Abstract

During the late Paleozoic, vascular land plants (tracheophytes) diversified into a remarkable variety of morphological types, ranging from tiny, aphyllous, herbaceous forms to giant leafy trees. Leaf shape is a key determinant of both function and structural diversity of plants, but relatively little is known about the tempo and mode of leaf morphological diversification and its correlation with tracheophyte diversity and abiotic changes during this remarkable macroevolutionary event, the greening of the continents. We use the extensive record of Paleozoic tracheophytes from South China to explore models of morphological evolution in early land plants. Our findings suggest that tracheophyte leaf disparity and diversity were decoupled, and that they were under different selective regimes. Two key phases in the evolution of South Chinese tracheophyte leaves can be recognized. In the first phase, from Devonian to Mississippian, taxic diversity increased substantially, as did leaf disparity, at the same time as they acquired novel features in their vascular systems, reproductive organs, and overall architecture. The second phase, through the Carboniferous–Permian transition, saw recovery of wetland communities in South China, associated with a further expansion of morphologies of simple leaves and an offset shift in morphospace occupation by compound leaves. Comparison with Euramerica suggests that the floras from South China were unique in several ways. The Late Devonian radiation of sphenophyllaleans contributed significantly to the expansion of leaf morphospace, such that the evolution of large laminate leaves in this group occurred much earlier than those in Euramerica. The Pennsylvanian decrease in taxic richness had little effect on the disparity of compound leaves. Finally, the distribution in morphospace of the Permian pecopterids, gigantopterids, and equisetaleans occurred at the periphery of Carboniferous leaf morphospace.

Keywords

1. Introduction

The origin and diversification of tracheophytes (vascular plants) in the Paleozoic was a key event, as life moved from the water to colonize land (Kenrick and Crane, 1997, Vecoli et al., 2010 and Kenrick et al., 2012). The earliest known tracheophyte megafossils, from the Late Silurian–Early Devonian, are characterized by a wide distribution, low taxic diversity, and simple morphological organization (Edwards et al., 1992 and Gensel, 2008). It has been hypothesized that the increase in Paleozoic

tracheophyte diversity throughout the Paleozoic was triggered by several key innovations, including increased vasculature complexity, monopodial stem branching, secondary xylem growth, formation of sporangium clusters, leaves, and heterospory (Niklas et al., 1983, Knoll et al., 1984 and Niklas, 1988). In turn, such innovations are thought to have promoted greater morphological variety and a rapid exploration and colonization of new niches (Bateman et al., 1998 and Hao and Xue, 2013a). As a result, Early Devonian floras were replaced by forests of lycopsids, progymnosperms, ferns, and early gymnosperms in the Middle–Late Devonian (Stein et al., 2007, Stein et al., 2012, Meyer-Berthaud et al., 2010, Decombeix et al., 2011, Cleal and Cascales-Miñana, 2014 and Wang et al., 2015), and highly diversified floristic communities were in place by the end of the Paleozoic (DiMichele et al., 1992, DiMichele et al., 2005 and Bateman et al., 1998).

The earliest documented tracheophytes had no leaves (Edwards et al., 1992 and Gensel, 2008), and the earliest known leaves were structurally very simple (Hao et al., 2003). However, during the first 180 Myr of their history, tracheophytes developed an extraordinary diversity of leaf shapes and sizes (Fig. 1; Li et al., 1995 and Taylor et al., 2009). As the primary photosynthetic organs of tracheophytes, leaves had a substantial impact on physiological and developmental aspects of plant evolution as well as, more widely, on the establishment of terrestrial food webs, ecosystems, and biogeochemical cycles (Beerling et al., 2001, Beerling, 2005 and Rowe and Speck, 2005). For these reasons, studies of leaves have found wide applications in paleoclimatological and paleoenvironmental reconstructions (e.g., Spicer, 1989, Wolfe, 1993, Wilf, 1997, Wilf et al., 1998, Uhl and Mosbrugger, 1999, Glasspool et al., 2004a, Glasspool et al., 2004b and Peppe et al., 2011).
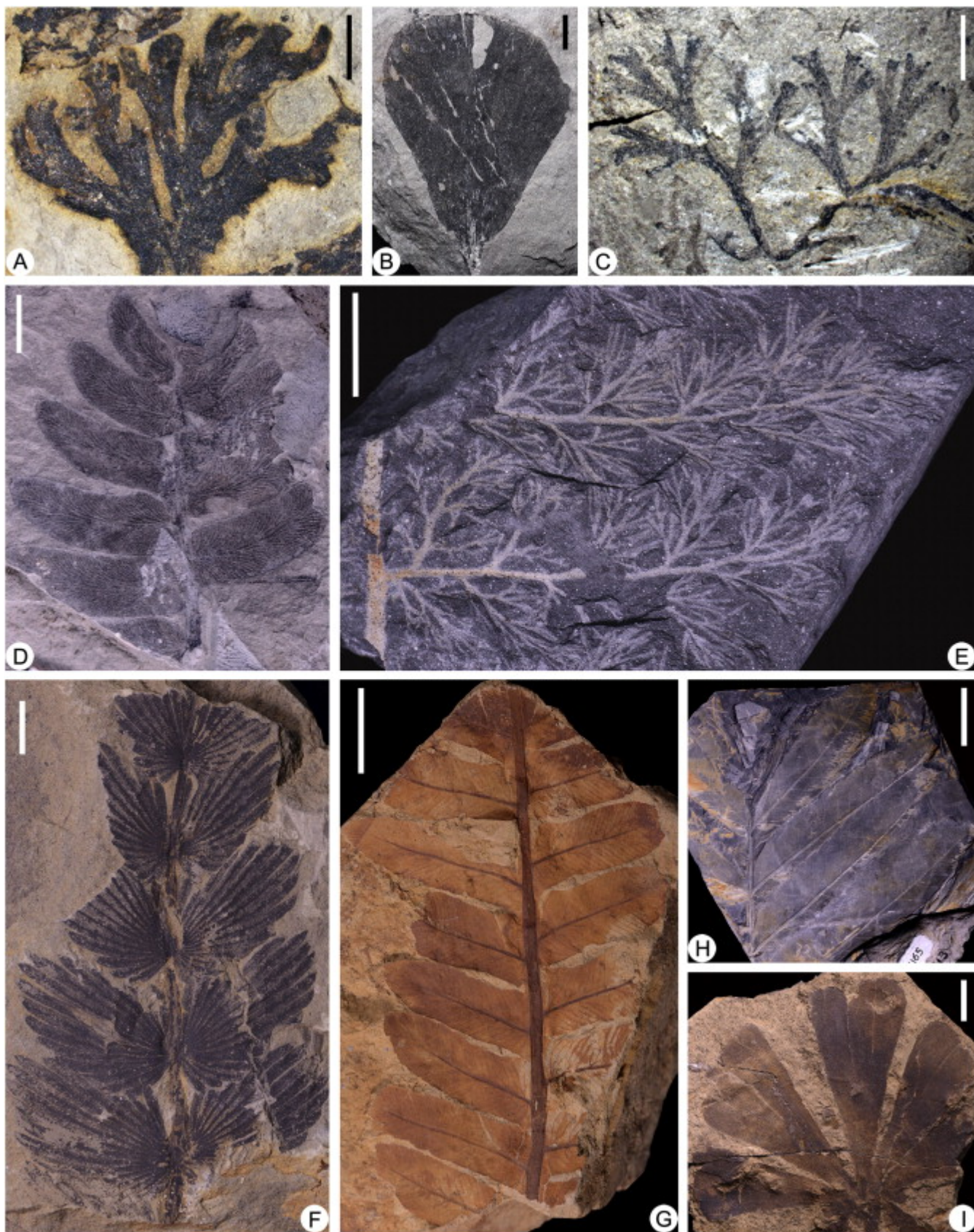
Fig. 1.

Examples of fossil leaves from the late Paleozoic of South China. (A) *Eophyllophyton bellum*. Specimen PUH.10-Eop.04. Early Devonian Posongchong Formation, Yunnan Province. Scale bar = 1 mm. (B) *Xihuphyllum megalofolium*. Specimen PKUB13679. Late Devonian Wutong Formation, Zhejiang Province. Scale bar = 10 mm.

(C) *Denglongia hubeiensis*. Specimen PKU-XH149. Late Devonian Huangjiadeng Formation, Hubei Province. Scale bar = 3 mm. (D) *Neuropteris* cf. *pseudogigantea*. Specimen PB9333. Mississippian Zishan Group, Jiangxi Province. Scale bar = 5 mm. (E) *Rhodeopteridium yingdeense*. Specimen PB8193. Mississippian Datang Stage, Guangdong Province. Scale bar = 10 mm. (F) *Lobatannularia cathaysiana*. Specimen PB6990. Lopingian Xuanwei Formation, Yunnan Province. Scale bar = 10 mm. (G) *Pecopteris lingulata*. Specimen PB7016. Lopingian Xuanwei Formation, Yunnan Province. Scale bar = 10 mm. (H) *Fujianopteris fukienensis*. Specimen PB9165. Guadalupian Tongziyan Formation, Fujian Province. Scale bar = 20 mm. (I) *Rhipidopsis lobulata*. Specimen PB7084. Lopingian Xuanwei Formation, Guizhou Province. Scale bar = 10 mm. (A–C) Specimens deposited at the School of Earth and Space Sciences, Peking University. (A) First published in Hao and Xue (2013b). (C) First published in Xue and Hao (2008). (D–I) Specimens deposited at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (photographs courtesy of Dr. Honghe Xu). (D) First published in Zhao and Wu (1982a). (E) First published in Zhao and Wu (1982b). (F, G, I) First published in Zhao et al. (1980). (H) First published in Liu and Yao (2004).

Both intrinsic (biotic) and extrinsic (abiotic) factors have been invoked to explain the great diversity of Paleozoic leaves. A previous study based on Paleozoic floras from North America and Europe (Boyce and Knoll, 2002) concluded that leaf disparity (= morphological diversity) peaked in the mid-Carboniferous (Namurian), but that later rises in tracheophyte taxic diversity did not affect the range of leaf morphologies. A subsequent study using a larger taxon sample with a near-global distribution revealed similar patterns (Boyce, 2005a). These findings led some researchers (Boyce and Knoll, 2002) to hypothesize that tracheophytes had exhausted their potential for evolving novel leaf traits by the mid-Carboniferous, and that diversity and disparity became decoupled thereafter.

The appearance of large laminate leaves in the Late Devonian–Early Carboniferous has been linked to the dramatic drop of atmospheric CO_2 levels (Beerling et al., 2001, Osborne et al., 2004 and Beerling, 2005). In this scenario, such low levels would promote an increase in the density of leaf stomata, which in turn would allow higher transpiration rates. These rates are essential to maintain a sufficiently low surface temperature in large leaves (Beerling et al., 2001). It has also been suggested that, in the step with the shifts in atmospheric CO_2 and climate, the Permo-Carboniferous floras from western Euramerica showed major reconstructions in their constituents and, progressively, some evolutionarily advanced lineages with new body plans began to appear in the fossil record (Montañez et al., 2007). However, it is not entirely clear whether diversity and disparity were *globally* decoupled during critical phases of late Paleozoic tracheophyte evolution; nor is it clear whether tracheophyte diversification was triggered by the appearance of new leaf traits driven by abiotic factors (e.g., low atmospheric CO_2 levels).

In this paper, we explore new databases of tracheophyte fossil-species (sensu Cleal and Thomas, 2010a and Cleal and Thomas, 2010b) based on the well documented and well sampled Paleozoic record from South China (Figs S1, 10A; Datasets S1–S3) (Gu and Zhi, 1974, Li et al., 1995, Wu, 1995, Xiong and Wang, 2011, Hao and Xue, 2013a and Xiong et al., 2013). South China was an important center of radiation and dispersal for Paleozoic tracheophytes (Hao and Xue, 2013a and Xue and Hao, 2014). One of the four major Paleozoic floristic realms, the Cathaysian flora, was widely represented in South China during the Carboniferous and Permian (Li et al., 1995, Wnuk, 1996, Hilton and Cleal, 2007 and Wang et al., 2012). In addition, South China represents a clearly delimited

tropical province, with distinct features relative to Euramerican provinces (Raymond, 1985, Wnuk, 1996, Scotese, 2001, Hilton and Cleal, 2007 and Wang et al., 2012).

The present study seeks to quantify temporal trends in leaf disparity and tracheophyte diversity in South China, augments the scope for paleobiodiversity studies on a regional scale, and permits detailed comparisons with previous analyses.

2. Material and methods

2.1. Taxon selection

Tracheophytes are abundant and diverse in late Paleozoic strata of South China (Gu and Zhi, 1974, Li et al., 1995, Xiong and Wang, 2011, Hao and Xue, 2013a and Xiong et al., 2013) and have been documented extensively in recent compendia (Xiong and Wang, 2011 and Xiong et al., 2013). Usually, the organs of Paleozoic tracheophytes (e.g., stems, seeds, roots, and leaves) are found disarticulated and might be ascribed to different fossil-taxa (Cleal and Thomas, 2010a and Cleal and Thomas, 2010b). Compared to other parts of the tracheophyte body, leaves are very common in the fossil record (Fig. 1). Their structure is extensively documented, thus providing a solid base for disparity analyses. Our taxon sample (Dataset S1) includes only those euphyllophytes in which leaves are preserved and can be coded for at least 85% of character states. Although the choice of this percentage threshold is arbitrary, it does ensure a meaningful coverage of leaf structures in a wide variety of taxa, while reducing the amount of missing data. Problematic and/or open nomenclature taxa, such as *Linopteris* sp. and *Alethopteris* sp., are also included as they add to the range of documented variation through their unique combination of traits. We refer to the fossil-genera and fossil-species in our sample as "leaf genera" and "leaf species", for simplicity.

2.2. Leaf characters

The Paleozoic tracheophyte record includes both simple and compound leaves. In seed plants, the homology of simple and compound leaves is debated, and it is not known with certainty whether individual leaflets of compound leaves are homologous to simple leaves, or whether the entire compound leaf is homologous to a simple leaf (Kaplan, 1975, Sattler and Rutishauser, 1992 and Champagne and Sinha, 2004). Among ferns, the homology of simple leaves and compound fronds is also debated (Vasco et al., 2013). In light of these problems, we produced two different data sets, one consisting of simple leaves only (Dataset S2), the other consisting of compound leaves only (Dataset S3).

Leaf characters for simple and compound leaves were collated from the literature (Gu and Zhi, 1974, Li et al., 1994, Li et al., 1995, Boyce and Knoll, 2002, Ellis et al., 2009, Taylor et al., 2009 and Hao and Xue, 2013a) and from personal observations. In particular, Ellis et al. (2009) provide guidelines for describing different morphologies objectively and reproducibly. Although angiospermous leaves are different from, and more complex than, non-angiospermous leaves (particularly in their venations), morphological descriptors are identical for both sets of leaves. As we

are interested in patterns of morphospace occupation, the selected characters may not necessarily imply biological homology. However, their use is justifiable in that they can be applied to structures (leaves) that share many features. In this study, we follow the practice adopted in disparity analyses of other organisms (Wills et al., 2012).

As we seek to measure the morphological variation of different types of leaves, our character selection strives to encapsulate as much of the observable and measurable features as possible. All characters are binary and refer for the most part to the presence or absence of particular features. Inapplicable or missing characters are coded as "?". Characters [S1]–[S73] describe the overall morphology of simple leaves, [C1]–[C80] describe the morphology of compound leaves, and [V1]–[V23] describe the veins of simple leaves and those of pinnules in compound leaves (Fig. 2; Online supplementary data, leaf characters). As a result, 96 and 103 characters apply, respectively, to simple and compound leaves (Datasets S2, S3).

Fig. 2.

Schematic illustrations of a simple (A; after Li et al., 1994, p. 684) and a compound leaf (B, after Gu and Zhi, 1974, p. 87), showing the terminology applied to the external leaf morphology, together with examples of character descriptors. See the online supplementary data for details of leaf characters.

Previous work has investigated leaf disparity using measurements of one or a few variables, such as leaf width (Guerin et al., 2012), leaf lamina area (Osborne et al., 2004), and leaf vein density (Uhl and Mosbrugger, 1999 and Feild et al., 2011). However, these features provide only a limited perspective on leaf variation. Multivariate analyses of leaf morphological traits (e.g., Boyce and Knoll, 2002) offer a more complete picture of leaf disparity.

2.3. Stratigraphic assignments

Leaf species were assigned to six time bins: Early–Middle Devonian; Late Devonian; Mississippian; Pennsylvanian; Cisuralian–Guadalupian and Lopingian. Age attributions follow the international stratigraphic subdivisions and are based on previous synoptic reviews (Li et al., 1995, Xiong and Wang, 2011 and Xiong et al., 2013). The Early and Middle Devonian are combined into a single time bin because only a small number of euphyllophytes from these time periods show leaves (Hao and Xue, 2013b). The Cisuralian and Guadalupian are also combined into a single time bin because of the paucity of tracheophyte fossils from the Cisuralian of South China (Li et al., 1995 and Xiong and Wang, 2011).

The dataset of simple leaves includes 95 species, distributed as follows: 4 Early–Middle Devonian; 17 Late Devonian; 8 Mississippian; 18 Cisuralian–Guadalupian and 48 Lopingian (Dataset S2; Table S1). There is no record of simple leaves in the Pennsylvanian of South China (Wu, 1995). The database of compound leaves includes 218 species, distributed as follows: 2 Late Devonian; 51 Mississippian; 15 Pennsylvanian; 52 Cisuralian–Guadalupian and 98 Lopingian (Dataset S3; Table S1). No compound leaves are known from the Early–Middle Devonian.

2.4. A note on Devonian primitive leaves

Following Tomescu (2009), the leaves of tracheophyte sporophytes (the spore-producing diploid multicellular stages of the plants) are laterally projecting organs generally sharing four defining characteristics: vascularization (leaf veins), determinate growth, bilateral symmetry (adaxial–abaxial polarity), and specific arrangement (phyllotaxis). By this definition, most Devonian basal euphyllophytes have no "true" leaves, although there are some exceptions (e.g., progymnosperms). Instead, they exhibit three- or sometimes two-dimensional lateral ultimate vegetative appendages, variously referred to as "incipient fronds", "dichotomous pinnule-like appendages", "branch–leaf complexes", or "proto-leaves" (Kenrick and Crane, 1997, Berry and Stein, 2000, Beerling et al., 2001, Hao and Xue, 2013a, Hao and Xue, 2013b and Gerrienne et al., 2014). However, such ultimate appendages do show some of the features that define typical leaves (such as vascularization, determinate growth, and/or specific arrangement), function as small photosynthetic organs, and have been regarded as precursors to true leaves (Kenrick and Crane, 1997, Sanders et al., 2009, Galtier, 2010, Hao and Xue, 2013a, Hao and Xue, 2013b and Gerrienne et al., 2014). We chose to extend our sample of Paleozoic euphyllophytes to the Devonian groups with lateral ultimate appendages, including *Eocladoxylon*, *Estinnophyton*, *Denglongia*, *Eviostachya*, *Metacladophyton*, and *Rotafolia*. We interpret their ultimate appendages as simple leaves and, therefore, include them in Dataset S2, because such leaves are borne on branches in a helical or whorl-like arrangement. The inclusion of these taxa is justified by the fact that we aim to reconstruct patterns of leaf morphological variation beginning with the inception of true leaf evolution.

2.5. Exclusion of lycopsids

We exclude lycopsids from our analyses because their leaves are quite distinct from those of euphyllophytes in terms of their morphology, development, and evolutionary origins (Kenrick and Crane, 1997, Tomescu, 2009 and Hao and Xue, 2013a). The vegetative leaves of Devonian lycopsids are usually borne on the stems and have been well studied (Berry et al., 2003 and Xue et al., 2005). In contrast, the vegetative leaves of Permo-Carboniferous lycopsids are usually detached but are associated with other organs. They have received little attention in studies of the Cathaysian flora and their fossil record is very scarce (Wang et al., 2002a, Wang et al., 2002b, Wang et al., 2009 and Wan et al., 2011). In Xiong and Wang's (2011, Supplementary material) database, 20 lycopsid species are assigned to the Wuchiapingian and 15 to the Changhsingian. However, only one species with leaves, assigned to the genus *Lepidophylloides*, is recorded in the Wuchiapingian, and no species with leaves are known from the Changhsingian. The fertile leaves (sporophylls) of Paleozoic lycopsids show spines, keels, alations, and heels developing in various combinations in different plants (Berry et al., 2003, Meng et al., 2013 and Wang et al., 2014b). However, the features of sporophylls require a different character-coding system relative to the taxa considered here, and fall outside the focus of the present paper. Therefore, they will not be considered further here.

2.6. Diversity

The diversity metrics for the six time bins are shown in Table S1. The metrics include: total studied species (number of leaf species coded in this study); studied species with simple leaves; studied species with compound leaves; total studied genera (number of leaf genera coded in this study); studied genera with simple leaves; and studied genera with compound leaves. The Lazarus taxa were not considered because of their very small numbers. To characterize floral similarities in two different time bins, A and B, we used the Sørensen Index $(SI)_{A-B} = 2 \times G_O / (G_A + G_B)$, where G_A, G_B, and G_O represent, respectively, the numbers of genera in A and B, and shared by A and B (Tables S2–S4).

2.7. A primer for character-based analyses of disparity and morphospace occupation

Despite the widespread use of character-based analyses of disparity in paleobiology, we think it appropriate to offer a simple introduction to the analytical and statistical protocols used in this paper. These protocols were fully expounded in Wills et al. (1994). More recently, Ruta et al. (2013a) offered additional clarifications, and Chartier et al. (2014) applied the methods to an analysis of angiosperms. Unlike traditional (i.e. measurement-based) and geometric (i.e. landmark-based) morphometrics, character-based analyses of disparity and morphological space (morphospace) occupation seek to measure phenotypic dissimilarity using scores of taxa, typically (but not exclusively) their different character-states, such as are tabulated in cladistic data matrices (however, any matrix of phenotypic traits can be used). Such states can be discrete, as in the present study (see also Brusatte et al., 2008, Brusatte et al., 2011, Shen et al., 2008, Ruta, 2009, Cisneros and Ruta, 2010, Young et al., 2010, Prentice et al., 2011, Thorne et al., 2011, Wills et al., 2012 and Ruta et al., 2013b), or include a mixture of discrete and continuous (e.g., Ruta et al., 2013a). Note that the selection of character-states simply aims to summarize different observable conditions, regardless of whether such conditions have the potential to provide phylogenetic reconstruction.

Character-based analyses of disparity are carried out according to a simple methodological protocol that includes the following steps. First, the tabulated characters are used to extract pairwise taxon distances. Different types of distances can be used, but generalized Euclidean distances are appropriate. This is because they ensure a complete representation of all taxa in a multivariate space in which intertaxon distances can be visualized as the lengths of the straight lines uniting any two taxa (Legendre, 2012).

Second, to evaluate similarities/dissimilarities among taxa, the distances are subjected to ordination, typically a principal coordinates analysis (PCoA). The original l taxa are placed in an l-dimensional space in such a way that many of the original distances among taxa are preserved. Consider a number l of objects (taxa). It is possible, for any two of those objects (say, i-th and j-th), to find their distance δ_{ij}. The ordination seeks to find l vectors or axes (say, $x_1, x_2, x_3, \ldots, x_l$) on which the length between two points x_i and x_j is as close as possible to the distance between the i-th and the j-th object. Formally, $\|x_i - x_j\| \approx \delta_{ij}$ for all $i, j \in 1, 2, 3, \ldots, l$. The l vectors are selected in such a way that they represent the specific collection of real numbers (from the R pool of all real numbers) that satisfy

the above formalization. We can choose N dimensions, such that the vectors form a N-dimensional vector space R^N where the mutual positions of all objects can be visualized.

Third, following ordination we obtain scores (coordinates) of taxa on all PCo axes. These coordinates are used to calculate disparity indices and to produce a graphic representation of objects in N dimensions (morphospace).

2.8. Disparity calculations

We employed identical disparity protocols for the datasets of simple and compound leaves. The Late Devonian and Mississippian compound leaves were grouped together, as the Late Devonian sample is very small. Pairwise generalized Euclidean distances were obtained in MATRIX v. 1.0 (Wills, 1998), and subjected to PCoA in GINKGO v. 1.5.5 (de Cáceres et al., 2007) (http://biodiver.bio.ub.es/ginkgo/Ginkgo.htm) applying the Cailliez method of negative eigenvalue correction (to ensure full euclideanarity of the multivariate space), and placing the centroid for the leaf taxa on the origin of the multivariate axes. The results from GINKGO were verified by running PCoA in the R ape library (Paradis et al., 2004). Morphospace plots using all combinations of the first three PCo axes were built in R and PAST v. 3.0 (Hammer et al., 2001; http://folk.uio.no/ohammer/past).

We employed three disparity metrics, namely: the sum of ranges (a measure of the amount of morphospace occupation; ranges are the absolute differences between the largest and smallest coordinate values on each axis), the sum of variances (a measure of the amount of taxon dispersal within occupied regions of morphospace; variances are the univariate variances of coordinate values on each axis), and the mean pairwise dissimilarity (namely, the "… proportion of characters scored differently [for any two taxa] over all those [characters] that can be compared between [those] two taxa"; Benson and Druckenmiller, 2014, p. 6). The sum of ranges and sum of variances were calculated in RARE v. 1.2 (Wills, 1998) using the PCo scores (coordinates) of taxa on the first 16 PCo axes in the case of simple leaves and the first 13 PCo axes in the case of simple leaves. Rarefaction analyses (Foote, 1992) were run in order to investigate the effect of sample size differences on both metrics. For each time bin, we built a complete rarefaction profile by bootstrapping 1000 times all taxon subsamples between 1 and the maximum number of taxa in the time bin. Mean, median, and 95% confidence intervals were calculated for each subsampling routine. For disparity plots using the sums of ranges and variances (Fig. 5), we show both the un-rarefied and the rarefied mean values per group with the associated confidence interval (Tables S5, S6). The smallest sample sizes at which we conducted rarefaction is $n = 8$ (Mississippian sample) for the simple leaf dataset (Tables S7–S8) and $n = 15$ (Pennsylvanian sample) for the compound leaf dataset (Tables S9–S10). To calculate the mean pairwise dissimilarity, we applied the protocols and codes of Benson and Druckenmiller (2014).

To evaluate differences among distributions of groups in morphospace, we used two non-parametric analyses, namely a permutational multivariate analysis of variance (PERMANOVA; H_0: no differences among group means; Anderson, 2001) and a one-way analysis of similarities (ANOSIM; H_0: mean of rank-converted distances within groups greater than, or equal to, mean of rank-converted distances

between groups; Clarke, 1993; see also Anderson and Walsh, 2013) (Table 1 and Table 2, S11, S12). These analyses were performed in PAST, using the Euclidean distance measure and scores on an identical number of axes to those used in the disparity analyses (see above).

Table 1.

PERMANOVA test for statistical significance between groups of simple leaves from each of the five time bins, Early–Middle Devonian ($n = 4$), Late Devonian ($n = 17$), Mississippian ($n = 8$), Cisuralian–Guadalupian ($n = 18$), and Lopingian ($n = 48$), based on PCo analyses.

p (same) overall	Pairwise comparisons, Bonferroni-corrected				
		Early–Middle Devonian	Late Devonian	Mississippian	Cisuralian–Guadalupian
0.0001□□	Late Devonian	1			
	Mississippian	1	0.888		
	Cisuralian–Guadalupian	0.087	0.001□□	0.001□□	
	Lopingian	0.343	0.001□□	0.002□□	1

□□

p < 0.005.

Table 2.

PERMANOVA test for statistical significance between groups of compound leaves from each of the four time bins, Late Devonian plus Mississippian ($n = 53$), Pennsylvanian ($n = 15$), Cisuralian–Guadalupian ($n = 52$), and Lopingian ($n = 98$), based on PCo analyses.

p (same) overall	Pairwise comparisons, Bonferroni-corrected			
		Late Devonian–Mississippian	Pennsylvanian	Cisuralian–Guadalupian
0.0001□□	Pennsylvanian	1		
	Cisuralian–Guadalupian	0.0006□□	0.0006□□	
	Lopingian	0.0006□□	0.0006□□	1

□□

p < 0.005.

In order to evaluate the extent to which different types of characters may affect patterns of morphospace occupancy, we partitioned our datasets into leaf lamina characters and leaf vein characters and ran PCoA on each partition (Fig. S2 for simple leaves; Fig. S3 for compound leaves).

2.9. Comparison of diversity and disparity

We used the number of studied leaf species and leaf genera as diversity proxies and correlated their values in the different time bins with un-rarefied sum of variances, un-rarefied sum of ranges, and mean pairwise dissimilarity. The plots of plant diversity and leaf disparity through time are shown in Fig. 6, Fig. 7 and Fig. 8. The strength and significance of all pairwise correlations were assessed

through Spearman's rho. The results are shown in Table S13, but we urge caution in their interpretation given the small number of variables.

3. Results

3.1. Morphospace occupation of simple leaves

The pattern of morphospace occupation is shown in two-dimensional plots delimited by combinations of PCo axes 1–3. In the case of simple leaves, Early–Middle Devonian taxa show the smallest occupation of morphospace. A modest expansion occurs in the Late Devonian (Fig. 3A–C), and characterizes progymnosperms (*Archaeopteris*) and a wide variety of sphenophyllaleans (Fig. 4A, B). Morphospace occupation increases remarkably in the Cisuralian–Guadalupian (Early–Middle Permian) and reaches a peak in the Lopingian (Late Permian), with Late Permian taxa largely overlapping the Early–Middle Permian taxa. The dramatic expansion in morphospace occupation during the Permian characterizes gigantopterids (*Gigantopteris*), equisetaleans, and *Rhipidopsis* (Fig. 4A, B).

Fig. 3.

Two-dimensional morphospace plots using PCo1–3 axes, showing patterns of morphospace occupation of simple leaves (A–C) and compound leaves (D–F). The convex hulls delimit taxa from different time bins. Abbreviations for time bins (upper left corner in (A) and (D)): E.–M. DEV, Early–Middle Devonian; L. DEV, Late Devonian; MISS, Mississippian; PENN, Pennsylvanian; CIS–GUA, Cisuralian–Guadalupian; LOP, Lopingian.

Fig. 4.

Leaf morphospace. (A–B) Two-dimensional morphospace plots of simple leaves using PCo1–3 axes. (C–D) Two-dimensional morphospace plots of compound leaves using PCo1–3 axes. Taxa belonging to different groups are shown with different symbols and colors. The convex hulls delimit taxa from Late Devonian (light green), Mississippian (red), and Lopingian (blue). Only two Late Devonian taxa were sampled for compound leaves.

We find similar results when only leaf lamina data are used (Fig. S2A–C). However, when only leaf vein data are used, simple leaves of Devonian and Mississippian taxa appear tightly clustered, and this pattern presumably reflects their limited variation in venation patterns. In contrast, the expansion in morphospace occupation exhibited by the Permian taxa reflects for the most part their great variety of venation patterns, including the complex venations of gigantopterids, the single veins of equisetaleans, and the parallel veins of *Cordaites* (Fig. S2D–F).

PERMANOVA (F = 2.983; p = 0.0001) returns significant results, indicating overall significant separation among group means (centroids) assigned to the five time bins, and it reports a significant separation for the pairwise comparisons of Permian taxa with both Late Devonian and Mississippian taxa (Table 1). However, the pairwise comparison between Late Devonian and Mississippian taxa is non-significant. The non-significant comparisons between Early–Middle Devonian taxa and taxa from other time bins require further scrutiny, given the paucity of Early–Middle Devonian taxa. ANOSIM (R = 0.01365; p = 0.3746) returns overall non-significant results (Table S11), probably indicating that

the dispersions of taxa among different time bins are not significantly distinct. A significant pairwise comparison occurs only between Late Devonian and Cisuralian–Guadalupian taxa (Table S11).

3.2. Disparity of simple leaves

For simple leaves, the sum of ranges increases from the Early–Middle Devonian to the Late Devonian (Fig. 5A), with the mean value in the latter period being almost twice the mean value in the former (Table S5). The sum of ranges declines in the Mississippian, rebounds to a Cisuralian–Guadalupian higher value, and then reaches a peak in the Lopingian (Fig. 5A). The mean value for the sum of ranges in the Lopingian is three times higher than that in the Early–Middle Devonian. Similarly, the sum of variances and the mean pairwise dissimilarity show two phases (Fig. 5C, E): in the first phase, Devonian and Mississippian taxa show comparable values; in the second phase, disparity increases remarkably during the Cisuralian–Guadalupian and then stabilizes during the Lopingian. The rarefied sum of ranges and sum of variances in the Permian bins are comparable but higher than that in the Devonian and Mississippian (Fig. 5B, D).

Fig. 5.

Leaf disparity through time, showing mean disparity values and associated 95% confidence intervals for sum of ranges (A–B, F–G), sum of variances (C–D, H–I), and mean pairwise dissimilarity (E, J). (A–E) Disparity of simple leaves. In (B) and (D), Early–Middle Devonian disparity was kept at original values ($n = 4$), while the rarefied values of other time bins were calculated at $n = 8$ (total taxon number in the Mississippian). (F–J) Disparity of compound leaves. For calculations of sum of ranges and sum of variances, the species of Late Devonian ($n = 2$) and Mississippian ($n = 51$) were grouped together. In (G) and (I), the rarefied values were calculated at $n = 15$ (total taxon number in the Pennsylvanian). Abbreviations for time bins as in Fig. 3.

3.3. Morphospace occupation of compound leaves

Rare compound leaves were reported from the Devonian, and only two Late Devonian taxa of South China were included in this study. The rarity of compound leaves in the Devonian is unlikely to be due to a sampling artifact or preservational bias, and may indicate that such structures had not diversified extensively. The major expansion in morphospace occupation occurs in the Mississippian (Fig. 3D–F) and coincides with the emergence of *Rhodeopteridium*, *Neuropteris*, and *Sphenopteris* (Fig. 4C, D), documenting an unprecedented differentiation of compound leaves presumably related to the breadth of ecological adaptations of tracheophytes at that time. After the Mississippian, morphospace occupation remains almost unchanged, but occupied regions in the Permian appear to be offset relative to the Carboniferous. The comparable amounts of morphospace occupation during most of the Carboniferous and Permian are unexpected, both because many new tracheophyte clades appear in these periods, and because extensive coal swamps with varied taxic diversity develop in the Permian of South China. Several Permian taxa, such as pecopterids and gigantopterids, plot outside but close to the Mississippian morphospace area (Fig. 4C, D).

The pattern of morphospace occupation based on leaf lamina characters is similar to the pattern based on all characters (Fig. S3A–C). With leaf vein data, Carboniferous taxa

(e.g., *Neuropteris*; *Sphenopteris*) contribute to the modest expansion observed in this period, while gigantopterids contribute to the dramatic morphospace expansion of the Permian (Fig. S3D–F). Statistical tests corroborate these qualitative patterns (PERMANOVA: F = 8.286; p = 0.0001; ANOSIM: R = 0.2245; p = 0.0001) (Tables 2, S12). Both PERMANOVA and ANOSIM report non-significant comparisons between Late Devonian–Mississippian and Pennsylvanian taxa, and between Cisuralian–Guadalupian and Lopingian taxa, but significant separation occurs between Carboniferous and Permian taxa (Tables 2, S12).

3.4. Disparity of compound leaves

For compound leaves, the sum of ranges declines from Mississippian to Pennsylvanian, rebounds in the Cisuralian–Guadalupian to a higher value comparable to the Mississippian value, and shows a steady increase (with the highest recorded value) through to the Lopingian (Fig. 5F). The Lopingian and Mississippian values differ significantly, based on non-overlap between error bars (Foote, 1992). The sum of variances changes very little across the four time bins (error bars overlap) (Fig. 5H). With rarefaction, both sum of ranges and sum of variances show little changes from Mississippian to Lopingian (Fig. 5G, I). The mean pairwise dissimilarity increases from Mississippian to Pennsylvanian, and decreases again in later times (Fig. 5J).

3.5. Comparison of diversity and disparity

As for the simple leaves, the number of studied species and genera increases from the Early–Middle Devonian to the Late Devonian, decreases in the Mississippian, and then rebounds in the Permian (Fig. 6A, B; Table S1). Along with this trend, the sum of ranges for simple leaves shows a Devonian increase, a Mississippian decline, and a Permian rebound to the Lopingian peak (Fig. 6A). Unlike the fluctuations in taxic diversity and sum of ranges, the sum of variances and the mean pairwise dissimilarity keep constant from the Early–Middle Devonian to the Mississippian, before their values jump to a high level in the Permian (Figs. 7A, B, 8A, B). Overall, significant correlations are found between the mean values of the sum of ranges and the generic and species diversity, as well as between the mean value of the sum of variances and the number of studied species (Table S13). Other correlations are non-significant. However, when focusing on the Permian alone, we find that the Lopingian saw a 2–3 times increase in the number of genera and species with simple leaves (Table S1), whereas the sum of variances and the mean pairwise dissimilarity show negligible changes, and the sum of ranges increases only by 16.6% in mean value (from 42.86 to 49.96) (Table S5).

Fig. 6.

Comparison of leaf disparity and diversity from the late Paleozoic of South China. (A, C) Sum of ranges of simple and compound leaves compared to the number of studied species in each time bin. Disparity symbols: squares and error bars; diversity symbols: dots. (B, D) Cross-plot of the number of studied genera of simple and compound leaves and the mean value of the sum of ranges in each time bin. Abbreviations for time bins as in Fig. 3.

Fig. 7.

Comparison of leaf disparity and diversity from the late Paleozoic of South China. (A, C) Sum of variances of simple and compound leaves compared to the number of studied species in each time bin. Disparity symbols: squares and error bars; diversity symbols: dots. (B, D) Cross-plot of the number of studied genera of simple and compound leaves and the mean value of the sum of variances in each time bin. Abbreviations for time bins as in Fig. 3.

Fig. 8.

Comparison of leaf disparity and diversity from the late Paleozoic of South China. (A, C) Mean pairwise dissimilarity of simple and compound leaves compared to the number of studied species in each time bin. Disparity symbols: squares and error bars; diversity symbols: dots. (B, D) Cross-plot of the number of studied genera of simple and compound leaves and the mean value of the mean pairwise dissimilarity in each time bin. Abbreviations for time bins as in Fig. 3.

In the case of compound leaves, a rapid increase of taxic diversity occurred from the Late Devonian (2 genera and 2 species) to the Mississippian (19 genera and 51 species) (Table S1). Diversity then falls greatly in the Pennsylvanian, rebounds in the Cisuralian–Guadalupian, and reaches its highest level in the Lopingian, when the genera are ca. 1.5 times and the species are twice the numbers of the Mississippian and Cisuralian–Guadalupian (Table S1; Figs. 6C, D, 7C, D, 8C, D). Compared to the diversity changes, the sum of ranges rises and falls in a similar manner (Fig. 6C, D), the sum of variances changes little (Fig. 7C, D), and the mean pairwise dissimilarity shows an inverse trend (increasing in the Pennsylvanian and decreasing in the Permian; Fig. 8C, D). However, a non-significant correlation occurs in all pairwise comparisons of diversity and disparity values (Table S13). Only 7.4%–14.3% of genera with simple leaves are shared between the Mississippian and the Permian bins, and only 5.1%–15.7% of genera with compound leaves are shared between each two Carboniferous and each two Permian bins (Tables S2–S4). This observation indicates that the components of the Carboniferous and Permian floras are apparently quite different, although the possible reasons for this, such as changes in climate and depositional settings, evolutionary trends of the plants themselves, or a combination of these factors, remain to be addressed. The paucity of Pennsylvanian records in South China makes a detailed analysis very difficult. When examined in the context of morphospace analysis, Permian simple leaves tend to spread remarkably into morphospace, a pattern that is clearly illustrated by newly appearing taxa in South China, such as gigantopterids (*Gigantopteris*), equisetaleans, and *Rhipidopsis*. As for Permian compound leaves, their occupied morphospace regions appear to be offset relative to the Carboniferous. Pecopterids (named for the fossil-genus *Pecopteris*; but see Cleal, 2015) and gigantopterids (*Fujianopteris*, *Gigantonoclea*, and *Trinerviopteris*) plot outside but in proximity to the morphospace region occupied by Mississippian taxa. Both groups began to appear in the Permian of South China, although pecopterids had already been a dominant group in the Pennsylvanian wetlands of Euramerica (DiMichele et al., 1992, DiMichele et al., 2005, DiMichele et al., 2009 and Cleal, 2015), and the origin of gigantopterids may also be earlier (e.g., Looy et al., 2014).

4. Discussion

4.1. Macroevolutionary pattern of euphyllophyte leaves

4.1.1. Timing of character acquisition

Our results highlight that the timing of character acquisition during tracheophyte evolution varies in different paleocontinents. Two examples are particularly interesting. (i) The oldest unequivocal laminate leaves in euphyllophytes are those of the Early Devonian (Pragian) *Eophyllophyton bellum* from South China (Fig. 9; Beerling et al., 2001, Meyer-Berthaud and Gerrienne, 2001, Hao and Xue, 2013a, Hao and Xue, 2013b and Gerrienne et al., 2014), and they considerably predate the oldest records of laminate leaves in other regions (Boyce and Knoll, 2002 and Osborne et al., 2004). Simple leaves of *Eophyllophyton* are small (ca. 5 mm in width), with dissected laminae and dichotomous venations (Hao and Beck, 1993 and Hao et al., 2003). (ii) In the sphenophyllaleans (a clade within sphenopsids) of South China, wedge- or fan-shaped laminate simple leaves first appeared early in the Late Devonian (Famennian), represented by *Sphenophyllum* (Fig. 10D) and *Xihuphyllum* (Chen, 1988 and Wang et al., 2008). Leaves of *Xihuphyllum* are of particular interest as they attained a large size, reaching ca. 70 mm in lamina length and ca. 50 mm in maximal width (Chen, 1988). In Euramerica, similar leaf forms of sphenophyllaleans occurred from the Mississippian onwards (Boyce, 2005b and Taylor et al., 2009). It is also noted that the Late Devonian radiation of sphenophyllaleans in South China contributed significantly to the expansion of the morphospace of simple leaves, whereas in Euramerica, the morphological diversity of sphenophyllalean leaves increased much later, in the Pennsylvanian (Westphalian) (Boyce and Knoll, 2002).

Fig. 9.

Artist's illustration of Early Devonian landscape at dawn, with plant community of *Eophyllophyton bellum*. Painting by Shougang Hao.

Fig. 10.

Vascular plant, geographic, and atmospheric evolution from Silurian to Permian. (A) Phytogeographic provinces in the Early Devonian (left), Mississippian (middle), and Lopingian (right) (Raymond, 1985, Wnuk, 1996, Scotese, 2001, Hilton and Cleal, 2007, Wang et al., 2012 and Hao and Xue, 2013a). Paleomaps modified from Scotese (2001, with permission). Green flags indicate the position of South China. (B) Plant diversity in South China (Xiong and Wang, 2011 and Xiong et al., 2013), and in North America, Europe, and Russia (Niklas, 1988). (C) Representative plant types. (D) Comparison between modeled reconstruction of changes in atmospheric CO_2 (Berner and Kothavala, 2001 and Royer et al., 2004) and leaf disparity (data from this study and from Boyce and Knoll, 2002). Representative plant types and leaf forms are based on various sources (Gu and Zhi, 1974, Li et al., 1994, Li et al., 1995, Dilcher et al., 2004, Wang et al., 2008, Xue and Hao, 2008, Taylor et al., 2009 and Hao and Xue, 2013a).

4.1.2. Group separation in Permian leaf morphospace

Morphological separation of simple leaves is first documented among Late Devonian sphenophyllaleans and progymnosperms, but is more striking among Permian gigantopterids (*Gigantopteris*), equisetaleans, and *Rhipidopsis* (Fig. 4A, B). The separation of compound leaves in the Permian is among the pecopterids and gigantopterids (Fig. 4C, D). Gigantopterids – some perhaps being climbers/scramblers in humid habitats (Yao, 1983, Li et al., 1994, Yao and Liu, 2004 and Seyfullah et al., 2014; but see Wang, 1999) – characterized the Late Permian floras of South China (Li et al., 1995) and their leaves resemble those of angiosperms in size, shape, and venation (Glasspool et al., 2004a and Glasspool et al., 2004b). The equisetaleans include the genera *Annularia* and *Lobatannularia*, both representing foliage of calamitean trees (Taylor et al., 2009 and Thomas, 2014). *Rhipidopsis* may have affinities with ginkgoaleans (Zhou, 2009). The pecopterid ferns had arisen earlier, in the Pennsylvanian wetlands of Euramerica (DiMichele et al., 1992, DiMichele et al., 2005, DiMichele et al., 2009 and Cleal, 2015). They continued to be important across the landscape there, into the Early Permian, and appeared in South China as well, during the Permian (Xiong and Wang, 2011).

Wetland plant communities had been greatly restricted to local, low-diversity patches, such as "wet spots" along permanent streams, in Euramerica at the beginning of the Permian (DiMichele et al., 2006, Tabor et al., 2013 and DiMichele, 2014), and were replaced spatially by conifers, cycads, and other seed plants later in the Permian (Cleal and Thomas, 2005 and DiMichele et al., 2009). The Permian leaf types of Euramerica were not well represented in previous studies because of the limited number of fossil localities and poor preservation. By contrast, wetland plant communities extended to the end of the Permian in South China, with the explosive diversification of pecopterids, gigantopterids, and equisetaleans.

4.1.3. Pennsylvanian preservational bias

Unlike in the Pennsylvanian of Euramerica (DiMichele et al., 1992, DiMichele et al., 2009 and Hilton and Cleal, 2007), wetland plant communities went through a major loss in biodiversity throughout the

Pennsylvanian and early Permian in South China, caused by the widespread occurrences of carbonate platforms and the paucity of floodplain environments (Fig. S1D; Li et al., 1995, Wu, 1995 and Hilton and Cleal, 2007). For this reason, only 15 species of compound leaves and no simple leaves were sampled in this study from the Pennsylvanian of South China. However, this reduction of taxic diversity of compound leaves had little effect on leaf disparity. Wetland plant communities began to recover in South China after the Late Cisuralian–Early Guadalupian (Li et al., 1995 and Hilton and Cleal, 2007), with a dramatic floristic replacement at the generic level. For simple leaves, the lack of a Pennsylvanian record urges caution in the interpretation of the apparent trend of increasing disparity from Mississippian to Permian.

4.1.4. Sampling bias

All paleodiversity studies face the issue of sampling bias, and this is particularly true for the terrestrial record (Knoll et al., 1979, Raymond and Metz, 1995, Wing and DiMichele, 1995, Benton, 2010, Cascales-Miñana et al., 2010, Cascales-Miñana et al., 2013 and Looy et al., 2014). The overwhelming majority of the leaf taxa sampled from South China represents plants within lowland floodplain communities of tropical climates (Fig. S1), and most lived in humid, peat-forming or non-peat forming wetland environments (Li et al., 1995 and Greb et al., 2006). Thus, our taxon sample is similar to the Paleozoic floristic assemblages analyzed in previous studies (Knoll et al., 1979, Niklas et al., 1980, Niklas, 1988, Boyce and Knoll, 2002 and Wang et al., 2010). Non-wetland taxa (possibly from upland communities) may have existed by the Late Devonian (Decombeix et al., 2011), and their occurrence has been confirmed in Carboniferous and Permian floras (Zhou, 1994, Falcon-Lang and Scott, 2000, Falcon-Lang and Bashforth, 2004 and DiMichele et al., 2009). However, their records are very patchy and insufficient to make a detailed study of their diversity pattern.

4.2. Role of CO_2 in shaping early leaf evolution

Beerling et al. (2001) highlighted the roles of atmospheric CO_2 in shaping early leaf evolution. Their working hypothesis was based on the observation that the stomatal density of tracheophytes showed a remarkable 100-fold increase, from 5–10 mm^{-2} on early plant axes to 800–1000 mm^{-2} on the cuticles of Late Carboniferous leaves (Beerling, 2005). This increase was linked to a major drop in atmospheric CO_2 levels in the late Paleozoic (Fig. 10D; Berner and Kothavala, 2001, Royer et al., 2004 and Berner, 2006). According to simulations, the rise in stomatal density in leaves may permit sufficient transpiration rates to cool leaf temperatures below the lethal range (Beerling et al., 2001). Thus, the development of photosynthetic structures with high stomatal densities, and correspondingly higher transpiration rates and higher cooling capacities, was suggested as an essential requirement for the evolution of laminate leaves. One prediction of Beerling et al.'s (2001) hypothesis is that the appearance of large laminate leaves was delayed by high atmospheric CO_2 levels. Only after such levels declined did large leaves gradually appear (Beerling et al., 2001 and Beerling, 2005). As a test of this scenario, Osborne et al. (2004) demonstrated a 25-fold increase of leaf lamina width, first in the Late Devonian progymnosperm *Archaeopteris* and later in the pteridosperms, based on morphometric analyses of fossil leaves from Europe. As shown in the present study, the timing of leaf trait

acquisition, including laminate blades, varies in different lineages as well as on different paleocontinents. However, large laminate leaves emerged in parallel in the sphenophyllaleans and progymnosperms from the Late Devonian onwards in South China, their leaf size being comparable to that of coeval progymnosperms from Europe (Osborne et al., 2004), possibly implying that independent lineages on different continents were subjected to the same size constraints. It is also worth considering that CO_2 levels may have driven the diversification of leaf shapes. The decline of atmospheric CO_2 level and the increase of leaf morphological diversity appear to be correlated (Fig. 10D). Thus, it would appear that the CO_2-related evolutionary hypothesis is consistent with the present findings. These suggest that, after atmospheric CO_2 levels had dropped by the end of the Devonian, leaf diversity increased dramatically, presumably because of the relaxation of thermodynamic constraints on leaf size.

It is worth noting, however, that different plant groups respond differently to decreasing CO_2 levels. We cannot assess Beerling et al.'s (2001) hypothesis directly with our material, because few fossil leaves from the Paleozoic preserve stomata (see also Edwards et al., 1998). Some recent studies have shown that the stomatal behaviors of extant ferns and seed plants have different metabolic control mechanisms, including responses to abscisic acid and epidermal cell turgor (Brodribb et al., 2009 and Brodribb and McAdam, 2011). Leaves of ferns and seed plants show additional differences in the relationship between leaf physiognomy and environmental factors, such as temperature (Peppe et al., 2014), so that different plant groups may need different models of biophysics and physiology.

4.3. Ecological scenario

Our results suggest an ecological scenario for the evolution of leaf morphologies and the tracheophytes as a whole. The data from the South China paleocontinent indicate that the initial expansion of tracheophytes – both in terms of taxic diversity and in terms of morphological disparity of both simple and compound leaves – went through two phases.

The first phase, from Early Devonian to Mississippian, witnessed plant invasion of largely empty ecospace with the appearance of new leaf morphologies, and the simultaneous increase in taxic diversity (Fig. 10B) (Niklas et al., 1980, Knoll et al., 1984, Niklas, 1988, Wang et al., 2010 and Xiong et al., 2013). This phase witnessed the rise and decline of the eophytic flora (e.g., Zosterophyllopsida, Trimerophytopsida, and early Lycopsida) in the Early–Middle Devonian and the expansion of the paleophytic flora in later times, with the introduction of heterospory among the spore producing plants, and of early gymnosperms (Wang et al., 2010 and Cleal and Cascales-Miñana, 2014). The disparity of simple leaves increased in the Late Devonian and that of compound leaves rapidly rose to a maximum level in the Mississippian. In tune with the increase of leaf disparity, other key changes in the tracheophyte body plan include: the emergence of complex vascular systems and the origin of secondary xylem (Meyer-Berthaud et al., 1999, Hilton et al., 2003, Rowe and Speck, 2005, Wang et al., 2006, Decombeix et al., 2011, Gerrienne et al., 2011 and Wang and Liu, 2015); the differentiation of plant architectures, with the appearance of shrubs, lianas, groundcovers, and trees of various sizes (Fig. 10C) (Mosbrugger, 1990, Bateman et al., 1998, Dilcher et al., 2004, Xue and Hao, 2008, Stein et

al., 2012 and Naugolnykh and Jin, 2014); the widespread occurrence of heterospory and the origin of seeds (DiMichele and Bateman, 1996 and Wang et al., 2014a). Peat-forming wetland communities became widespread in South China by the middle Mississippian (Visean) (Wu, 1995). Experiments with various arrangements of tissue types, in an ecologically undersaturated and low-competition landscape, resulted in the establishment of major body plans of euphyllophytes (Bateman et al., 1998).

The Carboniferous–Permian transition witnessed the second phase of leaf morphological evolution in South China. The percentage of genera of simple and compound leaves shared between the Carboniferous and Permian time bins ranges from 5.1–15.7%, indicating a great change in floristic composition, although the picture may be blurred by the paucity of Pennsylvanian records. In the Cisuralian–Guadalupian, there was a new, additional expansion in morphospace occupation by simple leaves, and an offset shift in the regions of morphospace occupied by compound leaves, a pattern that lasted until the Lopingian. This phase also saw an increase in taxic diversity from the early Permian onwards (Fig. 10B), apparently matching the recovery of wetland communities in South China, with abundant occurrences of gigantopterids, equisetaleans, and pecopterids (Li et al., 1995, Glasspool et al., 2004a, Glasspool et al., 2004b, Yao and Liu, 2004 and Xiong and Wang, 2011). However, these processes are complex when considered from a taphonomic perspective. Perhaps, the changes of leaf morphologies would have happened earlier but outside the "window of preservation" (sensu Looy et al., 2014), such as in upland or dryland environments of the same area. Large-scale migrations of wetland communities from Euramerica to Cathaysia during the late Pennsylvanian have been postulated (e.g., Hilton and Cleal, 2007). Some leaf morphologies are shared by Carboniferous and Permian taxa, suggesting a certain degree of conservatism across different plant groups.

The approximately twofold increase of taxic diversity in the Lopingian had little effect on disparity. The decoupling of leaf disparity and diversity further corroborates an ecologically driven model of tracheophyte evolution. Slight shifts in morphospace occupation in the Lopingian attest to continued morphological evolution, but by this time tracheophytes had specialized and diversified within existing leaf morphospace. It is more likely that the increasingly established ecological structures, particularly within wetland communities where ecological roles of each plant group are better defined (DiMichele et al., 1992 and DiMichele et al., 2005), made it more difficult for large increases in disparity to occur (cf.Ciampaglio, 2002). It is also possible that the range of gross morphologies of leaf forms increased and reached a maximum level, with constraints of increasing canalization of leaf development, as suggested byBoyce and Knoll (2002) and Boyce (2005a) in the case of the marginal and diffuse growth mode of the leaf lamina.

5. Summary

(1)

> The study of leaf evolution in Paleozoic tracheophytes from South China reveals a more complicated pattern than that retrieved in North America and Europe. Morphospace

occupation of simple leaves follows a stepwise trajectory, with a modest expansion in the Devonian followed by a dramatic expansion in the Permian. The expansion of compound leaf morphospace occurred rapidly from Late Devonian to Mississippian, with an offset shift in an otherwise similar amount of morphospace occupation during the Permian.

(2)

The evolution of leaf morphology in South Chinese Paleozoic tracheophytes shows several unique features. The radiation of sphenophyllaleans in South China during the Late Devonian contributed significantly to the expansion of leaf morphospace at that time, and these taxa developed large laminate leaves much earlier than in Euramerica. The Pennsylvanian loss of taxonomic richness in South China had little effect on the disparity of compound leaves. Most of the morphospace regions occupied by Carboniferous leaves were shared by Permian taxa, but Carboniferous and Permian leaves differ in many respects. The morphological separation of plant groups is particularly striking in the case of Permian pecopterids, gigantopterids, and equisetaleans.

(3)

Two major phases of leaf evolution are recognized in the Paleozoic of South China, and an ecological scenario for the evolution of leaves and the tracheophytes as a whole is proposed. In the first phase, morphological disparity of leaves increased progressively from Devonian to Mississippian, in parallel with an increase in taxic diversity. The Carboniferous–Permian transition witnessed the second phase of leaf evolution. New, additional expansion of morphologies of simple leaves, and an offset shift in the morphologies of compound leaves, occurred in the Cisuralian–Guadalupian. Slight shifts in morphospace in the Lopingian attest to continued morphological evolution, but during this time tracheophytes specialized and diversified, with ca. twofold increase of taxic diversity, within existing leaf morphospace.

Acknowledgments

Appendix A. Supplementary data

Supplementary material 1: Leaf characters, supplementary figures, tables, and dataset S1.

Supplementary material 2: Dataset S2.xls.

Supplementary material 3: Dataset S3.xls.

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