



Last Glacial Maximum, early Holocene and modern environments of the northern South China Sea region: Insight from SEM analysis of Oak (*Quercus*) pollen

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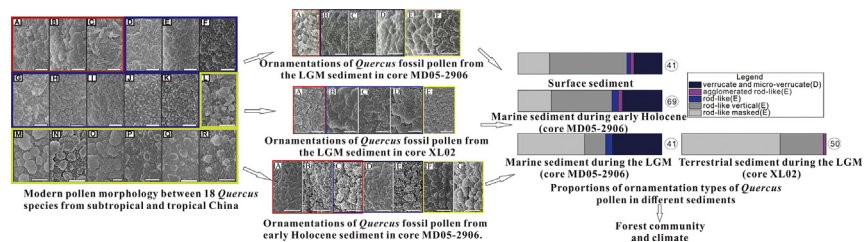
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HIGHLIGHTS

- The study clarified the potential significance of morphological diversity of *Quercus* pollen in the northern South China Sea (SCS).
- Occurrence of deciduous *Quercus* pollen and absence of deciduous oak in the northern SCS indicated extensive long-distance transport of pollen in an open marine setting.
- Evergreen *Quercus*-dominated pollen assemblages in sediment confirmed that evergreen forests had occupied the inland of the northern SCS during the LGM.

GRAPHICAL ABSTRACT



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ABSTRACT

Oak (*Quercus*) pollen was identified at the infra-generic (i.e. sub-genus to species) utilizing Scanning Electron Microscope (SEM) images of modern (i.e. 18 species from southern China) and fossil pollen grains from northern South China Sea (SCS) marine and terrestrial sediments. Key morphological characteristics of *Quercus* exine sculpture were used to separate the pollen into evergreen and deciduous groups, with this distinction applied to the fossil oak pollen from the Last Glacial Maximum (LGM) and early Holocene periods. The presence of *Quercus* pollen from the modern Pearl River and northern SCS suggests long distance transport from inland temperate to tropical regions surrounding the SCS. Fossil oak pollen from terrestrial and marine sediments from the northern SCS region suggests different pollen representation between these two sedimentary environments, with the terrestrial site dominated by evergreen *Quercus* types and the marine location showing greater representation of deciduous oak species. The presence of both evergreen and deciduous oak pollen in the LGM age marine sediments suggests only moderate cooling during this time period, while the dramatic increase of deciduous *Quercus* pollen in the marine core, as well as generally higher pollen influx values, reflects greater fluvial discharge, which in turn is linked to increased precipitation in the region during the early Holocene period.

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Various climate models based on pollen data have been proposed for the area inland of the northern South China Sea (SCS) during the Last Glacial Maximum (LGM), namely temperate (Sun and Li, 1999; Sun et al., 2003; Chang et al., 2013) to subtropical climates (Liew et al., 2006; Yue et al., 2012; Dai et al., 2015; Xue et al., 2015; Yu et al., 2017). Evidently, this remains debatable, because the high vegetation richness and low pollen identification rate in tropical and subtropical environments cause ambiguity in effective pollen proxies for humidity and temperature. This uncertainty impairs the establishment of a global general circulation model of glacial cycles and understanding of driving mechanism of global monsoons (Ruddiman, 2008; Wang et al., 2017). Pollen identification at family or genus level yields insensitive responses of pollen assemblages to moderate environmental alterations in tropical and subtropical regions, e.g. resulting in the development of a variety of climate reconstructions for the Sunda shelf and Amazon Basin regions that have dramatic implications for landscape interpretations during the LGM (i.e. extent of savanna versus rainforest cover) (Heaney, 1991; Bird et al., 2005; Bush et al., 2011; Bush, 2017).

Quercus is a dominant broadleaved component in pollen assemblages around the northern SCS, making up ~20% of pollen in the northern continental shelf and Chaoshan Plain (Yue et al., 2012; Dai et al., 2015) and 20–40% in the Leizhou Peninsula (Zheng and Li, 2000; Xue et al., 2015; Wang et al., 2012) during the LGM. Evergreen *Quercus* pollen is well represented and is an indicator of tropical and subtropical forests in southern China (Zheng et al., 2014). Correspondence between pollen ornamentation and molecular phylogenies has confirmed that infra-generic taxonomy of *Quercus* pollen is a valuable tool for reevaluating the fossil record of *Quercus* pollen (Denk and Grimm, 2009). Therefore, the infra-generic taxonomy of *Quercus* pollen may provide accurate information about forest dynamics and associated climate in the northern SCS since the LGM.

Scanning electronic microscopy (SEM) is a useful tool for pollen identification at the infra-generic to species levels (Denk and Grimm, 2009; Nakagawa et al., 2000) and can reveal details of vegetation changes. In this study, we used SEM to reveal the ornamentation of *Quercus* pollen derived from plants and sediments. The former included

18 oak species widely distributed across tropical and subtropical China, and the latter included surface samples from the Pearl River mouth and northern SCS, as well as fossil pollen from marine (MD05–2906) and continental (XL02) sediments from the LGM and early Holocene periods (Fig. 1). The objectives of this study were to 1) reveal diagnostic features of *Quercus* pollen at the infra-generic level, 2) determine the sources of different types of *Quercus* pollen deposited in the northern SCS, and 3) reevaluate the inland vegetation and climate during the LGM and early Holocene.

2. Material and method

2.1. Regional environment

The northern SCS is bordered by southern mainland China, Hainan Island, and Taiwan Island. It is connected to the East China Sea and Pacific Ocean by the Taiwan and Bashi Straits (Fig. 1). The regional vegetation is generally characterized by tropical and subtropical broadleaved evergreen forests composed mainly of Fagaceae, Lauraceae, Theaceae, Hamamelidaceae, and Magnoliaceae (Zhang, 2007). The percentages of tropical vegetation elements gradually increase as the latitude decreases. The zonal vegetation changes from central subtropical evergreen broadleaved forest to southern tropical monsoon forest and tropical moist rainforest in southeastern China (Fig. 1).

2.2. Sampling

In China, most tropical and subtropical broadleaved pollen has low prevalence. For example, Lauraceae are a major component of forests, but their pollen is not easily preserved in sediments because of the thin exine (Macphail, 1980; Hesse and Kubitzkik, 1983). Only several pollen taxa are well represented, such as Fagaceae, of which *Quercus* is the most abundant broadleaved component in pollen assemblages of the northern SCS. Therefore, its infra-generic taxonomy provides an opportunity to more accurately understand past forest and associated climate in East Asian monsoon regions (Nakagawa et al., 1996; Liu et al., 2007; Naryshkina and Evstigneeva, 2009; Denk and Grimm, 2009;

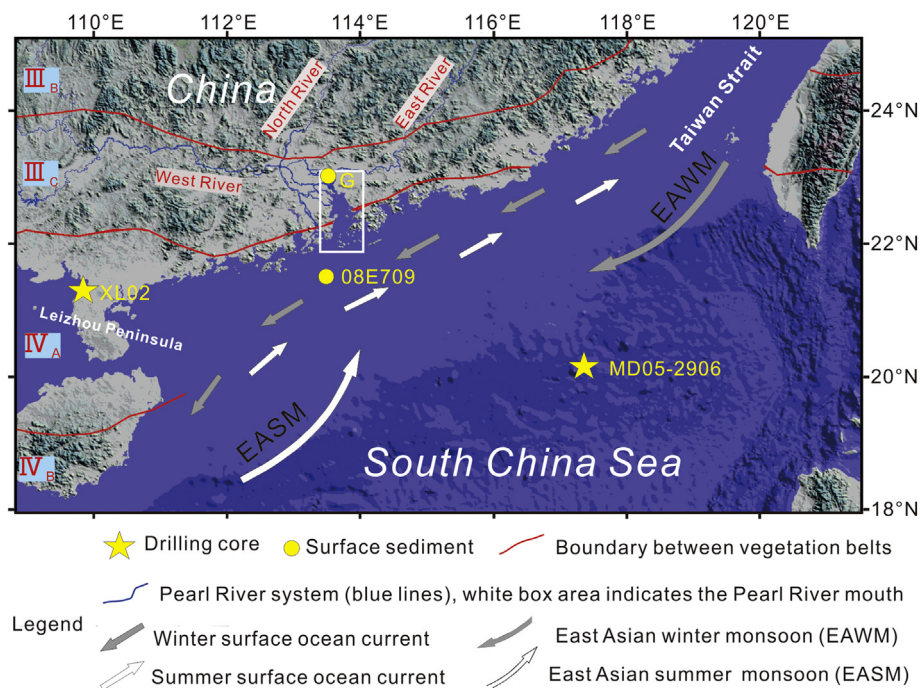


Fig. 1. Location of sediment samples and vegetation belts (III_B–IV_B). The Pearl River comprises the North, West, and East Rivers. The vegetation belts included III_B, central subtropical evergreen broadleaved forest, III_C, southern subtropical evergreen broadleaved forest, IV_A, northern tropical semi-evergreen monsoon and tropical moist forests, and IV_B, southern tropical monsoon forest and tropical moist rainforest. The vegetation belts were modified from Zhang, 2007.

Hayashi et al., 2012; Deng et al., 2013; Tekleva et al., 2014). Evergreen and deciduous *Quercus* pollen has hitherto extensively been used to indicate the shift of cold and warm climates in subtropical and tropical regions around China (Hayashi et al., 2012; Xu et al., 2013; Park et al., 2014; Fang et al., 2015; Park and Park, 2015). Such studies have mostly been based on the length of the polar axis, in which pollen of $>32\ \mu\text{m}$ was deciduous and that of $<32\ \mu\text{m}$ was evergreen (Dai et al., 2014). However, recent studies have demonstrated that pollen identification based on *Quercus* pollen exine sculptures was more reliable than pollen size (Wang and Pu, 2004; Denk and Grimm, 2009). Therefore, we selected *Quercus* pollen for SEM analysis to improve paleoclimatic reconstructions for the northern SCS region.

18 species of *Quercus* pollen were analyzed and were collected from several botanical gardens and the State Key Laboratory, Tongji University, in China (Table S1). These *Quercus* species are typical arboreal components in tropical and subtropical forests of China, including evergreen or deciduous subg. *Quercus* and evergreen sect. *Cyclobalanopsis* subg. *Cerris* (Table S2).

Core MD05-2906 ($20^{\circ}08.16'\text{N}$, $117^{\circ}21.59'\text{E}$) was drilled in the continental slope near Dongsha Island at a water depth of 1636 m, the total length of the core was 36.72 m. The sediments were composed of olive and gray clay (Dai et al., 2015; Dai and Weng, 2015). Core XL02 ($21^{\circ}18'\text{N}$, $109^{\circ}49'\text{E}$) was drilled on a peatland located in Leizhou Peninsula, southern China (Fig. 1), the total length of the core was 2 m. Based on established pollen assemblages (Xue et al., 2015), oak fossil pollen was extracted from precisely dated sediment samples in both cores (Table S3). Surface sediment samples composed of clay were taken in the Pearl River channel and northern SCS (Fig. 1), and their pollen

assemblages were examined (Dai et al., 2014). The sediment samples were processed with hydrochloric and hydrofluoric acids used to remove calcite and other minerals components and the oak pollen was then concentrated. The modern pollen samples were treated with hydrochloric acid in a water bath. Light microscopy was used to select *Quercus* pollen grains from the sediment samples for SEM observation. A total of 201 selected pollen grains were used to SEM analysis, in which 41 grains were from the modern sediments (including samples G and 08E709); 69 grains were from the marine sediment during the early Holocene (at a depth of 9.03 m in core MD05-2906, dated at 9.4–9.7 cal ka BP); 41 grains were from the marine sediments during the LGM (including two samples at a depth of 15.11–15.03 m in core MD05-2906, dated at 20.2–18.8 cal ka BP); 50 grains were from the terrestrial sediments during the LGM (including two samples at a depth of 1.08–0.96 m in core XL02, dated at 27.9–25.3 cal ka BP) (Figs. 1 and 7; Table S3). At least five pollen grains from each modern species were observed under the SEM.

2.3. SEM observation

For SEM observation, pollen grains extracted from the sediments were transferred onto aluminum stubs with adhesive carbon tape and coated with gold. A Hitachi S-4800 cold field emission SEM was run at 8 kV and 7 μA and a working distance of 9 mm. All observations were carried out at the Ningbo Institute of Industrial Technology, Chinese Academy of Sciences. The taxonomy of *Quercus* pollen was based on updated infra-generic classification of oaks, in which *Quercus* comprised subg. *Cerris* and subg. *Quercus* with eight sections (Denk et al., 2017).

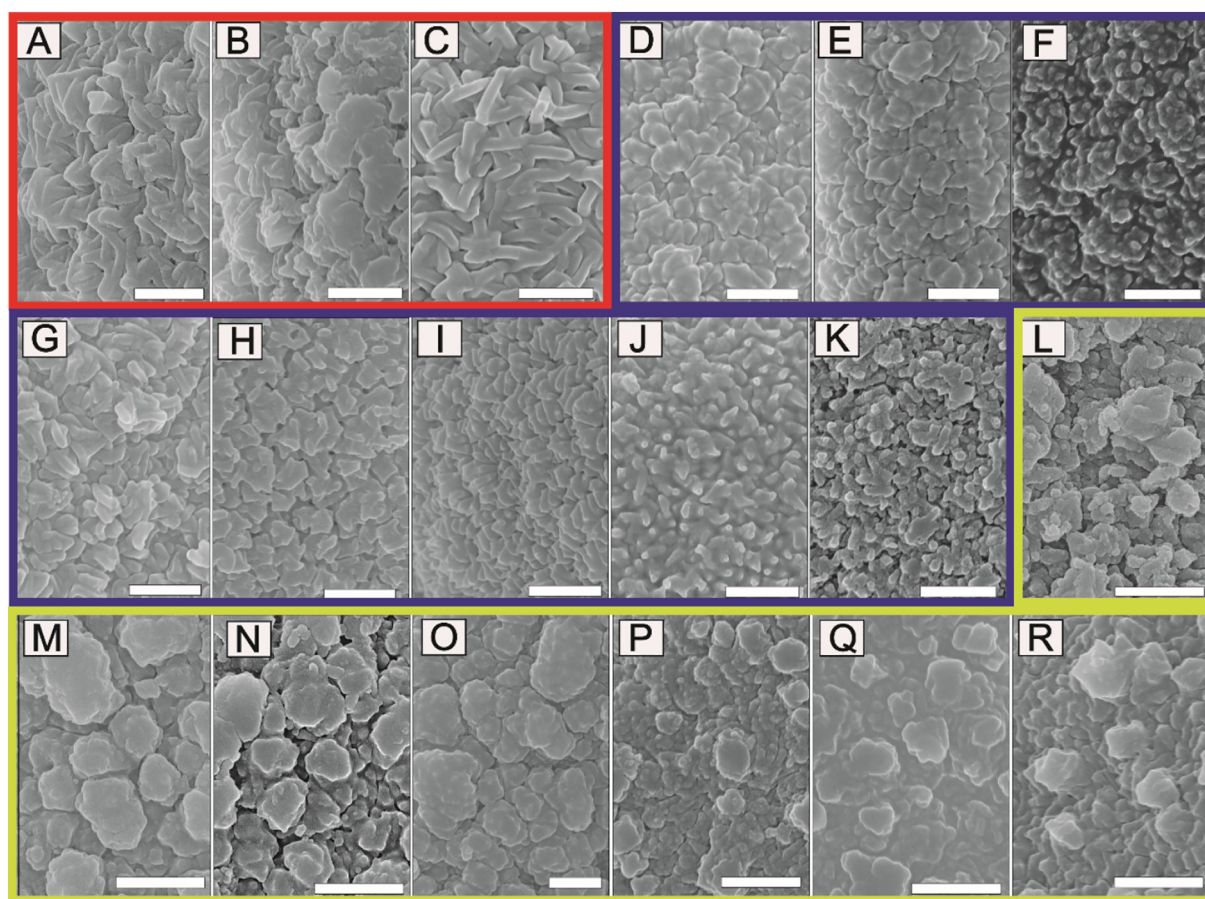


Fig. 2. Pollen morphological comparisons between 18 *Quercus* species from subtropical and tropical China: A, *Q. phillyraeoides*; B, *Q. semecarpifolia*; C, *Q. franchetii*; D, *Q. myrsinifolia*; E, *Q. sessilifolia*; F, *Q. stewardiana*; G, *Q. helferiana*; H, *Q. gilva*; I, *Q. gracilis*; J, *Q. hui*; K, *Q. glauca*; L, *Q. chenii*; M, *Q. griffithii*; N, *Q. fabri*; O, *Q. aliena*; P, *Q. variabilis*; Q, *Q. acutissima*; R, *Q. stewardii*. Colored boxes outline the various sections: red, sect. *Ilex*; blue, sect. *Cyclobalanopsis*; yellow, sect. *Quercus* and *Cerris*. Figs. 3–6 are the same. Scale bar = 1 μm . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

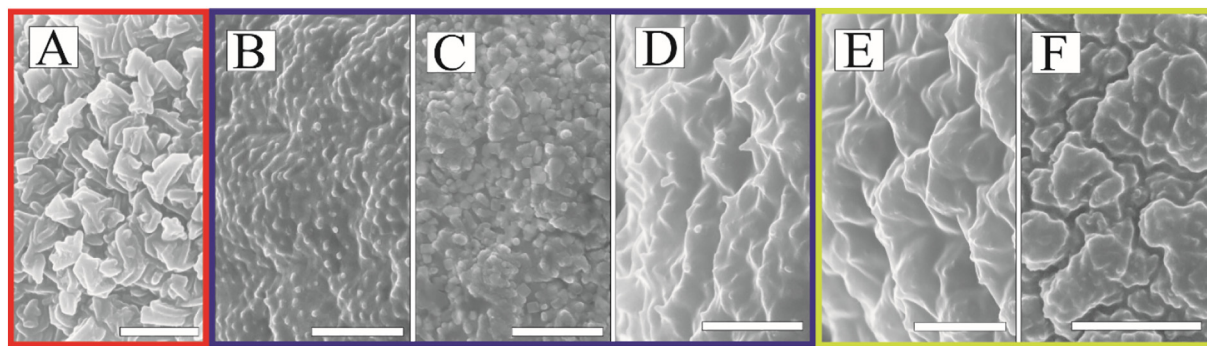


Fig. 3. Ornamentations of *Quercus* fossil pollen from the LGM sediment in core MD05-2906. A, rod-like; B–C, rod-like masked; D, rod-like vertical; E–F, verrucate. Scale bar = 1 μ m.

3. Results

3.1. Morphology of modern *Quercus* pollen in southern China

Quercus can be divided into evergreen and deciduous types (Wu, 1980). The former includes sect. *Ilex* and sect. *Cyclobalanopsis* subg. *Cerris*, and the latter includes sect. *Cerris* subg. *Cerris* and sect. *Quercus* subg. *Quercus* (Denk et al., 2017), among which sect. *Ilex*, *Cyclobalanopsis*, and *Quercus* are widely distributed across southern and southwestern China. In this study, we investigated the four sections of *Quercus* pollen (Table S1). Sect. *Ilex* including three species, their pollen was characterized by independent rod-like elements or agglomerated structures formed of rod-like elements oriented in different directions (Fig. 2A–C). Evergreen sect. *Cyclobalanopsis* included eight species. Their pollen has rod-like masked (Fig. 2D–F), agglomerated rod-like (Fig. 2G), and rod-like vertical ornamentations (Fig. 2H–K). Deciduous subg. *Quercus* included seven species. Their pollen had verrucate sculptures composed of numerous large agglomerations, and the base diameter of agglomerations was large (0.1–1 μ m) (Fig. 2L–R).

3.2. Morphology of *Quercus* pollen in cores MD05-2906 and XL02 during the LGM

Four sculpture types of *Quercus* pollen in marine sediments from core MD05-2906 were confirmed, namely rod-like (Fig. 3A), rod-like masked (Fig. 3B and C), rod-like vertical (Fig. 3D), verrucate (Fig. 3E and F; Fig. S1). The rod-like masked pollen type was dominant, and the verrucate type was relatively abundant (Fig. 7). Three sculpture types of *Quercus* pollen in lacustrine sediments from core XL02 were identified, namely agglomerated rod-like (Fig. 4A), rod-like masked (Fig. 4B–D), and rod-like vertical (Fig. 4E). The rod-like masked and rod-like vertical pollen types were dominant (Fig. 7; Fig. S2), the verrucate type was absent.

3.3. Morphology of *Quercus* pollen of core MD05-2906 during the early Holocene

Five sculpture types of *Quercus* pollen in marine sediments from core MD05-2906 were identified, namely rod-like (Fig. 5A and B), agglomerated rod-like (Fig. 5C), rod-like masked (Fig. 5D), rod-like vertical (Fig. 5E), and verrucate (Fig. 5F and G; Fig. S3).

3.4. Morphology of *Quercus* pollen in surface sediments from the northern SCS and the Pearl River

Five sculpture types of *Quercus* pollen from the Pearl River and surface sediments from the northern SCS were identified, namely rod-like (Fig. 6A), agglomerated rod-like (Fig. 6B), rod-like masked (Fig. 6C), rod-like vertical (Fig. 6D and E), and verrucate (Fig. 6F). Almost all pollen with verrucate sculpture was from the northern SCS sediment sample (Fig. 1; Fig. S4). Most pollen with rod-like and rod-like vertical sculptures were from the Pearl River sample (Fig. 1; Fig. S5), where the verrucate type was absent.

4. Discussion

4.1. Paleoenvironmental significance of morphological diversity of oak pollen

The findings of this study suggest that the morphological diversity associated with *Quercus* pollen could be used as a proxy for indicating pollen transportation and sedimentary processes in the marine environment. The morphology of the modern pollen showed that verrucate sculpture exclusively occurred in deciduous *Quercus*, this characteristic differed from evergreen oak (Fig. 2). Similar research has revealed that verrucate sculpture is a unique feature of deciduous *Quercus* pollen, such as sect. *Cerris* subg. *Cerris* and sect. *Quercus* subg. *Quercus* (Wang and Pu, 2004; Denk and Grimm, 2009). Therefore, deciduous *Quercus*

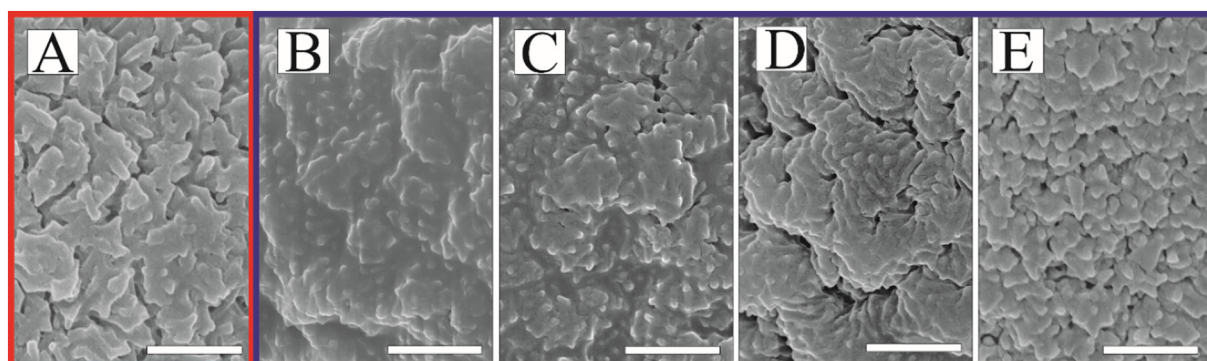


Fig. 4. Ornamentations of *Quercus* fossil pollen from the LGM sediment in core XL02. A, agglomerated rod-like; B–D, rod-like masked; E, rod-like vertical. Scale bar = 1 μ m.

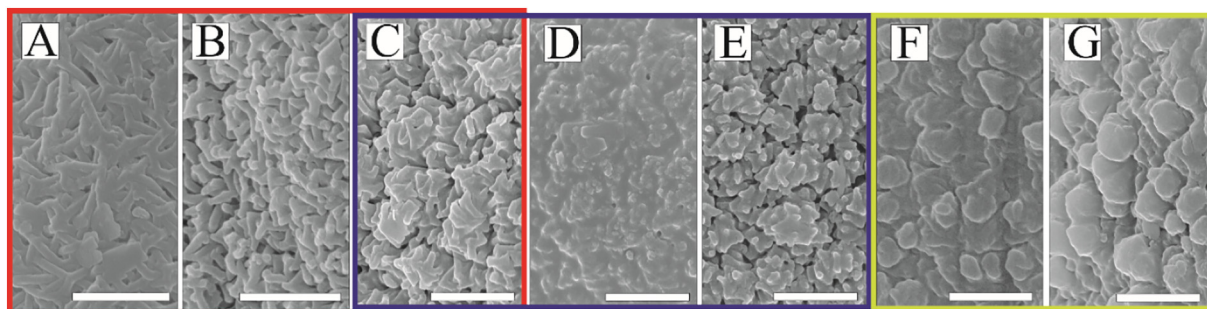


Fig. 5. Ornamentations of *Quercus* fossil pollen from early Holocene sediment in core MD05-2906. A–B, rod-like; C, agglomerated rod-like; D, rod-like masked; E, rod-like vertical; F–G, verrucate. Scale bar = 1 μ m.

fossil pollen is easily recognizable in sediments observed through the SEM. This result provides new insights into the evaluation of the pollen source area range. In East Asia, deciduous *Quercus* is extensively distributed across temperate hills or subtropical and tropical mountains (Wu, 1980). Because of the absence of deciduous oak in epicontinental vegetation communities of the northern SCS (Cao et al., 2013), the occurrence of deciduous *Quercus* pollen with verrucate sculpture in surface marine sediments may reflect the regional dispersal of pollen grains (Fig. 6F), which may be transported by boundary currents from the East China Sea over long distances (Fig. 1). This may be confirmed by modern pollen dispersal and clay mineral transport processes. Surface pollen distribution has shown that wind and ocean currents were important pollen carriers, they can transport *Picea* and *Abies* pollen from Taiwan Island and *Phyllocladus* pollen from Philippines to the northern SCS over long distance (Sun et al., 1999; Dai et al., 2014; Luo et al., 2014; Yu et al., 2017). Furthermore, spatial distributions of *Quercus* pollen have suggested their extensive source areas and dispersal in the northern SCS (Dai et al., 2014). Clay mineral records from core MD12-3434 located on the northern SCS demonstrated that Taiwan and Luzon were major sources of terrigenous sediments (Zhao et al., 2018), and ocean currents played a crucial role in carrying terrestrial particles to the northern SCS (Liu et al., 2016; Liu et al., 2018). Considering the absence and underrepresentation of deciduous *Quercus* pollen in Quaternary sediments of Taiwan island (Liew et al., 2006; Lee and Liew, 2010), the East China Sea and connected temperate regions could be a potential pollen source. Pollen may have been carried by rivers in the Taiwan Strait at periods of low sea levels. Therefore, a small amount of deciduous *Quercus* fossil pollen in the northern SCS does not necessarily signify the local presence of a temperate or montane oak community.

This study showed that *Quercus* pollen with rod-like and agglomerated rod-like sculptures belonged to sect. *Ilex* subg. *Cerris* (Denk and Tekleva, 2014; Zhang et al., 2018). We found that most modern species in sect. *Ilex* were distributed at elevations of >1500 m in southwestern China (Fig. S6). These species are associated with a relatively cold alpine climate and rarely occurred on the plains and hills of eastern and south-eastern China. Many studies demonstrated that the pollen in alluvial

deposits was derived from the drainage basin, and reflected the vegetation patterns on the river basin instead of local area (Brown et al., 2007; Xu et al., 2012; Lambert et al., 2017). In this study, a few of *Quercus* pollen of sect. *Ilex* in the Pearl River indicated that this pollen was derived from the upstream catchment of the river. Its abundance was likely associated with the strength of river flow and distribution of parent plants in the catchment (Fig. 1).

4.2. Forest community and climate reconstruction during the LGM in the northern SCS

Epicontinental vegetation in the northern SCS during the LGM has remained contentious. In cores XL02 and MD05-2906, *Quercus* was the most important broadleaved pollen, with average percentages of 30 and 15, respectively (Dai et al., 2015; Xue et al., 2015). Therefore, infra-generic taxonomy of *Quercus* pollen provided more detailed information about epicontinental forest components. Our results showed three sculpture types of *Quercus* fossil pollen in peat sediments (core XL02), with rod-like vertical and rod-like masked sculptures indicating that sect. *Cyclobalanopsis* pollen was predominant (Fig. 7) and that dense *Cyclobalanopsis* communities were distributed on adjacent areas, and even across the Leizhou Peninsula, close to the northern SCS during the LGM (~28–25 cal ka BP). The modern distribution of sect. *Cyclobalanopsis* is concentrated in south and southwest China, where there is a warm and humid climate (Liu and Hong, 1998) (Fig. S7), and the pollen of other evergreen broadleaved species, such as *Castanopsis*, *Lithocarpus*, and *Altingia*, was abundant in this pollen assemblage (Xue et al., 2015). We therefore deduced that evergreen broadleaved forests and subtropical climate prevailed in the northern SCS during the LGM. *Quercus* pollen in contemporary marine sediments (core MD05-2906) had four sculpture types, among which deciduous *Quercus* with verrucate pollen ornamentation was recognized (Fig. 3; Fig. S2) (Dai et al., 2018). The pollen assemblage of core MD05-2906 was characterized by a mixture of deciduous and evergreen *Quercus* pollen, which differs from the pollen of the terrestrial core (Fig. 7), despite both cores being located in similar tropical regions. Considering

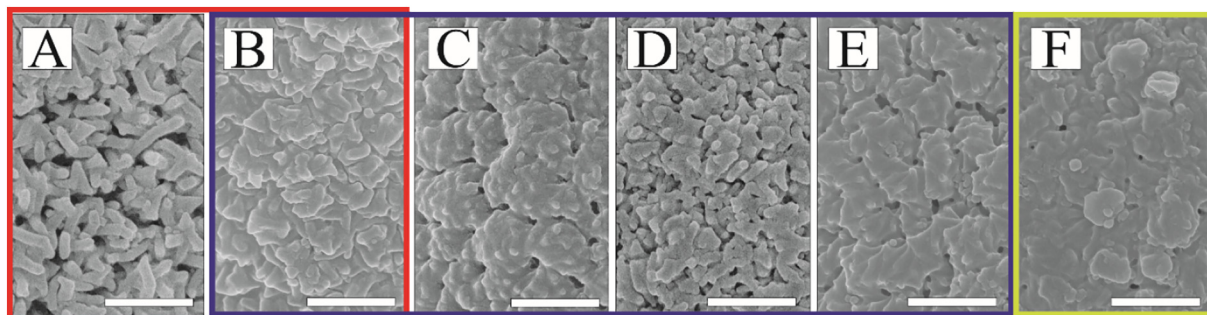


Fig. 6. Ornamentations of *Quercus* pollen in surface sediments from the Pearl River and northern South China Sea. A, rod-like; B, agglomerated rod-like; C, rod-like masked; D–E, rod-like vertical; F, verrucate. Scale bar = 1 μ m.

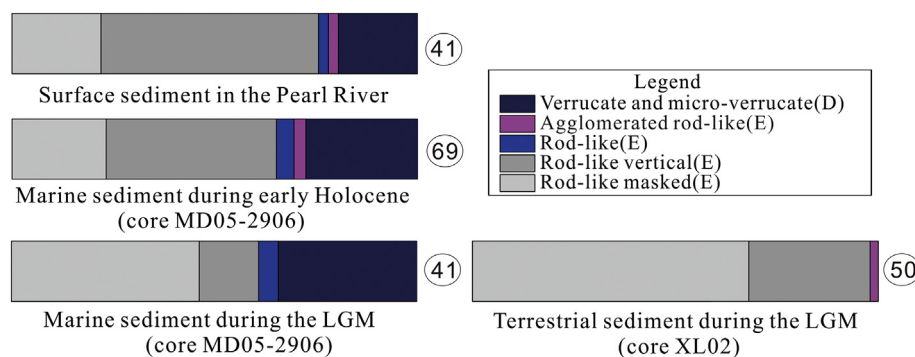


Fig. 7. Proportions of ornamentation types of *Quercus* pollen in different sediments. The numbers of pollen grains counted for each sediment sample are plotted on the right side of bars. D and E indicate types of deciduous and evergreen *Quercus* pollen, respectively.

that deciduous *Quercus* pollen can be transported by ocean current over long distance, and the pollen of no other deciduous broadleaved trees was found in core MD05-2906 (Dai et al., 2015), relatively higher proportion of deciduous *Quercus* pollen suggested that moderate cooling occurred during the LGM (Fig. 7), but did not reflect the wide distribution of deciduous oak on the inland northern SCS region during this period. The difference between marine and terrestrial pollen records can be attributed to different pollen sources, i.e., the former indicated regional pollen dispersal in an open setting, and the latter reflected local pollen deposition. The fact that broadleaved tree pollen was dominated by evergreen *Quercus* in both cores MD05-2906 and XL02 implied the existence of evergreen broadleaved forest in the inland hills, reflecting prevailing humid and warm climate in the northern SCS during the LGM (Fig. 7).

4.3. Hydrological condition and climate reconstruction during the early Holocene in the northern SCS

According to the paleoclimate precession cycle, higher insolation increased sea surface temperatures and the strength of the East Asian summer monsoon during the early Holocene in the northern SCS (Dykoski et al., 2005; Oppo, 2005). High-resolution pollen stratigraphy of core MD05-2906 showed the peaks in the sedimentary rate of non-arboreal and *Pinus* pollen during this period, indicating a notably enhanced pollen input associated with strong terrestrial runoff (Dai and Weng, 2015). Furthermore, our data showed the response of arboreal pollen to this event, when deciduous sect. *Quercus* pollen with verrucate sculpture and sect. *Ilex* pollen with rod-like sculpture were present in higher proportions than they are today (Fig. 7). As mentioned above, deciduous *Quercus* pollen was transported by ocean current through the Taiwan Strait from the north, its increase may be associated with stronger coastal weathering and terrigenous particle input. Multi-proxy geochemical evidences from cores ODP 1144 and KNG5 close to our study site displayed a maximum weathering flux at 10 ka in Taiwan Island, which was in response to intensifying monsoon precipitation in the northern SCS (Hu et al., 2012; Huang et al., 2016).

The Pearl River carried a high number of sect. *Ilex* pollen derived from the southwestern mountains, relatively high proportions of sect. *Ilex* pollen possibly indicate increased pollen discharge (Fig. 7). Similarly, a core from the Pearl River delta recorded fluvial-dominated sediment in the early Holocene (Wu et al., 2017; Xiong et al., 2018). The palynological record of core GLW31D located on the Pearl River mouth indicated that pollen transport occurred predominantly via water currents during the early Holocene (Li et al., 2017).

5. Conclusion

Our study has clarified the potential paleoclimatic significance of the morphological diversity of *Quercus* pollen in the northern SCS for the first time. Deciduous *Quercus* pollen was reliably identified, which

indicated extensive dispersion of pollen over long distances in an open marine setting. Evergreen *Quercus* dominated the broadleaved pollen assemblage, and abundant evergreen tree pollen in marine and terrestrial sediments confirmed that evergreen forests had occupied the mainland of the northern SCS during the LGM, when a subtropical climate prevailed. During the early Holocene, relatively high proportions of sect. *Ilex* and *Quercus* pollen were mainly derived from the catchment of the Pearl River and East China Sea, implying enhanced pollen discharge associated with abundant water flow and strongly coastal land weathering, and heavy precipitation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.07.062>.

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