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Pollen morphology of *Quercus* sect. *Ilex* and its relevance for fossil pollen identification in southwest China

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Abstract

Pollen grains of 16 modern species of *Quercus* were examined by scanning electron microscopy (SEM) and light microscopy (LM). The focus of this investigation was on a small group (*c.* eight species) of alpine, sclerophyllous oaks that may form a monophyletic group within sect. *Ilex*. The data were combined with published data for Polar axis (*P*) and Equatorial diameter (*E*) for more than 80 species. Based on pollen morphology *Quercus* pollen grains were divided into three types: (1) The *Cyclobalanopsis* type is smallest (generally < 23 µm) in size, with *P/E* ratios of approximately 1.08 and a psilate or fine-grained surface; (2) *Quercus* sect. *Ilex* type is 23–29 µm, the *P/E* ratio is approximately 1.24 (prolate) and it has a rugulate pollen surface; (3) the *Quercus* sect. *Quercus* type is generally > 29 µm in size, has a *P/E* ratio of approximately 1.04, and a clearly verrucate pollen surface. Based on a comparison with modern pollen size and ornamentation, fossil pollen grains of the Quaternary Qinghai Lake core can be assigned to the Chinese southwest mountain oak group of *Quercus* sect. *Ilex* (in particular *Quercus semecarpifolia*). In addition, we show that the pollen percentages of *Quercus* rapidly increased to the highest level during the glacial period. Using SEM for the identification of fossil *Quercus* pollen grains is essential to ensure the accuracy of differentiating evergreen *Quercus* types (sect. *Ilex* versus sect. *Cyclobalanopsis*) during the last glacial period in southwest China.

Keywords: *Quercus*, pollen morphology, *Quercus* sect. *Ilex*, Chinese southwest mountain oaks, southwest China, scanning electron microscopy

Quercus (oak) is a large genus (*c.* 400 species) of monoecious trees and shrubs in the family Fagaceae, which is found in North Africa, Asia, Europe, North America and South America (Colombia). There are *c.* 80 spp. of its species growing in China (Flora of China 1989–2013). The genus *Quercus* was initially classified into two subgenera, *Cyclobalanopsis* and *Quercus*, and the latter was further subdivided into five sections (*Heterobalanus*, *Cerris*, *Protobalanus*, *Quercus* and *Lobatae*) (Trelease 1924; Camus 1936–1938, 1938–1939, 1952–1954; Menitsky 1984; Nixon 1997). Subsequently, Manos and co-workers modified the taxonomy by dividing the section *Cerris* into the sections *Heterobalanus* (= *Brachylepides*) and *Cerris* (Manos et al. 1999, 2001;

Manos & Stanford 2001; Oh & Manos 2008; Yang et al. 2017) on the basis of molecular studies (cpDNA, ITS, *CRC*+ITS, and SNP data). Recently, Denk and Grimm (2009) and Denk and Tekleva (2014) concluded that there are six infrageneric groups of *Quercus* (*Cyclobalanopsis*, *Ilex*, *Cerris*, *Protobalanus*, *Quercus* and *Lobatae*) based on pollen ornamentation features, with *Quercus* section *Heterobalanus* (sect. *Heterobalanus*) entirely included in Group *Ilex* (Denk & Grimm 2009, 2010; Denk & Tekleva 2014; Denk et al. 2017a). Most recently, Denk et al. (2017b) proposed a new classification of oaks. Subgenus *Cerris* includes three sections, sect. *Cerris*, sect. *Ilex*, and sect. *Cyclobalanopsis*; subgenus *Quercus* includes the sections *Quercus*, *Lobatae*,

Protobalanus, *Virentes* and *Ponticae*. The species of *Quercus* have a wide global distribution, encompassing various ecological habitats. Within sect. *Ilex*, Menitsky (1984) recognised a distinct group of alpine evergreen sclerophyllous oaks that comprises at least eight species (his sect. *Heterobalanus*). Members of this group are very special not only in terms of plant morphology (i.e. tomentum, leaves and fruits) (Menitsky 1984; Zhou 1992; Zhou et al. 2003; Yang et al. 2009), but more importantly because of their unique distribution and habitat preference.

Most recently, it has been shown that sect. *Heterobalanus* may indeed form a natural group within sect. *Ilex* (Hipp et al. 2015; Deng et al. 2017), but it is currently uncertain whether all species originally included within sect. *Heterobalanus* belong to this natural group. Hence, in the following we refer to this group of oaks as ‘Chinese southwest mountain oaks.’ Most species in this group are gregarious, forming pure stands on the upper slopes and summits of ridges in southwest China (Jin 1981; Zhou et al. 2003). Their altitudinal distribution is mainly concentrated between 2400 and 3600 m (Zhou et al. 2007).

Pollen analysis has become an important method for the reconstruction of past vegetation. Examining the pollen morphology under light microscopy (LM), *Quercus* is easily distinguished from other Fagaceous genera, such as *Castanea*, *Castanopsis*, *Lithocarpus*, *Fagus*, *Trigonobalanus*, *Formanodendron* and *Colombobalanus* (Yamazaki & Takeoka 1959; Liu & Fang 1986; Wang & Chang 1988, 1991; Nixon & Crepet 1989). However, pollen identification of *Quercus* itself is difficult and the pollen classification is not straight-forward when using LM only. In addition, the recognition of two pollen morphotypes of *Quercus*, i.e. the evergreen pollen type (mainly including or synonymous with sects *Cyclobalanopsis* and *Ilex*) and the deciduous (sect. *Quercus*) pollen type (Jarvis et al. 1992; Liu et al. 2007) is insufficient for reliably interpreting the palaeoclimate and may produce taxonomic confusion. Because of the importance of Chinese southwest mountain oaks as a paleoenvironmental indicator, we conducted a detailed study of pollen morphology for many species in the genus *Quercus*, in particular for Chinese southwest mountain oaks and other species of sect. *Ilex*. The size and fine ornamentation measurements were collected using LM and scanning electron microscopy (SEM), and then statistical analysis was undertaken. Finally, fossil pollen grains of *Quercus* from a Quaternary core collected in Yunnan province, China, were identified as belonging to Chinese southwest mountain oaks based on the new pollen morphological results.

Material and methods

Materials

Pollen samples and plant species. — Pollen samples for the morphological study were collected from the Botanical Herbarium of Sun Yat-sen University and the Herbarium of the South China Institute of Botany, Chinese Academy of Sciences, China. A total of 16 species of the genus *Quercus* were collected, of which 15 species were from subgenus *Cerris* and one from subgenus *Quercus*. For the *Cerris* subgenus, 11 species were from sect. *Ilex* (including eight species of Chinese southwest mountain oaks and three other species) and three species from sect. *Cyclobalanopsis*. Their distributions and ecological features are listed in the present study (Table I).

A pollen morphology dataset of more than 80 species of *Quercus* was established based on information presented in previously published papers (Nakagawa et al. 1996; Cao & Zhou 2002; Wei 2003; Beug 2004; Wang & Pu 2004; Liu et al. 2007; Deng et al. 2013; Denk & Grimm 2009; Denk & Tekleva 2014).

Fossil pollen samples. — Qinghai Lake (25° 12' N, 98° 25' E) is a volcanic dammed lake, located at an elevation of 1885 m above sea level (a.s.l.), in the western Gaoligong Mountains of Tengchong County, Yunnan Province, China. In 2013, a core in length of 1442 cm was extracted from the centre of Qinghai Lake. The chronology of the core is based on 15 accelerator mass spectrometry (AMS) radiocarbon dating results, which were calibrated using the Clam software package (Blaauw 2010). According to the dating results, the age of the bottom of the core was 60.4 cal ka BP (i.e. at 1442 cm). The age-depth plot shows that the sedimentation rate was high during the Holocene and low during the last glacial period. Previous pollen results show abundant pollen of *Quercus* (including both deciduous and evergreen types), in particular at the level older than ~10 cal ka BP (Xiao et al. 2015; Yang et al. 2016). For further identification of the *Quercus* pollen, a new detailed pollen study was performed, in which the *Quercus* pollen from 200 to 740 cm (age: 30–13 cal ka BP) of the core was studied using SEM.

Methods

The modern pollen samples were prepared using the acetolysis method described by Erdtman (1953). A total of 360 samples were collected at 4 cm intervals for fossil pollen analysis. For each sample, 1 g of sediment was weighed and processed using heavy liquid separation (Moore & Webb 1979; Moore et al. 1991). In brief, the process is as follows: (1) 15% HCl added to remove carbonates; (2) then 10% KOH added to remove humic substances; (3) heavy liquid flotation, followed by mounting the sample in

Table I. Plant species collected for pollen morphological study. Relevant habitats and distributions are shown.

Species	Habitat	Altitude (m)	Distribution
<i>Quercus</i> subgenus <i>Cerris</i>			
Chinese southwest mountain oaks of sect. <i>Ilex</i>			
<i>Q. aquifolioides</i>	Evergreen, tree (10 m), found in mountain forest, often shrub (1–4 m)	2000–4500	China (Tibet), Bhutan, Burma
<i>Q. guyavifolia</i>	Evergreen, tree (15 m), found in mountain forest, brittle shrub (0.6–2 m)	2500–4000	China (Sichuan, Yunnan)
<i>Q. longispica</i>	Evergreen, tree (20 m), found in mountain forest, small tortuous shrub at high elevation	1500–4000	China (Guizhou, Sichuan, Tibet, Yunnan), Thailand
<i>Q. monimotricha</i> ^a	Evergreen, shrub (0.2–0.6m), found in mountain elfin forest	2000–4400	China (Sichuan, Yunnan), Myanmar
<i>Q. pannosa</i>	Evergreen, tree (15 m), found in mountain forest, small shrub at high elevation	2500–3900	Afghanistan, China (Tibet), India, Myanmar, Nepal
<i>Q. rehderiana</i> (syn. <i>Q. longispica</i>)	Evergreen, tree (12 m), found in mountain forests, small tortuous shrub at high elevation	1500–4000	China (Guizhou, Sichuan, Tibet, Yunnan)
<i>Q. semecarpifolia</i>	Evergreen, tree (20–30 m), found in mountain forest, columnar habit with domed crown	2600–4000	Afghanistan, China (Tibet, Yunnan), India, Myanmar, Nepal
<i>Q. senescens</i>	Evergreen, tree (10 m), found in mountain forest, often shrub (less than 3 m)	1900–3300	China (Guizhou, Sichuan, Tibet, Yunnan)
<i>Q. spinosa</i>	Evergreen, tree (4–10 m), found in mountain forest, shrub	1000–3100	China (Sichuan, Guizhou, Yunnan, Taiwan), Myanmar
Other species of sect. <i>Ilex</i>			
<i>Q. cocciferoides</i>	Semi-evergreen, tree (15 m), found on mountain slopes or in dry valleys, often bushy	1000–2500	China (Sichuan, Yunnan)
<i>Q. franchetii</i>	Evergreen, tree (15 m), found in mountain broadleaf forest	800–2600	China (Sichuan, Yunnan), Thailand, Vietnam
<i>Q. phillyraeoides</i>	Evergreen, tree (10 m), found in mountain forest, small tortuous shrub at high elevation	300–1200	Southwestern and Central China, Japan, Korea
Sect. <i>Cyclobalanopsis</i>			
<i>Q. fleuryi</i> ^a	Evergreen, tree (25 m), found in wet mountain subtropical forests	500–1500	Southwest China, Laos, Vietnam
<i>Q. glaucoides</i> ^a	Evergreen, tree (20 m), found in mountain forest, prefers calcareous, dry sites	500–2200	China (Guizhou, Sichuan, Yunnan), Mexico
<i>Q. jenseniana</i> ^a	Evergreen, tree (30 m), found in forests on mountain slopes, valleys, along streams	300–1700	Southwest and Central China
<i>Quercus</i> subgenus <i>Quercus</i>			
<i>Q. yunnanensis</i>	Deciduous, tree (15–20 m), found in mountain oak-pine forest	1000–2800	China (Guangdong, Guangxi, Guizhou, Sichuan, Yunnan)

^aSamples from the herbarium of Sun Yat-sen University, all others from the herbarium of the South China Institute of Botany, Chinese Academy of Science, China. The geographical data are based on Flora Republicae Popilaris Sinicae (Chen et al. 1980) and the online edition of *Oaks of the world* (<http://oaks.of.the.world.free.fr>).

a glycerine jelly. The fossil pollen grains were re-extracted with a capillary tube from the slide after LM observation and prepared for SEM examination (Tekleva et al. 2014).

Both modern and fossil pollen were identified using LM and SEM. Modern pollen mounted in glycerine jelly was examined in transmitted light using a Zeiss Axioscop (Germany) microscope. We measured Polar axis (*P*) and Equatorial diameter (*E*) of the pollen grains. In total, 200 pollen grains were analysed for each species.

Pollen for SEM examination was pulse sputter coated with a gold (60/40) target and examined with JEOL 880, Leica Stereoscan 440, Hitachi S800 and Zeiss Supra 55VP scanning electron

microscopes. SEM observation of modern pollen was at 3000 × and 20 000 × magnifications. Low magnification (3000 ×) was used to examine apertures, colpi and the arrangement of exine ornamentation, while details were investigated at higher magnification (20 000 ×).

The main magnification rates in the photographs are 3000 × and 20 000 ×.

Results

Pollen sizes of modern plant species

The pollen-grain observation for the 16 species under LM reveals that they are all tricolporate with

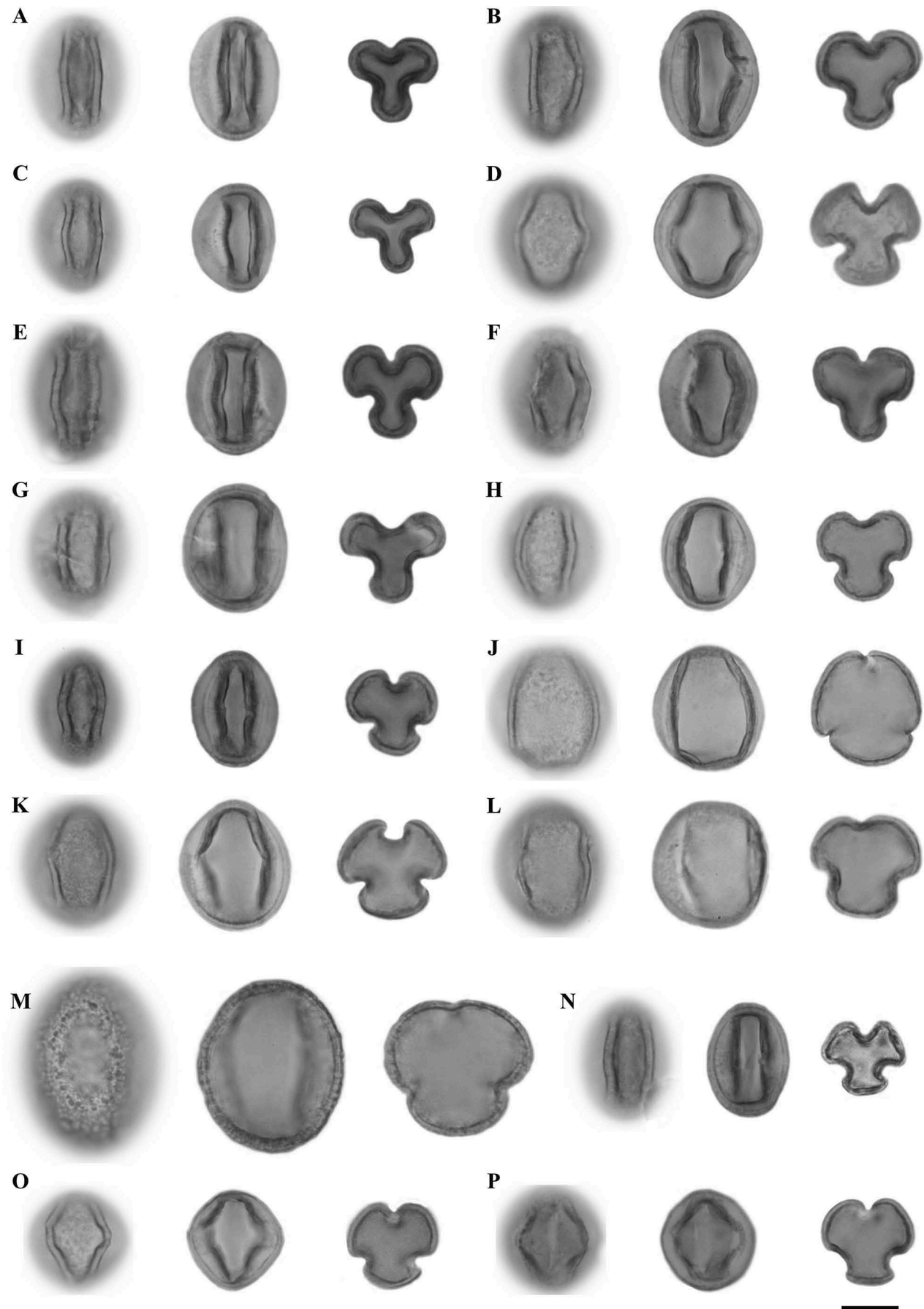


Figure 1. Light microscopy (LM) pollen morphology of *Quercus* (16 species), equatorial and polar view. **A.** *Q. aquifolioides*. **B.** *Q. guyavifolia*. **C.** *Q. longispica*. **D.** *Q. monimotricha*. **E.** *Q. pannosa*. **F.** *Q. rehderiana*. **G.** *Q. semecarpifolia*. **H.** *Q. senescens*. **I.** *Q. spinosa*. **J.** *Q. cocciferoides*. **K.** *Q. franchetii*. **L.** *Q. phillyraeoides*. **M.** *Q. yunnanensis*. **N.** *Q. fleuryi*. **O.** *Q. glaucoides*. **P.** *Q. jenseniana*. Scale bar – 10 μm .

relatively long and narrow colpi (Figure 1). The features of the apertures agree with previous observations (Benthem et al. 1984; Nakagawa et al. 1996; Wang & Pu 2004; Shah et al. 2005; Deng et al. 2013; Denk & Tekleva 2014). The exine ornamentation for most species is scabrate under LM; some are verrucate (*Quercus yunnanensis*). Due to the difficulty in recognising specific differences in exine characters by means of LM (Jarvis et al. 1992; Tang et al. 2016), differences in pollen size parameters (P , E , P/E ratio) are considered to be important criteria in distinguishing pollen types among *Quercus* when using LM only.

According to the measurements collected during this study, the length of P of all species in Chinese southwest mountain oaks of sect. *Ilex* (Figure 2) ranges from 22 to 34 μm , with three species (*Quercus aquifolioides*, *Q. guyavifolia* and *Q. longispica*) being relatively longer than the others, generally 27–32 μm . Size ranges of the other six species (i.e. *Q. monimotricha*, *Q. pannosa*, *Q. rehderiana*, *Q. semecarpifolia*, *Q. senescens* and *Q. spinosa*) are 23 to 28 μm . With regard to species of sect. *Ilex* outside the Chinese southwest mountain oaks (*Q. cocciferoides*, *Q. franchetii*, *Q. phillyraeoides*), the P lengths are slightly smaller (21–27 μm). As for sect. *Cyclobalanopsis* (*Q. fleuryi*, *Q. glaucoides* and *Q. jenseniana*), the length of P is in the range 22–26 μm (Figure 2). In contrast, the E of the Chinese southwest mountain oaks is much shorter than P , mainly ranging from 18 to 23 μm . Similar sizes are recorded for *Q. monimotricha* (15–18 μm) and other oaks of sect. *Ilex* (14–20 μm). In contrast, length of E in subgenus *Cyclobalanopsis* is around 20–24 μm which is very close to its P ranges and reflecting a spherical pollen grain. White oaks, subgenus *Quercus*, sect. *Quercus* (e.g. *Q. yunnanensis*) are markedly larger in terms of both their P (27–34 μm) and E (27–33 μm) ranges in comparison to all other species investigated in this study. This study further confirms that pollen grains of sect. *Cyclobalanopsis* and sect. *Quercus* have a ‘spheroidal’ shape (P/E ratio 0.88–1.14) (Punt et al. 2007), but the latter produce much bigger pollen. Concerning sect. *Ilex*, their pollen grains are prolate (P/E ratio 1.33–2.00).

Specific pollen comparison in *Quercus*

As mentioned earlier, pollen size (P , E , P/E ratio) can be used as a preliminary criterion to distinguish some sections within oaks (Jarvis et al. 1992; Nakagawa et al. 1996; Wang & Pu 2004). In this study, a dataset of pollen sizes has been compiled which includes 80 species of *Quercus* from around the world (Figure 3). The results show that P for the majority of species in sect. *Cyclobalanopsis* (29 species) is relatively short, centred between 22.7 and

26.5 μm , with the exceptions of *Q. austrocochinchinensis* (27.3–31.5 μm), *Q. gomeziana* (29.4–33.6 μm) and *Q. kerrii* (27.3–31.5 μm) (Wang & Pu 2004). In contrast, P ranges for sect. *Cerris*, sect. *Quercus* and sect. *Lobatae* are among the biggest, 28–36 μm , 31–39 μm and 36–42 μm , respectively. Chinese southwest mountain oaks (eight species) and other sect. *Ilex* (25 species) are intermediate, 25.1–30.5 μm and 25.3–32.3 μm , respectively. This means that P of the Chinese southwest mountain oaks is generally 4–6 μm longer than that of *Cyclobalanopsis*, but shorter than sect. *Quercus* or sect. *Lobatae*. With respect to E , the most remarkable feature is the greatest lengths in sect. *Cerris* (24.7–33.4 μm) and sect. *Quercus* (27.9–35.4 μm). However, the other taxa show high similarity among species including the sect. *Cyclobalanopsis* (21–24 μm), *Ilex* (Chinese southwest mountain oaks, 20–25 μm ; other species, 18.6–25.4 μm) and *Lobatae* (22.0–26.0 μm).

The P/E ratio can be used as a more effective criterion for pollen identification. Despite high diversity among the species, the general differences are still apparent. First, higher P/E ratios are observed in sect. *Lobatae* (1.63), suggesting ‘prolate’ pollen grains (Punt et al. 2007). The pollen of Chinese southwest mountain oaks has a variable P/E ratio, but the mean value 1.24 indicates more or less ‘prolate’ or ‘spheroidal’ grains. In contrast, sect. *Cyclobalanopsis* has a mean value of 1.08, indicating that most pollen grains are spherical.

A comparison of pollen size (P , E , P/E ratio) among the 80 species of *Quercus* reveals that sect. *Cyclobalanopsis*, *Protobalanus* and *Lobatae* have quite distinct values, allowing them to be roughly separated. Despite the P/E ratio values of sect. *Ilex* being relatively higher, their differences from other *Quercus* sections are still unclear, requiring more detailed morphological studies using both LM and SEM.

Ornamentation of the exine by SEM

Rod-like micro-rugulate type (characteristic of Chinese southwest mountain oaks). — Based on SEM photographs of Chinese southwest mountain oaks, the most important feature of the basic ornamentation is rod-shaped structures which are densely distributed on the exine surface except in the aperture regions. Each unit is multibaculate consisting of four to five very small, randomly oriented rods. This kind of exine surface was described as ‘rod-like micro-rugulate’ by Denk and Grimm (2009), where ‘rugulate’ denotes an ornamentation consisting of elongated exine elements more than 1 μm long, arranged in an irregular pattern that is intermediate between striate and reticulate (Punt et al. 2007).

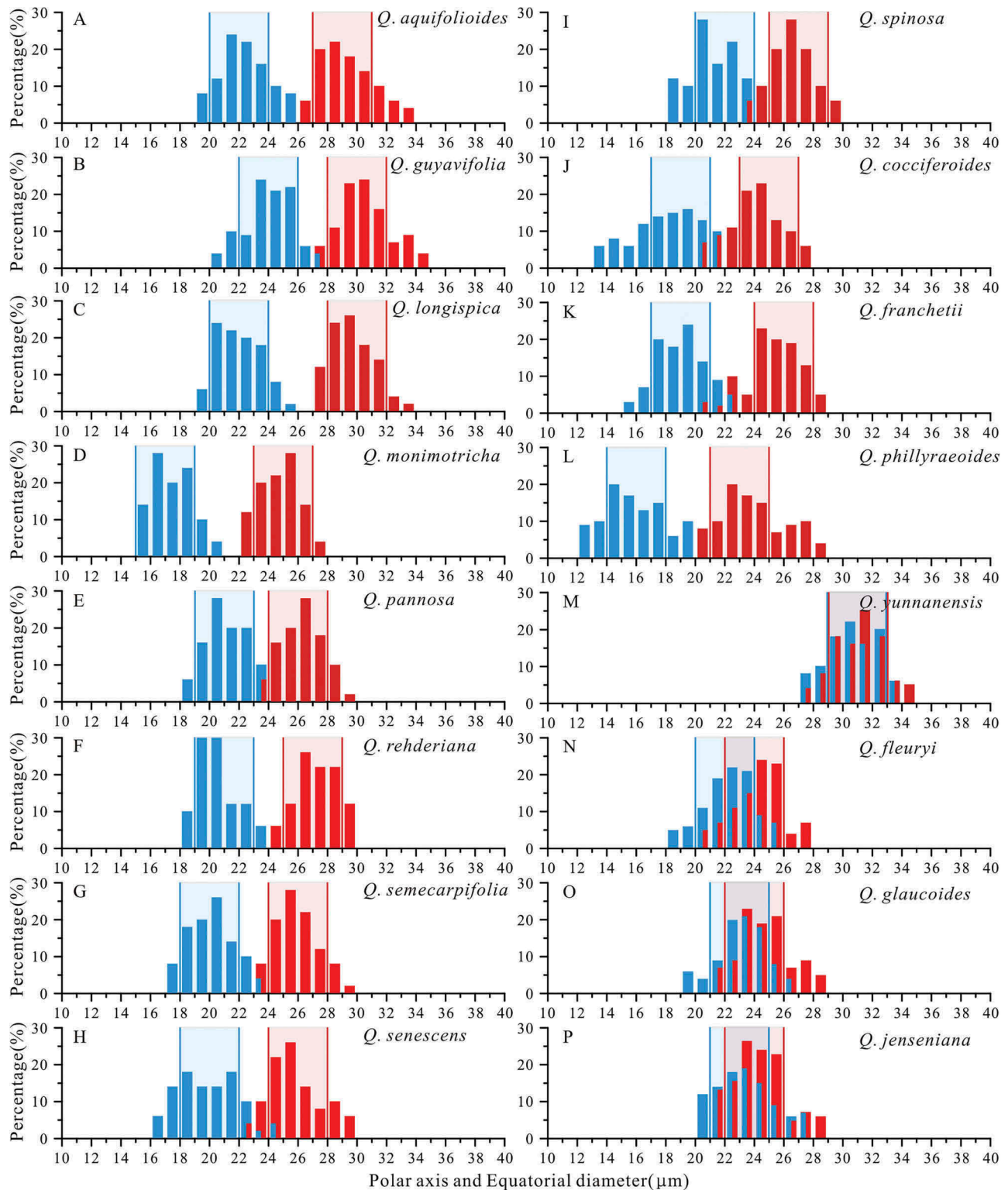


Figure 2. Bar charts of polar (red) and equatorial (blue) axis measurements of 16 species of *Quercus* to an accuracy of 1 μm (percentage of 200 grains measured under light microscopy [LM] for each species). The most common range (restricted to 4 μm) is shaded.

The current study reveals that the exine surface of Chinese southwest mountain oaks has a consistently rod-like structure (Figures 4, 5). We refer to this exine surface type as ‘rod-like micro-rugulate’

which is very clear under SEM, but is not visible under LM. The surface of the pollen of section *Ilex* (*Quercus cocciferoides*, *Q. franchetii* and *Q. phillyraeoides*) also has rod-shaped structures, but these

rods are obviously smaller or thinner. Consistent results were also reported by Denk and Tekleva (2014) for many species in sect. *Ilex* from southwest China (*Q. kingiana* and *Q. lodicosa*).

Verrucate type (characteristic of sect. Quercus)

For the sect. *Quercus*, which are deciduous broadleaved trees in Eurasia and either evergreen or deciduous broadleaved trees in the Americas, the pollen ornamentation takes the form of irregular verruca-like structures, randomly distributed on the exine surface except on regions inside the colpus (Figures 4, 5). Every unit is a distinct verruca of varying diameter size from 0.3 to 0.7 μm . This exine surface type was described as ‘micro-verrucate’ by Denk and Grimm (2009), where ‘verrucate’ denotes a wart-like exine element, more than 1 μm wide, that is broader than it is high and not constricted at the base (Punt et al. 2007). In our study, *Q. yunnanensis* was examined because of its typical verrucate structure. In fact, this structure is somewhat visible using LM (Liu et al. 2007).

Rod-like vertical type (characteristic of sect. Cyclobalanopsis)

The exine surface of sect. *Cyclobalanopsis* is micro-echinate and finegrained with various spines (Wei 2003; Wang & Pu 2004), and is described as ‘rod-like vertical’ by Denk and Grimm (2009). Our SEM photographs reveal that rod-shaped structures are the basic units on the exine surface (Figures 4, 5). Each unit is perpendicular with diverging rods or a relatively psilate structure which we refer to as the ‘rod-like vertical type.’ The diameter of each individual rod is usually less than 0.5 μm . Three exine types were classified by Deng et al. (2013): *Quercus fleuryi* is a ‘rod-like vertical’ type; *Q. glaucooides* and *Q. jenseniana* are ‘rod-like masked’ types.

Measurements of rod-like units and statistical analysis

Rod-like elements are the basic unit of the exine structure in Chinese southwest mountain oak species. In order to differentiate the eight species of these oaks, we calculated the length and width of the rods. At least 20 SEM high-resolution photographs of the equatorial zone between apertures at a magnification of 20 000 $\times$ were taken for each species. Investigation of the sculpturing was always done at the same position on the pollen grain, the sculpture elements were in a single plane and well exposed, and only the longest bar of each unit was measured.

A scatterplot of length versus width for the rods shows that some micro-rugulate differences can be

used for distinguishing pollen taxa (Figure 6). According to the measured values, the cluster of points representing *Quercus guyavifolia* is located separately on the right, with the longest rod length. The clusters of points for four species (*Q. monimotricha*, *Q. pannosa*, *Q. semecarpifolia* and *Q. spinosa*) are quite well separated, or partially overlapping by one or two species. The clusters of points for the other four species (*Q. aquifolioides*, *Q. longispica*, *Q. rehderiana* and *Q. senescens*) are completely or partially overlapping and it is difficult to separate them on the basis of their pollen ornamentation. Thus, some species within Chinese southwest mountain oaks can be identified using measurements of the micro-structure of the exine.

Discussion

Identification of fossil Quercus pollen

Many pollen records from lake sediments in southwest China confirm that the pollen assemblages from between the Holocene and the last glacial period vary greatly (Xiao et al. 2007, 2014a, 2014b, 2015, 2016; Shen et al. 2010; Tareq et al. 2011; Zhang et al. 2012; Chen et al. 2014; Yang et al. 2016). The pollen evidence shows that cold-tolerant trees increased markedly together with some herbs tolerant to dry conditions, such as *Artemisia* and *Amaranthaceae*, during the Last Glacial Maximum (LGM). In particular, a large amount of *Quercus* pollen has been found in the interval of the last glacial period, increasing from 20–30% to 50–60%. This change in pollen assemblages has been found in many records for southwest China (Kou et al. 2006; Chen et al. 2014; Xiao et al. 2015; Yang et al. 2016). For example, *Quercus* pollen grains from Tiancai Lake (3898 m a.s.l.) were abundant at a roughly constant level during the LGM (Xiao et al. 2014b). In general, *Quercus* in Quaternary pollen analysis is divided into deciduous and evergreen types on the basis of visible differences (i.e. pollen size, sculpture and aperture type). Jarvis et al. (1992) suggested that the deciduous oaks and evergreen oaks of southwest China can be reliably separated using LM. The previous fossil pollen studies shows that these criteria are actually problematic because of the low resolution of LM and possible occurrence of more diverse types of fossil oak pollen (Liu et al. 2007). A study from southwest Sichuan supports the suggestion that the pollen of the low and high elevation oaks cannot be distinguished by LM (Jarvis & Clay-Poole 1992). To date, few fossil pollen studies have differentiated the pollen of Chinese southwest mountain oaks of sect. *Ilex* from other *Quercus* types (Nakagawa et al. 1996, 2000; Takahashi et al. 2008). The use of SEM

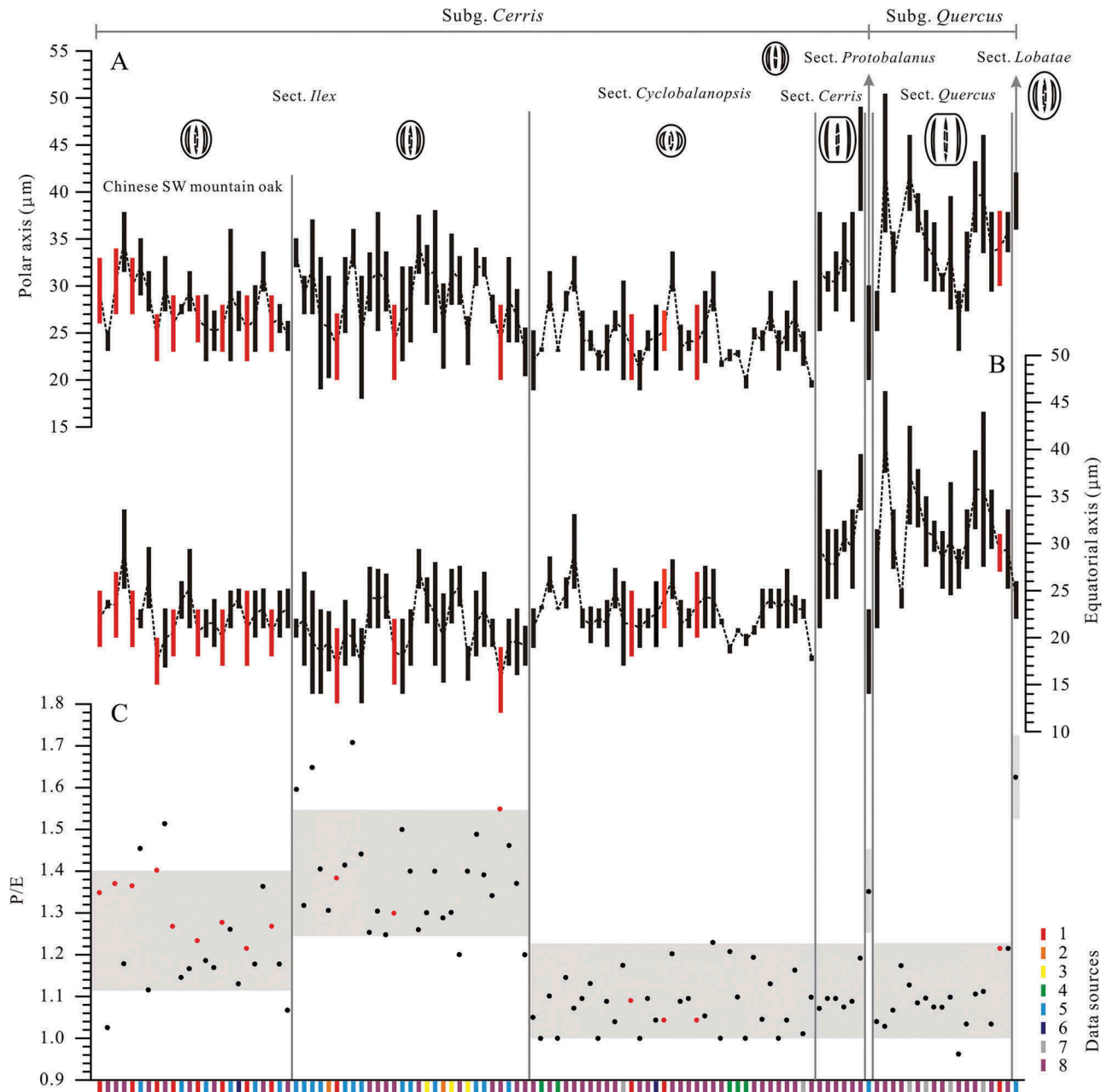


Figure 3. Pollen size of *Quercus*. **A.** Polar axis. **B.** Equatorial axis. **C.** Data shown are 'mid-values' ratios of polar axis and equatorial axis. Data summarised from: (1) this study (red); (2) Beug (2004) (orange); (3) Cao & Zhou (2002) (yellow); (4) Deng et al. (2013) (green); (5) Denk and Tekleva (2014) (cyan); (6) Nakagawa et al. (1996) (blue); (7) Wang et al. (1995) (grey); and (8) Wang and Pu (2004) (purple). Data for the groups *Protobalanus* and *Lobatae* are averaged values measured by scanning electron microscopy (SEM) (Denk and Tekleva 2014).

has helped to identify the species comprising the genus *Quercus*. Some studies show that the numerous species in *Quercus* can be grouped based on their ornamentation examined by SEM (Naryshkina & Evstigneeva 2009; Tekleva et al. 2014). Denk and Grimm (2009), for the first time, distinguished five pollen types of *Quercus* from 31 species based on tectum structures using SEM (rod-like vertical,

[micro]verrucate, rod-like masked, rod-like [micro]rugulate and [micro]verrucate scattered). In previous palynological studies, two pollen morphotypes of *Quercus* are usually recognised, i.e. the evergreen type (mainly including or synonymous with sect. *Cyclobalanopsis*) and the deciduous type (sect. *Quercus*) (Jarvis et al. 1992; Liu et al. 2007). This distinction is insufficient for correctly interpreting the

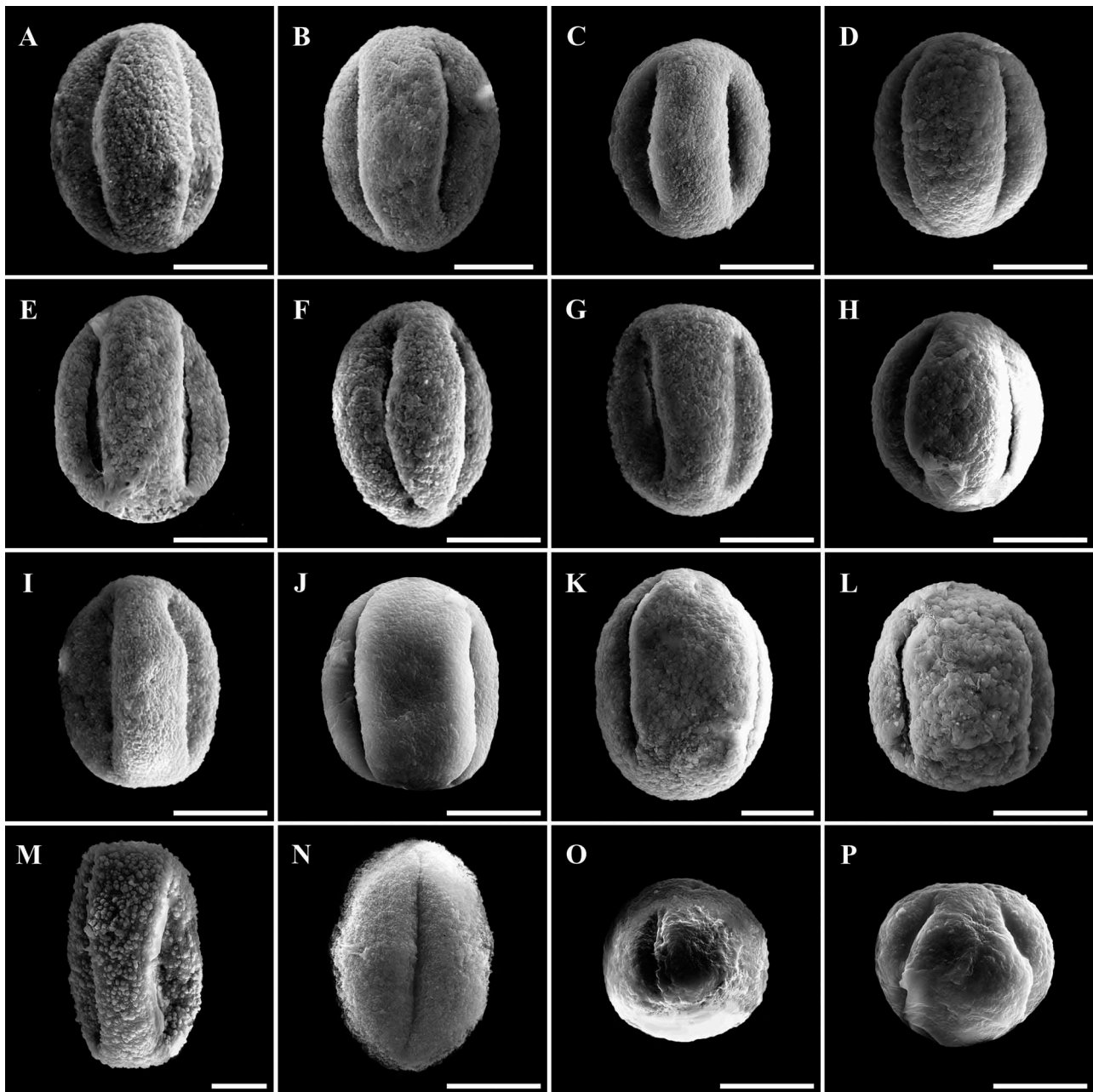


Figure 4. Scanning electron microscopy (SEM) pollen morphology of *Quercus* (16 species), equatorial view. **A.** *Q. aquifolioides*. **B.** *Q. guyavifolia*. **C.** *Q. longispica*. **D.** *Q. monimotricha*. **E.** *Q. pannosa*. **F.** *Q. rehderiana*. **G.** *Q. semecarpifolia*. **H.** *Q. senescens*. **I.** *Q. spinosa*. **J.** *Q. cocciferoides*. **K.** *Q. franchetii*. **L.** *Q. phillyreoides*. **M.** *Q. yunnanensis*. **N.** *Q. fleuryi*. **O.** *Q. glaucooides*. **P.** *Q. jenseniana*. Scale bars – 10 μm .

palaeoclimate and may produce taxonomic confusion. This is because the cold-tolerant alpine trees are usually assigned to the general ‘evergreen-type,’ despite them occupying a completely different habitat from other monsoonal evergreen *Quercus* (including sects *Cyclobalanopsis* and *Ilex*). Therefore, it is important to distinguish the pollen grains of Chinese southwest mountain oaks (particularly *Q. semecarpifolia* in the study region) from other evergreen sect. *Ilex* and/or *Cyclobalanopsis* from low altitudes.

In this study, a refined pollen analysis was used to investigate samples from a core from Qinghai Lake at 1700 m a.s.l. in Tengchong, Yunnan Province (Figure 7). The pollen percentages of *Quercus* rapidly increase to the maximum level during the period 30–11 cal ka BP. Similar results have also been reported by Xiao et al. (2015) and Yang et al. (2016).

We divided the *Quercus* pollen into three types based on LM and SEM examination:

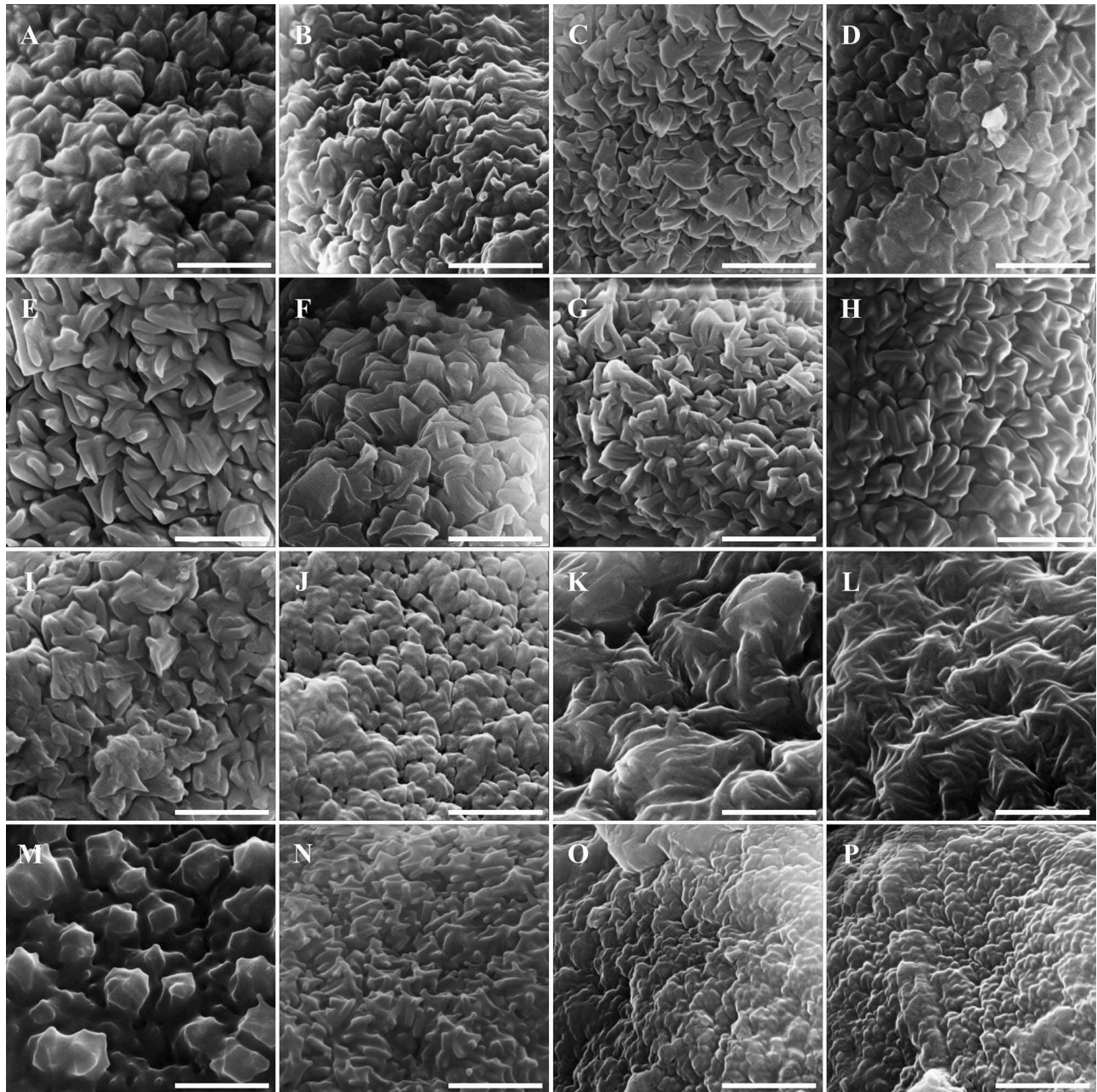


Figure 5. Scanning electron microscopy (SEM) photographs of pollen ornamentation for 16 species of *Quercus*, showing selected regions between apertures. **A.** *Q. aquifolioides*. **B.** *Q. guyavifolia*. **C.** *Q. longispica*. **D.** *Q. monimotricha*. **E.** *Q. pannosa*. **F.** *Q. rehderiana*. **G.** *Q. semecarpifolia*. **H.** *Q. senescens*. **I.** *Q. spinosa*. **J.** *Q. cocciferoides*. **K.** *Q. franchetii*. **L.** *Q. phillyreoides*. **M.** *Q. yunnanensis*. **N.** *Q. fleuryi*. **O.** *Q. glaucooides*. **P.** *Q. jenseniana*. Scale bars – 1 μm .

(1) Sect. *Cyclobalanopsis*-type (evergreen trees from low elevations). This pollen type is identified according to the following criteria: < 23 μm in size, P/E ratio ~ 1.08 and psilate or fine-grained pollen surface.

(2) Sect. *Ilex*, Chinese southwest mountain oaks-type (evergreen sclerophyllous trees from high elevations of southwest China and neighbouring regions). The critical identification features are: size 23–29 μm , P/E ratio ~ 1.24 , rod-like rugulate

type pollen surface, as observed by SEM to correlate with the specific length and width of the rod-like elements. Most pollen during the glacial period in the Qinghai core can be identified as *Quercus semecarpifolia*.

(3) Sect. *Quercus*-type (cold-tolerant, deciduous trees). This group includes the pollen > 29 μm in size, P/E ratio ~ 1.04 , tricolporate with a clearly verrucate or scabrate pollen surface.

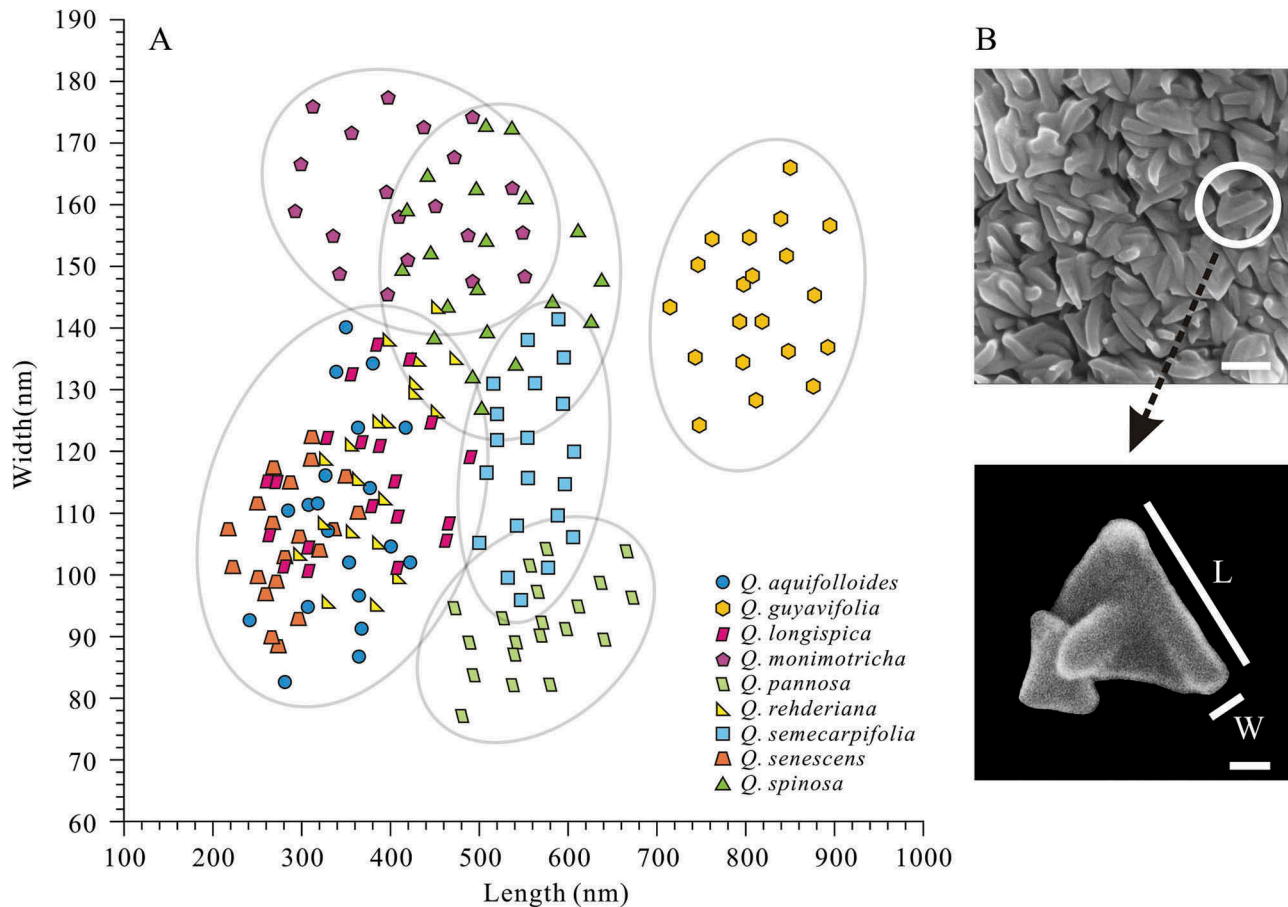


Figure 6. Plot of pollen surface rod size (length versus width) of eight species in Chinese southwest mountain oaks. **A.** Scatterplot. **B.** Measured location of rod-like rugulate surface. Scale bars – 1 μm (above), 100 nm (below).

In particular, selected pollen samples were examined with SEM. The pollen grains identified as Chinese southwest mountain oak-type require SEM examination at low magnification (3000 $\times$) for general surface comparison and with high magnification (20 000 $\times$) for detailed measurement of rod-like micro-rugulate units. Our scatterplot of length versus width of the rod structures of the fossil taxon of Chinese southwest mountain oak-type coincides with the cluster of points representing modern *Quercus semecarpifolia*, with a few points located in the areas occupied by the other two species of *Q. pannosa* and *Q. spinosa*. *Quercus spinosa* was included in sect. *Heterobalanus* (syn. sect. *Ilex*) by many authors (Flora of China Editorial Committee 1989–2013; Zhou et al. 2007; Yang et al. 2009), however, its distribution is not only in Yunnan, but mostly in the eastern part of mainland China, Taiwan Island and Burma where the climate condition is warmer. Therefore, *Q. spinosa* may be excluded from the Chinese southwest mountain oak group.

From the ecological and geographical point of view, the altitudinal distribution of Chinese southwest moun-

tain oaks ranges from 1700 to 4800 m, but is mainly concentrated between 2400 and 3600 m (Zhou et al. 2007). The characteristic climatic conditions at the locations where Chinese southwest mountain oaks thrive are as follows (Yang et al. 2009): mean temperature of the warmest month (MTW) = 12.0–19.5 $^{\circ}\text{C}$; warmth index (WI) = 33.2–88.9 $^{\circ}\text{C}$ month; annual biotemperature (BT) = –6.9 to –0.3 $^{\circ}\text{C}$; coldness index (CI) = –30.4 to –10.1 $^{\circ}\text{C}$ month; mean temperature of the coldest month (MTC) = –3.7 to 3.0 $^{\circ}\text{C}$; mean annual precipitation (MAP) = 701–897 mm.

The habitats occupied by Chinese southwest mountain oaks are characterised by a specific climate (Jarvis et al. 1992), which is quite different from other evergreen species of *Quercus*. Some studies have pointed out that low temperature, low precipitation and soil types limit the growth of most other evergreen broadleaved trees, so that the sclerophyllous Chinese southwest mountain oaks are dominant in the Himalaya–Hengduan Mountains (Zhou 1993; Yang et al. 2009).

The present assessment of fossil pollen confirms that pollen from the high plateau of southwest China

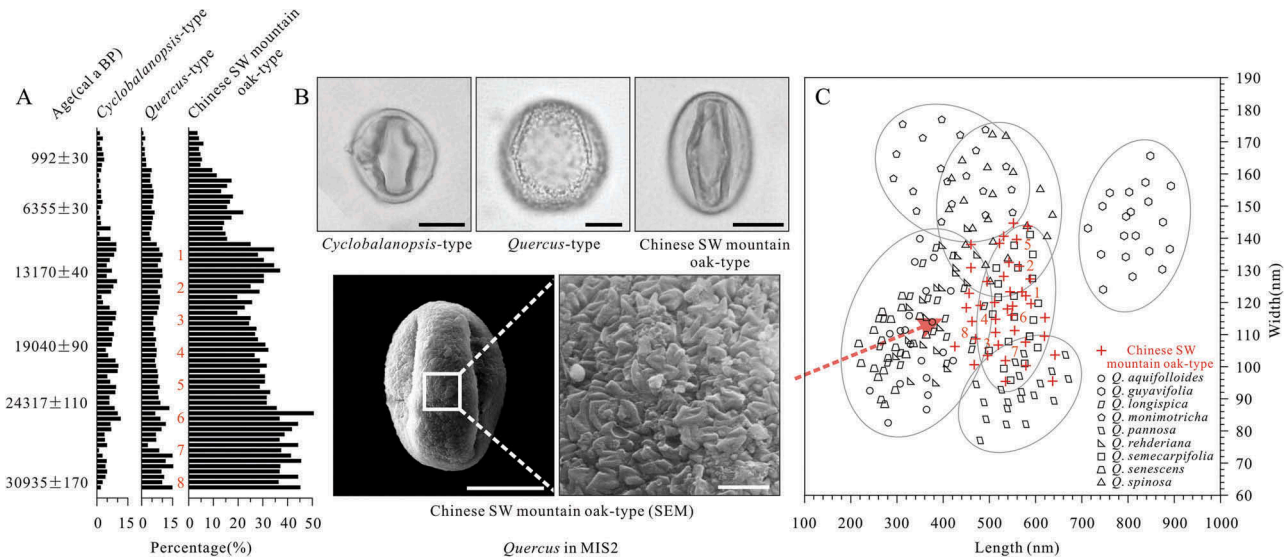


Figure 7. **A.** Relative amounts of fossil *Quercus* pollen. **B.** Light microscopy (LM) and scanning electron microscopy (SEM) pollen morphology of fossil *Quercus*, equatorial view. **C.** Rod sizes for the 'rod-like rugulate' type. Scale bars – 10 μ m (LM images), 10 μ m (SEM left image), 1 μ m (SEM right image).

previously identified as *Quercus* evergreen-type should be partly and/or totally attributed to the sclerophyllous taxa of *Quercus* sect. *Ilex*, and in particular to the group of Chinese southwest mountain oaks. In our study area of west Yunnan Province, *Q. semecarpifolia* (present-day distribution between 4000 and 2600 m a.s.l.) was dominant during the glacial period. Taking the present-day distribution at > 2600 m a.s.l. for *Q. semecarpifolia* and the associated pollen types of cold-tolerant temperate taxa like *Betula* into consideration, it appears that a remarkable vertical shift in the vegetation of the Tibetan Plateau occurred during the last glacial period, indicating colder conditions. This interpretation of local climate conditions explains why the pollen analysis conducted by Xiao et al. (2015) and Yang et al. (2016) found that unknown species of *Quercus* (evergreen-type/deciduous-type) were extremely abundant during the last glacial period.

Conclusion

Among the 80 species considered for the present study, the smallest pollen is found in members of *Quercus* sect. *Cyclobalanopsis* with a *P/E* ratio around 1.08, suggesting that pollen is spheroidal. The pollen of sect. *Quercus* (commonly called '*Quercus* deciduous-type' in pollen analysis) is also 'spheroidal' (*P/E* ratio ~1.09), but its absolute size is much bigger and it has distinct verrucate ornamentation. In contrast, pollen in sect. *Ilex* is moderately prolate and of intermediate size, indicating that Chinese southwest mountain oaks (sect. *Ilex*) pollen is generally bigger

than that of sect. *Cyclobalanopsis*, but smaller than that of sect. *Quercus*. Thus, pollen size and shape can be the primary criteria for distinguishing species in the genus *Quercus*.

The exine surface of Chinese southwest mountain oaks is 'rod-like micro-rugulate' under 20 000 $\times$ SEM magnification. Another subset of sect. *Ilex* has similar morphological characters as Chinese southwest mountain oaks, reflecting their close affinity. For specific pollen identification, the pollen of Chinese southwest mountain oaks can be further distinguished into *Quercus* *guyavifolia*, *Q. monimotricha*, *Q. pannosa*, *Q. semecarpifolia* and *Q. spinosa*, because on scatterplots based on rod-sizes (length versus width) of exine ornamentations under SEM the points for each individual species cluster together and these clusters overlap very infrequently.

The fossil pollen from Yunnan was studied using both LM and SEM techniques in order to identify the *Quercus* pollen. During the last glacial period, the pollen assemblages were dominated by *Quercus* (previously attributed to the evergreen-type). The current study shows that at least three types, i.e. sect. *Cyclobalanopsis*-type (*Quercus* evergreen-type), sect. *Ilex*-type (including taxa of the Chinese southwest mountain oaks) and sect. *Quercus*-type can be distinguished. Further SEM examination reveals that most fossil pollen in the studied core belongs to *Quercus* sect. *Ilex*, and the fossil data points coincide with those of *Q. semecarpifolia* on the scatterplot, suggesting its dominance during the glacial period. This result indicates an obvious downward shift of the vegetation belts from the

Tibetan Plateau. The fossil pollen interpretation presented here clarifies the identity of the extremely large quantities of unknown species of evergreen *Quercus* that have been found in cores from the last glacial period in southwest China.

Disclosure statement

No potential conflict of interest was reported by the authors.

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