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Pollen morphology of the Sapotaceae from Thailand and its taxonomic implications

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ABSTRACT

The external pollen morphology of the family Sapotaceae in Thailand was examined using the acetolysis method to determine its taxonomic significance. Pollen of 39 specimens belonging to 32 species was investigated by means of light and scanning electron microscopy. Pollen grains are found to be monads, isopolar, colporate, lalongate, and variable in size, shape, aperture number, colpus length and exine thickness. Exine ornamentation is also variable, showing more than one pattern on a single pollen grain. Principal component analysis based on 13 pollen characters identified three pollen groups: *Chrysophyllum*, *Madhuca* and *Pouteria* types based on pollen shape, size, the ratio of colpus length to the polar axis and exine sculpturing. Pollen morphology is taxonomically useful in the classification of the Thai Sapotaceae, especially in the taxonomic status of *Planchonella* and *Pouteria* species.

KEYWORDS: morphometric analysis, palynology, Sapotaceae, taxonomy, Ericales.

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INTRODUCTION

Sapotaceae is a pantropical family, widely distributed in tropical regions, i.e., South America, Africa and South-East Asia, with approximately 1,270 species belonging to 58 genera (Christenhusz *et al.*, 2017). Eleven genera and 51 species are recognized from Thailand (Chantaranothai, 2005 & 2014). The family is characterized by being trees or rarely shrubs with latex in all parts, simple and typically spiral leaves, fascicled and axillary flowers and fleshy fruits.

The Sapotaceae is one of the families in which generic limits are very difficult to recognize and several familial classifications, based on morphological information have been proposed (de Candolle, 1844; Bentham & Hooker, 1876; Engler, 1890; Baillon, 1891; Dubard 1912, 1915; Lam, 1939; Aubréville, 1964; Baehni, 1965; Pennington, 1991). The earlier systems were usually based on the presence or absence of the staminodes and corolla appendages, the number of corolla lobes related to the number of sepals, and of stamens related to the number of corolla lobes while characters of seed were used with the floral structures by Baillon (1891) and later authors. Formerly, Lam (1939) placed *Sarcosperma* Hook.f. in its own family, Sarcopermataceae, because of its opposite leaves and racemose inflorescence but the genus was put back in Aubréville's study (Aubréville, 1964). The classification into subfamilies, tribes and genera remains unstable even though more morphological characters have been incorporated into studies of the family. Recently, molecular phylogenetic studies based on cpDNA sequence data from the *ndh*F gene were used to create a classification (Anderberg & Swenson, 2003; Swenson & Anderberg, 2005). Using morphology and molecular data, recognition of three subfamilies has been proposed comprising Chrysophylloideae, Sapotoideae and Sarcospermatoideae (Swenson & Anderberg, 2005).

Pollen morphology of Sapotaceae has been reported from both local and floristic studies (Erdtman 1952; Ayensu, 1972; Sowunmi, 1974; Gupta & Sharma, 1977; Kunasit & Chantaranothai, 2021). However, the most extensive palynological survey of the family using light microscopy (LM), scanning electron microscopy (SEM) and transmission electron

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microscopy (TEM) of almost 400 species was undertaken by Harley (1986 & 1991) and proposed 12 pollen types. According to Harley's studies, pollen of the Sapotaceae is monad, isopolar, usually 3–5 -colporate, rarely 6-colporate, angul- or planaperture and has a more or less circular amb. The shape is typically prolate-spheroidal, subprolate or prolate, sometimes spheroidal and rarely oblate-spheroidal. The polar axis length is 16.0–92.2 µm. The colpi are usually narrow, 0.15–0.85 in proportion to polar length. The wall thickness at the pole is 1–3(–5) µm, and the equator is 1–5(–8) µm. The sculpturing appears in various types, including perforate, microfossulate, psilate, subpsilate, scabrate, granular, striate-rugulate, striate or regulate. The polar and equatorial areas sometimes have different exine sculpturing.

Overall, the palynological information presented by Harley (1986 & 1991) did not resolve the generic limits within the family, however, it did correlate well with Pennington's sectional classification of *Pouteria* Aubl. Moreover, these pollen types were discussed in a phylogenetic context for the subfamily Chrysophylloideae (Swenson *et al.*, 2008). By the work of Swenson and his colleagues, two sections of *Pouteria* were outlined - the *Pouteria* sensu stricto clade having only pollen type V, while other sections represented six different pollen types. The pollen information provided by Harley (1991) also supported Swenson's concept that *Beccariella* Pierre and *Planchonella* Pierre, which were a part of *Pouteria*, were distinct genera and not included in the *Pouteria* sensu stricto clade.

In Thailand, the pollen morphology of subfamily Chrysophylloideae, including *Chrysophyllum* L., *Pouteria*, *Synsepalum* (A.DC.) Daniell. and *Xantolis* Raf., has been reported by Kunasit & Chantaranothai (2021). In that paper, palynological characteristics are correlated well to most Thai genera in Chrysophylloideae in that *Chrysophyllum*, *Pouteria* I, *Pouteria* II, *Synsepalum* and *Xantolis* types were recognized, and support the phylogenetic classification of *Pouteria* by Swenson *et al.* (2007 & 2013). At present, the *Pouteria* species representing *Pouteria* I type, have been transferred to *Planchonella* Pierre, i.e., *Planchonella grandifolia* Pierre, *P. obovata* (R.Br.) Pierre and *P. stellibacca* (J.F.Maxwell) Swenson (Swenson *et al.*, 2007, 2013; Faria *et al.*, 2017). This study extends the overall palynological information available of Thai Sapotaceae and undertakes a phenetic analysis to assess taxonomic relationships of pollen morphology within the family.

MATERIALS & METHODS

Thirty-nine pollen samples belonging to 32 species of Thai Sapotaceae were collected from living specimens in the field and from herbarium specimens from BK, BKF, KKU, PSU and QBG (Table 1; herbarium codes follow Thiers *et al.*, 2021, continuously updated).

Mature anthers were used for pollen material. The pollen was prepared using the acetolysis technique of Erdtman (1960) for investigation under LM and SEM, and then mounted in silicone oil and sealed with paraffin for the LM study. Five to 10 pollen grains were observed for each sample and all quantitative characters were measured with an ocular micrometer using an Olympus CH30 microscope. For the SEM study, pollen suspended in ethanol was dropped onto a two-sided carbon tape which topped a stub, then sputter-coated with gold. For collapsed pollen, the grain underwent critical point drying before it was moved to the stub. Exine sculpturing of the pollen was investigated using a SNE-4500M SEM.

Pollen slides were deposited at KKU herbarium. Pollen terminology follows Walker & Doyle (1975) and Punt *et al.* (2007). Scientific names follow the Flora of Thailand (Chantaranothai, 2005 & 2014). Pollen character measurements followed those outlined in Fig. 1.

Morphometric analysis was conducted based on the arithmetic mean of the 12 quantitative (P, E, P/E, N, C, C/P, I, Ol, Ow, Ea, Em and Eap) and one qualitative (S) palynological characters (Table 2). The character states of the exine sculpturing were categorized into psilate and non-psilate types then analyzed together with those of quantitative data. Principal component analysis (PCA) was applied in R (version 4.1.1) using the PCAmixdata package (Chavent *et al.*, 2017) that allowed PCA to analyze both quantitative and qualitative variables.

Table 1. Specimens examined of Thai Sapotaceae pollen.

No.	Taxon	Collector No.	Herbarium
1–2	*Chysophyllum cainito* L.	*Kunasit 66*; *Buain 009-2004*	**KKU**; **PSU**
3	*Madhuca esculenta* H.R.Fletcher	*van de Bult 1022*	**BKF**
4	*M. floribunda* (Pierre ex Dubard) H.J.Lam	*Phengklai et al. 3611*	**BKF**
5	*M. klackenbergii* Chantar.	*Kunasit 134*	**KKU**
6	*M. krabiensis* (Aubrév.) Chantar.	*Kunasit 83*	**KKU**
7	*M. malaccensis* (C.B.Clarke) H.J.Lam	*Niyomdham et al. 2211*	**AAU**
8	*M. motleyana* (de Vries) J.F.Macbr.	*Niyomdham 2014*	**BKF**
9	*M. stipulacea* H.R.Fletcher	*Maxwell 89-343*	**BKF**
10	*M. thorelii* (Dubard) H.J.Lam	*Middleton et al. 5661*	**BKF**
11	*Manilkara hexandra* (Roxb.) Dubard	*Phengklai et al. 12824*	**BKF**
12	*M. kauki* (L.) Dubard	*Boonchu s.n.*	**BKF**
13	*M. littoralis* (Kurz) Dubard	*Niyomdham & Puudjaa 3353*	**BKF**
14	*M. zapota* (L.) P.Royen	*Namdar s.n.*	**AAU**
15–16	*Mimusops elengi* L.	*Kunasit 77*; *Kunasit 139*	**KKU**
17–18	*Palaquium garrettii* H.R.Fletcher	*Maxwell 00-4*; *BGO Staff s.n.*	**BKF**; **QBG**
19	*P. obovatum* (Griff.) Engl.	*Sirirugsa 1275*	**PSU**
20	*P. ottolanderi* Koord. & Valeton	*Middleton et al. 417*	**BKF**
21	*P. rostratum* (Miq.) Burck	*Kerr 14441*	**BK**
22	*P. sumatranum* Burck	*Boonkird 70*	**BKF**
23	*Payena acuminata* (Blume) Pierre	*Gardner & P. Tippayasri ST1600*	**BKF**
24–25	*P. asiatica* Chantar.	*Gardner & P. Tippayasri ST1361*; *Maxwell 86-150*	**BKF**; **PSU**
26	*P. lucida* A.DC.	*Gardner & Sidisunthorn ST1621*	**BKF**
27	*P. maingayi* C.B.Clarke	*Gardner ST0228*	**BKF**
28	*Pouteria campechiana* (Kunth) Baehni	*Kunasit 84*	**KKU**
29	*Planchonella grandifolia* Pierre	*Smitinand 5565*	**BKF**
30	*P. obovata* (R.Br.) Pierre	*Wongprasert 075-36*	**BKF**
31	*P. stellibacca* (J.F.Maxwell) Swenson	*Boonkongchart & Tanthana 109*	**BKF**
32–33	*Sarcosperma arboreum* Hook.f.	*Maxwell 01-112*; *La-ongsri & Norsaengsri 97*	**BKF**; **QBG**
34	*S. griffithii* Hook.f.	*Mitsuta et al. T-45321*	**BKF**
35–36	*Synsepalum dulcificum* (Schum. & Thonn.) Daniell	*Kunasit 86*; *Phaosrichai 02*	**KKU**; **QBG**
37–38	*Xantolis burmanica* (Collet & Hemsl.) P.Royen	*Maxwell 89-545*; *Thon 11*	**BKF**; **QBG**
39	*X. cambodiana* (Pierre ex Dubard) P.Royen	*Winit 1587*	**BK**

RESULTS

General pollen morphology

Pollen morphology is summarized in Table 2. The pollen are monads, isopolar, colporate, lalongate. The smallest grains belong to *Chrysophyllum cainito* L. (18.5–23 µm long) while the largest ones are found in *Palaquium obovatum* (Griff.) Engl. and *Payena lucida* A.DC. (up to 56 µm long). The pollen shape varies from oblate spheroidal to euprolate. Pollen of *Chrysophyllum cainito* and the genus *Planchonella* are strongly euprolate with the average ratio between polar length (P) and equatorial diameter (E) of more than 1.50. Only *Madhuca motleyana* (de Vries) J.F.Macbr. has an oblate spheroidal shape (Fig. 4L). The colpi are usually longer than half of

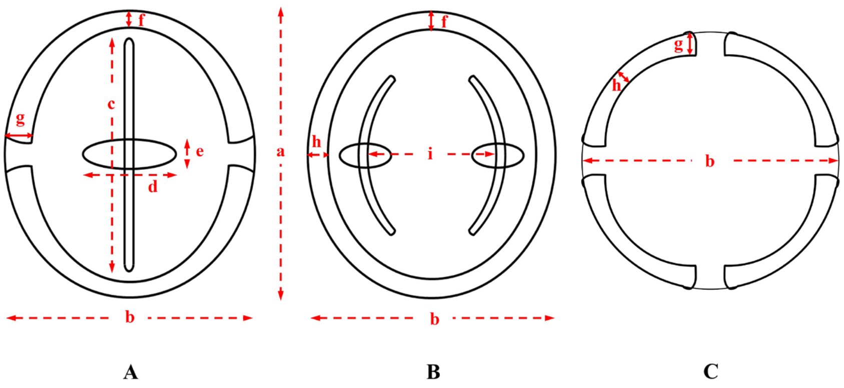

Figure 1. Diagram of pollen measurement under light microscope; A–B: equatorial view; C. polar view; a: polar length; b: equatorial diameter; c: colpus length; d: ora width; e: ora length; f: apocolpial exine thickness; g: apertural exine thickness; h: mesocolpial exine thickness; i: intercolpial width.

the polar length, rarely shorter, slit-like or wider. The ora is horizontally elliptic to circular. The exine is usually thinner at the apocolpium, equal or thicker at the mesocolpium, and thickest at the equator near the aperture. The sculpturing type is various with usually more than one pattern on a pollen grain, and also characterizes some individual species, e.g., the entirely smooth surface of *Pouteria campechiana*, and the striae-rugulae of *Synsepalum dulcificum* (Schum. & Thonn.) Daniell.

Morphometric analyses of the pollen

The PCA of 13 palynological characters is exposed by the first three principal components, correlated to the percentage of variance summarized in Table 3. The first three components together account for 81.35% of the total cumulative variance, contributing 59.78%, 13.18% and 8.38%, respectively. The PCA scores of each component are plotted in two dimensions. The plot belonging to the highest cumulative variance clearly separates group III from the other groups while groups I and II are closely approached (Fig. 2). The plot of the second highest one split group I from the others while groups II and III are assembled (Fig. 3). According to Table 4, most characters which a high factor loading of 0.5, are important characters in each component. Component 1 consists of the most quantitative characters, including equatorial diameter, the length of the polar axis, colpus and ora, the width of intercolpium and ora, the thickness of apocolpial, mesocolpial, and apertural exine, and the number of apertures. The C/P ratio and exine sculpturing are the predominant characters in component 2. For component 3, the P/E ratio and C/P ratio are considered significant characters.

Pollen type

The phenetic analysis determined high factor loadings which contributed significant characters in each component (Table 4). These characters, the equatorial diameter, the ratios of P/E and C/P, and exine sculpturing were used to simply divide pollen types.

KEY TO POLLEN TYPES

1. Pollen strongly euprolate with P/E ratio more than 1.50, 3–4-colporate; average of equatorial diameter up to 20 µm — *Chrysophyllum* type
1. Pollen oblate spheroidal to weakly euprolate with P/E ratio less than 1.50, 3–6-colporate; average of equatorial diameter usually more than 20 µm
   2. C/P ratio more than 0.5. Exine ornamentation not psilate — *Madhuca* type
   2. C/P ratio less than 0.5. Exine ornamentation psilate — *Pouteria* type

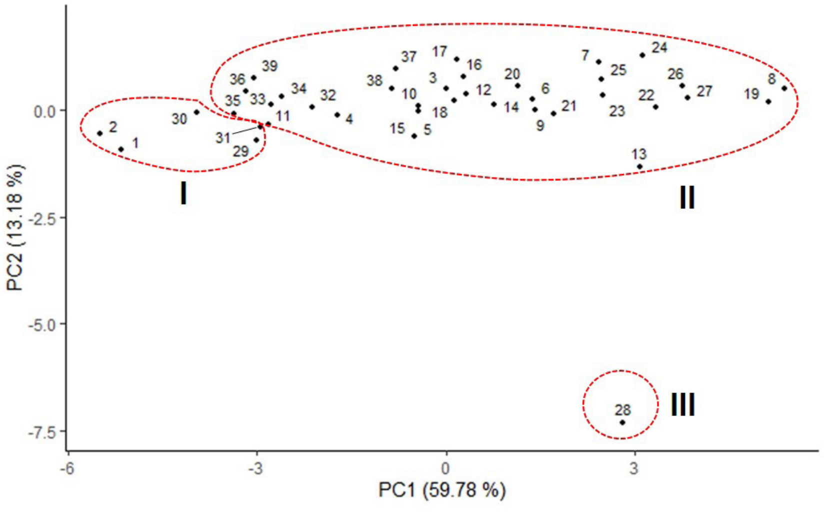

Figure 2. Plot of the first and second principal components accounting for 72.96% of variance.

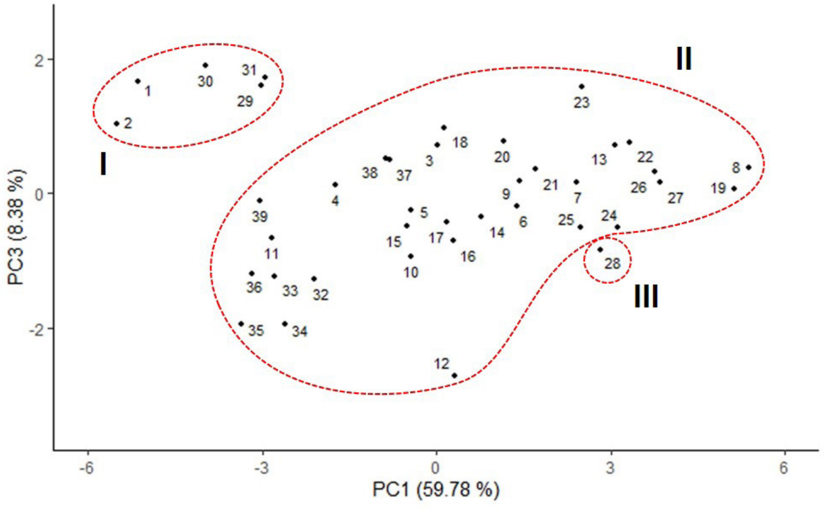

Figure 3. Plot of the first and third components accounting for 68.16% of variance.

Chrysophyllum type (Group I) (Fig. 4A–E)

Pollen grains 3–4-colporate, euprolate, P = 18.5–34 µm, E = 11–15 µm, P/E = 1.53–1.69. Colpi 12–25 µm long (C/P = 0.63–0.71), narrow. Ora 1–3 × 3–5 µm, more or less horizontal elliptic to circular. Intercolpium 6–12 µm wide. Exine thickness 0.8–1.5 µm at apocolpium and mesocolpium, 1.5–2.5 µm near the colpi and ora. Sculpturing scabrate, psilate or psilate at apocolpium and fossulate at mesocolpium.

Taxa included: *Chrysophyllum cainito*, *Planchonella grandifolia*, *P. obovata* and *P. stellibacca*.

Madhuca type (Group II) (Fig. 4H–M, Fig. 5)

Pollen grains 3–6-colporate, oblate spheroidal to euprolate, P = 19–56 µm, E = 17–52 µm, P/E = 0.98–1.46. Colpi 15–38 µm long (C/P = 0.53–0.84), narrow to wide. Ora 2–7 × 4–10 µm, more or less horizontal elliptic to circular. Intercolpium 6–28 µm wide. Exine thickness 1–2.5 µm at apocolpium, at least 1 µm at mesocolpium, 1.5–5 µm near the colpi

Table 2. Data of the examined Thai Sapotaceae species; P, E, C, I, Ol, Ow, Ea, Em and Eap shown in micrometer unit regarding mean ± standard deviation with a range in a parenthesis; P = polar length; E = equatorial width; P/E = shape of pollen grain from ratio between polar length and equatorial width; N = number of apertures (colporate); C = colpus length; I = intercolpial width; Ol = ora length; Ow = ora width; Ea = apocolpial exine thickness; Em = mesocolpial exine thickness; Eap = apertural exine thickness; S = sculpturing; fs = fossulate; gr = granulate; pf = perforate; ps = psilate; sb = scabrate; sr = striate-rugulate; ru = rugulate; + = compound sculpturing throughout pollen surface; / = compound sculpturing with different areas (apocolpium/ mesocolpium); np = non-psilate sculpturing ; p = psilate sculpturing; G = PCA group.

No.	Taxon	P	E	P/E	N	C	C/P	I	Ol	Ow	Ea	Em	Eap	S	G
1	*Chrysophyllum cainito*	20.90 ± 1.60 (19–23)	13.30 ± 0.82 (12–14)	1.57 (euprolate)	3	13.20 ± 0.92 (12–14)	0.63	7.70 ± 0.48 (7–8)	1.05 ± 0.16 (1–1.5)	3.50 ± 0.53 (3–4)	1.00 ± 0.00 (1)	1.00 ± 0.00 (1)	2.00 ± 0.00 (2)	sb (np)	I
2	*C. cainito*	19.95 ± 0.90 (18.5–21)	13.00 ± 1.25 (11–15)	1.53 (euprolate)	3	13.90 ± 1.10 (12–16)	0.69	7.00 ± 0.47 (6–8)	1.25 ± 0.26 (1–1.5)	2.80 ± 0.42 (2–3)	0.88 ± 0.10 (0.8–1)	1.00 ± 0.00 (1)	1.80 ± 0.26 (1.5–2)	sb (np)	I
3	*Madhuca esculenta*	34.50 ± 1.22 (32–35)	25.40 ± 1.14 (24–27)	1.36 (euprolate)	4	24.40 ± 2.07 (22–27)	0.70	15.50 ± 0.71 (15–16)	4.13 ± 0.63 (3.5–5)	5.50 ± 0.58 (5–6)	1.67 ± 0.25 (1.5–2)	2.17 ± 0.29 (2–2.5)	2.93 ± 0.19 (2.5–3)	fs+ru (np)	II
4	*M. floribunda*	28.29 ± 1.89 (25–31)	24.00 ± 1.63 (21–26)	1.17 (subprolate)	4–5	18.50 ± 1.73 (17–20)	0.65	12.60 ± 2.30 (10–15)	1.80 ± 0.27 (1.5–2)	4.60 ± 0.89 (4–6)	1.38 ± 0.25 (1–1.5)	1.50 ± 0.00 (1.5)	2.79 ± 0.27 (2.5–3)	fs+ru (np)	II
5	*M. klacken-bergii*	30.40 ± 2.01 (28–35)	25.30 ± 1.06 (24–27)	1.20 (subprolate)	4	21.00 ± 3.16 (17–26)	0.69	16.71 ± 1.60 (15–20)	4.00 ± 0.66 (3–5.5)	5.85 ± 0.58 (5–7)	1.50 ± 0.00 (1.5)	1.88 ± 0.23 (1.5–2)	2.71 ± 0.39 (2–3)	fs+gr (np)	II
6	*M. krabiensis*	35.75 ± 1.51 (34–39)	30.30 ± 1.83 (28–33)	1.17 (subprolate)	4–5	24.90 ± 1.52 (22–27)	0.69	15.20 ± 1.03 (14–17)	5.15 ± 0.58 (4–6)	8.70 ± 0.67 (8–10)	1.45 ± 0.16 (1–1.5)	2.30 ± 0.26 (2–2.5)	3.55 ± 0.44 (3–4)	fs+gr (np)	II
7	*M. malac-censis*	42.40 ± 1.90 (38–44)	33.00 ± 1.73 (30–35)	1.28 (subprolate)	4	32.90 ± 0.88 (31–34)	0.77	20.89 ± 0.78 (20–22)	4.40 ± 0.52 (4–5)	9.00 ± 0.67 (8–10)	2.00 ± 0.00 (2)	2.20 ± 0.26 (2–2.5)	3.28 ± 0.36 (3–4)	fs+gr (np)	II
8	*M. motleyana*	44.70 ± 1.57 (43–47)	45.40 ± 2.17 (43–50)	0.98 (oblate-spheroidal)	4–5	26.78 ± 1.48 (24–29)	0.59	22.50 ± 1.84 (21–27)	5.70 ± 0.48 (5–6)	9.00 ± 0.82 (8–10)	2.60 ± 0.39 (2–3)	3.00 ± 0.00 (3)	4.40 ± 0.52 (4–5)	pf+sb (np)	II
9	*M. stipulacea*	38.10 ± 2.81 (32–42)	30.00 ± 3.77 (22–34)	1.27 (subprolate)	4–5	26.10 ± 1.81 (23–29)	0.68	18.80 ± 2.04 (14–21)	4.15 ± 0.47 (3–5)	10.10 ± 0.74 (9–11)	1.85 ± 0.24 (1.5–2)	2.05 ± 0.16 (2–2.5)	3.05 ± 0.16 (3–3.5)	fs+gr (np)	II
10	*M. thorelii*	31.80 ± 1.48 (30–34)	27.00 ± 2.40 (24–32)	1.17 (subprolate)	4–5	23.50 ± 1.64 (22–26)	0.73	14.40 ± 2.59 (12–18)	4.20 ± 0.89 (3–6)	6.80 ± 1.55 (5–10)	1.36 ± 0.24 (1–1.5)	1.42 ± 0.20 (1–1.5)	2.55 ± 0.16 (2.5–3)	fs+ru (np)	II
11	*Manilkara hexandra*	27.40 ± 1.26 (25–29)	21.00 ± 1.05 (19–22)	1.30 (subprolate)	5	19.40 ± 0.70 (18–20)	0.70	9.70 ± 0.67 (8–10)	3.55 ± 0.44 (3–4)	3.75 ± 0.63 (3–5)	1.00 ± 0.00 (1)	1.00 ± 0.00 (1)	1.60 ± 0.21 (1.5–2)	pf+gr (np)	II
12	*M. kauki*	30.50 ± 1.87 (28–33)	29.50 ± 1.41 (26–30)	1.03 (prolate-spheroidal)	4	25.75 ± 2.50 (22–27)	0.84	18.20 ± 1.48 (16–20)	6.83 ± 1.47 (4–8)	7.33 ± 0.82 (6–8)	1.31 ± 0.26 (1–1.5)	1.67 ± 0.25 (1.5–2)	2.08 ± 0.20 (2–2.5)	fs+sb (np)	II
13	*M. littoralis*	43.10 ± 3.75 (38–48)	35.30 ± 2.71 (31–40)	1.22 (subprolate)	4	22.80 ± 2.04 (19–26)	0.53	21.70 ± 2.16 (19–25)	6.87 ± 1.17 (5–9)	10.33 ± 1.50 (8–12)	1.76 ± 0.25 (1.5–2)	2.38 ± 0.23 (2–2.5)	3.17 ± 0.35 (3–4)	fs+sb (np)	II

Table 2. Data of the examined Thai Sapotaceae species (Cont.).

No.	Taxon	P	E	P/E	N	C	C/P	I	Ol	Ow	Ea	Em	Eap	S	G
14	*M. zapota*	34.29 ± 0.49 (34–35)	30.67 ± 1.00 (29–32)	1.11 (prolate-spheroidal)	4	24.00 ± 1.00 (23–25)	0.69	19.75 ± 1.04 (19–22)	3.55 ± 0.50 (3–4)	7.00 ± 0.67 (6–8)	1.50 ± 0.00 (1.5)	2.00 ± 0.00 (2)	3.25 ± 0.27 (3–3.5)	sb (np)	II
15	*Mimusops elengi*	33.50 ± 1.35 (31–35)	27.10 ± 1.29 (25–29)	1.23 (subp-rolate)	3–4	23.50 ± 1.43 (22 ± 26)	0.70	17.20 ± 2.25 (13–20)	4.60 ± 0.70 (4–6)	7.80 ± 0.79 (7–9)	1.00 ± 0.00 (1)	1.38 ± 0.35 (1–2)	2.90 ± 0.21 (2.5–3)	pf+gr (np)	II
16	*M. elengi*	31.90 ± 1.29 (30–35)	26.90 ± 1.85 (25–30)	1.18 (subp-rolate)	3–4	25.00 ± 1.41 (23–27)	0.78	16.50 ± 10.8 (15–18)	4.00 ± 0.82 (3–5)	7.90 ± 0.99 (7–10)	1.55 ± 0.16 (1.5–2)	2.05 ± 0.16 (2–2.5)	3.05 ± 0.44 (2.5–4)	pf+gr (np)	II
17	*Palaquium garrettii*	35.10 ± 1.29 (33–37)	28.90 ± 1.20 (28–32)	1.21 (subp-rolate)	4	28.40 ± 1.43 (27–32)	0.80	17.20 ± 0.42 (17–18)	3.22 ± 0.44 (3–4)	5.70 ± 0.67 (5–7)	1.50 ± 0.00 (1.5)	2.05 ± 0.16 (2–2.5)	3.00 ± 0.24 (2.5–3.5)	fs+ru (np)	II
18	*P. garrettii*	38.90 ± 2.08 (36–42)	28.30 ± 1.83 (26–32)	1.37 (eup-rolate)	4–5	25.90 ± 1.85 (22–28)	0.66	13.40 ± 1.35 (12–16)	3.50 ± 0.53 (3–4)	6.30 ± 0.48 (6–7)	1.27 ± 0.25 (1–1.5)	2.11 ± 0.22 (2–2.5)	3.00 ± 0.00 (3)	fs+ru (np)	II
19	*P. obovatum*	53.40 ± 2.01 (50–56)	49.00 ± 1.89 (47–52)	1.08 (prolate-spheroidal)	5–6	34.63 ± 1.60 (32–36)	0.64	25.60 ± 0.55 (25–26)	4.95 ± 0.50 (4–5.5)	10.00 ± 0.94 (9–12)	1.86 ± 0.26 (1.5–2)	2.42 ± 0.38 (2–3)	3.67 ± 0.26 (3.5–4)	pf (np)	II
20	*P. ottolanderi*	43.88 ± 2.36 (40–48)	33.13 ± 2.75 (30–38)	1.32 (subp-rolate)	4–5	31.50 ± 1.91 (30–34)	0.71	19.00 ± 1.63 (17–21)	3.25 ± 0.50 (3–4)	6.43 ± 0.79 (6–8)	1.58 ± 0.20 (1.5–2)	1.83 ± 0.26 (1.5–2)	3.17 ± 0.29 (3–3.5)	fs+gr (np)	II
21	*P. rostratum*	41.60 ± 1.58 (40–45)	32.20 ± 2.57 (30–39)	1.29 (subp-rolate)	5–6	26.80 ± 1.23 (25–29)	0.64	15.80 ± 1.55 (14–19)	4.30 ± 0.82 (3–5)	9.70 ± 0.67 (9–11)	1.63 ± 0.22 (1.5–2)	1.86 ± 0.38 (1.5–2.5)	2.80 ± 0.26 (2.5–3)	fs+sb (np)	II
22	*P. sumatranum*	43.90 ± 1.37 (41–45)	38.50 ± 1.78 (35–40)	1.14 (prolate-spheroidal)	5	26.00 ± 1.83 (23–29)	0.59	18.80 ± 1.48 (16–21)	4.10 ± 0.74 (3–5)	9.30 ± 0.82 (8–10)	1.73 ± 0.25 (1.5–2)	2.35 ± 0.41 (2–3)	4.45 ± 0.50 (4–5)	fs+sb (np)	II
23	*Payena acumi-nata*	45.50 ± 2.51 (43–50)	36.10 ± 1.91 (34–39)	1.26 (subp-rolate)	4	28.17 ± 1.94 (25–30)	0.62	20.00 ± 0.53 (19–21)	3.25 ± 0.46 (2.5–4)	7.33 ± 1.12 (6–9)	1.61 ± 0.22 (1.5–2)	2.63 ± 0.23 (2–2.5)	4.31 ± 0.37 (4–5)	fs+gr (np)	II
24	*P. asiatica*	41.00 ± 3.02 (37–47)	35.30 ± 1.42 (34–38)	1.16 (subp-rolate)	4	32.70 ± 1.57 (30–35)	0.79	22.50 ± 1.51 (21–26)	5.20 ± 0.92 (4–7)	9.20 ± 1.03 (8–11)	1.70 ± 0.26 (1.5–2)	2.70 ± 0.26 (2.5–3)	3.80 ± 0.26 (3.5–4)	fs+gr (np)	II
25	*P. asiatica*	40.40 ± 2.99 (36–46)	35.60 ± 3.41 (29–41)	1.13 (prolate-spheroidal)	4	30.43 ± 1.81 (28–33)	0.75	22.56 ± 2.40 (19–26)	4.83 ± 1.27 (4–8)	8.22 ± 0.97 (7–10)	1.44 ± 0.30 (1–2)	2.38 ± 0.52 (2–3)	3.81 ± 0.26 (3.5–4)	fs+gr (np)	II
26	*P. lucida*	50.11 ± 4.08 (43–56)	41.56 ± 3.81 (37–49)	1.20 (subp-rolate)	4–5	34.67 ± 3.27 (29–38)	0.69	21.40 ± 1.44 (20–23)	4.55 ± 0.90 (3–6)	9.43 ± 0.98 (8–11)	1.69 ± 0.37 (1.5–2.5)	2.00 ± 0.50 (1.5–2.5)	4.00 ± 0.00 (4)	fs+gr (np)	II

Table 2. Data of the examined Thai Sapotaceae species (Cont.).

No.	Taxon	P	E	P/E	N	C	C/P	I	Ol	Ow	Ea	Em	Eap	S	G
27	*P. maingayi*	47.00 ± 5.37 (40–54)	41.60 ± 4.81 (34–48)	1.12 (prolate-spheroidal)	4	31.71 ± 1.70 (30–35)	0.67	24.30 ± 2.41 (22–28)	5.33 ± 1.12 (4–8)	8.80 ± 0.92 (8–11)	2.10 ± 0.21 (2–2.5)	2.30 ± 0.42 (2–3)	3.50 ± 0.47 (3–4)	fs+gr (np)	II
28	*Pouteria campechiana*	46.25 ± 3.65 (40–52)	41.38 ± 2.39 (38–44)	1.11 (prolate-spheroidal)	4	21.88 ± 2.30 (19–25)	0.47	28.00 ± 1.73 (25–30)	6.20 ± 0.84 (5–7)	10.20 ± 1.48 (8–12)	1.13 ± 0.22 (1–1.5)	1.29 ± 0.27 (1–1.5)	2.50 ± 0.35 (2–3)	ps (p)	III
29	*Planchonella grandifolia*	32.50 ± 0.97 (31–34)	20.00 ± 1.05 (18–21)	1.62 (eup-rolate)	3–4	21.13 ± 2.30 (18–25)	0.65	12.40 ± 0.55 (12–13)	2.60 ± 0.97 (2–5)	4.20 ± 0.79 (3–5)	1.00 ± 0.00 (1)	1.06 ± 0.18 (1–1.5)	2.05 ± 0.28 (2–2.5)	ps/fs (np)	I
30	*P. obovata*	28.00 ± 1.33 (26–30)	16.50 ± 0.85 (15–18)	1.69 (eup-rolate)	3	19.89 ± 1.17 (18–21)	0.71	10.11 ± 1.54 (8–12)	2.06 ± 0.39 (1.5–3)	3.22 ± 0.44 (3–4)	1.05 ± 0.16 (1–1.5)	1.50 ± 0.00 (1.5)	2.05 ± 0.16 (2–2.5)	fs (np)	I
31	*P. stellibacca*	30.70 ± 0.95 (29–32)	18.60 ± 0.52 (18–19)	1.65 (eup-rolate)	4	20.40 ± 1.58 (18–23)	0.66	9.75 ± 1.04 (9–12)	2.40 ± 0.46 (2–3)	5.40 ± 0.52 (5–6)	1.00 ± 0.00 (1)	1.38 ± 0.23 (1–1.5)	2.20 ± 0.26 (2–2.5)	ps/fs (np)	I
32	*Sarcosperma arboreum*	25.60 ± 1.71 (23–28)	22.40 ± 1.84 (20–26)	1.14 (prolate-spheroidal)	4	19.50 ± 1.51 (18–22)	0.76	13.10 ± 0.99 (12–15)	2.80 ± 0.48 (2.5–4)	6.30 ± 0.95 (5–8)	1.00 ± 0.00 (1)	1.50 ± 0.00 (1.5)	2.20 ± 0.26 (2–2.5)	fs+sb (np)	II
33	*S. arboreum*	23.40 ± 0.70 (23–25)	20.20 ± 1.32 (18–22)	1.15 (subp-rolate)	4	18.00 ± 1.25 (16–20)	0.76	11.60 ± 0.97 (10–13)	2.40 ± 0.39 (2–3)	5.40 ± 0.52 (5–6)	1.00 ± 0.00 (1)	1.50 ± 0.00 (1.5)	2.05 ± 0.16 (2–2.5)	fs (np)	II
34	*S. griffithii*	21.80 ± 0.42 (21–22)	20.60 ± 0.52 (20–21)	1.05 (prolate-spheroidal)	3–4	17.70 ± 1.25 (16–19)	0.81	13.60 ± 1.58 (11–16)	2.63 ± 0.49 (2–3.5)	5.70 ± 0.82 (5–7)	1.00 ± 0.00 (1)	1.30 ± 0.26 (1–1.5)	2.50 ± 0.00 (2.5)	fs (np)	II
35	*Synsepalum dulcificum*	20.00 ± 1.22 (19–22)	19.71 ± 2.29 (17–23)	1.01 (prolate-spheroidal)	4	15.33 ± 0.58 (15–16)	0.76	12.25 ± 1.71 (10–14)	2.00 ± 0.35 (1.5–2.5)	4.33 ± 0.82 (4–6)	1.00 ± 0.00 (1)	1.17 ± 0.24 (1–1.5)	1.86 ± 0.24 (1.5–2)	sr (np)	II
36	*S. dulcificum*	24.20 ± 1.23 (23–26)	19.20 ± 1.55 (17–22)	1.26 (subp-rolate)	4	19.86 ± 1.86 (17–22)	0.82	11.10 ± 1.60 (9–13)	2.17 ± 0.29 (2–2.5)	5.67 ± 0.58 (5–6)	1.00 ± 0.00 (1)	1.15 ± 0.23 (1–1.5)	1.93 ± 0.16 (1.5–2)	sr (np)	II
37	*Xantolis bur-manica*	36.00 ± 1.33 (34–38)	25.30 ± 1.83 (22–28)	1.42 (eup-rolate)	4	28.20 ± 1.75 (26–32)	0.78	13.60 ± 1.58 (12–17)	3.25 ± 0.82 (2.5–5)	5.15 ± 0.82 (4–6)	1.50 ± 0.00 (1.5)	1.65 ± 0.24 (1.5–2)	2.75 ± 0.26 (2.5–3)	fs (np)	II
38	*X. burmanica*	32.10 ± 1.52 (30–35)	22.30 ± 1.83 (19–25)	1.43 (eup-rolate)	4	23.90 ± 1.10 (22–26)	0.74	13.60 ± 0.97 (12–15)	3.65 ± 0.58 (2.5–4)	6.70 ± 0.67 (6–8)	1.50 ± 0.00 (1.5)	1.68 ± 0.24 (1.5–2)	2.90 ± 0.21 (2.5–3)	fs (np)	II
39	*X. cambodiana*	27.50 ± 1.08 (26–28)	18.80 ± 0.92 (18–20)	1.46 (eup-rolate)	5	21.80 ± 1.62 (19–25)	0.79	8.11 ± 1.17 (6–10)	2.30 ± 0.63 (1.5–3)	4.20 ± 0.42 (4–5)	1.06 ± 0.17 (1–1.5)	1.25 ± 0.27 (1–1.5)	2.00 ± 0.00 (2)	fs (np)	II

Table 3. Summary of variance, including eigenvalues, the proportion of variance of each component and the cumulative variance along the first three given components.

Component	Eigenvalue	Variance	Cumulative variance
1	7.772	59.786	59.786
2	1.713	13.181	72.967
3	1.090	8.387	81.356

Table 4. Loading score of 13 characters on the first three principal components.

Characters	PC1	PC2	PC3
Polar length (P)	.928	-.078	.263
Equatorial diameter (E)	.978	-.092	-.024
P/E ratio (P/E)	-.563	-.001	.729
Number of apertures (N)	.510	.131	-.129
Colpus length (C)	.834	.316	.077
C/P ratio (C/P)	-.362	.659	-.512
Intercolpial width (I)	.924	-.208	-.126
Ora length (OL)	.811	-.188	-.244
Ora width (OW)	.900	-.142	-.120
Apocolpial exine thickness (Ea)	.847	.267	.165
Mesocolpial exine thickness (Em)	.860	.318	.150
Apertural exine thickness (Eap)	.860	.225	.211
Sculpturing (S)	.026	.823	.017

and ora. Sculpturing usually two patterns in one grain, variable in scabrate, granulate, perforate, fossulate, regulate or striate-rugulate.

Taxa included: all species in *Madhuca*, *Manilkara*, *Mimusops*, *Palaquium*, *Payena*, *Sarcosperma*, *Synsepalum* and *Xantolis*.

Pouteria type (Group III) (Fig. 4F–G)

Pollen grains 4-colporate, oblate spheroidal (P/E = 1.00–1.25), P = 40–52 µm, E = 38–44 µm. Colpi 19–25 µm long (C/P = 0.47), narrow. Ora 5–7 × 8–12 µm, horizontal elliptic. Intercolpial 25–30 µm wide. Exine thickness 1–1.5 µm at apocolpium and mesocolpium, 2–3 µm near the colpi and ora. Sculpturing psilate.

Taxon included: *Pouteria campechiana*.

DISCUSSION

Most pollen grains examined in the present study show that they have highly overlapping features. However, the PCA indicated that most quantitative characters were included in the first principal component while exine sculpturing and pollen shape were predominant in the second and the third of that, respectively. As a result of the PCA, the first three principal components supported the pollen to be classified into three pollen groups.

Group I, *Chrysophyllum* type, displays the distinct euprolate shape with a P/E ratio of more than 1.50. This type matches Harley's work (1991) where the pollen of *Chrysophyllum cainito*, *Planchonella grandifolia* and *P. obovata* were placed together in pollen type VII by having a unique stratification of exine in which the equatorial region

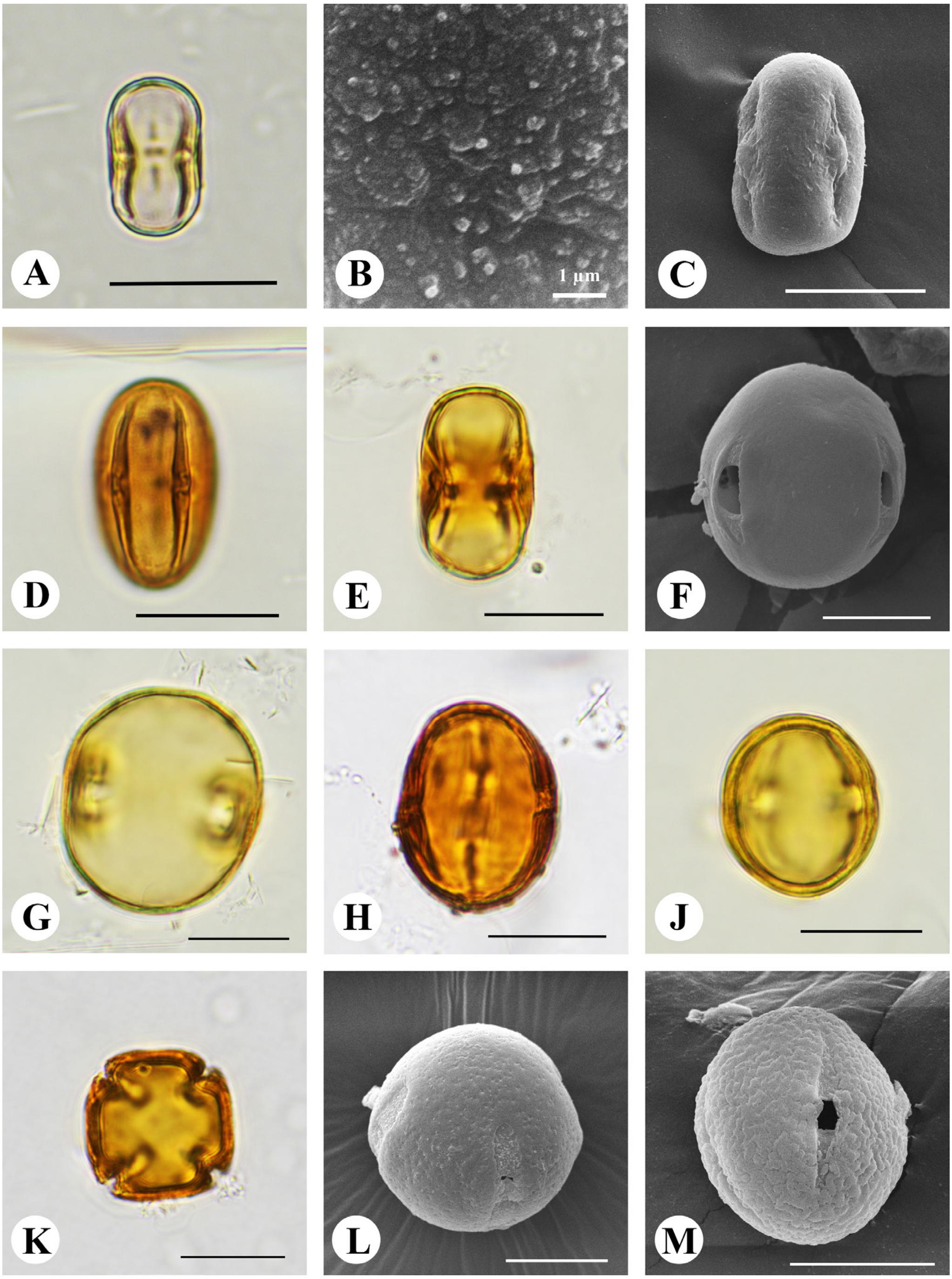

Figure 4. Pollen of Thai Sapotaceae. A, D–E, G–J, K: LM micrographs; B–C, F, L–M: SEM micrographs; A–E: *Chrysophyllum* type; A–B: *Chrysophyllum cainito* (*Kunasit 66*); A: equatorial view; B: mesocolpial surface; C: *Planchonella grandifolia*, equatorial view; D: *P. obovata*, equatorial view; E: *P. stellibacca*, equatorial view; F–G: *Pouteria* type, *Pouteria campechiana*, equatorial view; H–M: *Madhuca* type; H: *Madhuca esculenta*, equatorial view; J: *M. klackenbergii*, equatorial view; K: *M. krabiensis*, polar view; L: *M. motleyana*, subpolar view; M: *M. stipulacea*, subequatorial view. Scale bar = 20 µm otherwise individually indicated by a number.

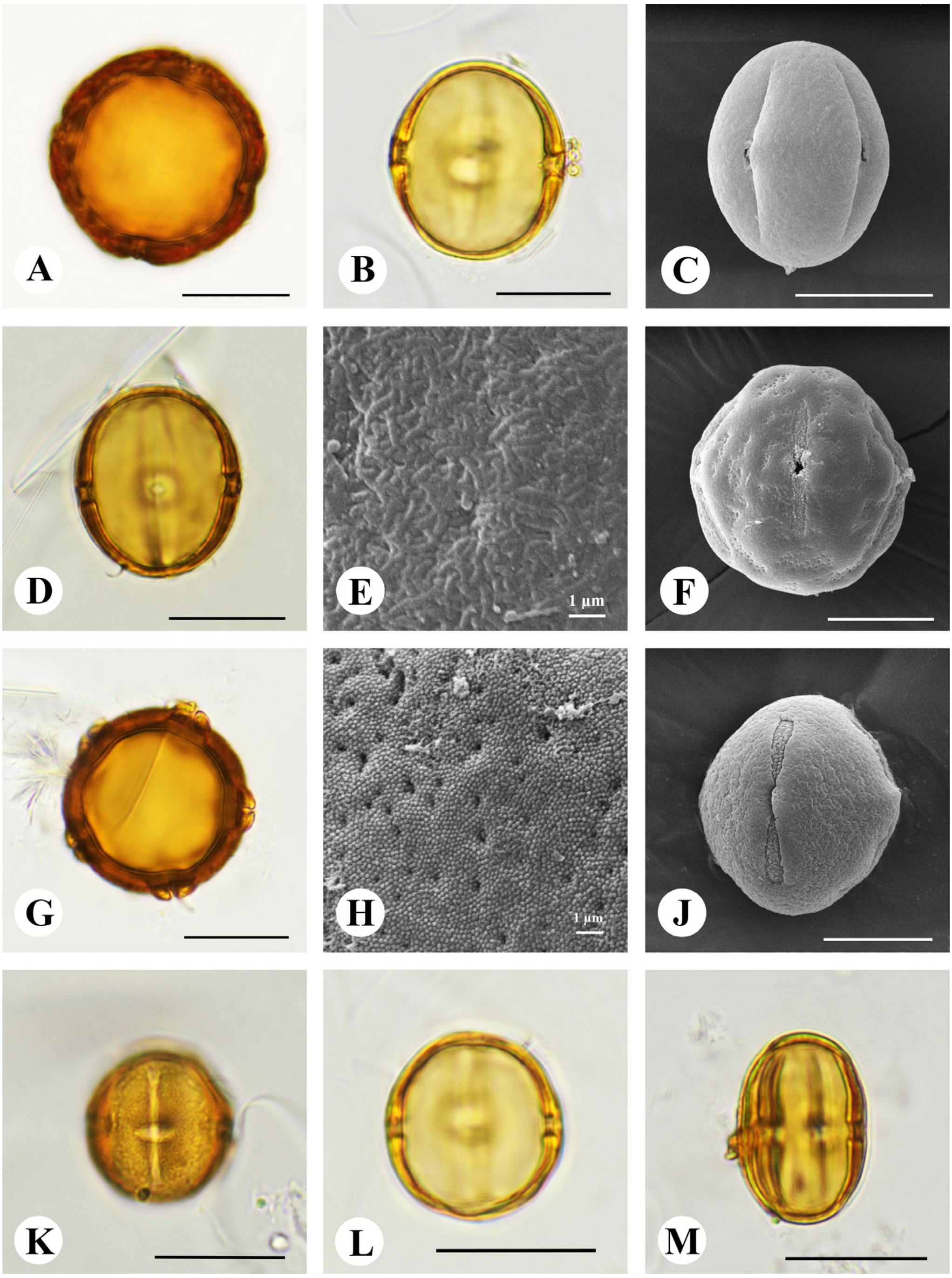

Figure 5. Pollen in *Madhuca* type. A–B, D, G, K–M: LM micrographs; C, E–F, H–J: SEM micrographs; A: *Manilkara littoralis*, polar view; B: *M. zapota*, equatorial view; C: *Mimusops elengi* (*Kunasit 139*), equatorial view; D–E: *Palaquium garrettii* (*Maxwell 00-4*); D: equatorial view; E: mesocolpial surface; F: *P. obovatum*, equatorial view; G: *P. sumatranum*, polar view; H: *Payena asiatica* (*Gardner & P. Tippayasri ST1361*), mesocolpial surface; J: *P. maingayi*, equatorial view; K: *Sarcosperma arboreum* (*Maxwell 01-112*), equatorial view; L: *Synsepalum dulcificum* (*Kunasit 86*), equatorial view; M: *Xantolis cambodiana*, equatorial view. Scale bar = 20 µm otherwise individually indicated by a number.

forms the continuous endexine with narrow endoaperture and having typically different ornamentation between the apocolpium and mesocolpium. The pollen ornamentation of more than one type specific to an area often occurred in many species and is likely involved in adaptations to storage and exit function. In the case of our study, only the pollen of *P. grandifolia* and *P. stellibacca* exposed the differentiated exine between the apocolpium and mesocolpium whereas that of *C. cainito* and *P. obovata* did a single pattern of ornamentation. Our *C. cainito* and *P. obovata* exine surface were quite distinct from those of Harley's showing the modified exine sculpturing. In addition, Pollen of *C. cainito* can be further separated from that of *P. grandifolia*, *P. obovata* and *P. stellibacca* if the pollen size, colpus length and sculpturing were considered specifically. The polar and colpus length of *Chrysophyllum* pollen are always less than 23 µm long and 14 µm long, respectively, while those of *Planchonella* are 26–34 µm long and 18–25 respectively. In addition, the pollen of the *Chrysophyllum* has scabrate ornamentation which is different from those *Planchonella* having fossulate and psilate. However, by the PCA results (Figs. 2 & 3) and the clear pollen shape with 0.729 of loading score (Table 4), pollen of these four species should be classified into the same group.

Group II, the *Madhuca* type, consists of most of the Thai species. The pollen is small to large, 19–56 µm in size. Two patterns of exine sculpturing throughout pollen grains are usually found in this group. According to the group with the highest number of species examined, their variations cause having diversely palynological characters but some of them are specific to a species or a group of species. A striate-rugulate exine ornamentation belongs to *Synsepalum dulcificum* (Fig. 5L). Remarkably, the exine surface of *S. dulcificum* reported by previous authors is slightly different from our study in that the finely striate-granular (Ayensu, 1972) and finely reticuloid exine patterns (Sowunmi, 1974) were recorded. In the case of Sowunmi's study, the pollen was observed only under the LM. The SEM should be applied for clearer ornamentation which is more specific than the LM. The pollen of *Madhuca krabiensis* has square-like amb (Fig. 4K) and only *Madhuca motleyana* has oblate-spheroidal pollen (Fig. 4L). *Palaquium obovatum* possesses sparsely perforate ornamentation (Fig. 5F) and a finely rugulate exine (Fig. 5E) is specific to *Madhuca esculenta*, *M. floribunda*, *M. thorelii*, and *Palaquium garrettii*. The pollen of *Madhuca* type in our study is found in types I, II, III, IV of Harley's study (1991). In the Harley study (1991), these four types were separated based on the shape at amb view, pollen shape, average polar length and exine sculpturing. After careful examination, we found that the first three characters were difficult to apply regarding the boundary and definition of the characters and that only granular and striate-rugulate sculpturing are distinct to segregate types I and II. All our samples in this group were tried to identify using Harley's artificial key but most of them were identified to her types IX, X, XI and XII which no member of the genera in this group is included in those types. One reason we thought is pollen of the same species of our and her pollen are quite different in size that is what to be used in the first couplet of her key. This demonstrated that our pollen was moderately incompatible with her classification criterion. Based on our reconsideration and phenetic analysis result (Figs. 2–3), thus, the pollen of our Group II should be assembled together rather than be classified into different groups.

Group III, the *Pouteria* type has a single species, *Pouteria campechiana*. This Group resembles Group II by its pollen shape and size, but it has clear psilate sculpturing and the lowest C/P ratio of all our samples. This group agrees well with Harley's type V (Harley, 1991) but has a noticeable difference regarding exine ornamentation between our and Harley's *P. campechiana* which coarsely reticulate/psilate and perforate/subpsilate types were reported (Harley, 1986 & 1991). *Pouteria campechiana* pollen with its prolate spheroidal shape obviously has different characters from the *Pouteria* pollen found in Group I, the *Chrysophyllum* type, with *P. grandifolia*, *P. obovata* and *P. stellibacca* having a firmly euprolate shape. The polar length of Group I, the *Chrysophyllum* type, is always less than 35 µm long, while that of Group III, *Pouteria* type is at least 40 µm long. The sculpturing and C/P ratio can also distinguish between these groups with *P. campechiana* having an absolutely smooth surface and the average C/P ratio less than 0.6 while those in Group I are fossulate at the mesocolpium and have a C/P ratio of at least 0.6.

The different pollen type between the *Planchonella* and *Pouteria* was mentioned in the palynological study of Thai Chrysophylloideae proposed by Kunasit & Chantaranothai (2021) which placed *Planchonella grandifolia*, *P. obovata* and *P. stellibacca* in *Pouteria* I type, and *Pouteria campechiana* in *Pouteria* II type. By the PCA result (Figs. 2 & 3), the recognition of these two groups was strongly supported and relative to the previous study except for the assembly of the former *Chrysophyllum* and *Pouteria* I types as *Chrysophyllum* type in our study. Both the present study and Kunasit & Chantaranothai (2021) supported the molecular phylogenetic classifications (Swenson *et al.*, 2007 & 2013; Faria, *et al.*, 2017) which *Planchonella grandifolia*, *P. obovata* and *P. stellibacca* were accepted while *P. campechiana* was still placed in *Pouteria*. As the palynological discussion to the phylogenetic study (Swenson *et al.*, 2008), *Pouteria campechiana* was indicated as *Pouteria* sensu stricto clade, including members of American *Pouteria* species which all represented Harley's pollen type V, unlike Australasian *Pouteria* transferred to other genera, e.g., species in *Planchonella*, it shows the variable pollen types, but not type V. Our study, therefore, agrees well with the taxonomic position of *Pouteria* species proposed by Swenson *et al.* (2007, 2008 & 2013).

The three pollen types proposed here do not match exactly with any classification of Sapotaceae so far published. The classification proposed by Swenson and Anderberg (2005) includes three subfamilies, namely Chrysophylloideae, Sapotoideae and Sarcospermatoideae. In this study, the pollen from samples of species in the Chrysophylloideae, i.e., *Chrysophyllum*, *Pouteria*, *Synsepalum* and *Xantolis*, are found in different groups. According to the previous report of Thai Chrysophylloideae (Kunasit & Chantaranothai, 2021), five pollen types, namely *Chrysophyllum*, *Pouteria* I, *Pouteria* II, *Synsepalum* and *Xantolis* have been proposed. However, in this present study, the pollen of *Synspelalum* and *Xantolis* are similar to those of our Group II, the *Madhuca* type, and do not form their own individual type. The former *Chrysophyllum* and *Pouteria* I types are here placed in our Group I, the *Chrysophyllum* type and the *Pouteria* II type, including *Pouteria campechiana* only is placed in our Group III, *Pouteria* type. All pollen grains of the Sapotoideae (*Madhuca*, *Manilkara*, *Mimusops*, *Palaquium* and *Payena*), and Sarcospermatoideae (*Sarcosperma*), are placed together in Group II, the *Madhuca* type where the pollen of *Madhuca esculenta*, *M. floribunda*, *M. klackenbergii*, *M. thorelii*, *Manilkara kauki*, *Palaquium garrettii*, and *P. sumatranum* is reported here for the first time.

Pollen grains from different collections of the same species, such as *Chrysophyllum cainito*, *Payena asiatica* and *Sarcosperma arboreum*, were palynologically similar. However, different collections of *Palaquium garrettii* were more variable with one having a longer polar axis and higher C/P ratio. In the case of *Mimusops elengi*, collections from different regions (southern and north-eastern Thailand) have pollen grains that are faintly different in exine thickness and a number of apertures, the north-eastern collection of which has thicker exine and frequently 4-colporate apertures while the other is thinner and often 3-colporate. This is also found in *Synsepalum dulcificum*, with the collection from the north-eastern region having a shorter polar length and more spherical-like shape than that from the north. The difference in palynological features between a collection of species often occurred in Harley's study (1991). For example, *Elaeoluma nuda*, one collection of which is in pollen type V while the other two collections examined are in pollen type X. Harley suggested that this variation emphasized the need to study at least two collections of a species wherever possible before trying to make decisions about taxonomic affinities. Collecting a pollen specimen at least two collections in all species examined is our limitation because of having poor flowering specimens and rare species with few collections.

CONCLUSION

The study of Thai Sapotaceae pollen shows that the pollen is monad, oblate spheroidal to euprolate in shape, 3–6-colporate, lalongate aperture and various exine ornamentation from psilate, fossulate, perforate, scabrate, granulate, rugulate to striate-rugulate. Three pollen types are presented based on pollen shape, C/P ratio and exine sculpturing. Even though the pollen morphology cannot define most of the genera, it shows the efficiency of a taxonomic character for Thai species, especially for the new taxonomic status of some species in the former *Pouteria* group.

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