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A new species of *Exbucklandia* (Hamamelidaceae) from the Pliocene of China and its paleoclimatic significance

Jingyu Wu [a,b], Bainian Sun [a,b,*], Yu-Sheng(Christopher) Liu [c], Sanping Xie [a], Zhicheng Lin [a]

[a] Key Laboratory of Western China's Environmental Systems of the Ministry of Education, Lanzhou University, Lanzhou 730000, China
[b] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Paleontology, Nanjing 210008, China
[c] Don Sundquist Center of Excellence in Paleontology, Department of Biological Sciences, East Tennessee State University, Box 70703, Johnson City, Tennessee 37614-1710, USA

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ABSTRACT

Eight fossil leaves identified as *Exbucklandia tengchongensis* sp. nov. (Hamamelidaceae) were collected from the Pliocene Mangbang Formation in Tengchong, Yunnan Province, Southwest China. The fossil leaves are characterized by the overall rounded lamina with entire margin, actinodromous venation, and cyclocytic stomata, which suggest the affinity within the genus *Exbucklandia*, particularly with *E. populnea*. A survey on the cuticles of the sun and shade leaves of modern *E. populnea* indicates that the shade leaves generally possess more pronounced undulate anticlinal cell walls and a much lower stomatal density than the sun leaves. Two morphotypes, i.e. sun vs. shade types, of the fossil leaves were therefore recognized. The distribution of the modern *Exbucklandia* suggests that the genus lives under a warm climate with a mean annual temperature (MAT) from 13 °C to 27 °C and a mean annual precipitation (MAP) from 800 mm to 2500 mm. Hence, *E. tengchongensis* might also live under a similar climatic condition in the Pliocene. Leaf margin analysis on the Tengchong flora supports this result. The little change of Neogene MAT in Southwest China is therefore supported.

1. Introduction

Exbucklandia is one of the 31 genera in the Hamamelidaceae. It today includes four species of evergreen trees, which are restricted to forests and ravines of South and Southeast Asia (Mabberley, 1985; Zhang et al., 2003). The trees of *Exbucklandia* grow naturally in a range from 500 m to 2000 m above sea level (Zhang and Lu, 1995). Recent molecular phylogeny of Hamamelidaceae supports that *Exbucklandia* is one of the primitive genera in this family (Li et al., 1999a,b; Qiu et al., 1998; Ickert-Bond and Wen, 2006). The fossils of *Exbucklandia* have been found in several places where many are out of the current distribution range of the genus, such as Northwest USA and Northwest China (Fig. 1). For example, these fossils include the leaves of *E. microdictya* from the Paleocene of Altai, Xinjiang, Northwest China (Guo et al., 1984), *E. oregonensis* from the Oligocene of Oregon, Northwest USA (Lakhanpal, 1958; Meyer, 1973), *E. miocenica* from the Miocene of Xiaolongtan, Yunnan, Southwest China (Tao et al., 2000), and *Exbucklandia* sp. of the late Middle Miocene of Idaho, Northwest USA (Baghai and Jorstad, 1995). Furthermore, infructescences of *Exbucklandia* have also been reported from the Miocene of Idaho and Washington, northwest USA (Brown, 1946; Lakhanpal, 1958; Manchester, 1999; Pigg and Wehr, 2002). The origin of similar distribution pattern in other seed plants has been extensively discussed by Manchester (1999) and Manchester et al. (2009).

Previous studies have shown that both fossil and modern leaf morphological features like size and shape of leaves and their cuticular structures such as cuticular thickness, stomatal size and density are variable due to insolation conditions (Kvacek and Walther, 1978; Strauss-Debenetti and Berlyn, 1994; Barbacka and van Konijnenburg-van Cittert, 1998; Kürschner et al., 1996; Kürschner, 1997). In general, the shade leaves are usually larger than sun leaves. Anatomically, the cuticles of shade leaves are often thinner with a deeply undulate cell wall and both a lower stomatal density and index than those of sun leaves (Poole et al., 1996; Kürschner, 1997; Barbacka and van Konijnenburg-van Cittert, 1998).These criteria have been successfully used in the study of fossil leaves (e.g. Denk and Velitzelos, 2002). Furthermore, ultrastructure of cuticular characters was also utilized to differentiate fossil sun and shade leaves (Guignard et al., 2001).

Fossil occurrences of *Exbucklandia* are rare and none of the previously reported leaf remains included cuticular investigations. In the present study, eight fossil leaves from the Pliocene of China are identified as a new species *E. tengchongensis* sp. nov. Based on the cuticular differences, both sun and shade morphotypes are recognized

* Corresponding author. Key Laboratory of Western China's Environmental Systems of the Ministry of Education, Lanzhou University, Lanzhou 730000, China. Tel./fax: +86 931 8915280.
E-mail address: bnsun@lzu.edu.cn (B. Sun).

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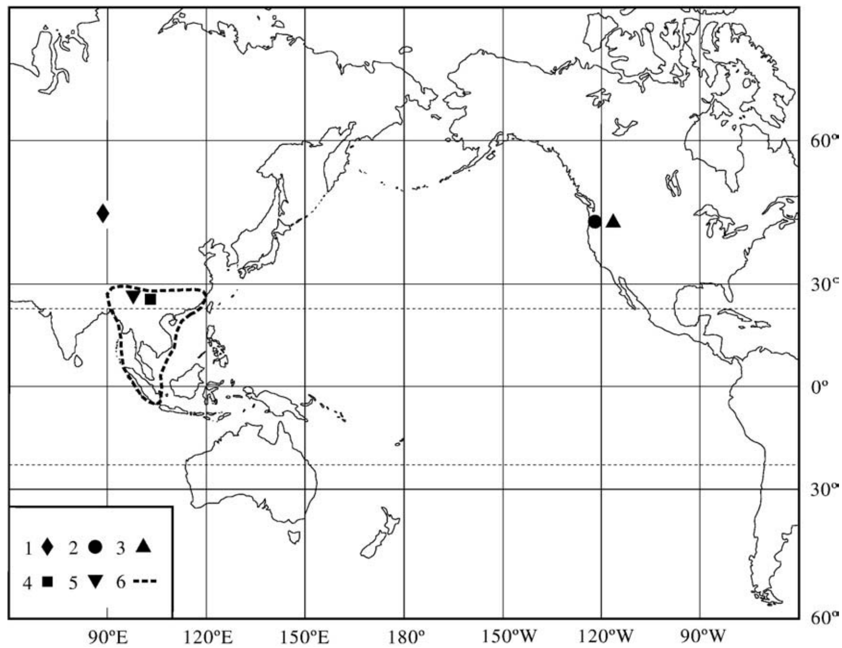

Fig. 1. Distribution map of fossils and modern plants of *Exbucklandia*. (1). Paleocene of Xinjiang, China. (2). Oligocene of Oregon, USA. (3). Miocene of Washington and Idaho, USA. (4). Miocene of Yunnan, China. (5). Pliocene of Yunnan, China (the present study). (6). Modern distribution region.

and confirmed by the comparative study of the sun and shade leaves of modern *E. populnea*.

2. Materials and methods

2.1. Fossil materials and preparation

The fossil leaves were collected from an open-cast diatomite mine about 1 km west of Tuantian town (24° 41′ N, 98° 38′ E), Tengchong County, Yunnan Province, Southwest China (Fig. 1). The fossil-bearing horizons occur in the diatomitic sediments of the Mangbang Formation. The Formation has been divided into three lithologic sections, which are in ascending order the lower unit consisting mainly of conglomerates and glutenites, the middle unit with basalts and the upper unit having siltstones, mudstones, claystones and diatomites, from where the fossil leaves were uncovered (Ge and Li, 1999; Shang, 2003). Based on K–Ar dating of the middle unit basaltic rocks of the Mangbang Formation and overlying Mingguang Formation andesitic rocks, the upper fossil-bearing unit studied here is considered to be late Pliocene (2.3–3.3 Ma) (Mu et al., 1987; Jiang, 1998; Guo and Lin, 1999; Li et al., 2000).

Carbonized leaf fragments were sampled from the middle part of leaf specimens, immersed in 10% HCl solution for 10 h to remove calcium carbonate, washed and then immersed in 50% HF solution for 24–48 h. After washing in dilute water, the samples were oxidized in 30% HNO_3 solution for 8–10 h. When the black color was changed to dark or light brown, the samples were removed and then neutralized by 5% NH_4OH for 10 min. The lower and upper cuticles were then separated through manipulation of a dissecting needle under a stereomicroscope. After staining in a 0.5% Safranine solution, the cuticles were mounted on slides, embedded in glycerine jelly and photographed under a light microscope (Leica DM4000B) at Lanzhou University. For SEM, cuticles were mounted on a stub and coated with the gold, examined under the scanning electron microscopy (JEOL JSM-5600LV) at the Lanzhou Institute of Chemical Physics, Chinese Academy of Sciences.

All specimens and cuticle slides are housed in the Institute of Paleontology and Stratigraphy, Lanzhou University, China.

2.2. Modern materials and preparation

The modern fresh leaves of *E. populnea*, mostly close to the fossil species, were chosen for a close comparison and differentiation of eco-morphotypes. They were collected from Kunming Arboretum, Yunnan Province, China. The leaves were cut into 1 × 1 cm and boiled for 5–10 min, then immersed into1:1 solution of glacial acetic acid and 30% H_2O_2, which was water bathed at 70 °C for 8–10 h. The epidermal and mesophyll cells were separated when the leaves became white. After neutralization, both the lower and upper epidermis can then be separated. The same procedures as those for fossil leaves were followed for both LM and SEM preparations.

2.3. Measurement and statistics

The area and the circumference of randomly selected epidermal cells were measured with an image analyzer (Leica QWin V3). Totally 29 cuticles from 12 modem leaves, and 80 cuticles from all 8 fossil specimens uncovered were measured.

The stomatal index was calculated using the following equation (Salisbury, 1927):

$$SI = \frac{sd}{sd + ed} \times 100 \tag{1}$$

where SI (%) represents the stomatal index, sd the stomatal number per unit leaf area and ed the epidermal cell density per unit leaf area.

In order to evaluate quantitatively the undulated degree of anticlinal walls of epidermal cells of sun and shade leaves, the undulation index (UI) is cited after Kürschner (1997) as follows:

$$UI = \frac{C_e}{C_o} = \frac{C_e}{2 \times \pi \times \sqrt{\frac{A_e}{\pi}}} \tag{2}$$

where UI (dimensionless) represents the undulation index, C_e (μm) the circumference of the cell, C_o (μm) the circumference of the circle with the same area as the cell, and A_e (μm^2) the area of the cell. The