



First Fossil *Fokienia* (Cupressaceae) in South China and Its Palaeogeographic and Palaeoecological Implications

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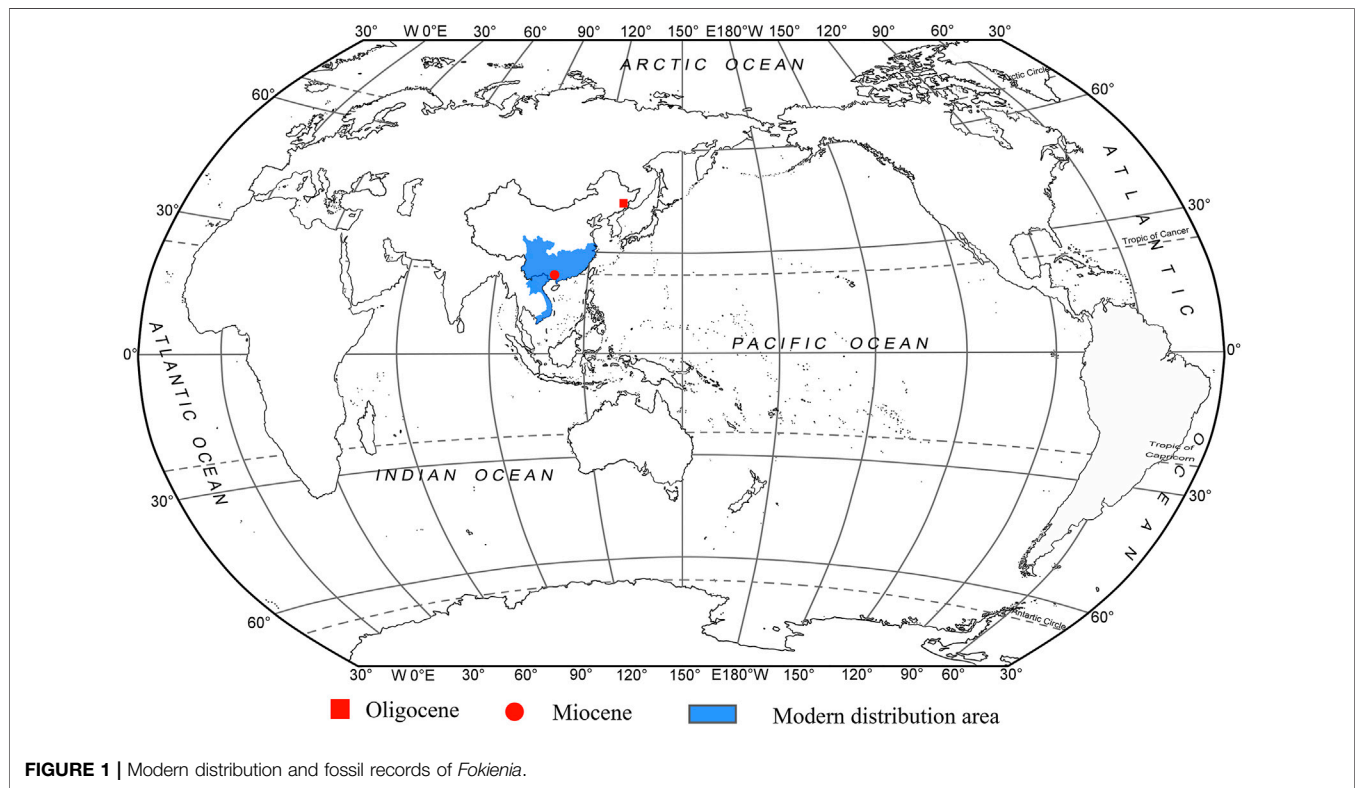
Fokienia A. Henry & H. H. Thomas is a monotypic genus of the Cupressoideae Rich. ex Sweet (Cupressaceae), native to subtropical evergreen mesophytic forests in South China, northern Laos and Vietnam. The fossil record of *Fokienia* is very scanty, with only one known occurrence of foliage in the Oligocene of Longjing, Jilin, China. Here we report the fossil foliage of *Fokienia* discovered in the Miocene Erzitang Formation of the Guiping Basin, South China, which is similar to that of the only extant species *Fokienia hodginsii* in both macromorphological and epidermal features. This species is the earliest fossil record within the modern distribution area of *Fokienia* and the only fossil species for which morphology and anatomy have been studied in detail. Fossil evidence suggests that the genus *Fokienia* was present at middle latitudes of the Northern Hemisphere in the Oligocene and spread to South China during the Miocene. Due to physiological adaptations to warm-wet environments and weak cold tolerance, *Fokienia* migrated southward, as global climate cooling gradually drove it to extinction in the mid-latitudes. The ecological niche of the extant species, and co-existing plant fossils, suggest that the fossil assemblage represents the remains of an evergreen broad-leaved and conifer mixed forest growing under humid and warm Miocene climate.

Keywords: Miocene, conifers, leaf epidermal characters, *Fokienia*, Cupressaceae

INTRODUCTION

The monotypic genus *Fokienia* A. Henry et H. H. Thomas belongs to the subfamily Cupressoideae Rich. ex Sweet within the Cupressaceae. The only extant species, *Fokienia hodginsii* (Dunn) Henry & Thomas is an evergreen tree species native to subtropical evergreen mesophytic forests in South China (except Hainan Island), northern Laos and Vietnam (Figure 1; Farjon, 2005). Here, *Fokienia* has significant economic value, its high-quality timber is extensively used for building materials, furniture construction and fine handicrafts. This conifer is also used in forest plantations, and its valuable essential oil is used in pharmaceuticals and cosmetics (Fu et al., 1999).

Fokienia hodginsii was firstly treated as a new species of *Cupressus* (sect. *Chamaecyparis*) *hodginsii* by Dunn (1908), and then Henry and Thomas (Henry, 1911) assigned this species to a new genus *Fokienia* based on the morphological characteristics of its seed cones, seeds and leaves. Recently extant species are sometimes referred as *Chamaecyparis hodginsii* (Dunn) Rushforth (Rushforth, 2007). Based on detailed analyses of the ontogeny of the seed cones (Farjon, 2005; Jagel and Dörken,



2015), morphological phylogenetic analysis (Farjon, 2005) and DNA sequence data (Gadek and Quinn, 1993), *Fokienia* is now considered to be separate from *Chamaecyparis*. Recent molecular phylogenetic analyses cluster these two genera into single subclade in Cupressaceae (Yang et al., 2012) and strongly support the sister relationships between *Chamaecyparis* p. p. and *Fokienia* (Gadek et al., 2000). However, combined analysis of molecular data and morphological characters revealed the varying placement of *Fokienia hodginsii* within the phylogenetic tree according to different sequence data (Little et al., 2004).

Fokienia is similar to most genera of the subfamily Cupressoideae in terms of leaf macromorphology, but can be effectively distinguished by the epidermal characteristics (Kvaček et al., 2000; Kvaček and Rember, 2007; Shi et al., 2011, 2012). Moreover, the macromorphology and anatomical characteristics of Cupressoideae foliage have been studied in detail (Kvaček et al., 2000; Wang, 2007; Shi et al., 2011, 2012; Wu et al., 2014, 2019; Zhang et al., 2015), which plays an important guiding role in the identification of *Fokienia*.

Fossils of *Fokienia* are very rare (**Figure 1**). Foliage of *Fokienia* sp. from the Oligocene Sanhe flora of Longjing, Jilin, China, is morphologically similar to that of extant *F. hodginsii* and seems to be the only reliable fossil record of this genus, but its leaf epidermal anatomy remains unknown. In this paper, we describe a new fossil species of *Fokienia* on the basis of foliage from the Miocene of South China and discuss the

phytogeographical and palaeoecological implications of this genus.

MATERIALS AND METHODS

The fossils studied here were collected from the Miocene Erzitang Formation in the Guiping Basin located east of Guiping City, Guangxi, South China. The fossil locality is on the northeastern edge of this basin, near Longsheng Village, Tianping Town, Tengxian County (**Figure 2**, 23°22'55.04"N, 110°44'13.31"E). The Erzitang Formation in this area consists of coal-bearing deposits. *Fokienia* leafy shoots and isolated leaves along with numerous other plant fossils are preserved as compressions in gray-black shales. Based on the mammal genus *Prolipotes yujiangensis* Zhou, Zhou & Zhao found in the Guiping Basin, Zhou et al. (1984) and Zhao (1988) suggested a Miocene age for the Erzitang Formation. Extant specimens were collected from Daiyunshan National Nature Reserve in Fujian Province, China and Bidoup-Nui Ba National Park of Hân Giao forest station in Đà Lạt District, Lâm Đồng Province, Vietnam.

Fossil and extant specimens were photographed using a Canon EOS 500D digital camera (Canon, Tokyo, Japan), and images were processed with DigiCamControl-Free Windows DSLR camera controlling solution (Duka, 2015) and Helicon Focus 6.6.1 (Helicon Soft Ltd., Kharkov, Ukraine). Fossils were treated by immersion in 10% hydrochloric acid for 12h, then in Schulze's



FIGURE 2 | Map showing the fossil locality (red triangle, modified from Han et al., 2018).

solution (70% HNO₃, saturated with KClO₃) for approximately 1 h followed by 5–10% KOH for 30 min (Ye, 1981). After each process the samples were washed with distilled water. The cuticles were separated with a needle under a stereomicroscope. The leaves of extant *F. hodginsii* were boiled to translucency in a mixed solution of 10% acetic acid and 10% H₂O₂ (1:1; Lin, 2007). After treatment with Schulze's solution followed by 8% KOH for 30 min each, the cuticles were separated. The cuticles of fossil and modern leaves were stained with 1% fuchsin solution and mounted on glass slides in glycerine jelly for observation and photography using an Axio Scope A1 stereoscopic microscope (Carl Zeiss, Oberkochen, Baden-Württemberg, German). Parts of unstained fossil and extant cuticles were mounted on stubs, then observed and photographed using a JSM-6330F scanning electron microscope (JEOL Ltd., Akishima, Tokyo, Japan) with an accelerating voltage of 10 keV. All the specimens are deposited in the Museum of Biology, Sun Yat-sen University with collection numbers beginning with TX.

SYSTEMATIC PALAEOLOGY

Family Cupressaceae Gray, 1822

Subfamily Cupressoideae Rich. ex Sweet, 1826

Genus *Fokienia* A. Henry & H. H. Thomas, 1911

Fokienia tianpingensis Wu & Jin, sp. nov.

Figures 3A,C,E–G; Figure 4; Figures 5A–D.

Etymology

The epithet “*tianpingensis*” refers to the town near the fossil locality.

Holotype

TX-2-1, leafy shoot, designated here (**Figure 3A**).

Paratypes

TX-2-2, TX-34-2, TX-35-1, TX-38-1, TX-39, TX-63-2, TX-70A-1.

Material

Eight leafy shoots and isolated leaves from the Miocene Erzitang Formation in the Guiping Basin; type locality near Tianping Town, Tengxian County, Guangxi, South China.

Diagnosis

Foliage shoots alternately branching in the same plane. Leaves dimorphic, in whorls of four. Facial and lateral leaves almost equal in length. Leaves amphistomatic, stomata in broad bands on underside of foliage shoots. Facial leaves with a few stomata, lateral leaves nonstomatal on the upper side of shoots. Adaxial surface of facial leaves with stomatal bands at the leaf apex. Anticlinal walls of ordinary epidermal cells straight, periclinal walls slightly granular. Stomata monocyclic, rarely incompletely amphicyclic, densely spaced, longitudinally oriented, with 4–6 subsidiary cells, sharing 1–2 subsidiary cells. Florin rings prominent. Stomatal zones papillate.

Description

Foliage comprising three preserved branching orders are flattened in the same plane, the ultimate branchlets arise from the axil of lateral leaves of the penultimate branchlets in an alternate manner (**Figures 3A,C,E**). The incompletely preserved shoot bearing penultimate branchlets is 1.8 cm long, weakly flattened and narrower, but thicker than the penultimate branchlets (**Figure 3C**). Vegetative branchlets are convex on the upper side (**Figures 3A,G**) and concave on the lower side (**Figure 3F**). Leaves are scale-like, decussate, in whorls of four, strongly dimorphic, differentiated into



FIGURE 3 | Foliage of *Fokienia tianpingensis* sp. nov. (**A, C, E–G**) and extant species *F. hodginsii* (Dunn) Henry et Thomas (**B, D, H**). (**A**) Branchlets of two orders, showing the alternate branching pattern, holotype TX-2-1. (**B**) Similar ultimate branchlets of extant species. (**C**) Incompletely preserved shoot bearing penultimate branchlets, TX-38-1. (**D**) Similar shoot of extant species with penultimate branchlets. (**E**) Longitudinal section of penultimate branchlet showing one resin canal per each leaf (arrows), TX-70A-1. (**F**) Compound cladode-like segment of the branchlet junction showing resin canals, TX-35-1. (**G**) Ultimate shoot, TX-2-2. (**H**) Lower side of shoot showing stomatal bands. Scale bars for (**A, G**) = 2 mm, (**B, C, E, H**) = 3 mm, (**D**) = 5 mm (**F**) = 1 mm.

laterals and facials (**Figures 3A,C,E,G**). The leaf base is decurrent, partly concealed by leaves of the lower pair (**Figures 3A,C,G**). Two lateral and two facial leaves constitute wedge-shaped, cladode-like segments stacked along branch axis. Each scale-like leaf has one resin canal (**Figures 3E,F**).

The lateral leaves are conduplicate, strongly bilaterally flattened and boat-shaped in surface view, 1.6–6.0 mm long (**Figures 3A,E–G**), but lateral leaves from penultimate shoots are smaller, 3.0–4.1 mm in length (**Figure 3C**). The margins of lateral leaves are entire. The apices of lateral leaves are acute or acuminate, slightly incurved, with free tips (**Figures 3A,F,G**). The facial leaves are dorsiventrally flattened and closely appressed to

the shoot axis. They are wedge-shaped oblanceolate in outline, with obtuse apices, shorter than, or approximately equal in length to, the lateral leaves in the same whorl, up to 1.3–5.6 mm long (**Figures 3A,F,G**), but in the penultimate shoot facial leaves are shorter, 2.0–3.9 mm in length (**Figure 3C**).

The leaves are amphistomatic. The lateral leaves are nonstomatal on the upper side of foliage shoots (**Figures 4C,D**). The epidermal cells are elongated along the longitudinal cell files, more or less rectangular in outline, often with oblique end walls (**Figures 4A,C–E**). The anticlinal walls are straight, with numerous pits (**Figure 5D**). The external cuticular surfaces are generally even, but some cavities are occasionally observed. The cavities are irregular in distribution and size, round

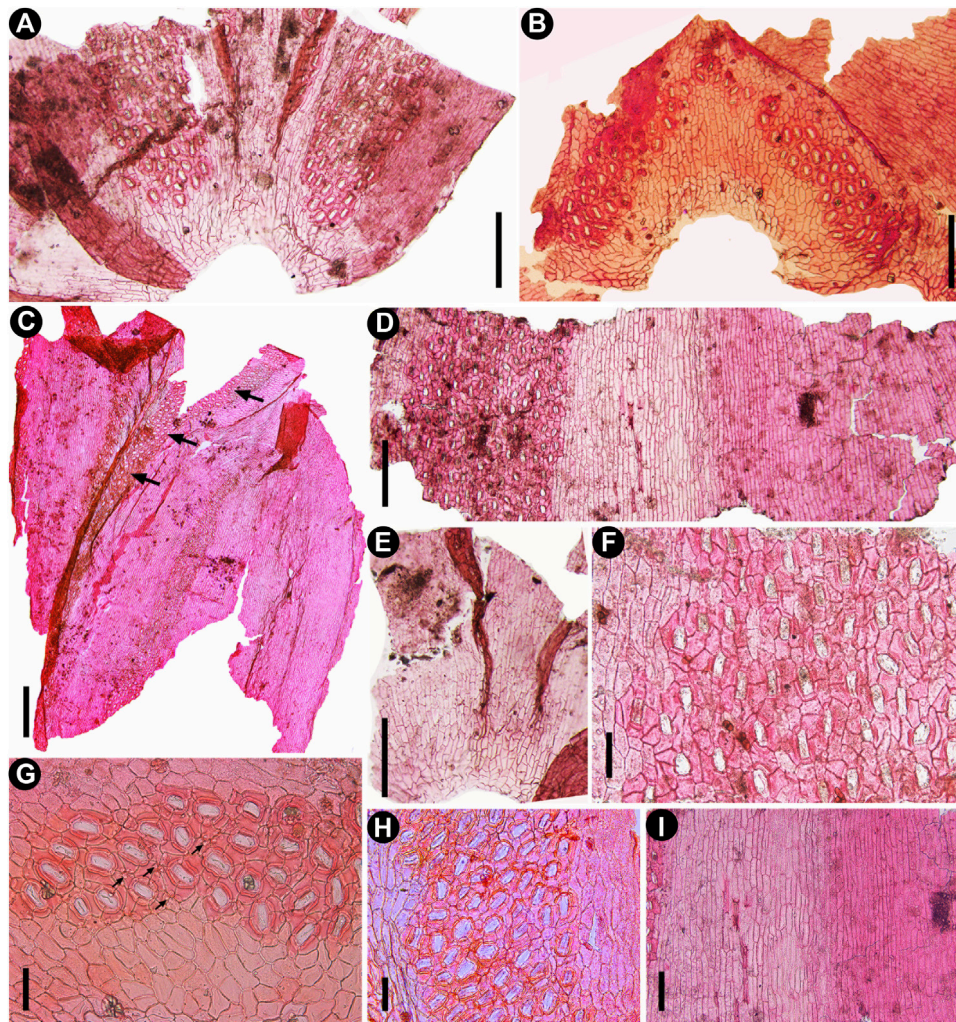


FIGURE 4 | Cuticular characters of fossil *Fokienia tianpingensis* sp. nov., LM. **(A)** Cuticle of facial and two lateral leaves showing the distribution of stomatal bands on the underside of a branchlet, TX-63-2. **(B)** Stomatal distribution on the adaxial surface of a facial leaf of the shoot underside, TX-63-2. **(C)** The cuticle of one facial and one lateral leaves (from left to right) showing stomatal distribution on the abaxial and adaxial (arrow) surfaces, TX-39. **(D)** Abaxial cuticle of a lateral leaf showing the nonstomatal surface on the upper side of the branchlet (right) and a broad stomatal band on the underside of the branchlet (left), TX-34-2. **(E)** Narrow stomatal zones along the sutures between facial and lateral leaves on the upper side of a branchlet, TX-63-2. **(F)** Enlargement of the stomatal band in **(D)** showing the stomatal density and shared subsidiary cells. **(G)** Enlargement of stomata in **(B)** showing papillae within the stomatal band (arrows). **(H)** Enlargement of the stomatal band on the underside of the lateral leaf in **(C)**. **(I)** Enlargement of nonstomatal zones of the lateral leaf in **(D)** on the upper side of branchlet (right) and on the underside (left). Scale bars for **(A, B, D, E)** = 200 μm, **(F-H)** = 400 μm, **(I)** = 100 μm.

in outline, with a thickened rim. The periclinal cell walls are smooth to finely granular (**Figure 5D**).

The abaxial leaf surface on the underside of shoots displays one broad median stomatal zone and two narrow lateral nonstomatal zones (**Figures 4A,C,D**). The morphology and arrangement of ordinary epidermal cells of nonstomatal zones are similar to those of the upper side. The stomatal zone is strongly papillate, running along the leaf margin from the base to the apical region, but is absent from the leaf apex. The stomata are irregularly arranged, mostly oriented longitudinally (**Figure 4F**). Adjacent stomata sharing 1–2 subsidiary cells (**Figure 4F**).

The adaxial surface of the lateral leaf has one lateral stomatal zone on the underside of the foliage shoots (**Figure 4C**).

Nonstomatal zones on each side of the stomatal zone only consist of a few files of ordinary epidermal cells, which are similar to those of the abaxial surface in morphology and arrangement (**Figure 4C**). A wide stomatal zone runs approximately the whole length of the leaf from the base, and stomata are closely spaced (**Figure 4C**).

The abaxial surfaces of facial leaves on the upper side of the shoots are generally nonstomatal with a few stomata running along the sutures between the facial and lateral leaves (**Figure 4E**). The epidermal cells are arranged in longitudinal files. The abaxial surfaces of facial leaves on the underside of foliage shoots possess broad median nonstomatal zones and two narrow lateral stomatal zones. The epidermal cells of nonstomatal zones are

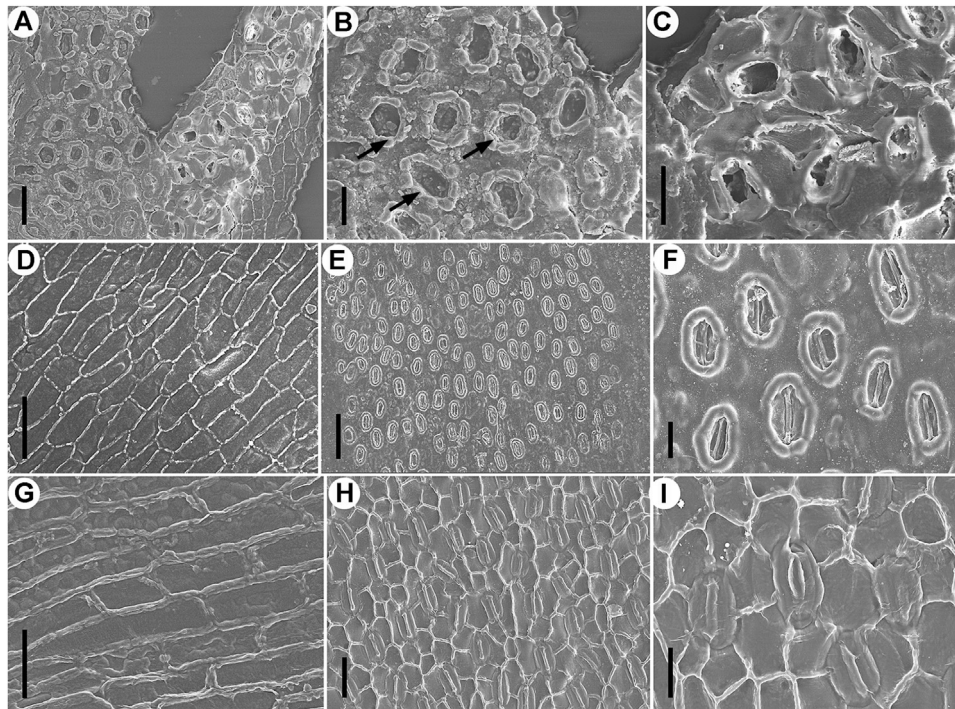


FIGURE 5 | Epidermal characters of *Fokienia tianpingensis* sp. nov. (**A–D**) and extant *Fokienia hodginsii* (Dunn) Henry & Thomas (**E–I**), SEM. (**A**) Abaxial cuticle of a lateral leaf on the underside of a branchlet showing a stomatal band, outer (left) and inner (right) view, TX-63–2. (**B**) Enlargement of the stomatal band (outer view) in (**A**) showing Florin rings (arrows) and papillae. (**C**) Enlargement of stomata (inner view) in (**A**) sharing subsidiary cells. (**D**) Abaxial cuticle of a lateral leaf on the underside of a branchlet showing the morphology and arrangement of ordinary epidermal cells of a non-stomatal zone, inner view, TX-63–2. (**E**) Abaxial surface of a lateral leaf on the underside of a branchlet, outer view. (**F**) Enlargement of stomata in (**E**). (**G**) Abaxial cuticle of a lateral leaf on the underside of a branchlet showing the morphology and arrangement of ordinary epidermal cells of a non-stomatal zone, inner view. (**H**) Abaxial cuticle of a lateral leaf on the underside of a branchlet showing a stomatal band, inner view. (**I**) Enlargement of stomata in (**H**) sharing subsidiary cells. Scale bars for (**A, D, G, H**) = 40 μm , (**B, C, F, I**) = 20 μm .

morphologically similar to those of the lateral leaves. The stomatal zones run along the sutures between the facial and lateral leaves (Figures 4A,C). The adaxial surfaces of facial leaves on both upper and lower sides of the shoots have two stomatal zones at the leaf apex running along the leaf margins (Figure 4B).

The stomatal complexes are monocyclic or very rarely incompletely amphicyclic, elliptical or sometimes elongate in shape (Figures 4F–H; Figures 5A,B). Stomata are densely spaced, generally longitudinally oriented, surrounded by 4–6 subsidiary cells, and adjacent stomata share 1–2 subsidiary cells (Figures 4D,F–H; Figures 5C). The subsidiary cells are polygonal, isodiametric or elongate in shape, and papillate (Figures 5A–C). The guard cells are slightly sunken, forming a usually closed aperture (Figure 5B). Florin rings are prominent, round or elliptical in outline (Figures 4G,H; Figures 5A,B).

DISCUSSION

Comparison With Extant Genera

In gymnosperms, members of the Podocarpaceae and Cupressaceae possess scale leaves, but only in the Cupressoideae and Callitroideae subfamilies some genera

produce branching in a single plane shoots with flattened whorled leaves (De Laubenfels, 1953). All genera of the subfamily Callitroideae are distributed in the Southern Hemisphere (Li, 1953; Li and Yang, 2002). The leaves of many genera within this subfamily, such as *Fitzroya* Hook. f., *Actinostrobus* Miq. and *Callitris* Vent., are arranged in alternating whorls of three, which are different from the leaves of our new fossil species from Tengxian in which leaves are arranged in whorls of four. The leaves of the new species form decussate whorls, whereas those of *Widdringtonia* Endl., *Diselma* Hook. f. and *Papuacedrus* H. L. Li are arranged in opposite decussate pairs (Farjon, 2005). The facial leaves of *Papuacedrus*, *Austrocedrus* Florin et Boutelje and *Libocedrus* Endl. are much smaller than their lateral leaves (Vidaković, 1991; Farjon, 2005), but the facial leaves of the present fossil are shorter or nearly equal to the lateral leaves. By these characters, new fossil species can be easily distinguished from the Callitroideae conifers.

The subfamily Cupressoideae comprises ten genera, including *Chamaecyparis* Spach, *Platyclusus* Spach, *Calocedrus* Kurz, *Thujopsis* Siebold et Zucc. ex Endl., *Cupressus* Gray, *Fokienia* A. Henry et H. H. Thomas, *Juniperus* L., *Microbiota* Kom., *Thuja* L. and *Tetraclinis* Mast. (Li, 1953; Gadek et al., 2000; Li and Yang, 2002; Farjon, 2005). Although all the above genera and new fossils

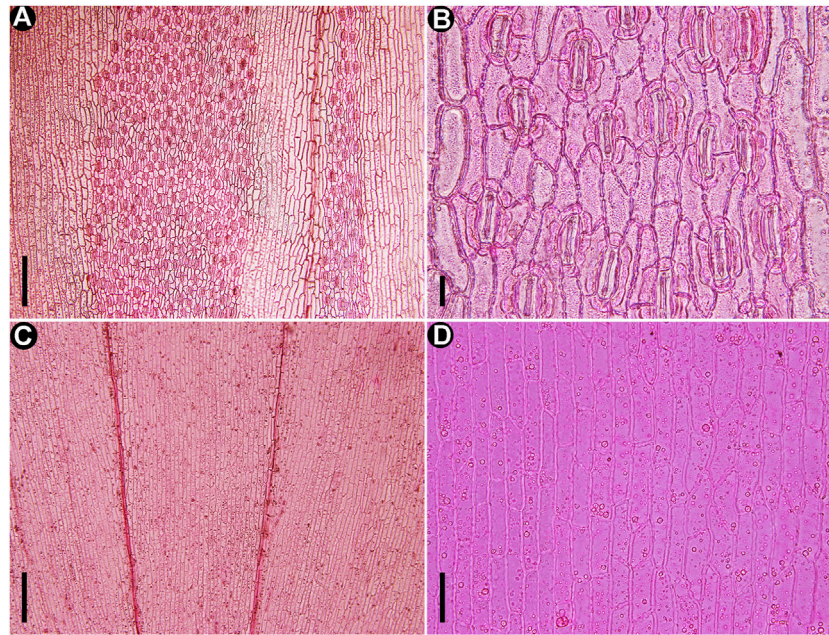


FIGURE 6 | Cuticles of extant *Fokienia hodginsii* (Dunn) Henry et Thomas, LM. **(A)** The stomatal distribution on the abaxial surfaces of lateral (left) and facial (right) leaves on the underside of shoot. **(B)** Enlargement of lateral leaf stomatal band in **(A)** showing densely arranged stomata sharing subsidiary cells. **(C)** Cuticles of lateral and facial leaves on the upper surface of a shoot. **(D)** Enlargement of the epidermal cells in **(C)**. Scale bars for **(A, C)** = 200 μm , **(B)** = 20 μm , **(D)** = 50 μm .

possess scale-like and whorled leaves, they can be easily distinguished from each other in macromorphological and cuticle characters, such as stomatal distribution, leaf shape and size. Among them, *Thujaopsis* resembles the present fossil in having alternate branching, flattened ultimate shoots and dimorphic foliage, but differs in having obtuse apices on its facial and lateral leaves, the obvious separation between lateral and facial leaves, larger leaves (about 4–7 mm) and nonstomatal upper sides of leaves (Shi et al., 2012). The genus *Thuja* is different from the present fossil in having obovate or rhombic facial leaves with one gland, stomata with a loose distribution and basically no shared subsidiary cells (Shi et al., 2012). *Cupressus* differs in having irregular leaf placement, obliquely pendulous branches, simple or weakly dimorphic leaves, and triangle to diamond-shaped facial leaves. *Juniperus* can readily be distinguished from the new fossil foliage by having branchlets usually arranged irregularly, not in flattened sprays, with non-dimorphic leaves in alternating opposite pairs or in whorls of three, rarely in whorls of four. In comparison with the present fossil, the genus *Calocedrus* differs in possessing a serrate margin of lateral leaves, and loosely-spaced stomata that rarely share subsidiary cells (Shi et al., 2012). In foliage gross morphology, the present fossils are also obviously different from most other genera of the Cupressoideae. The facial leaves of *Chamaecyparis* are ovate or rhomboid-ovate; leaves of *Platycladus* are generally less than 3 mm; the facial leaves of *Tetraclinis* are linear and lateral leaves are long spoon shaped; and the branches of *Microbiota* are scattered, spreading, sagging and extending downward (Little et al., 2004; Farjon, 2005). The genus *Fokienia* is characterized by

alternately branched flattened shoots, lateral leaves with entire margins, dense stomatal distribution and the stomata sharing subsidiary cells.

The new fossil species closely resembles the extant species of *Fokienia* in gross foliage morphology and epidermal characters. Both species have alternately branched shoots strongly flattened in the same plane, dimorphic decussate leaves in whorls of four, boat-shape lateral leaves with entire margins (Figure 3), papillate stomatal bands on abaxial surfaces of lateral and facial leaves on the lower side of shoots, but rarely on the adaxial surfaces of lateral leaves, as well as on the adaxial surface of facial leaves of both shoot sides, as well as monocyclic or very rarely incompletely amphicyclic stomata with distinct Florin rings, which are closely spaced and share subsidiary cells (Figures 4F–H; Figures 5A–C E,F,H,I; Figure 6) (Table 1). However, the facial and lateral leaves of the present fossils are smaller than those of the extant species, and the periclinal walls of the ordinary epidermal cells are slightly granular, while those of extant species are smooth (Figure 5G).

Comparison With Fossil Species of *Fokienia*

Fossils of *Fokienia* were rarely found in the past. *Fokienia shengxianensis* He, Sun & Liu from the Miocene of Zhejiang (He et al., 2012) was reassigned to *Calocedrus shengxianensis* (He, Sun & Liu) Zhang & Zhou (Zhang et al., 2015) based on sparsely spaced stomata that rarely share subsidiary cells. *Fokienia catenulata* (Bell) R.W. Brown and *Fokienia ravenscragensis* McIver & Basinger were revised to the extinct genus *Ditaxocladus* based on the oppositely branched leaf sprays and

TABLE 1 | Comparison of *Fokienia tianpingensis* sp. nov. with another fossil species and extant *Fokienia hodginsii*.

Character	<i>F. tianpingensis</i> sp. nov.	<i>F. hodginsii</i>	<i>Fokienia</i> sp.
Branching	Alternate, spread in a flatten spray	Alternate, spread in a flatten spray	Unknown
Leaf placement	Decussate, almost in whorls of 4	Decussate, almost in whorls of 4	Unknown
Leaf shape	Scale-like; facials wedge-oblongate; laterals boat-shape	Scale-like; facials wedge-oblongate; laterals boat-shaped	Scale-like; facials cuneate; laterals falcate
Facials apex	Obtuse or acuminate	Short, cuspidate apex in young tree, obtuse in old tree	Deltoid
Margins	Lateral and facial leaf margin entire	Lateral leaf margin entire; facial leaf margin serrate and scariose	Unknown
Leaf size (L × W mm)	Facials: 1.3–5.6 × 0.7–1.1 Laterals: 1.6–6.0 × 0.5–0.9	Facials: 2–7 × 1–2 Laterals: 4–10 × 2–4	Facials: 1.5 × 5.0 Laterals: 4.0–8.0 × 1.5–2.0
Distribution of stomata	Lateral leaves amphistomatic, stomata occur on the abaxial leaf surface of the underside of shoots and adaxial leaf surface. Facial leaves amphistomatic, stomata occur on the abaxial leaf surface of the underside of shoots and adaxial leaf surfaces of both shoot sides	Lateral leaves amphistomatic, stomata occur on the abaxial leaf surface of the underside of shoots and adaxial leaf surface. Facial leaves amphistomatic, stomata occur on the abaxial leaf surface of the underside of shoots and adaxial leaf surfaces of both shoot sides	Unknown
Stomata	Monocyclic or very rarely incompletely amphicyclic, round or elliptical in outline, arranged in bands	Monocyclic or very rarely incompletely amphicyclic, elliptical in outline, arranged in bands	Unknown
Epidermal cells	Rectangular and elongate rectangular, rarely quadrangular	Quadrangular, rectangular and elongate rectangular	Unknown
Anticlinal and periclinal cell walls	Straight, slightly granulated	Straight, smooth	Unknown
Florin rings	Present	Present	Unknown
Papillae	Present in stomatal bands and epidermal cells	Present in stomatal bands and epidermal cells	Unknown
Distribution	Tengxian, China	Southern China, northern Vietnam, and northern Laos	Longjing, China

oppositely clustered seed cones with much fewer cone scales (Brown, 1962; McIver and Basinger, 1990; McIver, 1992; Guo et al., 2012). *Fokienia* sp. from the Oligocene of Longjing, Jilin, is similar to the new extinct species in leaf morphology, but its epidermal characters are unknown. The facial leaves of the present fossils are wedge-oblongate with obtuse or acuminate apices and the lateral leaves are boat-shaped, while the facial leaves of *Fokienia* sp. are wedge-shaped with a deltoid apex and its lateral leaves are falcate. The facial leaves of the present fossil and those of *Fokienia* sp. are similar in size but the lateral leaves of the former are much smaller than those of the latter.

Palaeogeographic and Palaeoecological Implications

Available palaeobotanical evidence indicates that the oldest known fossil record of *Fokienia* is from the Oligocene of Longjing, Jilin, China (Figure 1; Guo and Zhang, 2002). Combined with the previous phylogenetic study of Cupressaceae (Mao et al., 2012; Qu et al., 2017) and fossil records, Yin et al. (2020) studied the phylogeography of *F.*

hodginsii based on the molecular markers of chloroplast and single-copy nuclear genes. This analysis revealed that *F. hodginsii* comprised two major phylogeographic lineages located on either side of the Tanaka-Kaiyong Line, which is considered to be a major phytogeographic boundary in southwest China, separating Sino-Japanese and Sino-Himalayan floristic subkingdoms of East Asia (Li and Li, 1997; Yin et al., 2020). The divergence time of these two major lineages was dated to the early Miocene (ca. 19.34–19.95 Ma) (Yin et al., 2020). Yin et al. (2020) speculated the ancestors of *Fokienia* migrated from the middle latitudes of the Northern Hemisphere to the subtropical regions after the formation of the East Asian monsoon. In addition, combined with the obvious phylogeographic structure and ENM results, it seems the *F. hodginsii* survived in four refuges during the last glacial episodes, which is consistent with the multiple refugia patterns of relict species in subtropical China (Yin et al., 2020). The *F. hodginsii* population has a relatively high genetic diversity, which may be related to its long history in a variety of geographical habitats (Yin et al., 2018; Yin et al., 2020). However, the fossils (*F. shengxianensis* He, Sun & Liu, *F. catenulata* (Bell) R.W. Brown and *F. ravenscragensis* McIver

& Basinger) used for the fossil calibration points have been reassigned to other genera. Consequently, the time to the most recent common ancestors of intraspecific lineages in *F. hodginsii* and phylogeography of the genus should be reconsidered. Now the fossil record of *Fokienia* is enriched by *Fokienia tianpingensis* sp. nov. from the Miocene Erzitang Formation, Tengxian, Guangxi. From the present two fossil records, we infer that *Fokienia* already existed in middle latitudes of the Northern Hemisphere at least as early as the Oligocene, as global climate cooling gradually drove it to extinction in the mid-latitudes and migrated southward to South China in the Miocene (**Figure 1**), which is consistent with the above phylogeographical context.

Extant *Fokienia* is generally a minor constituent of subtropical to warm temperate evergreen (mixed) mesophytic forest. This genus forms nearly pure stands at elevations of 350–2,300 m on slopes and ridges of mountains with soils derived from both granite and limestone or is associated with other conifers (e.g., *Dacrydium*, *Cunninghamia*, *Nothotsuga*, *Cephalotaxus*) and broad-leaved tree species of the families Fagaceae, Lauraceae, Theaceae and Magnoliaceae (Farjon, 2005, 2017). Being not cold-tolerant, *Fokienia* prefers a humid and warm climate, with precipitation in excess of 1,200 mm and a mean annual temperature range of 15.4–23.6°C. It rarely grows in frost-prone areas (Farjon, 2005; Tam et al., 2011; Huang et al., 2013).

Apart from *Fokienia*, a large number of fossils of gymnosperms and angiosperms have been found in Guiping Basin, e.g., representatives of Pinaceae (*Pinus* L., *Keteleeria* Carr.), Podocarpaceae (*Dacrycarpus* (Endl.) de Laub.), Burseraceae (*Canarium* Linn.), Fagaceae and Theaceae (Han et al., 2018; Wu et al., 2021). Among them, *Dacrycarpus* is a robust indicator for a very wet palaeoenvironment, as it requires high precipitation and is one of the least drought-tolerant genera, and is often distributed in tropical mountains. According to the taxonomic composition of the fossil flora and the niches of related modern species, it can be inferred that in the Miocene the Guiping Basin was covered in an evergreen broad-coniferous mixed forest growing under warm and humid climatic conditions.

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DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

JJ, CQ, TK, and NM designed the research. XW, JJ, and SJ collected fossil and modern leaves. XW, HZ, and SJ prepared and studied the cuticles with LM and SEM. JJ, XW, QY, TK, and NM analyzed and interpreted the results. All authors contributed feedback on drafts, revised and approved the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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