements. Havlena (1975) envisioned that the mesophytic elements may have originated from at least three different communities. The first type of assemblage was interpreted to have come from vegetation established on fluvial channel bars that existed *within* the peat swamp. This concept was used to account for the presence of Flözfern assemblages in seam partings (Havlena 1975, p. 14). A second assemblage was interpreted to have originated from communities established on bedrock-derived soils, exposed at higher elevations, that surrounded the basin. This scenario was used to explain Flözfern elements within "the sandy claystones and sandstones and sandstones between coal seams." The third assemblage of mesophytic elements (denudo-mesophytic) was believed to have originated kilometers inland from the depositional site. These were considered to represent extrabasinal floras that were established within valleys. Xerophytic elements (denudo-xerophytic) also were believed to have originated extrabasinally, with contribution from communities that grew on hilly plateaus.

Interseam Flözfern assemblages are preserved in river channel (fluviatile arkoses and arenites) and lake (mudstone and claystone; Pešek 1994) deposits, and the taphonomic conditions of these settings strongly control assemblage characters. Hence, the interpretation that can be ascribed to any particular plant assemblage is context specific. Although not clearly indicated, it appears from the literature that most assemblages are interpreted to have originated from variegated claystones and mudstones that are broadly assigned to lacustrine facies (Havlena 1961, 1970, 1971, 1975; Šetlík 1967, 1970; Šetlík-Rieger 1970). It is not known if these assemblages accumulated within intermontane lakes developed on alluvial plains, or if they represent accumulation within channel cutoffs. If these lithologies represent accumulation within intermontane lakes, the plant fossils may represent riparian contribution from either local (Spicer 1981) or regional (Spicer and Wolfe 1987) sources. On the other hand, if these assemblages are preserved within channel cutoffs, it is more likely that the phytoclasts represent local contribution (depending upon the stratigraphic position of the phytoclasts within the channel fill sequence). The distribution of phytoclasts within these rocks may provide the taphonomic data necessary to distinguish such sources (Gastaldo et al. 1996) and resolve this question.

INTERMONTANE SEDIMENT CYCLES AND THE OCCURRENCE OF FOSSIL PLANTS

Pešek (1994) reviewed the Carboniferous geology of central and western Bohemia, which records sedimentation patterns from the Westphalian to the Autunian(?). The maximum thickness of this sequence is 1,440 m encountered in the Kladno-Rakovník Basin. The lowermost lithologic units (Radnice [= Westphalian C] and Nýřany [= Westphalian D – Stephanian] mbrs. of the Kladno Fm.) are characterized by basal breccias over which lie fluviatile, lacustrine, and coal facies. The fluvial facies are cyclical, with basal arkosic or arenitic sandstones (with pebble to cobble conglomerates in the Nýřany Mbr.) overlain by mudstone, claystone, hydric paleosols (underclays), and coal. These cycles are more complete and coals are generally thicker in the Radnice Mbr. Coals are associated with the fluvial facies in the Radnice Mbr., whereas they are more commonly associated with the lacustrine facies in the Nýřany Mbr. Fluvial cycles are bounded by erosional surfaces, dominated by coarse clastics, and are generally asymmetrical (cycles become more symmetrical in the eastern part of the Mšeno-Roudnice Basin). Lacustrine facies are composed of mudstone and claystone, with an admixture of volcaniclastics. In the Nýřany Mbr., coals and paleosols are associated with the lacustrine facies. Pešek (1994) considers each member of this formation as a mesocycle, composed of numerous erosionally bounded fluvial cycles.

Plant fossils reported from the Radnice Mbr. represent elements of both the Flöznah and Flözfern assemblages, but details of preserving lithologies and collection horizons are not published. It is presumed that reported lycopsids and calamites were recovered from above coals, whereas pteridosperms, ferns, and cordaites originated from either fluviatile or lacustrine mudstones/claystones. Systematics of the plant fossils from the Nýřany Mbr. are broadly similar to those of the Radnice Mbr., but preservation of these assemblages is restricted to thin locally interbedded mudstones/claystones (Pešek 1994). It is within the Nýřany Mbr. that many archaic floral elements of the Westphalian are no longer encountered and those of the mesophytic are first reported in abundance (above the Mirošov Horizon; Šetlík ms noted in Pešek 1994; Havlena 1974).

The Týnek Formation (Stephanian A [=Stephanian B of Wagner 1977]) is similar lithologically to the Kladno Fm., although more highly variable both in composition and thickness across the Czech Republic. Basalmost sediments include locally thick conglomerates overlain by fluviatile and lacustrine facies, with a virtual absence of coal but the presence of paleosols (Šetlík 1970). Lithologies in these facies are variously colored, including mudstones/claystones that are gray, brown, red, dark green, or variegated. The sediments of this formation are considered as one mesocycle (Pešek 1994).

Plant fossils are reported from gray mudstones and claystones of the Týnek Fm., and are principally Flözfarn assemblages. Based upon the reported lithologic succession (Pešek 1994, p. 40), the mudstones cap fluvial cycles. Whether these assemblages represent parautochthonous or allochthonous assemblages is uncertain, but the floral assemblages preserved in these lithologies are mesophytic in character.

The overlying Slaný Formation (?Stephanian B) marks a radical change from the Týnek Formation, with the development of an overall finer-grained character. The Slaný Fm. records the deposition of varved claystones (in the lacustrine facies) and extensive peat accumulation. Fluviolacustrine facies are cyclical with basal arkosic sandstones with local conglomerates, overlain by thick mudstones and/or claystones (> 10 m thick), capped by coals. Three members are recognized—the Jelenice Mbr., the Malesice Mbr., and the Otruby Mbr. The Jelenice Mbr. is considered to represent one mesocycle, separated temporally from the remainder of the section. Pešek (1994) believes that this mesocycle was part of a megacycle that is incompletely preserved. The Malesice and Otruby mbrs. each are interpreted as mesocycles, both of which together constitute one megacycle.

Šetlík (1967) recognized three preservational modes of plant fossils in this formation: fragmentary phytoclasts may be distributed on specific bedding surfaces; they may occur bundled or laminated within claystones; or they are preserved as a heteromeric mixture of "crushed" parts. Systematically, these plants are similar to those in the Týnek Fm. Fusainized plant remains are common in stratigraphic members.

The youngest strata, the Líně Formation (Stephanian C to ?Autunian), are very thick, ranging from 113 to 1,022 m. They are dominated by deep-reddish claystones and mudstones, assigned to a lacustrine facies, with minimum coal formation. Fluviolacustrine cycles may begin with conglomerates or microbreccias, overlain by locally thick arenites and argillites (Pešek 1994). These cycles are asymmetric, with more fine-grained than coarse-grained clastics. All fluviolacustrine sequences are considered to represent a single mesocycle.

Plant fossils originate from gray and variegated claystones and mudstones, and the systematic diversity is lower than underlying units. Mesophytic and xerophytic elements are common. Again, the relationship between megafloral assemblage and stratigraphic position is not known exactly.

INFLUENCES ON SEDIMENTARY CYCLES

Large-scale geological processes operating regionally (intrabasinal) and globally (interbasinal) play a major role in the lithostratigraphic character of the geologic record. Regional influences in the Carboniferous of the Czech Republic include the tectonic activity associated with the Hercynian orogeny. Linearly trending intermontane basins developed in response to deep-rooted faulting, and the sediments that filled these basins originated from Proterozoic rocks exposed early in the history of the basins, the Central Bohemian Pluton, and later lithologies derived from the Bohemian Massif (Pešek 1994). Local changes in sediment availability, coupled with alterations in local climate and clastic pathways, may account for some of the cyclical variation recorded in the stratigraphic record.

Overprinted on these regional influences, though, is a strong global component that is coupled with continental-scale glaciation (Frakes et al 1992). Changes in the extent of polar glaciation have a direct impact on the distribution of rainfall in the tropics by affecting the atmospheric circulation and the latitudinal range and width of the intertropical convergence zone (Ziegler et al 1987;

Pfefferkorn 1995). During glacial maxima, the tropics experienced minimal seasonality of rainfall, resulting in ever-wet conditions. In contrast, during warmer intervals, seasonal moisture availability should have been more common in the tropics. This relationship has been used by Cecil (1990) to explain stratigraphic occurrence and variance in peat-accumulating and clastic-accumulating environments.

Broadly applying these insights to the intermontane Carboniferous strata of the Czech Republic may help to explain the cyclicity recorded in these strata. In turn, an understanding of the stratigraphic relationships of Flöznah and Flözfern assemblages within this context may provide the empirical data that could be used for predictive purposes related to the timing of biome replacement and turnover.

PALEOCLIMATE INFERENCES OF INTERMONTANE CYCLES

Two alternating depositional settings are documented in the Namurian to mid-Westphalian intermontane strata of the Czech Republic. Fining-upwards sequences of coarse clastic fluvial regimes are overlain by inceptisols or entisols (underclays) and histosols (peat swamps). The change from coarse-grained alluvial plain deposition to fine-grained deposition and the establishment of soils reflect a marked difference in the hydrologic regime responsible for the widespread development of these deposits.

The development of conglomeratic alluvial plain and braidplain (?) deposits is generally associated with a climatic regime in which there is heavy, seasonally distributed discharge. High discharge velocities are required not only to move these clasts from their site of origin, but also to aggregate them into thick bedforms and megaforms in river channels. Conglomeratic facies are reported to disconformably overlie fine-grained peat or lacustrine facies. This stratigraphic relationship is indicative of a regional change in baselevel. Such changes within intermontane basins may be due to tectonic subsidence resulting in a local baselevel change, a change in ocean levels affecting clastic pathways from the coast to the interior of continents, possibly a change in rainfall patterns, or a variable combination of each. The basal-most conglomeratic deposits within these fluvial facies may have developed in response to any of these mechanisms. If, though, their presence is related to climatic intervals of increased seasonal moisture availability (months of high rainfall alternating with months of low rainfall), these fluvial cycles could be the reflection of periods of glacial minima.

Underclay (inceptisol/entisol) formation and extensive peat (histosol) accumulation require ever-wet climates (Cecil 1990). In these regimes, rainfall is generally constant throughout the growing season. Additionally, there is a minimum both in seasonal rainfall fluctuation and the variance in the amount of yearly rainfall over thousands of years (10^4 years). Inceptisols/entisols are soils that have undergone rudimentary soil-forming processes. This is primarily because the soil-forming processes that affect these sediments occur in wetlands where there is a high water table and leaching of soluble minerals. Peats accumulate where stilted water tables develop above inceptisols (Gastaldo and Staub 1995), and organic accumulation continues until the system is perturbated. Cessation of peat accumulation occurs when organic matter degradation exceeds accumulation at the surface of the histosol. This may be in response to doming (Staub and Esterle 1994) or a change in rainfall patterns, exposing the peat body to drying. Ever-wet conditions within a single intermontane basin might be regionally controlled, resulting in the development of a temporally localized coal. Geographically equivalent correlative coals, found within different basins at the same time, would indicate the presence of a similar climate regime over a widespread area. Such a regime would be indicative of global, rather than regional, control of rainfall patterns. Minimal seasonality of rainfall in the tropics is associated with glacial maxima.

Lower Stephanian strata in the Týnek Formation exhibit a marked shift from this sedimentological pattern. Although fluvial facies are similar to older deposits, there is a noticeable absence of coals and, presumably, inceptisols/entisols. Rooted soils are reported for this interval (Šetlík 1970), but there have been no paleopedological investigations to determine their character. The presence of variously colored mudstones/claystones, though, would indicate the potential existed that more well-developed soils formed in these alluvial floodplains. If this is the case, spodosols, ultisols, and/or vertisols would reflect development under humid, warm-humid, or subhumid climates, respectively. Pešek (1994) interprets the climatic conditions under which these sediments were deposited as having been drier and warmer than the climatic conditions in the Westphalian. This warm interval coincides with the first major deglaciation of the southern hemisphere (Frakes et al. 1992).

A return to a more equitable climatic regime is proposed by Pešek (1994) with the deposition of the Slaný Formation (?Stephanian B). Coals again are found at the top of some fluvial cycles, and, in some instances, varved lake claystones occur in the lacustrine facies. Such controls of climatically-sensitive lithologies would indicate the reestablishment of ever-wet and seasonably wet conditions within these basins. These deposits coincide with the reestablishment of continental glaciation (Frakes et al. 1992). The Líně Formation appears to mark the change from the second Carboniferous icehouse into the greenhouse of the Permian.

INFERENCES FOR FLÖZNAH AND FLÖZFERN ASSEMBLAGES

It is becoming well documented that vegetational response in both tropical coastal lowlands and intermontane basins parallels changes in climate during glacial epochs (Neogene–Holocene). Most of these results have been derived from palynological studies of lake deposits in Central (Graham 1994) and South America (Islebe et al. 1995; Wijninga 1994) and Indonesia (Van der Kaars and Dam 1995). The overall pattern discerned from these investigations is that vegetational response has been complex, operating on a time scale (10^3–10^4 years) that may not be discernible in the megafossil record. For example, the Bandung intramontane basin of West-Java (Indonesian archipelago) records dramatic vegetational changes during the past 135,000 YBP. Dry intervals have been correlated with both the final glacial phases, just prior to glacial retreat, and the onset of glaciation. Warm, wet intervals with the development of open swamp vegetation have been found to occur during interglacial and full glacial phases. Changes in rainfall patterns in this island setting has been attributed to changes in the availability of moisture uptake by the northwest monsoons (Van der Kaars and Dam 1995).

Nevertheless, if the sedimentological character of intermontane deposits in continental settings is controlled by climates affected by moderate-term (10^4–10^6 years) and long-term (10^5–10^7 years) glacial waxing and waning, vegetational response to these shifts should be recorded in these lithologies. It is generally accepted that hygrophytic ecotypes, characteristic of the Flöznah assemblages found in association with inceptisols/entisols and coals, reflect a wetland biome that developed in response to ever-wet climatic conditions. These ever-wet conditions and the rocks that represent these intervals in coastal lowland settings can be correlated to periods of regression (late Highstand Systems Tracts) and accompanying glacial maxima (Lowstand Systems Tracts; Gastaldo et al. 1993). Similar ever-wet conditions would have existed within the interiors of landmasses located within the tropics. The presence of extensive and numerous coals within the intermontane basins of the Czech Republic is believed to reflect these ever-wet climates associated with glacial maxima. Therefore, Flöznah assemblages represent the successful biome that colonized the intermontane basins during periods without significant seasonal fluctuation in rainfall.

Flözfern assemblages, restricted to fine-grained clastics within fluviatile and lacustrine settings (interseam lithologies), were contributed by riparian vegetation capable of colonization during periods of seasonal moisture availability (particularly in the Namurian-Westphalian section). If intermontane clastic-dominated sequences developed in response to climate change during glacial minima, then Flözfern assemblages represent the replacement biome in these settings. There would not appear to be minimum turnover within the landscape, but rather wholescale replacement of the biome. But, without taphonomic data concerning the disposition of Flöznah assemblages throughout the Carboniferous sequence, and a more thorough investigation of systematic presence/absence in sequential Flöznah vs. Flözfern assemblages, this assertion must remain speculative. If, though, this assertion is valid, then it would be possible to evaluate the timing of the first appearance of those floristic elements that ultimately characterize the biome found in the Týnek Formation, following global deglaciation and the establishment of warmer climates. Such data would allow for a test of the proposal made by DiMichele and Aronson (1992) outside of the coastal lowlands settings of Euramerica.

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