

Discriminating fossil evergreen and deciduous *Quercus* pollen: A case study from the Miocene of eastern China

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Abstract

In palaeopalynology oaks are rarely identified beyond the generic level. In order to recognize fossil evergreen and deciduous oak pollen, we compiled distinguishing criteria from the literature, most under the SEM, on the living oaks. One of the most significant criteria is the nature of the sculpturing under the SEM. Evergreen oak pollen exhibit at least four kinds of sculpturing, *viz.* rod-like elements, uniformly fine granules, scabrate–verrucate, and rugulate micromorphology. The first two types of sculpturing are mostly limited to the evergreen oaks and can be used to identify fossil evergreen oak pollen, while the last two types can also be seen in many deciduous oaks. On the other hand, deciduous oak pollen grains have relatively uniform sculpturing, with only two types encountered: scabrate–verrucate and rugulate sculpturing. This sculpturing is mainly present in deciduous oaks, despite its occurrence in some evergreen oaks. An absolute discrimination between evergreen and deciduous oak pollen is thus impossible and would require additional evidence in the form of macrofossils. The diagnostic criteria are applied to a Miocene pollen assemblage from Zhejiang Province, eastern China and demonstrate the high diversity of fossil oaks in the vegetation. The fossil pollen includes three morphotaxa of deciduous origin, two morphotaxa of evergreen habit, and three oaks whose habit is uncertain.

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1. Introduction

The living species of *Quercus* L., the largest genus in the Fagaceae, are found in nearly all northern temperate forests and woodlands, often as dominant elements. They are also abundant in subtropical and tropical regions of the Northern Hemisphere (Menitsky, 1984; Jones, 1986; Menitsky, 2005). Their pollen grains, living and fossil, have been the subject of many studies, in the hope of

establishing a solid framework for an accurate recognition (Jarvis et al., 1992 and literature cited therein; Nakagawa et al., 1996; Zheng et al., 1999; Wei, 2003; Wang and Pu, 2004). However, the morphological overlap of pollen in ecologically or taxonomically distinct groups presents a serious obstacle to the interpretation of the palynological data (Jarvis et al., 1992).

By using the SEM on living oak pollen, three pollen types were first recognized (Yamazaki and Takeoka, 1959), *viz.* one for the deciduous oaks and two for the evergreen oaks (Tables 2 and 3). Subsequent work, covering many regions in the Northern Hemisphere, has

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demonstrated that the pollen morphology in *Quercus* under the SEM is highly diverse (Lieux, 1980; Solomon, 1983a,b; Van Benthem et al., 1984; Liu and Fang, 1986; Valdés et al., 1987; Wang and Chang, 1988; Wang and Pu, 2004). As the terminology used by different researchers was not standardized, their results are prone to confusion and contradictions. Therefore, these studies have had a limited impact on the determination of fossil oak pollen. The first objective of the present study is to summarize the information scattered in the literature and try to synthesize it using a uniform terminology.

Among the living oaks, the differences in their ecological habits are so large that it is practically no use if only generic determination is reached in the fossil analysis (Axelrod, 2000). The evergreen or deciduous habit is a well-known phenomenon in the ecology of *Quercus* (Jarvis et al., 1992). This phenomenon is of critical climatic significance. Possible origin of deciduousness could be in response to dry periods (Axelrod, 1966) or appears related to absence or low levels of winter light (Wolfe, 1987). Fossil oak pollen might therefore be expected to yield an ecological signal. By means of phase contrast microscopy, Van der Spoel-Walvius (1963) was able to distinguish two pollen types among the five common Northwest European species. These types were based on sexine characters. Subsequently Dupont and Dupont (1972) confirmed these results under the SEM and linked the two pollen types with the distinction between evergreen and deciduous species. Smit (1973) noticed that many evergreen oaks have pollen showing scattered elongated elements, while numerous deciduous ones have micro-verrucae and flatter parts of the tectum being covered with rounded spinuloid processes (also see Tables 2 and 3). This was confirmed later by Van Benthem et al. (1984). As their work only covered quite a limited number of oaks in Europe, the results may not be valid for other parts of the world. Jarvis et al. (1992) made an attempt to discriminate the modern evergreen oak pollen from the deciduous ones using LM. Although they claimed that they could differentiate them from one another after careful examination of pollen size, sculpture and aperture type, the application of the results is still limited due to the poor resolution of LM. The ability to distinguish evergreen from deciduous oak pollen is however critical for a better palaeoecological interpretation of Tertiary assemblages (Leopold and Clay-Poole, 2001). For example, Yamanoi (1992) and Saito and Morohoshi (1992) used evergreen and deciduous oak pollen to understand the “tropical spike” in Japan in Middle Miocene and the vegetation changes, respec-

tively. Although neither of these authors mentioned how the two types of oak pollen were distinguished, it seems that the size and ornamentation of the grains were the primary criteria used, viz. the deciduous oak pollen are generally larger and display a coarser sculpturing than the evergreen ones (see also Jarvis et al., 1992; Wang and Pu, 2004). However, the pollen size may be highly variable and surface coarseness is difficult to evaluate under the LM (Van Benthem et al., 1984). Furthermore, the pollen sculptural surfaces of Yamanoi’s deciduous and evergreen oaks look quite similar (plate 5, figs. 11 and 12 of Yamanoi, 1992). Therefore, the characters revealed under LM have limited value in this regard, but SEM, with its higher resolution power, is a powerful tool for separating the pollen grains (Fujiki and Miyoshi, 1995; Fujiki et al., 1996; Wang and Pu, 2004). Our second objective in this study is to establish criteria by which to recognize the living evergreen and deciduous oak pollen based on previously published work.

There is little doubt about the importance of fossil oak pollen in the reconstruction of palaeovegetation and palaeoclimate or even in tracing their palaeogeographical migration pattern, although Aizen and Patterson (1990) commented that specific patterns of (oak) migration cannot be established from palynological records because different species of oaks possess pollen of similar size and morphology. Oak is one of the few taxa to be well represented in the pollen record and is consequently a vital indicator of vegetation change (Jarvis et al., 1992; Nakagawa et al., 1996; Miyoshi et al., 1999). Sachse (1997) discussed the Miocene vegetation in Crete (Greece), based on evergreen and deciduous oak pollen, along with other lines of evidence. Our last objective is to discuss the ecology of a Miocene flora in eastern China, based on information from the evergreen and deciduous oak fossil grains.

2. Material and methods

In eastern China, seventeen Neogene floras have been documented (Liu et al., 1996). Among them, the Miocene megaf flora of Xiananshan in Zhejiang is one of the best-preserved assemblages in East Asia, containing at least 139 species of macrofossils, belonging to 96 genera and 46 families (Li and Guo, 1982; Li, 1984). The largest family is the Fagaceae (Li, 1984). Unfortunately, as no further study on the macrofossils has been carried out (Li and Guo, 1982; Li, 1984), the precise taxonomy of these fossils, particularly in Fagaceae, is still unknown. The clay sample belongs to the Xiananshan Formation from Ninghai County, Zhejiang Province, eastern China (28°50' N, 121°10' E; Fig. 1) and is dated as Miocene

on the basis of the well-preserved plant megafossils (Liu et al., 1996, 1997) and local stratigraphic correlations (Li, 1984). For details on the lithology of this formation, readers are referred to Li (1984).

The fossil pollen grains were extracted from a clay matrix sample containing a fossil leaf, presented by Professor Shuangxing Guo at the Nanjing Institute of Geology and Palaeontology, Academia Sinica. The method of pollen preparation, which involves single grain observations under LM and SEM, was followed according to the procedures outlined by Zetter (1989) and Zetter and Ferguson (2001). A total of 500 pollen grains were counted. More than 330 grains belong to *Quercus* (66%), of which 75% are considered as to be evergreen oaks, 15% are attributed to deciduous oaks, and 10% are of uncertain habit. Other remarkable elements in this pollen assemblage include *Zelkova* (4.3%), *Carya* (4%), *Fagus* (3.5%), *Buxus* (3.3%), *Ulmus* (2.6%), and *Castanopsis*

type (2.3%). The remaining genera are represented by less than 1%. The size of the pollen grains is based on SEM measurements. At least ten well-preserved grains representing each pollen type were measured for better understanding of the pollen size range. To simplify comparison between the various pollen grains, observations of the sculpturing were restricted to the mesocolpium.

The terminology used to describe the pollen morphology of oaks is far from uniform. Solomon (1983a) proposed a set of terms for the descriptions of the fine sculpture of the American white and red oaks. However, his terms are difficult to follow. For instance, the sculpturing illustrated in figures 7–9 in Solomon (1983a) is very similar, but it was referred to as scabrate, verrucate, and rugulate, respectively. We follow the glossary of Punt et al. (1994) in this study, simply because it is widely cited and represents the most recent work. For clarity, we also use plain English words to describe the

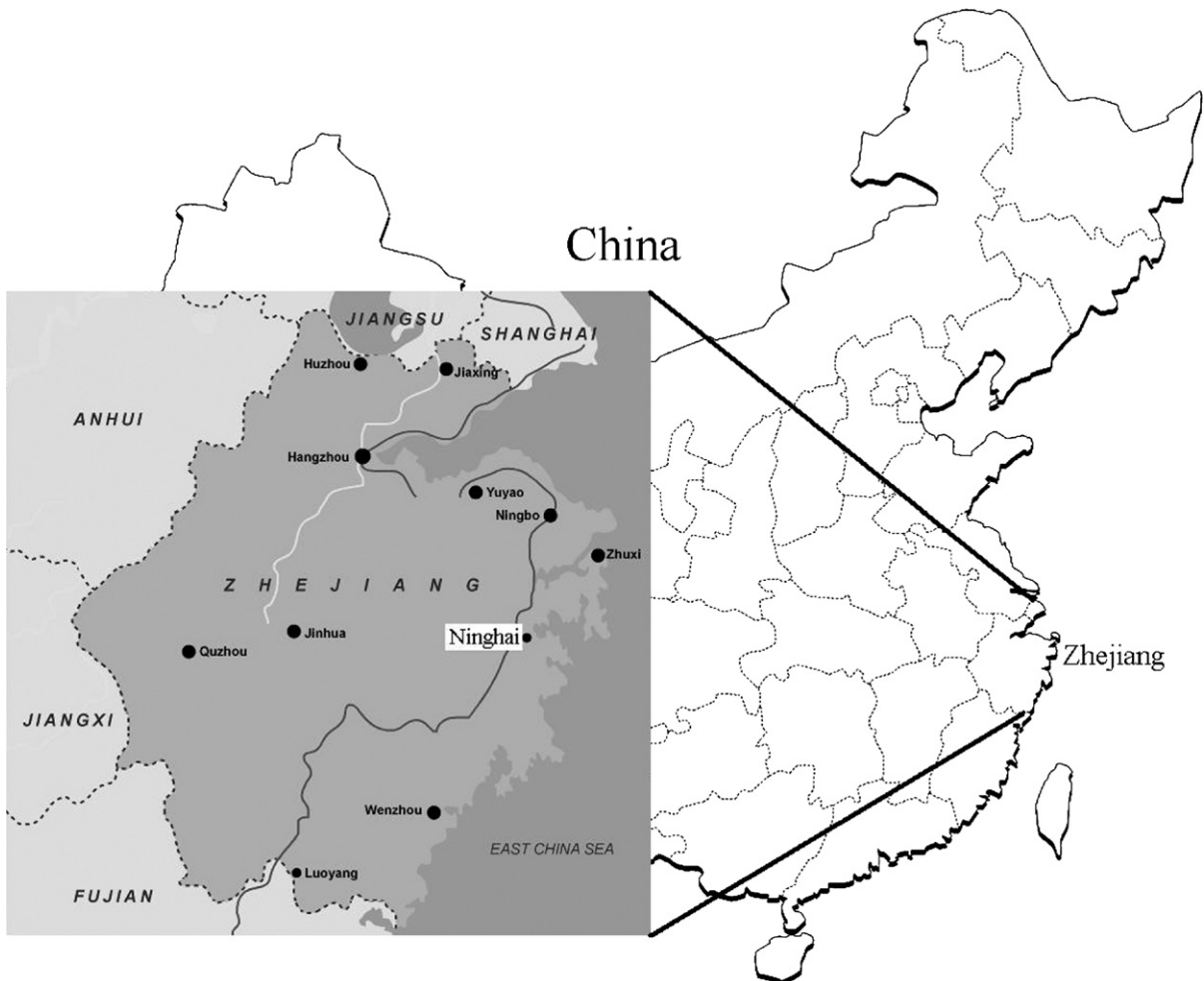


Fig. 1. Map showing the fossil locality.

evergreen oak pollen sculpture. The exine ornamentation of many evergreen oak pollen is often described as rugulate or something similar (Van Benthem et al., 1984; Valdés et al., 1987), but this is not consistent with the definition of this term (cf. Punt et al., 1994). In this study, we use “rod-like elements” to represent this unique sculpture in evergreen oak pollen. The elements, usually smaller than 1 µm, described as “dispersed rice hulls” by Yamazaki and Takeoka (1959), are generally straight, hooked or curved, and irregularly grouped in protruding clusters (Smit, 1973).

The figured specimens and the SEM stubs are housed in the Department of Palaeontology, University of Vienna, Austria.

3. Discrimination between the living evergreen and deciduous *Quercus* pollen grains

Due to their great variability and the frequent occurrence of introgressive hybridization, the extant species of *Quercus* are extremely difficult to classify. For example, an infrageneric classification for the Chinese oaks is not even proposed in the latest edition of the Flora of China (Huang et al., 1999). Although deciduous and evergreen habits are not used in the taxonomy of *Quercus* as shown in Table 3 where the inconsistency between the habits and classification scheme/pollen type does exist, their important ecological significance requires to be addressed, especially in palaeoenvironmental reconstruction.

Table 1
Comparison of pollen morphology from the extant Fagaceae

Genus	Size (µm)	Shape	Aperture	Exine structure under SEM	Sources
<i>Quercus</i>	21–44 × 17–40	Subspheroidal–subprolate; circular in polar view	3-colporate or 3-colporoidate (endoapertures not evident)	Tuberculately verrucate or spinose	2, 4
<i>Fagus</i>	32–40 × 35–46	oblate–spheroidal; circular in polar view	3(-4)-colporate	Granulate or verrucate, finely scabrate	1, 3
<i>Colombobalanus</i>	25 × 17	Prolate; trilobite or subtriangular in polar view	3-colporoidate or 3-colporate; planaperturate	Tectate–perforate, coarsely tuberculate or verrucate; well defined primary rugulate pattern; thick footlayer	2, 4
<i>Formanodendron</i>	18–29 × 20–29	Peroblate; obtusely triangular in polar view	3-colporate, angulaperturate and thickened at margin; endoaperture associate with a well-developed atrium	Densely granular or verrucate; tectate–imperforate, verrucately rugulate; footlayer unusually thin	2, 3, 4
<i>Trigonobalanus</i>	28 × 22	Prolate; trilobite to circular in polar view	3-colporate, planaperturate	Fine granular ornamentation over a primary rugulate exine; tectate–perforate; footlayer extremely thick	2, 4
<i>Castanea</i> / <i>Lithocarpus</i> / <i>Castanopsis</i>	14–23 × 11–17	Prolate supraprolate; circular in polar view	3-colporate	Rugulate, striate-rugulate or crassi-striate	1, 3

Sources: 1. Crepet and Daghljan (1980); 2. Nixon and Crepet (1989); 3. Wang and Chang (1991); 4. Wang et al. (1998).

Table 2

Brief summary of the pollen of living deciduous and evergreen oaks

Pollen Group	Sexine Sculpture	Geography	Sources
<i>Mainly deciduous</i>			
Group 1	Type 1 (Scabrate–verrucate)	Northern Hemisphere	1–4, 6–10, 13, 15
Group 2	Type 2 (Rugulate)	Mainly American red oaks	3, 5, 6
<i>Mainly Evergreen</i>			
Group 3	Type 3 (Rod-like elements)	Europe and Asia	1, 2, 6, 8
Group 4	Type 4 (Uniformly fine granular)	Montane evergreen oaks in SW China and many species of <i>Cyclobanopsis</i>	7, 9, 13, 14, 16
Group 5	Type 2 (Rugulate)	Northern Hemisphere	1–3, 5, 6, 8, 10–12, 15
Group 6	Type 1 (Scabrate–verrucate)	S. Europe	2, 8

Sources: 1. Yamazaki and Takeoka (1959); 2. Smit (1973); 3. Lieux (1980); 4. Solomon (1983a); 5. Solomon (1983b); 6. Van Benthem et al. (1984); 7. Liu and Fang (1986); 8. Valdés et al. (1987); 9. Wang and Chang (1988); 10. Jarvis et al. (1992); 11. Nilsson and Pragłowski (1992); 12. Fujiki and Miyoshi (1995); 13. Fujiki et al. (1996); 14. Nakagawa et al. (1996); 15. Zheng et al. (1999); 16. Wei (2003).

In terms of the size, shape, aperture, and exine structure, pollen grains of the modern *Quercus* are easily distinguished from those of other fagaceous genera such as *Castanea*, *Castanopsis*, *Lithocarpus*,

Table 3

Pollen types of the living deciduous and evergreen oaks and the correlation to the infrageneric classification of the genus *Quercus* (taxonomy of the Asian oaks after Menitsky, 1984, 2005)

Pollen Group	Sexine Sculpture		Section	Subgenus
<i>Mainly deciduous oaks</i>				
Group 1	Type 1	<i>Q. acutissima</i> (D), <i>Q. cerris</i> (D), <i>Q. variabilis</i> (D)	<i>Cerris</i>	<i>Quercus</i>
Group 1	Type 1	<i>Q. alba</i> (D), <i>Q. aliena</i> (D), <i>Q. bicolor</i> (D), <i>Q. canariensis</i> (D), <i>Q. chapmanii</i> (D), <i>Q. durandii</i> (D),	<i>Quercus</i>	<i>Quercus</i>
Group 1	Type 1	<i>Q. faginea</i> (D), <i>Q. lyrata</i> (D), <i>Q. macrocarpa</i> (D), <i>Q. margaretta</i> (D), <i>Q. michauxii</i> (D),	<i>Quercus</i>	<i>Quercus</i>
Group 1	Type 1	<i>Q. mongolica</i> var. <i>grosseserrata</i> (D), <i>Q. muehlenbergii</i> (D), <i>Q. oglethorpensis</i> (D),	<i>Quercus</i>	<i>Quercus</i>
Group 1	Type 1	<i>Q. petraea</i> (D), <i>Q. prinoides</i> (D), <i>Q. prinus</i> (D), <i>Q. pubescens</i> (D), <i>Q. robur</i> (D), <i>Q. serrata</i> (D),	<i>Quercus</i>	<i>Quercus</i>
Group 1	Type 1	<i>Q. similis</i> (D), <i>Q. stellata</i> (D), <i>Q. virginiana</i> (E)	<i>Quercus</i>	<i>Quercus</i>
Group 1	Type 1	<i>Q. dentata</i> (D), <i>Q. pontica</i> (D)	<i>Quercus</i>	<i>Quercus</i>
Group 1	Type 1	<i>Q. dolicholepis</i> (E), <i>Q. franchetii</i> (E)	<i>Ilex</i>	<i>Heterobalanus</i>
Group 2	Type 2	<i>Q. arkansana</i> (D), <i>Q. coccinea</i> (D), <i>Q. ellipsoidalis</i> (D), <i>Q. falcata</i> (D), <i>Q. georgiana</i> (D),	<i>Lobatae</i>	<i>Quercus</i>
Group 2	Type 2	<i>Q. ilicifolia</i> (D), <i>Q. imbricaria</i> (D), <i>Q. laevis</i> (D), <i>Q. laurifolia</i> (D), <i>Q. marilandica</i> (D),	<i>Lobatae</i>	<i>Quercus</i>
Group 2	Type 2	<i>Q. nigra</i> (D), <i>Q. nuttallii</i> (D), <i>Q. palustris</i> (D), <i>Q. phellos</i> (D), <i>Q. pumila</i> (D), <i>Q. rubra</i> (D),	<i>Lobatae</i>	<i>Quercus</i>
Group 2	Type 2	<i>Q. shumardii</i> (D), <i>Q. velutina</i> (D)	<i>Lobatae</i>	<i>Quercus</i>
Group 2	Type 2	<i>Q. incana</i> (D) (also Type 4)	<i>Ilex</i>	<i>Heterobalanus</i>
Group 2	Type 2	<i>Q. pyrenaica</i> (D)	<i>Quercus</i>	<i>Quercus</i>
<i>Mainly evergreen oaks</i>				
Group 3	Type 3	<i>Q. calliprinos</i> (E) (= <i>Q. coccifera</i> subsp. <i>calliprinos</i>), <i>Q. coccifera</i> (E)	<i>Ilex</i>	<i>Heterobalanus</i>
Group 3	Type 3	<i>Q. ilex</i> (E) (Syn. <i>Q. rotundifolia</i>), <i>Q. phillyreoides</i> (E) (also Type 4)	<i>Ilex</i>	<i>Heterobalanus</i>
Group 4	Type 4	<i>Q. aquifolioides</i> (E), <i>Q. guajavifolia</i> (E) (Syn. <i>Q. pannosa</i>), <i>Q. monimotricha</i> (E),	<i>Heterobalanus</i>	<i>Heterobalanus</i>
Group 4	Type 4	<i>Q. rehderiana</i> (E) (Syn. <i>Q. longispica</i>), <i>Q. semecarpifolia</i> (E), <i>Q. senescens</i> (E),	<i>Heterobalanus</i>	<i>Heterobalanus</i>
Group 4	Type 4	<i>Q. spinosa</i> (E) (Syn. <i>Q. gilliana</i>)	<i>Heterobalanus</i>	<i>Heterobalanus</i>
Group 4	Type 4	<i>Q. cocciferoides</i> (±E), <i>Q. engleriana</i> (E), <i>Q. incana</i> (D) (also Type 2),	<i>Ilex</i>	<i>Heterobalanus</i>
Group 4	Type 4	<i>Q. lanata</i> (E) (Syn. <i>Q. lanuginosa</i>), <i>Q. phillyreoides</i> (E) (also Type 3)	<i>Ilex</i>	<i>Heterobalanus</i>
Group 5	Type 2	<i>Q. acuta</i> (E), <i>Q. sessilifolia</i> (E) (Syn. <i>Q. paucidentata</i>)	<i>Acuta</i>	<i>Cyclobalanopsis</i>
Group 5	Type 2	<i>Q. gilva</i> (E)	<i>Gilva</i>	<i>Cyclobalanopsis</i>
Group 5	Type 2	<i>Q. glauca</i> (E), <i>Q. myrsinifolia</i> (E), <i>Q. salicina</i> (E)	<i>Glauca</i>	<i>Cyclobalanopsis</i>
Group 5	Type 2	<i>Q. augustinii</i> (E)	<i>Cyclobalanooides</i>	<i>Cyclobalanopsis</i>
Group 5	Type 2	<i>Q. kerrii</i> (E)	<i>Helferiana</i>	<i>Cyclobalanopsis</i>
Group 5	Type 2	<i>Q. chrysolepis</i> (E)	<i>Protobalanus</i>	<i>Quercus</i>
Group 5	Type 2	<i>Q. myrtifolia</i> (E)	<i>Lobatae</i>	<i>Quercus</i>
Group 6	Type 1	<i>Q. aegilops</i> (D) (Syn. <i>Q. macrolepis</i>), <i>Q. crenata</i> (±E), <i>Q. suber</i> (E), <i>Q. thracica</i> (E),	<i>Cerris</i>	<i>Quercus</i>
Group 6	Type 1	<i>Q. trojana</i> (D)	<i>Cerris</i>	<i>Quercus</i>

Note the inconsistency between the pollen types/infrageneric classification scheme and the ecological habits. For the pollen types, refer to Table 2. D=deciduous, E=evergreen, ±E=semi-evergreen.

Fagus, *Trigonobalanus*, *Formanodendron*, and *Colombobalanus* (Crepet and Daghljan, 1980; Nixon and Crepet, 1989; Wang and Chang, 1991; Wang et al., 1998). As in all species of *Quercus*, species of *Trigonobalanus*, *Formanodendron*, and *Colombobalanus* have tricolporate pollen grains with primarily rugulate micromorphology on their exine. However, their aperture types are different from those of *Quercus* (Table 1; Wang et al., 1998). A comparison of the pollen

characters in the different fagaceous genera is therefore provided to allow the recognition of oak pollen grains in fossil samples (Table 1).

Evergreen oaks include a wide range of species which retain their leaves throughout the year. They normally refer to the oaks from the Mediterranean and other southern European regions, southern East Asia, large mountainous regions of southwest China at an altitude of 2600–4000 m, and southern North America

(see Tables 2 and 3; Nixon, 1997; Liang et al., 1999; Huang et al., 1999).

A brief summary of how to discriminate the deciduous and evergreen oak pollen is provided in Table 2.

Jarvis et al. (1992) suggested that by careful examination of pollen size, sculpture and aperture type, deciduous oaks and evergreen oaks of southwestern China can be reliably separated using light microscopy. When a fossil assemblage is investigated, these criteria become problematic because of the low resolution of LM and possible occurrence of more diverse types of fossil oak pollen. Jarvis and Clay-Poole (1992) admitted that the pollen of the low and high elevation oaks from southwestern Sichuan cannot be distinguished using the light microscope. Tables 2 and 3, which compare the deciduous oak pollen with the evergreen ones, have been compiled from published accounts.

In summary most of the deciduous oaks have pollen grains with scabrate to verrucate sculpturing, upon which superimposed projections are present or absent. The only exceptions occur in evergreen species of *Q. suber* and some semievergreen hybrids (Group 6 of Type 1 sexine sculpture in Tables 2 and 3), in which the pollen grains display deciduous oak scabrate sculpturing (Smit, 1973; Valdés et al., 1987). However, except for the Mediterranean evergreen oaks (e.g. *Q. suber* and some semievergreen oaks) and North American evergreen oaks (Tables 2 and 3), the other evergreen oaks produce at least two exclusive types of pollen grain sculpturing. The first type, Type 3 in Table 2, has an ornamentation with partially fused rod-like elements, which are more or less uniform in size and shape. The rod-like elements, generally less than 1 µm long, are straight, hooked or slightly curved, and irregularly grouped into protruding clusters (Smit, 1973). These elements are never round. This type of pollen sculpturing is exclusive to the evergreen oaks from Europe and Asia and so far no North American evergreen oaks, e.g. *Q. myrtifolia*, are known to produce pollen grains with this ornamentation (Table 2). The second type of sculpturing, Type 4 in Table 2, is quite uniform consisting of fine granules, which are 0.2–0.4 µm (see Wei, 2003). This sculpturing is only found in Asian evergreen oaks (Tables 2 and 3). The North American evergreen oak pollen has rugulate sculpturing, upon which superimposed projections or nanno-spinules are present or almost absent. This type of sculpture is commonly seen in the deciduous oak pollen (Table 2).

Wang and Chang (1988) have compared pollen of species of *Cyclobalanopsis* and *Quercus*. They concluded that pollen of the subgenus *Cyclobalanopsis* could be

distinguished from that of deciduous *Quercus* species but could not be separated from evergreen *Quercus* species.

It is necessary to note that the boundaries among different types of oaks are not clear-cut, as presented in Table 3, where a disparity between the pollen types and their taxonomic treatment is evident. Comparatively, the sculpture types of deciduous oak pollen are less diverse than those of evergreen ones. While deciduous oaks have

Table 4

Comparisons of the fossil oak pollen from Zhejiang, eastern China in the Miocene

Taxa and Pollen Type	Size (µm)	P/E	Shape	Ornamentation
<i>Deciduous</i>				
<i>Q.</i> morphotaxon 1 (Plate I, 1–3; 10–12) Type 1	27–32 × 23–27	1.2	Subprolate	Scabrate, 2 kinds of scabrae: smaller ones more compact and fused; larger ones composed of several grouped smaller scabrae and scattered on them
<i>Q.</i> morphotaxon 2 (Plate I, 4–6) Type 1	24 × 24	1	Spheroidal	Scabrate, 2 kinds of scabrae, smaller ones more compact, larger ones scattered on them
<i>Q.</i> morphotaxon 2 (Plate I, 7–9) Type 1	32 × 29	1.1	Spheroidal	Scabrate, 2 kinds of scabrae, smaller ones more compact, larger ones scattered on them
<i>Evergreen</i>				
<i>Q.</i> morphotaxon 4 (Plate II, 1–12; Plate III, 1–6) Type 3	2.5–3.1 × 1.8–2.4	1.2–1.6	Prolate-Subprolate	Partially fused rod-like elements, elements slightly longer
<i>Q.</i> morphotaxon 5 (Plate III, 7–12) Type 4	1.9–2.2 × 1.6–1.9	1.2	Subprolate	Uniformly fine granules
<i>Uncertain status — could be either evergreen or deciduous</i>				
<i>Q.</i> morphotaxon 6 (Plate IV, 1–6) Type 1	1.9–2.2 × 1.6–1.7	1.2–1.3	Subprolate	Rugulate, superimposed nanno-spinules densely present
<i>Q.</i> morphotaxon 7 (Plate IV, 7–9) Type 1	19 × 19	1	Spheroidal	Irregularly rugulate, super-imposed nannospinule present
<i>Q.</i> morphotaxon 8 (Plate IV, 10–12) Type 1	25 × 20	1.3	Subprolate	Tectum fossulate, rugulate, superimposed elements sparsely present; heavily pitted

For pollen sexine sculpture types, refer to Table 2.

a similar ornamentation to some evergreen oaks, Type 3 of evergreen oak pollen grains is unique (Table 2).

4. Fossil descriptions

Based on a comparison with published fossils and living oak pollen morphology, three morphotaxa of deciduous oaks are recognized, while two morphotaxa of evergreen oak are found in the Miocene of Zhejiang, eastern China (Table 4). In addition, three morphotaxa of uncertain habit are recognized in this assemblage (Table 4). We follow the approach of Ferguson et al. (1998) whereby no specific epithets are assigned to the fossil pollen because it is still unclear how well the different morphotaxa of pollen grains correspond to oak species.

4.1. Deciduous oak pollen

As mentioned above, scabrate–verrucate pollen sculpturing occurs in both evergreen and deciduous oaks (Table 2), although the sculpturing is only present in a small number of evergreen oaks, most of which are adapted to arid environments in the Mediterranean region. On the other hand, the dominant deciduous oaks demonstrate similar pollen sculpturing (Tables 2 and 3). According to the fossil leaf assemblages from the same locality, Li (1984) found no fossil oaks showing any relationship to the evergreen oaks adapted to arid conditions. Therefore, it is highly likely that the scabrate–verrucate pollen from Zhejiang originated from deciduous oaks.

4.1.1. *Quercus morphotaxon 1* (Plate I, 1–3, 10–12)

Pollen grains subprolate, elliptic in equatorial view. Size 27–32 × 23–27 μm. Tricolporate; long narrow colpi (the oblique preservation of the grain, shown in the SEM in Plate I, 11 makes the colpus appear shorter). Exine tectate, tectum perforate, sexine thicker than nexine (Plate I, 1, 10). Sculpturing composed of two tiers of elements: a basal tier of compact and randomly grouped micro-scabrae, irregularly overlain by a second tier of larger and grouped scabrae (Plate I, 3, 12), which is recognized as Type 1 (Table 4).

The micromorphology of the pollen grains resembles that of the oak grain from the Miocene of Kreuzau in Germany, *Quercus* sp.1 (Ferguson et al., 1998). As suggested by Ferguson et al. (1998), this kind of pollen should be compared to the deciduous roburoid oaks.

4.1.2. *Quercus morphotaxon 2* (Plate I, 4–6)

Pollen grains spheroidal, almost circular in equatorial view. Size 24 × 24 μm (Plate I, 4, 5). Tricolporate, colpi

with genicula (Plate I, 4). Exine tectate, tectum perforate, sexine thicker than nexine (Plate I, 4). Sculpturing consisting of two tiers of elements: a basal tier of compact and round smaller scabrae overlain by an irregularly grouped second tier of larger, round and psilate scabrae (±1 μm) (Plate I, 6). This pollen is of Type 1 (Table 4).

The pollen grains display a close resemblance to those of *Quercus* sp.1 from the Pliocene of Germany (Van der Burgh and Zetter, 1998). This type of pollen is also of deciduous oak type (Table 2).

4.1.3. *Quercus morphotaxon 3* (Plate I, 7–9)

Pollen grains spheroidal, circular in equatorial view. Size 32 × 29 μm. Tricolporate, colpi with genicula (Plate I, 7). Exine tectate, tectum perforate, sexine thicker than nexine (Plate I, 7). Sculpturing having two tiers of elements: a basal tier of compact and regularly fused scabrae, irregularly covered by larger, round and psilate scabrae, which is of Type 1 (Plate I, 9; Table 4).

The micromorphology of the pollen sculpture is similar to that of *Quercus morphotaxon 2* in terms of the larger second tier elements, but the basal tiers of these two oaks are essentially different. Judging from the scabrate character of the pollen sculpturing, the pollen grains were derived from deciduous oaks (Table 2).

4.2. Evergreen oak pollen

4.2.1. *Quercus morphotaxon 4* (Plate II, 1–12; Plate III, 1–6)

Pollen grains subprolate to prolate, elliptical in equatorial view. Size 25–31 × 18–24 μm. Tricolporate, endoporous (Plate II, 1, 4, 7, 10; Plate III, 1, 4). Exine tectate, tectum perforate, sexine thicker than nexine (Plate II, 1, 4, 7, 10; Plate III, 1, 4). Sculpturing having unique partially fused rod-like elements (Plate II, 3, 6, 9, 12; Plate III, 3, 6), and therefore the pollen is of Type 3 (Table 4).

The rod-like sculpturing, as shown in Tables 2 and 3, is indicative of an evergreen oak.

4.2.2. *Quercus morphotaxon 5* (Plate III, 7–12)

Pollen grains subprolate, elliptical in equatorial view. Size 19–22 × 16–19 μm. Tricolporate, colpi with poorly developed genicula (Plate III, 7, 10). Exine tectate, tectum perforate, sexine almost the same thickness as nexine (Plate III, 7, 10). Sculpturing with uniformly fine granules (Plate III, 3, 6) and is thus considered to be Type 4 (Table 4).

The fine granules with a uniform size range have been so far mainly described from evergreen oaks, including montane and *Quercus* subgenus *Quercus* evergreen oaks

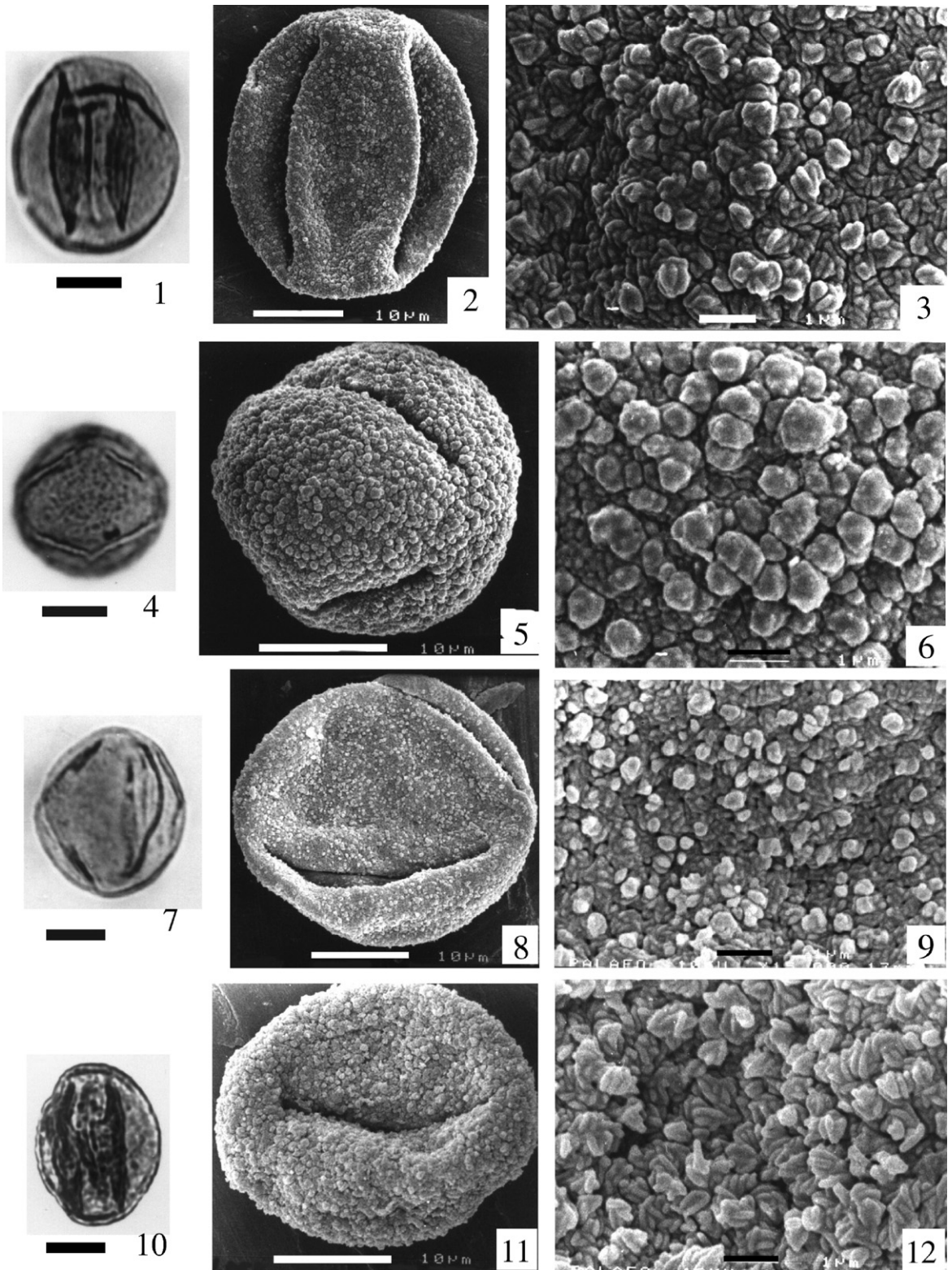


Plate I (caption on page 300).

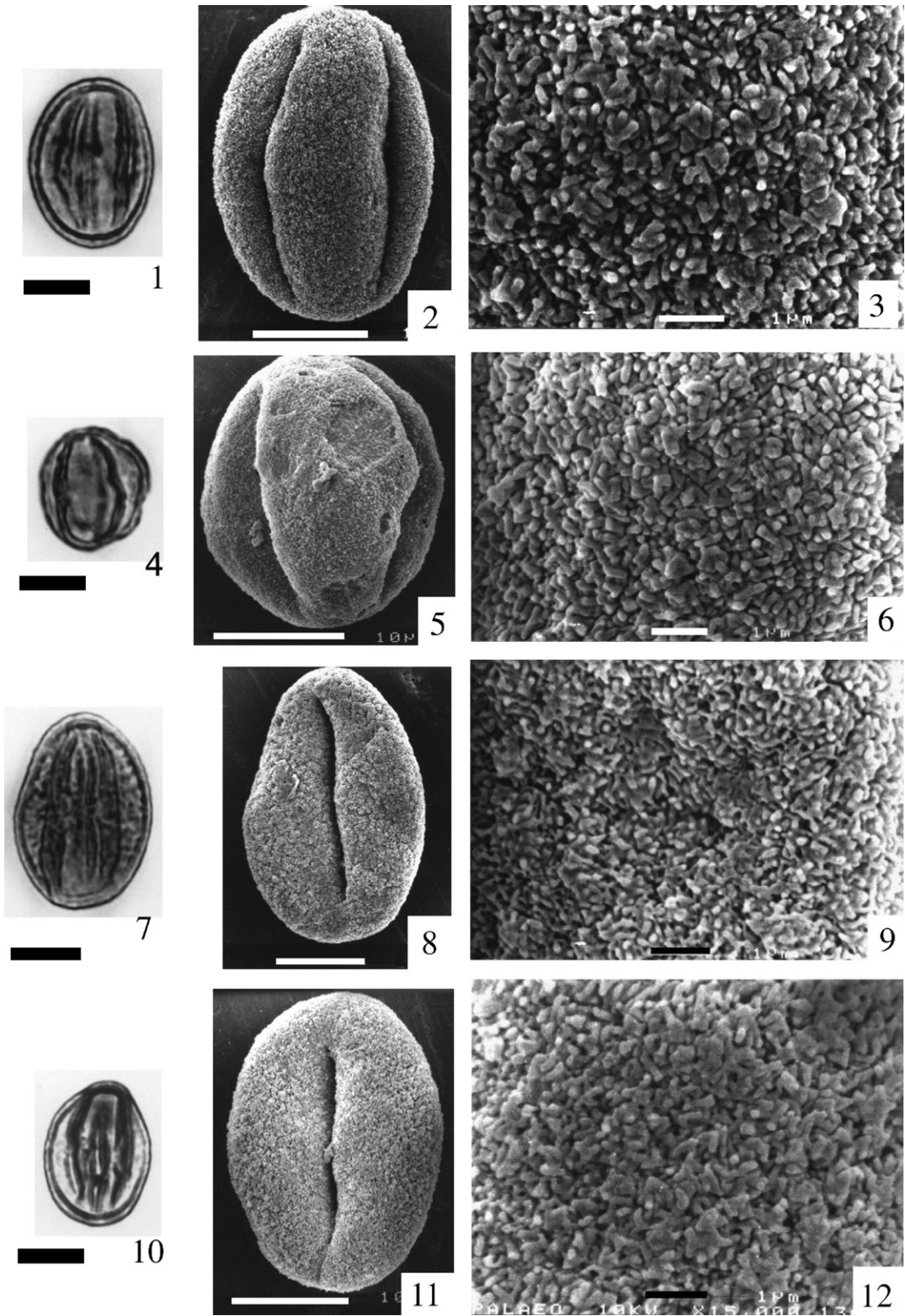


Plate II (caption on page 300).

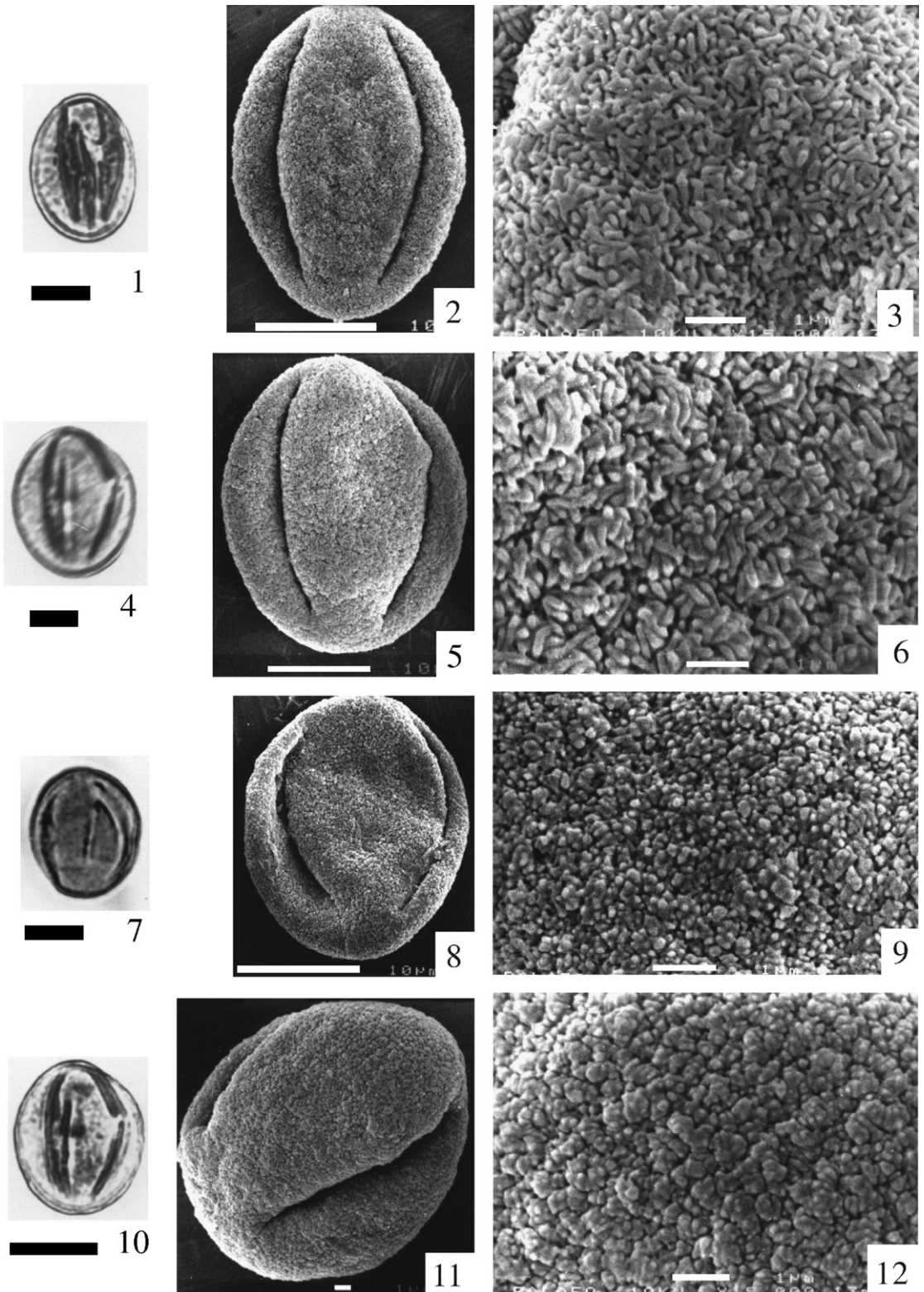


Plate III (caption on page 300).

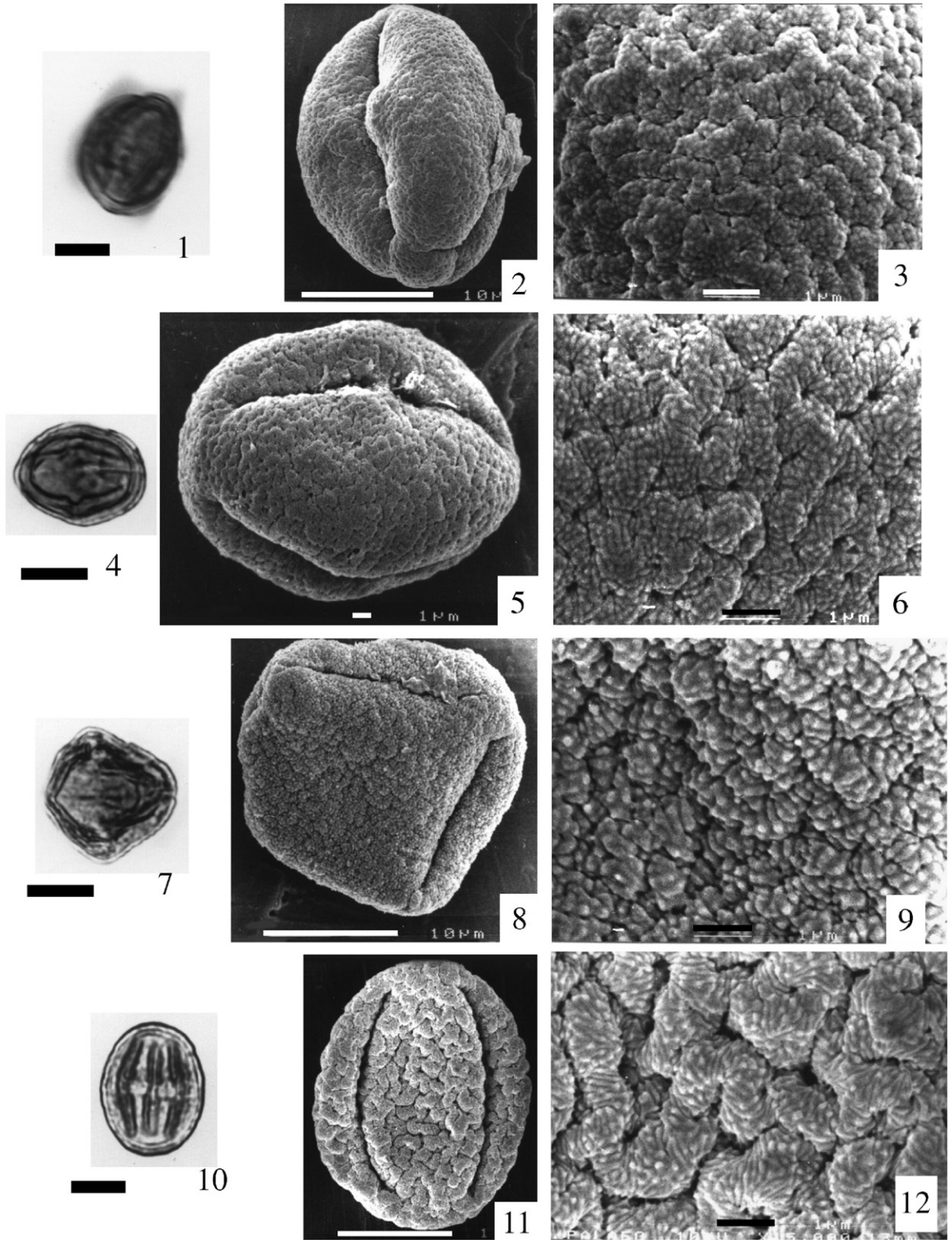


Plate IV (caption on page 301).

and *Quercus* subgenus *Cyclobanalepis* oaks, in southern and southwestern China (Wang and Chang, 1988; Wei, 2003). This indicates that the Chinese evergreen oaks, most likely the non-montane oaks, might have appeared in eastern China in Miocene times.

4.3. Oak pollen of uncertain habit

Three morphotaxa of oak pollen grains, representing oaks of uncertain habit, could be distinguished on the basis of their rugulate sculpturing.

Plate I. Fossil deciduous oak pollen. Scale bar for all the whole grains under the LM and SEM=10 µm, while the bar for sculpturing detail=1 µm.

1–3 and 10–12. *Quercus* morphotaxon 1 (1–3 and 10–12 denote two single grains, respectively)(see on page 296)

1. Equatorial view. LM.
2. Equatorial view. SEM.
3. Detail of sculpturing. SEM.
10. Equatorial view. LM.
11. Oblique equatorial view. SEM.
12. Detail of sculpturing. SEM.
- 4–6. *Quercus* morphotaxon 2 (single grain)
4. Equatorial view. LM.
5. Equatorial view. SEM.
6. Detail of sculpturing. SEM.
- 7–9. *Quercus* morphotaxon 3 (single grain)
7. Equatorial view. LM.
8. Equatorial view. SEM.
9. Detail of sculpturing. SEM.

Plate II. Fossil evergreen oak pollen. Scale bar for all the whole grains under the LM and SEM=10 µm, while the bar for sculpturing detail=1 µm.

1–12. *Quercus* morphotaxon 4 (including 4 single grains, i.e. 1–3, 4–6, 7–9, 10–12, respectively)(see on page 297)

1. Equatorial view. LM.
2. Equatorial view. SEM.
3. Detail of sculpturing. SEM.
4. Equatorial view. LM.
5. Equatorial view. SEM.
6. Detail of sculpturing. SEM.
7. Equatorial view. LM.
8. Equatorial view. SEM.
9. Detail of sculpturing. SEM.
10. Equatorial view. LM.
11. Equatorial view. SEM.
12. Detail of sculpturing. SEM.

Plate III. Fossil evergreen oak pollen. Scale bar for all the whole grains, except for fig. 11 (bar=1 µm), under the LM and SEM=10 µm, while the bar for sculpturing detail=1 µm.

1–6. *Quercus* morphotaxon 4 (including two single grains, i.e. 1–3 and 4–6).(see on page 298)

1. Equatorial view. LM.
2. Equatorial view. SEM.
3. Detail of sculpturing. SEM.
4. Equatorial view. LM.
5. Equatorial view. SEM.
6. Detail of sculpturing. SEM.
- 7–12. *Quercus* morphotaxon 5 (including two single grains, i.e. 7–9 and 10–12)
7. Equatorial view. LM.
8. Equatorial view. SEM.
9. Detail of sculpturing. SEM.
10. Equatorial view. LM.
11. Oblique equatorial view. SEM.
12. Detail of sculpturing. SEM.

Plate IV. Fossil oak pollen of unknown habit. Scale bar for all the whole grains, except for fig. 5 (bar = 1 μm), under the LM and SEM = 10 μm , while the bar for sculpturing detail = 1 μm .

- 1–6. *Quercus* morphotaxon 6 (including two single grains, i.e. 1–3 and 4–6). (see on page 299)
 1. Equatorial view. LM.
 2. Equatorial view. SEM.
 3. Detail of sculpturing. SEM.
 4. Equatorial view. LM.
 5. Equatorial view. SEM.
 6. Detail of sculpturing. SEM.
- 7–9. *Quercus* morphotaxon 7
 7. Equatorial view. LM.
 8. Equatorial view. SEM.
 9. Detail of sculpturing. SEM.
- 10–12. *Quercus* morphotaxon 8
 10. Equatorial view. LM.
 11. Equatorial view. SEM.
 12. Detail of sculpturing. SEM.

4.3.1. *Quercus* morphotaxon 6 (Plate IV, 1–6)

Pollen grains subprolate, elliptical in equatorial view. Size 19–22 \times 16–17 μm . Tricolporate, colpi with genicula (Plate IV, 2, 4). Exine tectate, tectum perforate, sexine thicker than nexine (Plate IV, 1, 4). Sculpturing rugulate, the rugulate elements densely covered by nannospinules (Plate IV, 3, 6).

4.3.2. *Quercus* morphotaxon 7 (Plate IV, 7–9)

Pollen grains spheroidal, rhombic in equatorial view (Plate IV, 7, 8). Size 19 \times 19 μm . Tricolporate, colpi with strong genicula (Plate IV, 7). Exine tectate, tectum perforate, sexine thicker than nexine (Plate IV, 7). Sculpturing weakly rugulate and covered by fewer nannospinules (Plate IV, 9).

The weakly rugulate sculpturing and sparse nannospinules distinguish it from *Q.* morphotaxon 6. The rhombic shape and rugulate micromorphology of sculpturing could suggest that the pollen is similar to that of *Trigonobalanus*, a tropical genus of the Fagaceae, especially that of *T. doichangensis* Forman (Nixon and Crepet, 1989). However, the unique proplate shape of *Trigonobalanus* pollen with its well developed atrium (Nixon and Crepet, 1989) is not reported from the current fossil. Additionally, no *Trigonobalanus* macrofossils have been reported at the same locality. For the present, we continue to classify this type of pollen grains under *Quercus*. More material is required to resolve its true identity.

4.3.3. *Quercus* morphotaxon 8 (Plate IV, 10–12)

Pollen grains subprolate, elliptical in equatorial view. Size 25 \times 20 μm . Tricolporate, endoporate (Plate IV, 10). Exine tectate, tectum strongly perforate with the pits linked to form fossulae, sexine thicker than

nexine (Plate IV, 10, 11). Sculpturing obviously rugulate and covered by numerous nannospinules (Plate IV, 12).

The pollen display pronounced rugulate sculpturing, divided by fossulae. Moreover, the arrangement of nannospinules is regular. Because of these two characters, it can be readily distinguished from the other fossil oak pollen grains.

5. Palaeoecological significance

In terms of the diversity of oak pollen grains from the Miocene of Zhejiang, eastern China, we have recognized three deciduous morphotaxa, two evergreen morphotaxa, with another three morphotaxa of uncertain habit (Table 4). The high diversity of oaks is supported by the macrofossil record from the same locality (Li, 1984). Based on the fossil leaves, the largest family is Fagaceae, with nineteen species, belonging to six genera, of which *Quercus* is the most abundant (Li, 1984). As mentioned above, the leaf fossils of *Quercus* have not yet been investigated in detail. The diversity of *Quercus* pollen grains would suggest that there were numerous oak species growing in the area during Miocene times. The palaeovegetation reconstructed from the fossil leaves is a notophyllous broadleaved evergreen forest (Liu and Zheng, 1995).

6. Conclusions

Based on the published work on extant oak pollen morphology, especially under the SEM, we have established the criteria (Tables 2 and 3) and apply them to distinguish deciduous and evergreen oak pollen from the

Miocene of Zhejiang, eastern China. The partially fused rod-like elements are almost exclusively present in the evergreen oak pollen in Europe and Asia, and uniformly fine granular ornamentation is mainly encountered in the Asian oaks, including montane evergreen oaks and *Quercus* subgenus *Cyclobalanopsis*. However, the North American evergreen oaks display similar sculpturing to the deciduous oaks. Although deciduous oak pollen lacks a unique ornamentation, the major type of sculpturing is scabrate or verrucate. In order to establish the presence of deciduous oaks unequivocally, it is necessary to take plant macrofossils into consideration.

The application of the criteria to the Miocene pollen assemblage from Zhejiang, eastern China confirms the evidence based on macrofossils from the same locality. Both lines of evidence suggest the palaeovegetation was a “notophyllous broadleaved evergreen forest”, in which evergreen and deciduous oaks were predominant.

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References

- Aizen, M.A., Patterson III, W.A., 1990. Acorn size and geographical range in the North American oaks (*Quercus* L.). *J. Biogeogr.* 17, 327–332.
- Axelrod, D.I., 1966. Origin of the deciduous and evergreen habits in temperate forests. *Evolution* 20, 1–15.
- Axelrod, D.I., 2000. A Miocene (10–12 Ma) evergreen laurel–oak forest from Camel Valley, California. *Univ. Calif. Publ. Geol. Sci.* 145, 1–34.
- Crepet, W.L., Daghlian, G.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 (5), 739–757.
- Dupont, R., Dupont, S., 1972. Etude de pollens de Chênes (genre *Quercus* L.) en microscopie électronique à balayage. *C. R. Séances Acad. Sci., Ser. D* 274 (17), 2503–2506.
- Ferguson, D.K., Pinggen, M., Zetter, R., Hofmann, C.-C., 1998. Advances in our knowledge of the Miocene plant assemblage from Kreuzau, Germany. *Rev. Palaeobot. Palynol.* 101, 147–177.
- Fujiki, T., Miyoshi, N., 1995. Pollen morphology of subgenus *Cyclobalanopsis* (*Quercus*, Fagaceae). *Jpn. J. Palynol.* 41 (1), 21–29.
- Fujiki, T., Morita, Y., Miyoshi, N., 1996. Pollen morphology of subgenus *Lepidobalanus* (*Quercus*, Fagaceae) in Japan. *Jpn. J. Palynol.* 42 (2), 107–116.
- Huang, C., Zhang, Y., Bartholomew, B., 1999. Fagaceae. In: *Flora of China* Editorial Committee (Editors), *Flora of China*. Vol. 4 (Cycadaceae through Fagaceae). Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis, pp. 314–402.
- Jarvis, D.I., Clay-Poole, S.T., 1992. A comparison of modern pollen rain and vegetation in southwestern Sichuan Province, China. *Rev. Palaeobot. Palynol.* 75, 239–258.
- Jarvis, D.I., Leopold, E.B., Liu, Y., 1992. Distinguishing the pollen of deciduous oaks, evergreen oaks, and certain rosaceous species of southwestern Sichuan Province, China. *Rev. Palaeobot. Palynol.* 75, 259–271.
- Jones, J.H., 1986. Evolution of the Fagaceae: the implications of foliar features. *Ann. Mo. Bot. Gard.* 73, 228–275.
- Leopold, E.B., Clay-Poole, S.T., 2001. Florissant leaf and pollen floras of Colorado compared: climatic implications. *Proc. Denver Mus. Nat. Sci., Ser. 4* (1), 17–69.
- Li, H.M., 1984. Neogene floras from eastern Zhejiang, China. In: Whyte, R.O. (Ed.), *The Evolution of the East Asian Environment*. Vol. II. Palaeobotany, Palaeozoology and Palaeoanthropology. Centre of Asian Studies, University of Hong Kong, Hong Kong, pp. 461–466.
- Li, H.M., Guo, S.X., 1982. Angiospermae. In: *Nanjing Inst. Geol. Min. Res. (Editor), Paleontological Atlas of East China, Part 3, Volume of Mesozoic and Cenozoic*. Geological Publishing House, Beijing, China, pp. 294–316.
- Liang, H.-P., Jen, H.-W., Liu, Y.-Q., 1999. A study on the morphology of foliar trichomes of evergreen oaks (*Quercus*) in China and its implication in taxonomy. *Acta Phytotaxon. Sin.* 28 (2), 112–121.
- Lieux, M.H., 1980. An atlas of pollen of trees, shrubs, and woody vines of Louisiana and other southeastern states, part II. *Platanaceae to Betulaceae. Pollen Spores* 22 (2), 191–243.
- Liu, L.-F., Fang, Z.-J., 1986. A study on pollen morphology of Quercoidae Oerster (Fagaceae) in China. *Guihaia* 6 (4), 243–251.
- Liu, Y.-S., Zheng, Y.H., 1995. Neogene floras. In: Li, X.X., et al. (Eds.), *Fossil Floras of China through the Geological Ages*. Guangdong Science and Technology Press, Guangzhou, China, pp. 506–551.
- Liu, Y.-S., Guo, S.X., Ferguson, D.K., 1996. Catalogue of Cenozoic megafossil plants in China. *Palaeontogr., Abt. B* 238, 141–179.
- Liu, Y.-S., Zetter, R., Ferguson, D.K., 1997. Fossil pollen grains of *Cathaya* (Pinaceae) in the Miocene of eastern China. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, vol. 58, pp. 227–235.
- Menitsky, Yu.L., 1984. *Duba Azii*. Nauka Publishers, Leningrad.
- Menitsky, Yu.L., 2005. *Oaks of Asia*. Science Publishers, Enfield, U.S.A.
- Miyoshi, N., Fujiki, T., Morita, Y., 1999. Palynology of a 250-m core from Lake Biwa: a 430,000-year record of glacial–interglacial vegetation change in Japan. *Rev. Palaeobot. Palynol.* 104, 267–283.
- Nakagawa, T., Yasuda, Y., Tabata, H., 1996. Pollen morphology of Himalayan *Pinus* and *Quercus* and its importance in palynological studies in Himalayan area. *Rev. Palaeobot. Palynol.* 91, 317–329.
- Nilsson, S., Praglowski, J., 1992. *Handbook of Palynology*, 2nd edition. Munksgaard, Copenhagen.
- Nixon, K.C., 1997. Fagaceae. In: *Flora of North America* Editorial Committee (Eds.), *Flora of North America North of Mexico*. Vol. 3. Oxford University Press, New York, pp. 436–506.
- Nixon, K.C., Crepet, W.L., 1989. *Trigonobalanus* (Fagaceae): taxonomic status and phylogenetic relationships. *Am. J. Bot.* 76 (6), 828–841.
- Punt, W., Blackmore, S., Nilsson, S., Le Thomas, A., 1994. *Glossary of pollen and spore terminology*. LPP Contributions Series, vol. 1. LPP Foundation, Utrecht, The Netherlands.
- Sachse, M., 1997. *Die Makrilia-Flora (Kreta, Griechenland) — ein Beitrag zur Neogenen Klima- und Vegetationsgeschichte des östlichen Mittelmeergebietes*. Doktor der Naturwissenschaften Thesis, ETH, Zürich, Switzerland.

- Saito, T., Morohoshi, F., 1992. Palynology of the Miocene Iwamura Group, Gifu Prefecture, Japan. Bull. Mizunami Fossil Mus. (19), 113–124.
- Smit, A., 1973. A scanning electron microscopical study of the pollen morphology in the genus *Quercus*. Acta Bot. Neerl. 22 (6), 655–665.
- Solomon, A.M., 1983a. Pollen morphology and plant taxonomy of white oaks in eastern North America. Am. J. Bot. 70 (4), 481–494.
- Solomon, A.M., 1983b. Pollen morphology and plant taxonomy of red oaks in eastern North America. Am. J. Bot. 70 (4), 495–507.
- Valdés, B., Díez, M.J., Fernández, I., 1987. Atlas Polínico de Andalucía Occidental. Instituto de Desarrollo Regional N° 43, Universidad de Sevilla EXCMA. Diputación de Cadiz.
- Van Benthem, F., Clarke, G.C.S., Punt, W., 1984. Fagaceae. The Northwest European Pollen Flora, 33. Rev. Palaeobot. Palynol. 42, 87–110.
- Van der Burgh, J., Zetter, R., 1998. Plant mega- and microfossil assemblages from the Brunssumian of ‘Hambach’ near Düren, B.R.D. Rev. Palaeobot. Palynol. 101, 209–256.
- Van der Spoel-Walvius, M.R., 1963. Les caractéristiques de l’exine chez quelques espèces de *Quercus*. Acta Bot. Neerl. 12, 525–532.
- Wang, P.-L., Chang, K.-T., 1988. Pollen morphology of *Cyclobalanopsis* and its relation to *Quercus*. Acta Phytotaxon. Sin. 26 (4), 282–289.
- Wang, P.-L., Chang, K.-T., 1991. The pollen morphology in relation to the taxonomy and phylogeny of Fagaceae. Acta Phytotaxon. Sin. 29 (1), 60–66.
- Wang, P.-L., Pu, F.-D., 2004. Pollen Morphology and Biogeography of Fagaceae. Guangdong Science and Technology Press, Guangzhou, China.
- Wang, P.-L., Pu, F.-D., Zheng, Z.-H., 1998. Palynological evidence for taxonomy of *Trigonobalanus* (Fagaceae). Acta Phytotaxon. Sin. 36 (3), 238–241.
- Wei, Z., 2003. Pollen Flora of Seed Plants. Yunnan Science and Technology Press, Kunming, China.
- Wolfe, J.A., 1987. Late Cretaceous–Cenozoic history of deciduousness and the terminal Cretaceous event. Paleobiology 13 (2), 215–226.
- Yamanoi, T., 1992. Palyno-floras of early Middle Miocene sediments in central Japan. Bull. Mizunami Fossil Mus. (19), 103–112.
- Yamazaki, T., Takeoka, M., 1959. Electronmicroscope investigations on the surface structure of the pollen membrane, based on the replica method. V. Especially, on the pollen of genus *Quercus*. J. Jpn. For. Soc. 41, 125–130.
- Zetter, R., 1989. Methodik und Bedeutung einer routinemäßig kombinierter lichtmikroskopischer und rasterelektronenmikroskopischer Untersuchung fossiler Mikroflora. Cour. Forschungsinst. Senckenberg 109, 41–50.
- Zetter, R., Ferguson, D.K., 2001. Trapaceae pollen in the Cenozoic. Acta Palaeobot. 41, 321–339.
- Zheng, Z.-H., Wang, P.-L., Pu, F.-D., 1999. A comparative study on pollen exine ultrastructure of *Nothofagus* and the other genera of Fagaceae. Acta Phytotaxon. Sin. 37 (3), 253–258.