



Research papers

Fokienia shengxianensis sp. nov. (Cupressaceae) from the late Miocene of eastern China and its paleoecological implications

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ABSTRACT

Twenty-one fossil foliage, identified as *Fokienia shengxianensis* sp. nov. (Cupressaceae), were collected from the upper Miocene Shengxian Formation in Tiantai and Ninghai counties, Zhejiang Province of eastern China. These fossils can likely be distinguished from other extant genera in the family Cupressaceae s.l. except *Fokienia* by leaf external morphology alone. Foliar cuticular comparison with the only modern species in this genus, *Fokienia hodginsii* Henry et Thomas, further suggests that the present fossil species closely resembles the modern counterpart. Paleoecologically, the occurrence of *Fokienia* from the Shengxian Formation appears to support that the fossil site was covered by subtropical evergreen broad-leaved forest and under warm and humid conditions during the late Miocene, consistent with evidence from previously published fossil plants.

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1. Introduction

Fokienia, one of the 30 genera in the Cupressaceae s.l., is a monotypic genus with only one modern species, *Fokienia hodginsii* (Farjon, 2005). Today, *Fokienia* occurs in southern China, northern Vietnam, and northern Laos (Zheng and Fu, 1978). This conifer is usually a minor constituent of a subtropical evergreen (mixed) mesophytic forest, which in an undisturbed state is dominated by numerous angiospermous trees, e.g., *Quercus* spp., *Lithocarpus* spp., *Pasania* spp., *Nyssa sinensis*, *Schima argentea*, *Schima superba*, and a few other conifers, e.g., *Cephalotaxus fortunei* and *Nothotsuga longibracteata* (Farjon, 2005). It grows in mountains at about 100–1800 m above sea level (Zheng and Fu, 1978) where the mean annual precipitation is 1200 mm or more (Farjon, 2005).

Fokienia is very rare in the fossil record. Mclver and Basinger (1990) reported fossil *Fokienia* foliage and attached seed cones from the Paleocene of Saskatchewan, central Canada. However, the taxonomic treatment of this fossil species has been questioned by Manchester et al. (2009), who suggested that it may belong to *Ditaxocladus*, an extinct cupressaceous genus. Another fossil record, represented by foliage

twigs with two nodes, was reported from the Oligocene of Jilin, northeastern China (Guo and Zhang, 2002). Generally, due to the great similarity of foliar characters in the Cupressaceae, their fossil identifications are best based on seed cone structure (Offler, 1984; Mclver and Basinger, 1987; Mclver, 1989; Mclver and Basinger, 1990). Unfortunately, cupressaceous remains usually consist of foliage only without attached seed cones (e.g., Chaney and Axelrod, 1959; Brown, 1962; Li and Guo, 1982; Guo and Zhang, 2002). However, recent work has suggested that cuticular characters of cupressaceous fossil leaves can be diagnostic (e.g., Kvaček et al., 2000; Kvaček and Rember, 2007; Shi et al., 2011).

In this paper, a total of 21 specimens of fossil foliage collected from the upper Miocene of Zhejiang Province, China, are described morphologically and anatomically as a new species, *Fokienia shengxianensis* sp. nov. These represent the first fossil with a description of the cuticle of *Fokienia*. Furthermore, paleoecological implications are briefly discussed.

2. Material and methods

2.1. Fossil material and preparation

The fossil leaf material was collected from the Shengxian Formation in Jiahu Village of Tiantai County, and Huangnitang Village of Ninghai County (29° 09' N, 121° 14' E: Fig. 1) in Zhejiang Province, eastern China. The formation is dominated by alternating basalts and

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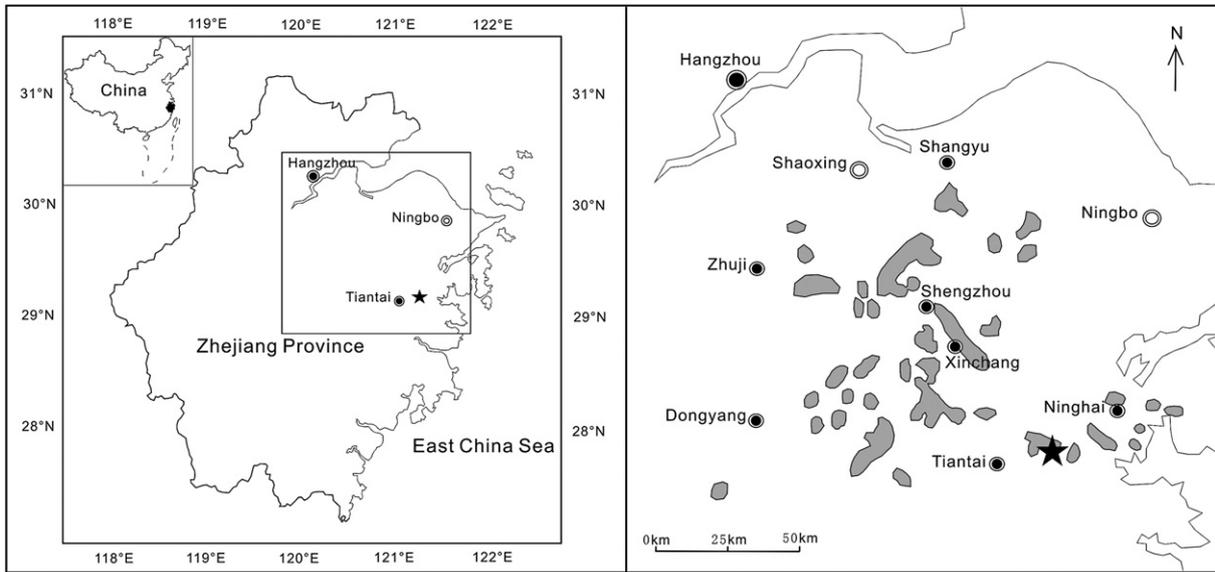


Fig. 1. Map showing the fossil locality (black star) of *Fokienia shengxianensis* sp. nov. (left) and distribution of the Shengxian Formation (right; after Yu et al., 1996).

sediment layers. Fossiliferous layers are exposed in an opencast diatomite mine, which consists of diatomaceous mudstone, shale and argillaceous siltstone. This sediment was originally named the “Xiananshan Formation” (Li and Guo, 1982; Li, 1984; Liu and Zheng, 1995; Liu et al., 1996, 2007, 2008; Tao et al., 2000; Li et al., 2008; Jia et al., 2009; Xiao, 2009; Li et al., 2010) after Li and Guo (1982), who briefly reported a Miocene macroflora from Xiananshan village, in the nearby Ninghai County of the same province. This old name, however, has been abandoned according to Yu et al. (1996). It is now clear that the Shengxian Formation is widely distributed all over the eastern part of Zhejiang Province, e.g., Shengxian, Xinchang, Tiantai, Ninghai and Shangyu counties (Fig. 1; Yu et al., 1996). The basaltic rocks within the formation were dated radiometrically at 10.5 ± 0.5 Ma in Ninghai County using the ^{40}Ar – ^{39}Ar method (Ho et al., 2003). Therefore, the age of the fossil flora is believed to be late Miocene (Li et al., 2010).

Twenty-one fossil leafy twigs of Cupressaceae were collected from the Shengxian Formation. Leaf compression fragments for cuticle analysis were lifted from the rock with a dissecting needle and then immersed in distilled water for 3 h. The fragments were then immersed in 10% HCl overnight to remove carbonates and followed by 65% HNO_3 for 3–6 days to oxidize the coaly material. When the color of samples changed to sandy beige or translucent, the samples were washed and then immersed in distilled water with 2 drops of 10% ammonia for 3–5 h to remove the humic substances, and washed in distilled water. The cuticles were mounted on slides, observed and photographed with a Leica DM4000B light microscope. For SEM, the cuticular material was mounted on four aluminum stubs, coated with gold, and examined under the scanning electron microscope (JEOLJSM-6380LV) at Lanzhou University.

2.2. Modern material and preparation

The fresh leaves of extant *Fokienia* for comparative study were collected from the Kunming Arboretum, Yunnan Province, south-western China. Cuticles were prepared according to the method described by Li et al. (2010).

All specimens and cuticle slides are housed in the Institute of Paleontology and Stratigraphy, Lanzhou University, China. For descriptions of leaf morphology, terms in Zheng and Fu (1978), Farjon (2005), and Paull and Hill (2009) are followed, while those of cuticular description follow Kvaček et al. (2000).

3. Results

Family: Cupressaceae Gray, 1822

Genus: ***Fokienia*** A. Henry et H.H. Thomas, 1911

Species: *Fokienia shengxianensis* He, Sun et Liu sp. nov.

(Plate I, 1–7; Plate II, 1–4; Plate III, 1–4; Plate IV, 1–2; Plate V, 1, 3, 5, 7, 9)
 Synonym: *Fokienia notoensis* Matsuo. Li and Guo, pp. 288, pl. 135, Fig. 9–9a, 1982.

Diagnosis: Foliage branches spread in flattened sprays. Leaves scale-like, dimorphic, decussate and almost in whorls of four. Facial leaves oblanceolate with obtuse apex. Lateral leaves boat-shaped with acute apex, overlapping margins of facial leaves, almost as long as or slightly longer than facial leaves. Epidermal cells mostly quadrangular, rectangular and elongate rectangular; hypostomatic; stomata cyclocytic, elliptical. Many papillae present around stomata.

Etymology: The epithet *shengxianensis* refers to the formation from which the specimens were collected.

Holotype: JH-1-4-290 (A, B) (Plate I, 1, 2).

Paratypes: JH-1-3-042, JH-2-045, JH-1-046, JH-1-052, JH-1-4-057 (Plate I, 5), JH-1-4-235 (A, B), JH-1-4-290 (A, B) (Plate I, 1, 2), JH-1-4-297 (Plate I, 3), JH-1-4-466 (A, B) (Plate I, 6, 7), JH-1-4-476 (Plate I, 4), JH-1-4-477, JH-1-4-478, JH-1-4-949, JH-1-956, JH-224, HNT-11 (Plate II, 2), HNT-25 (Plate II, 1), HNT-50 (Plate II, 3), HNT-51, HNT-215 (Plate II, 4).

All specimens and cuticle slides are housed in the Institute of Paleontology and Stratigraphy, Lanzhou University, China. The abbreviation JH means the fossil locality at Jiahu Village, while HNT denotes the fossil locality at Huangnitang Village.

Type locality: Jiahu Diatomite Mine in Tiantai County, Zhejiang Province, China.

Stratigraphy: Shengxian Formation.

Age: late Miocene.

3.1. Morphological description

Foliated branches spread in flattened sprays. Leaves are scale-like, dimorphic, decussate and almost in whorls of four. Facial leaves are closely appressed, narrowly oblanceolate, occasionally wedge-like; 0.8–8.9 mm in length and 0.6–2.6 mm in width; length to

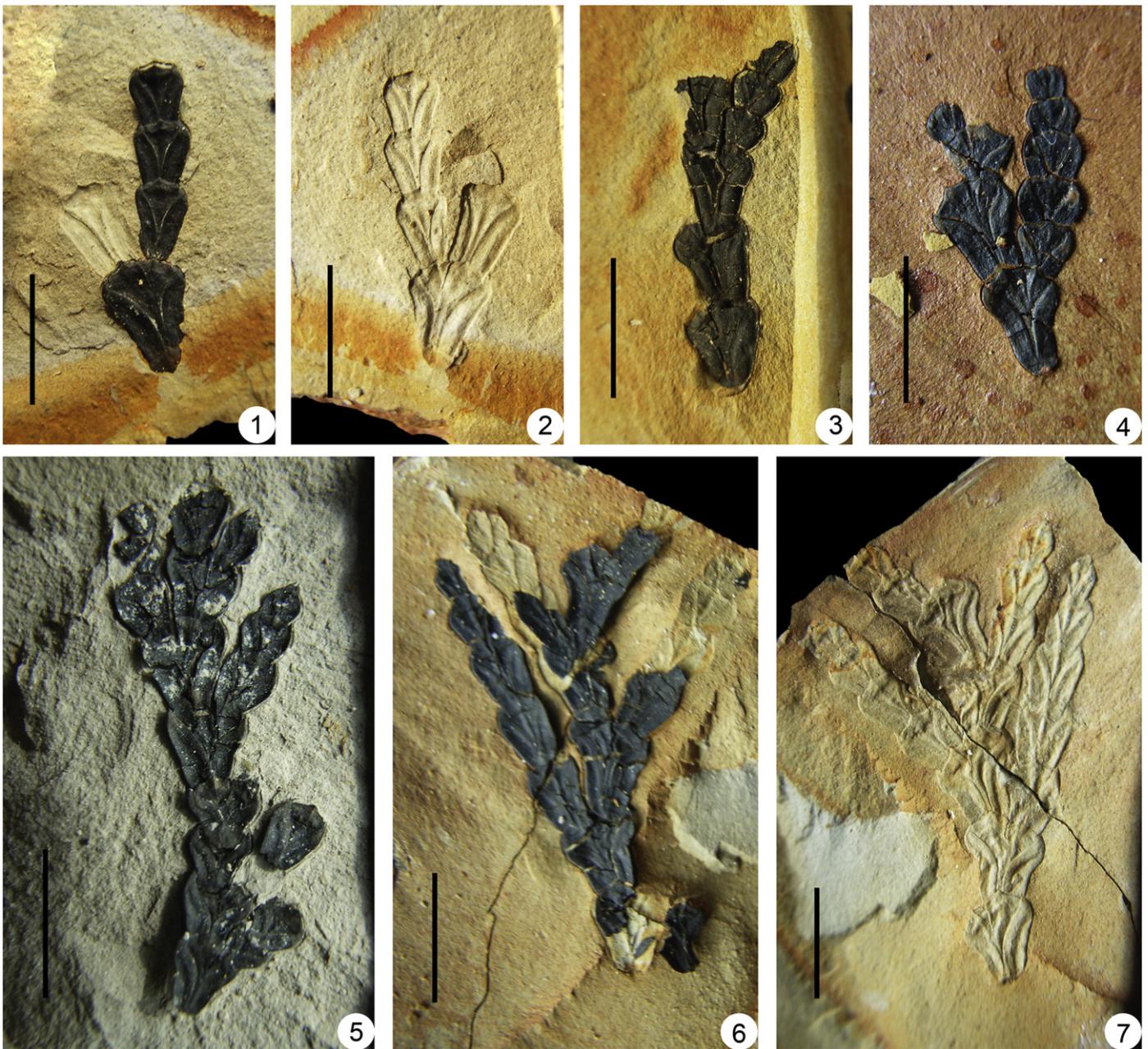


Plate I. Fossil foliage of *Fokienia shengxianensis* sp. nov. Scale bar = 5 mm. 1. Specimen no. JH-1-4-290 (A), showing the lateral leaves overlapping margins of facial leaves. 2. Specimen no. JH-1-4-290 (B). 3. Specimen no. JH-1-4-297. 4. Specimen no. JH-1-4-476, showing the lateral leaves are slight incurved. 5. Specimen no. JH-1-4-057. 6. Specimen no. JH-1-4-466 (A), showing the branches spread in flattened sprays. 7. Specimen no. JH-1-4-466 (B).

width ratio is 1.1 to 4.6; the apex of facial leaves are obtuse, occasionally acute. Lateral leaves are mostly boat-shaped, sometimes triangular, overlapping margins of facial leaves; 0.7–9.0 mm long, 0.4–1.4 mm wide, length to width ratio is 1.7 to 7.5, almost as long as or slightly longer than facial leaves; the apex of lateral leaves are acute, occasionally slightly obtuse, some slightly incurved (Fig. 2; Table 1).

3.2. Cuticular description

Facial leaf: Adaxial cuticle (Plate III, 1) is thick; epidermal cells are variable size, and mostly are quadrangular, pentagonal and rectangular, 18–41 μm (average 30 μm) long, 12–24 μm (average 17 μm) wide; anticlinal walls are straight; no stomata. Abaxial cuticle (Plate III, 2; Plate V, 1) is slightly thick; epidermal cells are irregular, mostly

quadrangular, pentagonal, elongate rectangular, occasionally linear, 16–43 μm (average 32 μm) long, 7–21 μm (average 14 μm) wide; anticlinal walls are mostly straight, sometimes curved or sinus-shaped; end walls are square; abaxial cuticle with stomata arranged in bands with 2–5 lines of stomata per band.

Lateral leaf: Adaxial cuticle (Plate III, 3) is thick; epidermal cells mostly rectangular, elongate rectangular and linear; 20–104 μm (average 47 μm) long, 9–23 μm (average 14 μm) wide; anticlinal walls are mostly straight, sometimes curved; no stomata. Abaxial cuticle (Plate III, 4; Plate V, 3) is slightly thicker; epidermal cells are quadrangular, rectangular, elongate rectangular and linear, pentagonal and occasionally shaped otherwise, 21–71 μm (average 35 μm) long, 11–24 μm (average 15 μm) wide, anticlinal walls are mostly straight, sometimes curved; end walls are square; abaxial cuticle with stomata arranged in bands and 2–8 lines of stomata per band.

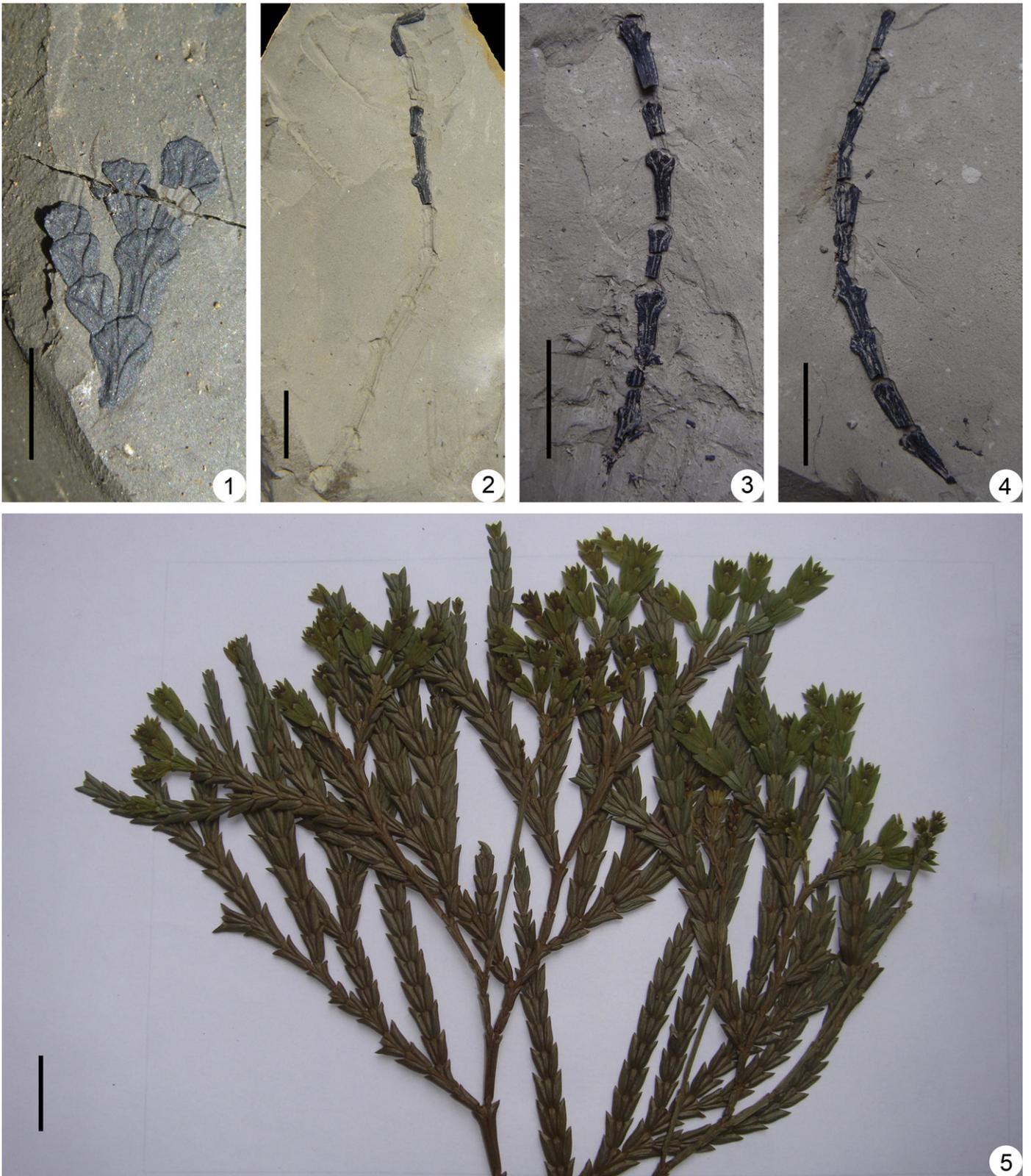


Plate II. The foliage of *Fokienia shengxianensis* sp. nov. and the living *Fokienia hodginsii*. 1, scale bar = 5 mm. 2–4, scale bar = 1 cm; 5, scale bar = 2 cm. 1. Specimen no. HNT-25.2. Specimen no. HNT-11.3. Specimen no. HNT-50.4. Specimen no. HNT-215.5. Modern foliage of *Fokienia hodginsii*.

Stomata (Plate IV, 1–2; Plate V, 5, 7, 9): Abaxial cuticle of both facial and lateral leaves have stomata mostly orientated parallel to the long axis of the leaf, fewer stomata with a little deflexion; stomata are 30–41 μm

(average 36 μm) long and 24–33 μm (average 26 μm) wide, mostly elliptical; stomata type is cyclocytic; guard cells are sunken and encircled by 5–7 distinctly protuberant subsidiary cells; Florin rings are present;

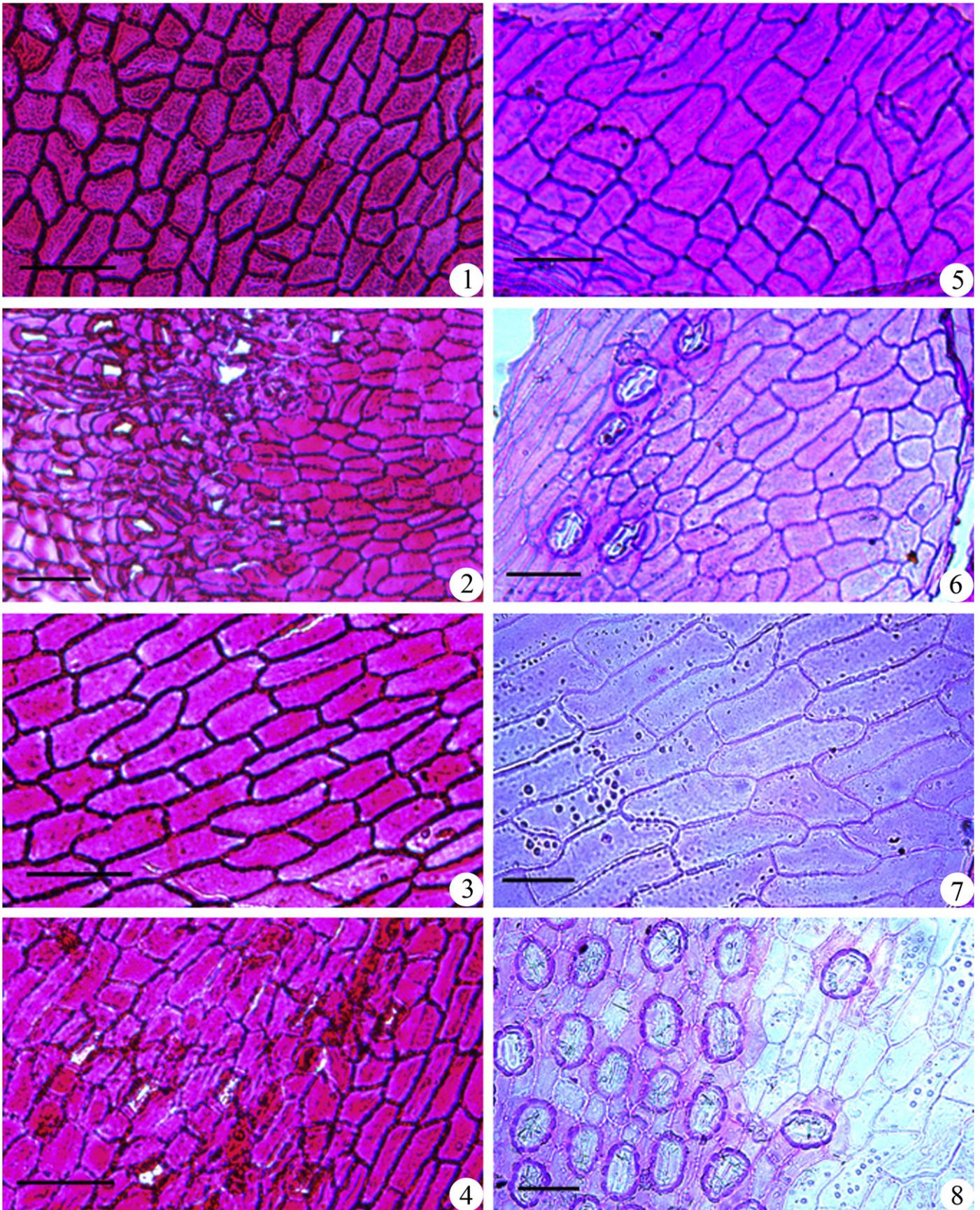


Plate III. Cuticles of *Fokienia shengxianensis* sp. nov. and *Fokienia hodginsii* under light microscopy. Scale bar = 50 μm . 1–4, Cuticles of *Fokienia shengxianensis* sp. nov. 1. Adaxial epidermis of facial leaf of specimen no. JH-1-4-290.2. Abaxial epidermis of facial leaf of specimen no. JH-1-4-290.3. Adaxial epidermis of lateral leaf of specimen no. JH-1-4-290.4. Abaxial epidermis of lateral leaf of specimen no. JH-1-4-290.5–6, Cuticles of *Fokienia hodginsii*. 5. Adaxial epidermis of facial leaf of *Fokienia hodginsii*. 6. Abaxial epidermis of facial leaf of *Fokienia hodginsii*. 7. Adaxial epidermis of lateral leaf of *Fokienia hodginsii*. 8. Abaxial epidermis of lateral leaf of *Fokienia hodginsii*.

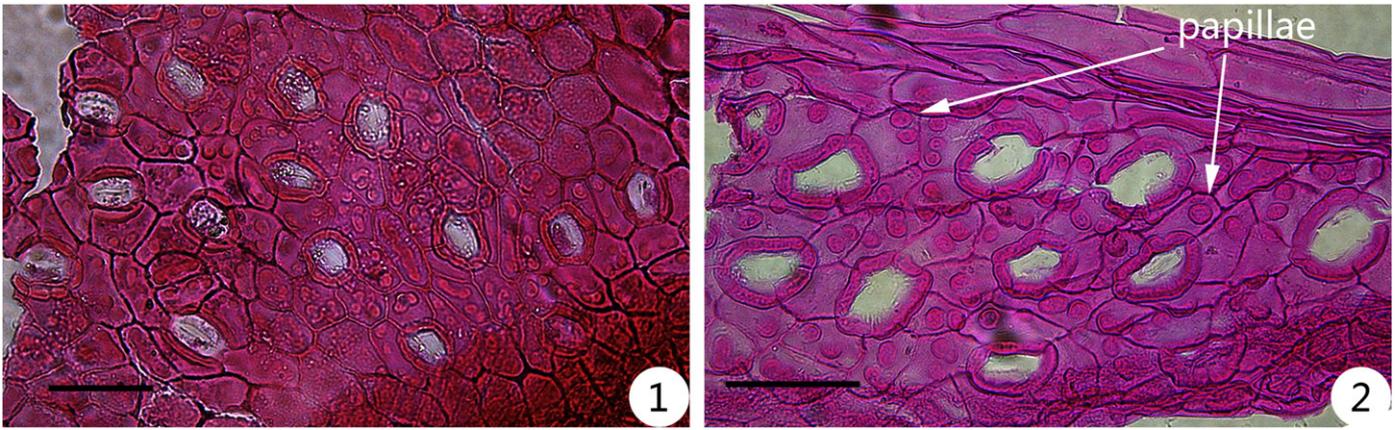


Plate IV. Stomata bands of *Fokienia shengxianensis* sp. nov. Scale bar = 50 µm. 1. Stomata bands of specimens no. JH-1-4-290. 2. Stomata bands of specimens no. JH-1-4-466, showing the papillae around the stomata.

papillae present around stomata; there are 4–9 papillae (average 7) per stomatal complex; the papillae are hemispherical, occurring on subsidiary cells (Plate V, 5).

4. Comparison and discussion

4.1. Comparisons

The present fossil leaves from the Shengxian Formation are scale-like and occur in whorls of four. In gymnosperms, scale leaves appear in families such as Cupressaceae s.s., Taxodiaceae s.s., and Podocarpaceae (de Laubenfels, 1953). Furthermore, leaves in the Cupressaceae s.s. are essentially whorled (de Laubenfels, 1953). Therefore, there is little doubt that the external foliar morphology alone strongly shows that the present fossils are of cupressaceous affinity.

The Cupressaceae s.s. includes two subfamilies, i.e., the Callitroideae and the Cupressoideae (Li, 1953; Li and Yang, 2002). Furthermore, the genera in the Callitroideae, which are distributed exclusively in the Southern Hemisphere (Li, 1953; Li and Yang, 2002), are different from the present fossils. The leaves of *Callitris*, *Actinostrobus* and *Fitzroya* are arranged in whorls of three. The leaves of *Widdringtonia*, *Diselma* and *Papuacedrus* are arranged in opposite pairs. The leaves of *Pilgerodendro* are all equal in size. The leaves of *Neocallitropsis* are awl-shaped (Farjon, 2005). The lateral leaves are much longer than the facial ones in *Austrocedrus* (Vidakovic, 1991) and in *Libocedrus* the lateral leaves are not close to the facial ones (refer to de Laubenfels, 1953). It is clear that our fossils cannot be placed to any genus of the Callitroideae. Thus, the present fossils should be assigned to the Cupressoideae and a comparative table is prepared for further discussion (Table 2).

4.1.1. Comparisons with the extant species in the Cupressoideae

Although the genera in Cupressoideae have scale and whorled leaves like in our fossils, there are some differences in the distribution of stomata, branches, leaf placement, leaf shape, leaf apex and leaf size between these genera and the fossils (Table 2). The Cupressoideae include the following ten genera, i.e., *Calocedrus*, *Chamaecyparis*, *Cupressus*, *Fokienia*, *Juniperus*, *Microbiota*, *Platycladus*, *Tetraclinis*, *Thuja* and *Thujopsis* (Li, 1953; McIver and Basinger, 1987; Gadek et al., 2000; Li and Yang, 2002; Farjon, 2005). First, within this subfamily only the genus *Fokienia* has hypostomatic leaves (Table 2). The present fossil is hypostomatic, like *Fokienia* (Table 2). Second, in leaf external morphology (Table 2), *Microbiota* differs from the present fossils because its branches are numerous, decumbent, spreading, and curved down in more or less plagiotropic frondose sprays (Farjon, 2005). The leaf placement in *Cupressus* is irregularly

disposed and spread, or plagiotropic and pendulous (Farjon, 2005), unlike that in the fossils. *Juniperus* differs from the present fossils in the absence of dimorphic leaves (Little et al., 2004; Farjon, 2005). It is evident that the other three genera, i.e., *Thuja*, *Chamaecyparis*, and *Tetraclinis*, are quite different from the present fossils. The facial leaves of *Thuja* are obovate-rhombic, while those of *Chamaecyparis* appear ovate or rhombic-ovate, and the lateral leaves of *Tetraclinis* are linear spatulate (Zheng and Fu, 1978; Farjon, 2005). Other genera such as *Platycladus*, *Thujopsis* and *Calocedrus* clearly differ from the present fossils. The leaves of *Platycladus* are often less than 3.0 mm long (Zheng and Fu, 1978). In *Thujopsis* the lateral leaves are not close to facial ones (de Laubenfels, 1953). In *Calocedrus* the leaf apices are incurved or recurved and its lateral ones meet the facial ones (Farjon, 2005). Based on the above comparisons, we can conclude that all the genera in Cupressoideae except for *Fokienia* differ from the present fossils (Table 2). Therefore, the present fossils can be safely placed within the genus *Fokienia*.

The cuticles of *Fokienia hodginsii*, the only extant species of the genus, are compared with those of the present fossil species (Table 3). The result shows that epidermal features of the fossil species and *F. hodginsii* are quite similar. Similarities are the hypostomatic leaves, the mostly quadrangular, rectangular to elongate rectangular epidermal cells, the straight anticlinal walls, the square end walls, and the cyclocytic, elliptical stomata, that are arranged in bands (Plate III, 1–8; Plate IV, 1–10). However, minor differences between *F. hodginsii* and the present fossils are to be seen such as slightly larger epidermal cells in the extant species, and the higher number of stomata in the stomatal bands in *F. hodginsii* (Plate III, 1, 4; Plate IV, 1–4). Moreover, there are fewer papillae around the stomata in *F. hodginsii* (Plate IV, 5, 6, 9, 10). Based on the epidermal features, we conclude that the present fossils belong to a species of *Fokienia*.

4.1.2. Comparison with the fossil species

Two fossil species of *Fokienia* have been published from the Paleocene to Miocene in Asia and North America (Table 4). A brief comparison with the present fossil is made in Table 4. It is clear that *Fokienia ravenscragensis* from the Paleocene of Canada uniquely possesses opposite branches (McIver and Basinger, 1990; McIver, 1992, 1994). Another fossil from the Oligocene of northeastern China, *Fokienia* sp., has a distinctive deltoid apex in the facial leaves (Guo and Zhang, 2002).

Several fossil leaves were previously as attributed to *Fokienia*, but their taxonomic status has since been revised. For example, *Fokienia praedecurrens* (Knowlton) Chaney and Axelrod (1959) has been transferred to *Tetraclinis salicornioides* (Unger) Kvaček, because the fossil leaves are morphologically indistinguishable from those of the widespread European Paleogene and Neogene species *T. salicornioides*

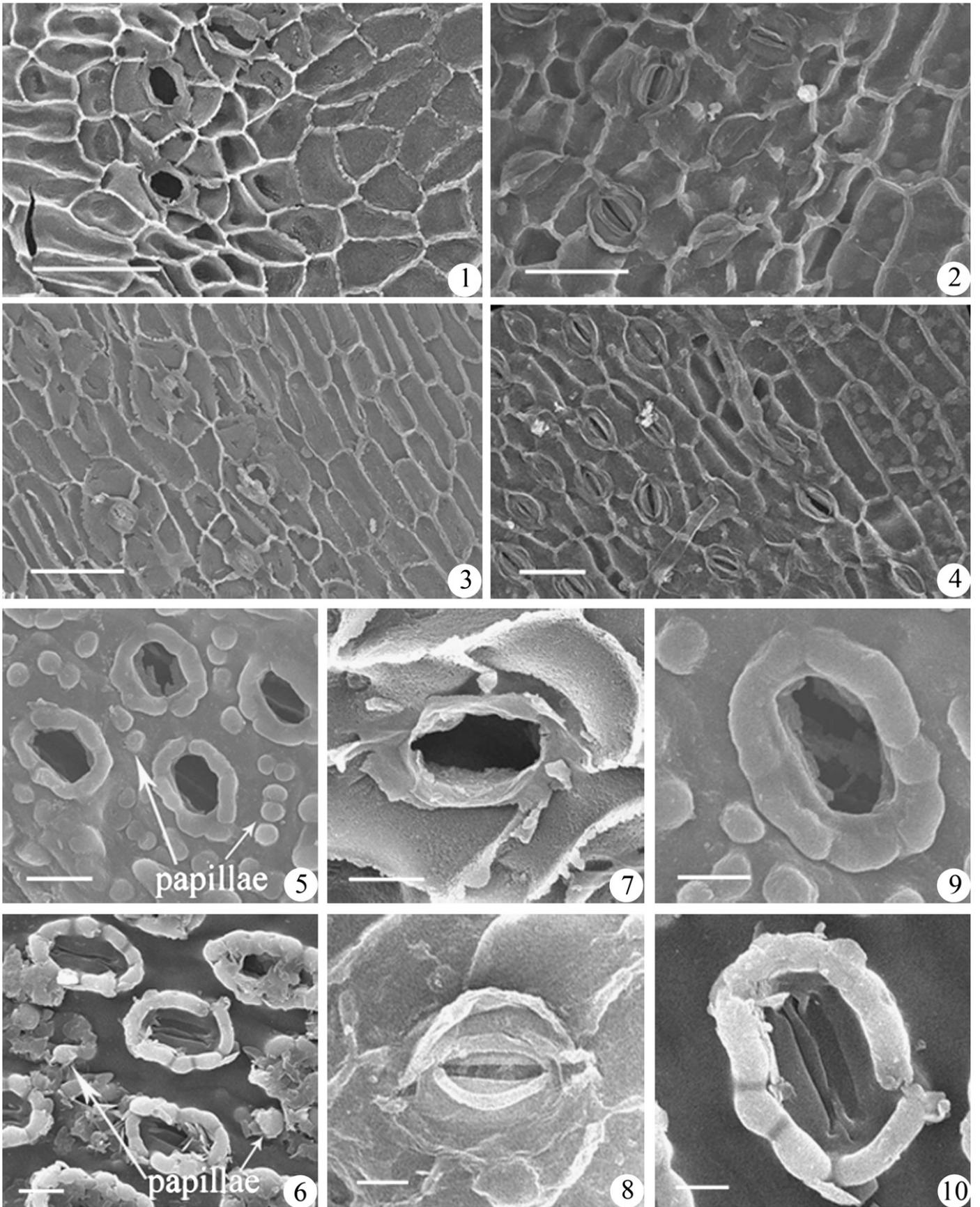


Plate V. Cuticles of *Fokienia shengxianensis* sp. nov. and *Fokienia hodginsii* under SEM. 1–4, scale bar = 50 μm; 5–6, scale bar = 20 μm; 7–10, scale bar = 10 μm. 1. Abaxial epidermis of facial leaf of specimen no. JH-1-4-290, inner view. 2. Abaxial epidermis of facial leaf of *Fokienia hodginsii*, inner view. 3. Abaxial epidermis of lateral leaf of specimen no. JH-1-4-290, inner view. 4. Abaxial epidermis of lateral leaf of *Fokienia hodginsii*, inner view. 5. Stomata and papillae of specimen no. JH-1-4-290, outer view. 6. Stomata and papillae of *Fokienia hodginsii*, outer view. 7. Stomata of specimen no. JH-1-4-290, inner view. 8. Stomata of *Fokienia hodginsii*, inner view. 9. Stomata of specimen no. JH-1-4-290, outer view showing the Florin ring. 10. Stomata of *Fokienia hodginsii*, outer view.

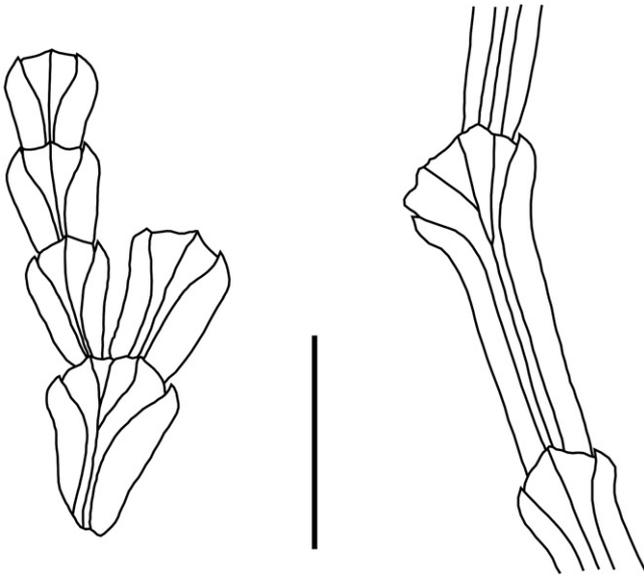


Fig. 2. Line drawing of the foliage of *Fokienia shengxianensis* sp. nov. based on JH-1-4-290 (left) and HNT-11 (right). Scale bar = 5.0 mm.

(Kvaček et al., 2000). *Fokienia notoensis* Matsuo (1963) was later assigned to *Libocedrus* (Ishida, 1970) and was then transferred to *Calocedrus* (Huzioka, 1972), because *Fokienia notoensis* is quite different from the extant *Fokienia* (Guo and Zhang, 2002). A specimen from the Miocene of Lújia Village, Ninghai County, Zhejiang Province (close to the type locality), was identified as *Fokienia notoensis* by Li and Guo (1982). It was described as having scale-like, decussate leaves with pointed apex, almost in whorls of four with lateral leaves overlapping the margins of the facial leaves. It is obvious that it is difficult to distinguish this specimen from the here described species. Thus we place it in the synonymy of *Fokienia shengxianensis*.

Mclver and Basinger (1990) suggested that in the absence of reproductive organs, any cupressaceous fossil foliage resembling that of *Fokienia* cannot be assigned to the extant genus, because in the absence of seed cones, the relationship of the vegetative remains to

extant members of the Cupressaceae cannot be clearly determined. Therefore, they proposed to use the name, *Fokieniopsis*, for vegetative remains. *Fokieniopsis* has frond-like foliage, opposite branching, pinnate, flattened branches arising in the axils of the lateral leaves. The leaves are scale-like, four-ranked, and arise in whorls giving a distinct jointed appearance to foliage. The facial leaves are appressed with an acuminate apex. The lateral leaves are lanceolate, decurrent, and commonly falcate. The apex is acute or attenuate and closely appressed to the facial leaf (Mclver and Basinger, 1990). The present fossils from eastern China appear to be not comparable with *Fokieniopsis* because the latter has opposite branches, which do not occur in the Chinese fossils.

Ditaxocladus planiphyllus was established by Guo et al. (1984) for fossil foliage from the Paleocene of northwestern China, showing a slight similarity to *Fokienia*. Mclver and Basinger (1990) transferred it to *Fokieniopsis* because the foliage resembles that of *Fokieniopsis catenulate*, as the cone scales differ from all other conifer cone scales and in not being attached to the foliage. However, this taxonomic revision was recently questioned by Manchester et al. (2009) who believe that *Fokienia* (Cupressaceae) reported from the Paleocene of North America (Brown, 1962; Mclver, 1992) does not belong to the extant genus *Fokienia*, but instead to the extinct Cupressaceous genus *Ditaxocladus* Guo & Sun (Guo et al., 1984; Manchester et al., 2009; S. R. Manchester, pers. comm.). *Ditaxocladus kivdensis*, another fossil species recently reported from the Paleocene of the Amur Province, Russia, also shows some similarities to the extant *Fokienia* in the morphology of shoots and foliage (Krassilov et al., 2009). However, the ultimate branchlets of *Fokienia* are alternate while they are strictly opposite in *Ditaxocladus* (Krassilov et al., 2009). Furthermore, all the above mentioned specimens from North America previously assigned to *Fokienia* and the extinct *Ditaxocladus* have pinnate-opposite leaves on each node of the branches which is quite different from the living *Fokienia hodginsii* (S. R. Manchester, pers. comm.). Therefore, we follow Manchester et al. (2009) who advocated that all the previously published fossils from North America assigned to *Fokienia* fossils should be transferred to *Ditaxocladus*. Opposite branching, one of the most important diagnostic characters of *Ditaxocladus*, is not seen in our fossils. Therefore, it is very clear that our fossils cannot be assigned to *Ditaxocladus*.

Table 1
The size and morphological features of *Fokienia shengxianensis* sp. nov.

Sample	Facial leaf				Leaf apex	Lateral leaf				
	Length	Width	Length to width ratio	Leaf shape		Length	Width	Length to width ratio	Leaf shape	Leaf apex
JHU-1-3-042	2.0–2.8	1.0–1.4	2	Wedge	Obtuse	2.0–3.0	0.5–1.0	3.0–4.0	Boat-shaped	Slightly obtuse
JHU-2-045	1.1–2.8	0.7–1.6	1.6–1.8	Narrowly oblanceolate	Acute	0.8–3.0	0.4–0.8	2.0–3.8	Boat-shaped	Acute
JHU-1-046	1.4–2.2	0.9–1.2	1.6–1.8	Narrowly oblanceolate	Obtuse	1.0–1.9	0.5–0.9	2.0–2.1	Boat-shaped	Acute
JHU-1-052	0.8–2.0	0.7–1.1	1.1–1.8	Narrowly oblanceolate	Acute	0.7–2.0	0.5–0.7	2.4–2.9	Boat-shaped	Acute
JHU-1-4-057	1.2–3.1	0.6–1.7	1.8–2.0	Narrowly oblanceolate	Obtuse	1.3–3.1	0.4–0.9	3.3–3.4	Boat-shaped/triangle	Acute
JHU-1-4-235	1.5–2.9	0.9–1.1	1.7–2.6	Wedge	Obtuse	1.0–3.0	0.6–1.1	1.7–2.7	Boat-shaped/triangle	Acute
JHU-1-4-290	2.1–4.5	1.2–2.5	1.8	Wedge/narrowly oblanceolate	Obtuse	2.0–4.2	0.7–1.0	2.9–4.2	Boat-shaped	Acute
JHU-1-4-291	0.8–1.8	0.4–1.0	1.8–2.0	Narrowly oblanceolate	Acute	0.9–1.8	0.3–0.8	2.3–3.0	Boat-shaped/triangle	Acute
JHU-1-4-297	1.2–3.0	0.7–1.9	1.6–1.7	Narrowly oblanceolate	Obtuse	1.2–3.1	0.4–0.9	3.0–3.4	Boat-shaped	Acute
JHU-1-4-466	1.8–3.9	0.9–3.1	1.3–2.0	Narrowly oblanceolate	Obtuse	1.4–4.0	0.5–1.1	2.8–3.6	Boat-shaped/triangle	Acute
JHU-1-4-476	1.1–3.3	0.4–2.2	1.5–2.8	Wedge/narrowly oblanceolate	Obtuse	1.0–3.6	0.4–0.9	2.5–4.0	Boat-shaped	Acute
JHU-1-4-477	1.3–3.1	1.0–1.7	1.3–1.8	Wedge/narrowly oblanceolate	Obtuse	1.2–3.1	0.5–1.0	2.4–3.1	Boat-shaped/triangle	Acute
JHU-1-4-478	1.7–4.0	1.1–2.4	1.5–1.7	Narrowly oblanceolate	Obtuse	1.3–4.2	0.6–1.0	2.2–4.2	Boat-shaped	Acute
JHU-1-4-949	2.0–3.3	1.2–1.6	1.7–2.1	Wedge/narrowly oblanceolate	Acute	2.0–3.3	0.6–0.8	3.3–4.1	Boat-shaped	Slightly obtuse
JHU-1-956	1.9–2.9	1.2–1.4	1.6–2.1	Narrowly oblanceolate	Obtuse	1.8–2.9	0.7–0.8	2.6–3.6	Boat-shaped	Slightly obtuse
JHU-224	1.6–3.9	1.1–2.3	1.5–1.7	Narrowly oblanceolate	Obtuse	1.6–3.0	0.5–1.0	3.0–3.2	Boat-shaped	Acute
HNT-11	4.7–8.0	1.3–3.2	2.5–3.6	Narrowly oblanceolate	Obtuse	4.4–7.9	0.7–1.4	5.6–6.3	Boat-shaped	Acute
HNT-25	1.4–3.9	1.2–2.6	1.2–1.5	Narrowly oblanceolate	Acute	1.2–3.8	0.6–1.0	2.0–3.8	Boat-shaped	Acute
HNT-50	5.2–8.9	1.3–3.0	3.0–4.0	Narrowly oblanceolate	Obtuse	5.0–9.0	0.7–1.2	7.1–7.5	Boat-shaped	Acute
HNT-51	4.0–4.4	1.8–2.4	1.8–2.2	Narrowly oblanceolate	Obtuse	3.4–4.3	0.8–0.9	4.3–4.8	Boat-shaped	Slightly obtuse
HNT-215	3.2–6.6	0.7–2.1	3.1–4.6	Narrowly oblanceolate	Obtuse	3.1–6.6	0.5–0.9	6.2–7.3	Boat-shaped	Slightly obtuse

Table 2
Comparison of stomata and foliage morphology of genera in the subfamily Cupressoideae (data from Farjon, 2005 and Zheng and Fu, 1978).

Genus	Distribution of stomata	Branches	Leaf placement	Leaf shape	Leaf apex	Leaf size
<i>Fokienia shengxianensis</i>	Hypostomatic	Foliated branches spread in flattened sprays	Decussate, almost in whorls of 4	Facials oblanceolate; laterals boat-shape	Facials obtuse; laterals acute	1.4–5.0×0.7–9.0 mm
<i>Calocedrus</i>	Amphistomatic	Arranged in a plane, spreading or ascending	Decussate, appearing in whorls of 4, imbricate; laterals meeting facials	Dimorphic; facials flattened; laterals boat-shaped	Facials obtuse-acuminate; laterals slightly incurved acute	2×1.5 mm on ultimate lateral branchlets to 15×3 mm on leading (whip) shoots
<i>Chamaecyparis</i>	Inconspicuous	Arranged in a plane, flattened	Decussate, imbricate	Dimorphic; facials ovate or rhombic-ovate; laterals boat-shaped	Unknown	The facials smaller than laterals
<i>Cupressus</i>	Amphistomatic	Ascending, rarely pendulous, often decussately arranged	Irregular disposed and spreading or plagiotropic and pendulous	Decussate, 4-ranked; juvenile leaves needlelike; adult leaves scale-like	Free apices	On ultimate branchlets 1–3×0.8–1.2 mm. on leading shot larger
<i>Fokienia</i>	Hypostomatic	Foliated branches spread in flattened sprays	Decussate, almost in whorls of 4	Facials closely appressed; laterals boat-shaped	Facials short, cuspidate apex in young tree, obtuse in old tree	2–7×1–2 mm on ultimate branchlets
<i>Juniperus</i>	Amphistomatic or epistomatic	Not arranged in a plane, terete or 3, 4, or 6 angled in cross section	Decussate or in whorls of 3, decurrent or non-decurrent	Leaves needlelike; usually not dimorphic	Obtuse or acute-pungent	Acicular to 25×4 mm
<i>Microbiota</i>	Amphistomatic	Numerous, decumbent, spreading	Decussate, broad decurrent, imbricate	Weak dimorphic	Facials rhombic with narrower acuminate apex or acute-pungent	1.5–3(–3.5)×0.6–1.5 mm
<i>Platycladus</i>	Amphistomatic	Arranged in a plane, spreading or ascending, flattened	Decussate, 4-ranked	Scale-like, on whip shoots monomorphic; on lateral branchlets dimorphic	Facials appressed, obtuse; laterals incurved, appressed or free, obtuse	Laterals on ultimate branchlets 1.5–2×1–1.5 mm. facials smaller than laterals
<i>Tetraclinis</i>	Epistomatic	Long and slender, more or less crooked angularly	Decussate, appearing in whorls of 4 on thinnest branchlets	Weakly dimorphic; facials linear; laterals linear-spathulate	Facials broad, acute apex	1.6–8×1–1.5 mm
<i>Thuja</i>	Amphistomatic	Arranged in a plane, flattened	4-ranked	Dimorphic; facials obovate-rhombic; laterals boat-shaped	Unknown	Facial smaller than the laterals, laterals less than 4 mm
<i>Thujopsis</i>	Amphistomatic, upper facials epistomatic	Arranged in a plane, flattened	Decussate, imbricate	Dimorphic; facials obovate-obdeltoid, laterals boat-shaped	Facials obtuse; laterals apex free, incurved, obtuse or acute	(1–)3–8×1–5 mm on flattened branchlets

Tetraclinis salicornioides (Unger) Kvaček is a widespread European Paleogene and Neogene species (Kvaček et al., 2000). Some fossil foliage from the Oligocene and Miocene of western North America was formerly assigned to *Fokienia* based on similarities in leaf morphology (Chaney and Axelrod, 1959). Meyer and Manchester (1997) indicated that the fossil foliage is morphologically indistinguishable from *T. salicornioides*. Our material clearly differs from *T.*

salicornioides because the leafy twigs of the latter are mostly opposite branching and anticlinal walls are very regular and finely undulate (Kvaček et al., 2000).

In conclusion, based on the comparison between the present fossils, extant species and previously published fossils, the foliage remains from China can be confidently identified as *Fokienia shengxianensis* sp. nov.

Table 3
Comparison of foliar cuticular characters between *Fokienia shengxianensis* sp. nov. and *Fokienia hodginsii*.

Character	<i>F. shengxianensis</i> sp. nov.	<i>F. hodginsii</i>
1. Stomata	Hypostomatic	Hypostomatic
1.1 Stomatic size (L×W μm, average)	36×26	40×29
1.2 Stomatic type	Cyclocytic	Cyclocytic
1.3 Stomatic shape	Elliptical	Elliptical
1.4 Stomatic arrangement	Arranged in bands; 2–8 tires per band	Arranged in bands; 2–10 tires per band
2. Epidermal cells		
2.1 Epidermal cells		
Size (L×W μm, average)		
2.1.1 Facials	Adaxial: 30×17; abaxial: 32×14	Adaxial: 41×23; abaxial: 50×18
2.1.2 Laterals	Adaxial: 47×14; abaxial: 35×15	Adaxial: 91×35; abaxial: 74×22
2.2 Epidermal cells shape	Quadrangular, rectangular and elongate rectangular	Quadrangular, rectangular and elongate rectangular
2.3 Anticlinal wall	Straight	Straight
2.4 End wall	Straight	Straight
3. Florin rings	Present	Present
4. Papillae	Many	Few

Table 4
Comparison of *Fokienia shengxianensis* sp. nov. with the previously published fossil species of *Fokienia*.

Character	<i>F. shengxianensis</i> sp. nov.	<i>Fokienia</i> sp.	<i>F. ravenscragensis</i>
References	Li and Guo, 1982; Present paper	Guo and Zhang, 2002	Mclver and Basinger, 1990; Mclver, 1992
Age	Late Miocene	Oligocene	Early Paleocene
Location	Tiantai and Ninghai, China	Longjing, China	Saskatchewan and Alberta, Canada
Branching	Arranged in a plane, flattened	Unknown (two notes of foliage twig)	Opposite
Leaf placement	Decussate, almost in whorls of 4	Unknown	Whorled, 4-ranked, persistent
Leaf shape	Scale-like; facials oblanceolate; laterals boat-shape	Scale-like; facials cuneate; laterals falciform	Scale-like; facials obovate to narrow oblanceolate; laterals lanceolate, commonly falcate
Leaf size (L×W mm)	Facials: 0.8–8.9×0.6–2.6; laterals: 0.7–9.0×0.4–1.4	Facials: 1.5×5.0; laterals: 4.0–8.0×1.5–2.0	Facials: 2.5–20.0×1.5–2.0; laterals: 2.5–20.0×0.5–1.5
Facials apex	Obtuse or acuminate	Deltoid	Acuminate or mucronate

4.2. Paleocology

Abundant plant fossils have been recovered from the Shengxian Formation, such as Leguminosae, Fagaceae, Lauraceae, Papilionaceae, Rosaceae, Ulmaceae, Cassalpinaceae, Aceraceae, Juglandaceae, Hamamelidaceae, Theaceae, Betulaceae, Aquifoliaceae, Smilacaceae and Pinaceae, Cupressaceae, Cephalotaxaceae, and Taxaceae (Li and Guo, 1982; Li, 1984; Liu et al., 1996; Li et al., 2008; Li et al., 2010; Ding et al., 2011). The association of these fossil plants suggested that this area was covered by an evergreen broad-leaved forest (Li, 1984). Previous paleoecological studies based on plant fossils suggested that the environment in eastern Zhejiang has been warm and humid during the Miocene (Li, 1984; Tao et al., 2000; Li et al., 2008; Jia et al., 2009; Xiao, 2009; Li et al., 2010; Ren et al., 2010). *Callimothallus pertusus*, a fossil epiphyllous fungus found on the surface of fossil *Smilax* leaves, also indicates a warm and humid environment because epiphyllous fungi usually grow under a humid subtropical–tropical climate (Ding et al., 2011). The inferred paleoecological conditions in eastern Zhejiang during the Miocene appear consistent with the habitat of the extant *Fokienia* (Table 5). As Table 5 shows, it is quite clear that several ecological factors required by the extant *Fokienia* appear to overlap with those reconstructed from other fossil plants at the fossil site, such as the mean annual temperature (MAT), and the annual precipitation. In addition, most associated plant groups in the modern habitat of *Fokienia* can be found in the Xiananshan flora (Shengxian Formation).

It is interesting to note that the diagnostic character in the abaxial cuticle of *Fokienia shengxianensis* is the presence of many papillae, which is quite different from that of the extant *F. hodginsii* (see above). It has been generally thought that the occurrence of many papillae would be xeromorphic leaf features and consequently might indicate a more or less arid environment (e.g., Alvin, 1983; Watson and Alvin, 1996; Axsmith and Jacobs, 2005). This seems to contradict to our paleoecological interpretation of the Miocene Xiananshan flora in eastern China. However, recent studies suggest that these so-called xeromorphic features cannot always be explained as an anti-transpirant adaptation because they may also perform self-cleaning (e.g., preventing entry of toxic gases), anti-herbivory, light reflectance, and water-repellence functions (e.g., Haworth and McElwain, 2008). Therefore, we tend to believe that the presence of many papillae on the cuticle of our fossil *Fokienia* likely indicate an ecological adaptation, such as self-cleaning in a wet and humid

Table 5
Comparison of ecology between the fossil site and the extant habitat of *Fokienia hodginsii*.

Ecological factor	Xiananshan flora (Shengxian Formation)	Current habitat of <i>Fokienia hodginsii</i>
Altitude	500–1200 m (see Ren et al., 2010)	100–1800 m
Mean annual temperature	9.91–19.74 °C (see Ren et al., 2010)	11.7–15 °C at distribution center (southern China)
Annual precipitation	1117.7–1564.4 mm (see Ren et al., 2010)	> 1200 mm
Relative humidity	Unknown	> 80% at distribution center (Southern China)
Vegetation type	Evergreen broad-leaved forest	Evergreen (mixed) mesophytic forest
Symbiotic plants	Leguminosae, Fagaceae, Lauraceae, Papilionaceae, Rosaceae, Ulmaceae, Cassalpinaceae, Aceraceae, Juglandaceae, Hamamelidaceae, Theaceae, Betulaceae, Aquifoliaceae, Smilacaceae and Pinaceae, Cupressaceae, Cephalotaxaceae, Taxaceae	Fagaceae, Nyssaceae, Theaceae and Pinaceae, Cephalotaxaceae
References	Li and Guo, 1982; Li, 1984; Liu et al., 1996; Li et al., 2008; Li et al., 2010; Ren et al., 2010; Ding et al., 2011.	Zheng and Fu, 1978; Lin et al., 2004; Farjon, 2005.

environment with elevated atmospheric CO₂ and SO₂ gases from active volcanic activities evidenced by the dominant basalts in the Shengxian Formation.

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