

Pollen morphology of Combretaceae from Thailand and its taxonomic significance

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ABSTRACT. The pollen morphology of 30 taxa from six genera of Thai Combretaceae, including one species each of *Anogeissus* and *Calycopteris*, two species each of *Lumnitzera* and *Quisqualis*, 11 species of *Combretum* and 13 species of *Terminalia* (including one introduced species), was investigated to determine its taxonomic significance. The pollen samples were acetolyzed and investigated under light and scanning electron microscopy. Pollen morphology of Thai Combretaceae was described, compared and discussed along with its taxonomic implications. The taxonomic significance of pollen morphological characters for Thai Combretaceae is limited. The pollen grains were found to be monads, radially symmetrical, isopolar, small- to medium-sized, heterocolpate (tricolporate alternating with subsidiary colpi). The taxa studied can be divided into two groups and nine subgroups according to the fusion of subsidiary colpi at the polar area and the exine sculpturing patterns. However, this grouping is not congruent with the taxonomic classification of the family based on morphological as well as molecular data.

KEY WORDS: Combretaceae, Pollen, Taxonomy, Thailand.

INTRODUCTION

The family Combretaceae belongs to the order Myrtales, and comprises ca 20 genera and 500 species (Heywood *et al.*, 2007; APG III, 2009). The family is distributed throughout the tropics, with some extensions to subtropical and warm-temperate regions (Exell & Stace, 1966; Heywood *et al.*, 2007; Stace, 2007). The family is divided into two subfamilies, Strephonematoideae and Combretoideae. The first one contains the single genus *Strephonema* Hook.f., and the latter contains most of the genera. The subfamily Combretoideae was previously divided into four tribes: Calycopter-ideae, Combreteae, Laguncularieae and Terminalieae (Exell, 1954). More recently, the subfamily was divided into only two tribes, Laguncularieae and Combreteae, and the latter tribe was subdivided into three subtribes: Combretinae, Pteleopsidineae and Terminaliinae (Exell & Stace, 1966; Stace, 2007). Only the subfamily Combretoideae is present in Thailand, with seven genera and 47 species (Nanakorn, 1985, 1986; Pooma & Suddee, 2014). The member of Combretaceae in

Thailand were classified into two tribes and three subtribes, including the tribe Laguncularieae containing the single genus *Lumnitzera* Willd.; the tribe Combreteae with two subtribes: Combretinae containing three genera: *Calycopteris* Lam. ex Poir., *Combretum* Loebl. and *Quisqualis* L., and Terminaliinae containing two genera: *Anogeissus* (DC.) Wall. ex Guillem. & Perr. and *Terminalia* L. (classification follows Stace, 1966).

Studies of pollen morphology of Combretaceae were carried out by a number of previous authors. Erdtman (1966) stated that pollen grains of Combretaceae are tricolporate or tricolporate with pseudocolpi, prolate to prolate-spheroidal in shape, with the sexine evidently thinner than the nexine. The pollen grains of this family are similar to those of Melastomataceae but differ from Myrtaceae, Punicaceae and Sonneratiaceae, which are all classified in the same order Myrtales according to APG III (2009). A more detailed study was produced by Patel *et al.* (1984), who recognized the Combretaceae pollen to be isopolar, radially symmetrical,

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tricolporate (rarely tetracolporate), or heterocolpate with three colporate alternating with three subsidiary colpi, and subsidiary colpi united or separated at the polar area, spheroidal to subprolate shape in equatorial view, circular or hexagonal outline in polar view, with the exine sculpturing diverse from striate, psilate, finely rugulate to rugulate. These authors also suggested that the Combretaceae pollen can be divided into five pollen groups based on the presence of subsidiary colpi and exine sculpturing. El Ghazali *et al.* (1998) investigated 18 genera and 130 species of Combretaceae and reported that the pollen are monads, isopolar, radially symmetrical, tricolporate or heterocolpate. Nine pollen types and two subtypes were recognized based on pollen class, aperture types, thickening of the exine around the endoapertures, costae endopori, pollen size, exine sculpturing and shape in polar view. They reported that pollen morphological data do not support the current taxonomic treatment of the family. Stace (2007) reported two pollen types: tricolporate and heterocolpate, the first type found in *Buchenavia* Eichler, *Laguncularia* C.F.Gaertn. and *Strephonema*, while the latter type is found in the other genera including *Anogeissus*, *Calycopteris*, *Combretum*, *Conocarpus* L., *Guiera* Adans. ex Juss., *Lumnitzera*, *Macrop-teranthes* F.Muell ex Benth., *Pteleopsis* Engl. and *Terminalia*. He pointed out that the exine sculpturing varies between species in the group with tricolporate grains but quite similar in the group with heterocolpate grains. Moreover, the pollen morphology cannot be used for clarifying the relationship between genera. However, these characters might help in identification of some taxa. The pollen morphology of the family has never been studied in Thailand. The aims of the present work were to classify, describe, and illustrate the pollen characteristics of Thai Combretaceae and to assess the taxonomic value of these characters.

MATERIAL AND METHODS

The pollen of 30 taxa of Combretaceae in Thailand (including one introduced species, *Terminalia ivorensis* A.Chev.) was examined using light microscopy (LM) and scanning electron microscopy (SEM). Pollen samples were collected from the field collections around Thailand and some taxa were taken from herbarium specimens

kept at Queen Sirikit Botanic Garden Herbarium (QBG). The list of voucher specimens included in this study is given in Appendix 1. The pollen grains were acetolyzed following the methods described by Erdtman (1966). For light microscopy, the acetolyzed pollens were mounted in silicone oil and sealed with paraplast. Permanent slides are kept at Khon Kaen University Herbarium (KKU). At least 15 pollen grains per taxa were used to measure the polar axis (P), equatorial axis (E), exine thickness in polar view (EX) and colpus length (CL). For scanning electron microscopy, acetolyzed pollen grains were suspended in a drop of absolute alcohol, then transferred to aluminum stubs, air-dried and coated with gold-palladium. SEM micrographs were taken with a Leo 1450VP SEM. The terminology and pollen size classes follow Walker & Doyle (1975) and Punt *et al.* (2007).

RESULTS

The description of pollen morphological characters is provided in alphabetical sequence by tribe, subtribe and genera, while the characters of the taxa are summarized in Table 1.

Tribe Combretae: subtribe Combretinae

Calycopteris (Fig. 2D–F):

Monads, radially symmetrical, isopolar, P = 18–23 μ m, E = 18–23 μ m, small, prolate-spheroidal, heterocolpate, colpus length 13–18 μ m, subsidiary colpi separated at the polar area, exine thickness 1–2 μ m, perforate-microrugulate

Combretum (Figs. 1A–C, 2G–I):

Monads, radially symmetrical, isopolar, P = 14–30 μ m, E = 14–29 μ m, small to medium, spherical, prolate-spheroidal, subprolate, oblate-spheroidal, heterocolpate, colpus length 11–27 μ m, subsidiary colpi fused or separated at the polar area, exine thickness 1–2 μ m, perforate-microrugulate, striate or microrugulate.

Quisqualis (Figs. 1D–F, 2J–L):

Monads, radially symmetrical, isopolar, P = 28–40 μ m, E = 29–42 μ m, medium, oblate-spheroidal or prolate-spheroidal, heterocolpate, colpus length 24–33 μ m, subsidiary colpi fused or separated at the polar area, exine thickness 2–3 μ m, microrugulate or reticulate.

Tribe Combreteae: subtribe Terminaliinae

Anogeissus (Fig. 2A–C):

Monads, radially symmetrical, isopolar, $P = 12\text{--}14\ \mu\text{m}$, $E = 11\text{--}14\ \mu\text{m}$, small, prolate-spheroidal, heterocolpate, colpus length $9\text{--}11\ \mu\text{m}$, subsidiary colpi separated at the polar area, exine thickness $1\text{--}1.5\ \mu\text{m}$, microechinate.

Terminalia (Figs. 1G–L, 3G–L):

Monads, radially symmetrical, isopolar, $P = 13\text{--}21\ \mu\text{m}$, $E = 12\text{--}19\ \mu\text{m}$, small, prolate-spheroidal or subprolate, heterocolpate, colpus length $9\text{--}18\ \mu\text{m}$, subsidiary colpi fused or separated at the polar area, exine thickness $1\text{--}2\ \mu\text{m}$, perforate-microrugulate or microrugulate.

Tribe Laguncularieae

Lumnitzera (Fig. 3A–F):

Monads, radially symmetrical, isopolar, $P = 20\text{--}30\ \mu\text{m}$, $E = 21\text{--}35\ \mu\text{m}$, small to medium, oblate-spheroidal, heterocolpate, colpus length $16\text{--}24\ \mu\text{m}$, exine thickness $1\text{--}4\ \mu\text{m}$, scabrate or reticulate.

DISCUSSION AND CONCLUSION

The study showed that the pollen grains of Thai Combretaceae are quite uniform. The basic pollen characters of the family are monads, isopolar, radially symmetrical, heterocolpate, (tricolporate alternating with subsidiary colpi), colpus $9\text{--}33\ \mu\text{m}$ in length, subsidiary colpi shorter or longer than colpi. Our results agree with the previous reports for the general characters of Combretaceae pollen by Erdtman (1966), Huang (1972), Patel *et al.* (1984), El Ghazali *et al.* (1998) and Stace (2007), except that the tricolpate grains were not observed in Thai Combretaceae. Patel *et al.* (1984) and El Ghazali *et al.* (1998) reported the fusion of subsidiary colpi at the polar area in some species of *Bucida* L., *Calopyxis* Tul. and *Quisqualis*. We also observed these characters in some taxa of *Combretum*, *Terminalia* and *Quisqualis*.

Pollen size and shape varied among species but did not appear to be diagnostic characters for the generic and infrageneric levels of this family. The size of pollen grains varied from small to medium ($P = 12\text{--}40\ \mu\text{m}$, $E = 11\text{--}42\ \mu\text{m}$). The members of

subtribe Terminaliinae have only a small sized-grains whereas subtribe Combretinae and Laguncularieae have a small to medium sized-grains. The largest size was found in *Q. indica* ($P = 37\text{--}40\ \mu\text{m}$, $E = 38\text{--}42\ \mu\text{m}$) and the smallest was found in *A. acuminata* ($P = 12\text{--}14\ \mu\text{m}$, $E = 11\text{--}14\ \mu\text{m}$). The pollen shape in equatorial view varied among species. Most species are prolate-spheroidal in pollen shape and a few species are oblate-spheroidal, subprolate and spherical. The amb outline is circular or hexagonal.

Even though the pollen morphological characters are insufficient to identify all species studied, the exine sculpturing is possibly a helpful character for distinguishing some species because it varies among species, and some species have specific features. Most species of Thai Combretaceae have perforate-microrugulate, microrugulate or striate exine sculpturing, while reticulate a type was found in two species, *Q. conferta* and *L. racemosa*, and a microechinate and scabrate exine was found only in a single species each, *A. acuminata* and *L. littorea* respectively.

Lacking a shared character among taxa in the same genus led to pollen morphological characters to be a considered of less taxonomic value for Thai Combretaceae. However, the pollen characters can be used to divide the Thai Combretaceae into two main groups with nine subgroups based on the fusion of subsidiary colpi at polar area and the exine sculpturing patterns.

Group I (Fig. 1): this group is characterized by the presence of subsidiary colpi fused at the polar area. There are three subgroups according to exine sculpturing patterns.

Subgroup I-A: a group of microrugulate exine sculpturing. This subgroup contains *Q. indica* and *T. catappa*.

Subgroup I-B: a group of perforate-microrugulate exine sculpturing. This subgroup contains *C. chinense*, *T. alata*, *T. calamansanai*, *T. corticosa* and *T. glaucifolia*.

Subgroup I-C: a group of striate exine sculpturing. This contains only a single species, *C. pilosum*.

Group II (Figs. 2–3): this group is characterized

by the presence of subsidiary colpi that separated at the polar area. It can be divided into six subgroups based on exine sculpturing patterns.

Subgroup II-A: a group of microechinate exine sculpturing. This contains only a single species, *A. acuminata*.

Subgroup II-B: a group of perforate-microrugulate exine sculpturing. This contains *C. griffithii*, *C. prosurcum*, *C. punctatum* ssp. *punctatum*, *C. punctatum* ssp. *squamosum*, *C. quadrangulare*, *C. sundaicum*, *Ca. floribunda*, *T. bellirica*, *T. chebula* var. *chebula*, *T. chebula* var. *nana*, *T. pedicellata*, *T. pierrei* and *T. triptera*.

Subgroup II-C: a group of microrugulate exine sculpturing. This contains *C. deciduum*, *C. trifoliatum* and *T. ivorensis*.

Subgroup II-D: a group of striate exine sculpturing. This subgroup contains *C. latifolium* and *T. arjuna*.

Subgroup II-E: a group of reticulate exine sculpturing. This subgroup contains *L. racemosa* and *Q. conferta*.

Subgroup II-F: a group of scabrate exine sculpturing. This subgroup contains only a single species *L. littorea*.

These grouping, however, are not congruent with the taxonomic groups based on macromorphological data (Exell & Stace, 1966; Stace, 2007). This is also in agreement with El Ghazali *et al.* (1998) who reported that the pollen characters cannot help in clarifying the taxonomic relationship in Combretaceae.

The taxonomic significance of pollen morphological characters in Thai Combretaceae is limited. Using the pollen characters alone does not help in resolving the classification of the family as well as they cannot be used to identify all species but they provide some information for distinguishing some taxa. Moreover, using these characters in combination with other characters such as anatomical or molecular data may help in clarifying the relationship between the closely related taxa and may help to further understand the taxonomic relationship within the family.

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APPENDIX 1

Specimens examined

Anogeissus acuminata, Phetchabun, Nam Nao National Park, *Krachai 445 (KKU)*; *Calycopteris floribunda*, Ubon Ratchathani, Khong Chiam, *Krachai 547 (KKU)*; *Combretum chinense*, Nan, Doi Phu Kha National Park, *Srisanga 1706 (QBG)*; *C. deciduum*, Chiang Mai, Fang, *Srisanga et al. 3132 (QBG)*; *C. griffithii*, Chiang Mai, Hang Dong, *Wattana & Pongamornkul 239 (QBG)*; *C. latifolium*, Khon Kaen, Nam Phong National Park, *Krachai 601 (KKU)*; *C. pilosum*, Udon Thani, Phu

Table 1. Pollen morphological characters of Combretaceae in Thailand (E = equatorial axis, P = polar axis, Size classes: M = medium sized-grains and S = small sized-grains, exine sculpturing: ME = microechinate, MR = microrugulate, PM = perforate-microrugulate, RE = reticulate, SC = scabrate, ST = striate, Subsidiary colpi: + = subsidiary colpi fused at the polar area, - = subsidiary colpi separated at the polar area).

Species	P (µm) (Range and mean ± SD)	E (µm) (Range and mean ± SD)	Shape	Size classes	exine thickness (µm)	colpus length (µm)	subsidiary colpi	exine sculp- turing	Group
Tribe Combretaceae: subtribe Combretinae									
<i>Calycopteris floribunda</i> (Roxb.) Lam. ex Poir.	18–23 (20.73 ± 1.53)	18–23 (20.53 ± 1.24)	Prolate spheroidal	s	1–2 (1.53 ± 0.29)	13–18 (15.4 ± 1.40)	-	PM	II-B
<i>Combretum chinense</i> Roxb.	19–25 (21.2 ± 1.42)	19–23 (21.06 ± 1.03)	Prolate spheroidal	s, m	1–2 (1.7 ± 0.31)	16–21 (18.06 ± 1.16)	+	PM	I-B
<i>C. deciduum</i> Collett & Hemsl.	23–26 (24.86 ± 0.91)	21–25 (23.06 ± 1.09)	Prolate spheroidal	s, m	1.5–2 (1.7 ± 0.25)	20–22 (21.53 ± 0.74)	-	MR	II-C
<i>C. griffithii</i> Van Heurck & Müll.Arg.	19–20 (19.53 ± 0.51)	17–21 (18.53 ± 1.06)	Prolate spheroidal	s	1.5–2 (1.63 ± 0.22)	15–17 (16.2 ± 0.67)	-	PM	II-B
<i>C. latifolium</i> Blume	23–30 (24.93 ± 1.98)	21–27 (24.06 ± 1.65)	Prolate spheroidal	s, m	1–2 (1.46 ± 0.22)	20–27 (22.06 ± 1.69)	-	ST	II-D
<i>C. pilosum</i> Roxb.	24–30 (26.8 ± 1.79)	21–27 (23.16 ± 1.52)	Subprolate	s, m	1–2 (1.53 ± 0.12)	20–27 (23.8 ± 2.19)	+	ST	I-C
<i>C. prostratum</i> Craib	16–19 (17.46 ± 0.83)	14–17 (15.93 ± 0.88)	Prolate spheroidal	s	1 (1 ± 0)	14–16 (15.33 ± 0.72)	-	PM	II-B
<i>C. punctatum</i> Blume ssp. <i>punctatum</i>	23–26 (24.13 ± 1.06)	22–28 (24.8 ± 1.69)	Oblate spheroidal	s, m	1.5–2 (1.73 ± 0.25)	17–23 (20.53 ± 1.45)	-	PM	II-B
<i>C. punctatum</i> ssp. <i>squamosum</i> (Roxb. ex G.Don) Exell	21–25 (23.4 ± 1.4)	22–26 (23.33 ± 1.39)	Prolate spheroidal	s, m	1–2 (1.6 ± 0.38)	17–22 (20.13 ± 1.80)	-	PM	II-B
<i>C. quadrangulare</i> Kurz	15–16 (15.46 ± 0.51)	14–17 (15.2 ± 0.86)	Prolate spheroidal	s	1–2 (1.33 ± 0.30)	11–13 (12.4 ± 0.63)	-	PM	II-B

Table 1. Continued.

Species	P (μm) (Range and mean ± SD)	E (μm) (Range and mean ± SD)	Shape	Size classes	exine thickness (μm)	colpus length (μm)	subsidiary colpi	exine sculp- turing	Group
<i>Combretum sundaicum</i> Miq.	25–28 (26.86 ± 0.91)	25–29 (26.8 ± 1.42)	Spherical	m	1–2 (1.93 ± 0.25)	20–23 (22.2 ± 1.01)	-	PM	II-B
<i>C. trifoliatum</i> Vent.	14–19 (15.53 ± 1.18)	14–16 (15 ± 0.75)	Prolate spheroidal	s	1–1.5 (1.1 ± 0.20)	11–15 (12.4 ± 0.91)	-	MR	II-C
<i>Quisqualis conferta</i> (Jack) Exell	28–35 (32.4 ± 2.26)	29–32 (30.4 ± 0.98)	Prolate spheroidal	m	2–2.5 (2.06 ± 0.17)	24–31 (27.46 ± 2.44)	-	RE	II-E
<i>Q. indica</i> L.	37–40 (38.73 ± 1.33)	38–42 (40.6 ± 1.40)	Oblate spheroidal	m	2–3 (2.4 ± 0.50)	28–33 (30.6 ± 1.72)	+	MR	I-A
Tribe Combreteae: subtribe Terminaliinae									
<i>Anogeissus acuminata</i> (Roxb. ex DC.) Wall. ex Guillem. & Perr.	12–14 (13.2 ± 0.67)	11–14 (12.8 ± 1.01)	Prolate spheroidal	s	1–1.5 (1.3 ± 0.25)	9–11 (10.2 ± 0.70)	-	ME	II-A
<i>Terminalia alata</i> B.Heyne ex Roth	17–21 (19.13 ± 1.12)	15–18 (16.86 ± 0.83)	Prolate spheroidal	s	1–2 (1.26 ± 0.31)	15–18 (16.26 ± 1.16)	+	PM	I-B
<i>T. arjuna</i> (Roxb. ex DC.) Wight & Arn.	15–17 (15.86 ± 0.51)	13–15 (13.93 ± 0.59)	Prolate spheroidal	s	1–1.5 (1.13 ± 0.22)	12–14 (13.33 ± 0.61)	-	ST	II-D
<i>T. bellirica</i> (Gaertn.) Roxb.	16–18 (16.93 ± 0.59)	16–19 (16.86 ± 0.91)	Prolate spheroidal	s	1–1.5 (1.2 ± 0.25)	12–15 (13.8 ± 1.01)	-	PM	II-B
<i>T. calamansanai</i> (Blanco) Rolfe	13–16 (14.46 ± 0.74)	12–14 (13.26 ± 0.59)	Prolate spheroidal	s	1–1.5 (1.06 ± 0.17)	10–13 (11.93 ± 0.70)	+	PM	I-B
<i>T. catappa</i> L.	17–20 (18.4 ± 0.98)	16–18 (17.2 ± 0.67)	Prolate spheroidal	s	1–1.5 (1.33 ± 0.24)	13–18 (16 ± 1.25)	+	MR	I-A
<i>T. chebula</i> Retz. var. <i>chebula</i>	14–16 (15.13 ± 0.83)	12–14 (13.3 ± 0.72)	Prolate spheroidal	s	1–1.5 (1.16 ± 0.24)	11–14 (12.33 ± 0.81)	-	PM	II-B

Table 1. Continued.

Species	P (µm) (Range and mean ± SD)	E (µm) (Range and mean ± SD)	Shape	Size classes	exine thickness (µm)	colpus length (µm)	subsidiary colpi	exine sculp- turing	Group
<i>T. chebula</i> var. <i>nana</i> Gagnep.	14-17 (15.93 ± 0.88)	12-15 (13.66 ± 0.81)	Subprolate	s	1-2 (1.36 ± 0.35)	11-14 (12.73 ± 0.79)	-	PM	II-B
<i>Terminalia coricosa</i> Pierre ex Laness.	18-21 (19.6 ± 0.98)	16-19 (17.4 ± 0.91)	Prolate spheroidal	s	1-1.5 (1.26 ± 0.25)	16-18 (16.86 ± 0.91)	+	PM	I-B
<i>T. glaucifolia</i> Craib	15-17 (16.13 ± 0.51)	14-16 (15.06 ± 0.59)	Prolate spheroidal	s	1-1.5 (1.3 ± 0.25)	12-15 (13.46 ± 0.83)	+	PM	I-B
<i>T. ivorensis</i> A.Chev.	14-17 15.53 ± 0.74)	13-16 (14.13 ± 0.74)	Prolate spheroidal	s	1 (1 ± 0)	12-15 (12.6 ± 0.82)	-	MR	II-C
<i>T. pedicellata</i> Nanakorn	17-21 (18.6 ± 1.12)	16-19 (17.33 ± 0.89)	Prolate spheroidal	s	1-1.5 (1.2 ± 0.25)	13-17 (14.8 ± 0.94)	-	PM	II-B
<i>T. pierrei</i> Gagnep.	14-17 (15.8 ± 0.86)	12-16 (13.66 ± 1.04)	Subprolate	s	1-1.5 (1.1 ± 0.2)	11-14 (13 ± 0.92)	-	PM	II-B
<i>T. triptera</i> Stapf	13-15 (13.53 ± 0.63)	12-13 (12.33 ± 0.48)	Prolate spheroidal	s	1 (1 ± 0)	9-12 (10.46 ± 0.91)	-	PM	II-B
Tribe Laguncularieae									
<i>Lumnitzera littorea</i> (Jack) Voigt	27-30 (28.6 ± 0.81)	27-35 (29.66 ± 2.63)	Oblate spheroidal	m	2-4 (2.9 ± 0.43)	19-24 (22.4 ± 1.45)	-	SC	II-F
<i>L. racemosa</i> Willd.	20-24 (22.06 ± 1.09)	21-26 (23.66 ± 1.34)	Oblate spheroidal	s, m	1-2 (1.66 ± 0.36)	16-19 (17.13 ± 0.83)	-	RE	II-E

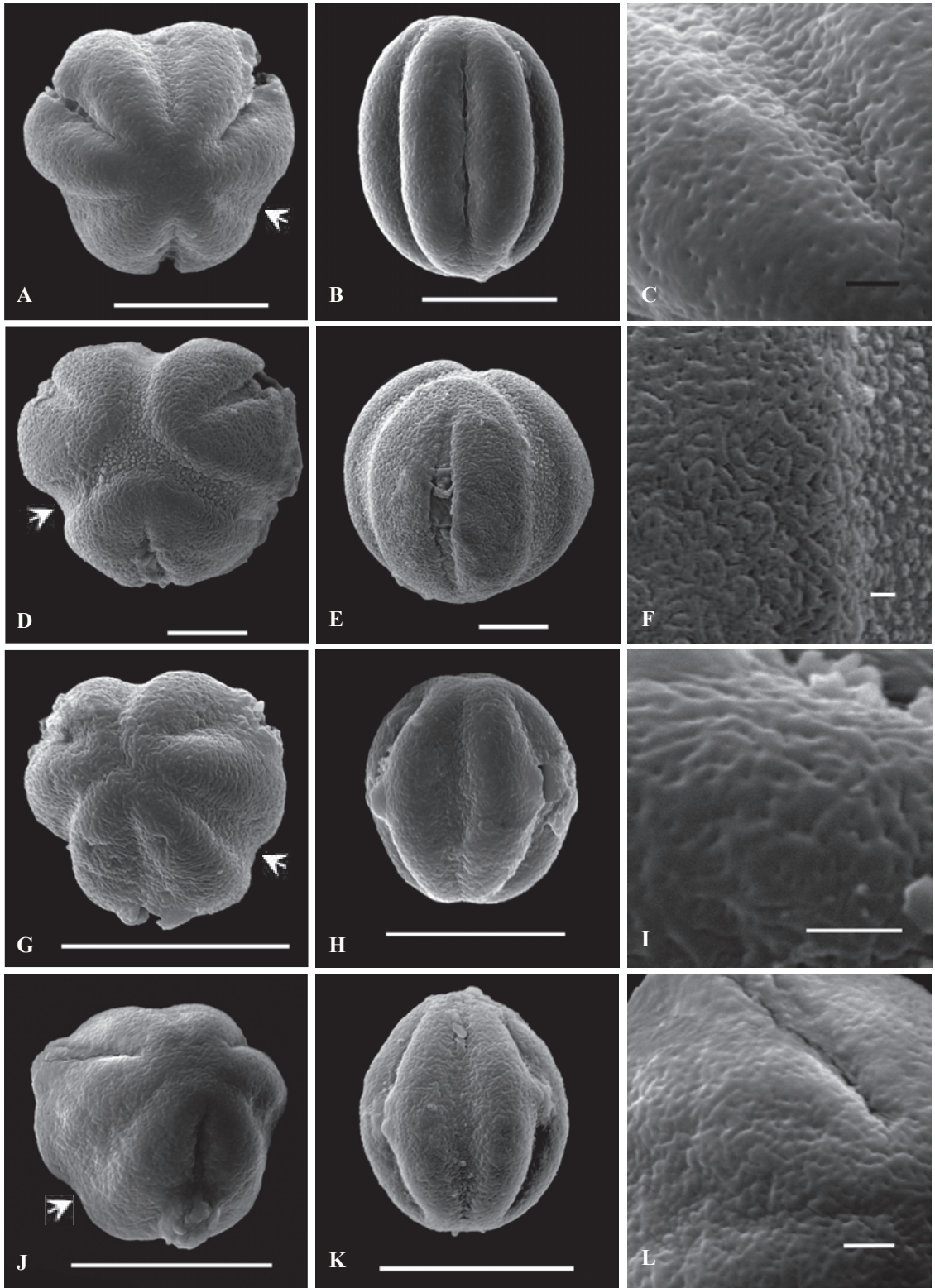


Figure 1. SEM micrographs of pollen grains. Group I: A–C: *Combretum chinense*; D–F: *Quisqualis indica*; G–I: *Terminalia alata*; J–L: *T. calamansanai*. A, D, G, J polar view; B, E, H, K equatorial view; C, F, I, L details of exine sculpturing. Scale bar = 10 μ m (A, B, D, E, G, H, J, K), 1 μ m (C, F, I, L); arrowheads indicate subsidiary colpi.

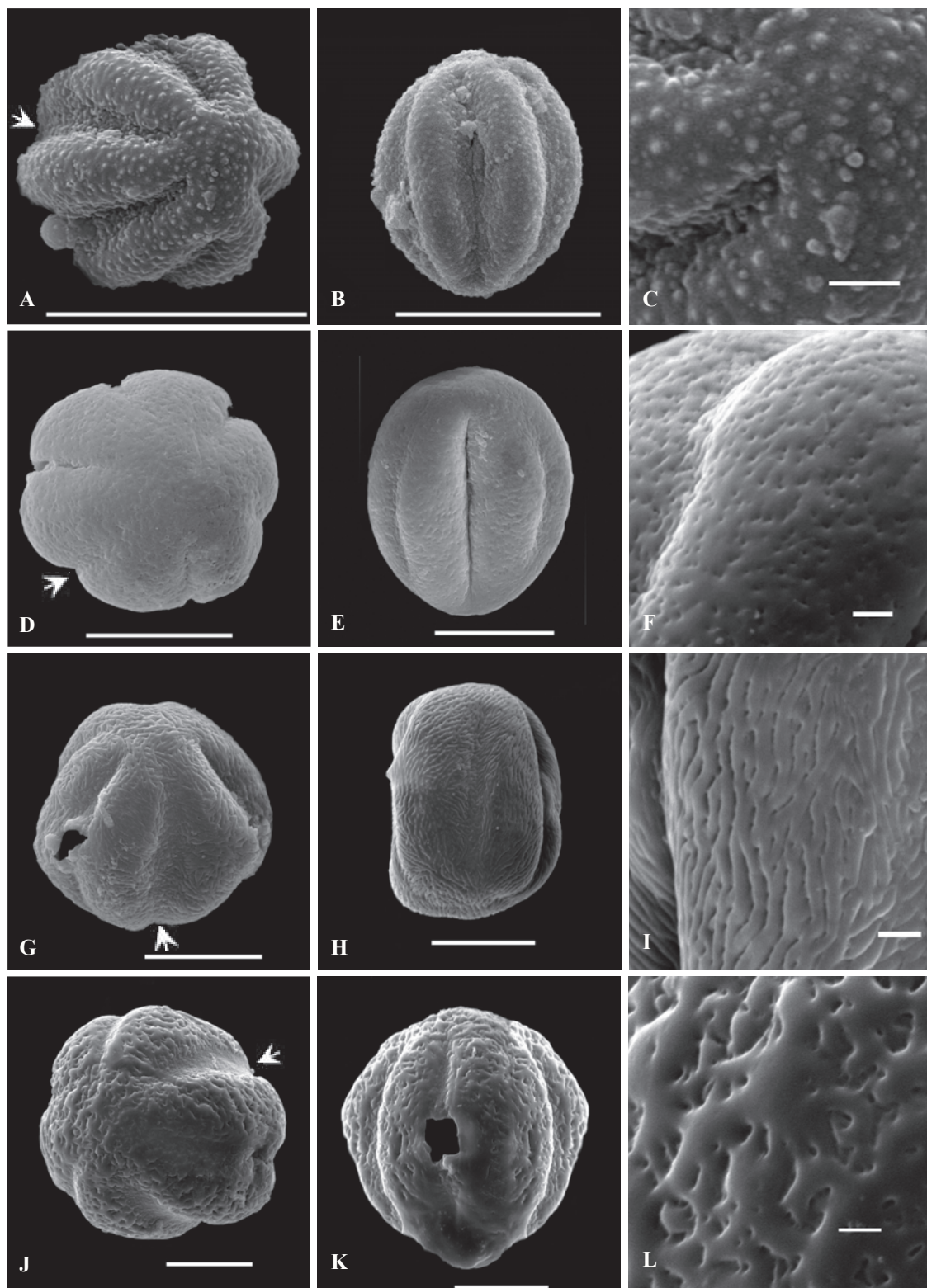


Figure 2. SEM micrographs of pollen grains. Group II: A–C: *Anogeissus acuminata*; D–F: *Calycopteris floribunda*; G–I: *Combretum latifolium*; J–L: *Quisqualis conferta*. A, D, G, J polar view; B, E, H, K equatorial view; C, F, I, L details of exine sculpturing. Scale bar = 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L); arrowheads indicate subsidiary colpi.

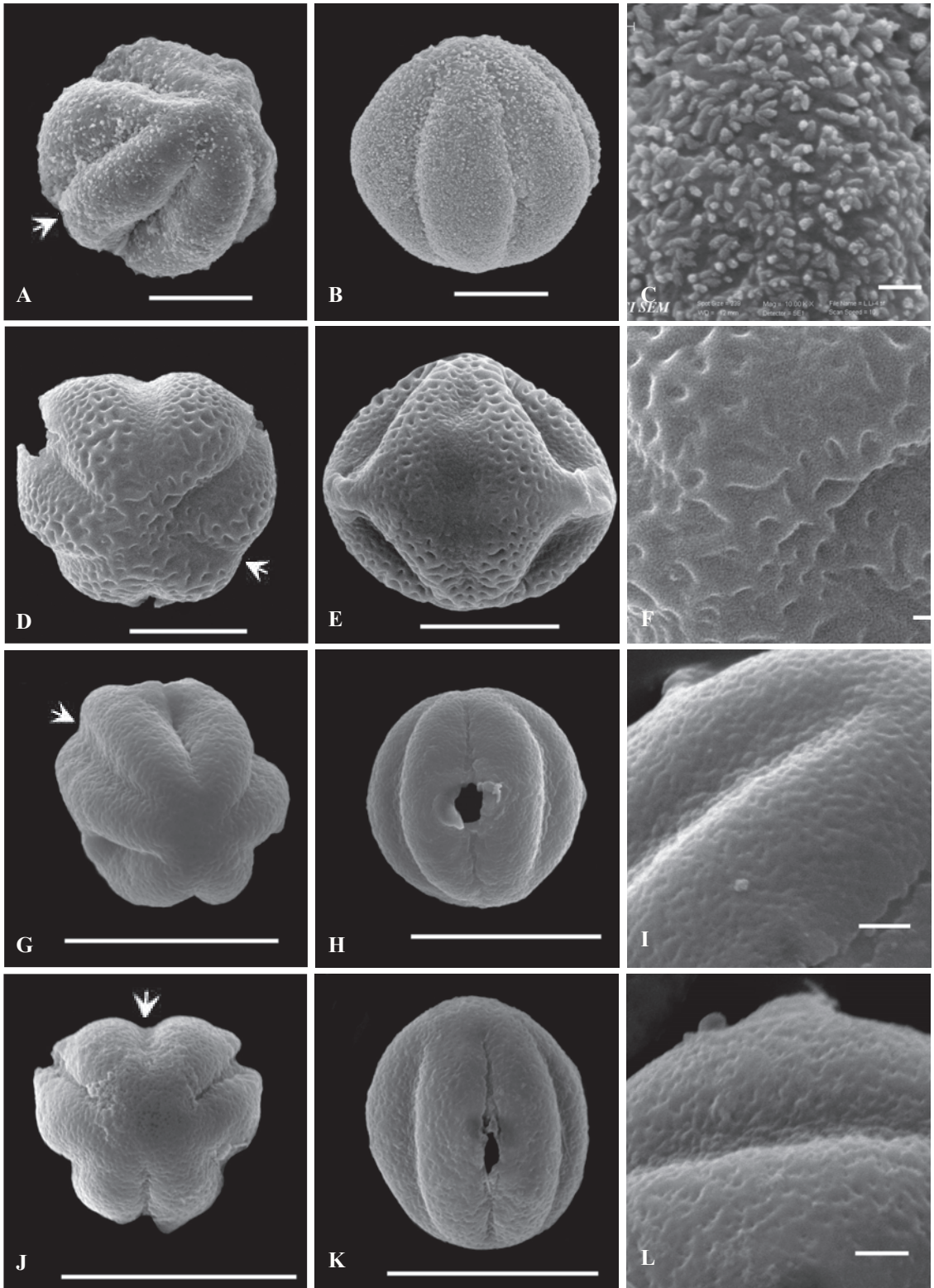


Figure 3. SEM micrographs of pollen grains. Group II: A–C: *Lumnitzera littorea*; D–F: *L. racemosa*; G–I: *Terminalia chebula* var. *chebula*; J–L: *T. triptera*. A, D, G, J polar view; B, E, H, K equatorial view; C, F, I, L details of exine sculpturing. Scale bar = 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L); arrowheads indicate subsidiary colpi.