



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

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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.

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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 *Ex-*

bucklandia 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

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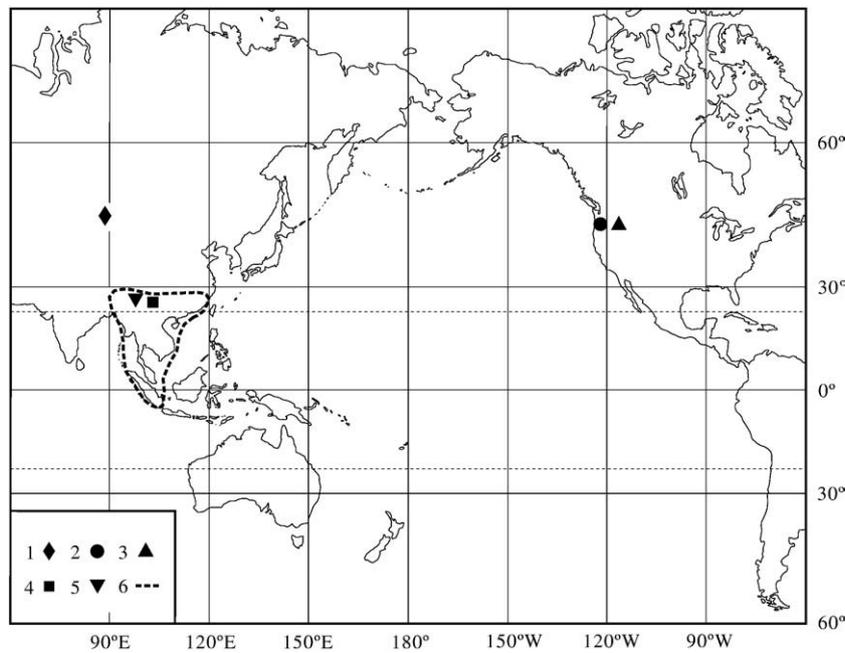


Fig. 1. Distribution map of fossils and modern plants of *Exbucklandia*. (1). Paleocene of Xinjiang, China. (2). Oligocene of Oregon, USA. (3). Miocene of Washington and Idaho, USA. (4). Miocene of Yunnan, China. (5). Pliocene of Yunnan, China (the present study). (6). Modern distribution region.

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% HNO₃ 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% NH₄OH 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% Safranin 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 ecomorphotypes. 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 into 1:1 solution of glacial acetic acid and 30% H₂O₂, 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 modern leaves, and 80 cuticles from all 8 fossil specimens uncovered were measured.

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

$$SI = \frac{sd}{sd + ed} \times 100 \quad (1)$$

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:

$$UI = \frac{C_e}{C_o} = \frac{C_e}{2 \times \pi \times \sqrt{\frac{A_e}{\pi}}} \quad (2)$$

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* (μm²) the area of the cell. The

undulation index is the ratio of the measured epidermal cell circumference and the circumference of a standard geometrical object, a circle with the same area as the cell.

Terminology on leaf architecture follows the Manual of Leaf Architecture (LAWG, 1999), while terms on foliar cuticle are after Wilkinson (1979).

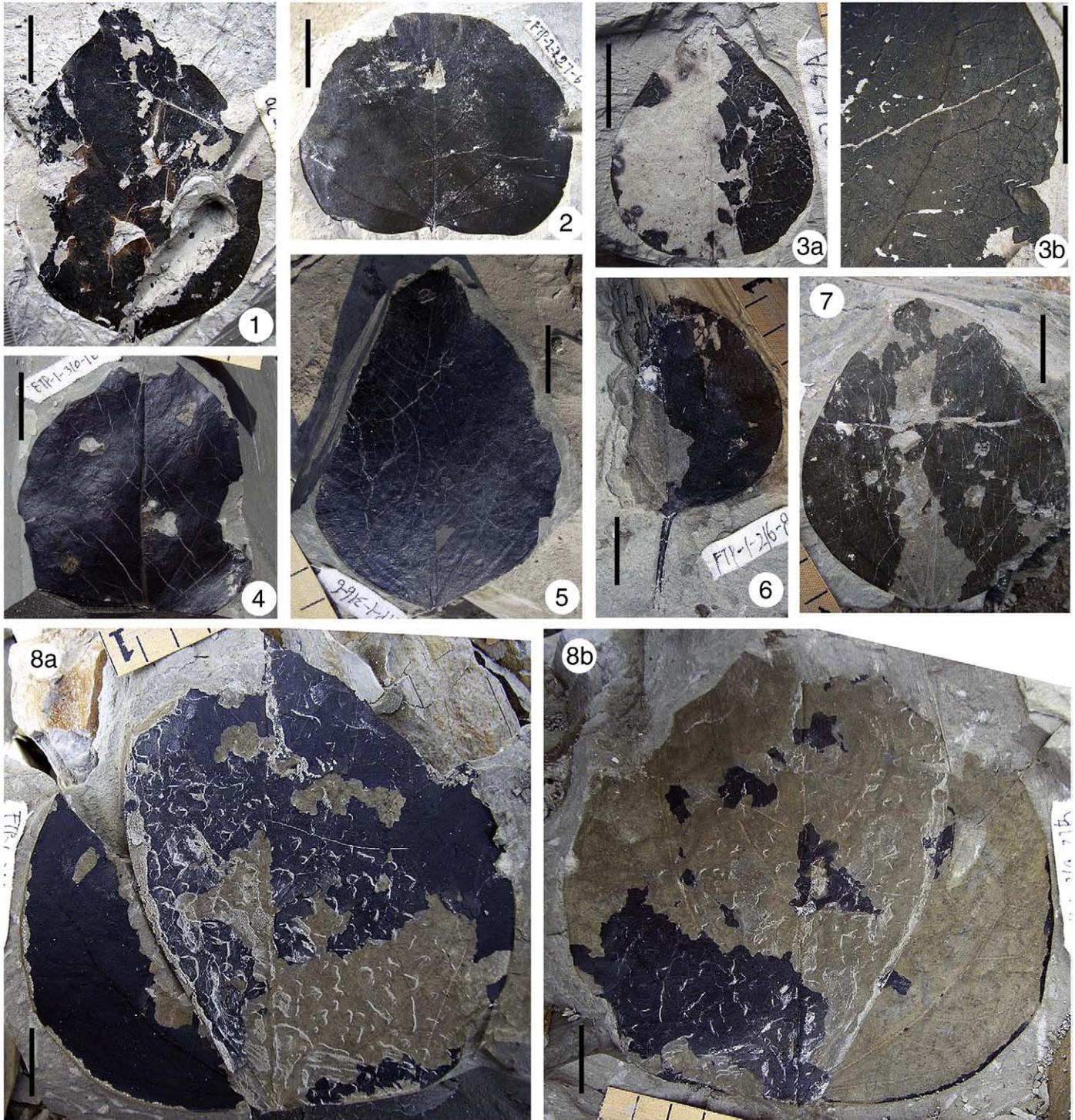


Plate I. Fossil leaves of *Exbucklandia tengchongensis*. Scale bar = 2 cm.

1. Specimen no. FTP-317-20.
2. Specimen no. FTP-227-6.
- 3a. Specimen no. FTP-221-9(A).
- 3b. Specimen no. FTP-221-9(B), showing secondary veins near the leaf margin.
4. Specimen no. FTP-310-16.
5. Specimen no. FTP-316-6.
6. Specimen no. FTP-216-8.
7. Specimen no. FTP-304-7.
- 8a. Specimen no. FTP-219-22 (A).
- 8b. Specimen no. FTP-219-22 (B).

3. Results

3.1. Systematic description

Order: Hamamelidales Griseb.
 Family: Hamamelidaceae R. Brown
 Genus: *Exbucklandia* R. W. Brown

Species: *Exbucklandia tengchongensis* J.Y. Wu et B.N. Sun, sp. nov. (Plate I, 1–8; Plate II, 4; Plate III, 1–4; Plate IV, 1–3, 7–10).
Specific diagnosis: Lamina rounded to broadly ovate-rounded; apex obtuse; base slightly cordate to rounded; length 5.8–14.5 cm, width 4.8–14.9 cm, length–width ratios 0.75–1.38; petiole length 2.9 cm, width 0.2 cm; margin entire; venation basal actinodromous with 5(3)–7 primary veins; secondaries brochidodromous;

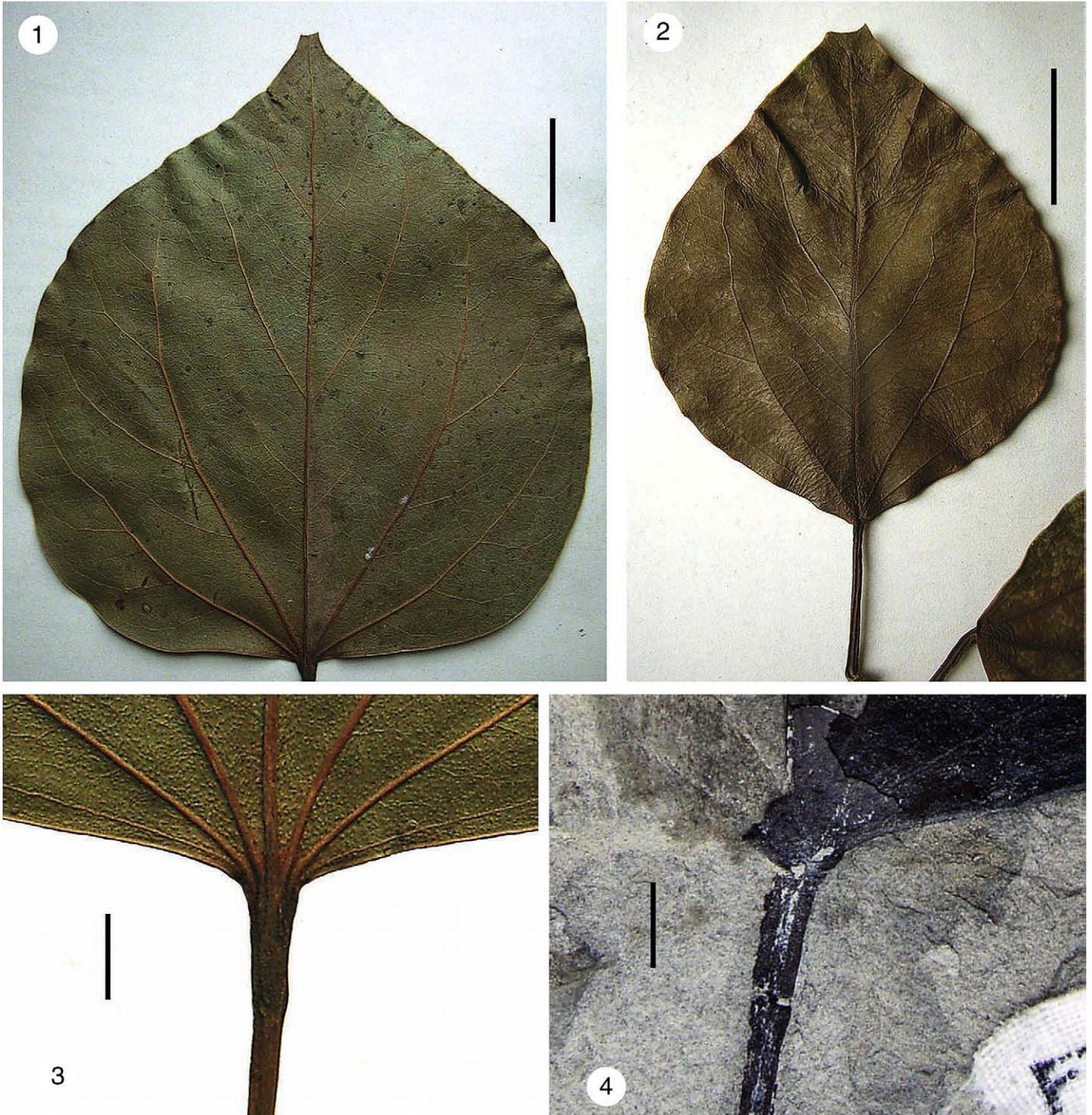


Plate II.

- 1, 2. Modern leaves of *Exbucklandia populnea* for comparison with the fossil leaves. Scale bar = 2 cm.
- 3, 4. Details of the leaf base and petiole, note 5–7 main veins arising from the base. Scale bar = 5 mm.
- 3. Modern leaf of *Exbucklandia populnea*.
- 4. Fossil leaf of *Exbucklandia tengchongensis*, specimen no. FTP-216-8.

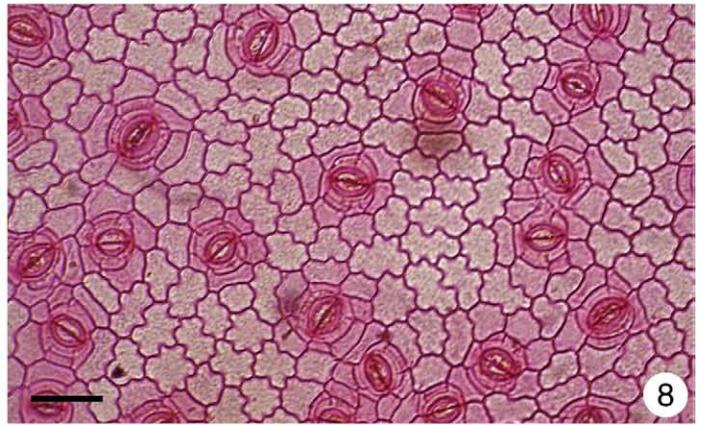
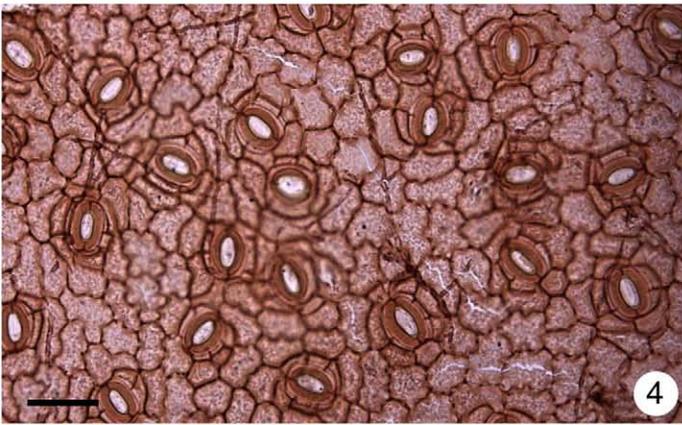
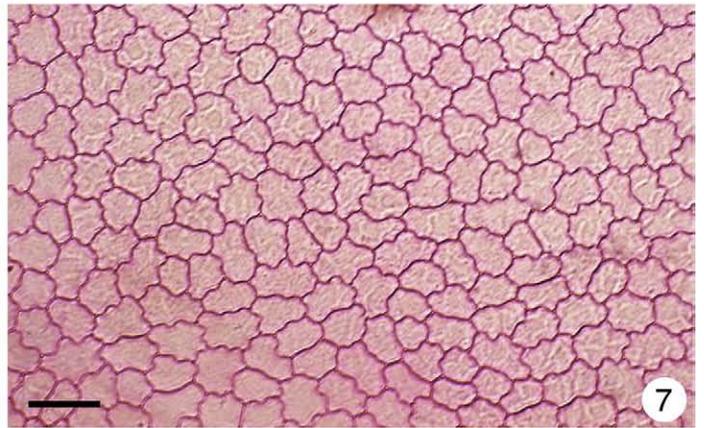
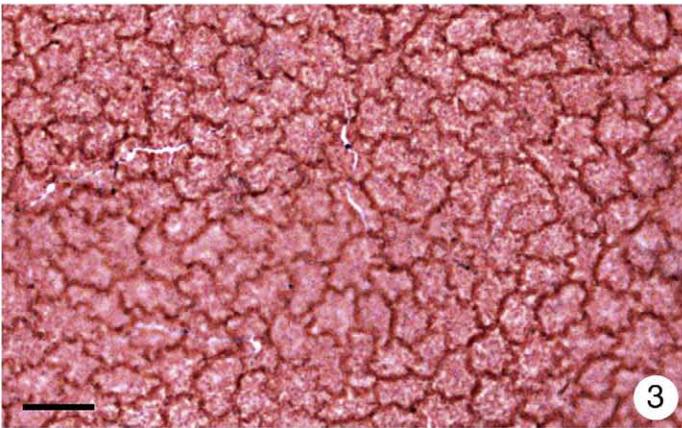
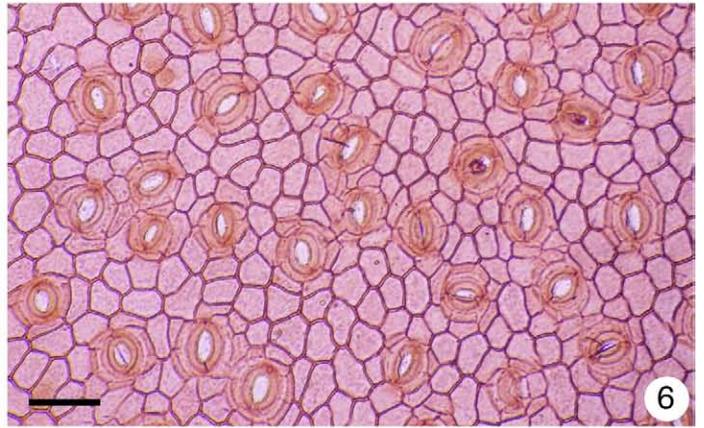
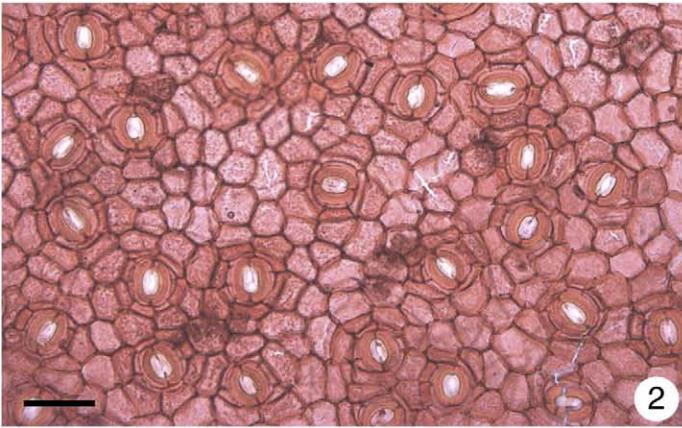
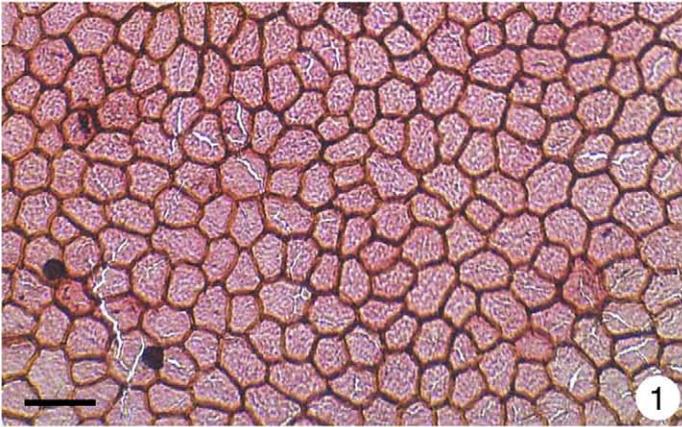


Plate III (caption on page 38).

marginal ultimate venation fimbrial. Adaxial cuticle thick, epidermal cells variable in size, mostly pentagonal, straight or undulated anticlines, periclinal smooth; abaxial cuticle thick but slightly thinner than adaxial cuticle, epidermal cells irregular, slightly

domed or flat, anticlines straight or undulated, stomata randomly orientated and cyclocytic, rounded or elliptical, with guard cells slightly sunk encircled by 5–6 distinctly protuberant subsidiary cells.

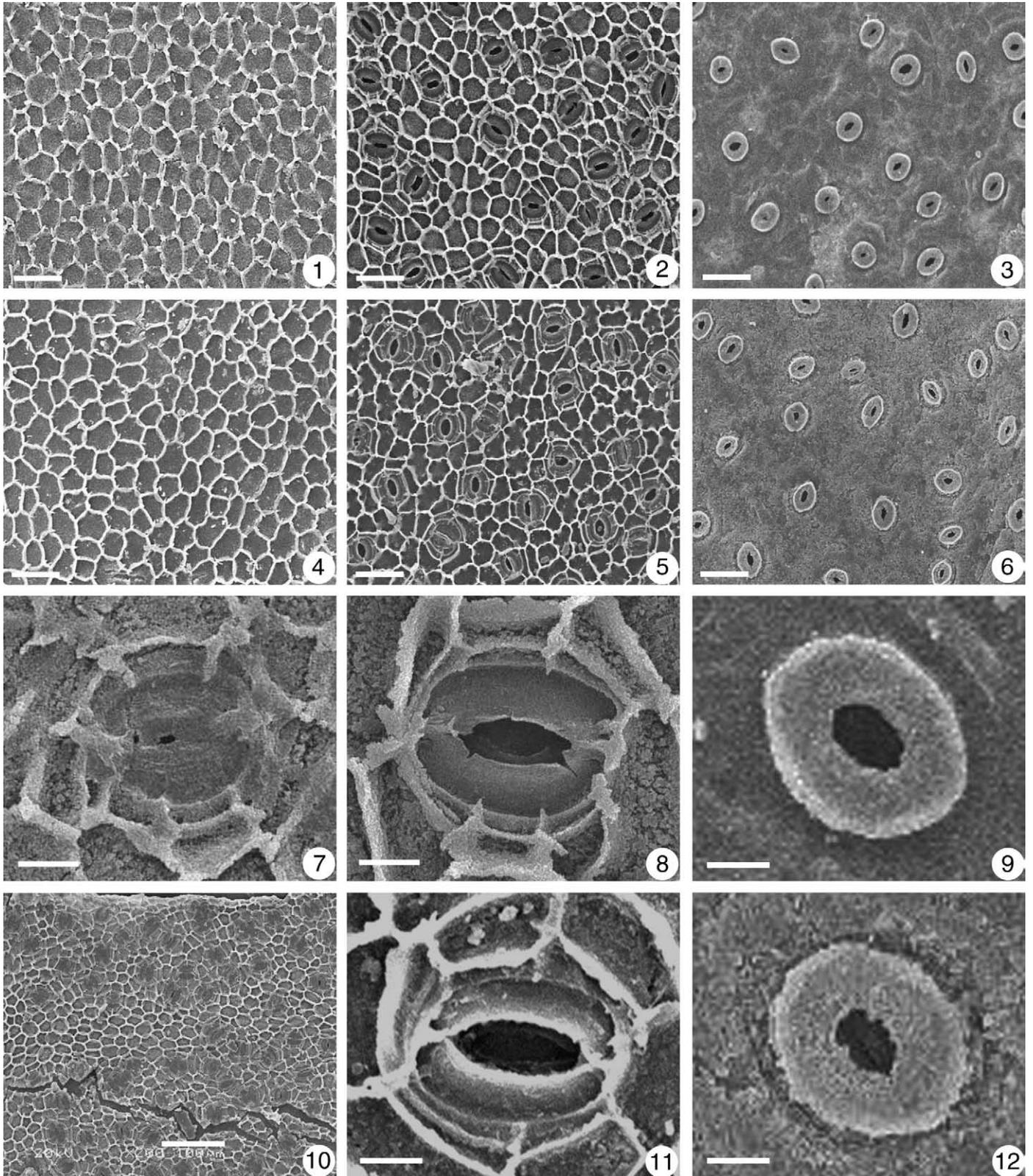


Plate IV (caption on page 38).

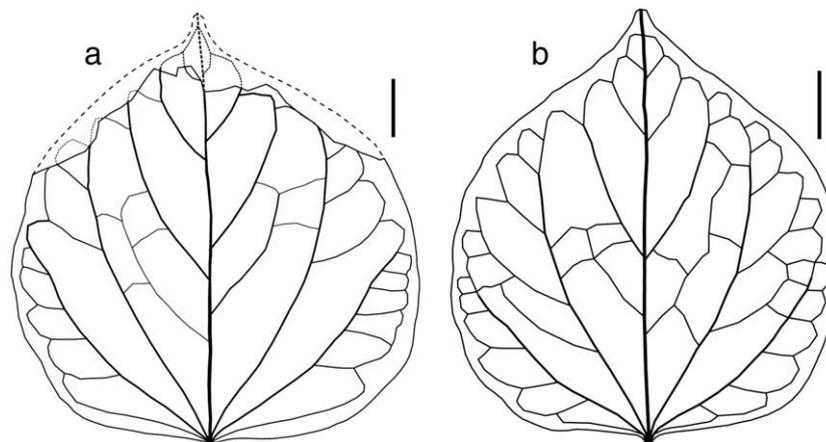


Fig. 2. Line drawing of leaf architecture of fossil and modern leaves, showing palmately veins, fimbrial veins and brochidromous secondary veins. Scale bar = 2 cm. a. Fossil leaf (see Plate I, 8b). b. Modern leaf of *Exbucklandia populnea* (see Plate II, 1).

Etymology: The epithet *tengchongensis* refers to the county where the specimens were collected.

Holotype designated here: FTP-219-22 (A, B) (Plate I, 8a, 8b; Plate III, 3, 4; Plate IV, 9).

Paratypes designated here: FTP-317-20 (Plate I, 1), FTP-227-6 (Plate I, 2; Plate III, 1, 2; Plate IV, 2, 8), FTP-221-9 (A, B) (Plate I, 3a, 3b; Plate IV, 1, 3, 7, 10), FTP-310-16 (Plate I, 4), FTP-316-6 (Plate I, 5), FTP-216-8 (Plate I, 6; Plate II, 4), FTP-304-7 (Plate I, 7).

Type locality: Tuantian town open-cast diatomite mine, Tengchong County, Yunnan Province, China (24° 41' N, 98° 38' E).

Stratigraphic position: Top member of the Mangbang Formation.

Age: Late Pliocene.

3.2. Description

3.2.1. Leaf morphology (Plate I; Plate II, 4; Fig. 2)

Lamina rounded to broadly ovate-rounded; apex obtuse; base slightly cordate to rounded; length 5.8–14.5 cm, width 4.8–14.9 cm;

petiole length 2.9 cm, width 0.2 cm; margin entire; venation basal actinodromous with 5(3)–7 primary veins, lateral primaries curved, inner pair extending more than three-fourths of the distance to the apex, second pair extending one-half of the distance to the apex, outermost pair shorter and much weaker; secondaries brochidromous, up to three pairs originating from midvein, arising abmedially from lateral primaries; tertiaries percurrent, less commonly reticulate, those between adjacent primary veins convex; intersecondaries occurring between midvein and inner pair of primaries; marginal ultimate venation fimbrial; higher order veins unclear.

3.2.2. Leaf cuticle (Plate III, 1–4; Plate IV, 1–3, 7–10)

Leaves hypostomatic; adaxial cuticle thick, epidermal cells variable in size, mostly pentagonal, 20–50 μm across with straight or undulated anticlines, periclinal smooth; abaxial cuticle thick while slightly thinner than adaxial cuticle, epidermal cells irregular, slightly domed or flat, anticlines straight or undulated, stomata randomly orientated and cyclocytic, 25–35 μm long and 20–30 μm wide,

Plate III. Cuticles of fossil and modern leaves. Under the light microscopy. Scale bar = 50 μm . (see plate on page 36)

- 1–4. Cuticles of *Exbucklandia tengchongensis*.
1. Upper epidermis of specimen no. FTP-227-6.
2. Lower epidermis of specimen no. FTP-227-6.
3. Upper epidermis of specimen no. FTP-219-22.
4. Lower epidermis of specimen no. FTP-219-22.
- 5–8. Cuticles of *Exbucklandia populnea*.
5. Upper epidermis of sun leaf.
6. Lower epidermis of sun leaf.
7. Upper epidermis of shade leaf.
8. Lower epidermis of shade leaf.

Plate IV. Cuticles of fossil *Exbucklandia tengchongensis* and modern *Exbucklandia populnea*. Under the SEM. (see plate on page 37)

- 1–6. scale bars = 50 μm . 7, 8, 9, 11, 12. scale bars = 10 μm . 10. Scale bars = 100 μm .
1. Upper epidermis of fossil leaf. Specimen no. FTP-221-9.
2. Lower epidermis of fossil leaf. Specimen no. FTP-227-6.
3. Lower epidermis of fossil leaf, outer surface. Specimen no. FTP-221-9.
4. Upper epidermis of modern leaf.
5. Lower epidermis of modern leaf.
6. Lower epidermis of modern leaf, outer surface.
7. Stomatal apparatus of fossil leaf. Specimen no. FTP-221-9.
8. Stomatal apparatus of fossil leaf. Specimen no. FTP-227-6.
9. Stomatal apparatus of fossil leaf, outer surface. Specimen no. FTP-219-22.
10. Lower epidermis of fossil leaf, showing the vein cells. Specimen no. FTP-221-9.
11. Stomatal apparatus of modern leaf.
12. Stomatal apparatus of modern leaf, outer side.

Table 1

Comparisons on the leaf architecture and cuticle of the fossil *Exbucklandia tengchongensis* with selected modern hamamelidaceous species, which resemble the fossil in leaf venation pattern.

Taxon	Leaf size (cm)	Leaf shape	Leaf base	Marginal ultimate venation	Pattern of anticlinal walls	Type of stomatal apparatus	References
<i>Exbucklandia tengchongensis</i>	5.8–14.5 × 4.8–14.9	Rounded, broadly ovate-rounded	Slightly cordate to rounded	Fimbriate	Straight or undulate	Cyclocytic	Present paper
<i>Exbucklandia populnea</i>	5.4–17.6 × 5.2–16.8	Rounded, broadly ovate-rounded	Cordate or occasionally broadly cuneate	Fimbriate	Straight or undulate	Cyclocytic	Present paper
<i>Exbucklandia tonkinensis</i>	8–12 × 6–10	Broadly ovate, sometimes 3-cuspidate	broadly cuneate	Fimbriate	Undulate	Cyclocytic	Pan et al., 1990; Zhang et al., 2003
<i>Exbucklandia longipetala</i>	8–13 × 5–9	Oblong-elliptic	Truncate	Fimbriate	undulate	Cyclocytic	Pan et al., 1990; Zhang et al., 2003
<i>Chunia bucklandioides</i>	10–15 × 8–14	Broadly ovate-rounded	Subcordate or truncate	Incomplete and looped	Straight or arched	Paracytic	Pan et al., 1990; Zhang et al., 2003
<i>Disanthus cercidifolius</i>	6–10 × 5–9	Broadly ovate-rounded	Slightly to deeply cordate	Incomplete	Slightly undulate	Paracytic	Pan et al., 1990; Zhang et al., 2003
<i>Mytilaria laosensis</i>	10–13 × 7–10	Broadly ovate-rounded	Cordate	Looped	Straight or arched	Stephanocytic	Pan et al., 1990; Zhang et al., 2003

rounded or elliptical, with guard cells slightly sunken encircled by 5–6 distinctly protuberant subsidiary cells. No trichome in the adaxial and abaxial cuticle.

3.3. Comparison

3.3.1. Recent species

The fossil leaves in the present study all share the leaf architectural characters, such as 5–7 actinodromous primary veins, 4–6 pairs of brochidromous secondary veins, obtuse apex, cordate base, entire margin and fimbrial marginal ultimate venation, which are common for several genera in the Hamamelidaceae (Wolfe, 1973, 1989; WGCP, 1978; Li and Hickey, 1988). Hamamelidaceous genera, such as *Exbucklandia*, *Chunia* and *Mytilaria* of the subfamily Exbucklandioideae (Endress, 1989a) and *Disanthus* of the subfamily Disanthoideae (Endress, 1989b), have leaves with similar leaf venation pattern and sometimes can be difficult to be separated (Wolfe, 1973, 1989; Li and Hickey, 1988). Fortunately, their cuticle structures are quite different. Within this family, the cyclocytic stomata are exclusively found in *Exbucklandia* and *Rhodoleia* of the subfamily Rhodoleioideae (Pan et al., 1990), while the stomatal type in the genera *Chunia* and *Disanthus* is paracytic type and the stephanocytic type in *Mytilaria* (Pan et al., 1990). A comparison in leaf architecture and cuticle is made between the current fossil and the related modern species in the Hamamelidaceae (Table 1). It is clear that the combination of leaf architectural and cuticular features warrants the classification of the

fossil leaves to *Exbucklandia*. Moreover, because of similar lamina size, the fossil species matches the modern *E. populnea* the most.

3.3.2. Previously fossil species

A fossil leaf of *E. oregonensis* from the Middle Oligocene of Oregon was reported by Lakhanpal (1958) and Meyer (1973). This fossil is similar to the modern *Exbucklandia* on the lamina shape and size, but it possesses primary three main veins (Meyer, 1973), which differentiate to the five primary veins of the present fossils. Baghai and Jorstad (1995) also reported a species from the Middle Miocene of Idaho, *Exbucklandia* sp. This fossil is different from the present fossil species in that the former has a distinct and much smaller, ovate lamina.

The Paleocene *E. microdictya* from Altai of China and the Miocene *E. miocenica* from Xiaolongtan of China both possess generic leaf architecture characters such as broadly ovate-rounded shape, 5 actinodromous primaries and brochidromous secondary veins. However, the leaves of both fossil species are much smaller than those of the present fossil. *E. microdictya* is about 5.4 cm long by

Table 2

Comparison of leaf size and cuticular differences in *Exbucklandia tengchongensis* and *E. populnea* presented as mean values ± St. Dev. UI = the undulation index; SD = the stomatal density; SI = the stomatal index; n = the number of cuticles.

Sample	Length × width (cm)	UI	SD (n/mm ²)	SI (%)	n
Fossil leaves					
FTP-317-20	11.2 × 8.5	1.19 ± 0.06	250 ± 8	8.2 ± 0.4	14
FTP-227-6	6.1 × 8.1	1.16 ± 0.03	219 ± 14	8.4 ± 0.5	11
FTP-221-9	5.8 × 4.8	1.22 ± 0.04	218 ± 11	8.4 ± 0.7	15
FTP-310-16	7.6 × 7.2	1.16 ± 0.04	221 ± 8	8.6 ± 0.6	8
FTP-316-6	9.9 × 7.2	1.17 ± 0.04	217 ± 10	8.3 ± 0.7	8
FTP-216-8	6.4 × 6.9	1.14 ± 0.05	208 ± 12	7.9 ± 0.5	8
FTP-304-7	8.4 × 7.2	1.17 ± 0.05	231 ± 11	8.3 ± 0.4	10
FTP-219-22	14.5 × 14.9	1.32 ± 0.03	168 ± 7	7.5 ± 0.4	16
Modern leaves					
Sun	5.4–12.8 × 5.2–11.7	1.16 ± 0.04	220 ± 9	8.8 ± 0.6	14
Shade	9.7–17.6 × 8.9–16.8	1.29 ± 0.05	162 ± 11	8.0 ± 0.4	15

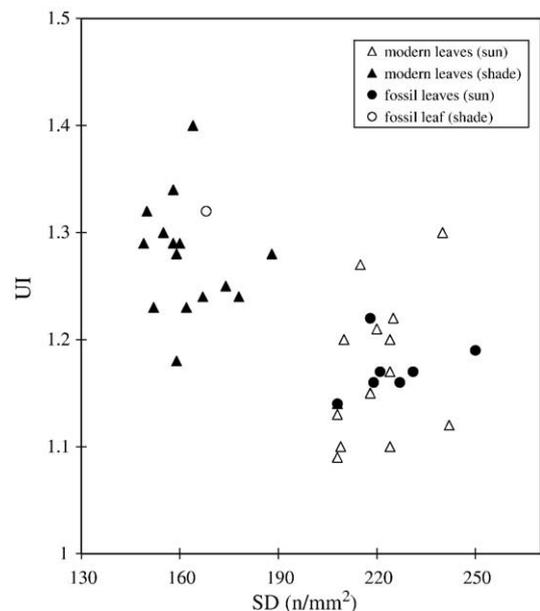


Fig. 3. Epidermal cell undulation index (UI) vs. stomatal density (SD) of the sun and shade leaves of the modern *Exbucklandia populnea* and fossil *Exbucklandia tengchongensis*; values are means.

3.4 cm wide (Guo et al., 1984), and *E. miocenica* is only 3 cm long by 2.5 cm wide (Tao et al., 2000). As none of these fossil species preserves cuticles, a further comparison appears to be limited.

Based on the comparison of leaf architecture and foliar cuticles between the present fossil from Yunnan and those of modern hamamelidaceous plants and previously published fossils, it is concluded that due to the unique combination of leaf architectural characters and foliar cuticular features the present fossil represents a new species.

4. Discussion

4.1. Distinguish sun and shade leaves

When we observed the cuticles of all the eight fossil leaves, we found that one specimen (No. FTP-219-22) possesses undulated anticlinal cell walls (Plate III, 3, 4) and a lower stomatal density; however, the straight anticlinal cell walls (Plate III, 1, 2) and a higher stomatal density are found in the other 7 leaves. In order to understand if this difference represents interspecific, intraspecific or ecological variations, an observation to various modern sun and shade leaves of *Exbucklandia populnea* was made. Our results confirm that the modern shade leaves usually exhibit a bigger lamina with larger epidermal cells than the sun leaves. Moreover, the anticlinal cell walls are generally straight or slightly arched in the sun leaves (Plate III, 5, 6), whereas undulate in the shade leaves (Plate III, 7, 8).

A comparison is made on the size of lamina and epidermal cells and the mean stomatal parameters of both the present fossil and modern *E. populnea* (Table 2). The mean stomatal density of sun leaves in modern *E. populnea* is 220 per mm², the mean undulation index 1.16. Correspondingly, the shade leaves show values 162 per mm² and 1.29. On the calculation of fossil leaves, we found that the mean stomatal density of the specimen FTP-219-22 is 168 per mm² and the undulation index 1.32, as compared to 208–250 per mm² and 1.14–1.22 in the other 7 fossil leaves (Table 2, Fig. 3). Distinctly, the fossil leaf of specimen FTP-219-22 and the shade leaves of modern *Exbucklandia populnea* possess a bigger size than the sun leaves.

Sun leaves in seed plants usually have smaller stomata but a higher stomatal density as compared with shade leaves (Zhang et al., 1995; Sun et al., 2003; Lichtenthaler and Babani, 2004; Lichtenthaler et al., 2007; Sarijeva et al., 2007). Kürschner (1997) studied the foliar cuticles of modern *Quercus petraea* and concluded that the stomatal density in the sun leaves is considerably increased as compared with the shade leaves, whereas the stomatal index is only slightly higher in the sun leaves. Moreover, sun leaves are also characterized by straight to rounded epidermal cell walls, while shade leaves are represented by a pronounced undulation of the epidermal cell walls (Kürschner, 1997). This is also true for the modern leaves of *Exbucklandia* (Table 2). Sun leaves usually tend to be fossilized preferentially (Roth and Dilcher, 1978; Spicer, 1981; Ferguson, 1985, 2005; Kürschner et al., 1996; Kürschner, 1997; Gastaldo, 2001; Royer, 2001). For example, Kürschner (1997) observed that 90% of his Miocene *Quercus pseudocastanea* leaves represent sun morphotypes. Similarly, we have only found one fossil leaf (Specimen No. FTP-219-22), showing a higher undulation index and lower stomatal density, highly likely represents a shade morphotype and, the majority of other 7 leaf specimens represent sun morphotypes.

4.2. Paleoclimate significance

There are only four species of *Exbucklandia* now distributed in Southeast Asia and South China. According to their geographic range, the climatic requirements appear to be 13–27 °C of mean annual temperatures (MAT) and 800–2500 mm of mean annual precipitations (NMBC, 1983; Harger, 1995; Luo et al., 1998; Li et al., 2005).

Leaf margin analysis on 33 fossil woody dicots from the Tengchong flora shows the percentage of entire-margined species is about 48% (Tao and Du, 1982), which might indicate that the MAT was about 16 °C in the late Pliocene of Southwest China (Wilf, 1997). This is therefore consistent with the temperature range of *Exbucklandia*. Furthermore, the modern MAT in Tengchong area is now around 15.2 °C. The little difference of the MATs between the modern and reconstruction suggests that the mean annual temperature in Southwest China was not greatly changed in the Pliocene, which has also been confirmed from other nearby Neogene floras in Southwest China (Xu et al., 2004, 2008).

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