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Pollen atlas for selected subfamilies of Euphorbiaceae from Southern China: a complementary contribution to Quaternary pollen analysis

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ABSTRACT

In this paper we examine pollen types from four representative subfamilies of Euphorbiaceae in southern China, including 34 species (21 genera) of Crotonoideae, Euphorbioideae, Acalyphoideae and Phyllanthoideae. The morphology of the investigated species is described and illustrated with high-resolution photographs observed by transmitted light microscope. These descriptions and illustrations are presented at the species level, and pollen types and identifying features are also noted. This study is a complementary contribution to Quaternary pollen analysis, and should aid in the identification of pollen types assigned to Euphorbiaceae, especially in Southern China, as well as elsewhere in the tropical and subtropical regions of East Asia.

KEYWORDS

pollen morphology; comparative characteristics; Crotonoideae; Euphorbioideae; Acalyphoideae; Phyllanthoideae

1. Introduction

As one of the largest and most diversified families of angiosperms, the Euphorbiaceae has about 8000 species in over 300 genera (Webster 1975, 1987, 1994a, 1994b; Radcliffe-Smith 2001). Jensen et al. (1994) suggested that on the basis of serological data there appear to be two main groups of Euphorbiaceae: Phyllanthoideae and Oldfieldioideae (Picrodendraceae); and Acalyphoideae, Crotonoideae and Euphorbioideae. However, molecular phylogenetic analysis assessed the systematic position of Picrodendraceae based on a comparative study of floral structure of the recently established family Picrodendraceae (part of Euphorbiaceae *sensu lato*) in Malpighiales (Sutter et al. 2006); and Wurdack et al. (2004) analysed plastid rbcL DNA sequence data of the pantropical family Phyllanthaceae (Malpighiales) and related biovulate lineages of Euphorbiaceae *sensu lato*. These phylogenic works suggest the dismemberment of Phyllanthoideae, considering a family other than Euphorbiaceae or Phyllanthaceae (Radcliffe-Smith 2001; APG 2016). The classification of Euphorbiaceae *sensu lato* has a long history (e.g. Webster 1975, 1994a, 1994b; Jensen et al. 1994; Radcliffe-Smith 2001; APG 2003, 2009, 2016), which is complicated beyond the scope of this paper. In this study, we follow the most fundamental division in Euphorbiaceae *sensu lato* with a grouping of two biovulate subfamilies (Phyllanthoideae and Oldfieldioideae) and three uniovulate ones (Acalyphoideae, Crotonoideae and Euphorbioideae) (Webster 1975, 1987, 1994a, 1994b).

The Euphorbiaceae *sensu lato* includes great diversity in growth form, from tall rain forest trees to lianas, shrubs, perennial and annual herbs, geophytes, succulents and floating aquatics (Webster 1987). *Euphorbia*, for example – one of the largest genera in the subfamily Euphorbioideae – has around 2000 species from tiny annual plants to large and long-lived trees, and their geographical distribution is cosmopolitan and largely in tropical and subtropical regions. So, palaeoecological interpretation based on pollen records of Euphorbiaceae is a significant challenge, and improving pollen identification is an effective way to refine pollen signals from a palaeoecological point of view. However, pollen types of Euphorbiaceae show high diversity according to previous studies; for example, early investigations of *Phyllanthus* (Phyllanthoideae) show much variation in pollen types based on a large collection of specimens from worldwide reported by Punt (1967, 1972, 1980, 1987) and Meewis and Punt (1983); and later the pollen morphology and taxonomy of the *Phyllanthus* species native to New Caledonia were studied by Loberau-Callen et al. (1988). Webster and Carpenter (2002) examined pollen morphology and provided new insights into phylogenetic relationships among the neotropical taxa of *Phyllanthus*. Moreover, Santiago et al. (2004) examined eight South American species of the genus *Phyllanthus*, subgenus *Phyllanthus*, section *Choretropsis*, endemic to Brazil. Chen et al. (2009) carried out a palynological study of Malesian *Phyllanthus*, and recently Wu et al. (2016) investigated the pollen morphology of 89 of the 127 Malesian *Phyllanthus* species, presented a pollen key for the

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pollen classes and types, and discussed evolutionary trends in pollen morphology and infrageneric classification in *Phyllanthus*. Yao and Zhang (2016) examined the pollen morphology of Chinese *Glochidion* (Phyllanthaceae), and its taxonomic implications. El-Ghazaly and Chaudhary (1993) distinguished seven pollen types, with a detailed diagnosis of each type based on the pollen morphology of 60 species from *Euphorbia*, and discussed the geographical distribution of the types, as well as putative evolutionary relationships between them. Park (1997) re-evaluated a sectional boundary and previous taxonomic treatments, based on pollen morphology of *Euphorbia* (Euphorbioideae), section *Tithymalopsis*, and related species. Pollen morphology, exine structure and systematics of the subfamily Acalyphoideae have been intensively investigated in many representative tribes (Nowicke et al. 1998, 1999; Takahashi et al. 2000; Nowicke and Takahashi 2002). Sagun et al. (2006) reported on the pollen morphology and ultrastructure of *Acalypha* (Acalyphoideae), and evaluated pollen exine structure variation, phylogeny and evolutionary trends. de Souza et al. (2017) found the pollen morphological characteristics more variable in the Acalyphoideae compared to the relatively homogeneous Euphorbioideae, according to their selected species from the Caatinga ecoregion in Brazil. Sagun and van der Ham (2003) investigated the pollen morphology of the Flueggeinae (a subtribe of Phyllantheae) and evaluated the relationships between the eight constituent genera. An early study by Lobreau-Callen and Cervera (1997) focused on pollen exine ultrastructure of the apetalous Crotonoideae, with five tribes and one subtribe. High diversity in pollen morphology of the subfamily Crotonoideae from north-eastern Brazil has been documented, and three pollen types and seven subtypes were recognised based on aperture type, polarity, shape, size and details of exine sculpture (de Souza et al. 2016). A new investigation by Yu et al. (2018) on the pollen of *Trigonostemon* and the related genera *Dimorphocalyx*, *Ostodes*, *Tritaxis* and *Jatropha* (outgroup) shows that the two major pollen types within *Trigonostemon* correlate well with macromorphological characters, and species belonging to the *Trigonostemon reidioides* type have pollen with '*Croton* pattern' ornamentation (Yu et al. 2018).

Most of these previous studies on Euphorbiaceae pollen morphology mainly focused on taxonomic and evolutionary significance; however, the distinguishing features of Euphorbiaceae remain poorly documented regarding an identification guide or pollen atlas for Quaternary palynology. An illustrated and descriptive atlas of pollen, particularly for those families (such as Euphorbiaceae) with a high diversity of pollen types, is an indispensable reference for Quaternary pollen analysis and palaeoecological interpretation. As useful references for Quaternary pollen identification, many pollen atlases from different parts of the world were published before 1998, as listed by Hooghiemstra and Van Geel (1998), followed by many new pollen atlases published since 2000 (so far, no new world pollen atlas has been published since 1998). In China, there are 67 genera of Euphorbiaceae with some 406 species (Editorial Committee of Flora of China 1994); however, only a limited number of pollen types of Euphorbiaceae have been examined so far as an indispensable reference to Quaternary palynological studies (e.g. Huang 1972; IBCAS 1982; Wang et al. 1995; Wei 2003). Considering diverse pollen types of Euphorbiaceae frequently occur in Quaternary sediments, especially from southern China, it is necessary to investigate more pollen types covering representative subfamilies of Euphorbiaceae. In this paper, we present pollen descriptions and transmitted light photographs for 34 species from 21 genera of four subfamilies (Acalyphoideae, Crotonoideae, Euphorbioideae, Phyllanthoideae) from southern China. This study is a complementary contribution to Quaternary pollen analysis, and our results should aid Quaternary pollen identification and subsequent interpretation of past vegetation history and palaeoecology based on fossil pollen data.

2. Material and methods

To examine pollen morphological characters, pollen grains of 34 plant species belonging to 21 genera were extracted from specimens collected from the Herbarium of Sun Yat-sen University (SYSU) and Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). All pollen specimens were collected from South China (Figure 1). The samples were prepared in the Quaternary Environmental Laboratory of SYSU and NIGPAS, and a list of voucher specimens used in this study as well as notes on the pollen plates are summarised in Table 1. Slides were prepared by mounting the pollen grains in glycerine jelly after acetolysis (treatment with an acetolytic mixture of nine parts acetic anhydride and one part sulphuric acid). All pollen grains were observed and photographed in both polar and equatorial views at a magnification of ×600 or ×1000 using

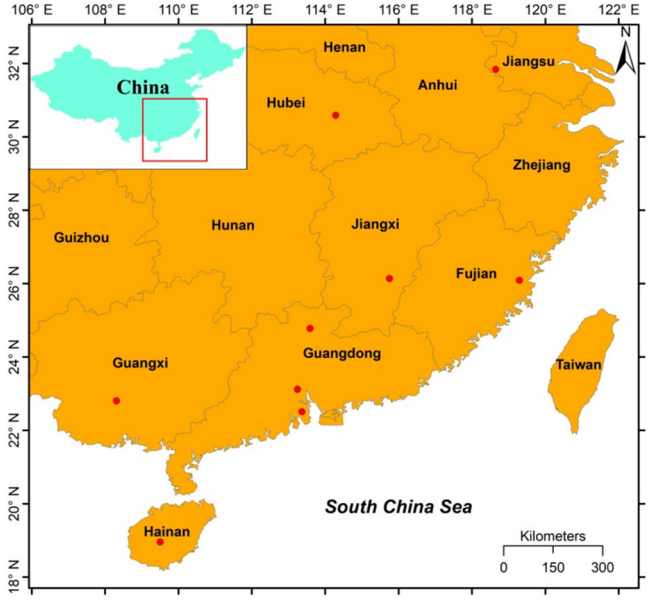

Figure 1. Map showing the localities (dots) of the pollen specimens collected from South China (for detailed information, see Table 1). Modified from original downloaded map from http://srtm.csi.cgiar.org/ (@CGIAR - Consortium for Spatial Information).

Table 1. List of pollen species examined in this study,[a] with voucher information and plate numbers if illustrated here.

Subfamily	Genus	Species	Life form	Locality	Voucher	Morphological key	Plate
Crotonoideae	*Aleurites*	*Aleurites moluccanus*	Tree	Guangzhou	YZ487, Yang	Inaperturate	Plate 1, figures 1–2
	Croton	*Croton tiglium*	Small tree or shrub	Hainan	YZ137, Yang		Plate 1, figures 5–6
		C. lachnocarpus	Shrub	Jiangxi	YZ772, Yang		Plate 1, figures 7–8
	Vernicia	*Vernicia fordii*	Tree	Nanjing	VF2018, Mao		Plate 1, figures 3–4, 4a
	Jatropha	*Jatropha curcas*	Small tree or shrub	Hainan	YZ783, Yang		Plate 1, figures 11–12
	Codiaeum	*Codiaeum variegatum*	Small tree or shrub	Guangzhou	YZ485, Yang		Plate 1, figures 9–10
Euphorbioideae	*Sapium*	*Sapium sebiferum*	Tree	Nanjing	SS 2011, Mao	Tricolporate	Plate 3, figures 1–3, 3a
	Euphorbia	*Euphorbia characias*[b]	Semishrub or herb	France	YZ777, Yang		Plate 2, figures 1–4
		Euphorbia heterophylla	Shrub	Guangzhou	YZ778, Yang		Plate 2, figures 5–8
		E. milii	Small shrub	Shaoguan	YZ377, Yang		Plate 2, figures 9–12
	Excoecaria	*E. formosana*	Shrub	Guangxi	YZ789, Yang		Plate 3, figures 4–5
Acalyphoideae	*Mallotus*	*Mallotus apelta*	Small tree or shrub	Guangzhou	YZ793, Yang		Plate 3, figures 6–9
		M. japonicus	Small tree or shrub	Fujian	YZ56, Yang		Plate 3, figures 10–13
		M. paniculatus	Small tree	Fujian	YZ48, Yang		Plate 3, figures 14–17
	Macaranga	*Macaranga denticulata*	Tree	Guangzhou	YZ170, Yang		Plate 3, figures 18–21
	Alchornea	*Alchornea trewioides*	Small tree or shrub	Guangzhou	YZ358, Yang		Plate 4, figures 1–4
	Cleidion	*Cleidion brevipetiolatum*	Small tree	Hainan	YZ773, Yang		Plate 3, figures 22–25
	Acalypha	*Acalypha hispida*	Shrub	Guangzhou	YZ780, Yang		Plate 4, figures 5–9
	Ricinus	*Ricinus communis*	Small tree or shrub	Guangzhou	YZ775, Yang		Plate 4, figure 10–14
Phyllanthoideae	*Phyllanthus*	*Phyllanthus embilica*	Small tree or shrub	Shenzhen	YZ445, Yang	Stephanocolporate	Plate 4, figures 23–24; Plate 5, figures 1–3
		P. flexuosus	Shrub	Guangxi	YZ795, Yang	Tricolporate	Plate 5, figures 4–7
		P. rheophyticus	Shrub	Hainan	YZ796, Yang	Tetracolporate	Plate 5, figures 8–11
	Glochidion	*Glochidion puberum*	Shrub	Hunan	YZ787, Yang	Tricolporate	Plate 5, figures 18–21
		G. wilsonii	Shrub	Hubei	YZ788, Yang	Tetracolporate	Plate 5, figures 22–25
		G. lanceolarium	Tree or shrub	Hainan	YZ786, Yang		Plate 6, figures 1–4
		G. zeylanicum	Small tree or shrub	Shenzhen	YZ400, Yang		Plate 6, figures 5–8
	Flueggea	*Flueggea virosa*	Shrub	Hainan	YZ384, Yang	Tricolporate	Plate 5, figures 12–15
		F. suffruticosa	Shrub	Hunan	YZ797, Yang		Plate 5, figures 16–17
	Aporosa	*Aporosa yunnanensis*	Small tree or shrub	Shenzhen	YZ433, Yang		Plate 4, figures 15–18
		A. chinensis	Small tree or shrub	Guangzhou	YZ102, Yang	Tricolporate or tetracolporate	Plate 4, figures 19–22
	Baccaurea	*Baccaurea ramiflora*	Tree	Hainan	YZ784, Yang		Plate 6, figures 9–12
	Bridelia	*Bridelia tomentosa*	Small tree or shrub	Hainan	YZ790, Yang	Tricolporate	Plate 6, figures 13–17
		B. balansae	Tree	Hunan	YZ1584, Yang		Plate 6, figures 18–22
	Antidesma	*Antidesma japonicum*	Tree or shrub	Guangdong	YZ792, Yang		Plate 6, figures 23–26

[a]Pollen specimens (32 species) are kept at the Quaternary Environmental Laboratory, School of Earth Science and Geological Engineering, Sun Yat-sen University, and two specimens (VF2018, SS2011) are kept at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), unless otherwise noted.
[b]Species introduced from France since the 1990s, a subspecies *Euphorbia characias wulfenii* (*not subsp.*) (Hoppe ex W.D.J.Koch) Radcl.-Sm.

a Nikon E200 microscope equipped with a COOLSNAP 5.0 camera, and an Olympus BX51 microscope equipped with a DP72 Charge Coupled Device (CCD) camera. The pollen dimensions obtained and mentioned in the description of each species are the average of measurements of at least 20 pollen grains. Pollen terms used in our descriptions are standard (for definitions, see Kremp 1965; Punt et al. 2007; Hesse et al. 2009).

3. Descriptions of pollen morphology

3.1. Crotonoideae

Five genera were investigated in the subfamily Crotonoideae, including *Aleurites* J. R. et G. Forst., *Vernicia* Lour., *Croton* Linn., *Codiaeum* A. Juss. and *Jatropha* Linn. Six species of these genera are examined for pollen description, namely *Aleurites moluccanus* (L.) Willd, *Vernicia fordii* (Hemsl.) Airy-Shaw, *Croton tiglium* Linn., *C. lachnocarpus* Benth., *Codiaeum variegatum* (L.) Rumph. ex A. Juss. and *Jatropha curcas* Linn.

Aleurites J.R. & G. Forst.
Aleurites moluccanus (L.) Willd

Plate 1, figures 1, 2

Pollen grains spheroidal, inaperturate, 50 (55) 70 μm in diameter; sexine thicker than nexine, sculpture presents a pattern covered by triangular prism baculate processes, clavae with acute ends, a set of (4)-5-7-(-8) triangular verrucae forms a visible circle and radiated pattern, but some circles not clear.

Vernicia Lour.
Vernicia fordii (Hemsl.) Airy-Shaw

Plate 1, figures 3, 4, 4a)

Pollen grains spheroidal, inaperturate, 55 (66.5) 75 μm in diameter; sexine thicker than nexine, sculpture coarsely reticulate (Plate 1, figures 3, 4a); muri with verrucae forming triangular prism shape (Plate 1, figure 4); the triangular prism was formed by three protuberances. As the focus moves downwards, the verrucae appeared to join into muri. A set of 5–8 verrucae form a visible circle.

Croton Linn.
Croton tiglium Linn.

Plate 1, figures 5, 6

Pollen grains spheroidal, inaperturate, 27 (30.5) 47 μm in diameter; sexine thicker than nexine, sculpture coarsely reticulate, muri with bead-like grains, usually 6–7 such grains arranged in a circle, and linked at the base of the exine (Yang et al. 2015).

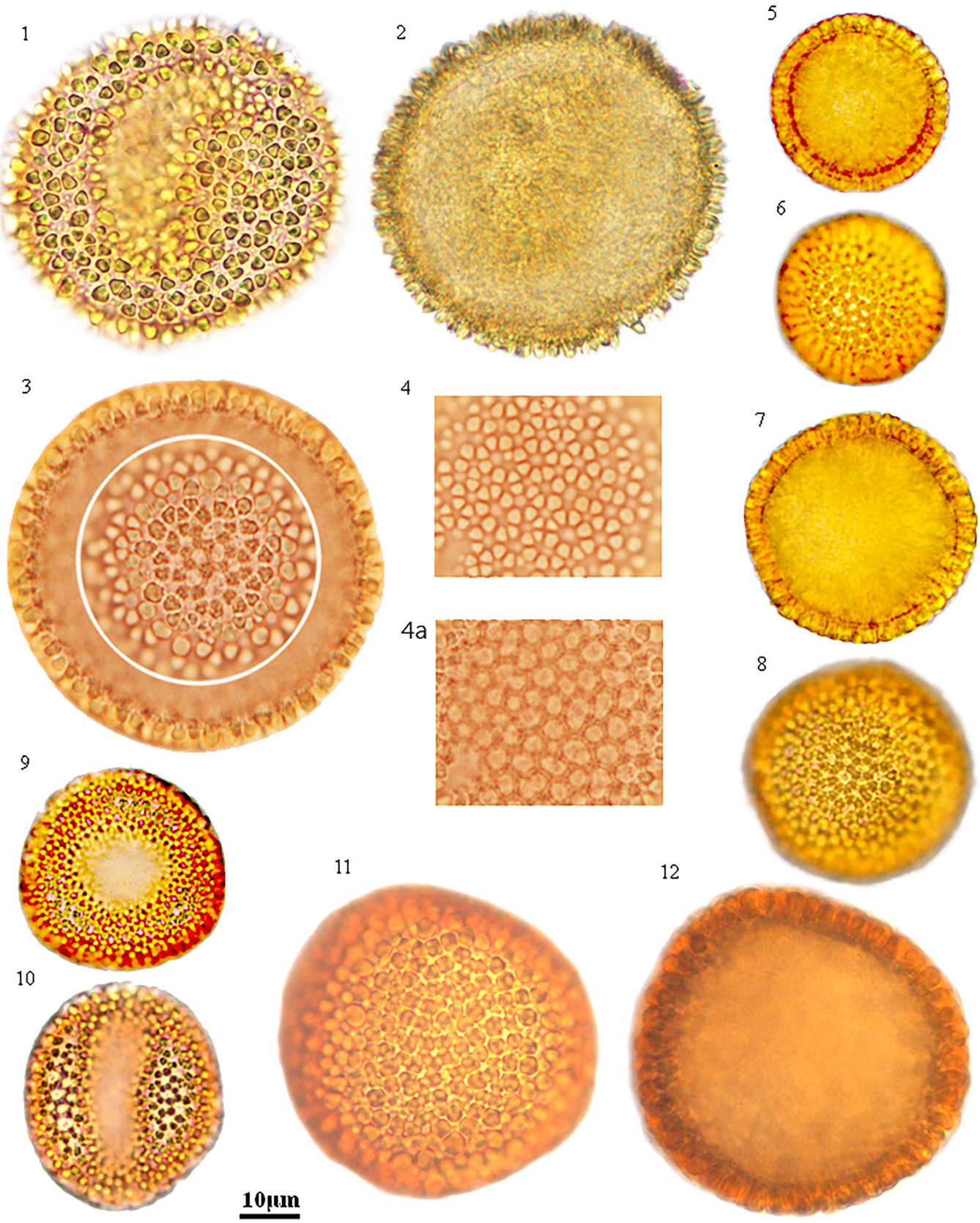

Plate 1. Light microscopic photographs of some species of the subfamily Crotonoideae. 1–2, *Aleurites moluccanus*; 3–4,4a, *Vernicia fordii* (3, a combined photo showing optical section and sculpture pattern; 4, upper focus showing verrucae sculpture; 4a, low focus showing coarsely reticulate pattern); 5–6, *Croton tiglium*; 7–8, *Croton lachnocarpus*; 9–10, *Codiaeum variegatum*; 11–12, *Jatropha curcas*.

Croton lachnocarpus Benth.

Plate 1, figures 7, 8

Pollen grains spheroidal, inaperturate, 30 (38) 47 μm in diameter, sculpture coarsely reticulate. The exine ornamentation resembles that of *C. tiglium* except in size.

Codiaeum A. Juss.
Codiaeum variegatum (L.) Rumph. ex A. Juss.

Plate 1, figures 9, 10

Pollen grains ellipsoidal, subcircular in polar view, inaperturate, 30 (34.5) 40 × 35 (38) 43 μm in diameter, sculpture with different sizes of strumae, 5–7 verrucae arranged in a circle and formed coarse reticulum, verrucae smaller than those of *Croton* and *Vernicia*, similar to coarse granule; exine ca. 2–3 μm thick with a wavy contour.

Jatropha Linn.
Jatropha curcas Linn.

Plate 1, figures 11, 12

Pollen grains subspheroidal, inaperturate, 50 (55) 75 μm in diameter, exine ca. 5 μm thick, sculpture verrucate, the protruding verrucae irregular in size and shape, relatively larger than those of its close relatives; each verruca has 4–6 bead-like structures; pollen wall with clearly clavate columellae, with indistinct stratification (Yang et al. 2015).

3.2. Euphorbioideae

In this subfamily, five representative species of three genera are examined for pollen description: *Euphorbia characias* subsp. *wulfenii* (Hoppe ex W.D.J.Koch) Radcl.-Sm., *E. heterophylla* Linn., *E. milii* Des Moul., *Sapium sebiferum* (L.) Roxb., *Excoecaria formosana* (Hayata) Hayata & Kawak, from *Euphorbia* Linn., *Sapium* Jacq., and *Excoecaria* Linn., respectively.

Euphorbia Linn.
Euphorbia characias subsp. *wulfenii* (Hoppe ex W.D.J.Koch) Radcl.-Sm.

Plate 2, figures 1–4

Pollen grains oblate spheroidal, subcircular in polar view, 50 (52) 54 × 48 (50) 52 μm in diameter, tricolporate, colpus slender and long, pore ellipsoidal and lolongate, ca. 12 μm, sexine thicker than nexine, exine gradually thinner around pores, exine ca. 3 μm thick, sculpture reticulate but appears finely granulate as the focus moves downwards.

Euphorbia heterophylla Murray

Plate 2, figures 5–8

Pollen grains oblate spheroidal, subcircular in polar view, 50 (53) 54 × 46 (47) 50 μm in diameter, tricolporate, colpus slender and long, pore lolongate and ellipsoidal, ca. (12 × 8) μm, exine ca. 5-6 μm thick, sculpture coarsely reticulate, texture coarsely granulate forming spines, contour fluctuating and not psilate.

Euphorbia milii Des Moul.

Plate 2, figures 9–12

Pollen grains prolate, trilobed circular in polar view, 35 (38) 40 × 38 (40) 44 μm in diameter, tricolporate, colpus slender and long, exine ca. 3 μm, exine around pore slightly thickened to 4–5 μm, sculpture finely reticulate, muri finely granulate.

Sapium Linn.
Sapium sebiferum (L.) Roxb.

Plate 3, figures 1–3, 3a

Pollen grains prolate, trilobed circular in polar view, 30 (35) 45 × 34 (40) 46 μm in diameter, tricolporate, colpus wide at the poles and constricted in the middle, pore lalongate and ellipsoidal, ca. 5 × 11 μm in diameter, sculpture mimics reticulate pattern, muri with fine granulate ornamentation.

Excoecaria Linn.
Excoecaria formosana (Hayata) Hayata & Kawak

Plate 3, figures 4, 5

Pollen grains subprolate, subcircular in polar view, 50 (52) 54 × 59 (50) 53 μm in diameter, tricolporate, colpus slender and long, pore circular, nexine and sexine similar in thickness, sexine with pilum, sculpture granulate-reticulate, contour of optical section irregular.

3.3. Acalyphoideae

Six genera are selected in the subfamily Acalyphoideae: *Mallotus* Lour., *Macaranga* Thou., *Alchornea* Sw., *Cleidion* Bl., *Acalypha* Linn. and *Ricinus* Linn. Eight species of these genera are investigated for pollen description, namely *Mallotus apelta* (Lour.) Müll. Arg., *M. japonicus* (Thunb.) Müll. Arg., *M. paniculatus* (Lam.) Müll. Arg., *Macaranga denticulata* (Blume) Müll. Arg., *Alchornea trewioides* (Benth.) Müll. Arg., *Cleidion brevipetiolatum* Pax & K. Hoffm., *Acalypha hispida* Burm.f. and *Ricinus communis* Linn.

Mallotus Lour.
Mallotus apelta (Lour.) Müll. Arg.

Plate 3, figures 6–9

Pollen grains spheroidal, subcircular in polar view, 22 (22) 28 × 24 (24) 30 μm in diameter, tricolporate, colpus slender and short, pore wide and lalongate, sexine and nexine similar in thickness but thicker around aperture, ca. 2 μm, sculpture coarsely granulate.

Mallotus japonicus (Thunb.) Müll. Arg.

Plate 3, figures 10–13

Pollen grains 22 (22) 28 × 24 (26) 30 μm, morphological characteristics similar to those of *M. apelta*.

Mallotus paniculatus (Lam.) Müll. Arg.

Plate 3, figures 14–17

Pollen grains 16 (18) 20 × 16 (18) 20 μm in diameter, Morphological characteristics similar to those of the above species except in size.

Macaranga Thou.
Macaranga denticulata (Blume) Müll. Arg.
Plate 3, figures 18–21

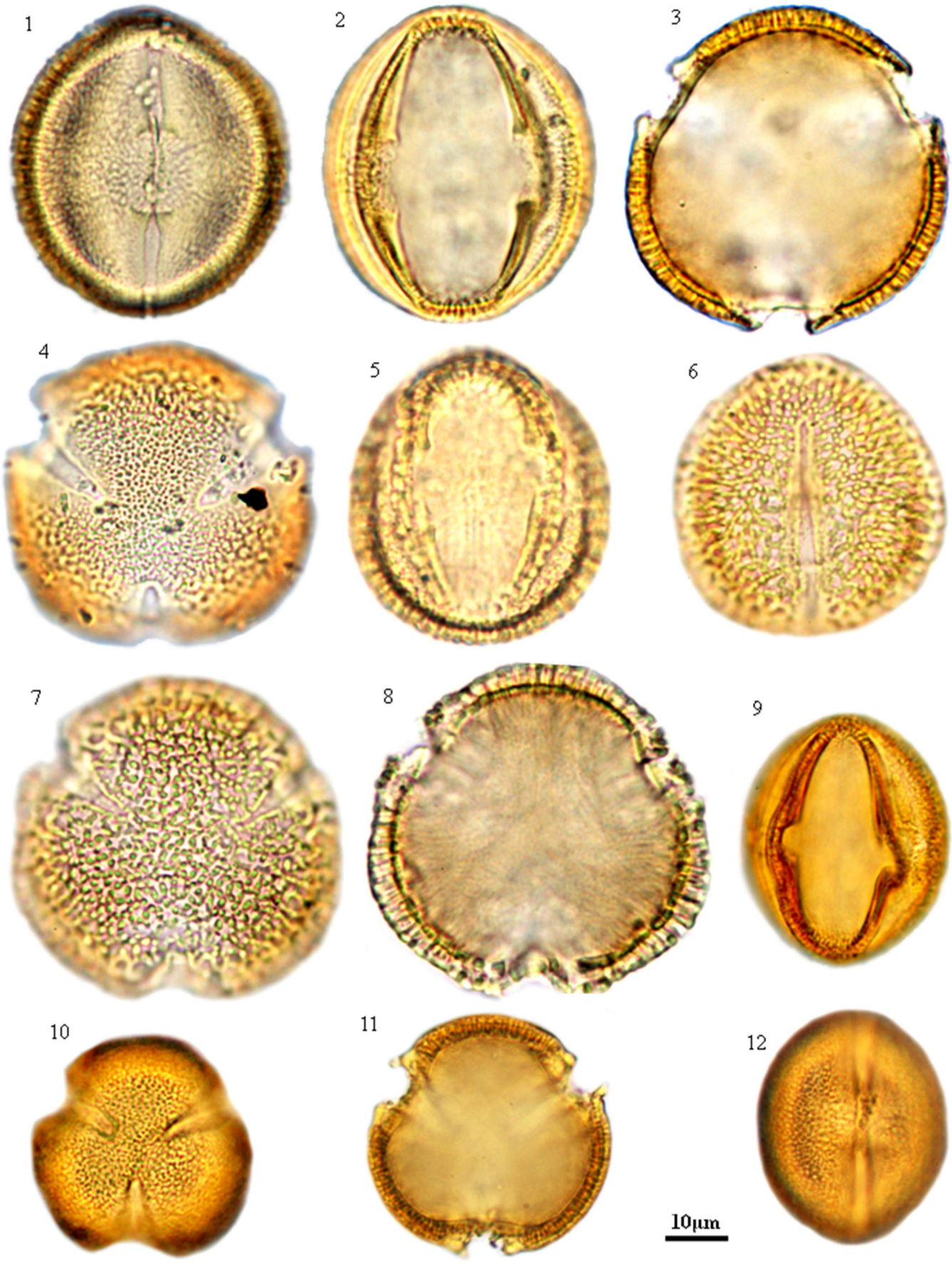

Plate 2. Light microscopic photographs of some species of Euphorbioideae. 1–4, *Euphorbia characias* subsp. wulfenii; 5–8, *Euphorbia heterophylla*; 9–12, *Euphorbia milii*.

Plate 3. Light microscopic photographs of some species of Euphorbioideae and Acalyphoideae. 1–3, 3a, *Sapium sebiferum*; 4–5, *Excoecaria formosana*; 6–9, *Mallotus apelta*; 10–13, *Mallotus japonicus*; 14–17, *Mallotus paniculatus*; 18–21, *Macaranga denticulata*; 22–25, *Cleidion brevipetiolatum*.

Pollen grains spheroidal, subcircular in polar view, 13 (17) 19 × 15 (18) 20 μm in diameter; tricolporate, colpi slender and short, pore lalongate; exine ca. 1.5–3 μm thick, sexine and nexine similar in thickness but thicker around aperture, sculpture finely reticulate, different from that of *Mallotus* (Yang et al. 2015).

Cleidion Bl.

Cleidion brevipetiolatum Pax & K. Hoffm.

Plate 3, figures 22–25

Pollen grains oblate spheroidal, trilobed circular in polar view, 16 (17) 20 × 16 (18) 21 μm in diameter, tricolporate, colpus slender and short, pore lalongate, sexine thicker than nexine, nexine thicker around aperture, sculpture faintly coarsely granulate.

Alchornea Sw.

Alchornea trewioides (Benth.) Müll. Arg.

Plate 4, figures 1–4

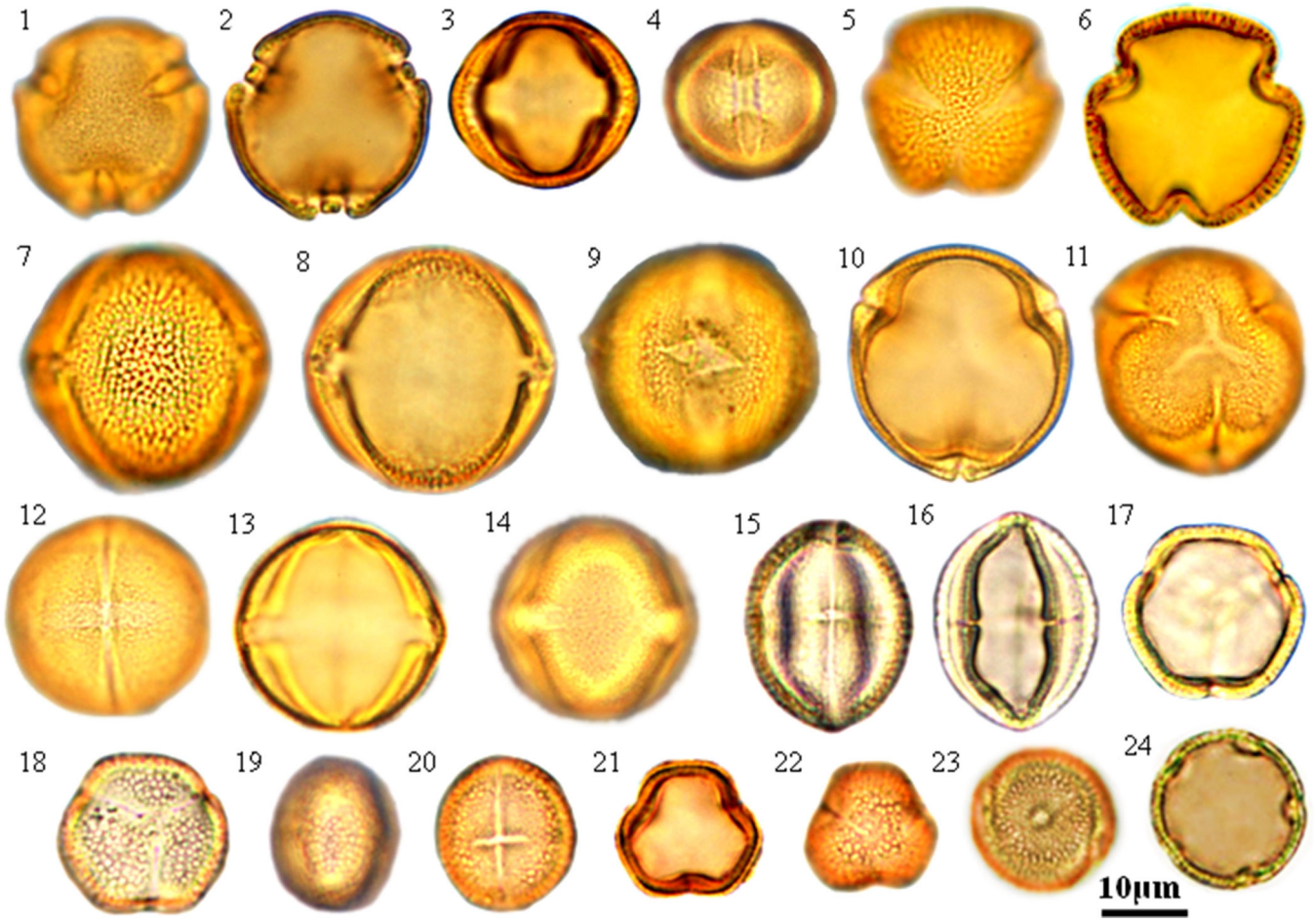

Plate 4. Light microscopic photographs of some species of Acalyphoideae and Phyllanthoideae. 1–4, *Alchornea trewioides*; 5–9, *Acalypha hispida*; 10–14, *Ricinus communis*; 15–18, *Aporusa yunnanensis*; 19–22, *Aporosa chinensis*; 23–24, *Phyllanthus embilica* (also see Plate 5, figures 1–3).

Pollen grains spheroidal, semi-circular in polar view, 13 (21) 25 × 17 (22) 27 μm in diameter, tricolporate, colpi with colpus membrane, colpus membrane edge sags, with ligulate protrusions in polar view, pore lalongate, sculpture unclearly granulate or mimic reticulate and more coarsely granulate around colpus and aperture.

Acalypha Linn.
Acalypha hispida Burm.f.

Plate 4, figures 5–9

Pollen grains spheroidal, trilobed circular in polar view, 24 (26) 28 × 25 (25) 33 μm in diameter, tricolporate, colpus wide but narrowing to the poles, pore rhombic, exine and nexine similar in thickness, sculpture reticulate, muri with pilum and stripe array ornamentation.

Ricinus Linn.
Ricinus communis Linn.

Plate 4, figures 10–14

Pollen grains spheroidal, semi-circular in polar view, 23 (25) 27 × 24 (27) 31 μm in diameter, tricolporate, colpi long and almost extending to the poles, colpus slender and narrow at ends, pore lalongate and rectangle, exine protruding around pore, sculpture faint reticulate, lumina irregular in shape and size, exine ca. 2–2.5 μm thick.

3.4. Phyllanthoideae

In this subfamily, seven genera (*Phyllanthus* Linn., *Glochidion* T.R. & G. Forst., nom. cons., *Flueggea* Willd., *Aporosa* Bl., *Baccaurea* Lour., *Bridelia* Willd. and *Antidesma* Linn.) with 15 representative species are observed for pollen description: *Phyllanthus embilica* Linn., *P. flexuosus* (Siebold & Zucc.) Müll. Arg., *P. rheophyticus* Gilbert & Li, *Glochidion puberum* (L.) Hutch., *G. wilsonii* Hutch, *G. lanceolarium* (Roxb.) Voigt, *G. zeylanicum* (Gaertn.) A. Juss., *Flueggea virosa* (Roxb. ex Willd.) Royle, *F. suffruticosa* (Pall.) Baill., *Aporosa yunnanensis* (Pax & K. Hoffm.) F.P. Metcalf, *A. chinensis* (Roxb. Ex Benth.) Merr., *Baccaurea ramiflora* Lour., *Bridelia tomentosa* Bl., *B. balansae* Tutcher, *Antidesma japonicum* Siebold & Zucc.

Aporosa Bl.
Aporosa yunnanensis (Pax & K. Hoffm.) F.P. Metcalf

Plate 4, figures 15–18

Pollen grains subprolate, semi-circular in view polar, 15 (17) 20 × 16 (18) 22 μm in diameter, tricolporate, colpus slender and long extending almost to the poles, pore lalongate, nexine around pore slightly thickened, sculpture reticulate, lumia regular in size and shape, but slightly smaller towards edge of colpus.

Aporosa chinensis (Roxb.) Müll. Arg.

Plate 4, figures 19–22

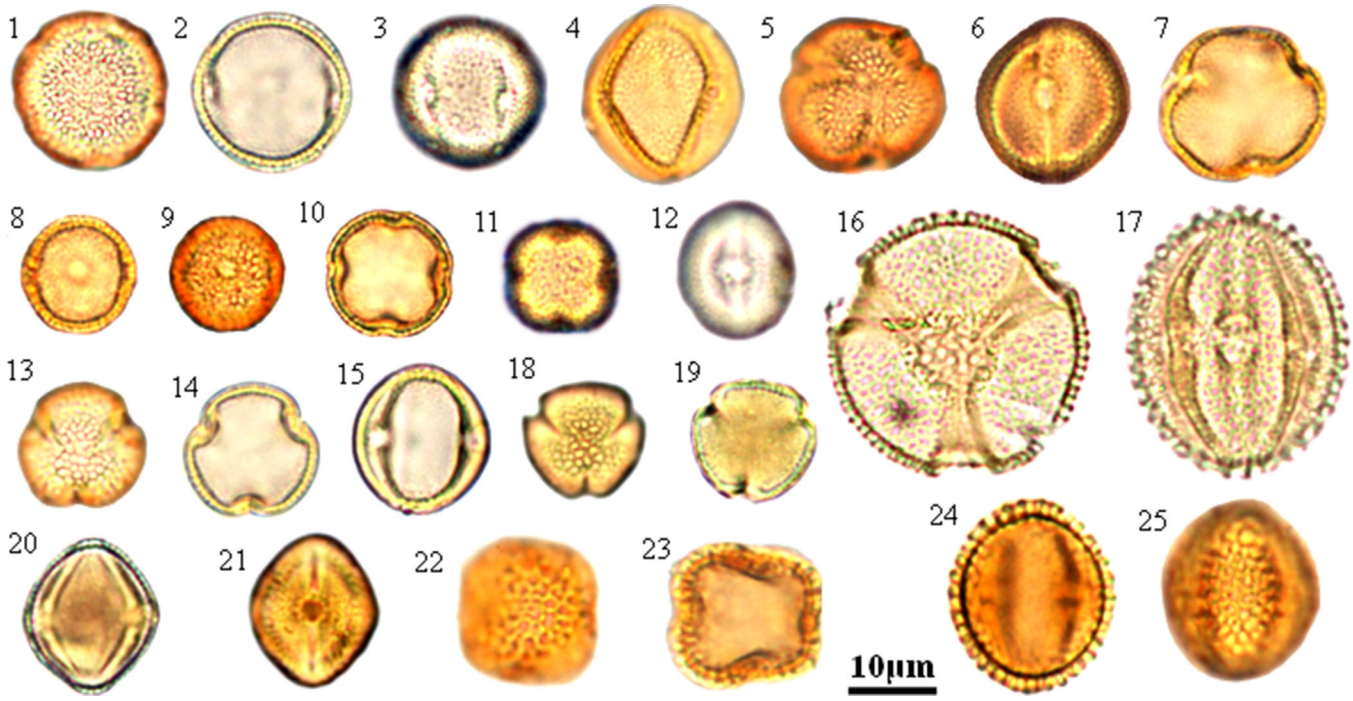

Plate 5. Light microscopic photographs of some species of Phyllanthoideae. 1–3, *Phyllanthus embilica* (also see Plate 4, figures 23–24); 4–7, *Phyllanthus flexuosus*; 8–11, *Phyllanthus rheophyticus*; 12–15, *Flueggea virosa*; 16–17, *Flueggea suffruticosa*; 18–21, *Glochidion puberum*; 22–25, *Glochidion wilsonii*.

Pollen grains 15 (17) 20 × 16 (18) 22 μm in diameter, Morphological characteristics similar to those of *A. yunnanensis* except in size.

Phyllanthus Linn.

Phyllanthus embilica Linn.

Plate 4, figures 23–24; Plate 5, figures 1–3

Pollen grains spherical, 4–6-lobate circular in polar view, 18 (19) 23 × 17 (18) 19 μm in diameter, 5-colporate dominant, rarely 4- or 6-colporate, colpus short, pore circular, 1.5–2 μm × 2–3 μm, sculpture finely reticulate.

Phyllanthus flexuosus (Siebold & Zucc.) Müll. Arg.

Plate 5, figures 4–7

Pollen grains spheroidal, trilobed circular in polar view, 18 (20) 23 × 17 (18) 19 μm in diameter, tricolporate, colpus slender and long, pore circular, sculpture finely reticulate.

Phyllanthus rheophyticus Gilbert & Li

Plate 5, figures 8–11

Pollen grains spheroidal, 4-lobed circular in polar view, 12 (15) 20 × 11 (13.5) 19 μm in diameter. Pollen grains normally 4-colporate, a few penta-colporate; colpus slender and short, pore circular; exine ca. 1 μm thick, sexine and nexine similar in thickness; nexine around pore slightly thickened, sculpture finely reticulate, morphological characteristics similar to those of *P. embilca* except pore number and size.

Flueggea Willd.

Flueggea virosa (Roxb. ex Willd.) Royle

Plate 5, figures 12–15

Pollen grains subprolate, trilobed circular in polar view, 13 (17) 22 × 11 (15.5) 18 μm in diameter, tricolporate, colpus slender and long, pore circular, ca. 2.5–3.5 μm in diameter, exine two layered, ca. 1–1.5 μm in thickness, sculpture clearly reticulate, lumina regular.

Flueggea suffruticosa (Pall.) Baill.

Plate 5, figures 16, 17

Pollen grains subprolate, trilobed circular in polar view, 28 (30) 32 × 28 (30.5) 32 μm in diameter, tricolporate, colpus slender and long, pore lalongate, sexine thicker than nexine, sculpture reticulate, lumina reticulate and irregular.

Glochidion T.R. & G. Forst., nom. cons.

Glochidion puberum (L.) Hutch.

Plate 5, figures 18–21

Pollen grains spheroidal, trilobed circular in polar view, 12 (14) 18 × 16 (18) 22 μm in diameter, tricolporate, rarely tetracolporate, colpus slender and long, pore subcircular, exine ca. 2–3 μm in thickness, sculpture coarsely reticulate.

Glochidion wilsonii Hutch.

Plate 5, figures 22–25

Pollen grains spheroidal, 4-lobed circular in polar view, 12 (17) 18 × 16 (22) 24 μm in diameter, mostly tetracolporate, colpus slender and short, pore circular, sculpture coarsely reticulate, exine with pilum, contour scabrate and wavy.

Glochidion lanceolarium (Roxb.) Voigt

Plate 6, figures 1–4

Pollen grains spheroidal, 5-lobed circular in polar view, 14 (20) 22 × 16 (21) 24 μm in diameter, tetracolporate, colpus slender and long, pore subcircular, sculpture coarsely reticulate.

Glochidion zeylanicum (Gaertn.) A. Juss.

Plate 6, figures 5–8

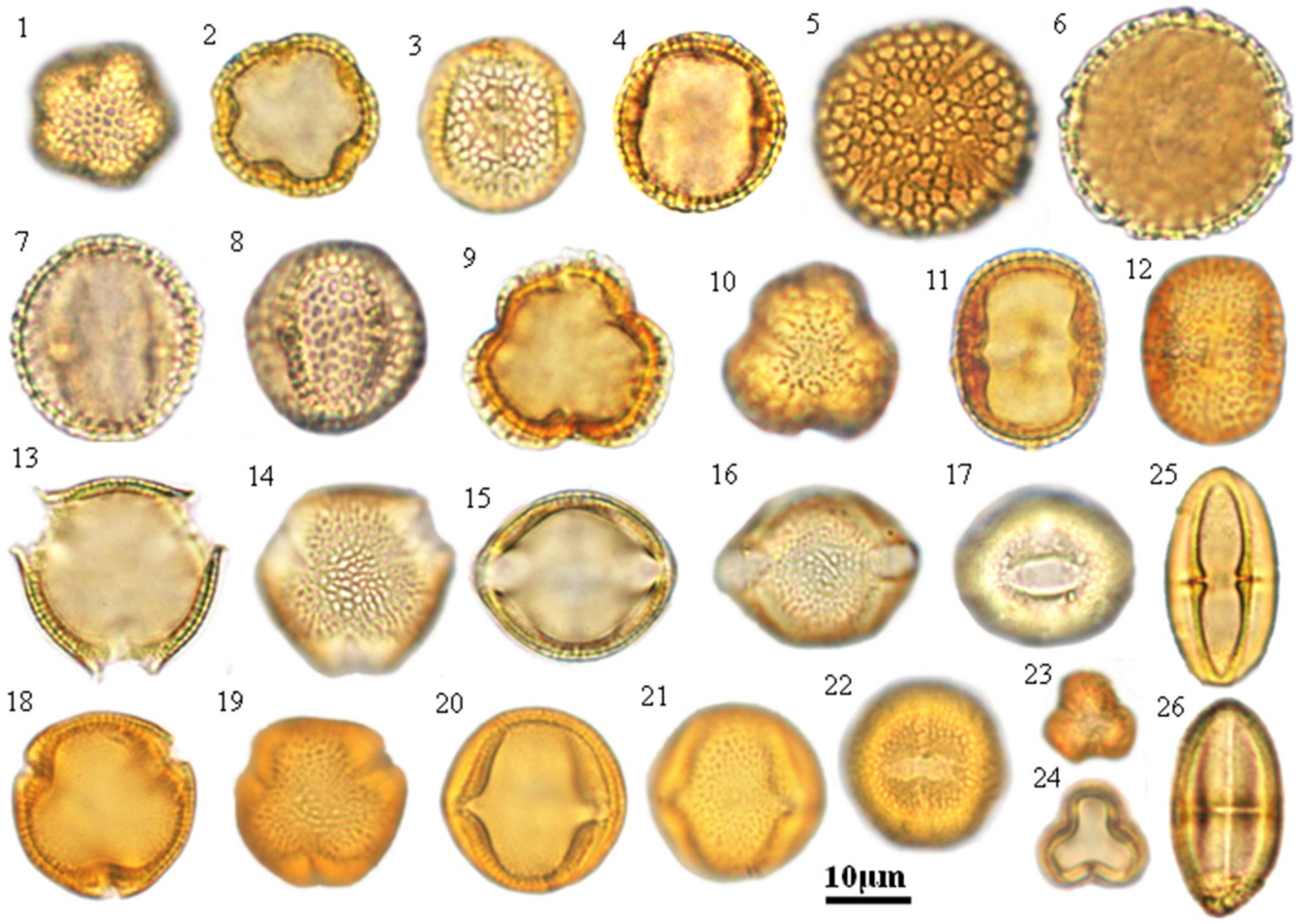

Plate 6. Light microscopic photographs of some species of Phyllanthoideae. 1–4, *Glochidion lanceolarium*; 5–8, *Glochidion zeylanicum*; 9–12, *Baccaurea ramiflora*; 13–17, *Bridelia tomentosa*; 18–22, *Bridelia balansae*; 23–26, *Antidesma japonicum*.

Pollen grains spheroidal, 4-lobed circular in polar view, 20 (24) 27 × 22 (27) 32 μm in diameter, mostly tetracolporate, pore outline faint, sculpture coarsely reticulate.

Baccaurea Lour.
Baccaurea ramiflora Lour.

Plate 6, figures 9–12

Pollen grains ellipsoidal, trilobed or 4-lobed circular in polar view, 17 (23) 30 × 18 (23) 28 μm in diameter. tricolporate to tetracolporate, colpus slender, pore lalongate with unclear outline, exine with pilum, sculpture coarsely reticulate.

Bridelia Willd.
Bridelia tomentosa Bl.

Plate 6, figures 13–17

Pollen grains spheroidal or subsphaeroidal, semi-angular in polar view, 22 (23) 24 × 19 (21) 24 μm in diameter, angulaperturate, tricolporate, pore lalongate and ellipsoidal, sculpture clearly reticulate, lumina in various sizes and shapes.

Bridelia balansae Tutcher

Plate 6, figures 18–22

Pollen grains spheroidal or subspheroidal, trilobed circular in polar view, 20.5 (21) 32 × 20.5 (22) 23.5 μm in diameter; tricolporate, pore lalongate; sexine and nexine similar in thickness, sculpture clearly striate-reticulate, lumina heterobrochate; muri near colpus striate and becoming reticulate. In mesocolpium, ornamentation is striato-reticulate and contour is wavy (Yang et al. 2015).

Antidesma Linn.
Antidesma japonicum Siebold & Zucc.

Plate 6, figures 23–26

Pollen grains perprolate, trilobed circular in polar view, 22 (25) 28 × 10 (13) 18 μm in diameter, tricolporate, colpus slender and long, pore lalongate and thickened around aperture forming cross with colpus, exine faintly layered, sculpture faintly granulate.

4. Notes on pollen types and distinguishing features

The binary division in Euphorbiaceae *sensu lato* provided by de Jussieu (1823, 1824) is based on ovule number, with a grouping of two biovulate subfamilies (Phyllanthoideae and Oldfieldioideae) and three uniovulate ones (Acalyphoideae, Crotonoideae, and Euphorbioideae) (Webster 1975, 1987, 1994a, 1994b). As one of five subfamilies of Euphorbiaceae *sensu lato*, Oldfieldioideae (Picrodendraceae) is an apparently diverse assemblage of mostly southern hemisphere trees and shrubs that traditionally have been allied with genera of Phyllanthoideae and Porantheroideae (Hayden 1994), while

Table 2. Comparative characteristics of pollen morphology for the investigated subfamilies of Euphorbiaceae.

Subfamily	Crotonoideae	Euphorbioideae	Acalyphoideae	Phyllanthoideae
Size	Larger than 30 μm	Larger than 30 μm	Smaller than 30 μm	Smaller than 30μm
Aperture	Inaperturate	Tricolporate with spherical or prolate, lalongate pore	Tricolporate with lalongate pore	Tricolporate to zonocolporate with spherical or lalongate pore and colpus forming a cross
Ornamentation	Exine tuberculate or bacubate forming *Croton*-type sculpture	Microreticulate and muri with granulate	Granulate or reticulate	Macroreticulate
Representative genera	*Aleurites*, *Croton*, *Vernicia*, *Jatropha*, *Codiaeum*	*Sapium*, *Euphorbia*, *Excoecaria*	*Mallotus*, *Macaranga*, *Alchornea*, *Cleidion*, *Acalypha*, *Ricinus*	*Phyllanthus*, *Glochidion*, *Flueggea*, *Aporosa*, *Baccaurea*, *Bridelia*, *Antidesma*

China in the northern hemisphere is home to another four subfamilies of Euphorbiaceae *sensu lato*, according to the Flora of China (Editorial Committee of Flora of China 1994) and the updated online eflora of China (www.efloras.org: vol. 11), namely Acalyphoideae, Crotonoideae, Euphorbioideae and Phyllanthoideae. Based on the pollen morphological characteristics investigated here, we found morphological categories of Euphorbiaceae in support of the subfamily taxonomy. Previous studies suggested that each subfamily has its own unique morphological characteristics distinguishable from those of the other subfamilies (Nowicke et al. 1998, 1999; Takahashi et al. 2000; Nowicke and Takahashi 2002; de Souza et al. 2016, 2017). According to previous palynological studies and our new observations, we outlined pollen morphological characteristics for each subfamily investigated in this study (Table 2).

The pollen morphology and size of Euphorbiaceae display notable differences at the level of species or genera: diameter ranges from 13.5 μm (*Flueggea virosa*) to 66.5 μm (*Aleurites fordii*) and the longest axis is generally less than 50 μm (Wang et al. 1995). However, both processing and mounting media can influence pollen size (e.g. Andersen 1960; Cushing 1961; Reitsma 1969); for instance, acetolysis and glycerine jelly are thought to increase size (e.g. Cushing 1961; Reitsma 1969). This issue is also discussed by Faegri and Iversen (1989). In our study, we used glycerine jelly after acetolysis, thus pollen size could be larger than normal, but not significantly so according to our comparison with the published pollen descriptions for some species. Pollen morphology of this family mostly includes colporate types, and rarely inaperturate types. For colporate pollen, tricolporate is the dominant type; however 4–5-colporate or stephanocolpate forms are also found in some genera and species. Exine ornamentation varies from reticulate to granulate, striate, tuberculate and so on. We can identify fossil pollen grains from Quaternary deposits to the genus level in some cases; however, it remains difficult to distinguish some species and genera accurately. Therefore, we examined practical classification for Euphorbiaceae pollen grains according to morphological characteristics which are summarised in Table 2.

The subfamily Crotonoideae, *sensu* Webster, consists of 13 tribes and approximately 73 genera, of which three genera – *Croton*, *Jatropha* and *Manihot* – account for half of the 2000 species (Nowicke 1994). Crotonoideae now appear to be an exception to pollen diversity and have surprisingly uniform pollen morphology, united by the *Croton* pattern (Erdtman 1952; Nowicke 1994; Webster 1994a; Lobreau-Callen and Suarez-Cervera 1997; de Souza et al. 2016): triangular supratectal elements attached to a network of muri having short or irregular columellae. In this paper, we observed *Aleurites*, *Croton*, *Vernicia*, *Jatropha* and *Codiaeum*, which are of the inaperturate type. Pollen morphological characteristics of these genera can be summarised as follows: pollen grains spherical, 30–80 μm in diameter, inaperaturate; exine ca. 1.5–8 μm in thickness; sexine far thicker than nexine; sculpture with *Croton* pattern, clavate or tuberculate; each design rosette with 5–8 short bars or verrucae and the design densely or sparsely arranged. However, this study dealt with a limited number of species from Crotonoideae, so further investigation to cover more species is needed prior to making an overall assessment of pollen morphological characteristics in this subfamily. According to previous studies (Nowicke 1994; Webster 1994a; Lobreau-Callen and Suarez-Cervera 1997; de Souza et al. 2016), this subfamily mainly has three pollen morphological types: inaperturate with plicate pila, pantoporate, and colpate. However, the triangular supratectal elements, muri, and modified columellae feature the pollen type of *Croton*, representing the key pollen morphology of most species in the subfamily Crotonoideae.

Previous studies on the pollen morphology of Euphorbioideae suggested the uniformity of pollen characters of this family, with tricolporate with margo and tectate perforate types (Punt 1987; Park and Lee 1988; Nowicke 1994). However, most pollen morphological studies have focused mainly on the tribe Euphorbieae (El-Ghazaly 1989; Suárez-Cervera et al. 2001; Lee and Park 2006; Noh and Park 2008). Punt (1962) intensively studied the pollen morphology of this subfamily using light microscopy. The results suggested a close relationship between Euphorbieae and Hippomaneae (Punt 1962). These two tribes show a similarity in endexine structure, but they display different intine thickness along each side of the aperture. However, these subtle characters are only identifiable under scanning electron microscopy and transmission electron microscopy (Suárez-Cervera et al. 2001; Park and Lee 2013). In China, the Euphorbioideae include two tribes, Euphorbieae and Hippomaneae. Our materials also include these tribes, including *Sapium*, *Euphorbia* and *Excoecaria*. From observation and description under a light microscope, the morphological characteristics of the above genera in this subfamily can be summarised as follows: tricolporate, pollen diameter mostly more than 30 μm, pore spherical or ellipsoidal and lalongate,

Table 3. Pollen morphological comparison for the investigated genera of Acalyphoideae.

Genus	*Mallotus*	*Macaranga*	*Alchornea*	*Cleidion*	*Acalypha*	*Ricinus*
Size	ca. 20–30 μm	Smaller than 20 μm	ca. 22 μm	ca. 18 μm	ca. 25 μm	ca. 26–28 μm
Aperture	Lalongate pore, almost extending and connecting with other pores	Not thickened	With ligulate protrusions in aperture in polar view, and wide colpus narrowing to the poles	Similar to *Mallotus*, but thickened	Rhombic aperture with wide colpus but narrowing to the poles	Pore elongate and rectangle with slender colpus and narrow, extending to the poles
Ornamentation	Microreticulate, but with foveolate lumina	Granulate to reticulate, different from *Mallotus*	Unclearly granulate or reticulate-like	Faintly granulate	Striate -reticulate with fine granules	Microreticulate with irregular lumina

exine with two layers having the same thickness, sculpture finely reticulate, muri with granules.

Acalyphoideae has 115 genera in 20 tribes, with the largest aggregation of taxa within the Euphorbiaceae (Webster 1994a). This subfamily is remarkably diverse in terms of exine structure and morphology (e.g. Takahashi et al. 1995; Fernández-González and Lobreau-Callen 1996). Almost all species of this subfamily are 3-colporate, and the endoaperture frequently has well-defined polar margins but diffuse lateral ones. The structure of the tectum and exine is more variable (Nowicke et al. 1998; Nowicke and Takahashi 2002). Lobreau-Callen and Suarez-Cervera (1994) concluded that some species from Acalyphoideae are suboblate to subprolate, mostly 3-colporate, and tectate with a wide range of sculpture/ornamentation. To better understand the diverse pollen morphology of this subfamily, we examined pollen morphological characteristics in detail, focusing on pollen size, aperture and ornamentation for some genera in Acalyphoideae, namely *Mallotus*, *Macaranga*, *Alchornea*, *Cleidion*, *Acalypha* and *Ricinus*. We provide a pollen morphological comparison for the investigated genera of Acalyphoideae, summarised in Table 3. Pollen grains are mainly tricolporate, colpus slim and long, pore mostly lalongate, and size relatively smaller. Some pollen types of this subfamily are frequently found in subtropical Quaternary sediments. Some species can be identified to the genus level – for example, *Alchornea*, *Mallotus* and *Macaranga*. The main characteristics of *Mallotus* are its slender colpus, lalongate pore that is nearly connected to the neighboring aperture, and with coarsely reticulate sculpture (Table 3). The pollen morphological characteristics of *Mallotus* are similar to those of *Cleidion*, although the pore thickens close to the aperture for *Cleidion*, which is different from *Mallotus*. *Macaranga* pollen grains are relatively smaller in size, generally less than 20 μm, the sexine and nexine are layered clearly and the same thickness, and the sculpture is granulate-reticulate different from *Mallotus*. *Alchornea* pollen has a wider colpus and sharpens towards the poles. In polar view, the pore has ligulate protrusions, and it is easy to identify fossil pollen grains in strata. *Acalypha* pollen grains show a wider colpus whcih gradually narrows to the poles, a rhomboid pore, and reticulate sculpture formed by fine granules with a striate pattern. As *Ricinus* is a cultivated plant, its pollen grains scarcely occur in Quaternary sediments. *Ricinus* pollen grains are ca. 26–28 μm in diameter, relatively bigger than those of the five genera discussed above, with an elongate, rectangular pore, a slender and narrow colpus, extending to the poles, and microreticulate sculpture with irregular lumina.

The subfamily Phyllanthoideae consists of 54–60 genera and ca. 2000, species mostly from pantropical areas, but many occur in southern temperate zones and some northern temperate zones as well (Kathriarachchi et al. 2006; Byng 2014) There are some 18 genera with ca. 164 species and 14 varieties in China (Li 1994). The largest genera and the approximate number of species in each are the following: *Phyllanthus* (1270), *Acalypha* (450), *Glochidion* (300), *Cleistanthus* (140), *Antidesma* (100), *Aporosa* (90), *Uapaca* (60), *Baccaurea* (50), *Bridelia* (50) and *Flueggea* (15) (Webster 1994a; Radcliffe-Smith 2001; Sagun and van der Ham 2003; Stevens 2010; Yao and Zhang 2016). This paper focuses on *Phyllanthus*, *Glochidion*, *Flueggea*, *Aporosa*, *Baccaurea*, *Bridelia* and *Antidesma*, and we found that key pollen types are tricolporate to stephanocolporate, with slim colpi, circular or lalongate pore crossed with colpus forming decussation, relatively smaller pollen, and clearly reticulate sculpture. Pollen grains of *Phyllanthus* are spherical, 3–6-colporate, colpus slender and short, pore circular, sculpture clearly reticulate. Santiago et al. (2004) found that the pollen shape and number of colpi varied within and between some species. Wu et al. (2016) identified five pollen classes (colporate pollen, incomplete synaperturate pollen, synaperturate pollen, clypeate pollen and porate pollen) based on a pollen morphological study of 89 species. In general, the pollen morphology of *Phyllanthus* is close to that of *Glochidion*; its exine ornamentation is more finely reticulate compared with that of *Glochidion*, but it is difficult to differentiate between these pollen types. Pollen grains of *Flueggea* are usually tricolporate, and the colpus width is different from that of *Phyllanthus*. *Aporosa* pollen grains are very similar to those of Anacardiaceae and Rutaceae in morphology, but the pore is lalongate, forming a crisscross with the colpus, which is different from the morphology of the other two subfamilies. The sexine of *Baccaurea* pollen grains has a pilum and muri and is composed of granulae. *Bridelia* pollen grains have lalongate pores, an elliptical or egg-shaped aperture and striate reticulate sculpture. *Antidesma* pollen has similar morphological features to *Castanopsis* and *Lithocarpus* in Fagaceae; however, the colpus crosses with the pore forming a decussation and the pollen grains have a longer polar axis. In these aspects, *Antidesma* is different from *Castanopsis* and *Lithocarpus*.

According to our new investigation of selected taxa, pollen types of four subfamilies (Acalyphoideae, Crotonoideae, Euphorbioideae, Phyllanthoideae) from Euphorbiaceae show

moderately high diversity in general (Table 2). Their pollen grains show diverse shapes, with a large variation in size – ranging from 13.5 μm to ~75 μm in diameter, but mostly less than 30 μm. Pollen grains are mostly prolate, with a few spherical or ellipsoid and colporate or inaperturate. Of the colporate pollen grains, most are tricolporate, but tetracolporate, 5-colporate or stephanocolporate forms also occur. Exine sculpture is reticulate, granulate, striate or verrucate (such as the *Croton* type). At the subfamily level, Crotonoideae pollen grains are inaperturate, large in size and with regularly arranged verrucate sculpture. Euphorbioideae pollen grains are tricolporate, more than 30 μm in size, with pores of various shapes, and finely reticulate sculpture on muri with granules. Acalyphoideae pollen grains are relatively small and tricolporate, with a slender and long colpus (Table 3). Phyllanthoideae pollen grains are also usually relatively small, tricolporate to stephanocolporate, with slender colpi and a small and circular pore; individual species may have an elongated pore crossing the colpi, and clearly reticulate sculpture. Some pollen types of Euphorbiaceae can be identified to the genus level, such as *Euphorbia*, *Mallotus*, *Macaranga*, *Alchornea*, *Phyllanthus*, *Glochidion*, *Aporosa*, *Bridelia* and *Antidesma*. There is a potential to interpret the palaecological significance of these genera in terms of their diverse habitats.

5. Concluding remarks

In this study, we have examined four selected subfamilies (Crotonoideae, Euphorbioideae, Acalyphoideae and Phyllanthoideae), including 21 genera and 34 species whose fossil pollen grains are frequently found in Quaternary sediments. Our illustrated and descriptive pollen atlas will aid Quaternary pollen analysis in southern China, as well as in the surrounding subtropical and tropical areas. The pollen morphology of some species overlaps, especially within the same genus, which may make it difficult, if not impossible, to identify some grains. This is inevitable for closely related pollen types. Further investigation can be aimed at widening our examination to cover many more genera and species of Euphorbiaceae that have yet to be investigated palynologically, to create a robust basis for pollen analysis and palaeoecological interpretation of Quaternary sediments. Pollen identification of the selected subfamilies of Euphorbiaceae can improve palaeoecological and palaeobiogeographical research based on Quaternary fossil pollen.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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References

Andersen ST. 1960. Silicone oil as a mounting medium for pollen grains. Danmarks Geologiske Undersgelse (Series). IV1:1–24.

APG (Angiosperm Phylogeny Group). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and

families of flowering plants: APG II. Botanical Journal of the Linnean Society. 141:399–436.
APG (Angiosperm Phylogeny Group). 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society. 161(2):105–121.
APG (Angiosperm Phylogeny Group). 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society. 181(1):1–20.
Byng JW. 2014. The flowering plants handbook. Hertford: Plant Gateway Limited.
Chen YJ, Chen SH, Huang TC, Wu MJ. 2009. Pollen morphology of Philippine species of *Phyllanthus* (Phyllanthaceae; Euphorbiaceae sensu lato). Blumea. 54(1):47–58.
Cushing EJ. 1961. Size increase in pollen grains mounted in thin slides. Pollen et Spores. 3(2):265–274.
de Jussieu A. 1823. Considérations sur la famille des Euphorbiacées. Mémoires du Muséum d'Histoire Naturelle (Paris). 10:317–355.
de Jussieu A. 1824. De Euphorbiacearum generibus medicisque earumdem viribus tentamen. Paris: Didot.
de Souza LR, Carneiro-Torres DS, Saba MD, dos Santos F. 2017. Pollen morphology of the Acalyphoideae and Euphorbioideae (Euphorbiaceae) of the Caatinga ecoregion in Brazil. Plant Systematics and Evolution. 303(9):1161–1118.
de Souza LR, Carneiro-Torres DS, Saba MD, Santos F. 2016. Pollen morphology of Crotonoideae (Euphorbiaceae) from seasonally dry tropical forests, Northeastern Brazil. Plant Systematics and Evolution. 302(7):795–817.
Editorial Committee of Flora of China. 1994. Flora of China. 44(1–3): Euphorbiaceae. Beijing: China Science Press.
El-Ghazaly G, Chaudhary R. 1993. Morphology and taxonomic application of Orbicules (Ubisch Bodies) in the Genus *Euphorbia*. Grana Palynologica. 32(sup002):26–32.
El-Ghazaly G. 1989. Pollen and orbicule morphology of some *Euphorbia* species. Grana. 28(4):243–259.
Erdtman G. 1952. Pollen morphology and plant taxonomy. Uppsala: Almqvist & Wiksells.
Faegri K, Iversen J. 1989. Textbook of pollen analysis. (revised by Faegri K, Kaland PE, Krzywinski K). New York (NY): Wiley & Sons.
Fernández-González D, Lobreau-Callen D. 1996. The pollen of the Acalypheae tribe (Acalyphoideae, Euphorbiaceae) (in French). Grana. 35(5):266–284.
Hayden WJ. 1994. Systematic anatomy of Euphorbiaceae subfamily Oldfieldioideae I. Overview. Annals of the Missouri Botanical Garden. 81(2):180–202.
Hesse M, Halbritter H, Weber M, Buchner R, Frosch-Radivo A, Ulrich S. 2009. Pollen terminology. An illustrated handbook. Berlin: Springer Verlag.
Hooghiemstra H, Van Geel B. 1998. World list of Quaternary pollen and spore atlases. Review of Palaeobotany and Palynology. 104(2): 157–182.
Huang T. 1972. Pollen flora of Taiwan. Taiwan: National Taiwan University Botany Department Press.
IBCAS (Institute of Botany and South China Institute of Botany, Chinese Academy of Sciences). 1982. Angiosperm pollen flora of tropic and subtropic China. (in Chinese). Beijing: Science Press; p. 1–453.
Jensen U, Vogel-Bauer I, Nitschke M. 1994. Leguminlike proteins and the systematics of the Euphorbiaceae. Annals of the Missouri Botanical Garden. 81(2):160–179.
Kathriarachchi H, Samue R, Hoffmann P, Mlinarec J, Wurdack KJ, Ralimanana H, Stuessy TF, Chase MW. 2006. Phylogenetics of tribe Phyllantheae (Phyllanthaceae; Euphorbiaceae sensu lato) based on nrITS and plastid *matK* DNA sequence data. American Journal of Botany. 93(4):637–655.
Kremp G. 1965. Morphologic encyclopedia of palynology. Tucson: The University of Arizona Press; p. 1–263.
Lee ED, Park KR. 2006. A palynotaxonomic study of *Euphorbia* section *Zygophyllidium* (Euphorbiaceae). Korean Journal of Electron Microscopy. 36:195–208. (in Korean).
Li PT. 1994. Glochidion. Flora Republica Popularis Sinicae.Tomus 44. Angiospermae Dicotyledoneae Euphorbiaceae. Beijing: Science Press; p. 133–162.
Loberau-Callen D, Punt W, Schmid M. 1988. Pollen morphology and taxonomy of the *Phyllanthus* species (Euphorbiaceae) native to New Caledonia. Review of Palaeobotany and Palynology. 53:283–304.
Lobreau-Callen D, Cervera MS. 1997. Pollen exine ultrastructure of the apetalous Crotonoideae. Review of Palaeobotany and Palynology. 98(3–4):257–291.
Lobreau-Callen D, Suarez-Cervera M. 1994. Pollen ultrastructure of Hymenocardia Wallich ex Lindley and comparison with other Euphorbiaceae. Review of Palaeobotany and Palynology. 81(2–4):257–278.
Meewis B, Punt W. 1983. Pollen morphology and taxonomy of the subgenus *Kirganelia* (Jussieu) Webster (Genus *Phyllanthus*, Euphorbiaceae) from Africa. Review of Palaeobotany and Palynology. 39(1–2):131–160.
Noh MA, Park KR. 2008. Pollen morphology of *Euphorbia* subsection *Meleuphorbia*. Korean Journal of Electron Microscopy. 38:329–338. (in Korean).
Nowicke JW, Takahashi M, Webster GL. 1998. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae) part 1. Tribes Clutieae, Pogonophoreae, Chaetocarpeae, Pereae, Cheiloseae, Erismantheae pro parte, Dicoelieae, Galearieae and Ampereae. Review of Palaeobotany and Palynology. 102(3–4):115–152.
Nowicke JW, Takahashi M, Webster GL. 1999. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae) part 2. Tribes Agrostistachydeae. Review of Palaeobotany and Palynology. 105(1–2):1–62.
Nowicke JW, Takahashi M. 2002. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae), part 41. Tribes Acalypheae pro parte. Review of Palaeobotany and Palynology. 121(3–4):231–336.
Nowicke JW. 1994. A palynological study of Crotonoideae (Euphorbiaceae). Annals of the Missouri Botanical Garden. 81(2):245–269.
Park KR. 1997. Pollen morphology of *Euphorbia* subgenus *Agaloma* section *Tithymalopsis* and related species (Euphorbiaceae). Grana. 36(1):11–16.
Park KR, Lee JH. 2013. Pollen morphology of subfamily Euphorbioideae (Euphorbiaceae). Korean Journal of Plant Taxonomy. 43(1):1–11.
Park KR, Lee S. 1988. A palynotaxonomic study of the Korean Euphorbiaceae. Korean Journal of Plant Taxonomy. 18(2):69–94.
Punt W. 1962. Pollen morphology of Euphorbiaceae with special reference to taxonomy. Wentia. 7:1–116.
Punt W. 1967. Pollen morphology of the genus *Phyllanthus* (Euphorbiaceae). Review of Palaeobotany and Palynology. 3(1–4):141–150.
Punt W. 1972. Pollen morphology and taxonomy of section *Ceramanthus* Baillon s.l. of the genus *Phyllanthus* (Euphorbiaceae). Review of Palaeobotany and Palynology. 13(3–4):213–228.
Punt W. 1980. Pollen morphology of the *Phyllanthus* species (Euphorbiaceae) occurring in New Guinea. Review of Palaeobotany and Palynology. 31:155–177.
Punt W. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. Botanical Journal of the Linnean Society. 94(1–2):127–142.
Punt W, Hoen PP, Blackmore S, Nilsson S, Thomas AL. 2007. Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology. 143(1–2):1–81.
Radcliffe-Smith A. 2001. Genera Euphorbiacearum. London (Kew): Cromwell Press.
Reitsma TJ. 1969. Size modification of recent pollen grains under different treatments. Review of Palaeobotany and Palynology. 9(3–4):175–202.
Sagun VG, Levin GA, van der Ham R. 2006. Pollen morphology and ultrastructure of *Acalypha* (Euphorbiaceae). Review of Palaeobotany and Palynology. 140(1–2):123–143.
Sagun VG, van der Ham R. 2003. Pollen morphology of the Flueggeinae (Euphorbiaceae, Phyllanthoideae). Grana. 42(4):193–219.
Santiago LJM, Louro RP, Emmerich M, Barth OM. 2004. The pollen morphology of *Phyllanthus* (Euphorbiaceae) section *Choretropsis*. Botanical Journal of the Linnean Society. 144(2):243–250.
Stevens PF. 2010. Angiosperm Phylogeny Website: Version 9, June 2008. [Accessed 14th September 2010]. http://www.mobot.org/MOBOT/research/APweb/.

Suárez-Cervera M, Gillespie L, Arcalís E, Le Thomas A, Lobreau-Callen D, Seoane-Camba JA. 2001. Taxonomic significance of sporoderm structure in pollen of Euphorbiaceae: tribe Plukenetieae and Euphorbieae. Grana. 40(1–2):78–104.

Sutter DM, Forster PI, Endress PK. 2006. Female flowers and systematic position of Picrodendraceae. Plant Systematics and Evolution. 261(1–4):187–215.

Takahashi M, Nowicke JW, Webster GL, Orli SS, Yankowski S. 2000. Pollen morphology, exine structure, and systematics of Acalyphoideae (Euphorbiaceae), part 3. Tribes Epiprineae, Adelieae, Alchorneae, Acalypheae pro parte. Review of Palaeobotany and Palynology. 110(1–2):1–66.

Takahashi M, Nowicke JW, Webster GL. 1995. A note on remarkable exines in Acalyphoideae (Euphorbioideae). Grana. 34(5):282–290.

Wang FX, Qian NF, Zhang YL, Yang HQ. 1995. Pollen flora of China. (in Chinese). Beijing: Science Press; p. 1–461.

Webster GL, Carpenter KJ. 2002. Pollen morphology and phylogenetic relationships in neotropical *Phyllanthus* (Euphorbiaceae). Botanical Journal of the Linnean Society. 138(3):325–338.

Webster GL. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon. 24(5–6):593–601.

Webster GL. 1987. The saga of the spurges: a review of classification and relationships in the Euphorbiales. Botanical Journal of the Linnean Society. 94(1–2):3–46.

Webster GL. 1994a. Classification of the Euphorbiaceae. Annals of the Missouri Botanical Garden. 81(1):3–32.

Webster GL. 1994b. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Annals of the Missouri Botanical Garden. 81(1):33–144.

Wei ZX. 2003. Pollen flora of seed plants. (in Chinese). Kunming: Yunnan Science and Technology Press.

Wu MJ, Huang TS, Liu CC, Chen YJ, Chang YS, Hsu CL, Wu SY, Tseng AY, Chang YC, Liu CC, Kaewmuan A. 2016. Pollen morphology and taxonomy in Malesian *Phyllanthus* (Phyllanthaceae). Journal of Japanese Botany. 91(Suppl):257–292.

Wurdack KJ, Hoffmann P, Samuel R, de Bruijn A, van der Bank M, Chase MW. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte, Euphorbiaceae sensu lato) using plastid RBCL DNA sequences. American Journal of Botany. 91(11): 1882–1900.

Yang S, Zheng Z, Mao LM, Ferguson D, Huang KY, Chen BS, Ranhotra PS. 2015. Selected pollen grains from tropical Hainan Island, south China: an identification key to Quaternary pollen. Review of Palaeobotany and Palynology. 222:84–103.

Yao G, Zhang DX. 2016. Pollen morphology of Chinese *Glochidion* (Phyllanthaceae) and its taxonomic implications. Nordic Journal of Botany. 34(1):102–110.

Yu RY, van der Ham R, van Welzen P. 2018. Pollen morphology of *Trigonostemon* and its relatives (Euphorbiaceae). Grana. 58(2):114–128.