

A palynotaxonomic study of the genus *Filipendula* (Rosaceae)

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Abstract Pollen grains from 15 species (18 taxa) of the genus *Filipendula* were examined with light and scanning electron microscopy. It was revealed that the pollen grains are isopolar, tricolporate, with scabrate or scabrate-microechinate surface. The pollen morphology was compared with the conventional classification systems of the genus by different authors, and supported Shimizu's system (1961), in which the genus was divided into three subgenera. The monotypic subgen. *Hypogyna* is characterized by pollen lacking fastigium and thickened costae colpi. The other monotypic subgen. *Filipendula* differs from others by pollen having larger grain, larger pore size, longitudinally elliptic fastigium and thickened costae colpi. The largest subgen. *Ulmaria* is distinguished by pollen having rounded or latitudinally elliptic fastigium and thickened costae colpi. Sectional classification was not supported by the pollen morphology due to insufficient variability.

Key words *Filipendula*, palynology, systematics.

Genus *Filipendula* Mill. (Rosaceae) includes about 20 species and is predominantly distributed in the temperate and subarctic northern hemisphere, especially in northeastern Asia including Korea, Japan, northeastern China and eastern Siberia (Ohwi, 1953; Shimizu, 1961; Schanzer, 1994). Infrageneric classifications of *Filipendula* have been proposed by Juzepczuk (1941) and Popov (1957). The former divided the genus into three subgenera and two sections, while the latter into two subgenera and two sections (Table 1). In their systems, however, only indigenous species to their own country were included. After them, Shimizu (1961) revised the whole genus, amending the two former systems. In his system (Table 1), 15 species all over the world were classified into two monotypic subgenera *Hypogyna* T. Shimizu and *Filipendula*, and one large subgenus *Ulmaria* Moench with four sections *Ulmaria* Hill, *Albicoma* Juz., *Sessilia* T. Shimizu and *Schalameya* Juz., based mainly on morphological characters such as roots, stipules, leaves, flowers and achenes. Sergievskaya (1967) revised Shimizu's system (1961) and made a different one in which the genus was divided into four subgenera, by retaining only Shimizu's sect. *Ulmaria* within subgenus *Ulmaria* and transferring the remaining sections into subgenus *Aceraria* as in Juzepczuk (1941). Schanzer (1989, 1994) provided a new taxonomic treatment of the

genus on the basis of morphological and geographical data. He divided the genus into four sections: *Hypogyna*, *Schalameya*, *Albicoma* and *Filipendula*. In his treatment, however, no species of section *Sessilia* (Shimizu, 1961) or *Gymnocarpa* (Sergievskaya, 1967) were included and *F. hexapetala* Gilib., the type species of the monotypic subgenus *Filipendula* (Shimizu, 1961; Sergievskaya, 1967) or *Eu-Filipendula* (Juzepczuk, 1941), was treated as a species in the name of *F. vulgaris* of section *Filipendula* including most species of subgenus *Ulmaria* (Juzepczuk, 1941; Shimizu, 1961; Sergievskaya, 1967). The sections of Sergievskaya (1967) do not correspond with subgenera of any previous authors. The four systems of Juzepczuk (1941), Shimizu (1961), Sergievskaya (1967), and Schanzer (1994) are incongruent with each other to a certain extent (Table 1).

Pollen morphology has been used to elucidate taxonomic relationships in many angiosperm taxa (Erdtman, 1972), including Rosaceae (Reitsma, 1966; Eide, 1981). The pollen morphology of *Filipendula* was optically observed from limited number of local species (Ikuse, 1955; Kim & Chung, 1986) and has never been utilized in constructing or evaluating the infrageneric systems. The present study aimed to provide the palynological data for the taxonomy of the genus *Filipendula*, and to evaluate the infrageneric systems mentioned above on the basis of a new set of characters.

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Table 1 Comparison of the infrageneric systems of the genus *Filipendula* (from Schanzer, 1994)(Bold-typed species were investigated in this study)

Juzepczuk (1941)	Shimizu (1961)	Sergievskaia (1967)	Schanzer (1994)
	Subgen. Hypogyna T. Shimizu	Subgen. Hypogyna T. Shimizu	Sect. Hypogyna (T. Shimizu) Shantser
	1. <i>F. occidentalis</i> (S. Watson) Howell	1. <i>F. occidentalis</i> (S. Watson) Howell	1. <i>F. occidentalis</i> (S. Watson) Howell
Subgen. Aceraria Juz.	Subgen. Ulmaria Moench	Subgen. Aceraria Juz.	
Sect. Schalameya Juz.	Sect. Schalameya Juz.	Sect. Aceraria Serg.	Sect. Schalameya Juz.
1. <i>F. kamtschatica</i> Maxim.	2. <i>F. kamtschatica</i> Maxim.	2. <i>F. kamtschatica</i> Maxim.	2. <i>F. kamtschatica</i> Maxim.
2. <i>F. glabra</i> Nakai ex Kom. & Aliss.	3. <i>F. glaberrima</i> Nakai	3. <i>F. koreana</i> Nakai	3. <i>F. glaberrima</i> Nakai
3. <i>F. purpurea</i> Maxim.	4. <i>F. yezoensis</i> Hara	4. <i>F. auriculata</i> (Ohwi) Kitam.	4. <i>F. formosa</i> Nakai
4. <i>F. palmata</i> (Pall.) Maxim.	5. <i>F. purpurea</i> Maxim.	5. <i>F. glaberrima</i> Nakai	5. <i>F. multijuga</i> Maxim.
	6. <i>F. multijuga</i> Maxim.	6. <i>F. vestita</i> (Wall.) Maxim.	6. <i>F. tsuguwoi</i> Ohwi
	7. <i>F. palmata</i> (Pall.) Maxim.	7. <i>F. palmata</i> (Pall.) Maxim.	7. <i>F. kiraishiensis</i> Hayata
	8. <i>F. rubra</i> (Hill) B. L. Rob.	8. <i>F. purpurea</i> Maxim.	
Sect. Albicoma Juz.	Sect. Albicoma Juz.	Sect. Albicoma Juz.	Sect. Albicoma Juz.
5. <i>F. angustiloba</i> (Turcz.) Maxim.	9. <i>F. angustiloba</i> (Turcz.) Maxim.	9. <i>F. angustiloba</i> (Turcz.) Maxim.	8. <i>F. angustiloba</i> (Turcz.) Maxim.
6. <i>F. intermedia</i> (Glehn) Juz.		10. <i>F. intermedia</i> (Glehn) Juz.	9. <i>F. palmata</i> (Pall.) Maxim.
	Sect. Sessilia T. Shumizu	Sect. Gymnocarpa Serg.	10. <i>F. rubra</i> (Hill) B. L. Rob.
	10. <i>F. vestita</i> (Wall.) Maxim.	12. <i>F. kiraishiensis</i> Hayata	
	11. <i>F. kiraishiensis</i> Hayata	13. <i>F. formosa</i> Nakai	
	12. <i>F. formosa</i> Nakai	14. <i>F. tsuguwoi</i> Ohwi	
	13. <i>F. tsuguwoi</i> Ohwi	15. <i>F. multijuga</i> Maxim.	
Subgen. Ulmaria Moench	Sect. Ulmaria Hill	Subgen. Ulmaria Moench	Sect. Filipendula
7. <i>F. ulmaria</i> (L.) Maxim.	14. <i>F. ulmaria</i> (L.) Maxim.	16. <i>F. ulmaria</i> (L.) Maxim.	11. <i>F. vestita</i> (Wall.) Maxim.
8. <i>F. denudata</i> (J. Presl & C. Presl) Fritsch		17. <i>F. denudata</i> (J. & C. Presl) Fritsch.	12. <i>F. ulmaria</i> (L.) Maxim.
9. <i>F. stepposa</i> Juz.		18. <i>F. stepposa</i> Juz.	13. <i>F. stepposa</i> Juz.
10. <i>F. megalocarpa</i> Juz.		19. <i>F. megalocarpa</i> Juz.	14. <i>F. megalocarpa</i> Juz.
Subgen. Eu-Filipendula Juz.	Subgen. Filipendula	Subgen. Filipendula	15. <i>F. vulgaris</i> Hill (= <i>F. hexapetala</i> Gilib.)
11. <i>F. hexapetala</i> Gilib.	15. <i>F. hexapetala</i> Gilib.	20. <i>F. hexapetala</i> Gilib.	

1 Material and methods

The materials used in the study were taken from the specimens loaned from several herbaria (GH, KYO, SNU, SNUA, TI) (Table 2).

Pollen grains were collected from herbarium specimens and processed by Erdtman's acetolysis method modified by Livingstone (Lee & Kim, 1978). Acetolysed pollen grains were embedded in glycerine jelly to make permanent slides, which were observed with a light microscope (LEITZ Laborlux 12). For scanning electron microscopy, the acetolysed pollen grains preserved in 70% ethanol were placed on a stub, dried, coated with gold by an ion-sputter (JOEL-JFC1100), and observed with scanning electron microscope (JEOLSS EM-ASID-4A) at 20 kV.

2 Results

General description

Pollen grains are isopolar, radially symmetrical, monads, varying in shape from suboblate to subprolate (polar length (P) / equatorial diameter (E))= 0.97–1.15 in average, Table 3), amb shapes circular,

with tricolporate aperture (Figs. 1–39). The grain size falls in the range of 14.00–23.24 $\mu\text{m} \times$ 13.72–22.82 μm (P×E, minimum-maximum), the smallest in *F. yezoensis* (15.19 $\mu\text{m} \times$ 14.22 μm in average; Fig. 34) and the largest in *F. hexapetala* (21.11 $\mu\text{m} \times$ 21.83 μm in average; Fig. 35) (Table 3). The endoaperture is equatorially elongate. The endoaperture is not fastigiate (arrow) only in *F. occidentalis* (Fig. 9). The fastigium is longitudinally elliptic (arrow) in *F. hexapetala* (Fig. 26) and latitudinally elliptic or round in the remaining species. The colpus is 12.41–17.08 μm long, mostly acute at the ends or sometimes blunt. Contrary to other species, the costa colpi (inner margin) is not thickened (arrow) in *F. occidentalis* (Fig. 1). The colpus surface is mostly microgranulate or psilate (arrow) in *F. formosa* only (Fig. 32). Sculpturing patterns of the grain surface are mostly scabrate, or rarely scabrate-microechinate. The size of the supra-ectal processes is somewhat even in most species but conspicuously variable in *F. rubra* (Fig. 35) and *F. palmata* (Fig. 33). The numbers of processes vary from 3 to 23 per 4 μm^2 . The palynological groupings of the species are summarized in the following key.

Table 2 Collection data for voucher specimens (Herbarium abbreviation follows Holmgren et al., 1990)

Taxon	Locality	Collected date	Voucher
Subgen. <i>Hypogyna</i>			
<i>F. occidentalis</i> (S. Watson) Howell	Mt. Rocky, USA	1936-06-08	Anonymous (GH)
Subgen. <i>Filipendula</i>			
<i>F. hexapetala</i> Gilib.	Newfoundland, Canada	1928	M. Ayre s.n. (GH)
	Nova Scotia, Canada	1920-07-08	C. H. Bissel s.n. (GH)
Subgen. <i>Ulmaria</i>			
Sect. <i>Ulmaria</i>			
<i>F. ulmaria</i> (L.) Maxim.	Newfoundland, Canada	1908-07-22	E. H. Eames 7009 (GH)
Sect. <i>Albicoma</i>			
<i>F. angustiloba</i> (Turcz.) Maxim.	Harbin, China	1937-06-01	Anonymous (GH)
	Tuberdai, China	1925-06-24	P. H. Dorsett 3420 (GH)
	no exact locality	1942-07-11	T. Kira s.n. (KYO)
Sect. <i>Sessilia</i>			
<i>F. formosa</i> Nakai	Mt. Chiri, Korea	1960-08-01	T. B. Lee s.n. (SNUA)
	Mt. Chiri, Korea	1982-07-04	T. B. Lee s.n. (SNUA)
<i>F. kiraishiensis</i> Hayata	Teadongju Kangsan, China	1938-07-24	S. Okamoto s.n. (KYO)
<i>F. tsuguwoi</i> Ohwi	Mt. Shiraiwa, Miyazaki Pref., Japan	1958-10-23	T. Shimizu 3418 (KYO)
<i>F. vestita</i> (Wall.) Maxim.	Yunnan, China	no exact collected date	T. T. Yu s.n. (GH)
	Yunnan, China	1939-09-08	K. M. Feng s.n. (GH)
sect. <i>Schalameya</i>			
<i>F. glaberrima</i> Nakai	Mt. Keumkang, Korea	1933-07-29	B. S. Doo s.n. (SNU)
	Myoungdangbong, Korea	1934-07-17	B. S. Doo s.n. (SNU)
<i>F. kamtschatica</i> Maxim.	Hondo, Japan	1955-08-05	M. Mizushima 16534 (TI)
	no exact locality	1980-06	T. Shimizu s.n. (GH)
	Tsutanuma, Japan	1940-07-11	H. Ohashi s.n. (TI)
<i>F. multijuga</i> Maxim. var. <i>multijuga</i>	Mt. Kamihiruzen, Japan	1962-07-29	G. Murata 27195 (KYO)
<i>F. multijuga</i> var. <i>ciliata</i> Koidz.	Futakuchitoge, Japan	1985-07-29	H. Ohashi 11690 (GH)
<i>F. palmata</i> (Pall.) Maxim. var. <i>palmata</i>	Kamtchatka, USSR	1928-07-16	E. Hulten s.n. (GH)
<i>F. palmata</i> f. <i>nuda</i> (Grub.) T. Shimizu	Heungkyori, Korea	1964-07-12	T. B. Lee s.n. (SNUA)
<i>F. purpurea</i> Maxim. var. <i>purpurea</i>	Yamagata Pref., Japan	1990-07-03	H. Ohashi 28143 (GH)
<i>F. purpurea</i> var. <i>auriculata</i> Ohwi	Oizumi, Japan	1942-06-10	T. Makino 129397 (TI)
	Hondo, Japan	1922-07-20	K. Shiota 1085 (GH)
	Mt. Iide, Nigata Pref., Japan	1965-07-22	M. Togashi 9963 (GH)
<i>F. rubra</i> (Hill) B. L. Rob.	Nova Scotia, Canada	1919-07-14	R. W. Woodward s.n. (GH)
	New Hampshire, USA	1910-07-17	E. F. Williamson s.n. (GH)
<i>F. yezoensis</i> H. Hara	Japan	1903-06-20	Anonymous (GH)
	Mt. Seuilbong, Korea	1940-07-25	B. S. Doo s.n. (SNU)
	Dongkunung, Korea	1944-05	B. S. Doo s.n. (SNU)

Key to the *Filipendula* pollen

- 1a. Pollen lacking fastigium and thickened costae colpi.....subgen. **Hypogyna**
 1b. Pollen with fastigium and thickened costae colpi.2
 2a. Fastigium longitudinally elliptic. Average pollen size >21 $\mu\text{m} \times 22 \mu\text{m}$ (P \times E).....subgen. **Filipendula**
 2b. Fastigium round or latitudinally elliptic. Average pollen size <20 $\mu\text{m} \times 20 \mu\text{m}$ subgen. **Ulmaria**

As shown in the pollen key above to *Filipendula* groups, the monotypic subgen. *Hypogyna*, consisting of *F. occidentalis* (Figs. 1, 5, 9, 25), is distinguished by pollen lacking fastigia and thickened costae colpi. The monotypic subgen. *Filipendula*, including species *F. hexapetala* (Figs. 2, 6, 10, 26), is characterized by

pollen having larger grains, larger pore sizes, longitudinally elliptic fastigia and thickened costae colpi. Finally subgen. *Ulmaria*, comprising the remaining 13 species, is characterized by pollen with rounded or latitudinally elliptic fastigia and thickened costae colpi. Thus, the classification of the genus into the

three subgenera *Hypogyna*, *Filipendula* and *Ulmaria*, as recognized by Shimizu (1961) is strongly supported by the pollen morphology.

The pollen characters are, however, not useful to distinguish the sections (Juzepczuk, 1941; Shimizu, 1961; Sergievskaya, 1967; Schanzer, 1994) although some species are distinguishable from others within the section.

3 Discussion

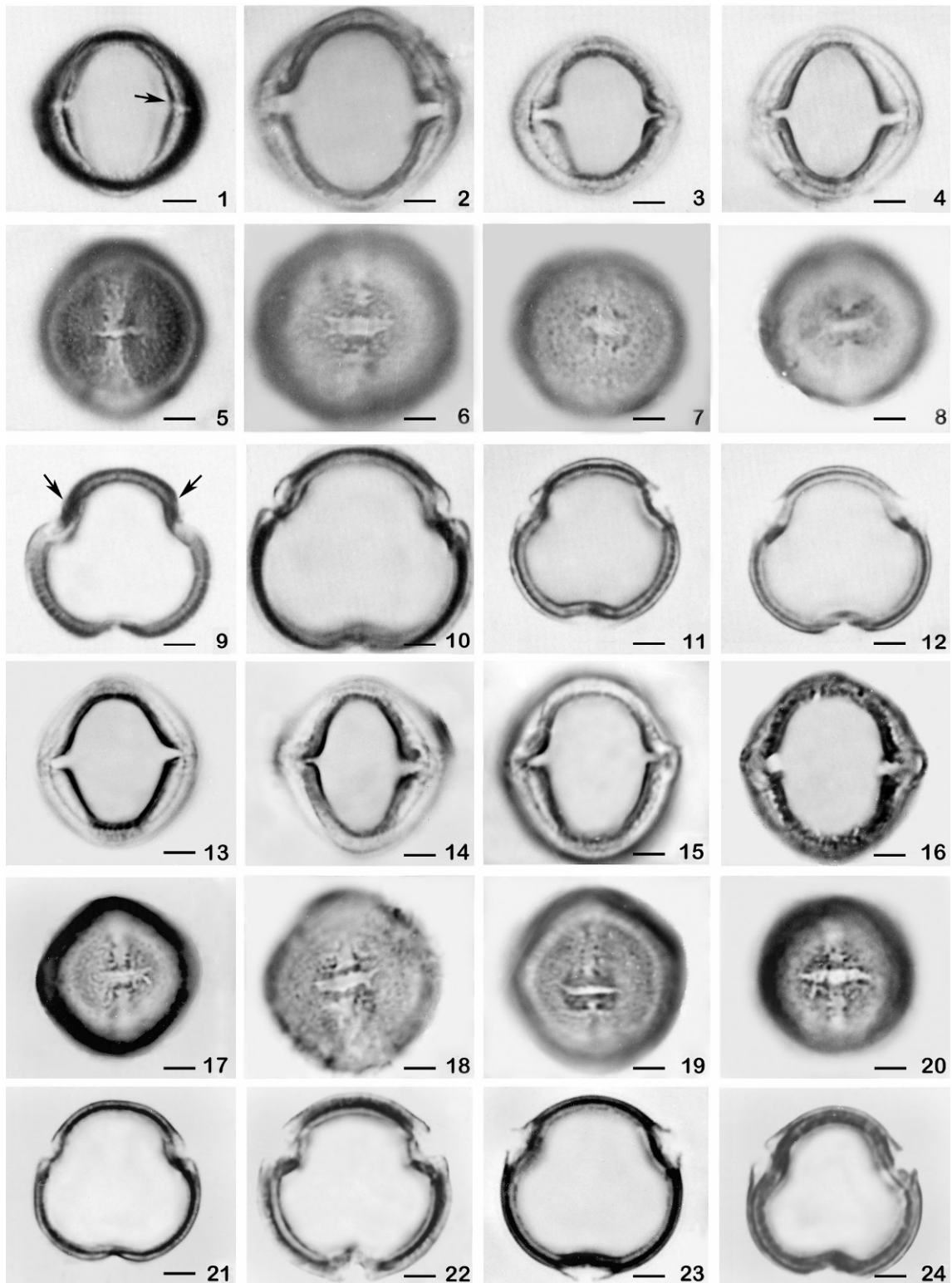
The present palynological data support Shimizu's (1961) classification of *Filipendula*, in which the genus was divided into two monotypic subgenera and one large subgenus consisting of 13 species in four sections.

Shimizu (1961) newly added *F. occidentalis* to the genus *Filipendula* and treated it as a monotypic subgen. *Hypogyna*. It possesses the unique morphology characterized by hypogynous perianths and indistinct calyx tubes, in contrast to all the other species which possess perigynous perianths and distinct calyx tubes. The pollen morphology showed that *F. occidentalis* is well separated from the other species by lacking a fastigium and thickened costae colpi which occur in all the other members of the genus. Palynologically it was supported that *F. occidentalis* (subgen. *Hypogyna*) occupies the most primitive position (Shimizu, 1961; Schanzer, 1994) because fastigium and costa colpi are not general and presumably apomorphic in the angiosperm pollen (Walker & Doyle, 1975). The primitive position of

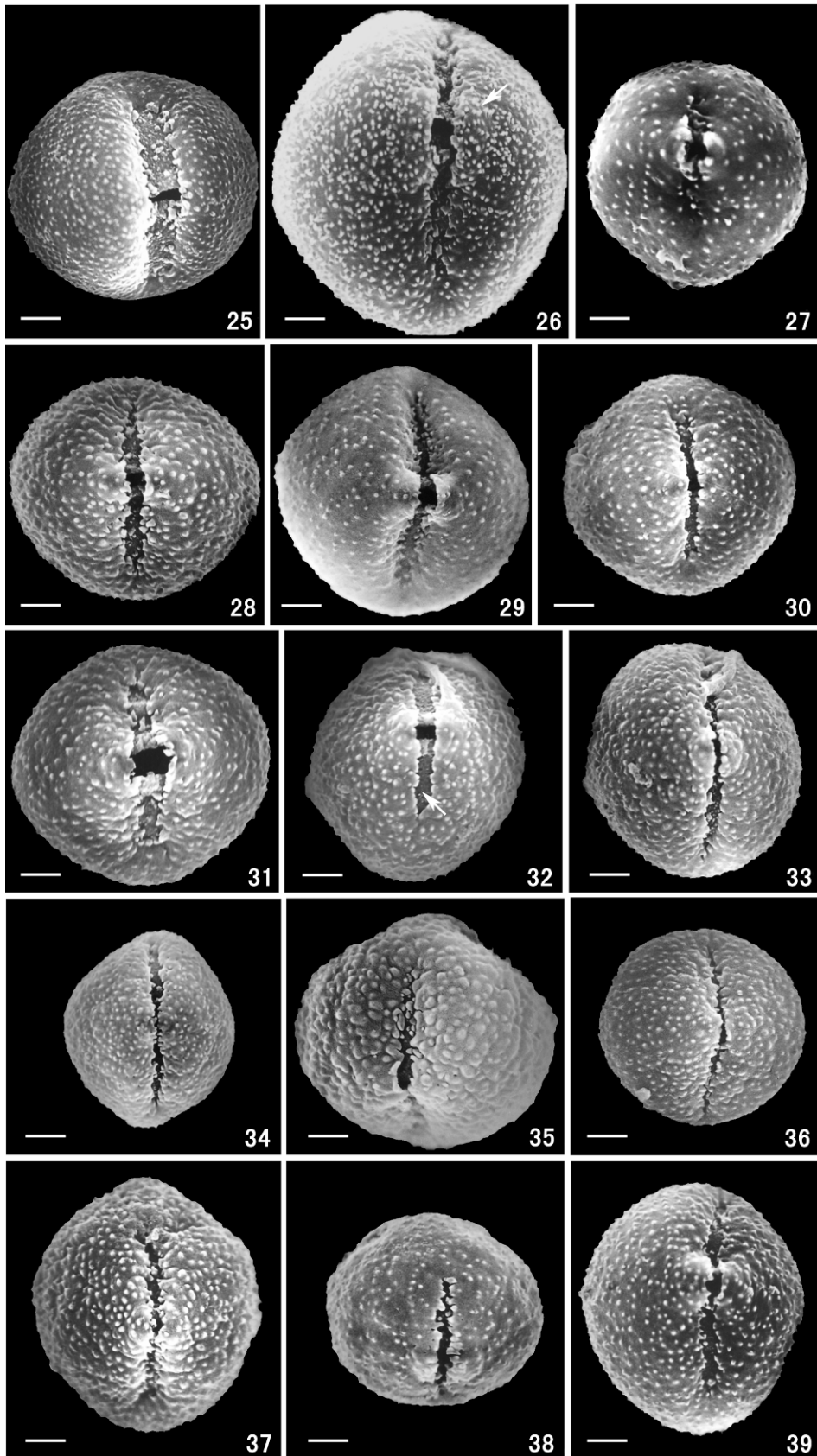
Table 3 Pollen measurements of the *Filipendula* species (Species of subgenera are divided by solid lines and those of sections by dotted lines)

Species name	*	Polar axis (P)(μm)**	Equatorial Diameter (E)(μm)**	P/E ratio**	Colpus length (μm)**	Exine thickness (μm)**	Pore size (μm)***	Protrusion number/4 μm^2	Protrusion diam. (μm)
<i>F. occidentalis</i>		19.71 \pm 1.05	19.80 \pm 1.44	1.00 \pm 0.07	15.81 \pm 1.73	1.92 \pm 0.20	0.58 \times 5.96	21–23	0.07
<i>F. hexapetala</i>	(1)	21.11 \pm 1.03	21.83 \pm 0.81	0.97 \pm 0.04	17.08 \pm 1.01	2.24 \pm 0.21	1.50 \times 6.13	11–13	0.26
	(2)	20.90 \pm 0.41	20.59 \pm 0.37	1.02 \pm 0.03	16.76 \pm 0.33	2.31 \pm 0.14	1.52 \times 6.09	11–13	0.26
<i>F. ulmaria</i>		17.12 \pm 0.62	16.98 \pm 0.28	1.01 \pm 0.03	13.72 \pm 0.79	1.79 \pm 0.25	1.08 \times 5.12	7–10	0.29
<i>F. angustiloba</i>	(1)	19.12 \pm 0.89	18.57 \pm 1.01	1.03 \pm 0.04	14.93 \pm 1.12	1.67 \pm 0.31	0.88 \times 5.33	7–10	0.27
	(2)	19.94 \pm 0.14	18.05 \pm 0.29	1.11 \pm 0.04	15.47 \pm 0.35	1.57 \pm 0.14	0.75 \times 5.91	7–10	0.27
	(3)	18.82 \pm 0.43	16.89 \pm 0.27	1.11 \pm 0.05	14.67 \pm 0.49	1.63 \pm 0.22	0.56 \times 5.52	7–10	0.27
<i>F. tsuguwoi</i>		16.87 \pm 0.36	16.72 \pm 0.29	1.01 \pm 0.02	13.54 \pm 0.72	1.60 \pm 0.30	0.54 \times 5.32	5–7	0.26
<i>F. kiraiishiensis</i>	(1)	18.84 \pm 1.05	18.97 \pm 1.30	1.00 \pm 0.07	14.13 \pm 0.99	2.56 \pm 0.17	1.08 \times 5.58	4–6	0.28
	(2)	19.05 \pm 0.37	18.59 \pm 0.30	1.02 \pm 0.06	14.67 \pm 0.37	2.51 \pm 0.09	1.23 \times 5.58	4–6	0.28
<i>F. formosa</i>	(1)	18.13 \pm 0.90	16.67 \pm 0.72	1.09 \pm 0.32	14.63 \pm 0.68	1.35 \pm 0.33	0.42 \times 4.86	7–10	0.29
	(2)	18.79 \pm 0.03	17.37 \pm 0.04	1.08 \pm 0.05	15.47 \pm 0.05	1.43 \pm 0.20	0.47 \times 4.91	7–10	0.29
<i>F. vestita</i>	(1)	17.68 \pm 0.87	17.40 \pm 1.18	1.02 \pm 0.06	13.39 \pm 0.95	1.22 \pm 0.15	1.04 \times 5.42	6–9	0.29
	(2)	16.21 \pm 0.38	15.82 \pm 0.35	1.03 \pm 0.07	13.48 \pm 0.41	1.28 \pm 0.11	1.20 \times 5.36	6–9	0.29
<i>F. yezoensis</i>	(1)	16.21 \pm 0.99	15.74 \pm 1.08	1.03 \pm 0.06	12.90 \pm 0.89	1.22 \pm 0.28	0.79 \times 4.17	17–20	0.15
	(2)	15.72 \pm 0.98	14.64 \pm 0.71	1.07 \pm 0.05	12.41 \pm 1.19	1.41 \pm 0.28	0.79 \times 4.25	10–12	0.18
	(3)	15.19 \pm 0.31	14.22 \pm 0.37	1.07 \pm 0.06	12.18 \pm 0.34	1.56 \pm 0.12	0.67 \times 4.91	10–12	0.18
<i>F. rubra</i>	(1)	19.89 \pm 1.18	19.38 \pm 0.72	1.03 \pm 0.06	16.10 \pm 1.14	1.28 \pm 0.32	1.08 \times 4.50	11–13	0.29
	(2)	19.19 \pm 0.39	19.40 \pm 0.37	0.99 \pm 0.12	15.32 \pm 0.37	1.31 \pm 0.14	1.03 \times 4.93	11–13	0.29
<i>F. kamschatica</i>	(1)	17.56 \pm 0.90	16.55 \pm 0.98	1.06 \pm 0.08	14.13 \pm 0.52	1.28 \pm 0.44	0.54 \times 4.92	8–10	0.33
	(2)	16.69 \pm 0.77	16.51 \pm 0.49	1.01 \pm 0.05	12.68 \pm 1.33	1.12 \pm 0.26	0.67 \times 5.58	4–6	0.28
	(3)	17.04 \pm 0.22	16.98 \pm 0.43	1.09 \pm 0.06	13.93 \pm 0.27	1.27 \pm 0.10	0.28 \times 5.74	8–10	0.28
<i>F. multijuga</i>									
var. <i>multijuga</i>		19.32 \pm 1.30	17.26 \pm 0.71	1.12 \pm 0.06	16.10 \pm 1.03	2.05 \pm 0.33	0.63 \times 5.54	6–8	0.27
var. <i>ciliata</i>		17.93 \pm 1.04	17.23 \pm 0.86	1.04 \pm 0.05	14.40 \pm 1.14	1.35 \pm 0.27	0.68 \times 5.75	4–6	0.28
<i>F. palmata</i>									
var. <i>palmata</i>		17.51 \pm 0.97	17.09 \pm 0.87	1.03 \pm 0.04	13.70 \pm 1.02	0.96 \pm 0.37	0.75 \times 4.29	7–10	0.29
f. <i>nuda</i>		20.06 \pm 1.10	20.49 \pm 1.12	0.98 \pm 0.04	16.63 \pm 0.74	2.24 \pm 0.40	1.35 \times 5.42	5–7	0.31
<i>F. glaberrima</i>	(1)	18.13 \pm 1.02	17.30 \pm 1.10	1.05 \pm 0.07	14.31 \pm 0.98	1.15 \pm 0.39	0.48 \times 4.83	11–13	0.27
	(2)	18.94 \pm 0.27	17.53 \pm 0.25	1.08 \pm 0.04	14.60 \pm 0.29	1.13 \pm 0.11	0.36 \times 5.04	11–13	0.27
<i>F. purpurea</i>									
var. <i>purpurea</i>		17.54 \pm 1.55	16.10 \pm 1.06	1.09 \pm 0.06	13.90 \pm 1.74	0.96 \pm 0.47	0.41 \times 5.55	11–13	0.22
var. <i>auriculata</i>	(1)	17.43 \pm 0.56	15.59 \pm 1.10	1.12 \pm 0.06	13.86 \pm 0.63	0.77 \pm 0.22	0.42 \times 5.58	11–13	0.23
	(2)	18.54 \pm 0.92	16.06 \pm 1.23	1.15 \pm 0.07	15.08 \pm 1.25	0.64 \pm 0.33	0.45 \times 5.64	7–10	0.25
	(3)	16.34 \pm 1.20	16.55 \pm 1.13	0.99 \pm 0.06	11.61 \pm 1.15	0.91 \pm 0.30	0.42 \times 5.54	7–10	0.21

*, Serial numbers of duplicates are the same as those of SPECIMENS EXAMINED in the text; **, Mean \pm standard deviation; ***, Polar diameter (mean) \times Equatorial diameter (mean).



Figs. 1–24. Light microscopic photographs of pollen grains of *Filipendula* species. 1–4, 13–16. Equatorial view focused on costa colpi. 5–8, 17–20. Aperture at equator. 9–12, 21–24. Polar cross-section. 1, 5, 9. *F. occidentalis*. 2, 6, 10. *F. hexapetala*. 3, 7, 11. *F. ulmaria*. 4, 8, 12. *F. angustiloba*. 13, 17, 21. *Filipendula vestita*. 14, 18, 22. *F. kiraishiensis*. 15, 19, 23. *F. multijuga* var. *ciliata*. 16, 20, 24. *F. multijuga* var. *multijuga*. 1. Arrow: costa colpi not thickened. 9. Arrow: pollen lacking fastigia. Scale bars=4 μ m.



F. occidentalis is well matched with the trend of fruit morphology in which the stigma was differentiated from broad to narrow, the style from long to short, and the ovary from slender and lanceolate to broad within the genus (Shimizu, 1961; Lee & Lee, 1998).

Except Schanzer (1994), all the previous authors (Juzepczuk, 1941; Popov, 1957; Shimizu, 1961) treated *F. hexapetala* as its own monotypic subgen. *Filipendula*. This monotypic subgenus is characterized by some unique characters in the genus, such as many lateral leaflets, tuberous roots, solid stems, and large calyx tubes. But Schanzer (1989, 1994) synonymized *F. hexapetala* to *F. vulgaris* and insisted that some of the above mentioned characters, i.e. root tubers and strongly dissected leaves, are only a kind of adaptation to the dry habitat. He revised the subgen. *Ulmaria* of Sergievskaya (1967) by adding *F. vulgaris* plus shifting a few other species between the sects. *Ulmaria* and *Sessilia* (Table 1). Palynologically, the monotypic subgen. *Filipendula* is distinguished from the other two subgenera by possessing a longitudinally elliptic fastigium, large pollen grains, and large pore, which are unique pollen characters in the genus. The distinct position of subgenus *Filipendula* inferred from pollen morphology is also supported by the fruit morphology in which the fruit is laterally attached and hairless (Lee & Lee, 1998). Schanzer's treatment merging *F. vulgaris* (to which *F. hexapetala* was synonymized by himself) to sect. *Filipendula* is not supported by the present pollen data at all. In addition, the high correlation observed between the pollen size and the floral part sizes in *F. hexapetala* (Juzepczuk, 1941; Popov, 1957; Shimizu, 1961) is interesting in terms of the functional significance of pollen size characters (Lee, 1978), i.e. the larger the pollen grains, the higher the nutrition contents for the pollen tube to penetrate the style.

The largest subgen. *Ulmaria* s.l. (Popov, 1957; Shimizu, 1961) is delimited by lacking the floral, vegetative, and pollen features, which are possessed by the other two subgenera. Juzepczuk (1941) divided subgen. *Ulmaria* s.l. into two subgenera *Ulmaria* s.s. and *Aceraria*, which was rejected by Popov (1957) and Shimizu (1961). Because there is no supporting evidence to distinguish the two subgenera, the present palynological result does not support Juzepczuk's

system, which was later adopted by Sergievskaya (1967).

Within the subgen. *Ulmaria* (*sensu* Shimizu), the subgroupings by different authors are quite incongruous with each other. The present authors tried to find the palynological characters supporting the subgroups, but failed. The pollen morphology of the subgenus has not been differentiated enough to support or reject the sectional classification. Shimizu (1961) and Lee & Lee (1998) pointed out the evolutionary tendency would have proceeded from sect. *Schalameya*, through sect. *Albicoma* and sect. *Sessilia*, to sect. *Ulmaria* by "means of shortening of the ventral margins of achene." Based on the palynological results, however, such a trend was not clear.

Finally, it is noted that the pollen character, such as amb shape and surface protrusion number, is variable within *F. yezoensis*. According to the previous study (Lee & Lee, 1998), fruit shape and size are also variable in this taxon. This seems to be the reason why Kim & Chung (1986) and Sergievskaya (1967) divided this taxon into two different species, *F. koreana* and *F. yezoensis*. In the present paper, we temporarily accepted Shimizu (1961) and Schanzer (1989), in which *F. koreana* was treated as the synonym of *F. yezoensis*. Further studies on the populations would be needed to resolve the taxonomic treatment of the two taxa.

Since last a few decades, molecular systematics studies have contributed to the evaluation of many taxonomic systems. This approach has not been applied to the whole genus *Filipendula*, but it has been used for subfamily Rosoideae (Eriksson et al., 2003), subtribe Geinae (Smedmark et al., 2005), and *Geum* and relatives (Smedmark & Eriksson, 2002), in which *Filipendula* was always the most basal group or an outgroup. Molecular studies of the whole genus would be needed to evaluate the classification systems proposed by previous authors and to test our conclusions based on the palynological results presented here.

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Fig. 25–39. Scanning electron microscopic photographs of pollen grains of *Filipendula* species. Equatorial view with a colpus. 25. *F. occidentalis*. 26. *F. hexapetala*. Arrow: fastigium longitudinally elliptic. 27. *F. tsuguwoi*. 28. *F. ulmaria*. 29. *F. angustiloba*. 30. *F. vestita*. 31. *F. kiraishiensis*. 32. *F. formosa*. Arrow: colpus surface microgranulate or psilate. 33. *F. palmate* var. *palmate*. 34. *F. yezoensis*. 35. *F. rubra*. 36. *F. glaberrima*. 37. *F. kamschatkana*. 38. *F. multijuga* var. *multijuga*. 39. *F. purpurea* var. *purpurea*. Scale bars=3 μm.

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