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# *Lagerstroemia* (Lythraceae) pollen from the Miocene of eastern China

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**Abstract**
A newly discovered fossil pollen taxon is described as *Lagerstroemia cathayensis* sp. nov. on the basis of a combination of morphological characters including prolate shape with no or weakly developed pseudocolpi and rugulate-verrucate tectum. The fossil pollen was recovered from a Miocene deposit in Zhejiang province, eastern China. It resembles pollen of extant *Lagerstroemia subcostata* Koehne and *L. limii* Merrill, both species still occurring near the fossil site in Zhejiang province and further extending into other regions of southern China, Japan, India and the Philippines. This record represents the only description of Cenozoic pollen grains of the genus *Lagerstroemia* from East Asia examined by means of scanning electron microscopy. The occurrence of *Lagerstroemia* together with some temperate plants (i.e. *Keteleeria, Acer, Carpinus, Fagus*) at the fossil site suggests that the climate in eastern China during the Miocene was similar to that of today.

**Keywords:** Lagerstroemia cathayensis, *Lythraceae, pollen, Miocene, eastern China*



The genus *Lagerstroemia* (Lythraceae), horticultural plants known as crape myrtles, comprises around 56 living species spread from India, Southeast Asia, southern China, Japan and Korea to northern Australia and New Guinea (Furtado & Srisuko, 1969; Graham, 2007). This distribution pattern in circum-east Indian and west Pacific Oceans raises an intriguing biogeographic question about how this pattern originated. Fossil evidence could provide concrete evidence for a better understanding of this question. The fossil history of *Lagerstroemia* is, however, limited (Muller, 1981*a*; Tanai & Uemura, 1991; Tiwari & Mehrotra, 2000; Mehrotra et al., 2004 and references cited therein; Pigg & De Vore, 2005; Cheng et al., 2007). In the course of evaluating the fossil pollen records of extant angiosperms (Muller, 1981*a*) and summarizing the geologic history of the Lythraceae (Graham & Graham, 1971; Eyde, 1972), all concluded that there were no authentic fossil pollen records of the genus *Lagerstroemia*, although the morphology of the pollen grains is very distinctive (see Muller, 1981*b*; Kim et al., 1994; Fujiki et al., 2001). In fact, fossil pollen of the genus was reported from the Pleistocene of northern Taiwan in 1972 (see Chung & Huang, 1972: plate 129, Figures 18–21). Fossil pollen of *Lagerstroemia* are rarely documented (Yamanoi 1992*a*, *b*). One of the serious problems with the microfossil records of *Lagerstroemia* is that the identification is rarely straightforward. It is hard to reach an unambiguous identification without the aid of a scanning electron microscope (SEM) (Ferguson et al., 2007). For example, it is difficult to establish the identity of some *Lagerstroemia*-like pollen grains, such as the Chinese fossil pollen *Verrutricolporites pachydermis* Sun, Kong et Li (Sun et al., 1980) and *Rugulitriporites* cf. *vestibulipori* Muller (Zhang & Zhan, 1991), with only light microscopy (LM) at a low resolution. Both of these fossil species have been transferred to a single fossil pollen taxon (*Planotricolporites lagerstromiaformis*) with an affinity to *Lagerstroemia* (Song et al., 2004). It is hard to believe that only a single species was represented throughout the Late Cretaceous

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and Cenozoic of China, as China ranks as one of the countries with a high number of extant species.

The authors have isolated and confirmed by SEM observations numerous authentic pollen grains of *Lagerstroemia* in a Miocene pollen assemblage from Zhejiang Province, eastern China (Figure 1). The main purpose of the present paper is to describe these fossil pollen grains in detail, using both LM and SEM investigations.

## Material and methods

As a result of Neogene volcanism in eastern China, several large plant assemblages have become entombed in ancient maar lakes, such as the Shanwang flora in Shandong (Hu & Chaney, 1940; Yang & Yang, 1994; Sun, 1999; Wang et al., 2006) and the Xianan Shan flora in Zhejiang (Figure 1; Li & Guo, 1982; Li, 1984; Liu et al., 2007). The latter flora was uncovered from the intercalations in the Sheng Xian Group, probably representing temporary lake or fluvial deposits formed after volcanic eruptions (Li, 1984). The Sheng Xian Group, lying unconformably upon rocks of Jurassic to Cretaceous age, includes the Xianan Shan Formation in the lower part (Figure 2). The Xianan Shan Formation is mainly composed of lacustrine sediments such as fire-clay, diatomaceous earth, and lignite. An abundant assemblage of megafossil plants, mostly leaves, is well preserved in the clay, in which a rich fossil pollen assemblage is also preserved (Liu et al., 2007). Figure 2 presents the columnar section of Xianan Shan Formation in Xianan Shan, Ninghai County. It is unfortunate that the megafossil assemblage was only briefly described more than two decades ago (Li & Guo, 1982; Li, 1984) because it is no longer exposed. Because no fossil vertebrates were ever found, the geological age of this flora is considered to be Miocene on the basis of correlations of plant megafossils and local stratigraphy (Li, 1984).

The fossil pollen grains were isolated from a sample of clay, on which a fossil leaf is preserved. The sample was collected by Professor Shuang-Xing Guo from the fossiliferous clay layer in the upper part of the Xianan Shan Formation (Figure 2).

The pollen preparation method developed by Zetter (1989) and outlined in detail by Ferguson et al. (2007) was followed. This method allows single pollen grains to be manipulated for better observations under light and scanning electron microscopy. Cross-sections of the exine, obtained by exerting local pressure on the pollen grain using a human hair mounted on a dissecting needle (see Zetter, 1989), were also examined under SEM. A total of 500 pollen grains in the assemblage were counted. Dominant elements include *Quercus* (66%; mostly evergreen), *Zelkova* (4.3%), *Carya* (4%), *Fagus* (3.5%), *Buxus* (3.3%), *Ulmus* (2.6%), and

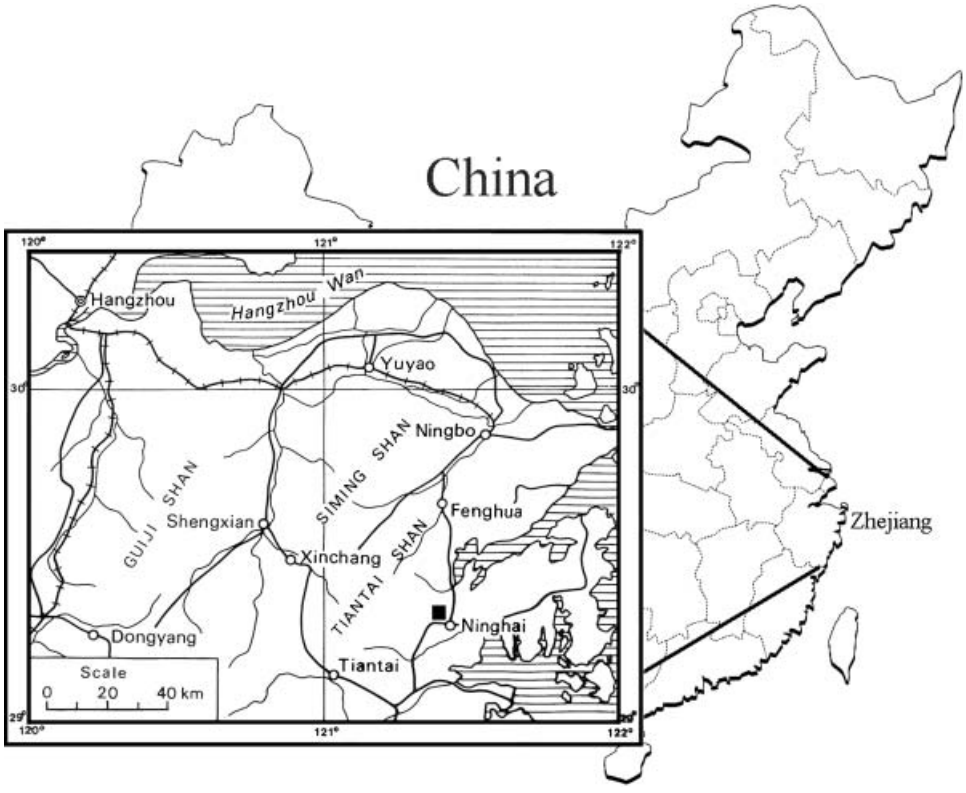



Figure 1. Map showing the fossil locality (Black Square) near Ninghai of Zhejiang Province, eastern China (modified from Li, 1984).

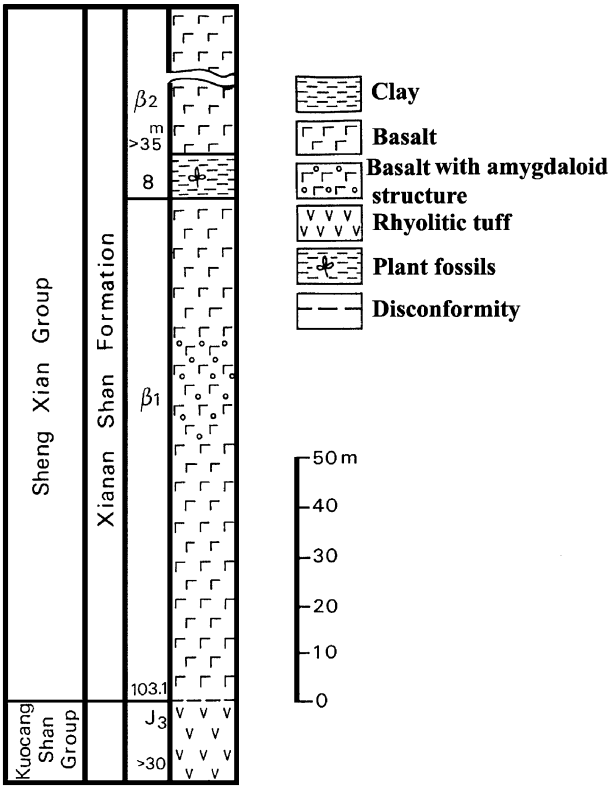



Figure 2. The profile section of Xianan Shan Formation in Xianan Shan, Ninghai County, Zhejiang province, eastern China (after Li, 1984).

*Castanopsis* (2.3%), which suggest that the palaeovegetation must have been a mixed evergreen and deciduous broadleaved forest, developed under a seasonal warm and humid climate. Pollen grains of *Lagerstroemia* counted are about 1% of the total.

The description of pollen morphology follows Punt et al. (1994). The figured specimens and the SEM stubs have been deposited in the Institute of Palaeontology, University of Vienna, Austria.

Pollen grains of two living species of *Lagerstroemia* from China are examined for comparison with the Miocene pollen grains in the present study. The pollen samples of both living species are from the Herbarium of the Institute of Botany in Beijing (PE): 1) *Lagerstroemia limii* Merrill; Location: Jiande County, Zhejiang Province, eastern China; Field No.: 29441; Date: 1st July 1958 – Collector: unknown. 2) *Lagerstroemia subcostata* Koehne; Location: Hangzhou City, Zhejiang Province, eastern China; Field No.: 0724; Date: 24th July 1958 – Collector: unknown.

## Results

*Systematic description*

Family: Lythraceae J. St.-Hil.
Genus: *Lagerstroemia* L.
Species: *Lagerstroemia cathayensis* sp. nov. (Figures 3, 4)

*Diagnosis.* Pollen grains subprolate, tricolporate; pseudocolpi absent or weakly developed, endopores round, colpi of various lengths, the apices attenuate or sometimes rounded. Exine thick, tectate; tectum rugulate to verrucate, rugulae/verrucae psilate.

*Holotype.* Figure 3G, L, Q. Slide China 1/8.

*Etymology.* The specific epithet *cathayensis* - refers to the ancient name for China.

*Type locality, stratum and age.* Clay stratum of the upper part of Xianan Shan Formation, Xianan Shan, Ninghai County, Zhejiang Province, eastern China. Miocene in age.

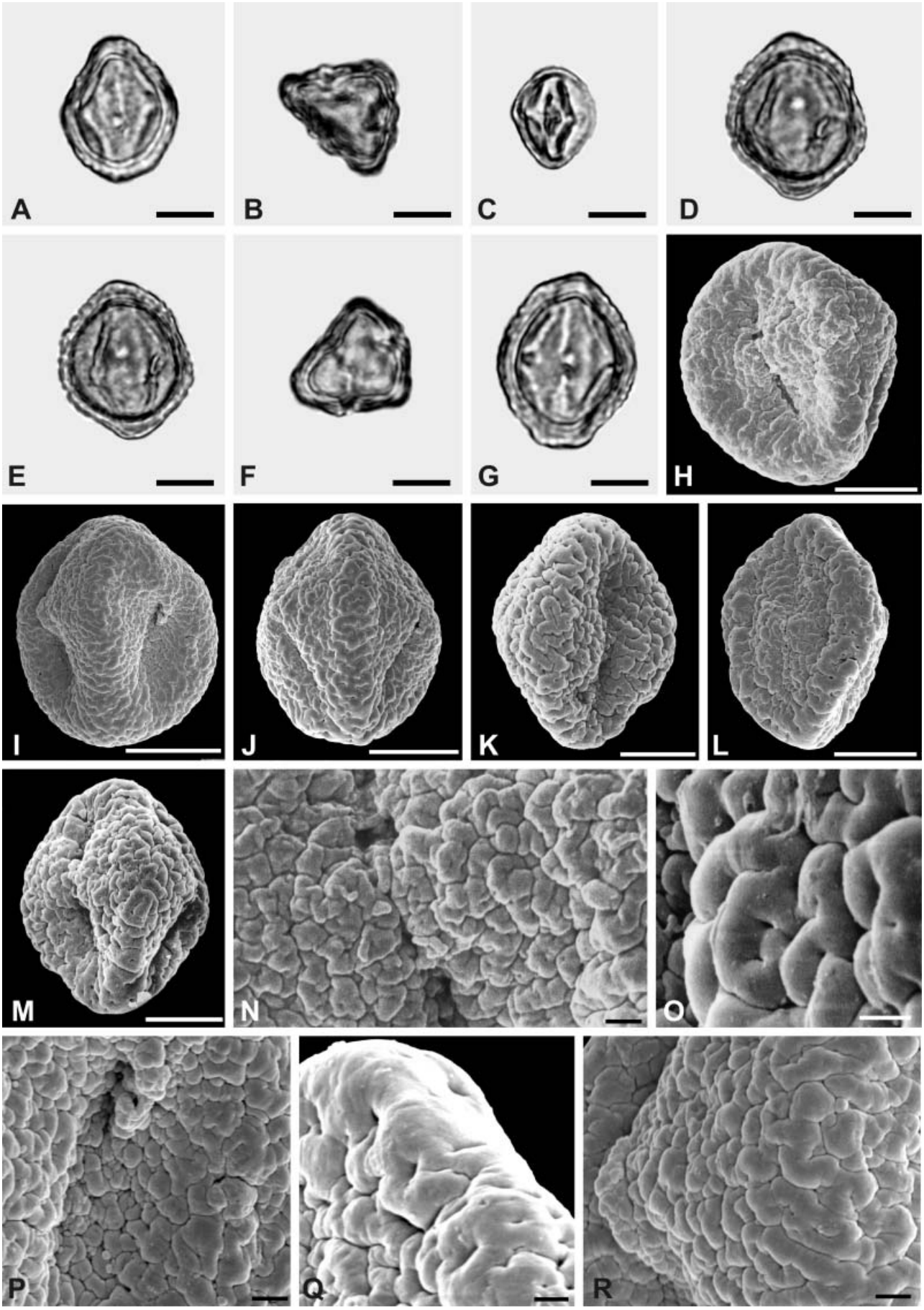
*Paratypes.* Figures 3A–F, H–K, M–P, R; 4A–D.

*Number of samples examined.* Five grains were observed.

*Description.* Pollen grains subprolate, equatorial axis 20–25 μm, polar axis 30–34 μm, mostly isopolar, radially symmetrical, sometimes pear-shaped in equatorial view (Figure 3A, C–E, G–M), mostly concave triangular in polar view (Figure 3B, F). Pollen grains tricolporate, endopores large, round, diameter ca. 1.5–2 μm (Figure 3A, C–E, G). Colpi generally ca. 26–27 μm long, varying in length, one frequently shorter than the other two, the apices attenuate or sometimes rounded (Figure 3C, H). Exine tectate, somewhat punctate (Figure 3K–M, O), 2–3 μm thick in interapertural zone, sometimes thicker in polar region (Figure 3D, E, G); coarser granulation around the inner endoapertural area (Figure 4D). Columellae slightly rough (Figure 4A, B), shorter near the apertures with a thicker tectum, longer with a thinner tectum in the polar regions (Figure 4A–C). Tectum rugulate to verrucate, verrucae of various sizes and morphology, psilate (Figure 3H–R), typically more randomly arranged in the mesocolpium than near the apertures. Ectexine thickened around pore area, endexine thin (Figure 3B, F).

→

Figure 3. **A–R**. *Lagerstroemia cathayensis*. **A–G**. LM, **H–R**. SEM. **A**, **C–E**, **G**. *Lagerstroemia cathayensis*, variation of fossil pollen grains in equatorial view. **B**, **F**. Variation of fossil pollen grains in polar view. **H–M**. Variation of *Lagerstroemia cathayensis* in equatorial view, SEM. **N**, **P**, **R**. Details of the sculpture in apertural area. **O**. Detail of the sculpture on the meridional ridge. **Q**. Detail of the sculpture in the polar area. Scale bars −10 μm (A–M); 1 μm (N–R).



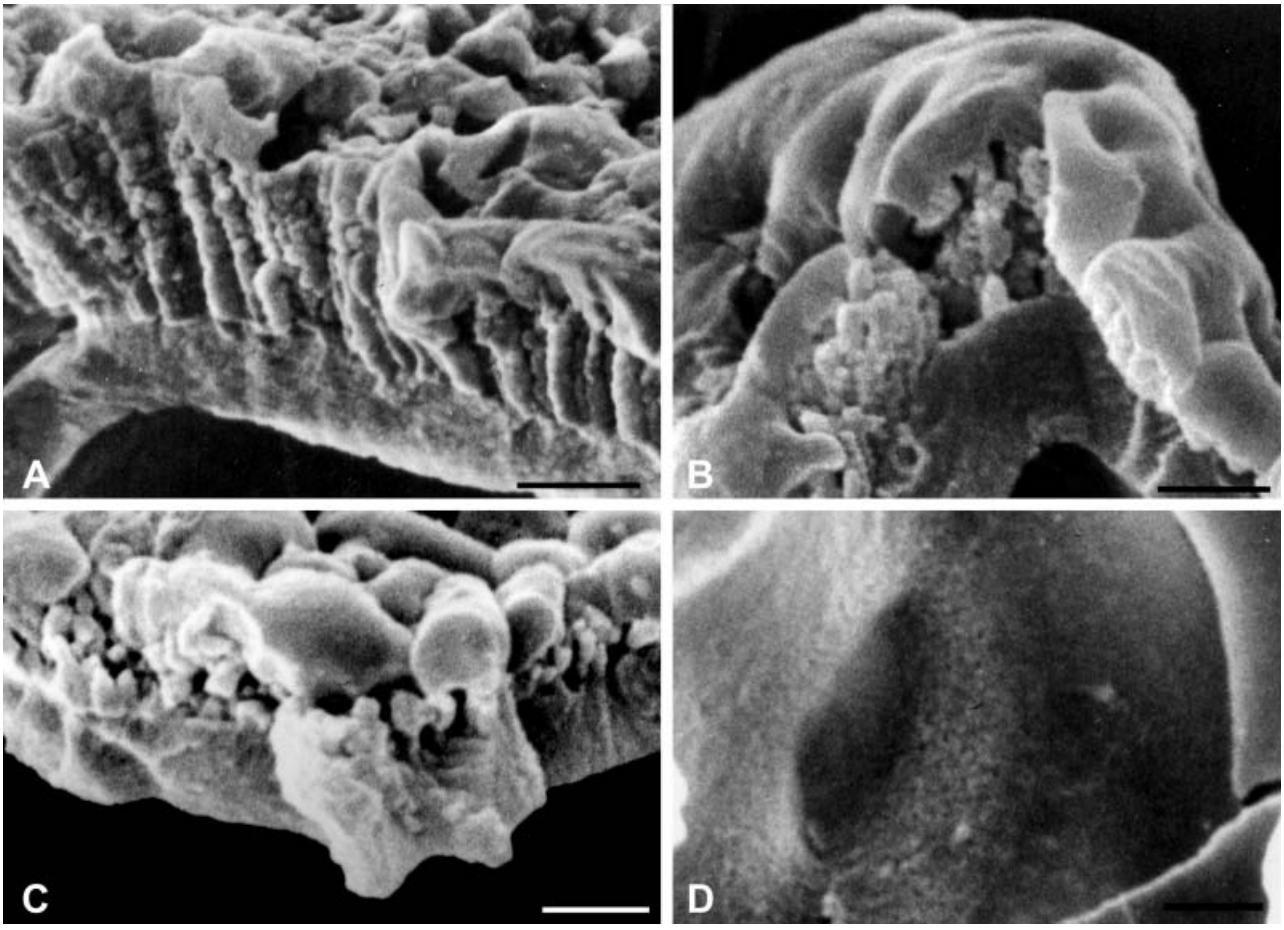



Figure 4. **A–D**. *Lagerstroemia cathayensis*, SEM. **A**. Detail of the pollen wall structure at the transition between mesocolpium and polar area. Note the granulate columellae. **B**. Elongated columellae in the polar area. **C**. Detail of the pollen wall structure in the mesocolpial area. **D**. Detail of the inner endoapertural area. Note the coarser granulation around the endoaperture. Scale bar −1 μm.



## Comparison and discussion

Although a few fossil pollen species of *Lagerstroemia* have been reported since the 1970s, detailed descriptions of the fossil pollen morphology are still rare simply because of the limited utilization of SEM for fossil material. The present description is mainly based on SEM observations supplemented by LM.

Modern lythraceous pollen grains, representing about 24 genera, have been intensively studied since the early 1980s (Muller, 1981*b*; Graham et al., 1985, 1987, 1990; Booi et al., 2003). The pollen is tricolporate (sometimes 4-colporate), heterocolpate (sometimes syncolpate) with psilate, microrugulate, microreticulate to finely striate surface ornamentation (Booi et al., 2003). Pollen morphology at the generic level in the Lythraceae is reviewed (Table I). It is evident that the fossil pollen from China described here can be assigned to the Lythraceae based on the prolate, tricolporate grains with rugulate to verrucate tectum (Table I).

Pollen of modern *Lagerstroemia* has been well-documented in recent years (Graham et al., 1987; Bortenschlager & Thammathaworn, 1990; Kim et al., 1994). It is apparent that the pollen of *Lagerstroemia* has a unique set of characters, being prolate to prolate-spheroidal, tricolporate with 6 weakly developed pseudocolpi and with mostly prominent mesocolpial ridges. Based on differences in size, shape, amb, pseudocolpi, sculpture, and margo, Kim et al. (1994) recognized five intuitively generated pollen groups, except for three species which produce unique pollen grains and are therefore referred to Group VI (Table II). The groupings more or less correspond to the sectional classification of Furtado and Srisuko published in 1969 (Kim et al., 1994). By way of comparison, pollen of two extant species from around the fossil locality, i.e. *L. subcostata* Koehne, and *L. limii* Merrill, were examined in the same way as the fossil grain using LM and SEM (Figure 5). It is clear that the morphology of the pollen exine in the two extant species, being rugulate and verrucate, closely resembles that of the Chinese fossil pollen. In a more thorough survey of pollen morphology in *Lagerstroemia*, Kim et al. (1994) examined 39 (of

Table I. Comparison of pollen morphology in extant genera of the Lythraceae.

| Genus | Exine | Aperture | Distinctive characters | Sources |
|---|---|---|---|---|
| *Adenaria* | scabrate | tricolporate | ectexine bridge over the endoaperture, a scabrate/granular tectum | 2 |
| *Ammannia* | finely striate | tricolporate with 6 distinct pseudocolpi | | 2 |
| *Capuronia* | psilate to faintly scabrate-punctate | tricolporate | sharply delimited apertures, absence of pseudocolpi, a psilate/sparsely punctate tectum | 2 |
| *Crenea* | verrucate | tricolporate with 6 pseudocolpi | scabrate to verrucate tectum | 1, 2 |
| *Cuphea* | | 3-syncolporate | syncolporate | 2, 5 |
| *Decodon* | scabrate bordering apertures | tricolporate, colpus membrane granular | faint elongated depressions paralleling the colpi | 2 |
| *Didiplis* | striate-rugulate in mesocolpal region | tricolporate | tectum of fine striae organized similar to that in *Ammannia* | 2 |
| *Diplusodon* | verrucate, margins of verrucae irregular and lobate | tricolporate, colpi faint | pseudocolpi absent, poorly developed or seemingly absent colpi, tectum coarsely/deeply verrucate/rugulate | 2 |
| *Galpinia* | verrucate, more psilate along mesocolpial ridge | tricolporate | tectum on either side of poorly defined colpus irregularly granular but being more psilate nearer poles/mesocolpium | 2 |
| *Haitia* | scabrate | tricolporate with 6 pseudocolpi | well-developed pseudocolpi & scabrate tectum | 3 |
| *Heimia* | scabrate | tricolporate | lack both pseudocolpi & verrucate/rugulose tectum | 3 |
| *Hionanthera* | finely striate, striae arranged parallel | tricolporate with 6 faint pseudocolpi | faint pseudocolpi & finely striate tectum | 3 |
| *Lafoensia* | scabrate to finely verrucate | tricolporate with 6 pseudocolpi | psilate tectum along mesocolpial ridges & poles, but scabrate on aperture borders | 1, 3 |
| *Lagerstroemia* | scabrate to finely verrucate | tricolporate with or without pseudocolpi | great variation, prolate-spheroidal, tricolporate with 6 faint pseudocolpi, mesocolpial ridges prominent | 1, 3, 5 |
| *Lawsonia* | psilate | tricolporate with 6 pseudocolpi | well-delimited pseudocolpi, psilate tectum near apertures where it is faintly verrucate/rugulate or coarsely granular | 3, 5 |
| *Lythrum* | striate, striae parallel to colpi | tricolporate with 3 pseudocolpi | 3 prominent granular pseudocolpi alternat-ing with 3 apertures, tectum finely striate | 3, 5, 6 |
| *Nesaea* | striate, striae parallel to colpi or irregularly oriented | tricolporate with 6 pseudocolpi | well-defined pseudocolpi with pronounced mesocolpial ridges | 3 |
| *Pehria* | minutely scabrate, faint margo | tricolporate | lack pseudocolpi | 3 |
| *Pemphis* | psilate to faintly scabrate | tetracolporate with 8 faint pseudocolpi or tricolporate with 3 faint pseudocolpi | | 3, 7 |
| *Peplis* | striae oriented transversely across mesocolpial bands | tricolporate with 3 conspicuous pseudo-colpi | wall thickest ca. 1 μm in mesocolpial region, thinner at colpi/pseudocolpi; mesocolpia restricted to bands 2–3 μm wide | 3, 5 |
| *Physocalymma* | rugulate/short tiner-lanced striae | tricolporate | well-defined colpi alternating with a poorly defined intercolpar concavity, tectum rugulate | 4 |
| *Pleurophora* | scabrate | tricolporate with 3 faint pseudocolpi | | 4 |
| *Rotala* | scabrate to finely verrucate, rugulate bordering colpus | tri- to tetracolporate with 6 faint pseudo-colpi | | 4, 5 |
| *Tetrataxis* | prominent mesoco-lpial ridges, psilate | tricolporate | 3 apertural fields each with a central pore separated by prominent meridional ridges extending to poles | 4 |
| *Woodfordia* | scabrate | tricolporate | lack pseudocolpi; only weakly developed meridional ridges in polar view | 4, 5 |

Sources: 1. Muller (1981*b*); 2. Graham et al. (1985); 3. Graham et al. (1987); 4. Graham et al. (1990); 5. Wang et al. (1995); 6. Booi et al. (2003); 7. Wei (2003).

Table II. Comparison of *Lagerstroemia* pollen groups based on the differences in size, shape, amb, pseudocolpi, sculpturings, and margo (after Kim et al. 1994). Sectional taxonomy follows Furtado and Srisuko (1969).

| Pollen group | Characters | Section |
|---|---|---|
| I. | amb circular; pseudocolpi indistinct; margo distinct; ectexine greatly thickened; sexine psilate-punctuate in polar/mesocolpial regions and scabrate-finely verrucate in the remaining areas (antesepalous) and very coarsely rugulate overall sculpturing (antepetalous). | *Lagerstroemia* |
| II. | pollen diminutive; exine very thin; pseudocolpi absent and distinct margo indistinct; sexine verrucate to finely rugulate (antesepalous) and coarsely rugulate near the colpus (antepetalous). | *Lagerstroemia* |
| III. | pseudocolpi absent or indistinct; margo absent or poorly developed; meridional ridges distinct; sexine psilate-punctate in polar and meridional regions, scabrate-finely verrucate near the apertural regions (antesepalous) and uniformly densely rugulate (antepetalous). | *Adambea* |
| IV. | pseudocolpi absent or indistinct; margo narrow, distinct; meridional ridges prominently developed; sculpturing psilate-punctate to scabrate punctate. | *Trichocarpidium* & *Lagerstroemia* |
| V. | Most distinctive; tectum smooth or very finely granular; pseudocolpi lacking. | *Trichocarpidium* & *Adambea* |
| VI. | collective group for unique pollen types that cannot be easily assigned to Groups I–V. | *Trichocarpidium* & *Adambea* |



the ca. 56) species of the genus and provided enough illustrations for comparisons. It is confirmed that the Chinese Miocene pollen species is closely comparable to not only the two extant species, but also another modern species in terms of exine morphology: *L. micrantha* Merrill, all of which belong to Group III. In the most recent taxonomic treatment of Chinese *Lagerstroemia*, the presence of *L. micrantha* in China could not be confirmed (Qin et al., 2007). The other two species (*L. subcostata* and *L. limii*) are therefore considered to represent the best match for the Chinese fossil pollen.

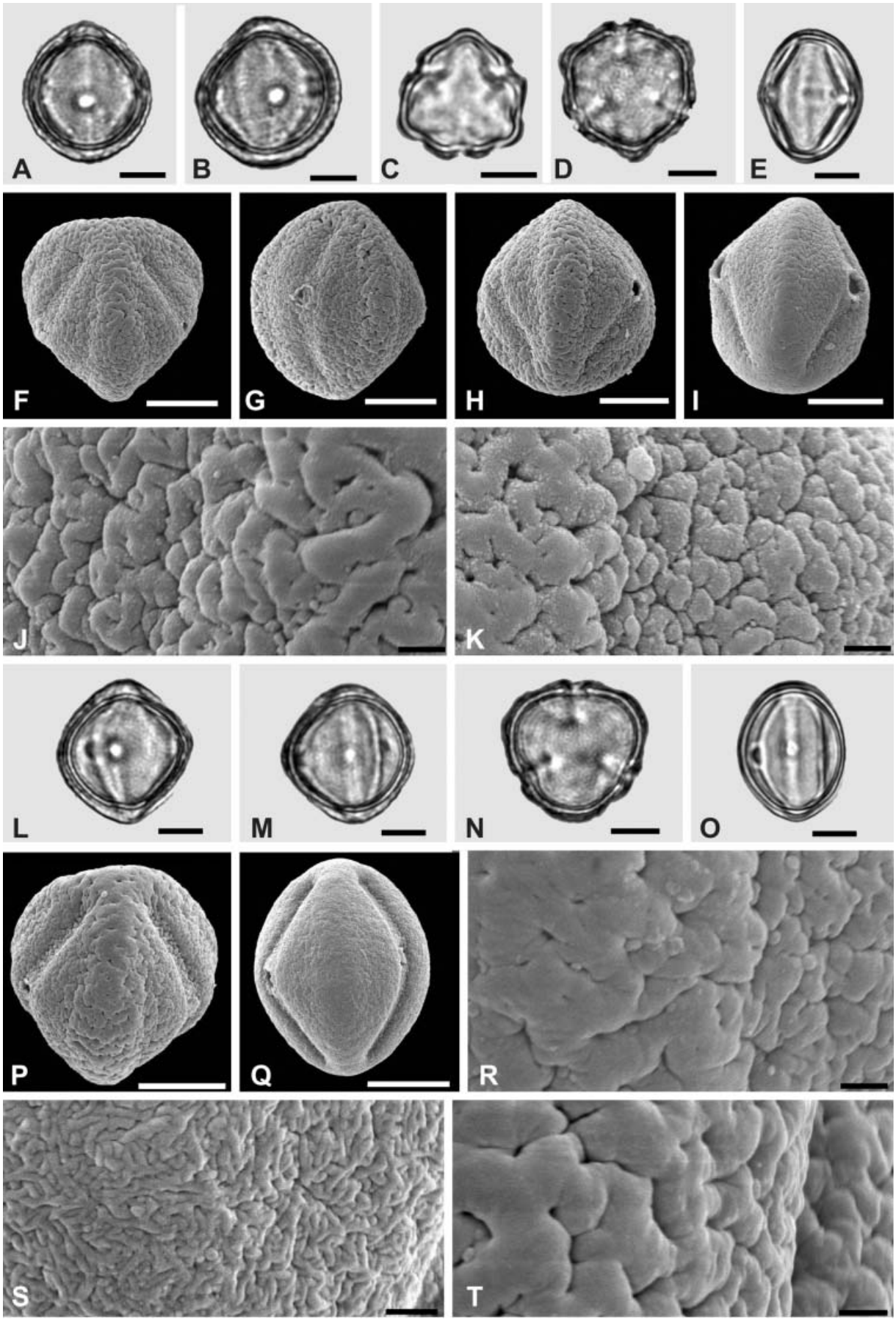
Fossil *Lagerstroemia* pollen grains have only been illustrated occasionally. As yet the infrageneric affiliation of these fossil pollen grains has not been discussed. These records include fossil *Lagerstroemia* pollen grains from the early Miocene of Thailand and the Pleistocene of Thailand and Japan (Watanasak, 1990; Fujiki et al., 2001; Songtham et al., 2005; Rugmai et al., 2008). They represent some of the very few published SEM images of fossil *Lagerstroemia* pollen grains. These fossil grains, with much finer exine sculpturing, are therefore quite different from our Chinese grains. Also, these fossil grains could represent pollen from antisepalous stamens (see below) due to their finer exine sculpturing, so it is not a good argument for erecting a new species. In Songtham et al. (2005) and Rugmai et al. (2008) the pollen grains are not given a specific epithet. Therefore, a new species is proposed largely based on the morphology of exine sculpturing under SEM.

Under SEM the pollen of recent *Lagerstroemia* displays variable exine morphology, viz. coarse and fine verrucae within the same species. This dimorphism is dependent on the anther from which the pollen was derived (Muller, 1981*b*; Pacini & Bellani, 1986; Kim et al., 1994; Fujiki et al., 2001). Generally, the flowers of *Lagerstroemia* produce two types of anthers, i.e. large ones on the long stamens (antisepalous) and small ones on the shorter stamens (antipetalous). The coarse grains mainly correspond to those from short stamens, while the fine grains are produced by the anthers of long stamens (Fujiki et al., 2001). Since the Chinese fossil pollen grains have a coarse sculpture, it appears likely that they represent grains from short stamens.

Pollen grains of the genus *Decodon* (Lythraceae), which is now restricted to eastern North America but had a widespread distribution throughout the Northern Hemisphere (including high latitudinal areas of East Asia) in the Cenozoic (Ferguson et al., 1997; Matsumoto et al., 1997), display a close resemblance to those of *Lagerstroemia* under SEM and LM. As a result, the two genera have sometimes been confused (e.g. Menke, 1976). The pollen grains of *Decodon* are distinguished from those of *Lagerstroemia* by their dumbbell-shaped colpi.

→

Figure 5. **A–K**. *Lagerstroemia limii*. **A–E**. LM overview of pollen grains. **A**, **B**. Equatorial view (pollen grain of antepetalous stamen). **C**, **D**. Polar view (pollen grain of antepetalous stamen). **E**. Equatorial view (pollen grain of antesepalous stamen). **F–K**. SEM micrographs. **F–H**. Equatorial view (pollen grains of antepetalous stamen). **I**. Equatorial view (pollen grain of antesepalous stamen). **J**, **K**. Details of exine sculpture in the area of the mesocolpial ridge and the mesocolpium (rugulate, foveolate) (pollen grain of antepetalous stamen). **L–T**. *Lagerstroemia subcostata*. **L–O**. LM overview of pollen grains. **L**, **M**. Equatorial view (pollen grains of antepetalous stamen). **N**. Polar view (pollen grain of antepetalous stamen). **O**. Equatorial view (pollen grain of antesepalous stamen). **P–T**. SEM micrographs. **P**. Equatorial view (pollen grain of antepetalous stamen). **Q**. Equatorial view (pollen grain of antesepalous stamen). **R**, **T**. Details of the mesocolpial ridge and the mesocolpium (rugulate, foveolate) (pollen grain of antepetalous stamen). **S**. Detail of the mesocolpial ridge and the mesocolpium (pollen grain of antesepalous stamen). Scale bars −10 μm (A–I, L–Q); 1 μm (J, K, R–T).



Fossil leaves attributable to *Lagerstroemia* also occur in the stratum from which the pollen was extracted (S.-X. Guo, pers. comm.). This provides circumstantial evidence in support of the identification.

## Paleoecological significance

*Lagerstroemia* prefers a subtropical or warm-temperate climate (Graham, 2007) and cannot survive cold winters (Qin et al., 2007). If its ecological requirements have not changed through time, the Miocene site in Zhejiang of eastern China must have experienced mild, wet winters like those of today. The fossil pollen species resembles two modern species (*L. subcostata* and *L. limii*), which are found to occur in Zhejiang Province and other places in southern China, southern Japan, India and the Philippines. *Lagerstroemia subcostata* grows along forest margins and streamsides and occurs at low to medium elevations, while *L. limii* is found in mixed forests at low altitudes (Qin et al., 2007). These subtropical species confirm the paleoclimatic interpretation reached by Liu et al. (2007) based on the presence of abundant evergreen *Quercus*. This would suggest that the environmental conditions at the fossil site in the Miocene of eastern China are similar to those of today.

## Conclusions

The present study reports a new species of *Lagerstroemia* from the Miocene of eastern China, based on well-preserved pollen grains. This represents the first record of microfossils in *Lagerstroemia*, confirmed by scanning electron microscopy, and therefore represents an important contribution to historical biogeography. Two recent species from Southeast Asia, *L. subcostata* Koehne and *L. limii* Merrill, are closely comparable with the fossil.

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