Chapter 4

Pollen morphology of *Ficus* subsection *Urostigma* (Moraceae)

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Abstract

The pollen morphology of *Ficus* subsection *Urostigma* has been studied using light microscopy and scanning electron microscopy. It conforms to the description of *Ficus* pollen in the literature except for the observed rare occurrence of 4-porate pollen, which was unknown so far in the genus. Due to minor variability it was not possible to distinguish any pollen types. No significant pollen morphological differences were found between species with active pollination and species with passive pollination.

Key words: *Ficus*, Moraceae, pollen, pollination.

Introduction

Ficus L. subsect. *Urostigma* (Gasp.) Berg and *F.* subsect. *Conosycea* (Miq.) Berg form section *Urostigma* (Gasp.) Endl. of *F.* subgenus *Urostigma* (Gasp.) Miq. *Ficus* subsect. *Urostigma* comprises 28 species, which are distributed from West Africa and Madagascar through the Asian mainland to Japan and through southern Malesia to Australia and the Pacific (Berg & Wiebes, 1992; Berg & Corner, 2005; Chantarasuwan et al., 2013). All species are trees, many are hemi-epiphytic, some are terrestrial. The syconiums (figs) are usually borne below the leaves, sometimes on the older branches. Staminate flowers occur mostly near the ostiole of the syconium or are regularly dispersed among the pistillate flowers; in some species (e.g., *F. arnottiana* (Miq.) Miq. and *F. virens* Aiton var. *dispersa* Chantaras.) they occur both around the ostiole (abundant) and dispersed (scarce). *Ficus* subsect. *Conosycea* comprises 66 species (Berg & Corner, 2005), their figs are mostly sessile and the staminate flowers are dispersed, as in some of the species of subsect. *Urostigma* (see above).

Literature on the pollen morphology of *Ficus* is scarce (Langeveld & van der Ham, 2005). Recent studies include those by Khan et al. (2001) and Tzeng et al. (2009). The latter provided detailed descriptions and scanning electron micrographs of 28 *Ficus* taxa occurring in Taiwan, three of which belong to subsect. *Urostigma*. According to the available studies, pollen grains of *Ficus* are very small to small monads (largest = equatorial diameter 6–22 µm), 2- or sometimes 3-porate, and quite uniform. The shape of 2-porate grains is ellipsoid, often slightly asymmetrical, one side being more convex than the other (Fig. 4-1G; 4-2E, M; 4-3 E,K). The orientation of the polar axis in 2-porate grains is hard or impossible to determine. The shape of 3-porate grains is triangular in polar view and oblate in equatorial view. Nearly all species have 2-porate pollen, many species (c. 50% according to the literature studied) have minor percentages of 3-porate pollen as well. *Ficus palmata* Forssk. (= *F. pseudosycomorus* Decne.) is reported to have exclusively 3-porate pollen (Horowitz & Baum, 1967). The pores are circular and vary in size from 0.7–2.5 µm. The exine is thin, flexible, up to 1 µm thick and tectate. Mostly, the nexine and sexine are equally thick; sometimes the nexine is slightly thicker. The infratectum is granular with indistinct columellae. The ornamentation is psilate or slightly scabrate.

The relationship between *Ficus* and its pollinators is a classical story (Ramirez, 1969; Wiebes, 1979). All species are pollinated by fig wasps (Agaonidae). Two pollination types have been distinguished: 1. Active pollination, in which pollen is deliberately collected by the wasps and stored in their pollen pockets, and 2. Passive pollination, in which the wasps receive the pollen from the flowers, scattered over their body. Both passive and active pollination are found in section *Urostigma* (Kjellberg et al., 2001).

The aims of the present study is to describe the pollen of *Ficus* subsect. *Urostigma*, trying to find pollen morphological markers supporting the taxonomy (Chantarasuwan et al., 2013) and phylogeny (Chantarasuwan et al., in prep.) of this group, and to assess if there is any difference between the pollen of species with the passive pollination type and species with the active type.

Materials and methods

All material studied belongs to *Ficus* section *Urostigma*. Pollen of 12 out of the 28 species of subsect. *Urostigma* and two species of subsect. *Conosycea* (*F. altissima* Blume and *F. amplissima* J.E.Sm.) was examined (Table 1). The latter two species were included for comparison, because the species of subsect. *Conosycea* share some morphological characters with subsect. *Urostigma* (e.g., deciduousness, staminate flowers dispersed, and the colour of the ovaries partly red). The classification used is according to Chantarasuwan et al. (2013). Among the species studied, *F. prolixa* G.Forst. and *F. virens* var. *dispersa* could have passive pollination, while the other species (including *F. virens* Aiton var. *matthewii* Chantaras.) probably have active pollination (Kjellberg et al., 2001; Kjellberg personal communication, 2012). The pollen samples were taken from collections preserved in the herbaria of the Naturalis Biodiversity Center at Leiden (L) and the Muséum National d'Histoire Naturelle in Paris (P).

All samples were prepared for light microscopy (LM) and scanning electron microscopy (SEM), following the techniques described by Van der Ham (1990). Ten pollen grains per sample were measured. The terminology used follows Punt et al. (2007). The shape of asymmetrical 2-porate pollen grains is described as 'gibbous' in the present study. Although the orientation of the polar axis in 2-porate grains is hard or impossible to determine, the smallest diameter of the grains is still given here as P.

Results

Ficus subsection *Urostigma*

The pollen grains are very small to small, 2– or sometimes 3–porate, rarely 4–porate monads; P x E = 7.7–13.6 x 11.4–19.7 µm. The shape 2–porate grains is ellipsoid or gibbous, while that of 3–porate grains is triangular in polar view and oblate in equatorial view; 4–porate grains are quadrangular in polar view; P/E = 0.56–0.81. The pores are circular and 1.2–4.7 µm diam. The exine is less than 1 µm thick, and the ornamentation is nearly always scabrate (elements < 1 µm: finely punctate, microrugulate or microverrucate).

Table 4-1 Pollen characters of *Ficus* subsect. *Urostigma* and *Conosycea*

Taxa	Distribution	P x E (µm)	P/E	Shape	Aperture system	Pore (µm)	Ornamentation	Figures
Subsect. *Urostigma*								
F. arnottiana	India, Sri Lanka, Nepal	9.8 x 16.4	0.60	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.3	microverrucate	4-1 A–C
F. cordata	Africa	11.8 x 16.4	0.72	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.3–3.9	microverrucate	4-1 D–F
F. densifolia	India, Sri Lanka	11.5 x 15.5	0.73	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.3	microrugulate	4-1 G–I
F. geniculata var. geniculata	SE Asia	9.7 x 15.4	0.62	ellipsoid, gibbous	2-porate	1.6	indistinctly punctate	4-1 J–L
F. ingens	Africa	11.6 x 16.2	0.71	ellipsoid, gibbous	2-porate	2.3–3.1	indistinctly punctate	4-1 M–O
F. orthoneura	SE Asia	11.5 x 14.1	0.81	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	1.6	microrugulate	4-2 A–C
F. prolixa	W Pacific	7.7 x 11.4	0.67	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	1.2	indistinctly microverrucate	4-2 D–F
F. pseudoconcinna	Sulawesi	9.3 x 14.0	0.66	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.0	indistinctly microverrucate	4-2 G–I
F. religiosa	India to SE Asia	13.6 x 18.9	0.72	ellipsoid, gibbous	2-porate	1.6–2.3	indistinctly microverrucate	4-2 J–L
F. salicifolia	Africa	12.9 x 19.7	0.65	ellipsoid, gibbous, triangular, quadrangular	2-, 3- and 4-porate (50 : 20 : 1)	3.9–4.7	microverrucate	4-2 M–O
F. superba	SE Asia, W Malesia	8.3 x 13.0	0.63	ellipsoid, gibbous	2-porate	1.6	indistinctly microverrucate	4-3 A–C
F. virens var. dispersa	Malesia, W Pacific	10.8 x 16.5	0.65	ellipsoid, gibbous	2-porate	2.3	indistinctly microverrucate	4-3 D–F
F. virens var. matthewii	India, Sri Lanka	11.9 x 17.0	0.70	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.3–3.9	microverrucate	4-3 G–I
Subsect. *Conosycea*								
F. altissima	SE Asia, Malesia	10.7 x 14.8	0.72	ellipsoid, gibbous	2-porate	2.3	microverrucate	4-3 J–L
F. amplissima	India, Sri Lanka	9.2 x 16.4	0.56	ellipsoid, gibbous	2-porate	2.3	psilate	4-3 M–O

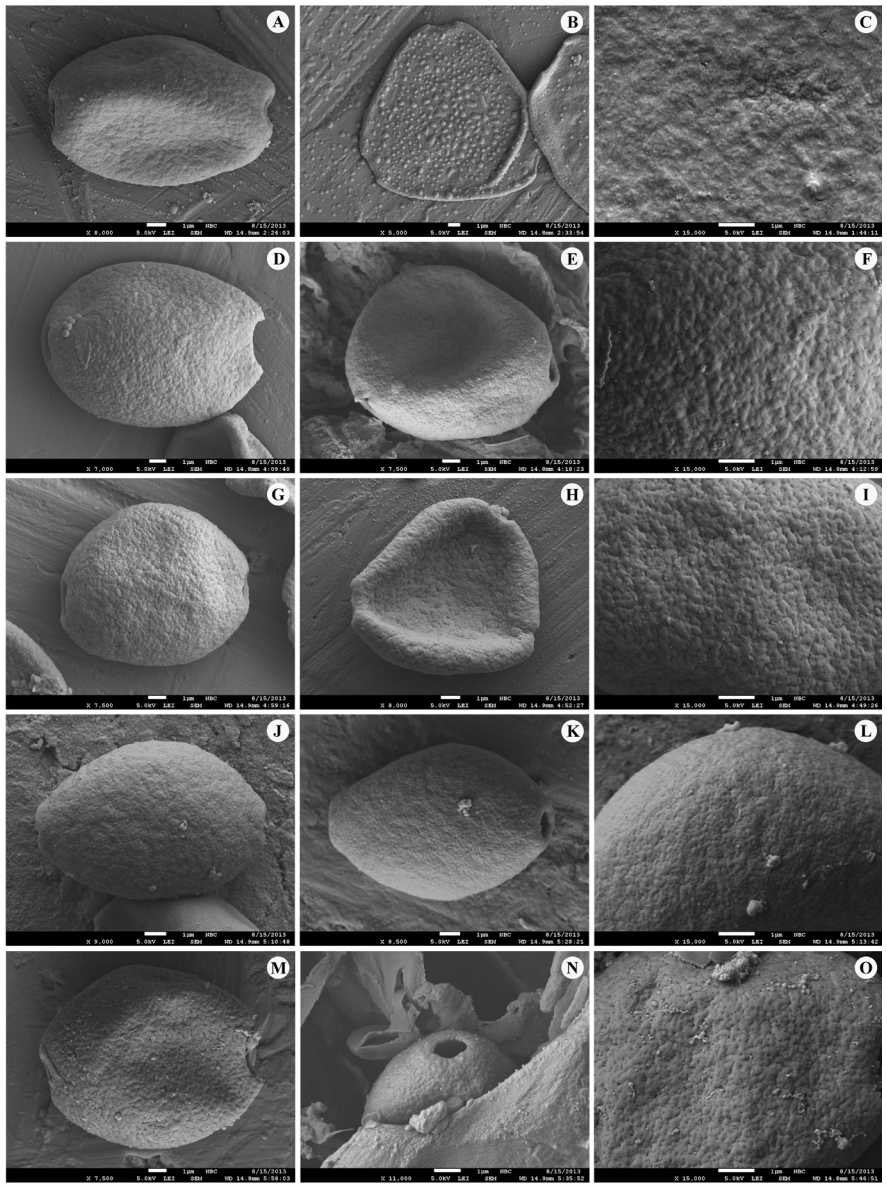

FIGURE 4-1. A-C. Pollen of *F. arnottiana* (from *Kurz s.n.*): A. ellipsoid grain, B. triangular grain in polar view, C. indistinctly microverrucate surface; D-F. Pollen of *F. cordata* (from *Robert J. Rodin 2969*): D. ellipsoid grain, E. triangular grain in surface view, *F.* indistinctly microverrucate surface; G-I. Pollen of *F. densifolia* (from *Etienne 5156*): G. gibbous grain, H. triangular grain in polar view, I. microrugulate surface; J-L. Pollen of *F. geniculata* var. *geniculata* (from *Chantarasuwan 220910-1*): J. gibbous grain, K. grain with circular pore, L. indistinctly punctate surface. M-O. Pollen of *Ficus ingens* (from *Lotsy & Goddijn 379*): M. ellipsoid grain, N. circular pore, O. indistinctly punctate surface. All photographs by B. Chantarasuwan.

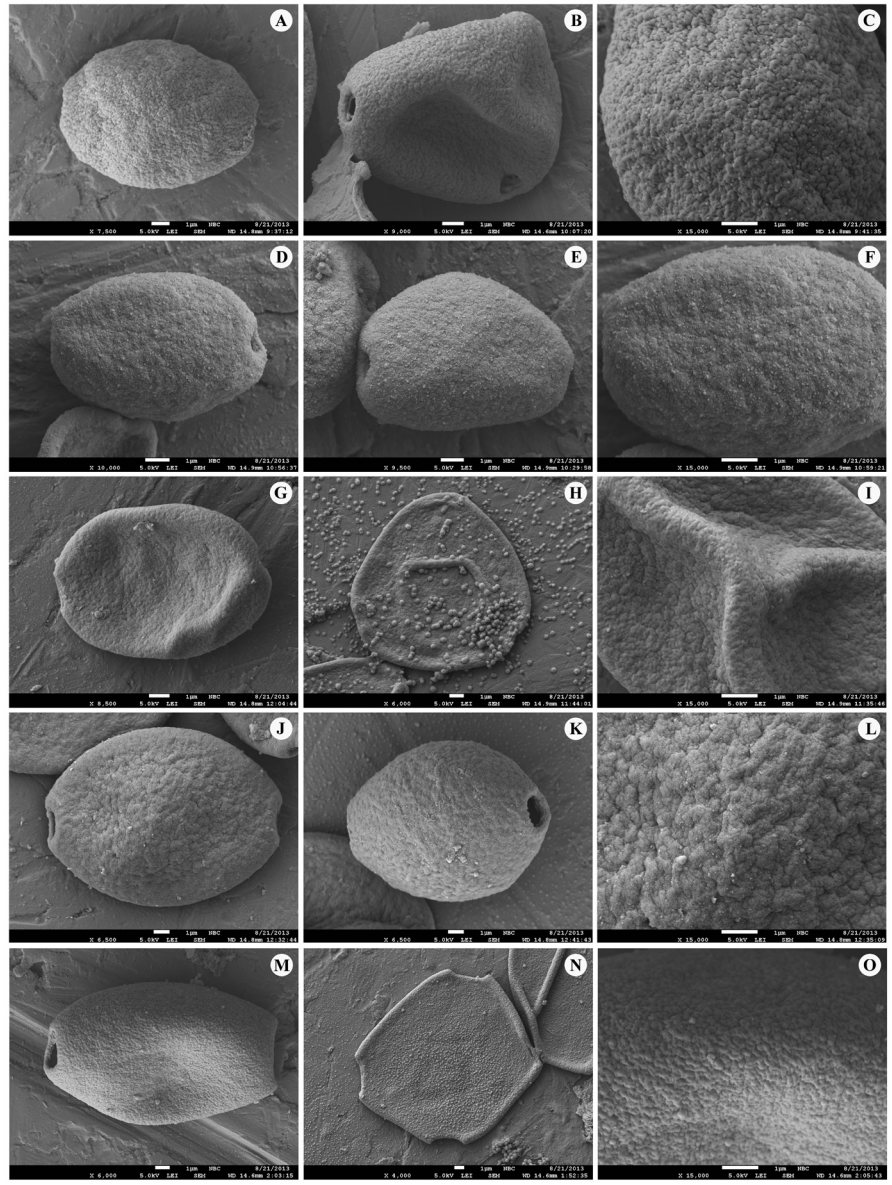

FIGURE 4-2. A-C. Pollen of *F. orthoneura* (from *M.M. Cavalerie & Fortunat 2050*): A. ellipsoid grain, B. triangular grain in polar view, C. microrugulate surface; D-F. Pollen of *F. prolixa* (from *Florence 10308*): D. ellipsoid grain, E. gibbous grain, F. indistinctly microverrucate surface; G-I. Pollen of *F. pseudoconcinna* (from *T.C. Whitmore & K. Sidiyasa TCW3429*): G. ellipsoid grain, H. triangular grain in polar view, I. indistinctly microverrucate surface; J-L. Pollen of *F. religiosa* (from *W. Koelz 4030*): J. ellipsoid grain, K. grain with circular pore, L. indistinctly microverrucate surface; M-O. Pollen of *Ficus salicifolia* (from *J. Léonard 4959*): M. ellipsoid grain, N. quadrangular grain in polar view, O. microverrucate surface. All photographs by B. Chantarasuwan.

***Ficus arnottiana* (Miq.) Miq. (Fig. 4-1A–C)**
Material: Sri Lanka. Maison, 1864, *Kurz s.n.* (P).

Pollen grains small, 2– or sometimes 3–porate; P x E = 9.8 x 16.4 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.60. Proportion of 2– and 3–porate grains about 50/1. Pores circular, about 2.3 µm diam. Exine thin (<1 µm), microverrucate.

***Ficus cordata* Thunb. (Fig. 4-1D–F)**
Material: South–West Africa. Namib desert, 17 Dec 1947, *Robert J. Rodin 2969* (P).

Pollen grains small, 2– or sometimes 3–porate; P x E = 11.8 x 16.4µm. Shape of 2–porate grains ellipsoid or gibbous, of 3– porate grains triangular in polar view and oblate in equatorial view; P/E = 0.72. Proportion of 2– and 3–porate grains about 50/1. Pores circular, 2.3–3.9 µm diam. Exine thin (< 1 µm), microverrucate.

***Ficus densifolia* Miq. (Fig. 4-1G–I)**
Material: Réunion. 7 Apr 1975, *Etienne 5156* (P).

Pollen grains small, 2– or sometimes 3–porate; P x E = 11.5 x 15.5 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.73. Proportion of 2– and 3–porate grains about 50/1. Pores circular, about 2.3 µm diam. Exine thin (<1 µm), microrugulate.

***Ficus geniculata* Kurz. var. *geniculata* (Fig. 4-1J–L)**
Material: Thailand. Phitsanulok, 22 Sept 2010, *Chantarasuwan 220910-1*(L).

Pollen grains small, 2–porate; P x E = 9.7 x 15.4 µm. Shape ellipsoid or gibbous; P/E = 0.62. Pores circular, about 1.6 µm diam. Exine thin (<1 µm), indistinctly punctate.

***Ficus ingens* (Miq.) Miq. (Fig. 4-1M–O)**
Material: South Africa. Magaliesberge, Aug 1925, *Lotsy & Goddijn 379* (L)

Pollen grains small, 2–porate; P x E = 11.6 x 16.2 µm. Shape ellipsoid or gibbous; P/E = 0.71. Pores circular, 2.3–3.1 µm diam. Exine thin (<1 µm), indistinctly punctate.

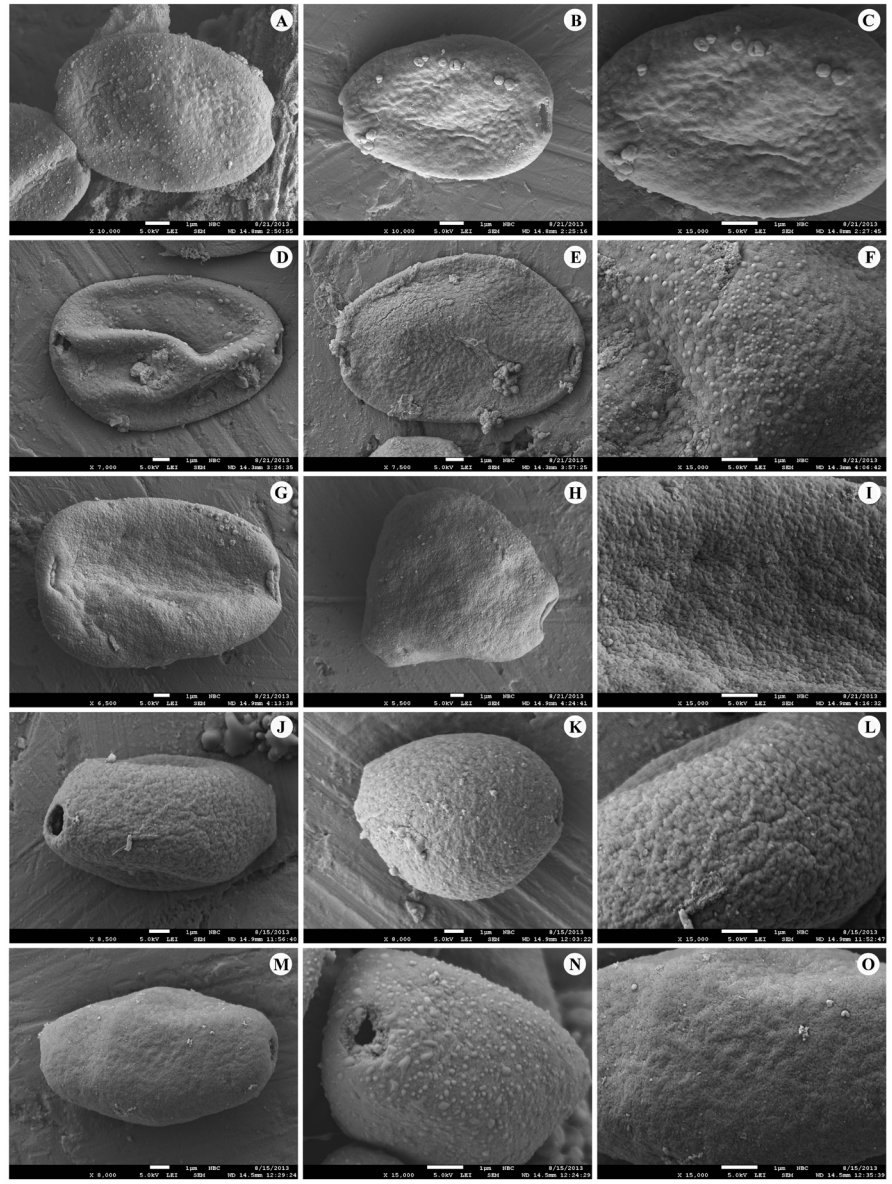

FIGURE 4-3. A-C. Pollen of *F. superba* (from *F.S.P. Ng FRI 5047*): A. ellipsoid grain, B. a grain show circular pore, C. indistinctly microverrucate surface; D-F. Pollen of *F. virens* var. *dispersa* (from *Floyd NGF 6457*): D. a grain show 2–porate, E. gibbous grain, F. indistinctly microverrucate surface; G-I. Pollen of *F. virens* var. *matthewii* (from *Ridsdale 722*): G. ellipsoid grain, H. triangular grain in polar view, I. microverrucate surface; J-L. Pollen of *F. altissima* (from *Chantarasuwan 281111-2*): J. ellipsoid grain with circular pore, K. gibbous grain, L. microverrucate surface; M-O. Pollen of *Ficus amplissima* (from *Wirawan et al. 1133*): M. ellipsoid grain, N. circular pore, O. psilate surface. All photographs by B. Chantarasuwan.

***Ficus orthoneura* H.Lév. & Vaniot (Fig. 4-2A–C)**
Material: China. Kouy–Tchéou, 6 Jun 1904, *M.M. Cavalerie & Fortunat 2050* (P).

Pollen grains small, 2– or sometimes 3–porate; P x E = 11.5 x 14.1 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.81. Proportion of 2– and 3–porate grains about 50/1. Pore circular, about 1.6 µm diam. Exine thin (<1 µm), microrugulate.

***Ficus prolixa* G. Forst. (Fig. 4-2D–F)**
Material: Tahiti. Mont Hiurai, 10 May 1990, *Florence 10308* (L).

Pollen grains very small, 2– or 3–porate; P x E = 7.7 x 11.4 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.67. Proportion of 2–porate and 3–porate grains about 50/1. Pore circular, about 1.2 µm diam. Exine thin (<1 µm), indistinctly microverrucate.

***Ficus pseudoconcinna* Chantaras. (Fig. 4-2G–I)**
Material: Indonesia. Sulawesi, 17 Sep 1984, *T.C. Whitmore & K. Sidiyasa TCW3429* (L).

Pollen grains small, 2– or sometimes 3–porate; P x E = 9.3 x 14.0 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.66. Proportion of 2– and 3–porate grains about 50/1. Pores circular, about 2.0 µm diam. Exine thin (<1 µm), indistinctly microverrucate.

***Ficus religiosa* L. (Fig. 4-2J–L)**
Material: India. Punjab, 23 Jan 1933, *W. Koelz 4030* (L).

Pollen grains small, 2–porate; P x E = 13.6 x 18.9 µm. Shape ellipsoid or gibbous; P/E = 0.72. Pores circular, about 1.6–2.3µm diam. Exine thin (<1 µm), indistinctly microverrucate.

***Ficus salicifolia* Vahl (Fig. 4-2M–O)**
Material: Libye. Djebel Uweinat, 12 Dec 1968, *J. Léonard 4959* (P).

Pollen grains small, 2– or sometimes 3–porate, rarely 4–porate; P x E = 12.9 x 19.7 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view, of 4–porate grains quadrangular in polar view; P/E = 0.65. Proportion of 2– , 3– and 4–porate grains about 50/20/1. Pore circular, 3– 4.7 µm diam. Exine thin (<1 µm), microverrucate.

***Ficus superba* (Miq.) Miq. (Fig. 4-3A–C)**
Material: Malaysia. Johore, 16 Apr 1967, *F.S.P. Ng FRI 5047* (L).

Pollen grains very small, 2–porate; P x E = 8.3 x 13.0 µm. Shape ellipsoid or gibbous; P/E = 0.63. Pores circular, about 1.6 µm diam. Exine thin (< 1 µm), indistinctly microverrucate.

***Ficus virens Aiton var. dispersa* Chantaras. (Fig. 4-3D–F)**
Material: Papua New Guinea. New Britain, West Nakanai, *Floyd NGF 6457* (L).

Pollen grains small, 2–porate; P x E = 10.8 x 16.5 µm. Shape ellipsoid or gibbous; P/E = 0.65. Pores circular, about 2.3 µm diam. Exine thin (< 1 µm), indistinctly microverrucate.

***Ficus virens Aiton var. matthewii* Chantaras. (Fig. 4-3G–I)**
Material: India. South India, Cardamom Hills, *Ridsdale 722* (L).

Pollen grains small, 2– or sometimes 3–porate; P x E = 11.9 x 17.0 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.70. Proportion of 2– and 3–porate grains about 50/1. Pore circular, 2.3–3.9 µm diam. Exine thin (< 1 µm), microverrucate.

Ficus subsect. Conosycea
The pollen grains are very small to small, 2–porate; P x E = 9.2–10.7 x 14.8–16.4 µm. The shape 2–porate grains is ellipsoid or gibbous; P/E = 0.56–0.72. The pores are circular and about 2.3 µm diam. The exine is less than 1 µm thick, and the ornamentation is nearly always scabrate (elements < 1 µm: finely punctate, microverrucate), or sometimes psilate.

***Ficus altissima* Blume (Fig. 4-3J–L)**
Material: Thailand. Chiang Rai, Doi Po, 28 Nov 2011, *Chantarasuwan 281111-2* (L).

Pollen grains small, 2–porate; P x E = 10.7 x 14.8 µm. Shape ellipsoid or gibbous; P/E = 0.72. Pores circular, about 2.3 µm diam. Exine thin (< 1 µm), microverrucate.

***Ficus amplissima* J.E. Sm. (Fig. 4-3M–O)**
Material: Sri Lanka. Wilpattu National Park, 13 Jul 1969, *Wirawan et al. 1133* (P).

Pollen grains small, 2–porate; P x E = 9.2 x 16.4 µm. Shape ellipsoid or gibbous; P/E = 0.56. Pores circular, about 2.3 µm diam. Exine thin (< 1 µm), psilate.

Discussion

The pollen morphology of the species of *Ficus* subsect. *Conosycea* and *F.* subsect. *Urostigma* described in the present study conforms to the general description of *Ficus* pollen in the literature (see Introduction), though, as far as known, 4-porate pollen grains (observed in *F. salicifolia*) were unknown in the genus. Subsect. *Urostigma* shows very little pollen diversity, which is the general picture in the genus *Ficus* (Langeveld & van der Ham, 2005). Minor variation occurs in all characters, but this does not seem to be useful in distinguishing pollen types, subdividing subsection *Urostigma* or supporting clades as found by Chantarasuwan et al. (in prep.).

Neither is much difference observed between subsect. *Urostigma* and the two species of subsect. *Conosycea*. In our study, subsect. *Conosycea* showed only 2-porate pollen, but only two species were included in the observation and five out of the 12 species of subsect. *Urostigma* also have exclusively 2-porate pollen.

The pollen of the two species, which could have passive pollination (*F. prolixa* and *F. virens* var. *dispersa*), cannot be distinguished from the other species, which show active pollination. This supports the results found earlier in larger sets of species (Khan et al. 2001; Kjellberg, 2001; personal communication F. Kjellberg, 2012; Rønsted et al., 2005, 2008; Tzeng et al., 2009; Cruaud et al., 2012). Our conclusion is that pollen morphology is not useful in distinguishing taxonomic groups, clades, or groups of species with either the active or passive pollination mode.

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