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Stepwise evolution of Paleozoic tracheophytes from South China: Contrasting leaf disparity and taxic diversity

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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.

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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; 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; 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; 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; 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, 2012; Meyer-Berthaud et al., 2010; Decombeix et al., 2011; Cleal and Cascales-Miñana, 2014; Wang et al., 2015), and highly diversified floristic communities were in place by the end of the Paleozoic (DiMichele et al., 1992, 2005; Bateman et al., 1998).

The earliest documented tracheophytes had no leaves (Edwards et al., 1992; 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; 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; 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; Peppe et al., 2011).

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; 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,b) 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; Xiong et al., 2013). South China was an important center of radiation and dispersal for Paleozoic tracheophytes (Hao and Xue, 2013a; 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; 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; 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; Xiong et al., 2013) and have been documented extensively in recent compendia (Xiong and Wang, 2011; 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,b). Compared to other parts of the tracheophyte body, leaves are very common in the fossil