Diversity of Fagaceae on Hainan Island of South China During the Middle Eocene: Implications for Phytogeography and Paleoecology

Xiaoyan Liu[1,2,3]*, Hanzhang Song[2] and Jianhua Jin[2]*

[1] School of Geography, South China Normal University, Guangzhou, China, [2] State Key Laboratory of Biocontrol and Guangdong Provincial Key Laboratory of Plant Resources, School of Life Sciences, Sun Yat-sen University, Guangzhou, China, [3] Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China

The Fagaceae family is currently widespread throughout tropical and temperate regions of South America and the Northern Hemisphere, especially East Asia, and has likely been so since the Eocene, according to fossil records. In China, Fagaceae fossils are rare in the lowest latitudes of South China. Here, we describe 12 species in 5 genera of Fagaceae (i.e., *Berryophyllum*, *Castaneophyllum*, *Quercus, Castanopsis*, and *Lithocarpus*) based on leaf morphology and trichomes. These fossils are recovered from the Changchang Formation of Changchang Basin, Hainan Island, South China, indicating that Fagaceae has been distributed in the tropical low latitudes since the Eocene. Given that our fossils are closely related to the tropical and subtropical extant species, we speculate that Fagaceae lineages have likely diverged since the Eocene and that each extant lineage, such as *Quercus* sect. *Cyclobalanopsis*, became highly differentiated no later than middle Eocene. Based on the current living conditions of the extant species, we further speculate that the climate of Hainan Island was warm and wet during the middle Eocene, suitable for the growth and differentiation of the family.

Keywords: Fagaceae, Eocene, South China, phytogeography, paleoecology

INTRODUCTION

The woody angiosperms family Fagaceae, which includes beeches and oaks, defines the structure of subtropical and tropical evergreen forests (Tang, 2015; Wilf et al., 2019). The family is subdivided into ten extant genera: *Fagus* L., *Formanodendron* Nixon et Crepet, *Trigonobalanus* Forman, *Colombobalanus* Nixon et Crepet, *Castanopsis* (D. Don) Spach, *Castanea* Miller, *Notholithocarpus* Manos, Cannon et S. Oh, *Lithocarpus* Bl., *Quercus* L., and *Chrysolepis* Hjelmqvist (Larson-Johnson, 2016). Widely distributed in temperate, subtropical, and tropical regions of the Northern Hemisphere and South America (Huang et al., 1999; Chen, 2007), Fagaceae is most diverse in South and Southeast Asia and North America (Zhou, 1999; Chen, 2007; Denk et al., 2017; Xu et al., 2019). Of the approximately 927 species in 10 genera, China hosts 294 species in 6 genera: *Fagus, Formanodendron, Castanopsis, Castanea, Lithocarpus,* and *Quercus,* most of which are found in South and Southwest China (Li, 1996; Huang et al., 1999). Characterizing the evolution and distribution of Fagaceae in this region is important for understanding this keystone family.

Fagaceae has several distinct features that help define the family, as well as its genera. Its diagnostic leaf characteristics are simple leaves with obliquely-oriented tertiary veins, anomocytic and/or cyclocytic stomatal complexes, and specific trichome complements (Jones, 1986). Of the nine main morphotypes, the two most common are the craspedodromous "chestnut"-like forms or the coarsely round-toothed, deciduous forms, both found among the genera *Castanopsis*, *Castanea*, *Lithocarpus,* and *Quercus*. Trichome is one of the important characteristics of Fagaceae and can be divided into glandular, intermediate, and non-glandular. Simple uniseriate trichome, a glandular trichome, usually occurs in *Lithocarpus*, *Notholithocarpus* and few species of *Q.* sect. *Cyclobalanopsis* (Luo and Zhou, 2001; Liu et al., 2009; Deng et al., 2013). Stellate trichomes are widely present in *Castanopsis*, *Castanea*, *Quercus*, and *Lithocarpus*, representing a symplesiomorphic feature (Liu et al., 2009). Appressed parallel tufts (APT) trichome is unique trichome type in the genus *Lithocarpus*. Therefore, above genera are distinguishable based on the combining characters of venation, tooth type and trichomes.

The Cenozoic is arguably the most important geologic era for the evolution of global angiosperms (Xing et al., 2015) and although the earliest fagaceous fossils were found in the Late Cretaceous, it wasn't until later in the Cenozoic that the family evolved and spread. These earliest fagaceous fossils include *Antiquacupula sulcata* Sims, Herendeen et Crane and *Protofagacea allonensis* Herendeen, Crane et Drinnan with inflorescences and fruit characteristics similar to some taxa of Fagaceae and Nothofagaceae (Herendeen et al., 1995; Sims et al., 1998). From a single Cretaceous site in Georgia USA into the Paleocene, the family became widely distributed in Europe, Asia, and North America (**Figure 1**). Fagaceous fossils from this epoch are mainly assigned to extinct fossil genera, e.g., *Berryophyllum* Jones et Dilcher, *Castaneophyllum* Jones et Dilcher, and *Trigonobalanoidea* Crepet et Nixon (Takhtajan, 1982; Jones and Dilcher, 1988; Crepet and Nixon, 1989a; Kvaček and Walther, 2010). Although *Trigonobalanoidea* has some similar fruits with the extant *Trigonobalanus doichangensis* (A. Camus) Forman and *T. excels* Loz.-Contr., Hern.Com. et Henao-S., there remain many differences (Crepet and Nixon, 1989a) and there is currently no convincing evidence for modern genera Fagaceae during the Paleocene.

The warm and wet climate of the Eocene was critical for the diversification, differentiation, and formation of modern flora, including Fagaceae. Based on numerous reports of leaves, fruits, and dispersed pollen, the fossil record of Fagaceae is well known in for the Northern Hemisphere (**Figure 1**) and one record from the early Eocene in South Argentina (Wilf et al., 2019). Fagaceae became more diverse and widely distributed with the appearance of many modern genera including *Fagus*, *Trigonobalanus*, *Castanopsis*, *Castanea*, *Lithocarpus*, and *Quercus* (**Figure 1**; MacGinitie, 1953, 1969; Axelrod, 1966a,b, 1998a; Writing Group of Cenozoic Plants of China [WGCPC], 1978; Crepet and Daghlian, 1980; Takhtajan, 1982; Mai and Walther, 1985; Kvaček and Walther, 1989; Manchester, 1994; Zhou, 1996; Manchester and Dillhoff, 2004; Vikulin, 2011), as well as two extinct genera (*Berryophyllum* Jones et Dilcher and *Castaneophyllum* Jones et Dilcher). Into the Oligocene, however,

the distribution of other genera has been reduced with the exception of *Quercus* which remain widely distributed in Europe, Asia, and North America (**Figure 1**, Writing Group of Cenozoic Plants of China [WGCPC], 1978; Takhtajan, 1982; Daghlian and Crepet, 1983; Manchester and Crane, 1983; Crepet and Nixon, 1989b; Kvaček and Walther, 1989, 2004, 2010; Meyer and Manchester, 1997). From the Miocene, some extant genera had begun to flourish in Europe, Asia, and North America while *Berryophyllum* and *Castaneophyllum* had almost disappeared (**Figure 1**, Axelrod, 1956, 1962; Wolfe and Tanai, 1980; Takhtajan, 1982; Kvaček and Walther, 1989; Palamarev and Tsenov, 2004; Hably, 2013).

In China, previously reported Fagaceae fossils were mainly recovered from the Eocene to Pleistocene strata in the northern and southwestern regions, including Liaoning, Shandong, Tibet, Sichuan, and Yunnan (Writing Group of Cenozoic Plants of China [WGCPC], 1978; Liu et al., 1995; Tao et al., 2000; Xiao et al., 2006; Xing et al., 2013; He et al., 2014; Wu et al., 2014; Li et al., 2015). Reports on Fagaceae fossils from the tropical low latitudes of South China are rare. The fossil history and its biogeographic implications of Fagaceae have been previously discussed (Zhou, 1999; Chen, 2007) given the continuous increase of this family's fossil record in recent years (Mindall et al., 2007, 2009; Vikulin, 2011; Xing et al., 2013; He et al., 2014; Wu et al., 2014; Jia et al., 2015; Li et al., 2015; Xu et al., 2016; Wilf et al., 2019), the diversity, and phytogeographic history of the family need to be further studied.

In this study, we studied 41 leaf fossils of Fagaceae recovered from the middle Eocene of Changchang Formation, Changchang Basin, Hainan Island, South China. Twelve species within 5 genera (*Berryophyllum* Jones et Dilcher, *Castaneophyllum* Jones et Dilcher, *Castanopsis*, *Lithocarpus,* and *Quercus*) have been described based on the leaf morphology and trichomes via Scanning Electron Microscopy (SEM). The present discovery documents a tropical low latitude distribution of Fagaceae in the middle Eocene. Moreover, our fossils are closely related to the extant tropical and subtropical elements, providing an important contribution to the understanding of the historical biogeography of this family and the paleoecology of Hainan Island during the middle Eocene.

MATERIALS AND METHODS

The present fossils were collected from the Changchang Formation of Changchang Basin (**Figure 2**, 19°38′03″N, 110°27′04″E), located near Jiazi Town, Qiongshan County, in the northeastern part of Hainan Island, South China and housed in the Museum of Biology, Sun Yat-sen University, Guangzhou, China.

The Changchang Formation is composed of two parts: the lower coal-bearing part is ca. 52–54 m thick and consists of clastic terrigenous and coal deposits with mudstone, coaly shale, oil-bearing shale, muddy siltstone, and sandstone, and coal; the upper part is ca. 37–40 m thick and consists predominantly of lacustrine and fluvial mudstones, siltstones, and sandstones (Spicer et al., 2014). Numerous well-preserved plant macrofossils,

FIGURE 1 | Fossil records of Fagaceae in the Cenozoic. PA, Paleocene; EO, Eocene; OL, Oligocene; MI, Miocene; PLI, Pliocene; PLEI, Pleistocene; SA, South America; NA, North America; A, Asia; EU, Europe. References for the fossil records are listed in S1 (**Supplementary Material**).

FIGURE 2 | Geographic map of the fossil locality. Base map modified after the Standard Map Service of the National Administration of Surveying, Mapping and Geoinformation of China (http://bzdt.ch.mnr.gov.cn/).

including the fagaceous leaf fossils investigated here, were mainly collected from the lower part of the Changchang Formation. These deposits also contain diverse pollen and spore assemblages (Zhang, 1980; Lei et al., 1992; Yao et al., 2009; Hofmann et al., 2019), as well as bivalve and gastropod remains, and fish bones and scales. The age of the Changchang Formation was originally

considered to be the late Palaeocene to early/middle Eocene based on floral composition (Guo, 1979). Later, the Changchang Formation is dated on the basis of palynological data as the middle Oligocene (Zhang, 1980), the late early Eocene to early late Eocene (Lei et al., 1992), and early middle Eocene (Yao et al., 2009). Recently, Spicer et al. (2014) dates the Changchang Formation as middle Eocene (Lutetian–Bartonian, ca.48–38 Ma) based on comprehensive analysis on the macrofossil flora, its similarity with the adjacent deposit Youganwo Formation in Maoming Basin, Guangdong Province, South China, and previously published palynological data. Here we followed the age assessment by Spicer et al. (2014).

Leaf fossils were photographed using a Canon EOS 500D digital camera (Canon, Tokyo, Japan). Small cuticular fragments of some species were recovered from the leaf fossils. Remnant rock particles adhering to the leaf fossils were removed using 40% HF for 24 h. The specimens were then rinsed in distilled water and mounted on stubs, coated with gold, and then examined and photographed using a JSM-6330F SEM (JSM, Tokyo, Japan).

We examined the extant specimens of *Quercus*, *Lithocarpus*, and *Castanopsis* represented in herbaria of the South China Botanical Garden, Chinese Academy of Sciences (IBSC, Guangzhou), Sun Yat-sen University (SYS, Guangzhou), Harvard University (HUH, Boston) and the University of Florida (FLAS, Gainesville). Leaf terminology follows Ellis et al. (2009). The following states and abbreviations are used for interpreting tooth types: convex (CV), straight (ST), concave (CC), retroflexed (RT; tooth flank is basally concave and apically convex). Tooth shape is described in terms of the distal and proximal flank curvatures relative to the midline of the tooth. The distal flank shape is always given first, e.g.: CV-ST indicates that the tooth is concave on the distal flank and straight on the proximal flank.

RESULTS

Order Fagales Engl. 1892
Family Fagaceae Dumort. 1829
Genus *Berryophyllum* Jones et Dilcher, 1988
Species *Berryophyllum relongtanense* (Colani) Z. K. Zhou (**Figure 3**)
Specimens examined CC-998 (a, b), CC-1107
Description Leaf lanceolate (**Figure 3A**), 4.6–5.4 cm long, 1.5–1.6 cm wide, base cuneate (**Figure 3B**). Margin entire near base, serrate from > 1/3 of the leaf to the apex (**Figure 3A**), teeth CC-ST with rounded sinus (**Figure 3C**). Midvein thick, straight or slightly bend; secondary veins pinnate, opposite at base, alternate from the third pairs to apex, craspedodromous, with angles 30–40° between the midvein and secondary veins (**Figure 3A**); Tertiary veins mostly opposite percurrent; Quaternaries regular, rectangular to polygonal reticulate (**Figure 3C**). Leaf surface rugose with solitary trichomes and stomata (**Figures 3D–F**).
Comparison The present specimens are assigned to *Berryophyllum* because they have lanceolate leaves, cuneate bases, serrate margins with CC-ST teeth and craspedodromous secondary veins (**Figures 3A–C**). They are similar to

Dryophyllum puryearensis Berry, *D. anomalum* Berry, and *B. tennesseensis* (Berry) Jones et Dilcher from the early Eocene of southeastern North America on the leaf shape (Berry, 1916; Jones and Dilcher, 1988), but they are different on venations. The present fossils are distinguished with *B. dewalquei* (Sap. et Mar.) Zhou (1996) and *B. yunnanense* (Colani) Zhou (1996) by the leaf shape, the trend and angle of secondary veins and the teeth (Writing Group of Cenozoic Plants of China [WGCPC], 1978; Zhou, 1996). Our specimens conform to the diagnosis of *B. relongtanense* (Colani) Z. K. Zhou previously recognized from Writing Group of Cenozoic Plants of China [WGCPC] (1978) and Zhou (1996).

Species *Berryophyllum hainanensis* X-Y Liu et J-H Jin sp. nov. (**Figure 4**).
Diagnosis Leaf narrowly lanceolate, apex elongate, acuminate or caudate bending to the right. Margin serrate up to the apex, teeth CC-ST to CC-CV with rounded sinus. Midvein straight to slightly bend in apex; secondary veins pinnate, nearly opposite, craspedodromous, bend inward in margin, with angles 40–50° between the midvein and secondary veins; Tertiary veins mixed percurrent; Quaternaries regular, rectangular to polygonal reticulate. Leaf surface rugose with verrucae.
Holotype CC-1244 (a, b)
Paratypes CC-1103, CC-1118 (a, b)
Etymology The specific epithet "*hainanensis*" refers to the Hainan Island from which the specimens were collected.
Description Leaf narrowly lanceolate (**Figures 4A–E**), preserved part 4.3–9.0 cm long, 1.5–1.6 cm wide, apex elongate, acuminate or caudate bending to the right (**Figures 4A,E**). Margin serrate up to the apex, irregular spaced (**Figures 4A,B,D,E**), teeth CC-ST to CC-CV with rounded sinus (**Figures 4B–D,F**). Midvein straight to slightly bend in apex; secondary veins pinnate, nearly opposite, craspedodromous, bend inward in margin, with angles 40–50° between the midvein and secondary veins (**Figures 4A,C,D**); Tertiary veins mixed percurrent; Quaternaries regular, rectangular to polygonal reticulate (**Figure 4C**). Leaf surface rugose with verrucae (**Figure 4G**).
Comparison The present specimens are distinguished from *B. relongtanense* which is also known from the same site, because they are narrowly lanceolate in shape while *B. relongtanense* is lanceolate. The present fossils are also different from the linear or extremely narrowly lanceolate leaves of *Berryophyllum tenuifolia* Jones and Dilcher (1988) and the lanceolate leaves of *B. dewalquei*, *B. yunnanense*, and *B. relongtanense* (Writing Group of Cenozoic Plants of China [WGCPC], 1978; Zhou, 1996). Our fossils are similar to *Dryophyllum berendtianum* (Goepp.) Kirchh. from the Eocene of Ukraine and Kaliningrad, Russia (Takhtajan, 1982) on having elongate acuminate or caudate apex with clear teeth. However, the teeth of our fossils have more irregular spaced teeth and narrower leaves than *D. berendtianum*. The features of narrowly lanceolate leaf shape with elongate acuminate or caudate apex, irregularly spaced CC-ST to CC-CV teeth and pinnate secondary veins without forming a loop convinced us to assign these fossils to a new species *B. hainanensis* sp. nov (**Figure 4**).
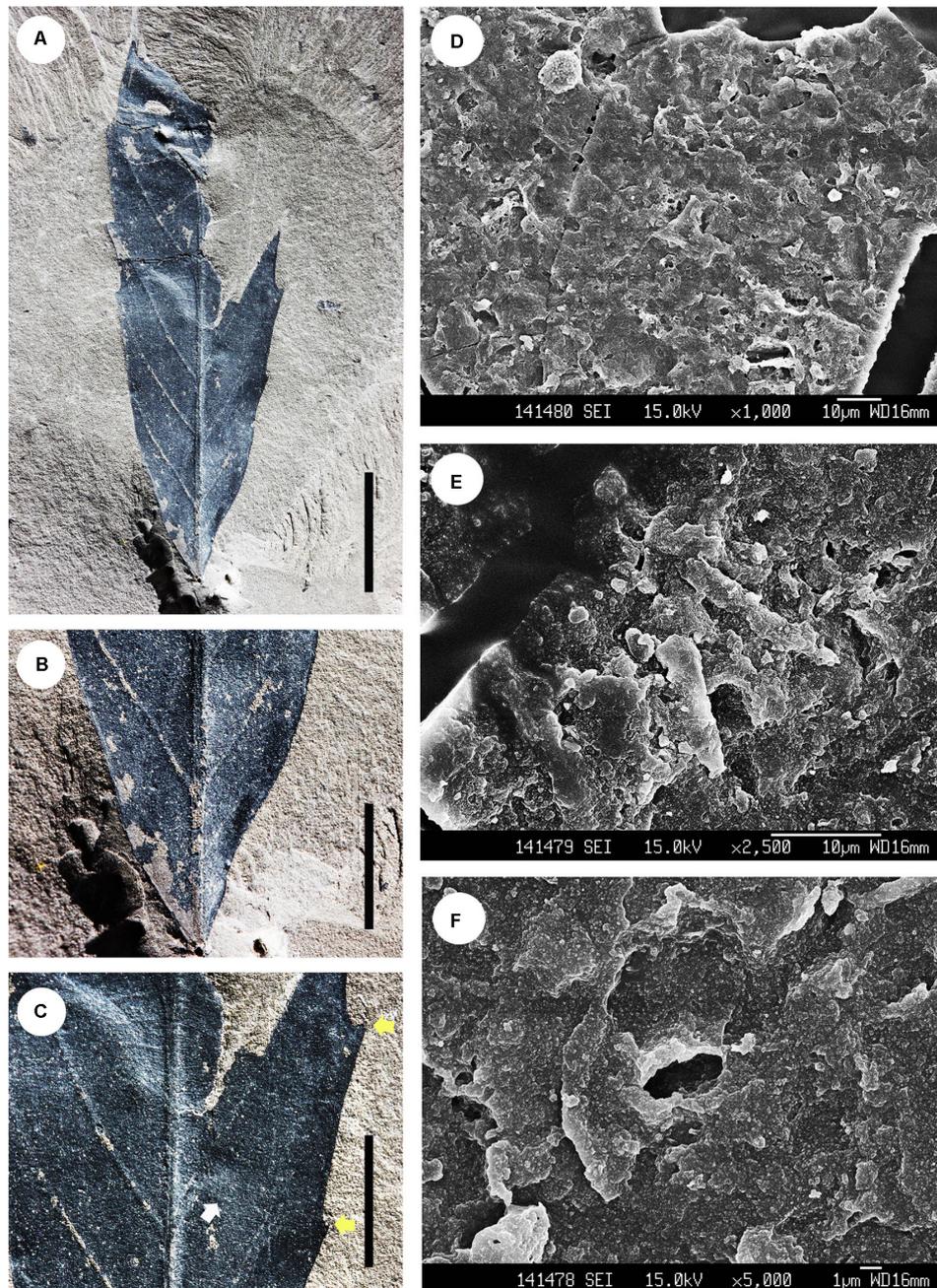
FIGURE 3 | Morphology of *Berryophyllum relongtanense* (Colani) Z.K. Zhou. **(A)** Specimen No. CC-998, showing leaf morphology; **(B)** enlargement of **(A)**, showing the base of the specimen; **(C)** enlargement of **(A)**, yellow arrows indicate leaf margin with teeth, white arrow indicates the tertiary and quaternary venations; **(D)** SEM image showing rugose structures on the outer surface of leaf; **(E)** showing solitary trichomes on the outer surface of leaf; **(F)** showing stomata on the outer surface of leaf. Scale bars: 10 mm **(A)**; 5 mm **(B,C)**.

Genus *Castaneophyllum* Jones et Dilcher, 1988

Species *Castaneophyllum hainanensis* X-Y Liu et J-H Jin sp. nov. (**Figure 5**)

Diagnosis Leaf lanceolate, base cuneate, symmetric. Margin entire near base, serrate from > 1/3 of the leaf to the apex, teeth ST-CC to CC-CC with rounded sinus; Tip slightly bend inward. Midvein thick, straight; secondary veins at least 10 pairs, pinnate, nearly opposite, craspedodromous, bend in ward near the margin; Tertiary veins mixed percurrent; Quaternaries regular, rectangular to polygonal reticulate. Leaf surface rugose with solitary trichomes.

Holotype CC-1260

Paratypes CC-1111, CC-1117, CC-1242, CC-1250
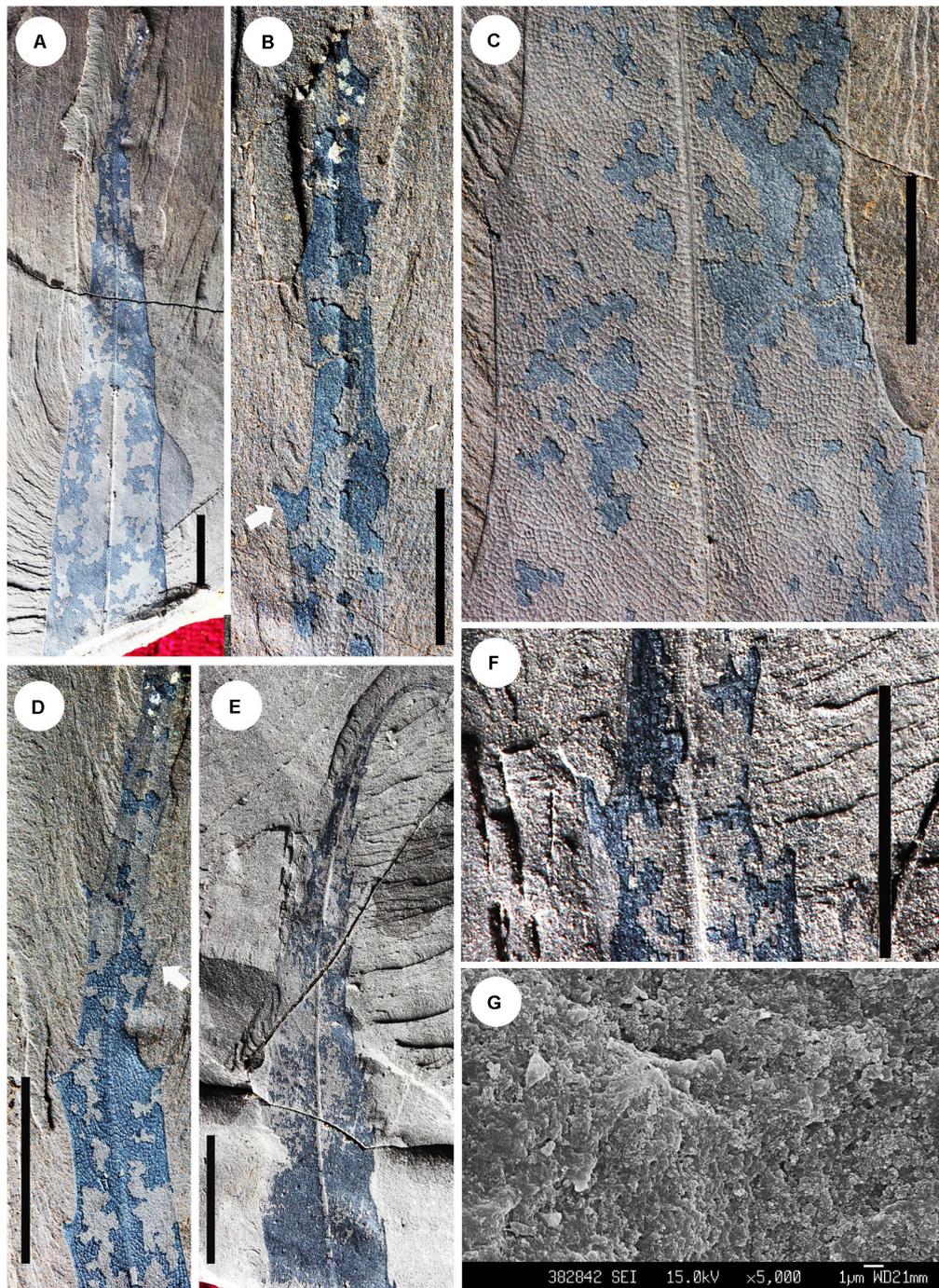
FIGURE 4 | Morphology of *Berryophyllum hainanensis* sp. nov. **(A)** Holotype. Specimen No. CC-1244a, showing leaf morphology; **(B)** specimen No. CC-1244b, arrow indicates the tooth; **(C)** enlargement of **(A)**, showing the tooth and venation; **(D)** enlargement of **(A)**, showing the apex with teeth (white arrow); **(E)** paratype. Specimen No. CC-1118a, showing the leaf shape; **(F)** enlargement of **(E)**, showing the teeth; **(G)** granular microstructure on the surface. Scale bars: 10 mm **(A,C,D)**; 5 mm **(B,E,F)**.

Etymology The specific epithet "*hainanensis*" refers to the Hainan Island from which the specimens were collected.

Description Leaf lanceolate (**Figure 5A**), preserved part 3.2–10.1 cm long, 1.2–2.0 cm wide, base cuneate, symmetric (**Figure 5A**). Margin entire near base, serrate from > 1/3 of the leaf to the apex (**Figure 5A**), teeth ST-CC to CC-CC with rounded sinus; Tip slightly bend inward (**Figure 5B**). Midvein thick, straight;
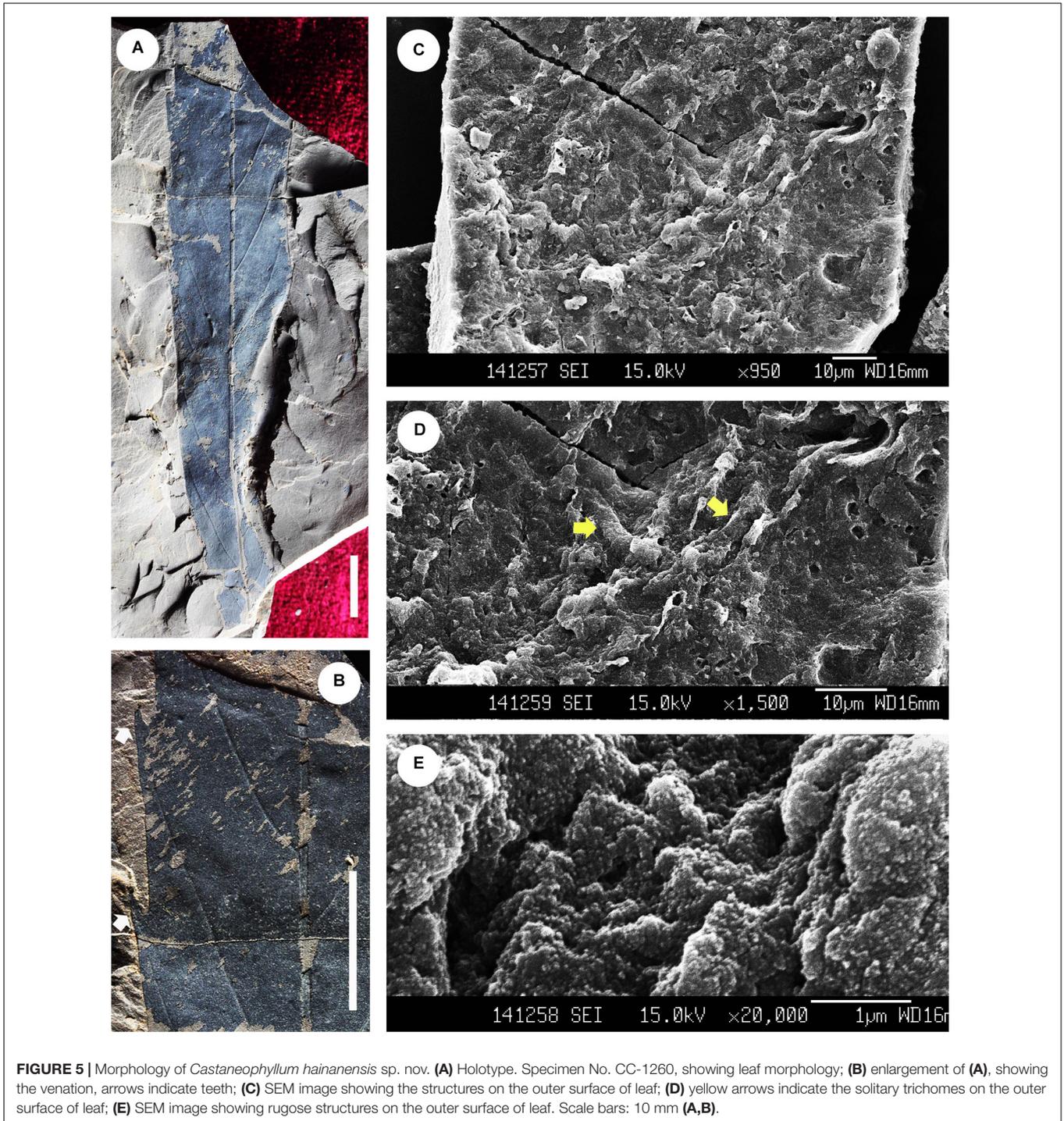
FIGURE 5 | Morphology of *Castaneophyllum hainanensis* sp. nov. **(A)** Holotype. Specimen No. CC-1260, showing leaf morphology; **(B)** enlargement of **(A)**, showing the venation, arrows indicate teeth; **(C)** SEM image showing the structures on the outer surface of leaf; **(D)** yellow arrows indicate the solitary trichomes on the outer surface of leaf; **(E)** SEM image showing rugose structures on the outer surface of leaf. Scale bars: 10 mm **(A,B)**.

secondary veins at least 10 pairs, pinnate, nearly opposite, craspedodromous, bend inward near the margin, with angles 50° between the midvein and secondary veins (**Figure 5A**); Tertiary veins mixed percurrent; Quaternaries regular, rectangular to polygonal reticulate (**Figure 5B**). Leaf surface rugose with solitary trichomes, 20.6–35.6 μm (mean = 27.6 μm) long, 2.0–5.1 μm (mean = 4.3 μm) wide (**Figures 5C,D**).

Comparison The present specimens are attributed to the *Castaneophyllum* rather than *Castanea* because their lanceolate leaf shape, craspedodromous and bend inward secondary veins and mixed percurrent tertiary veins are consistent with the *Castaneophyllum* (**Figures 5A,B**). Our specimens differ to *Castanea* on the secondary and tertiary veins. The secondary veins of *Castanea* are decurved near the midribs with two adjacent secondary veins near the midribs closer than those

near the margin. The tertiary veins of *Castanea* are opposite percurrent. This new species is similar to *Castaneophyllum tennesseense* (Berry) Jones et Dilcher (1988) from the Eocene of Tennessee, North America on the lanceolate leaf shape, but it is different on the teeth characters and arrangement of the secondary veins. Our specimens are distinguished from *C. moorii* (Lesq.) Jones et Dilcher (1988) which is elliptic to narrowly elliptic, 23 cm long and secondary veins closely spaced from the Eocene of Tennessee, by the leaf shape, size and venations. Our fossils greatly differ from *C. fushunense* (Chen et Wang) Z.K. Zhou from the Eocene of Fushun, Liaoning Province in teeth type and angles between midvein and secondary veins (Writing Group of Cenozoic Plants of China [WGCPC], 1978; Zhou, 1996).

Species *Castaneophyllum lanceolata* X-Y Liu et J-H Jin sp. nov. (**Figure 6**)

Diagnosis Leaf lanceolate, apex elongate acuminate, base cuneate. Margin entire near base, serrate from > 1/3 of the leaf to the apex, teeth ST-CV to CC-CV with rounded sinus. Midvein thick, straight; secondary veins 15 pairs, opposite from base to middle, pinnate from middle to apex, craspedodromous, bend in ward near the margin; Tertiary veins opposite percurrent; Quaternaries unclear. Leaf surface rugose with solitary trichomes.

Holotype CC-1106 (a, b)

Etymology The epithet "*lanceolata*" refers to the specimen has elongate lanceolate leaf.

Description Leaf lanceolate (**Figure 6A**), preserved part 12.6 cm long, 1.8 cm wide, length/width ratio 7, apex elongate acuminate with the angle 15°, base cuneate with the angle 30° (**Figures 6B,C**). Margin entire near base, serrate from > 1/3 of the leaf to the apex (**Figure 6A**), teeth ST-CV to CC-CV with rounded sinus (**Figures 6D–F**). Midvein thick, straight; secondary veins 15 pairs, opposite from base to middle, pinnate from middle to apex, craspedodromous, bend in ward near the margin, with angles 45° from base to the 3/4 of the leaf and declining up to the apex (**Figures 6A,E**); Tertiary veins opposite percurrent (**Figure 6F**); Quaternaries unclear. Leaf surface rugose with solitary trichomes, 15.6–18.8 μm (mean = 17.2 μm) long, 1.3–2.5 μm (mean = 1.9 μm) wide (**Figures 6G,H**).

Comparison The present fossil is attributed to *Castaneophyllum* because its leaves lanceolate with elongate acuminate apex, cuneate base, and serrate margin, secondary and tertiary veins (**Figures 6A–F**). This new species differs from *C. hainanensis*, described above, by the venation and tooth type. The present fossil is very similar to *C. tennesseense* (Jones and Dilcher, 1988), for both having lanceolate leaf and variable teeth type, but the present fossil has more elongate acuminate apex and smaller leaf than *C. tennesseense*. Our specimen with the length of 12.6 cm is much smaller than *C. moorii* and *C. fushunense* (Writing Group of Cenozoic Plants of China [WGCPC], 1978; Zhou, 1996).

Species *Castaneophyllum* cf. *moorii* (Lesq.) Jones et Dilcher (**Figure 7**)

Specimen examined CC-1136

Description Leaf lanceolate, symmetric, preserved part 4.4 cm long, 1.6 cm wide (**Figure 7A**). Margin serrate (**Figure 7A**), teeth ST-ST with rounded sinus (**Figure 7B**). Midvein thick, straight; secondary veins more than 9 pairs irregularly spaced, nearly opposite, craspedodromous, with stable angles 55° (**Figure 7A**); Tertiary and quaternaries veins unclear. Leaf surface rugose with stellate trichomes with 9 solitary branches; Branches 22.7–32.7 μm (mean = 27.7 μm) long, 1.8–2.3 μm (mean = 2.1 μm) wide (**Figures 7C–E**).

Comparison The present fossil is confirmed to *Castaneophyllum* because its lanceolate leaf shape, serrate margin, secondary and tertiary veins (**Figures 7A,B**). It is closest to *C. moorii* by having consistent characteristics of teeth type, similar angles between the midvein and secondary veins and the arrangement of secondary veins, but they are different in leaf shape and size. The present specimens are similar to *Q. relongtanense* Colani and *Quercus* cf. *relongtanense* Colani from the Miocene-Pliocene of To-tang, Yunnan Province, Southwest China (Colani, 1920) in venation, but our specimens have ST-ST teeth with rounded sinus and stellate trichomes, while the To-Tang species are lacking the details of leaf margin and surface.

Genus *Castanopsis* (D. Don) Spach, 1842
Species *Castanopsis* sp. (**Figure 8**)
Specimen examined CC-343, CC-401, CC-1276
Description Leaf lanceolate, preserved part 5.2–6.7 cm long, 2.9–3.2 cm wide (**Figure 8A**, apex acuminate (**Figure 8F**). Margin serrate, teeth irregularly spaced (**Figures 8F,G**). apex acuminate (**Figure 8F**). Margin serrate, teeth regularly spaced (**Figures 8A,F,G**), ST-RT with rounded sinus (**Figures 8B,C,H,I**). Midvein thick, straight; secondary veins more than 12 pairs regularly spaced, nearly opposite, craspedodromous, slightly bend in ward near the margin, with angles 40–50° (**Figures 8A,B**). Tertiary and quaternaries veins unclear. Leaf surface rugose with stellate trichomes with 6–10 solitary branches; Branches 22.7–29.1 μm (mean = 25.9 μm) long, 2.0–4.5 μm (mean = 3.25 μm) wide (**Figures 8D,E**).

Comparison we decided to assign the present specimen to *Castanopsis* based on the venation and ST-RT teeth with rounded sinus (**Figures 8A–C**). Our fossils resemble the extant *C. sclerophylla* on the tooth type and secondary veins, but they are different in the arrangement of the teeth. Our specimens have teeth from base to apex, while only the top 1/3 part of *C. sclerophylla* has teeth. This new species is similar with the extant *C. sclerophylla* (Lindl. et Paxton) Schottky in the characteristic of leaf shape and teeth type, but they are obviously different in secondary veins and trichomes. Our specimen has stellate trichomes (**Figures 8D,E**), while *C. sclerophylla* has thin-walled peltate trichomes. Our fossil has similar stellate trichomes with *C. mekongensis* A. Camus, but their leaf shape, size and angles between midvein and secondary veins are quite different. The present specimen is also distinctive from the previously fossil records of *Castanopsis* in the Cenozoic of China and North America (Wolfe, 1968; Tao et al., 2000; Wu et al., 2014; Li et al., 2015) by the teeth arrangement and small angle between midvein and secondary veins. Although *Castaneophyllum* cf. *moorii* also has stellate trichomes, these specimens are assigned to *Castanopsis* rather
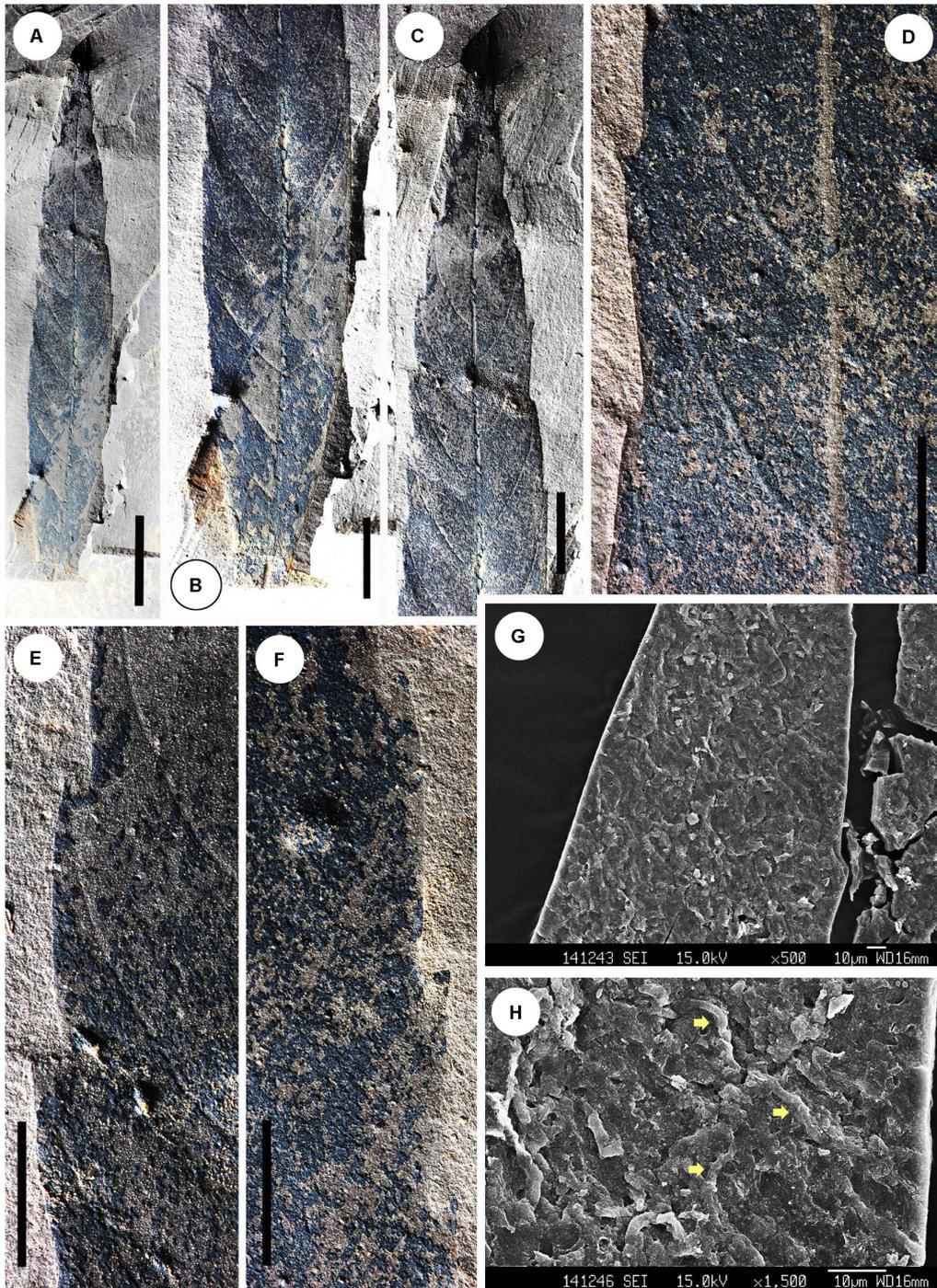
FIGURE 6 | Morphology of *Castaneophyllum lanceolata* sp. nov. **(A)** Holotype. Specimen No. CC-1106a, showing leaf morphology; **(B)** enlargement of **(A)**, showing the secondary veins from middle to base; **(C)** enlargement of **(A)**, showing the secondary veins from middle to apex; **(D)** enlargement of **(A)**, showing the teeth; **(E)** enlargement of **(A)**, showing the secondary veins end to the margin; **(F)** enlargement of **(A)**, showing the tertiary veins; **(G)** SEM showing rugose outer surface; **(H)** yellow arrows indicate solitary trichomes. Scale bars: 10 mm **(A–C)**; 5 mm **(D–F)**.

than *Castaneophyllum* for their ST-RT teeth and regularly spaced secondary veins.

Genus *Lithocarpus* Bl., 1826

Species *Lithocarpus changchangensis* X-Y Liu et J-H Jin sp. nov. (**Figure 9**)

Diagnosis Leaf elliptic, base cuneate with a short petiole. Margin serrate from 1/4 of the leaf to apex, teeth regularly

FIGURE 7 | Morphology of *Castaneophyllum* cf. *moorii* (Lesq.) Jones et Dilcher. **(A)** Specimen No. CC-1136, showing leaf morphology; **(B)** enlargement of **(A)**, showing teeth, tertiary veins and quaternary veins; **(C)** stellate trichomes and rugose structures on the outer surface; **(D)** yellow arrow indicates stellate trichomes; **(E)** SEM image showing stomata. Scale bars: 10 mm **(A)**; 5 mm **(B)**.
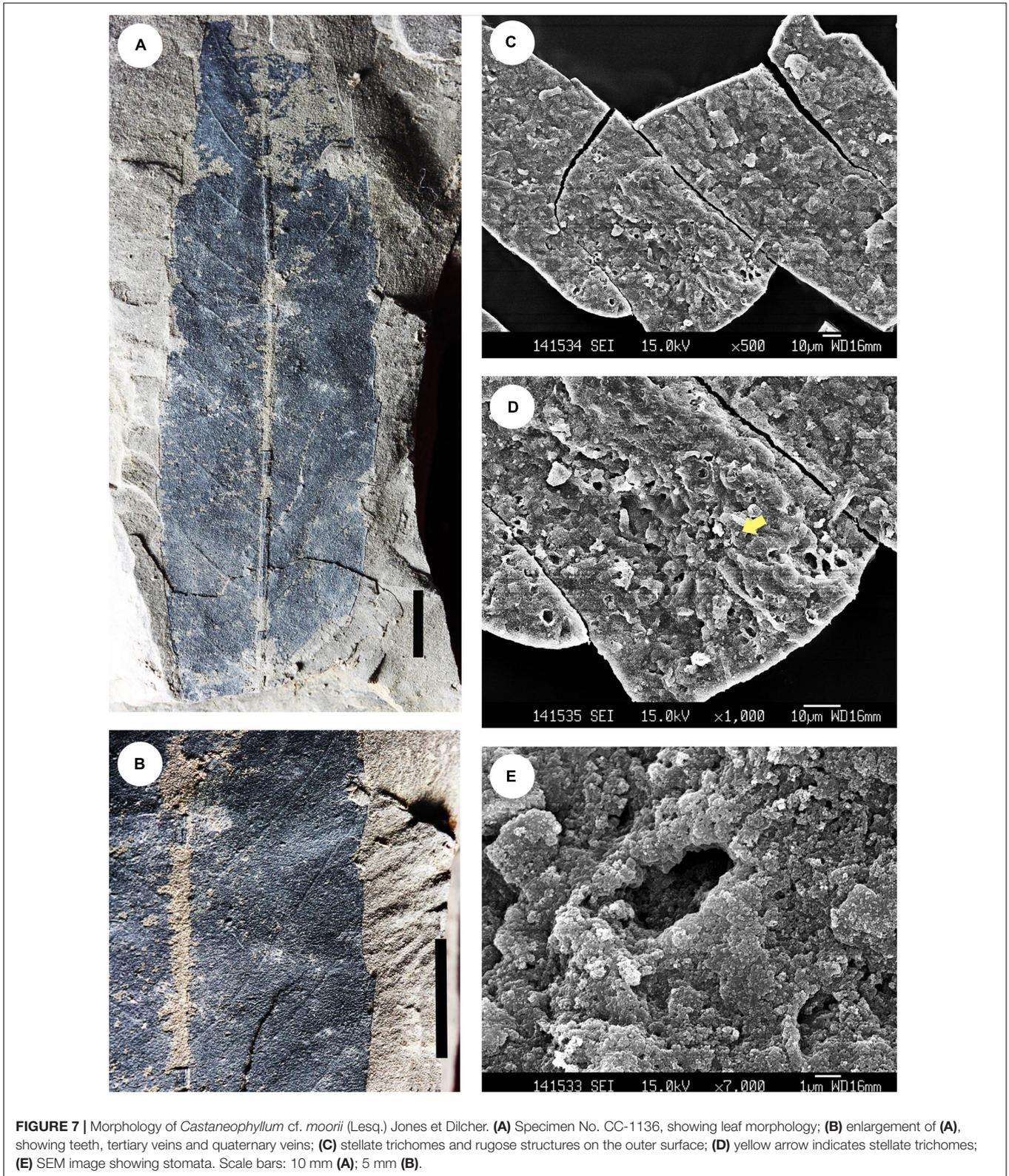
spaced, ST-ST or CV-CV with rounded sinus. Midvein straight; secondary veins thin, secondary veins more than 8 pairs regularly spaced, pinnate, craspedodromous. Tertiary veins opposite percurrent; Quaternaries unclear. Leaf surface rugose with appressed parallel tufts (APT) trichomes.

Holotype CC-1113
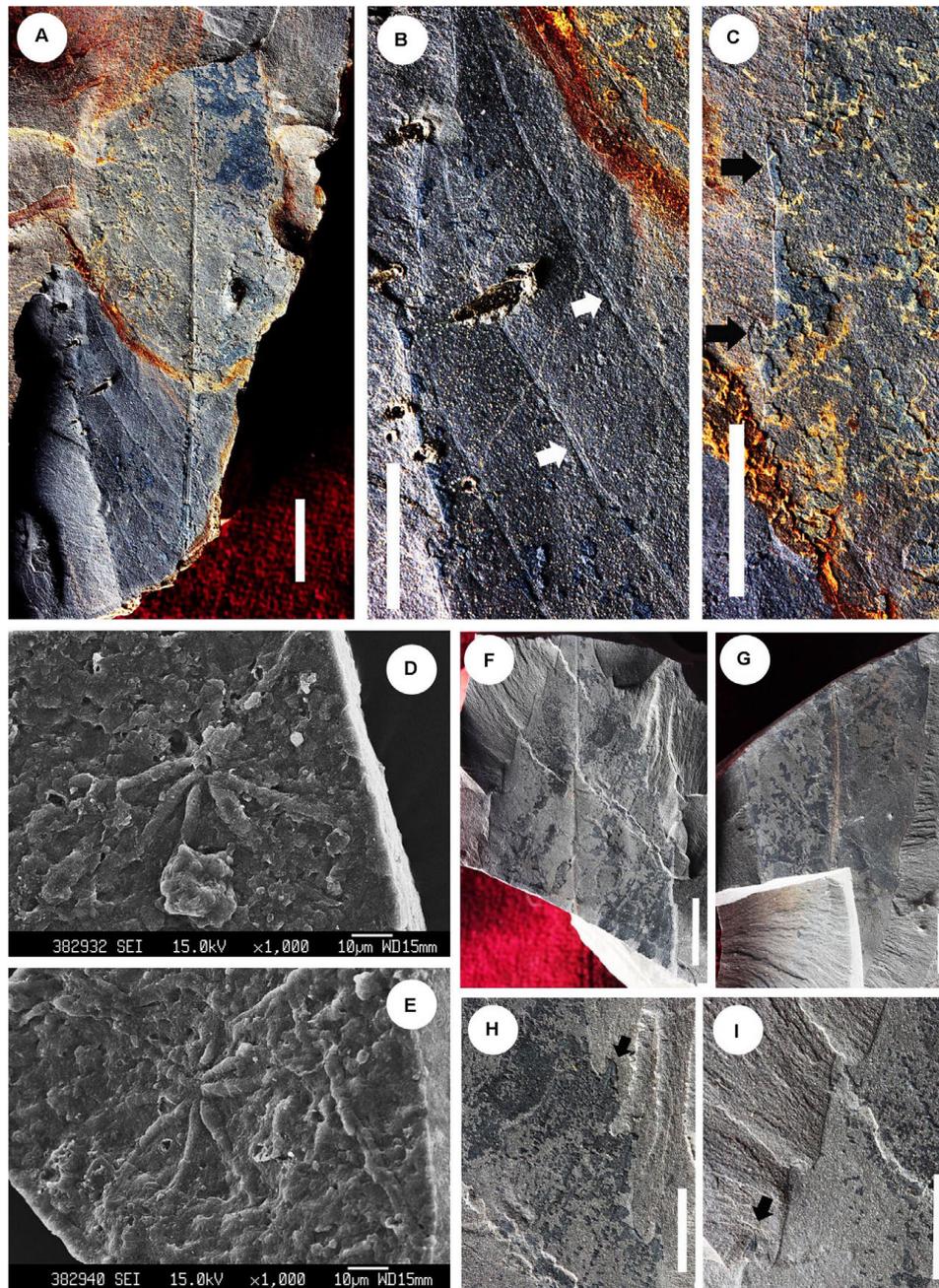
FIGURE 8 | Morphology of *Castanopsis* sp. **(A)** Specimen No. CC-1276, showing the leaf morphology; **(B)** enlargement of **(A)**, showing the secondary veins (white arrows) and tertiary veins; **(C)** enlargement of **(A)**, showing the teeth (black arrows); **(D,E)** SEM images showing the rugose outer surface and stellate trichomes. **(F)** Specimen No. CC-401, showing the leaf morphology; **(G)** specimen No. CC-343, showing the leaf morphology; **(H,I)** enlargement of **(F)**, showing the teeth (black arrows) and tertiary veins. Scale bars: 10 mm **(A,F,G)**; 5 mm **(B,C,H,I)**.

Paratypes CC-1126, CC-1237, CC-1238, CC-1281, CC-1284

Etymology The specific epithet "*changchangensis*" refers to the Changchang Formation from which the specimens were collected.

Description Leaf elliptic, preserved part 4.1–6.0 cm long, 1.2–1.8 cm wide (**Figure 9A**), base slightly asymmetry, cuneate with a short petiole, 4 mm long, 1 mm wide (**Figure 9B**).

Margin serrate from 1/4 of the leaf to apex, teeth regularly spaced (**Figure 9A**), ST-ST or CV-CV with rounded sinus, respectively (**Figure 9C**). Midvein straight; secondary veins thin, secondary veins more than 8 pairs regularly spaced, pinnate, craspedodromous (**Figures 9A,C**). Tertiary veins opposite percurrent (**Figure 9C**); Quaternaries unclear. Leaf surface rugose with appressed parallel tufts (APT) trichomes with 2
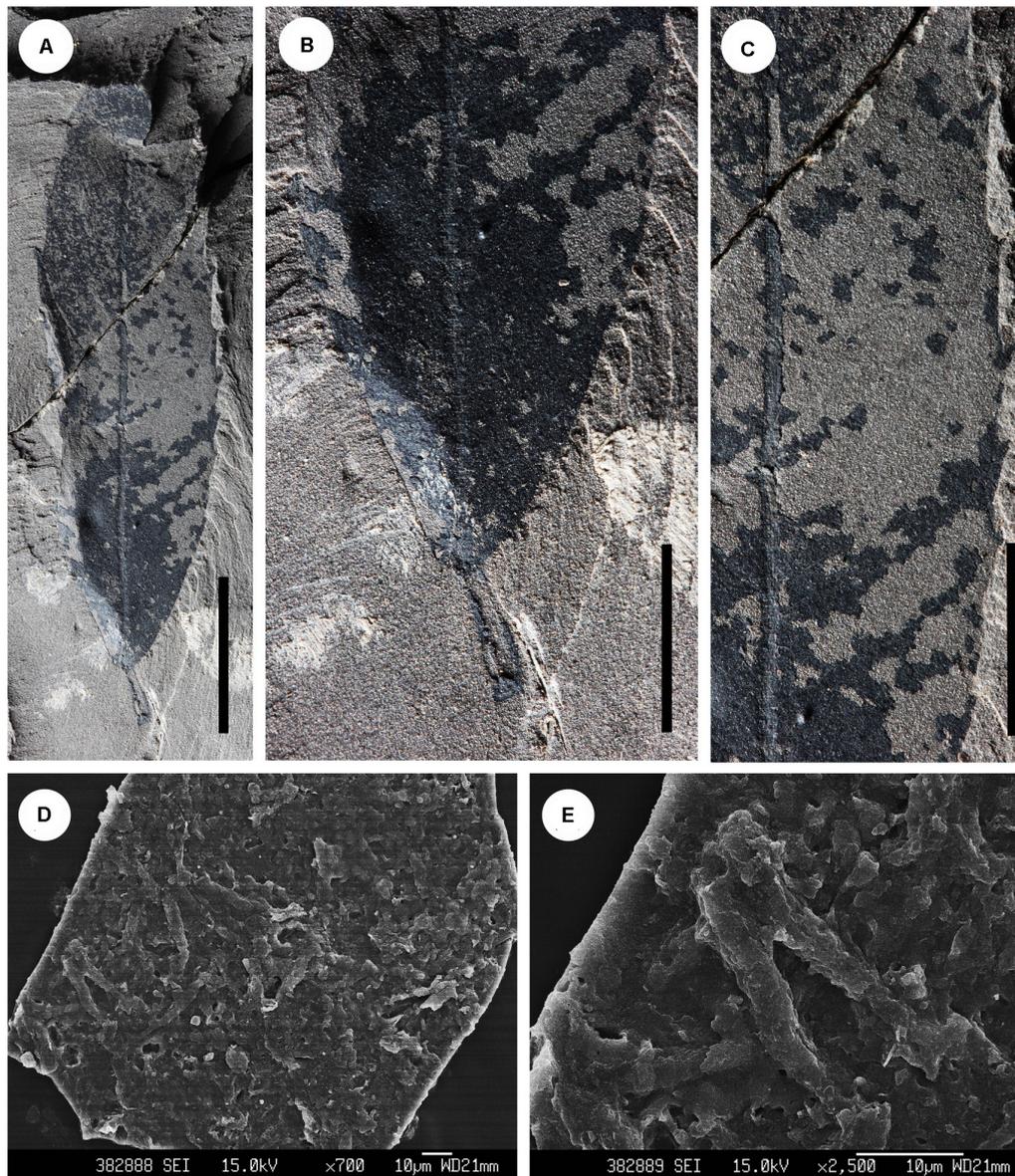
FIGURE 9 | Morphology of *Lithocarpus changchangensis* sp. nov. **(A)** Holotype. Specimen No. CC-1113, showing the leaf morphology; **(B)** enlargement of **(A)**, showing the base and petiole; **(C)** enlargement of **(A)**, showing the teeth and venation; **(D)** SEM image showing the rugose outer surface of leaf; **(E)** SEM image showing the appressed parallel tufts (APT) trichomes. Scale bars: 10 mm **(A)**; 5 mm **(B,C)**.

thick-walled, unicellular elements; Branches 3.7 μm long, 0.8 μm wide (**Figures 9D,E**).

Comparison Appressed parallel tufts (APT) trichome is unique trichome type in the genus *Lithocarpus*. The present fossils are confirmed to be *Lithocarpus* mainly based on leaf shape, venation and appressed parallel tufts (APT) trichomes with 2 thick-walled, unicellular elements (**Figure 9**). The tooth type and the secondary veins of the present fossils are similar to the extant *L. fordianus* (Hamsl.) Chun, but our fossils with the length of 4.1–6.0 cm are much smaller than *L. fordianus* with the length of 10–25 cm. The present fossils are different from all reported fossil records *Lithocarpus* leaves

from the Cenozoic of China, Europe and North America. Therefore, our fossils are assigned to a new species *Lithocarpus changchangensis* sp. nov.

Genus *Quercus* L. 1753
Subgenus *Cerris* Oerst.
Section *Cyclobalanopsis* (Oerst.) Benth. et Hook.
Species *Quercus paleohypargyrea* X-Y Liu et J-H Jin sp. nov. (**Figure 10**)

Diagnosis Leaf elliptic, base cuneate with a petiole. Margin serrate from 1/5 of the leaf to apex, teeth regularly spaced, CC-CV to CC-CC with rounded sinus. Midvein slightly curved;
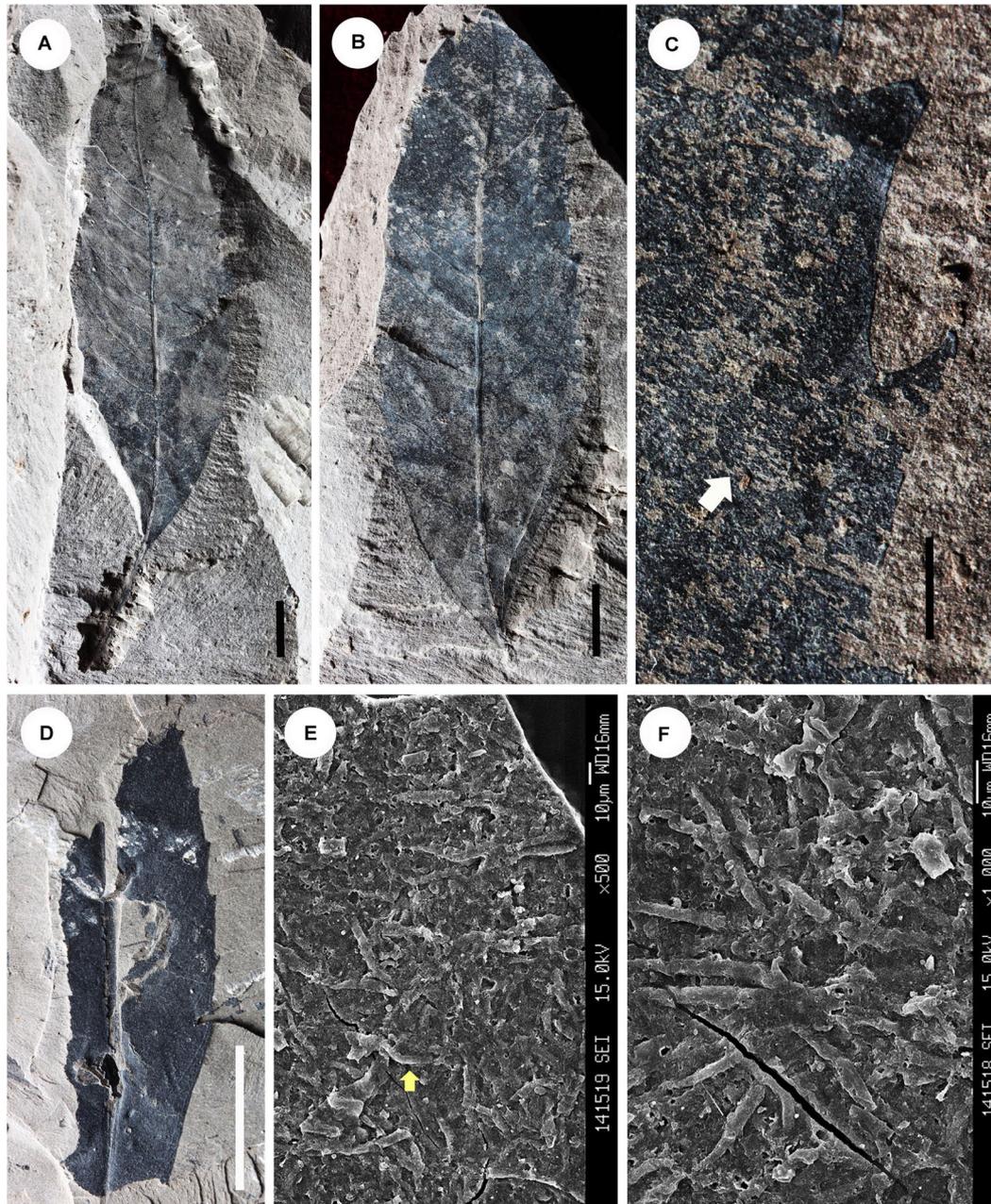
FIGURE 10 | Morphology of *Quercus paleohypargyrea* sp. nov. **(A)** Holotype. Specimen No. CC-1277a, showing the lanceolate leaf, more secondary vein; **(B)** counterpart of **(A)**, showing the median vein slightly bend; **(C)** Enlargement of **(A)**, showing the teeth and tertiary and quaternary veins (white arrow); **(D)** paratype Specimen No. CC-1108, showing the leaf morphology; **(E)** SEM image of **(D)**, showing the rugose outer surface and stellate trichomes (yellow arrow); **(F)** enlargement of E, showing the details of the stellate trichome. Scale bars: 10 mm **(A,B,D)**; 2 mm **(C)**.

secondary veins thin, 15–23 pairs regularly spaced, pinnate, craspedodromous, straight or slightly curved. Tertiary veins mixed percurrent; Quaternary veins regular, rectangular to polygonal reticulate. Leaf surface rugose with stellate trichomes with 4–8 solitary branches.

Holotype CC-1277 (a, b)

Paratypes CC-1108 (a, b), CC-1236, CC-1259

Etymology The specific epithet "*paleohypargyrea*" refers to its close affinity to the extant *Quercus hypargyrea* (Seemen ex Diels) C.C. Huang et Y.T. Chang.

Description Leaf elliptic, preserved part 3.8–8.9 cm long, 1.1–3.0 cm wide, base cuneate with the petiole 3.5–12 mm in length, 1–1.5 mm in width (**Figures 10A,B**). Margin serrate from 1/5 of the leaf to apex, teeth regularly spaced (**Figure 10B**),

CC-CV to CC-CC with rounded sinus (**Figure 10C**). Midvein slightly curved; secondary veins thin, 15–23 pairs regularly spaced, pinnate, craspedodromous, straight or slightly curved (**Figures 10A–D**). Tertiary veins mixed percurrent (**Figure 10C**); Quaternary veins regular, rectangular to polygonal reticulate (**Figure 10C**). Leaf surface rugose with stellate trichomes (some might be broken into separate ones) with 4–8 solitary branches; Branches 20.3–45.6 μm (mean = 32.3 μm) long, 2.6–6.7 μm (mean = 4.3 μm) wide (**Figures 10E,F**).

Comparison Our specimens are attributed to *Quercus* sect. *Cyclobalanopsis* by leaf shape, regularly spaced teeth and secondary veins as well as mixed percurrent tertiary veins (**Figures 10A–D**). The new species closest to *Q. hypargyrea* (Seemen ex Diels) C.C. Huang et Y.T. Chang, but they are significantly different: firstly, our fossils have cuneate base, while *Q. hypargyrea* is cuneate to subrounded; secondly, our specimens have15–23 pairs of secondary veins which is more than *Q. hypargyrea* (10–15); thirdly, the present fossils are longer and thinner than *Q. hypargyrea* (Huang et al., 1999). *Quercus paleohypargyrea* is distinctive by elliptic leaf shape, cuneate base, serrate margin with regularly spaced CC-CV to CC-CC teeth, multiple regularly spaced, pinnate, straight or slightly curved secondary veins, which is significantly different from the previously reported Cenozoic *Q.* sect. *Cyclobalanopsis* from China and North Amercia (MacGinitie, 1953; Axelrod, 1956, 1966b, 1992, 1995, 1998a,b, 2000; Writing Group of Cenozoic Plants of China [WGCPC], 1978; Tao et al., 2000). *Quercus paleohypargyrea* differs to the aforementioned *Castaneophyllum* cf. *moorii* and *Castanopsis* sp. which also have stellate trichomes by CC-CV to CC-CC teeth and pinnate secondary venation.

Species *Quercus paleolamellosa* X-Y Liu et J-H Jin sp. nov. (**Figure 11**).

Diagnosis Leaf elliptic, apex elongate acuminate, base cuneate, slightly asymmetric with the petiole. Margin serrate from 1/4 to 1/3 of the leaf to apex, teeth regularly spaced, CC-CV with rounded sinus. Midvein slightly curved; secondary veins thin, 15–23 pairs regularly spaced, pinnate, craspedodromous, straight or slightly curved. Tertiary veins mixed percurrent; Quaternary veins regular, rectangular to polygonal reticulate. Leaf surface rugose with stellate trichomes.

Holotype CC-1112 (a, b)

Paratypes CC-1110 (a, b), CC-1116, CC-1241(a, b), CC-1247, CC-1248, CC-1255, CC-1261, CC-1285

Etymology The specific epithet "*paleolamellosa*" refers to its close affinity to the extant *Quercus lamellosa* Smith.

Description Leaf elliptic, preserved part 4.5–8.3 cm long, 1.3–2.3 cm wide (**Figure 11A**), apex elongate acuminate (**Figure 11B**), base cuneate, slightly asymmetric with the petiole 9 mm in length, 0.8 mm in width (**Figure 11A**). Margin serrate from 1/4 to 1/3 of the leaf to apex, teeth regularly spaced (**Figures 11A,D**), CC-CV with rounded sinus (**Figure 11C**). Midvein slightly curved; secondary veins thin, 15–23 pairs regularly spaced, pinnate, craspedodromous, straight or slightly curved (**Figures 11A,C,D**). Tertiary veins mixed percurrent (**Figure 11C**); Quaternary veins regular, rectangular to polygonal reticulate (**Figure 11C**). Leaf surface rugose with stellate trichomes, branches 15.2–25.8 μm

(mean = 20.5 μm) long, 2.4–3.0 μm (mean = 2.7 μm) wide (**Figures 11E,F**).

Comparison The present fossils are assigned to *Quercus* sect. *Cyclobalanopsis* base on the leaf morphological characteristics such as oval long elliptic leaf, regularly spaced teeth and secondary veins and the mixed percurrent tertiary veins (**Figures 11A–D**). The new species is most similar to the extant *Q. lamellosa* Smith on the elliptic leaf shape and stellate trichomes. However, the secondary veins of our fossils are curved close to the leaf margin, while those of *Q. lamellosa* are straight. In addition, the teeth of the present fossils are CC-CV in a uniform size, sometimes curved inward like a hook, while the teeth of *Q. lamellosa* are thin and long, sometimes spiny. Our specimens are distinguished from the previously described fossils of *Quercus* sect. *Cyclobalanopsis* from the Cenozoic of China and North American by the leaf characteristics of large size, ovate, obovate or oblong shape, and the number of secondary veins (Writing Group of Cenozoic Plants of China [WGCPC], 1978; Meyer and Manchester, 1997). This new species is distinct from *Q. paleohypargyrea*, known from the same site, by the shape and size of teeth and secondary veins.

Species *Quercus* cf. *myrsinifolia* Blume (**Figures 12A–D**)

Specimen examined CC-1272 (a, b), CC-1282, CC-1283

Description Leaf lanceolate, preserved part 4.2–5.9 cm long, 1.6–2.0 cm wide, apex acuminate (**Figure 12A**). Margin serrate, teeth regularly spaced (**Figure 12A**), CC-CC with rounded sinus (**Figure 12B**). Midvein thick, straight; secondary veins thin, at least 12 pairs regularly spaced, nearly opposite, craspedodromous, slightly curved with the angles 60–40° from base to apex (**Figure 12A**). Tertiary veins mixed percurrent (**Figure 12B**); Quaternary veins regular, rectangular to polygonal reticulate. Leaf surface rugose with stomata 16.2 μm long, 13.0 μm wide (**Figures 12C,D**).

Comparison The present fossils can be assigned to *Quercus* sect. *Cyclobalanopsis* base on the leaf shape, regularly spaced teeth and secondary veins as well as the mixed percurrent tertiary veins (**Figures 12A,B**). These specimens are similar to the extant *Q. myrsinifolia* Blume in the characteristics of gradually stronger midvein, nearly parallelled secondary veins, slender cuneate teeth and trichomes. However, the present specimens are different from *Q. myrsinifolia* by the lanceolate leaf shape and elongate acuminate apex. Our fossils are different with *Q. sinomiocenicum* Hu et Chaney from the Miocene of Lintong, Shandong Province in the leaf shape, teeth type and venation (Nanjing Institute of Geology and Mineral Resources [NIGMR], 1982). This species is distinguished from *Q. paleohypargyrea* and *Q. paleolamellosa* from the same locality by the lanceolate leaf shape and tooth size.

Species *Quercus paleoargyrotricha* X-Y Liu et J-H Jin sp. nov. (**Figures 12E–I**).

Diagnosis Leaf lanceolate, apex elongate acuminate. Margin serrate, teeth small, regularly spaced, CC-CV with rounded sinus. Midvein thick, straight; secondary veins thin, 12–15 pairs regularly spaced, opposite to pinnate from base to apex, craspedodromous, slightly curved. Tertiary veins mixed
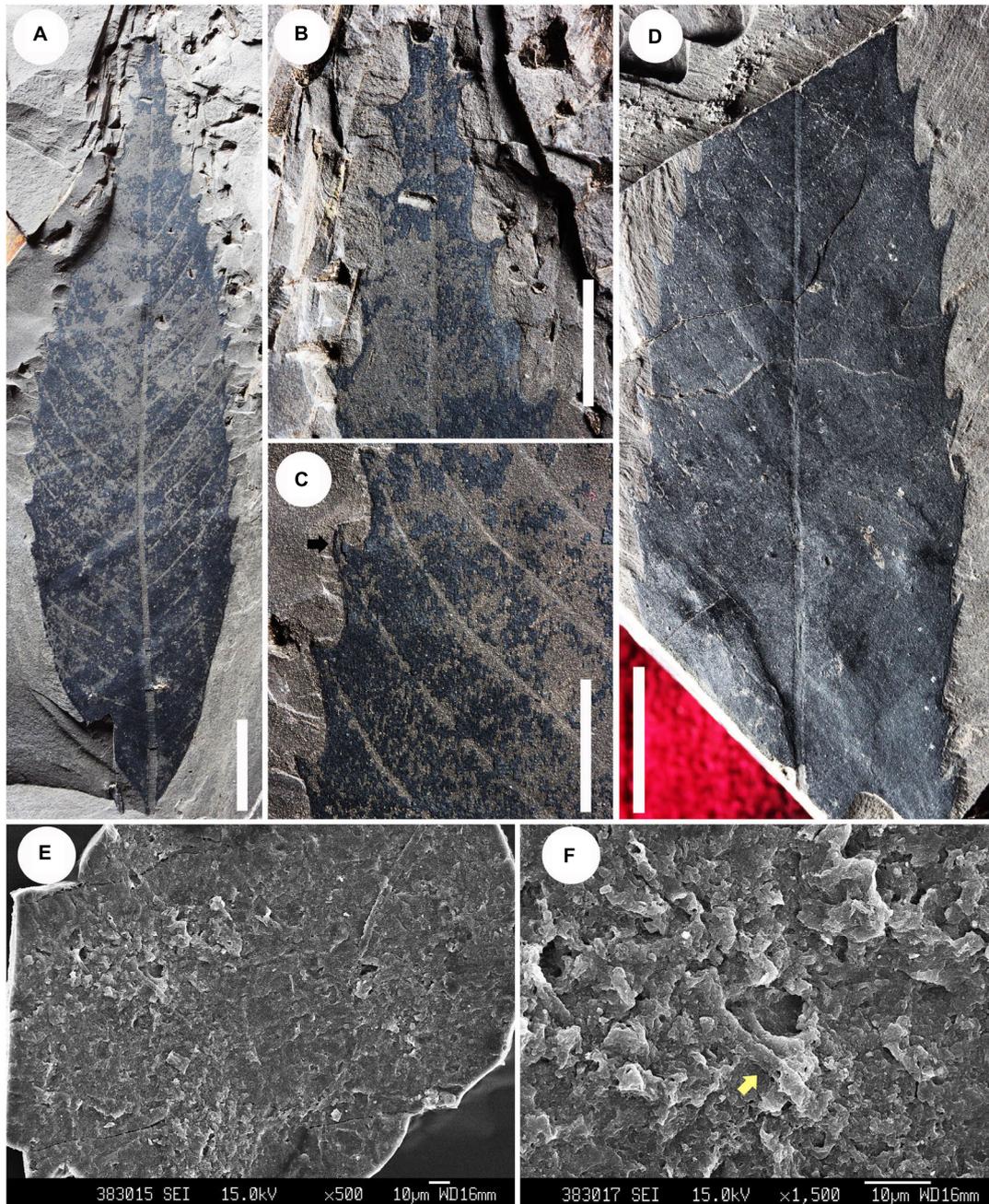
FIGURE 11 | Morphology of *Quercus paleolamellosa* sp. nov. **(A)** Holotype. Specimen No. CC-1112a, showing the lanceolate leaf and plenty of veins; **(B)** enlargement of **(A)**, showing the acuminate apex with teeth; **(C)** enlargement of **(A)**, showing the teeth (black arrow); **(D)** paratype. Specimen No. CC-1261, showing the teeth and venation. **(E)** SEM image of **(D)**, showing the rugose outer surface and solitary trichomes; **(F)** enlargement of **(E)**, showing the details of the solitary trichomes (yellow arrow). Scale: 10 mm **(A,D)**; 5 mm **(B,C)**.

percurrent; Quaternary veins regular, rectangular to polygonal reticulate. Leaf surface rugose with stellate trichomes and air hole of stomata.

Holotype CC-1287 (a, b)

Paratype CC-961

Etymology The specific epithet "*paleoargyrotricha*" refers to its close affinity to the extant *Quercus argyrotricha* A. Camus.

Description Leaf lanceolate, preserved part 5.5–7.7 cm long, 2.1–2.5 cm wide, apex elongate acuminate (**Figures 12E,F**). Margin serrate, teeth small, regularly spaced (**Figures 12E,F**), CC-CV with rounded sinus (**Figure 12G**). Midvein thick, straight; secondary veins thin, 12–15 pairs regularly spaced, opposite to pinnate from base to apex, craspedodromous, slightly curved (**Figures 12E–G**). Tertiary veins mixed percurrent
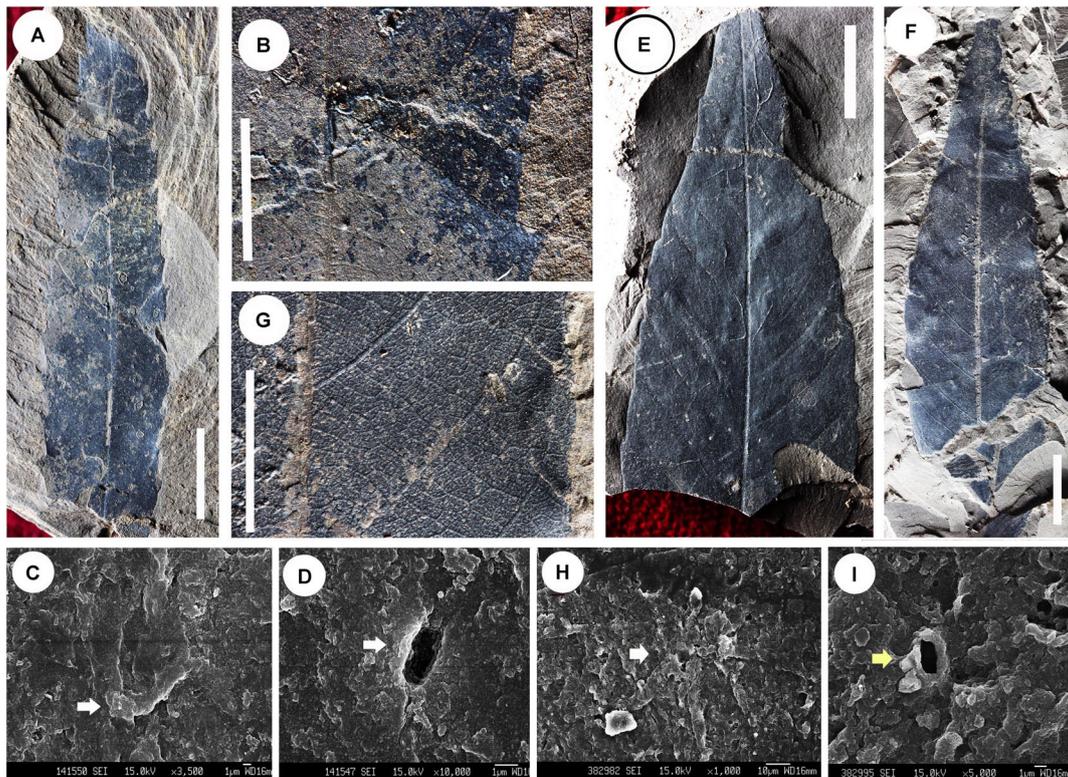
FIGURE 12 | Morphology of *Quercus* cf. *myrsinifolia* Blume **(A–D)** and *Q. paleoargyrotricha* sp. nov. **(E–I)**. **(A)** Specimen No. CC-1272a, showing the lanceolate leaf morphology; **(B)** enlargement of **(A)**, showing the teeth, secondary veins and mix percurrent tertiary veins; **(C)** SEM image showing the outer surface and a stoma (white arrow); **(D)** SEM image showing the air hole of a stoma (white arrow); **(E)** holotype. Specimen No. CC-1287a, showing the morphology of the leaf apex; **(F)** paratype. Specimen No. CC-961, showing the morphology of the leaf; **(G)** enlargement of **(F)**, showing the tooth, secondary veins and mix percurrent tertiary veins; **(H)** SEM image showing the stellate trichome (white arrow); **(I)** SEM image showing the air hole of a stoma (yellow arrow). Scale bars: 10 mm **(A,E,F)**; 5 mm **(B,G)**.

(**Figure 12G**); Quaternary veins regular, rectangular to polygonal reticulate (**Figure 12G**). Leaf surface rugose with stellate trichomes with 6–8 solitary branches, 16.2 μm long, 13.0 μm wide and air hole of stomata, rectangular, 2.8 μm long, 1.3 μm wide (**Figures 12H,I**).

Comparison The present specimens are assigned to *Quercus* sect. *Cyclobalanopsis* because the leaf shape, regularly spaced teeth and secondary veins, and mixed percurrent tertiary veins (**Figures 12E–G**). The new species is most similar to the extant *Q. argyrotricha* A. Camus in the characteristics of sparsely serrated margin, craspedodromous, slightly curved secondary veins, and stellate trichomes. However, the present specimens differ from *Q. argyrotricha* by the leaf shape, teeth details, and number of secondary veins. Our specimens have well-preserved trichomes (**Figure 12H**), while the previous reported fossil records from Cenozoic of east and west North America and southwest China lack trichome (Axelrod, 1956, 1992; Meyer and Manchester, 1997; Tao et al., 2000). The present specimens are different from *Q. paleohypargyrea* and *Q. paleolamellosa*, described above, in teeth shape and trichome branches.

Species *Quercus changchangensis* X-Y Liu et J-H Jin sp. nov. (**Figures 13A–C,E–H**).

Diagnosis Leaf lanceolate, apex elongate acuminate, base cuneate with petiole. Margin serrate from 1/3 of the leaf to apex, teeth regularly spaced, CC-RT with rounded sinus. Midvein thick to thin from base to apex, straight; secondary veins thin, 9 pairs regularly spaced, opposite to pinnate from base to apex, craspedodromous, with stable angles 50–60°, slightly curved near the margin. Tertiary veins mixed percurrent; Quaternary veins regular, polygonal reticulate. Leaf surface rugose with simple uniseriate trichomes and air hole of stomata.

Holotype CC-960

Paratype CC-1102

Etymology The specific epithet "*changchangensis*" refers to the Changchang Formation from which the specimens were collected.

Description Leaf lanceolate, 6.4–7.7 cm long, 1.5–1.8 cm wide, apex elongate acuminate (**Figure 13A**), base cuneate with petiole 10 mm long, 1 mm wide (**Figure 13C**). Margin serrate from 1/3 of the leaf to apex, teeth regularly spaced (**Figure 13A**), CC-RT with rounded sinus (**Figure 13B**). Midvein thick to thin from base to apex, straight; secondary veins thin, 9 pairs regularly spaced, opposite to pinnate from base to apex, craspedodromous, with stable angles 50–60°, slightly curved near the margin (**Figures 13A,B**). Tertiary veins mixed percurrent
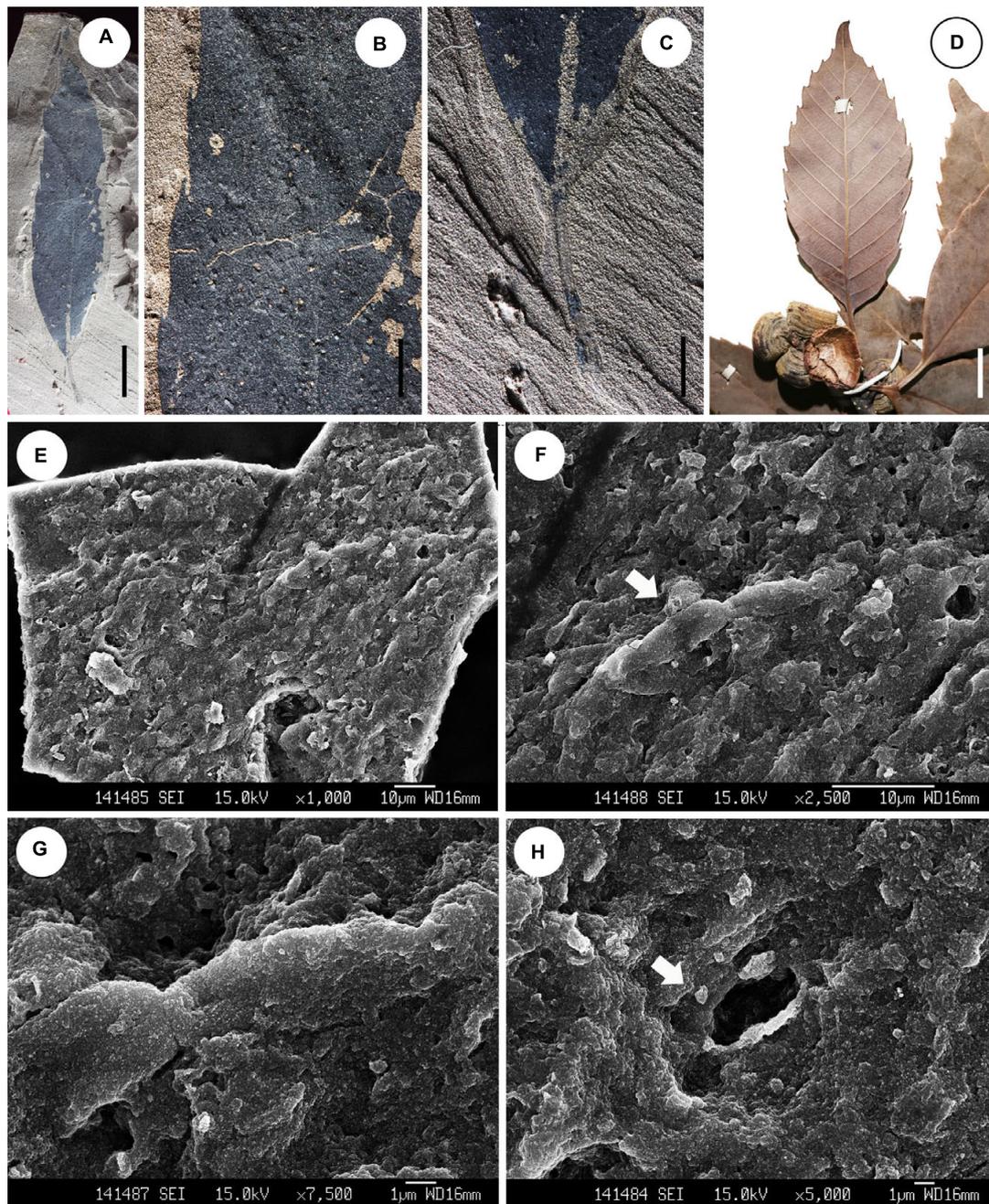
FIGURE 13 | Morphology of *Quercus changchangensis* sp. nov. **(A–C,E–H)** and the extant *Q. schottkyana* Rehd. et Wils. **(D)**. **(A)** Holotype. Specimen No. CC-960, showing the lanceolate leaf morphology; **(B)** enlargement of **(A)**, showing the teeth; **(C)** enlargement of **(A)**, showing the cuneate base and petiole; **(D)** elliptic leaf of *Q. schottkyana,* the Herbarium of the Sun Yat-sen University (SYS), No. 17306, collected by J. F. Rock; **(E)** SEM image showing the rugose outer surface of *Q. changchangensis*; **(F)** enlargement of **(E)**, white arrow indicates a uniseriate trichome; **(G)** enlargement of **(F)**, a cell of the uniseriate trichome; **(H)** outer face of *Q. changchangensis*, white arrow indicates the air hole of a stoma. Scale bars: 10 mm **(A,D)**; 5 mm **(B,C)**.

(**Figure 13B**); Quaternary veins regular, polygonal reticulate (**Figure 13B**). Leaf surface rugose with simple uniseriate trichomes composed of a single column of 3–4 thin-walled structures, apparently cells, 32.9 μm long, 3.9 μm wide and air hole of stomata, rectangular, 5.3 μm long, 2.8 μm wide (**Figures 13E–H**).

Comparison The present specimens are attributed to *Quercus* sect. *Cyclobalanopsis* because their leaf shape, regularly spaced teeth and secondary veins, and mixed percurrent tertiary veins (**Figures 13A–C**). This new species resembles the extant *Q. schottkyana* Rehd. et Wils. on the leaf shape and simple uniseriate trichomes (**Figures 13A,D**). This new species is

distinct from the extant *Q. schottkyana* Rehd. et Wils. and *Q. glauca* Thunb. which have simple uniseriate trichomes with the length of 160 and 265 µm in length, respectively (Luo and Zhou, 2001), by having much smaller simple uniseriate trichomes. Most of the previously described fossils reported fossil leaves of *Q.* sect. *Cyclobalanopsis* from the Cenozoic of China have no trichomes, except for *Q. praedelavayi* Y.W. Xing et Z.K. Zhou described from late Miocene of XundianXianfeng Basin with typical stellate trichomes including 16 branches (Xing et al., 2013). The present fossils are easily distinguished from *Q. praedelavayi* and above 4 species of *Quercus* described herein by the simple uniseriate trichome and lanceolate leaf with CC-RT teeth.

DISCUSSION

Phytogeographic Implications

Previously published fossil records indicate that *Berryophyllum* was widely distributed in strata from the Paleocene to the Eocene in Asia, North America, and Europe (**Figure 14A**; Writing Group of Cenozoic Plants of China [WGCPC], 1978; Takhtajan, 1982; Jones and Dilcher, 1988; Crepet and Nixon, 1989a; Mai, 1995; Zhou, 1996; Tao et al., 2000; Kvaček and Walther, 2010). The distribution range decreased since the Oligocene and finally disappeared from North America (**Figure 14A**; Tao et al., 2000; Kvaček and Walther, 2010). In China, this genus was present as early as Eocene in Fushun, Liaoning, and in Zhanhua, Shandong and become abundant in Yunnan after the Oligocene (**Figure 14A**; Tao et al., 2000). The present *Berryophyllum* fossils discovered on Hainan Island in South China indicates that the genus has been distributed in the low latitude tropical region at least since the Eocene.

Castaneophyllum has been in Asia and North America since the Paleocene (**Figure 14B**; Takhtajan, 1982; Jones and Dilcher, 1988). This genus not only appeared in Asia and North America but also spread to Europe in the Eocene (**Figure 14B**; Kvaček and Walther, 1989, 2010). However, fossil records of the genus only occurred in Europe and central Asia during the Oligocene (**Figure 14B**; Takhtajan, 1982; Kvaček and Walther, 1989, 2010). In China, the genus was only previously found in the Eocene in Fushun, Liaoning (**Figure 14B**; Tao et al., 2000). The *Castaneophyllum* fossils recovered here from Hainan Island are the lowest latitudinal distribution of the record for the genus.

Castanopsis fossils were widely distributed in Asia, North America, South America, and Europe during the Eocene, with the richest reproductive fossil records located in North America (**Figure 14C**; Wolfe, 1968; Huzioka and Takahasi, 1970; Takhtajan, 1982; Crepet and Nixon, 1989a; Manchester, 1994; Wilf et al., 2019). In China, however, *Castanopsis* fossils were mainly recovered from Yunnan, Sichuan, Zhejiang, and Guangxi during the Miocene to the Pliocene (**Figure 14C**; Tao and Du, 1982; Tao and Chen, 1983; Liu, 1993; Tao et al., 2000; Xia et al., 2009; Guo, 2011; Wu et al., 2014; Li et al., 2015). The *Castanopsis* fossils recovered here from the Eocene stratum on Hainan Island are both the earliest fossil records of the genus in China and also the lowest latitudinal distribution of the record in the world.

Lithocarpus was extensively distributed in North America and Europe in the Eocene, then extended into Asia during the Oligocene-Miocene, and finally almost disappeared from North America and Europe after the Miocene (**Figure 15A**; Andreansky and Kovaca, 1966; Axelrod, 1966a, 1998a; Takhtajan, 1982; Kvaček and Walther, 1989; Vikulin, 2011). In China, *Lithocarpus* fossils were mainly found from the Oligocene and Miocene strata of Yunnan, and diversified in the Miocene (**Figure 15A**; Writing Group of Cenozoic Plants of China [WGCPC], 1978; Tao et al., 2000; Guo, 2011; Mu et al., 2015). Additionally, they also occurred in the Pleistocene stratum of Guangxi (**Figure 15A**; Tao et al., 2000). The *Lithocarpus* fossils here from Hainan Island have similar implications compared to *Castanopsis* in that they have the earliest record in China and the lowest distribution latitudes in the world.

Quercus, including subgenus *Quercus* and subgenus *Cerris* (including *Q.* sect. *Cyclobalanopsis*, Denk et al., 2017), has the richest and widest distribution of both modern and fossil species. The fossil records suggest that *Q.* subg. *Quercus* has been widely distributed in East and South Asia, western North America, and southern Europe since the Eocene (**Figure 15B**; MacGinitie, 1941, 1953, 1969; Bones, 1979; Takhtajan, 1982; Daghlian and Crepet, 1983; Manchester, 1983, 1994; Mai and Walther, 1985; Kvaček and Walther, 1989; Vikulin, 2011; Tao et al., 2000). *Quercus* also occurred in the Eocene stratum in Fushun, Liaoning (**Figure 15B**; Tao et al., 2000). The fossil records of *Q.* sect. *Cyclobalanopsis* can be also dated back to the Eocene in western North America and eastern Germany (**Figure 15C**; Kvaček and Walther, 1989; Manchester, 1994). In China, the earliest reliable *Q.* sect. *Cyclobalanopsis* fossils were discovered from the Oligocene stratum in Yunnan and Guangdong provinces (**Figure 15C**; Writing Group of Cenozoic Plants of China [WGCPC], 1978; Liu et al., 2019). The *Quercus* fossils here from Hainan Island have a wide variety of species, including 5 species of *Q.* sect. *Cyclobalanopsis*, which are the lowest latitudinal distribution of the genus in the fossil record. Among these, the fossils assigned to *Q.* sect. *Cyclobalanopsis* are the earliest fossil records in China, as well as the earliest fossil records of the section in China. The above fossils suggest that the intragenus differentiation and the diversity evolution of the *Q.* sect. *Cyclobalanopsis* already started as early as the Eocene in South China.

Overall, as the earliest fossils of Fagaceae, such as *Berryophyllum* and *Castaneophyllum* were mainly distributed in high latitude regions, and the present occurrence of above five genera of Fagaceae from the middle Eocene Changchang Formation of Changchang Basin, Hainan Island of South China, a possible divergence pattern for the family is proposed that the family might be boreotropical origin and then migrated southward by the middle Eocene and highly differentiated at that time. The extinct genera, *Berryophyllum* and *Castaneophyllum* arrived at the low latitude of South China at least by the middle Eocene, and 7 fossils species in extant *Castanopsis, Lithocarpus,* and *Quercus* section *Cyclobalanopsis* show the diversity of the family in the middle Eocene of South China.
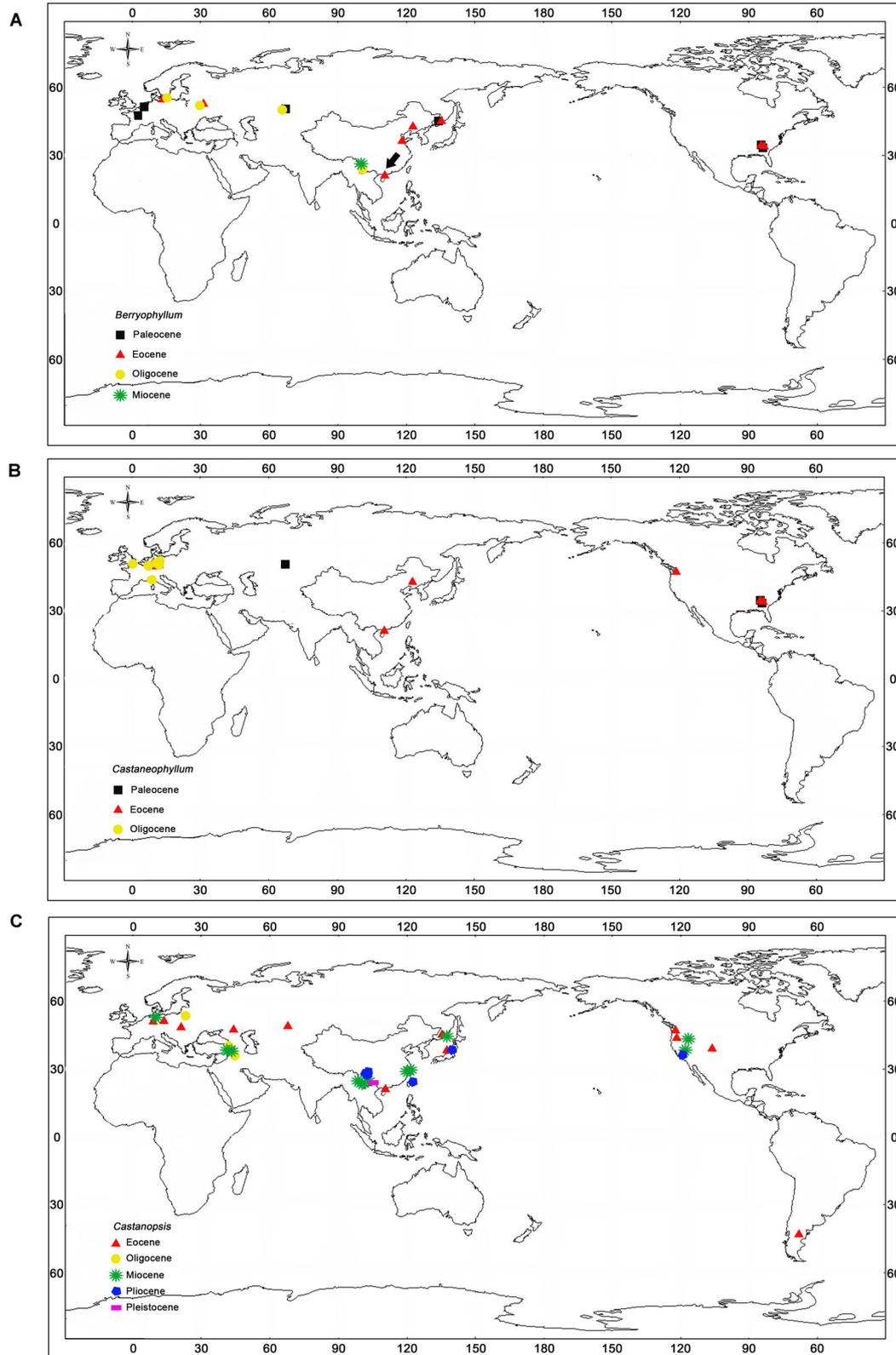
FIGURE 14 | Distribution of the fossil records for the genera *Berryophyllum*, *Castaneophyllum* and *Castanopsis*. (A) Distribution of the fossil records of *Berryophyllum*; (B) distribution of the fossil records of *Castaneophyllum*; (C) distribution of the fossil records of *Castanopsis*.
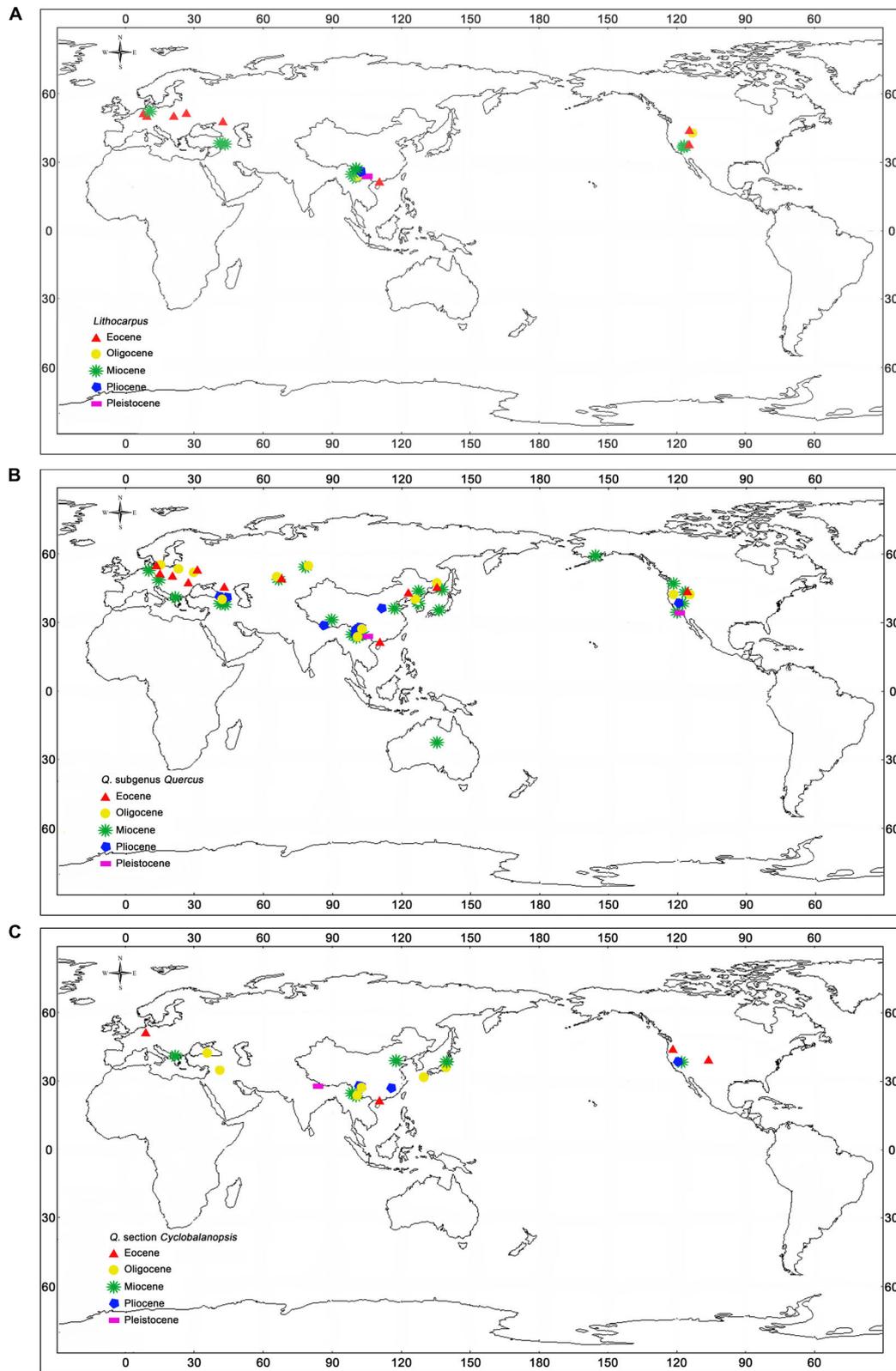
FIGURE 15 | Distribution of the fossil records for the *Lithocarpus*, *Quercus* subgenus *Quercus* and *Q.* section *Cyclobalanopsis*. **(A)** Distribution of the fossil records of *Lithocarpus*; **(B)** distribution of the fossil records of *Q.* subgenus *Quercus*; **(C)** distribution of the fossil records of *Q.* section *Cyclobalanopsis*.

Paleoecological Implications

The five species described here are assigned to the extinct genera *Berryophyllum* and *Castaneophyllum* complexes. Both the *Berryophyllum* and *Castaneophyllum* complexes could likely thrive in these many environments due to their considerable variation in ecologically important parameters (e.g., leaf area and length to width ratios) and due to their interbreeding complex, similar to the extant *Quercus* (Jones and Dilcher, 1988). The interbreeding strategy, highly adaptive in the fluvial and near coastal environments (Jones and Dilcher, 1988), is supported by the reconstructed environment of our fossil locality; Changchang Basin is very close to the coastal areas. In the Eocene Hainan Island, the presence of *Berryophyllum* and *Castaneophyllum* complexes, as well as a great number of aquatic ferns, *Salvinia* (Wang et al., 2014), *Alseodaphne* (Li et al., 2009), palms (Zhou et al., 2013), and other angiosperms from the same layer, indicates a wet environment in the basin during that time.

The other 7 species presented in this study have been assigned to the extant evergreen genera *Castanopsis*, *Lithocarpus,* and *Quercus* section *Cyclobalanopsis*. They are the most diverse groups within the family Fagaceae, confined to East and Southeast Asia, and are important dominants in the evergreen broad-leaved forests (EBLF) in tropical and subtropical Asia (Tang, 2015). *Castanopsis* is generally distributed at lower altitudes, whereas *Lithocarpus* and *Quercus* section *Cyclobalanopsis* at higher altitudes, but sometimes they have been found to coexist in the same altitudinal range and be co-dominant in the same EBLF (Tang, 2015). Indochina, Southwest China, and South China have the highest species diversity of these three genera (Tang, 2015). The floristic composition of Hainan Island shows a strong tropical characteristics, with mostly tropical genera, e.g., *Lithocarpus* and some subtropical genera, e.g., *Castanopsis* and *Quercus* (Jiang et al., 2002). Many tropical genera, including *Sabalites* (Zhou et al., 2013), *Alseodaphne* (Li et al., 2009), *Palaeocarya* (Jin, 2009) closely related to extant *Engelhardtia* (Juglandaceae), and *Morinda* (Rubiaceae; Shi et al., 2012), have been recovered from the middle Eocene Changchang Formation of Changchang Basin, South China. *Castanopsis, Lithocarpus,* and *Q.* section *Cyclobalanopsis*, collected from the same layer with the above taxa, are the most abundant and diverse taxa (except for Lauraceae). This indicates that these three genera of Fagaceae dominated the evergreen tropical and subtropical forests in South China by at least the middle Eocene.

Palynological and Climate Leaf Analysis Multivariate Program (CLAMP) studies show the mean annual temperatures of 14.2–19.8°C and ∼22 ± 4.7°C, respectively, the mean annual precipitations of 784.7–1,113.3 mm, and growing season precipitation (GSP, effectively the mean annual precipitation) of 2020 ± 1220 mm, respectively for the middle Eocene Changchang Formation of Changchang Basin, South China (Yao et al., 2009; Spicer et al., 2014). Based on the above analysis of the living environment for the nearest living relatives of these fossils, we speculate that the climate of Hainan Island was warm and wet during the middle Eocene, which was suitable for the growth and differentiation of Fagaceae, especially for *Quercus* sect. *Cyclobalanopsis* which was well-developed and highly differentiated during the middle Eocene.

DATA AVAILABILITY STATEMENT

All datasets presented in this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

JJ and XL conceived and designed the study, conducted taxonomic treatments, phytogeographic, and paleoecological interpretations. JJ, HS, and XL photographed specimens and arranged the figures. XL carried out the cuticle experiments and data analyses and wrote the manuscript. HS formatted the references and figure captions. All authors read and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00255/full#supplementary-material

REFERENCES

Andreansky, G., and Kovaca, E. (1966). Der verwandtschaftskreis der eichernfer unteroligozanen flora von kiseged bei Eger (Obcrungam): egri Muz Evk. *Am. J. Bot.* 2, 7–42.

Axelrod, D. I. (1956). *Mio-Pliocene Floras from West Central Nevada*. Berkeley, CA: University of California Publications in Geological Sciences.

Axelrod, D. I. (1962). *A Pliocene Sequoiadendron Forest from Western Nevada*. Berkeley, CA: University of California Publications in Geological Sciences.

Axelrod, D. I. (1966a). *The Eocene Copper Basin Flora of Northeastern Nevada*. Berkeley, CA: University of California Publications in Geological Sciences.

Axelrod, D. I. (1966b). *The Pleistocene Soboba Flora of Southern California*. Berkeley, CA: University of California Publications in Geological Sciences.

Axelrod, D. I. (1992). *The Middle Miocene Pyrimid Flora of Western Nevada*. Berkeley, CA: University of California Publications in Geological Sciences.

Axelrod, D. I. (1995). *The Miocene Purple Mountain Flora of Western Nevada*. Berkeley, CA: University of California Publications in Geological Sciences.

Axelrod, D. I. (1998a). *The Eocene Thunder Mountain Flora of Central Idaho*. Berkeley, CA: University of California Publications in Geological Sciences.

Axelrod, D. I. (1998b). *The Oligocene Haynes Creek Flora of Eastern Idaho*. Berkeley, CA: University of California Publications in Geological Sciences.

Axelrod, D. I. (2000). *A Miocene (10-12Ma) Evergreen Laurel-Oak Forest from Carmel Valley*. California: University of California Publications in Geological Sciences.

Berry, E. W. (1916). *The Lower Eocene Floras of Southeastern North America*. Reston, VA: United States Geological Survey.

Bhandari, S., Momohara, A., and Paudayal, K. N. (2009). Late Pleistocene plant macro-fossils from the Gokarna Formation of the Kathmandu Valley, Central Nepal. *Bull. Depart. Geol.* 12, 75–88. doi: 10.3126/bdg.v12i0.2252

Bones, T. J. (1979). Atlas of fossil fruit and seeds from North Central Oregon. *Oregon Mus. Sci. Ind. Occ. Pap. Nat. Sci.* 1, 1–23.

Borgardt, S. J., and Pigg, P. B. (1999). Anatomical and developmental study of petrified *Quercus* (Fagaceae) fruit from the middle Miocene, Yakima Canyon, Washington, USA. *Am. J. Bot.* 86, 307-325.

Chen, Y. Q. (2007). *The Phylogeny and Biogeography of Fagaceae*, Ph. D. thesis, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming.

Colani, M. (1920). *Étude sur les Florès Tertiaires de Quelques Gisements de Lignite de l'Indochine et du Yunnan. Series: Bulletin du Service Geologique de l'Indochine, v. 8, Fasc. 1.* Hanoi: Imprimerie d'Extreme-Orient.

Crepet, W. L., and Daghlian, C. P. (1980). Castaneoid inflorescences from the middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. *Am. J. Bot.* 67, 739–757. doi: 10.1002/j.1537-2197.1980.tb07704.x

Crepet, W. L., and Nixon, K. C. (1989a). Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications. *Am. J. Bot.* 76, 842–855. doi: 10.1002/j.1537-2197.1989.tb15062.x

Crepet, W. L., and Nixon, K. C. (1989b). Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications. *Am. J. Bot.* 76, 1493–1505. doi: 10.1002/j.1537-2197.1989.tb15131.x

Daghlian, C. P., and Crepet, W. L. (1983). Oak catkins, leaves and fruits from the Oligocene Catahoula Formation and their evolutionary significance. *Am. J. Bot.* 70, 639–649. doi: 10.1002/j.1537-2197.1983.tb12444.x

Deng, M., Li, Q. S., Yang, S. T., Liu, Y. C., and Xu, J. (2013). Comparative morphology of leaf epidermis in the genus *Lithocarpus* and its implication in leaf epidermal feature evolution in Fagaceae. *Plant Syst. Evol.* 299, 659–681. doi: 10.1007/s00606-012-0751-0

Denk, T., Grimm, G. W., Manos, P. S., Deng, M., and Hipp, A. L. (2017). "An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns," in *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L*, eds E. Gil-Pelegrín, J. J. Peguero-Pina, and D. Sancho-Knapik (Berlin: Springer), 13–38. doi: 10.1007/978-3-319-69099-5_2

Ellis, B., Daly, D. C., Hickey, L. J., Johnson, K. R., Mitchell, J. D., Wilf, P., et al. (2009). *Manual of Leaf Architecture*. Ithaca: Cornell University Press.

Guo, S. X. (1979). "Late Cretaceous and early Tertiary floras from the southern Guangdong and Guangxi with their stratigraphic significance," in *The Mesozoic and Cenozoic Red Beds of South China*, ed. Mesozoic and Cenozoic Red Beds of South China (Beijing: Science Press), 223–230.

Guo, S. X. (2011). The late Miocene Bangmai flora from Lincang county of Yunnan, southwestern China. *Acta Palaeontol. Sin.* 50, 353–408.

Hably, L. (2013). The late Miocene flora of Hungary. *Geol. Hungar. Ser. Palaeontol. Fasciculus* 59:175.

He, Y. L., Na, L., Wang, Z. X., Wang, H. F., Yang, G. L., Xiao, L., et al. (2014). *Quercus yangyiensis* sp. nov. from the late Pliocene of Baoshan, Yunnan and its paleoclimatic significance. *Acta Palaeontol. Sin.* 88, 738–747. doi: 10.1111/1755-6724.12234

Herendeen, P. S., Crane, P. R., and Drinnan, A. N. (1995). Fagaceous flowers, fruits, and cupules from the Campanian (Late Cretaceous) of central Georgia, USA. ιInt. *J. Plant Sci.* 156, 93–116. doi: 10.1086/297231

Hofmann, C. H., Kodrul, T. M., Liu, X. Y., and Jin, J. H. (2019). Scanning electron microscopy investigations of middle to late Eocene pollen from the Changchang Basin (Hainan Island, South China) – Insights into the paleobiogeography and fossil history of *Juglans*, *Fagus*, *Lagerstroemia*, *Mortoniodendron*, *Cornus*, *Nyssa*, *Symplocos* and some Icacinaceae in SE Asia. *Rev. Palaeobot. Palynol.* 265, 41–61. doi: 10.1016/j.revpalbo.2019.02.004

Huang, C. C., Zhang, Y. T., and Bartholomew, B. (1999). "Fagaceae," in *The Flora of China*, eds C. Y. Wu and P. H. Raven (Beijing: Science Press), 380–400.

Huzioka, K., and Takahasi, E. (1970). The Eocene flora of the ube coal-field, southwest Honshu, Japan. *J. Mining Coll. Akita Univ. Int. J. Min. Coll.* 4, 1–88.

Jia, H., Jin, P. H., Wu, J. Y., Wang, Z. X., and Sun, B. N. (2015). *Quercus* (subg. *Cyclobalanopsis*) leaf and cupule species in the late Miocene of eastern China and their paleoclimatic significance. *Rev. Palaeobot. Palynol.* 219, 132–146. doi: 10.1016/j.revpalbo.2015.01.011

Jiang, Y. X., Wang, B. S., Zang, R. G., Jin, J. H., and Liao, W. B. (2002). *Tropical Forest Biodiversity and Its Formation Mechanism in Hainan Island*. Beijing: Science Press.

Jin, J. H. (2009). Two Eocene fossil fruits from the Changchang Basin of Hainan Island, China. *Rev. Palaeobot. Palynol.* 153, 150–152. doi: 10.1016/j.revpalbo.2008.07.010

Jones, J. H. (1986). Evolution of the Fagaceae: the implications of foliar features. *Ann. Miss. Bot. Gar.* 73, 228–275.

Jones, J. H., and Dilcher, D. L. (1988). A study of the *Dryophyllum* leaf forms from the Paleogene of sontheastern North America. *Palaeontogr. Abt. B.* 208, 53–80.

Kvaček, Z., and Walther, H. (1989). Paleobotanical studies in Fagaceae of the European Tertiary. *Plant Syst. Evol.* 162, 213–229. doi: 10.1007/978-3-7091-3972-1_11

Kvaček, Z., and Walther, H. (2004). Oligocene flora of Bechlejovice at Děčín from the neovolcanic area of the České středohoří Mountains, Czech Republic. *Acta Mus. Nat. Pragae Ser. B Hist. Nat.* 60, 9–60.

Kvaček, Z., and Walther, H. (2010). European Tertiary Fagaceae with chinquapin-like foliage and leaf epidermal characteristics. *Feddes Repert.* 121, 248–267. doi: 10.1002/fedr.201100005

Larson-Johnson, K. (2016). Phylogenetic investigation of the complex evolutionary history of dispersal mode and diversification rates across living and fossil Fagales. *New Phyto.* 209, 418–435. doi: 10.1111/nph.13570

Lei, Y. Z., Zhang, Q. R., He, W., and Cao, X. P. (1992). *Tertiary, Geology of Hainan Island*. Beijing: Geological Publishing House.

Li, H. M., and Guo, S. X. (1982). "Angiospermae," in *Paleontological Atlas of East China part 3, volume of Mesozoic and Cenozoic*, ed. Nanjing Institute of Geology and Mineral Resourses (Beijing: Geological Publishing House), 236–316.

Li, J. Q. (1996). On the phylogeny of the Fagaceae. *Acta Phytotaxon. Sin.* 34, 597–609.

Li, J. Z., Qiu, J., Liao, W. B., and Jin, J. H. (2009). Eocene fossil *Alseodaphne* from Hainan Island of China and its paleoclimatic implications. *Sci. China Ser. D Earth Sci.* 52, 1537–1542. doi: 10.1007/s11430-009-0120-1

Li, R. Y., Sun, B. N., Wang, Q. J., Ma, F. J., Xu, X. H., Wang, Y. F., et al. (2015). Two new *Castanopsis* (Fagaceae) species based on cupule and foliage from the upper Miocene of eastern Zhejiang, China. *Plant Syst. Evol.* 301, 25–39. doi: 10.1007/s00606-014-1051-7

Liu, M. Q., Deng, M., and Zhou, Z. K. (2009). Taxonomic and ecological implications of leaf cuticular morphology in *Castanopsis*, *Castanea*, and *Chrysolepis*. *Plant Syst. Evol.* 283, 111–123. doi: 10.1007/s00606-009-0220-6

Liu, X. Y., Xu, S. L., Han, M., and Jin, J. H. (2019). An early Oligocene fossil acorn, associated leaves and pollen of the ring-cupped oaks (*Quercus* subg. *Cyclobalanopsis*) from Maoming Basin, South China. *J. Syst. Evol.* 57, 153–168. doi: 10.1111/jse.12450

Liu, Y. S. (1993). A palaeoclimatic analysis on early Pleistocene flora of Changsheling Formation, Baise Basin, Guangxi. *Acta Palaeontol. Sin.* 32, 151–169.

Liu, Y. S., Momohara, A., and Mei, S. W. (1995). A revision on the Chinese megafossils of *Fagus* (Fagaceae). *Journ. Jap. Bot.* 71, 168–177.

Luo, Y., and Zhou, Z. K. (2001). Leaf epidermis of *Quercus* subgen. *Cyclobalanopsis* (Oerst.) Schneid (Fagaceae). *Acta Phytotaxo. Sin.* 39, 489–501.

MacGinitie, H. D. (1941). *A Middle Eocene Flora from the Central Sierra Nevada.* Washington, DC: Carnegie Institution of Washington publication.

MacGinitie, H. D. (1953). *Fossil Plants of the Florissant Beds, Colorado.* Washington, DC: Carnegie Institution of Washington Publication.

MacGinitie, H. D. (1969). *The Eocene Green River Flora of North Western Colorado and Northeastern Utah.* California: University of California.

Mai, D. H. (1995). *Tertiäre Vegetations Geschichte Europas.* Heidelberg: Spektrum Akademischer Verlag.

Mai, D. H., and Walther, H. (1985). Dieobereozänen floren des weisselster-beckens und seiner Randgebiete, Jahrb. *Staatl. Mus. Mineral. Dresden.* 33:220.

Manchester, S. R. (1983). Eocene fruits, wood and leaves of the Fagaceae from the Clarno Formation of Oregon. *Am. J. Bot.* 70:74.

Manchester, S. R. (1994). Fruits and seeds of the middle Eocene Nut Beds flora, Clarno Formation, Oregon. *Palaeontogr. Am.* 58:280.

Manchester, S. R., and Crane, P. R. (1983). Attached leaves, inflorescences and fruits of *Fagopsis*, an extinct genus of fagaceous affinity from the Oligocene florissant flora of Calorado, U.S.A. *Am. J. Bot.* 70, l147–l164.

Manchester, S. R., and Dillhoff, R. M. (2004). *Fagus* (Fagaceae) fruits, foliage, and pollen from the middle Eocene of Pacific Northwestern North America. *Can. J. Bot.* 82, 1509–1517. doi: 10.1139/b04-112

Meyer, H. W., and Manchester, S. R. (1997). *The Oligocene Bridge Creek Flora of the John Day Formation, Oregon.* Berkeley, CA: University of California Press.

Mindall, R. A., Stockey, R. A., and Beard, G. (2007). *Cascadiacarpa spinosa* gen. et sp. nov (Fagaceae): castaneoid fruits from the Eocene of Vancouver Island, Canada. *Am. J. Bot.* 94, 351–361. doi: 10.3732/ajb.94.3.351

Mindall, R. A., Stockey, R. A., and Beard, G. (2009). Permineralized *Fagus* nuts from the Eocene Vancouver Island. *Can. Int. J. Plant Sci.* 170, 551–560. doi: 10.1086/596335

Mu, X. Y., Li, J. X., Xia, X. F., and Zhao, L. C. (2015). Cupules and fruits of *Lithocarpus* (Fagaceae) from the Miocene of Yunnan, southwestern China. *Taxon* 64, 795–808. doi: 10.12705/644.10

Nanjing Institute of Geology and Mineral Resources [NIGMR] (1982). *Paleontological atlas of East China: Part 3. Volume of Mesozoic and Cenozoic.* Beijing: Geological publishing house.

Palamarev, E., and Tsenov, B. (2004). Genus *Quercus* in the late Miocene flora of Baldevo Formation (Southwest Bulgaria): taxonomical composition and palaeoecology. *Phytol. Balc.* 10, 147–156.

Shi, X. G., Jin, J. H., Ye, C. X., and Liu, W. Q. (2012). First fruit fossil record of *Morinda* (Rubiaceae) from China. *Rev. Palaeobot. Palynol.* 179, 13–16. doi: 10.1016/j.revpalbo.2012.04.001

Sims, H. J., Herendeen, P. S., and Crane, P. R. (1998). New genus of fossil Fagaceae from the Santonian (Late Cretaceous) of central Georgia, USA. *Int. J. Plant Sci.* 159, 391–404. doi: 10.1086/297559

Spicer, R. A., Herman, A. B., Liao, W. B., Spicer, T. E. V., Kodrul, T. M., Yang, J., et al. (2014). Cool tropics in the middle Eocene: evidence from the Changchang flora, Hainan Island, China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 412, 1–16. doi: 10.1016/j.palaeo.2014.07.011

Takhtajan, A. (ed.) (1982). *Magnoliophyta Fossilia URSS, Ulmaceae-Betulaceae.* St. Petersburg: Russian Academy of Sciences.

Tang, C. Q. (2015). *The Subtropical Vegetation Of Southwestern China: Plant Distribution, Diversity And Ecology.* Berlin: Springer.

Tao, J. R., and Chen, M. H. (1983). "Cenozoic flora of Lincang in the southern Hengduan Mountains," in *Studies in Qinghai-Xizang (Tibet) Plateau—Special Issue of Hengduan Mountains Scientific Expedition (I)*, eds Team of Comprehensive Scientific Expedition to the Qinghai-Xizang (Tibet) Plateau and Chinese Academy of Sciences (Kunming: Yunanan People's Publishing House), 74–95.

Tao, J. R., and Du, N. Q. (1982). Neogene flora of Tengchong Basin in western Yunnan, China. *Acta Bot. Sin.* 24, 273–281.

Tao, J. R., Zhou, Z. K., and Liu, Y. S. (2000). *The Evolution of the Late Cretaceous—Cenozoic Floras in China.* Beijing: Science Press.

Vikulin, C. B. (2011). Thermophilic beech (Fagaceae): *Quercus, Lithocarpus, Castanopsis* from the late Eocene of the southern European Russia. *Read. Mem. A.N. Krishtofovich.* 7, 128–147.

Wang, L., Xu, Q. Q., and Jin, J. H. (2014). A reconstruction of the fossil *Salvinia* from the Eocene of Hainan Island, South China. *Rev. Palaeobot. Palynol.* 203, 12–21. doi: 10.1016/j.revpalbo.2013.12.005

Wilf, P., Nixon, K. C., Maria, A., and Gandolfo, C. N. R. (2019). Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests. *Science* 364:972.

Wolfe, J. A. (1968). Paleogene biostratigraphy of nonmaine rocks in King County, Washington, U.S.A. *Geol. Surv. Prof. Pap.* 571, 1–33.

Wolfe, J. A., and Tanai, T. (1980). The Miocene Seldovia point flora from the Kenai group, Alaska, U.S.A. *Geol. Surv. Prof. Pap.* 1105, 1–52.

Writing Group of Cenozoic Plants of China [WGCPC] (1978). *Cenozoic Plants from China: Fossil Plants of China.* Beijing: Science Press.

Wu, J. Y., Ding, S. T., Li, Q. J., Zhao, Z. R., Dong, C., and Sun, B. N. (2014). A new species of *Castanopsis* (Fagaceae) from the upper Pliocene of western Yunnan, China and its biogeographical implications. *Palaeoworld* 23, 370–382. doi: 10.1016/j.palwor.2014.10.005

Xia, K., Su, T., Liu, Y. S., Xing, Y. W., Frédéric, M. B., and Jacques Zhou, Z. K. (2009). Quantitative climate reconstructions of the late Miocene Xiaolongtan megaflora from Yunnan, southwest China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 276, 80–86. doi: 10.1016/j.palaeo.2009.02.024

Xiao, L., Sun, B. N., Yan, D. F., Xie, S. P., and Wei, L. J. (2006). Cuticular structure of *Quercus pannosa* Hand.-Mazz. from the Pliocene in Baoshan, Yunnan Province and its palaeoenvironmental significance. *Acta Micropalaeontol. Sin.* 23, 23–30.

Xing, Y. W., Gandolfo, M. A., and Linder, H. P. (2015). The Cenozoic biogeographical evolution of woody angiosperms inferred from fossil distributions. *Global Ecol. Biogeogr.* 24, 1290–1301. doi: 10.1111/geb.12383

Xing, Y. W., Hu, J. J., Jacques, F. M. B., Wang, L., Su, T., Huang, Y. J., et al. (2013). A new *Quercus* species from the upper Miocene of southwestern China and its ecological significance. *Rev. Palaeobot. Palynol.* 193, 99–109. doi: 10.1016/j.revpalbo.2013.02.001

Xu, H., Su, T., Zhang, S. T., Deng, M., and Zhou, Z. K. (2016). The first fossil record of ring-cupped oak (*Quercus* L. subgenus *Cyclobalanopsis* (Oersted) Schneider) in Tibet and its paleoenvironmental implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 442, 61–71. doi: 10.1016/j.palaeo.2015.11.014

Xu, X., Dimitrov, D., Shrestha, N., Rahbek, C., and Wang, Z. (2019). A consistent species richness-climate relationship for oaks across the Northern Hemisphere. *Glob. Ecol. Biogeogr.* 28, 1051–1066.

Yao, Y. F., Bera, S., Ferguson, D. K., Mosbrugger, V., Paudayal, K. N., and Jin, J. H. (2009). Reconstruction of paleovegetation and paleoclimate in the early and middle Eocene, Hainan Island, China. *Clim. Chang.* 92, 169–189. doi: 10.1007/s10584-008-9457-2

Zhang, Q. R. (1980). *Stratigraphy and Palaeontology.* Yichang: Yichang Institute of Geology.

Zhou, W. J., Liu, X. Y., Xu, Q. Q., Huang, K. Y., and Jin, J. H. (2013). New coryphoid fossil palm leaves (Arecaceae: Coryphoideae) from the Eocene Changchang Basin of Hainan Island, South China. *Sci. China Earth Sci.* 56, 1493–1501. doi: 10.1007/s11430-013-4681-7

Zhou, Z. K. (1996). Studies on *Dryophyllum* complex from China and its geological and systematic implications. *Acta Bot. Sin.* 38, 666–671.

Zhou, Z. K. (1999). Fossils of the Fagaceae and their implications in systematics and biogeography. *Acta Phytotaxo. Sin.* 37, 369–385.