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Tracing the Evolution of Plant Diversity in Southwestern China

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Biodiversity hotspots are key regions for understanding the evolutionary history of biodiversity as well as the processes initiating and maintaining it [1,2]. As a biodiversity hotspot, southwestern China is known worldwide for its modern taxonomic richness with numerous endemic and relic plants [3–5]. However, it is still unclear how this high regional plant diversity evolved, largely due to a lack of well-dated fossil evidence. Southwestern China is rich in Cenozoic sedimentary basins, preserving numerous fossil floras [6], and recent paleobotanical progress on these floras sheds new light on this topic.

One of the most important questions on the evolution of plant diversification concerns when modern plant diversity first appeared and, specifically, the pinpointing of the earliest occurrence of a flora that is floristically comparable to present vegetation in the same region. Until recently, it was thought that many taxa in southwestern China originated during the Miocene, evidenced by molecular analyses using fossil records for calibration [7]. Previously, most fossil floras in southwestern China were dated using stratigraphic or floristic comparison [8], which were limited by their low resolution and reasoning circularity. Recently, radiometric dating of volcanic ash materials from the plant-fossil-bearing deposits have substantially revised the ages of some important Cenozoic plant fossil-bearing basins in southwestern China, e.g., Jianchuan Basin [9], Lühe Basin [10], Mangkang Basin [11], and Wenshan Basin [12]. The Lühe flora from central Yunnan Province is dominated by Fagaceae and Betulaceae, and has long been considered to be late Miocene in age. However, recent U-Pb and ⁴⁰Ar/³⁹Ar radiometric dating of tuff layers in the fossil-bearing outcrops indicates an age of ~32 Ma for the flora [10]. Even though some taxa in this flora, such as *Sequoia* and *Metasequoia*, have disappeared from southwestern China, most taxa still survive there, e.g., *Betula*, *Cryptomeria*, *Dipteronia*, *Fraxinus*, *Quercus*, and *Tsuga* [10,13,14]. Besides, the Kajun flora in Mangkang Basin, eastern Xizang and Wenshan flora in southeastern Yunnan also show high floristic similarity to modern vegetation in southwestern China [11,12]. The ages of both these floras were previously thought to be late Miocene [8,15], but radiometric dating has now confirmed these two floras to be 34.6–33.4 Ma and 33 Ma, respectively [11,12]. It seems that regional tectonics near the end of the Eocene created many of the fossil-bearing basins in southwestern China.

The floras mentioned above are floristically different from older floras in southwestern China. For example, the middle Eocene (~47 Ma by U-Pb dating) Jianglang flora in the central Qinghai-Tibetan Plateau bears around 70 morphotypes and some important components in modern vegetation of southwestern China, such as Fagaceae and Betulaceae, are absent from the current collection of more than 2000 fossil specimens. Several extinct taxa, such as *Cedrelospermum*, *Lagokarpos*, and *Limnobiophyllum*, occurred in the flora [16]. The middle Eocene Relu flora in western Sichuan Province is characterized by *Comptonia*,

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Hemiptelea, Myrtaceae, and *Palibinia* [17], which are quite different from those in the modern regional flora. Therefore, the modernization of plant diversity in southwestern China should have been taking place in the late Eocene to early Oligocene.

Both climate and topography may be major factors stimulating the modernization of the flora. Current evidence suggests that there was a prolonged regional dry climate during the early and middle Eocene, and the transition from an arid to a humid climate occurred before the Eocene–Oligocene transition (between 45 and 42 Ma), associated with the rise of eastern Tibet to near present elevations and the reorganization of the monsoon system [18]. Currently, the prevailing monsoon climate of southwestern China is characterized by wet summers and dry winters [19], but the humid climate during the late Eocene did not necessarily represent the establishment of modern monsoonal climate. Modelling [20] and leaf-form analysis [11,16] suggest wet winters and dry summers in some parts of the region during the Eocene, and we know that winters and early springs have become drier since the Miocene, with inevitable impacts on plant diversity. Some genera such as *Cedrus*, *Metasequoia*, and *Sequoia* cannot survive under the modern monsoonal climate due to the poor drought resistance of young shoots [21–23], whereas many other genera, e.g., *Betula*, *Elaeagnus*, *Quercus*, *Rosa*, and *Ulmus* have thrived and diversified since then. Diversification within the region is complex and linked to interplay between orography and climate [24].

The topography is another important factor in shaping the modernization of plant diversity. The landscape of southwestern China was mainly established before the Neogene. Phytopaleoaltimetric reconstruction of the Mangkang basin suggests an uplift of ~900 m during the latest Eocene (~34.6 Ma) to the earliest Oligocene (~33.4 Ma) when it achieved its present elevation of 3900 m [10]. Another work in Gongjue Basin with carbonate clumped isotope thermometry suggested an even earlier elevational change from 700 m in the early Eocene to 3800 m in the middle Eocene [18]. All these rises were closely associated with the clockwise rotation and extrusion of Indochina in southeastern Qinghai-Tibetan Plateau initiated as early as the late Paleogene [25].

Generally, both tectonism and the development/fluctuations in monsoonal climate have played important roles in shaping modern plant diversity in southwestern China, but much is still unclear about how the modernization of plant diversity in southwestern China took place, as well as its underlying driving mechanisms. In the future, paleobotanical studies in Paleogene sediments within a high resolution absolute chronostratigraphic framework are needed to establish the sequence and spatial patterns of floristic change. By combining paleoclimate signals derived from fossil evidence, computed tomography (CT) analysis of undisturbed sedimentary core samples, and geochemical analyses and modelling, as well as past landscape reconstructions, the evolutionary history of modern plant diversity can be better understood in this globally important biodiversity center and provide critical processes for bringing together fossil and molecular phylogenetic data.

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