Palaeoecology of *Macroneuropteris scheuchzeri*, and its implications for resolving the paradox of 'xeromorphic' plants in Pennsylvanian wetlands

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ABSTRACT

The medullosan pteridosperm *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zodrow was widespread and abundant in the Middle to Late Pennsylvanian forests of tropical Pangaea. On the basis of its thick cuticles, few adaxial stomata, sunken stomata, and dense trichomes, it has been inferred to be a xeromorphic plant. Here we test that hypothesis by analyzing its facies distribution, especially in relation to coals, at 273 site collections from ~45 stratigraphic horizons accessioned in the Smithsonian National Museum of Natural History, Washington, D.C., U.S.A. The collections represent mostly (par)autochthonous assemblages and cover the taxon's complete known temporal range west of the Appalachians in west-central Pangaea. Chi-square analysis of facies-occurrence data indicates that *M. scheuchzeri* had a strong preference for mineral-enriched wetlands that immediately preceded and followed the development of peat swamps and mires (coals), particularly during the late Middle Pennsylvanian (late Moscovian) times, coincident with a period of reduced polar ice volume. In the Late Pennsylvanian, following an interval of global warming and tropical wetland reorganization, palaeoequatorial climate shifted to an overall drier mode. This was accompanied by the disappearance of *M. scheuchzeri* from Europe and its limitation, west of the Appalachians, to the wettest available habitats on the landscape. Thus, our data falsify the hypothesis that *M. scheuchzeri* was a conventional xerophyte, but highlight the paradox of a plant with apparent xeromorphic features confined to a wetland habitat. We consider several possible explanations for this association: (1) response to nutrient deficiency, (2) response to substrate salinity (due to growth in coastal mangrove habitats), (3) response to the composition of the Palaeozoic atmosphere, (4) return on investment (long leaf lifespan), and (5) phylogenetic constraint reflecting ancestral conditions. Our findings have broader implications for interpreting a wide variety of other Pennsylvanian wetland plants, which similarly show 'xermorphic' features.

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1. Introduction

The medullosan pteridosperm *Macroneuropteris scheuchzeri* (Cleal et al., 1990; *Neuropteris scheuchzeri* in older literature) is abundant and widespread in the Middle and Upper Pennsylvanian successions of tropical Pangaea (Darrah, 1969). East of the Appalachian Orogen (in Europe and Atlantic Canada), where it has been particularly well documented (Laveine and Behlis, 2007), it ranges from the lower Bashkirian (uppermost Langsettian) (Crookall, 1959) to the lower Kasimovian (upper Cantabrian), with a principal range from upper Duckmantian through middle Cantabrian (Bell, 1938; Zodrow, 2003; Laveine and Behlis, 2007). West of the Appalachian Orogen (in the United States), though less well documented, it is known from the

upper Bashkirian (lower Atokan) (Eble et al., 2009) to mid-Gzhelian (early Wolfcampian) (Blake et al., 2002; DiMichele et al., 2005) (Fig. 1). It is perhaps best known as the overwhelmingly dominant taxon in the famous Mazon Creek biota of Illinois, U.S.A. (Moscovian), where it is one of four species that comprise ~60% of the flora (Darrah, 1969, as *Neuropteris decipiens*; Pfefferkorn, 1979).

In terms of its palaeoecology, *M. scheuchzeri* presents something of a paradox. Based on aspects of its pinnule anatomy (i.e., thick cuticles, sunken stomata, dense trichomes), spiny rachis structure following pinnule abscission, and the inferred deciduous nature of its pinnules, many authors have argued that it was adapted for conservative water use and drought resistance (Schabilion and Reihman, 1985; Cleal and Zodrow, 1989; Zodrow, 2003; Knaus and Lucas, 2004). This, in turn, implies a water-stressed habitat. Other aspects of morphology, however, suggest hygrophilic habitat preferences, particularly the occurrence of features interpreted as hydathodes (anatomical modifications of leaf vein endings that permit water to be exuded without

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transpiration) on *M. scheuchzeri* pinnules (Schabilion and Reihman, 1985). Furthermore, the facies context of this plant, as known from the literature (not primarily focused on its palaeoecological preferences), is incongruent with growth in water-stressed environments. For example, (par)autochthonous assemblages dominated by *M. scheuchzeri* occur in peat-forming wetlands (Beeler, 1983), ponds (DiMichele et al., 2005) and clastic swamps (Falcon-Lang, 2009), habitats where instances of drought are inferred to have been rare or absent. Analysis of extant leaves (Givnish, 1987) indicates a considerable number of conflicting factors that influence leaf form and physiology, including strong effects of ancestry, raising the question of the degree to which morphology alone is diagnostic of any particular ecological strategy.

In order to assess the conflicting, morphologically based interpretations of the ecology of *M. scheuchzeri*, we undertook a quantitative assessment of its facies distribution to elucidate, as directly as possible, the ecological preferences of this species. Here, we survey the abundance and facies context of *M. scheuchzeri* in areas west of the Appalachian Orogen throughout its stratigraphic range. In addition to determining the specific habitat preferences of this species, we document its patterns of ecological expansion and contraction through time, which mirrored changes in global climate (Fielding et al., 2008a, 2008b).

2. Fossil plant collections

We surveyed the distribution and abundance of *Macroneuropteris scheuchzeri* in fossil plant collections of the Smithsonian's National Museum of Natural History, Washington D.C., U.S.A. These collections were made by various combinations of the authors over a thirty-year period, but with one of us (WD) always supervising the sampling protocols, thus ensuring consistency. We examined 273 separate collections from ~45 stratigraphic horizons (allowing for approximate correlations among basins for some horizons), totaling >12,000 individual hand sample specimens. These span the late Bashkirian through the early Asselian (mid-Atokan through early Wolfcampian) range of the taxon west of the Appalachian Orogen, an interval of approximately 18 million years duration (approximately 298–316 million years ago), distributed across Illinois and Indiana, in addition to a few records from Texas and West Virginia that encompass the uppermost part of the species range (Fig. 1).

Importantly, these collections were made from any deposit in which plant fossils could be found, regardless of preservational quality, provided that material was identifiable at generic level or better (i.e., the collecting efforts were not trophy-hunting expeditions). In addition, *M. scheuchzeri* was not the object of the initial collection strategy, so samples are not collector-biased for or against that taxon. In our study, all collections were examined and included in the analysis, regardless of whether *M. scheuchzeri* was present or absent.

2.1. Criteria for identification

In order to identify *Macroneuropteris scheuchzeri* (which is most typically represented by isolated pinnules in the collections), the following diagnostic characters were used (Cleal et al., 1990; Zodrow, 2003; Laveine and Behlis, 2007; Laveine and Legrand, 2008): Pinnules lanceolate (Fig. 2A–D), occasionally falcate (Fig. 2E–F), large (up to 120 mm long and 35 mm wide), with entire margins and occasional lobations, especially at the base. Pinnule bases cordate (Fig. 2B, C, F), occasionally forming basal ovoid pinnules. Pinnule apices bluntly or sharply acute to acuminate (Fig. 2A–E, G–H). Mid-rib thin but well marked, extending most of the pinnule length (Fig. 2A, C–D, G–H). Venation dense, arching, with each vein branching 4–5 times before reaching the margin at angle of ~80° (Figs. 2C, and 3). In each collection, at least several specimens show abaxial, and occasionally adaxial, apically directed, adpressed, stiff, short trichomes (Fig. 3). In many collections the characteristic "spiny" rachis segments accompanied pinnules.

To verify determination, cuticle preparations were made from selected stratigraphic horizons ranging from early Moscovian through late Kasimovian (upper Atokan through upper Missourian). All sampled pinnules showed features in conformance with the criteria established by Cleal et al. (1990, 1996) for the identification of *Macroneuropteris* in general, and *M. scheuchzeri* specifically, as follows: brachyparacytic stomata on adaxial surfaces and prominent multicellular trichomes and papillae on abaxial surfaces.

2.2. Geological context of collections

The collections examined in this analysis come a wide variety of palaeoenvironments, but can be grouped into two general geological contexts: (1) Predominantly wetland clastic facies, which, in the coal basins of the eastern United States (Illinois, Indiana, and West Virginia), account for a total of 169 out of a total of 215 collections (78.6%), and in the eastern shelf of the Midland Basin in Texas, account for 34 of 58 total collections (58.6%). These collections occur either directly above or below coal beds, generally in gradational contact with them. As coals are interpreted as having formed under humid climates, or in the case of some of the older (Atokan) coals, under perhumid conditions (Cecil et al., 1985, 2003; Cecil, 1990), clastic beds in direct gradational contact are interpreted to have formed in widespread wetlands transitional to, or from, those in which peat formed. (2) The remainder of the collections represents a diversity of deposits formed under more strongly seasonal climatic regimes in which peat did not form, and where better-drained landscapes were widespread within basinal lowlands. In the eastern coal basins, there are 46 such collections (21.4%) and in Texas, 24 (41.4%). These collections permit us to assess the occurrence of *M. scheuchzeri* in such settings.

In all instances, the Texas collections, from western Pangaea, represent slightly more seasonal climatic regimes than found in the more easterly regions of west-central Pangaea. For the beds associated with coals or coaly shales, in particular, localized wetland facies appear to have formed under humid to moist subhumid conditions (Tabor and Montañez, 2004).

The overwhelming dominance of collections from humid climates reflects a general taphonomic megabias of the plant fossil record, particularly in older time periods, towards plant preservation in wetland settings during periods of wetter climate (Behrensmeyer et al., 2000; Falcon-Lang et al., 2009, 2011b; Dolby et al., 2011; Gastaldo and Demko, 2011; Falcon-Lang et al., 2012), when short-term preservation and long-term burial were more likely in basinal settings. Even many of the 70 collections from seasonally dry climates appear to have been areas of relatively high local water tables, reflecting the strong biases toward burial and removal of organic matter from the vadose zone of surface oxidation. Under seasonally dry climates, wet-substrate depositional environments are often localized and may serve as catchments for plant debris from sites near, but outside, the immediate burial environment. Nonetheless, seasonally dry climates create conditions much less favorable for long-term preservation of organic material due to sporadic, sometimes extended periods of lowered water tables, during which oxidative destruction of potential plant fossils occurs (see discussion in Gastaldo and Demko, 2011).

2.3. Plant assemblages and taphonomy

Where *M. scheuchzeri* remains were found, they occurred in grey to buff mudstone and shale, coaly shale, or in small lenses and channels of very fine to fine-grained sandstone. Assemblages typically consisted of dense accumulations of unoriented plant material, including a great mixture of organs of different sizes and shapes. Some laminations were dominated by isolated pinnules of *M. scheuchzeri* whereas other, interbedded laminations commonly comprised large pteridosperm stems, foliar-frond axes, and rootlets.
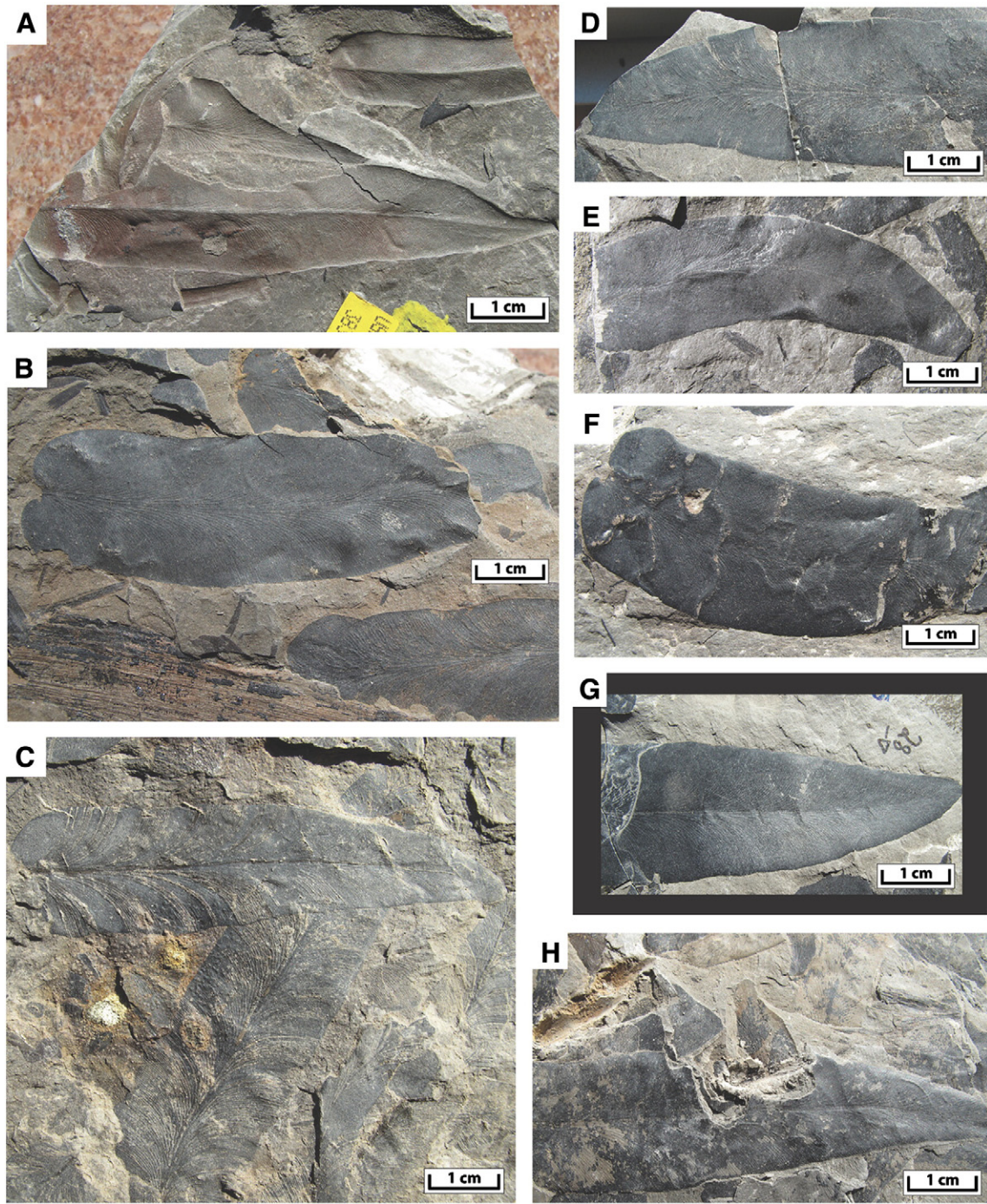
Fig. 2. *Macroneuropteris scheuchzeri* pinnules from various sites analyzed in this study (see Fig. 1 for details of stratigraphic intervals) demonstrating the fundamental conservatism of the morphological features used to identify the species throughout its range in several U.S. basins. A) Atokan, Brazil Formation, USNM locality number 38392, Roaring Creek, Indiana, USNM Specimen Number 543977. B) Virgilian, Waynesburg Coal, Dunkard Group, USNM locality number 42290, Patriot Mining, West Virginia, USNM Specimen Number 543978. C) Late Desmoinesian, Cottage Coal, USNM locality number 43513, Peabody Cottage Grove Mine, Illinois, USNM Specimen Number 543979. D) Middle Desmoinesian, Springfield Coal, USNM locality number 38372, Peabody Lynnville Mine, Indiana, USNM Specimen Number 543980. E) Late Desmoinesian, Baker Coal, USNM locality number 38417, Solar Sources Four Rivers Mine, Indiana, USNM Specimen Number 543981. F) Late Desmoinesian, Baker Coal, USNM locality number 38405, Solar Sources Mining, Indiana, USNM Specimen Number 543982. G) Early Desmoinesian, Murphysboro Coal, Creek Paum Mine, Illinois, USNM Specimen Number 543983. H) Missourian, Womac Coal, USNM Field Number 1993-4, Malone Mine, Illinois, USNM Specimen Number 543984.

Fig. 1. Distribution and relative abundance of *Macroneuropteris scheuchzeri* in U.S. stratigraphic successions studied for this analysis, compared with its range in Europe, correlated via global and regional time scales (using Heckel et al., 2007; Davydov et al., 2010; Falcon-Lang et al., 2011a). Pennsylvanian series boundaries are shown at traditional Appalachian levels. Global stage boundary dates follow Peterson (2011), while North American stage boundary date estimations follow Heckel (2008) and Falcon-Lang et al. (2011a). Dotted boundary for top of Virgilian shows previous level of Virgilian-Wolfcampian boundary (at base of Admire Group) used in older literature. Duckmantian-Bolsovian boundary date is from Waters and Condon (2012). Western European stage boundaries are shown as dotted lines where correlations with American and global successions are uncertain. Abbreviations: FAD, first appearance datum; LAD, last appearance datum. Formations: Cbn, Carbondale; Shb, Shelburn; Pta, Patoka; Bd, Bond; Matt, Mattoon; Way, Waynesburg; Mky, Markley; Wah, Washington.
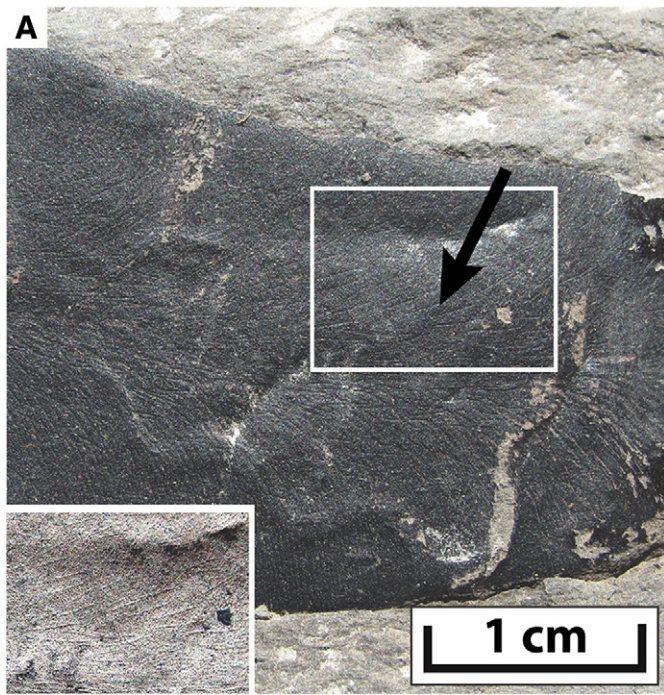
Fig. 3. *Macroneuropteris scheuchzeri* pinnule to show details of venation and adpressed trichomes (at arrow); enlargement of specimen illustrated in Fig. 2F, USNM Specimen Number 543982. Late Desmoinesian, Baker Coal, USNM locality number 38405, Solar Sources Mine, Indiana. Boxes in centre is enhanced in lower left to emphasize trichomes (by image color inversion and sharpening in Adobe Photoshop to show dark trichomes on a light grey background).

We interpret these assemblages to be autochthonous to parautochthonous (*sensu* Bateman, 1991), meaning that the debris was preserved with little, or no evidence, of transport from the place where it entered the depositional environment (autochthonous) or was transported some indeterminate distance but within the original habitat/environment of growth (parautochthonous). We stress that the caducous nature of *M. scheuchzeri* pinnules means that isolated pinnules are commonly encountered; these, however, are not a necessary indication of "transport" given that they most often occur in mats and in association with other kinds of pteridosperm remains (Falcon-Lang, 2009), such as stems and foliar-frond axes, and notably without preferential orientation suggestive of currents.

No doubt some assemblages were subject to varying degrees of decay. There is, however, no reason to believe that *M. scheuchzeri* has been preferentially concentrated by such decay relative to other plants of Pennsylvanian habitats, given that most species of the flora had thick, xeromorphic foliage. Thus, we conclude that the great majority of the collections studied capture the composition of the original plant communities in general terms.

3. Analytical methods

3.1. Facies context

For the purpose of our analysis, each collection was assigned to one of three facies-types:

(1) Below or within coals: Facies from below or within coals comprising dark grey, organic-rich, finely laminated shales that show dense accumulations of stem and foliar debris (Fig. 4A, B), widespread rooting, and grade into the overlying or surrounding coal. Included in this category are thin clastic beds within coals, often referred to as "partings". Plant assemblages are (par)autochthonous in this context (meaning parautochthonous and/or autochthonous, as described above). These deposits represent clastic swamp environments.

(2) Above coals: Facies overlying coal seams comprising medium to dark grey, organic-rich shale conforming to typical 'roof shales' in variably sharp to gradational contact with the top of the coal bed. Plant assemblages are mostly (par)autochthonous in this context, although in a few instances it was not possible to differentiate a parautochthonous from an allochthonous origin. In most instances, *M. scheuchzeri* forms dense accumulations (e.g., Fig. 5C, D). These deposits represent drowned final phases of the peat-forming vegetation or poorly-drained coastal plains, and most often reflect deposition under tidal (though not necessarily saline) influence (e.g., Kvale et al., 1989; Archer et al., 1995).

(3) Not Associated with coals: Facies not associated with coals, comprising a variety of habitat conditions from permanently water-logged but localized to seasonally dry habitats. Most of these formed under seasonally dry climatic regimes unfavorable to the accumulation of peat, such as channel-fill sediments formed contemporaneously with seasonally dry paleosols, and encompass a diverse array of plants varying greatly among the deposits (e.g., Leary, 1981; Feldman et al., 2005). Some of these come from sequences of floodplain or coastal plain deposits in which conditions were unfavorable for peat formation even if the landscape or local depositional environment was periodically quite wet, such as deposits capturing plants that grew within channel belts in what may have been, overall, seasonally dry environments (e.g., DiMichele et al., 2010). Thus, this group is more heterogeneous and contains a greater variety of depositional settings and original habitat conditions than the other two. We have chosen to lump these together rather than create a large array of very specific habitat types each represented by one or a few examples.

3.2. Abundance scores

Each collection comprises a varying number of discrete hand specimens, ranging from as few as 10 specimens to several hundred. For each collection, the number of hand specimens containing *M. scheuchzeri* was assessed, and ranked as follows: absent (no *M. scheuchzeri* present in the collection), rare (present on <10% of specimens), common (present on 10–50% of specimens), or abundant (present on >50% of specimens). This is a modification of the quadrat method of Pfefferkorn et al. (1975); see Wing and DiMichele (1995) for further discussion of this method.

3.3. Hypotheses

The null hypotheses under examination in this study are the following: (1) *Macroneuropteris scheuchzeri* was uniformly distributed among the three facies-types, or between two of these contexts (above and below coals); (2) the distribution of *M. scheuchzeri* among the three, or between the two (above and below coals), facies-types was uniform among the four time bins analyzed: Atokan, Desmoinesian, Missourian, Virgilian-Wolfcampian; and (3) *M. scheuchzeri* was uniformly distributed throughout its stratigraphic range in terms of the relative frequencies of absent/rare or common/abundant occurrences. The alternative hypotheses are, therefore, that *M. scheuchzeri* was not uniformly distributed among the three facies-types, or between the two coal-related contexts; that it was not uniformly distributed among the various facies-types within the temporal framework of the time bins analyzed; and that it was not uniformly distributed through time in term of its abundance categories. Should any of the null hypotheses be rejected, the tests we have chosen (Chi Square, see below) cannot give us a direct assessment of the directionality of the differences in abundance. However, these are clear by inspection of the observed data relative to the calculated expected values.

Fig. 4. Baker Coal exposure in Cottage Grove Mine, Illinois. A marks the position of a non-fossiliferous, seat earth paleosol with which the subcoal channel is laterally coextensive. B marks the position of a channel that was filled with fossiliferous siltstone in gradational contact with the base of the coal bed. A sharp zone of contact between A and B is marked by the dotted line. C marks the position of the Baker Coal, which is of Desmoinesian age (see Falcon-Lang et al., 2009 for details). Coal dips and thickens into a channel present on the landscape prior to the onset of peat formation, contemporaneous in part with the formation of the paleosol on its flanks beneath the coal. Note people for scale, to the immediate left of letter C.

3.4. Statistical analysis

Abundance scores (i.e. absent, rare, common, and abundant occurrences of *M. scheuchzeri*) were tallied in several different ways: (1) For each facies-type (i.e., below coal, above coal, or not associated with coal), (2) for each stratigraphic bin (i.e., Atokan, Desmoinesian, Missourian, Virgilian-Wolfcampian), and (3) for each facies-type within each stratigraphic bin. This hierarchical organization of the data allowed us to organize it for the series of analyses outlined below. For a subset of the analyses (discussed below), abundant and common occurrences
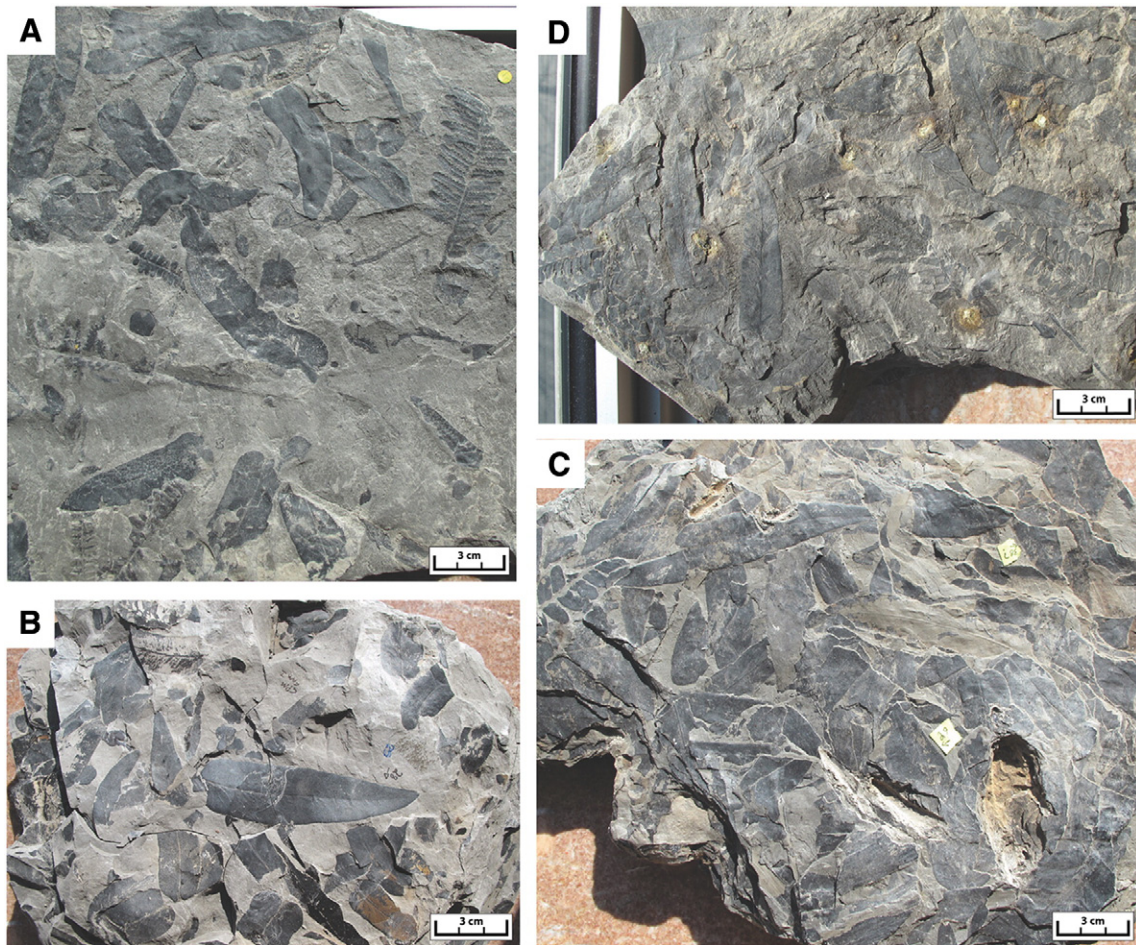

Fig. 5. *Macroneuropteris scheuchzeri* (par)autochthonous accumulations – representative examples. *M. scheuchzeri* is frequently preserved as dense accumulations of caducous pinnules at all stratigraphic levels at which it is found. A) USNM Locality 38417, Solar Sources Four Rivers Mine, Indiana, Below Baker Coal, Upper Desmoinesian, USNM Specimen Number 543973. B) Creek Paum Mine, Illinois, Below Murphysboro Coal, Lower Desmoinesian, USNM Specimen Number 543974. C) Field Locality 1993–4, Malone Mine, Illinois, Above Womac Coal, Lower Missourian, USNM Specimen Number 543975. D) USNM Locality 43513, Cottage Grove Mine, Illinois, Above Cottage Coal, Upper Desmoinesian, USNM Specimen Number 543976.

Table 1
Chi-square analyses of ecological distribution of *Macroneuropteris scheuchzeri* for the combined data set. Analysis 1 includes data from all ecological categories. Analysis 2 includes data only from the "above coal" and "below coal" ecological categories.

	Above	Below	Not Associated	P-value
	observed/ expected	observed/ expected	observed/ expected	
Combined data abundant				0.00
+ common	35/38.90	48/28.02	7/23.08	
rare + absent	83/79.10	37/56.98	63/46.92	
Combined data abundant			Not included	0.00
+ common	35/48.25	48/34.75		
rare + absent	83/69.75	37/50.25		

were grouped together while rare and absent occurrences were grouped together. We did this because both common and abundant occurrences (such as those illustrated in Fig. 5) provide a reliable indication that a collecting site sampled an area that was ecologically suitable for the growth and reproduction of *M. scheuchzeri*. Rare rankings, however, are somewhat ambiguous. They may suggest a site not ecologically suitable for extensive colonization, or be an allochthonous occurrence, depending on sedimentary context. Thus we infer that rare and absent rankings denote habitats or locations that this species probably found unfavorable or was unable to colonize.

Data were analyzed using chi-square, a widely used statistical test that examines categorical variables (Sokal and Rohlf, 1995). In this instance, we are using the statistic as a goodness-of-fit test to compare

Table 2
Chi-square analyses of the ecological distribution of *Macroneuropteris scheuchzeri* by time bin (Virgilian, Missourian, Desmoinesian, and Atokan). There are two analysis for each time bin: the first analysis of each pair includes all data and the second analysis includes only the "above coal" and "below coal" ecological categories.

	Above	Below	Not Associated	P-value
	observed/ expected	observed/ expected	observed/ expected	
Virgilian abundant				0.00
+ common	6/5.78	18/8.67	2/11.56	
rare + absent	12/12.22	9/18.33	34/24.44	
Virgilian abundant			Not included	0.02
+ common	6/9.6	18/14.4		
rare + absent	12/8.4	9/12.6		
Missourian abundant				0.00
+ common	1/2.00	11/9.3	0/3.50	
rare + absent	3/2.00	3/4.7	7/3.50	
Missourian abundant			Not included	0.02
+ common	1/2.82	11/9.18		
rare + absent	3/1.18	2/3.82		
Desmoinesian abundant				0.62
+ common	22/22.88	17/14.96	5/6.16	
rare + absent	30/29.12	17/19.04	9/7.84	
Desmoinesian abundant			Not included	0.48
+ common	22/23.58	17/15.42		
rare + absent	30/28.42	17/18.58		
Atokan abundant				0.31
+ common	6/5.18	2/1.29	0/1.53	
rare + absent	38/38.82	9/9.71	13/11.47	
Atokan abundant			Not included	0.70
+ common	6/6.40	2/1.60		
rare + absent	38/37.60	9/9.40		

Table 3
Chi-square analysis of the abundance of *Macroneuropteris scheuchzeri* through time based on the quantitative analysis of study samples analyzed by time bin.

	Atoken	Desmoinesian	Missourian	Virgilian	P-value
	observed/ expected	observed/ expected	observed/ expected	observed/ expected	
abundant + common	8/22.42	44/32.97	12/7.91	26/26.7	0.00
rare + absent	60/45.58	56/67.03	12/16.09	55/54.3	

the empirical distribution of *M. scheuchzeri* in the three facies-types and through time against expected distributions calculated from the row and column totals. We do not have an *a priori* reason to expect a particular distribution, such as one might with coin flipping or dice rolling. Two abundance-categories are being examined (rare-absent or common-abundant) according to their distribution by facies-type (below coal, above coal, not associated with coal) or by time bin (using U.S. stratigraphic units: Atokan, Desmoinesian, Missourian, Virgilian-Wolfcampian). These tests were run in two different groups: (1) all data and (2) data organized by time bin. Two types of analyses were carried out on the all-data group: (1) using all three facies-types and (2) using only the above and below coal groups, given that *M. scheuchzeri* occurred primarily in these settings. The data binned into stratigraphic groups were analyzed using the same statistical test and the same facies-types as that for the all-data analysis (all three facies-types; above and below coal facies only), to examine distributional patterns and possible changes in those patterns through time.

4. Results

The analysis of the entire data set (Table 1) shows that *Macroneuropteris scheuchzeri* is not uniformly distributed among the facies-types and abundance categories. Table 1 depicts two analyses. The first includes abundant/common and rare/absent abundance categories (Table 1, column 1) grouped by the three facies-types (Table 1, columns 2–4). This analysis indicates, with a probability of <0.01, that the null hypothesis of a uniform distribution can be rejected. By inspection of the observed and expected abundances, it appears that the species is more common below coals than expected and less common than expected in environments not associated with coal. This latter point is accentuated in the second analysis, in which the not-associated-with-coal category is dropped (Table 1), and where, again, the null hypothesis of a uniform distribution can be rejected (probability of <0.01). Inspection of the observed and expected values in this analysis indicates that the species is less common than expected above coals and more common than expected below.

In the second set of analyses (Table 2) abundant/common and rare/absent patterns of occurrence are binned by each of the four stratigraphic time units (see Fig. 1). As in the first analysis, each time bin is divided into an analysis that includes all three facies-types (the first row of each time bin analysis) and one that evaluates distribution patterns only above and below coals (the second row of each analysis). These analyses indicate that the null hypothesis of uniform distribution cannot be rejected for the Atokan or Desmoinesian. The sample numbers from the Atokan are quite low, which makes detection of significant deviations from expectations difficult. Whereas in the Desmoinesian, where sample numbers are greater, there is a small, non-significant, but consistent pattern of difference between observed (more abundant below, less abundant above and in non-associated) and expected. In contrast, all analyses of the patterns from the Missourian and Virgilian-Wolfcampian are significant at a probability of <0.02, indicating that the null hypothesis of a uniform distribution among abundance categories and facies-types contexts can be rejected. Inspection of the observed and expected patterns points to higher than expected abundances below coal beds and lower than expected abundance in environments not in direct association with coal.

In the final analysis (Table 3), patterns of occurrence are evaluated by comparing the total numbers of samples with abundant/common vs. absent/rare occurrences across the four time bins. The null hypothesis of a uniform distribution across abundance categories and time can be rejected at a probability of <0.01. Inspection of the observed vs. expected abundances indicates that the species is less often abundant-common and more often rare-absent than expected in the Atokan, at the lower end of its North American range (Table 3), more often abundant-common and less often rare-absent in the Desmoinesian and Missourian than expected (Table 3), and as expected in the Virgilian-Wolfcampian (Table 3).

In summary, *M. scheuchzeri* is more rare than expected, were its distribution uniform, during the its earlier range, in the Atokan. During the Desmoinesian, the species is more common than expected but shows no particular preference for ecological position above or below coals, although it could be argued that it is less common than expected in deposits not associated with coal beds. In the Missourian through Wolfcampian, *M. scheuchzeri* is differentially abundant below coals or within organic-shale partings of coals, both in analyses when all three facies-types are assessed and in the more restrictive analyses of only above and below coal occurrences. During these latter two intervals, of Late Pennsylvanian age, the species shows levels of abundance intermediate between its most abundant Desmoinesian occurrences and its nadir in the Atokan.

5. Interpretation of palaeoecological patterns

Macroneuropteris scheuchzeri has long been known from wetland deposits including clastic swamps and peat swamps and mires. This study has refined that understanding, at least in that portion of its geographic range to the west of the Appalachian Orogen, demonstrating lower than expected occurrences in environments with periodic water stress, and concentrations greater than expected in shales grading into coal deposits from below. These patterns overall indicate that this species exhibited a general preference for the wettest areas of clastic, wetland environments, particularly those beginning as clastic swamps with a tendency to accumulate organic matter and develop into peat-forming systems. A center of distribution of *M. scheuchzeri* in hygrophilic settings is supported further by its patterns of facies occurrence. During its long stratigraphic range in areas of west-central and western Pangaea — at least 18 million years (Fig. 1), from the latest Bashkirian or earliest Moscovian (early Atokan) through the early Asselian (early Wolfcampian), *M. scheuchzeri* appears to have tracked poorly-drained clastic environments. In the late Moscovian (Desmoinesian) of North America, this species shows a period of significant abundance paired with a widespread ecological distribution. This is concurrent with its period of greatest abundance and widest distribution east of the Appalachian Orogen (Zodrow, 2003; Fig. 1).

Macroneuropteris scheuchzeri was extant during a time of glacially-driven alternations between humid and more seasonal climates across tropical Pangaea, and the amplitude and mode of these climatic alternations changed through the studied interval (DiMichele et al., 2001; Falcon-Lang, 2004; Fielding et al., 2008b; Rygel et al., 2009). Prior to, and during the early phases, of its range (beginning in the Atokan; early to mid-Moscovian), the tropics were dominantly subjected to humid-to-perhumid climates, meaning that they were relatively wet year-round, even during the more seasonal portions of glacial-interglacial cycles, when peat was not forming (Cecil et al., 2003; Cleal and Thomas, 2005; Cleal et al., 2009). These conditions often led to the development of oligotrophic, domed phases during accumulation of some peat deposits and intense leaching of sulfate, iron, and carbonate from the terrestrial landscape (Cecil et al., 1985; Cecil, 1990; Eble et al., 2001; Greb et al., 2002). *M. scheuchzeri* was rare at this time.

In contrast, during the later Moscovian (Desmoinesian) and into the Late Pennsylvanian, polar ice masses appear to have diminished during part of the Kasimovian (Missourian) (Fielding et al., 2008b; Heckel, 2008; Rygel et al., 2009), as a consequence of global warming (Horton and Poulsen, 2009). Various lines of evidence — geochemistry (Cecil et al., 1985; Greb et al., 2002), palynology (Eble et al., 2001; Eble, 2002; Eble et al., 2003), plant megafossils (Pfefferkorn and Thomson, 1982; Phillips and Peppers, 1984; Cleal et al., 2009), the distribution of coals (Phillips and Peppers, 1984; Schutter and Heckel, 1985) and paleosols (Schutter and Heckel, 1985; Falcon-Lang et al., 2009; DiMichele et al., 2010; Falcon-Lang and DiMichele, 2010) — indicate that this was a time of much more seasonal climates at all phases of any given glacial-interglacial cycle. Peat swamps appear to have been largely planar, peats (coals) were of higher sulfur content, and vertic paleosols were increasingly common in those rocks between and beneath coals. It was at this time that *M. scheuchzeri* reached its peak in abundance and distribution throughout the west-central Pangaean tropics.

These data suggest that climatic patterns and changes therein correlate closely with the expansion of *M. scheuchzeri*. This species appears to have been most abundant during the wetter phases of glacial-interglacial cycles and expanded its range during times of the widespread prevalence of wet climatic regimes. At its zenith of abundance and biogeographic distribution, during the Desmoinesian (late Moscovian), wet climates were still present, indicated by extensive coal formation in parts of tropical Pangaea. However, these phases of glacial-interglacial cycles were punctuated by an increasing climatic contrast between wetter and drier phases. Major compositional and structural changes took place in wetland tropical landscapes across the Desmoinesian-Missourian boundary (Middle-to-Late Pennsylvanian: Falcon-Lang et al., 2011a). Considerable evidence (e.g., Phillips and Peppers, 1984; Schutter and Heckel, 1985; Cecil, 1990; Winston, 1990; DiMichele et al., 2001; Fielding et al., 2008a, 2008b; Heckel, 2008; Rygel et al., 2009; Bishop et al., 2010) suggests a shift in the climate cycle to increased overall dryness (greater seasonal dryness during both the drier intervals and wetter intervals of glaciogenic cycles) at this time, a change reflecting a period of intensified global warming and ice melting in the south polar regions. Beginning at the time of this major climatic shift, the distributional pattern of this species documents continued ecological confinement to the wettest, swampy environments of the Late Pennsylvanian, particularly those associated with some clastic influx. This pattern is accompanied by an overall decrease in abundance. This distributional pattern suggests that *M. scheuchzeri* showed considerable sensitivity to drought stress.

Macroneuropteris scheuchzeri does not extend into the Late Pennsylvanian, Missourian-equivalent age rocks in Europe (Fig. 1). That it was there in abundance until the early Kasimovian does not necessarily indicate that suitable habitats were lacking in the European portions of tropical Pangaea during the Kasimovian and later but, rather, that the plant perhaps could not recolonize the region after being extirpated. The late Moscovian-Kasimovian was a time of significant uplift of the Variscan mountain range in central-through-western Europe (Cleal et al., 2009; Falcon-Lang et al., 2012). Thus, the disappearance and failure to return of such a formerly widespread and abundant species suggests that there may have been migrational barriers between wetlands in the uplifting Variscan Foreland, where *M. scheuchzeri* had been abundant earlier, and those of intermontane basins and areas south of the Variscan Orogen, which mostly developed in the Moscovian-Kasimovian (Opluštil and Cleal, 2007).

During the Late Pennsylvanian, *M. scheuchzeri* survived in the present-day U.S.A. in a much-restricted remnant of its former range, mostly in swampy environments, and with fewer abundant or common occurrences than in the Middle Pennsylvanian. With continued drying of the equatorial climate in central and western Pangaea in

the Early Permian, *M. scheuchzeri* likely went extinct. Throughout its spatial and temporal distribution, rather than appearing to be drought tolerant, or even preferring such environments, as has been suggested often, this species seems to have been extremely sensitive to drought, and consequently was restricted to consistently wet-substrate environments (Tables 1 and 2).

6. Discussion: ecological re-evaluation

The patterns of ecological distribution found in this study conflict with the hypothesis that *Macroneuropteris scheuchzeri* was adapted to habitats with a significant period of moisture limitation and suggest instead that this species was drought-sensitive and restricted to habitats with available water for most of the year. This is an interesting finding, given that *M. scheuchzeri* possesses many features characteristic of extant drought-resistant plants. As Edwards (1998) notes, however, climate signals are hard to interpret from Palaeozoic plants, due to their phylogenetic distance from modern plants, as well as the drastically different environments that they may have experienced. Additionally, the "nearest living relative" approach, in which the environmental signals of the closest modern relative are used as the basis for inferring such signals from extinct plants (Mosbrugger and Utescher, 1997; Edwards, 1998), is inapplicable to seed ferns, a group that has no modern representatives. Attempts to infer environmental conditions from seed fern structures using extant plants as models should be viewed with considerable caution, particularly where the extant plants are angiosperms. Consider, for example, the large differences in leaf architecture, as related to leaf physiology, documented between angiosperms and all other plant groups (Boyce, 2008; Boyce et al., 2009, 2010; Boyce and Lee, 2010).

Other than the ecological distribution documented in this study, there are other lines of evidence suggesting that *M. scheuchzeri* may not have been adapted to soil-moisture deficits. Schabilion and Reihman (1985) showed that this species possessed hydathodes (see introduction for definition). These structures are associated with a wide variety of plants and habitats, including fresh and salt-water, aquatic to desert settings. Hydathodes do, however, allow water to be transported constantly through the plant even while the stomata are closed. They also have been reported from a variety of other medullosan taxa (e.g., Reihman and Schabilion, 1978; Oestry-Stidd, 1979; Krings and Kerp, 1997, 1999; Krings et al., 2001; Cleal and Shute, 2003; Cleal et al., 2007), and even in marattiealean tree ferns (Scott, 1933; Lesnikowska and Galtier, 1991). Additionally, medullosans had vascular systems that, while allowing for rapid rates of water transport (large diameter, thin-walled tracheids, with abundant areas for water transport between adjacent tracheidal cells, etc.), likely would have made them extremely vulnerable to water stress (Wilson et al., 2008). These lines of evidence, all somewhat ambiguous, do not, in and of themselves, indicate that *M. scheuchzeri* grew under conditions of constantly high soil moisture, lacking drought (either ecological or physiological), but they are not inconsistent with such an inference. Apparently some medullosans with these characters could exist in drylands because they are a common component of such settings (Falcon-Lang, 2003a, 2003b; Falcon-Lang et al., 2011b); however, that does not exclude the possibility of other explanations for the 'xeromorphic' leaf features in other settings.

Based on the ecological patterns found in this survey, we can speculate on the ecological significance of the morphological features of *M. scheuchzeri*. We offer five hypotheses for consideration and note that these are not mutually exclusive, nor should their effects be considered restricted to *M. scheuchzeri*, given the large number of 'xeromorphic' plants that populated the Pennsylvanian-age tropical wetlands. The number and range of factors that can affect leaf morphology are great (see the review of leaf form and function in extant plants by Givnish, 1987; the review of leaf xeromorphy by Shields,

1950; the review of plant physiological responses to stress by Chapin, 1991), and are much more easily understood when working from function to form that in the reverse direction, as we must do with fossils. Three of these five hypotheses overlap significantly, all related to the responses of plants to environmental stress, including nutrient deficiency, substrate salinity, and atmospheric composition (Hypotheses 1–3). Another (Hypothesis 4) is related to the "cost of doing business", in part related to environmental stress both abiotic and biotic, but more fundamentally tied to metabolic investment. Finally, we consider the role of evolutionary history (phylogeny) in constraining morphological change and ecological preferences.

6.1. Hypothesis 1: nutrient deficiency?

Wetland environments are typically nutrient deficient, particularly in nitrogen compounds available to plants (e.g., Pinay et al., 2002). This is particularly notable where inundation lasts for long periods, creating anoxia and reducing the activities of nitrogen-fixing organisms, although such patterns are typically complex and depend upon both soil conditions and the nature of the parent vegetation (e.g., Yu and Ehrenfeld, 2009).

In empirical studies of plant physiology, xeromorphic features have been linked to nitrogen limitation (Mothes, 1931, 1932; Müller-Stoll, 1948), possibly as a consequence of complex physiological reactions. Nitrogen stress has been shown to reduce root water uptake; evidently because root hydraulic conductance is more limited by low nitrogen than is the hydraulic conductance of stomata (Radin and Boyer, 1982). Finally, as a number of studies (e.g., Radin and Boyer, 1982; Boyer et al., 1985; Boyce, 2009) have shown, plant growth in general, including leaf size, cell size, and lamina thickness, are strongly affected by plant water reductions in water throughput, caused in part by nutrient stress, can lead to enhancement of xeromorphic characteristics.

Macroneuropteris scheuchzeri, and many other Pennsylvanian wetland plants, thus may have been 'physiological xerophytes', broadly speaking. As originally conceived (Andrews, 1911, p. 286), morphological xerophytism was envisioned as a response to high concentrations of solutes in the soil, particularly salts, which create an unfavorable osmotic differential between plant tissues and the surrounding aqueous environment, restricting the ability of plants to absorb water. However, as Mothes (1932) demonstrated, this tends to result in a combination of xeromorphic features and succulence. By contrast, nutrient deficiency alone also can create xeromorphism, but of a less extreme sort. This may be seen in such modern plants as cranberries (*Vaccinium macrocarpon*), blueberries (*Vaccinium corymbosum*), and other members of the Ericaceae, which favor waterlogged and/or very dry but acidic soils, but not saline environments.

Overall, we believe this to be the most influential causative agent for the xeromorphic features seen in *M, scheuchzeri* and other Pennsylvanian-age wetland plants, such as many other pteridosperms, the arborescent lycopsids, cordaitaleans, calamitaleans, and even some of the ferns. However, as noted in studies of modern plants (e.g., see reviews of Shields, 1950; Givnish, 1987, and Chapin, 1991), there are more causes of xeromorphy than simply nutrient limitation. So, although low nutrient conditions in late Palaeozoic wetlands appear to be an important consideration, they must be considered in light of other aspects of life during that time in Earth history, some of which we discuss below

6.2. Hypothesis 2: halophyte?

Although this species probably did not occur in habitats having one or more lengthy periods during the year with soil-moisture deficits, it is still possible that its xeromorphic features reflect adaptations to physiological drought in the sense of Andrews (1911).

Physiological drought is, among other things, a condition that ensues when there is a high non-diffusible solute concentration in soil water that exceeds the solute concentration in the tissues of the plant's roots, thus inhibiting passive movement of water into roots by osmosis (Philip, 1958). Falcon-Lang (2009), based on the ecological setting of a rooted trunk of *M. scheuchzeri*, interpreted this species as a mangrove-like plant, adapted for growth in coastal wetlands. This scenario suggests that *M. scheuchzeri*, or at least some populations of it, might have grown under brackish water conditions, the osmotic characteristics of which would have decreased water availability and therefore possibly imposed drought-like conditions, despite abundant water resources.

There are, however, other factors that may contribute to the xeromorphy of extant plants growing in brackish to salt water, such as nutrient deficiency, discussed above. Nutrient deficiency is a likely proximate cause of the xeromorphic leaf features shown by *Rhizophora mangle* (red mangrove) (Feller, 1996), for example. Whereas this angiosperm is not necessarily an ideal model system for interpreting *M. scheuchzeri*'s xeromorphic features, given its considerable phylogenetic distance, it does illustrate the potential complexity of the ecological significance of xeromorphic features in mangrove habitats. Thus, even if some populations of *M. scheuchzeri* did inhabit brackish, coastal regions, this cannot be demonstrated for all populations, and xeromorphy in this habitat may reflect other, less obvious causes.

6.3. Hypothesis 3: response to Palaeozoic atmospheric composition?

The late Palaeozoic was a time of very low CO_2, <400 ppm (e.g., McElwain and Chaloner, 1995; Ekart et al., 1999; Beerling, 2002; Royer et al., 2007a, 2007b) and very high O_2 (Scott and Glasspool, 2006; Berner, 2009; Glasspool and Scott, 2010), estimated by Scott and Glasspool (2006) to have been continuously above 26%. Under these atmospheric conditions, the high, saturating levels of light to which canopy and open-grown plants are exposed would have had potentially severe physiological consequences. Oxygen inhibits photosynthesis in plants, even at O_2 levels as low as 2% or less (Björkman, 1966). This phenomenon, known as the Warburg effect (Turner and Brittain, 1962), is exacerbated under conditions of low CO_2, particularly under conditions of light saturation. The effect is reduced significantly or does not occur under low light intensities. Additionally, under water deficit, photosynthetic rates in terrestrial plants are significantly reduced by stomatal closure, resulting in CO_2 reduction within leaf tissues, thus affecting carbon fixation and exposing chloroplasts to excessive light energy. This may generate active forms of oxygen and potentially cause oxidative damage to chloroplasts and other plant tissues (Smirnoff, 1993). Furthermore, the generally low levels of CO_2 may have slowed CO_2 diffusion into leaf tissues even with stomata open, as internal CO_2 concentrations likely would have been close to, or perhaps even higher than, atmospheric levels. Low CO_2 exacerbates photorespiration, by encouraging the reaction of O_2 with Rubisco.

Xeromorphy may, in part, reflect a gas-exchange tradeoff, between CO_2 conservation and O_2 exclusion. As studies of nutrient limitation have shown, morphological xeromorphy induced by low nitrogen conditions may secondarily protect chloroplasts from excessive light exposure (Steemann Nielsen, 1940 — in this capacity, xeromorphy would not be a primary adaptation, but rather an exaptive consequence, in the term of Gould and Vrba, 1982). In the case of *M. scheuchzeri*, we believe this to be unlikely, but worth considering.

As Falcon-Lang (2009) has shown, *Macroneuropteris scheuchzeri* appears to have been a plant of open habitats, possibly a leaning, thicket former, living under conditions of high insolation. Some pteridosperms with climbing or scrambling and thicket-forming habits, particularly the mariopterids, also are suspected of having been exposed to high light levels and were likewise strongly xeromorphic

(Krings et al., 2003). However, not all pteridosperms were xeromorphic. Some, such as *Laveineopteris rarinervis*, lack xeromorphic characteristics and may have been understory/subcanopy plants (Shute and Cleal, 2002), which would have buffered their physiologies to some degree from the potential CO_2–O_2 interaction.

Of course, such atmospheric-compositional factors would be expected to have affected all plants on the late Palaeozoic earth, with, perhaps, especially strong affects on wetland plants due to the other stresses they face. The nearly obligately swamp dwelling, yet xeromorphic, Carboniferous arborescent lycopsids, for example, dealt with these constraints possibly in the same way as the extant lycopsid *Isoetes*, which acquires CO_2 almost entirely from the soil and, in many species, has little or no gas exchange with the atmosphere. Green (2010) has designated this the Lycopsid Photosynthetic Pathway (LPP). LPP is similar to the CO_2 pathways found in many aquatic angiosperms, the so-called 'aquatic CAM' (Crassulacean Acid Metabolism) pathway (e.g., Sternberg et al., 1984; Keeley, 1998; see review in Green, 2010); such plants acquire CO_2 from sediment through aerenchymatous roots and transport into the aerial organs, accomplished by the possession of morphologies and physiologies that permit major reduction of gas exchange with the atmosphere. Perhaps some medullosan species had CAM-like physiologies in which thick cuticles, sunken stomata, and leaf hairs may have served to reduce CO_2 loss (or O_2 contamination, which would have reduced photosynthetic efficiency) via transpiration.

Aspects of this hypothesis, like the others, seem to be worthy of consideration as a contributor to xeromorphic morphology in *M. scheuchzeri* and in the larger spectrum of late Palaeozoic wetland plants. Once again, this is not likely to be a sole explanation, but it does overlap significantly with other aspects of response to environmental stress, such as nutrient deficiency and return on investment.

6.4. Hypothesis 4: return on investment?

Is it possible that the apparent xeromorphy of *M. scheuchzeri* leaves is a reflection of the "expense" of those leaves? Medullosans were found empirically by Baker and DiMichele (1997) to be the most expensive of the common arborescent coal-swamp plants on a per unit volume basis, more costly than lycopsids, ferns or calamitaleans. In addition, medullosan leaves could be quite large, a meter, or so in *M. scheuchzeri* (Laveine and Behlis, 2007), and up to many meters for some species of *Alethopteris* (Laveine, 1986), supported by a large diameter woody petiole, which was apparently shed with the leaf (Falcon-Lang, 2009). Furthermore, these leaves appear to have been retained on the plant for an extended period of time, as reflected in the persistent attachment of leaf bases to the stems of many species (Pfefferkorn et al., 1984; Wnuk and Pfefferkorn, 1984), including *M. scheuchzeri* (Falcon-Lang, 2009), often being retained after death as skirts around the lower parts of trunks. It thus seems safe to assume that the up-front costs of making a large, tough, long-lived pteridosperm leaf must be paid back through sustained photosynthetic output over a long time interval.

In a broad review of leaf morphology and physiology in extant plants, Givnish (1987, see primary citations therein) notes the following patterns of form and function, which may have relevance to the question of xeromorphy in *Macroneuropteris scheuchzeri*: leaf thickness tends to increase not only with decreasing rainfall, but with increasing leaf lifespan; evergreen leaves tend to have a lower photosynthetic capacity per unit leaf mass than deciduous leaves; evergreen leaves are common in plants on nutrient poor soils or in areas with little seasonality; amphistomatous leaves (stomata on both leaf surfaces) are more common in sunny and/or dry habitats, with hypostomatous leaves (stomata only on the lower surface) predominanting elsewhere (lower-insolation or wetter-substrate sites). Most of these particular morphological characteristics are those that

accompany 'xeromorphy', particularly those related to long leaf life-span and stomatal distribution. And the habitat preferences of plants with long-lived or xeromorphic leaves include those with little sea-sonality, low nutrient status, and wet substrate settings, as in tropical environments inhabited by *M. scheuchzeri*.

Recent studies of extant plants (Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004) have found clear links between leaf life span and biomass per unit area that divide leaves into two major groups: (1) leaves with high investment in biomass per unit area, long leaf life span, relatively low photosynthetic output per unit mass, and slow rates of dark respiration, and (2) leaves with low in-vestment in biomass per unit area, short leaf lifespans, relatively high rates of photosynthetic output per unit biomass, and faster rates of dark respiration. This has been described as the "leaf econom-ics spectrum" (Wright et al., 2004). The more heavily constructed leaves are more expensive to produce, tend to be biomechanically tougher or thicker, and generally have lower nutrient content per unit volume, which leads to reduced insect predation as a conse-quence (Wilf et al., 2001; Royer et al., 2007a, 2007b). The less well defended species also are engaging in a classic ecological "trade-off", sacrificing biomass to predation for high benefits derived from that biomass while functioning (reviewed in Royer et al., 2007a, 2007b). These modern findings have been extended to the fossil record, where similar patterns have been identified and a means of calibra-tion developed empirically for angiosperm leaves (Royer et al., 2007a, 2007b).

Macroneuropteris scheuchzeri foliage, with its high expense of con-struction, both on a per unit-volume basis, and as represented by large fronds, fits well into group (1) above. In addition, insect damage has been identified on the foliage and stems of Pennsylvanian wet-land plants (Scott and Taylor, 1983; Labandeira and Phillips, 1996a, b), though apparently at lower levels than at later times in geological history (Scott et al., 1992; Labandeira and Sepkoski, 1993; Labandeira, 1998). Conrad Labandeira (personal communication, 2011) notes that Pennsylvanian tropical wetland insect herbivory was lower than that found in the Permian tropics of Laurasia and Gondwana, that there is evidence of host specificity, and that pteridosperms, in-cluding *M. scheuchzeri,* demonstrate the highest levels of attack among the floras examined. Medullosans also were endowed with a variety of chemicals, such as resins (van Bergen et al., 1995; Bray and Anderson, 2009), common in their leaves and stems (e.g., Seyfullah et al., 2009), to accompany their heavy construction, again in keeping with Labandeira's observations and model (1) above.

To the extent that these various elements fit together into a coher-ent picture, medullosans, and *M. scheuchzeri* in particular, may have had large, robust, well defended and physiologically "slow" leaves, in conformance with such modern plants in which return-on-investment strongly underpins evolutionary ecology. Although perhaps not a primary influence on xeromorphic morphology, the linkages between 'slow' leaf physiology and xeromorphy are striking and should be considered part of any explanation thereof.

6.5. Hypothesis 5: phylogenetic niche conservatism?

Could the xeromorphy of some medullosans, and specifically *Macroneuropteris scheuchzeri*, be a reflection of inherited vine-like an-cestral features, and thus the result of phylogenetic morphological conservatism, rather than proximate evolutionary adaptation (Givnish, 1987; Coddington, 1988; papers in Orzack and Sober, 2001; Little et al., 2010)? Could these features have constrained the ecological opportunities available to medullosans (e.g., Stopes, 1907; Freckleton et al., 2002; Webb et al., 2002), which would be the essence of phylogenetic niche conservatism? These possibilities are somewhat more difficult to evaluate than the others, because of their complexity, but are nonetheless essential considerations (Losos, 2008). We conclude that neither the habit of *M. scheuchzeri*

nor its ancestry, given the very general level at which medullosan phylogeny is understood, alone adequately account for its xeromorphic morphological features.

A vine-like growth habit in the medullosan pteridosperms certain-ly appears to have been the primitive condition of the clade. This has been inferred mainly from constructional anatomy (e.g., Baxter, 1949). Throughout the clade, regardless of stem size or inferred growth habit, vascular cylinders, including secondary xylem, are di-vided into discrete bundles (e.g., Steidtmann, 1944; Stidd, 1981) with large diameter tracheary elements, permitting high fluid flow rates even though the total amount of stem and leaf vascular tissue is relatively small (Wilson et al., 2008). Both of these traits are found in modern lianas (Burnham, 2009; Isnard and Silk, 2009). Though having limited wood to provide support, cortical sclerenchy-ma in stems and leaves appears to have offered structural support in many medullosan species, a conclusion also derived from biogeo-chemical studies of medullosan tissues (Wilson and Fischer, 2011). Theses morphological bases of inference are supplemented by historical-stratigraphic patterns; a vine-like habit has been inferred for the earliest medullosans (Dunn et al., 2003; Burnham, 2009) and these growth forms were carried forward in the clade as the medullo-sans diversified. Studies of the cuticular details of adpression fossils (see review of Krings et al., 2003) also provide strong evidence for vine-like or scrambler habit, including a diversity of climbing mecha-nisms, in a wide range of derived late Palaeozoic seed ferns. And more direct examination of preserved stems (Krings and Kerp, 2006: Wnuk and Pfefferkorn, 1984) likewise reveals lianescent or non-self-supporting habits in the more derived and stratigraphically younger members of the clade.

Based on the anatomy of described medullosans, there is no evi-dence that any ever "escaped" the fundamental vine-like architecture of their ancestors. Some, including *M. scheuchzeri*, unquestionably evolved self-supporting, upright habits and were probably moderate-sized to quite large trees (Weber and Sterzel, 1896; Sterzel, 1918; Pfefferkorn et al., 1984; Galtier, 2008), but still retained vestiges of the ancestral morphology and its limitations. For example, Falcon-Lang (2009) describes a small *M. scheuchzeri* tree found in growth position. This specimen had a base 446 mm in diameter, ta-pering rapidly to 74 mm over 2 meters. Fronds remaining attached to the tree appear to have formed a skirt, which may have helped it stand in a semi-erect posture. More generally, the largest and youn-gest known medullosan stems are between 25 and 50 cm in diameter, and had evolved xylary modifications that added considerable strength to the stem (Weber and Sterzel, 1896; Sterzel, 1918), per-mitting upright habits.

The vine-like basic medullosan body plan manifested by *M. scheuchzeri* may not, however, be relevant to the matter of its xero-morphy. Modern angiospermous and pteridophytic climbing plants, though often xeromorphic, are not uniformly so. Rather, climbers tend to be highly efficient in water transport and at risk of vascular embolisms, due to their large diameter vessels or tracheids (Schnitzer, 2005). And although many pteridosperm taxa have xero-morphic features (e.g., many species of the small tree *Alethopteris* – Mickle and Rothwell, 1982; Zodrow, 2007; the vines *Mariopteris*, *Pseudomariopteris*, *Karinopteris*, *Lescuropteris* – Krings et al., 2003), many others either do not, or they show mixtures of features, only some of which may reflect xeromorphy (e.g., *Laveineopteris* – Shute and Cleal, 2002; *Neuropteris* – Cleal et al., 1999; *Odontopteris* – Cleal et al., 2007). There is no evidence that any medullosans had root sys-tems that deeply penetrated the substrate (Steidtmann, 1944; Rothwell and Whiteside, 1974), but modern angiospermous and pter-idophytic vines also have a wide range of rooting morphologies, so this line of evidence also is non-diagnostic of habit. In fact, *Macro-neuropteris scheuchzeri*, specifically, is known to have inhabited not only the mineral substrate habitats we have examined in this paper, but peat-substrate environments also (Beeler, 1983), where high

water tables and nearly aseasonally wet climates would have been common, resulting in selection against deeply penetrating root systems regardless of growth form.

Unfortunately, there is no phylogenetic analysis of the medullosan genera or species upon which to examine these patterns. However, given the abundance of xeromorphy among the medullosans, even if largely confined to the mariopterid vines, alethopterids and some neuropterids, it is possible that such attributes may have been phylogenetic constraints, passed on passively during speciation within these groups. Even if they were important in the life history and ecology of the plants, they may not have been proximate adaptations in need of ecological-evolutionary explanation, but, rather, reflections of inherited ancestral conditions.

6.6. Additional considerations

There are several additional factors that may be considered when assessing xeromorphy in Pennsylvanian lowland, wetland plants. Perhaps most important is recognition that "xeromorphic" morphologies are quite widespread among Pennsylvanian-age plants, particularly those of tree habit, or, as noted above, those that were woody vines with the potential for reaching the canopy or growing in open areas. Xeromorphy is visible in distantly related groups such as the arborescent lycopsids, cordaitalean gymnosperms, medullosan seed ferns, and sphenopsids. Even the large fronds of some marattialean tree ferns had strongly revolute pinnules with abundant abaxial trichomes and rachial scales (e.g., Millay, 1997), which could be interpreted as xeromorphic features.

Perhaps related to this pervasive xeromorphy are recent observations that all of these plants had much lower evapotranspiration capacities on a unit-area basis than those of modern flowering plants, thus greatly the reducing the amount of water loss possible per unit area of leaf-lamina surface (Boyce et al., 2009; Boyce and Lee, 2010). In contrast with these findings about transpirative capacity, however, the medullosans also have been shown to have had capacities for rapid transport of water through their vascular systems to the point of dispersal to the atmosphere, as did vine-like lyginopterid seed ferns and the ground-cover sphenopsid scrambler, Sphenophyllum (Wilson et al., 2008; Wilson and Knoll, 2010). This presents us with somewhat of a dilemma — based on the work of Wilson et al. (2008) and Wilson and Knoll (2010), some Pennsylvanian plants, including medullosans, had the capacity to get water to the evaporative surfaces nearly as rapidly and efficiently as some flowering plants, while, based on the work of Boyce et al. (2009, 2010), these same plants seem to lack the ability to vent that water to the atmosphere at a rate comparable to its uptake and transport. The key to this may be the scaling of total evaporative surface area of the leaf array relative to the total water transport capacity of the stem and leaf — which ought to be in balance. Seed ferns had highly divided, multiply compound leaves or "fronds". Particularly in light of xeromorphic morphology, this type of frond construction may have reduced the distance between veins and stomata, allowing more rapid movement of water through high-resistance mesophyll tissues and, at the same time, reduced boundary layer effects, allowing more rapid removal of water from the evaporative surface via transpiration (Schuepp, 1993). Although any given small surface may have experienced low rates of water loss, it is possible that the whole plant exhibited a large surface area through which water might have been translocated in relatively larger volumes than might be estimated from a small surface area. On the other side of this equality, the overall small size of the vascular system may have limited the total volume of water transport, even if the rate of transport was high on a per-tracheid basis. Evolutionary adjustment of these biomechanical attributes would have permitted medullosans to compensate somewhat for limiting constraints, such as low vein densities and low stomatal conductivities at the smallest spatial scales, and the need for conserving CO_2 while moving water through a large

leaf array. The balance point between vascular system size and leaf surface area might be found at different places in different taxa.

By placing M. scheuchzeri in a firmer ecological context, this study raises questions about the ecological significance of the xeromorphic features of the plant and of other supposedly xeromorphic Pennsylvanian-age plants with the centers of ecological distribution in wetland habitats. It opens the door for a reexamination of the ecology of M. scheuchzeri and other xeromorphic plants of the time, and the nature of the environmental and palaeogeographic controls on their temporal distribution and strong morphological conservatism.

7. Conclusions

1. Analysis of the distribution of Macroneuropteris scheuchzeri through time indicate that it was a species that was centered in wet substrate environments, often with a propensity to accumulate organic matter.
2. The xeromorphic features of M. scheuchzeri cannot be used alone to infer that this species preferentially inhabited seasonally dry settings. Rather, these features may reflect a variety of physiological and historical causes.
3. Many, distantly related plants living in late Paleozoic wetland settings were morphological xeromorphs. Thus, the contrast of morphological and physical habitat indicators of growth environment is widespread among plants from this time.
4. Both morphology and physical environmental indicators must be taken into account when assessing or interpreting the autecology of any particular fossil-plant species. Furthermore, comparisons with other plants in the same environments can broaden understanding of morphological phenomena.

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