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Pollen Morphology of *Pieris* D. Don (Lyonieae, Ericaceae) and Its Taxonomic Significance

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Pollen morphology of 6 species in the genus *Pieris* was examined using light and scanning electron microscopes. Judd's infrageneric classification of *Pieris* was re-examined in the light of new palynological characters. The genus *Pieris* is stenopalynous in having 3-colporate and oblate pollen tetrads. However, a continuous and serial variation in the exine sculpture, tetrad diameter, polar and equatorial length of pollen and apocolpial exine thickness was revealed within the genus. *Pieris nana* is characterized by having the smallest pollen and the smallest rugulae in the rugulate sculpture. Considering other distinct morphological characters, we confirm the recognition of the monotypic subgenus Arcterica based on this species. Within the other subgenus, Pieris, members of the sections Pieris and Phillyreoides can be distinguished by subtle differences in colpus width, septum thickness and ratio of colpus length to tetrad diameter. *Pieris formosa* is distinguished by its psilate exine with clear secondary striate sculpture. *Pieris japonica* and *P. cubensis* are not well differentiated in the palynological characters, and act as a bridge between sect. Pieris and sect. Phillyreoides. On the basis of palynological characters a dichotomous key of these taxa was also prepared.

Key words: *Pieris*, pollen morphology, taxonomic significance.

The genus *Pieris* D. Don (Ericaceae–Vaccinioideae–Lyonieae) (Kron et al. 2002) comprises seven allopatric and rather distinctive species occurring in Eastern Asia, Eastern America, and Cuba (Judd 1982) and is closely related to several genera in the tribe Andromedeae sensu Stevens (1971).

Until the mid of 20th century, the generic limit of *Pieris* was not very well defined. Some of its species such as *P. nana, P. floribunda* and *P. phillyreifolia* were segregated as distinct genera (Nuttall 1843, Small 1914, 1933, Makino 1961, Ohwi 1965). The genus *Pieris*, as circumscribed by Stevens (1971) along with the genus *Arcterica* Cov., is a member of the *Lyonia* group of the tribe Andromedeae (Ericaceae subfamily Vaccinioideae). From the phenetic standpoint, Judd (1979) did not find sufficient morphological and anatomical distinctions between the monotypic genus *Arcterica* and *Pieris* on the basis of 50 selected characters, and treated *Arcterica nana* as an isolated species within *Pieris*; *P. nana* (subgenus Arcterica). This genus is considered to be a monophyletic group easily separated from related genera by a number of features; including the leaf arrangement and anatomy, timing of inflorescence development, flower, filament and spur morphology, seed morphology (Judd 1979, 1982), chromosome number, secondary metabolites (toxic

diterpenes), and molecular characters (Kron et al. 1999, 2002). However, the infrageneric classification of *Pieris* is still in dispute. Judd (1982) has divided the genus *Pieris* into two subgenera; the monotypic subgenus Arcterica (Cov.) Judd (including *P. nana*) and subgenus Pieris, which has been divided into two sections, sect. Pieris (including *P. japonica*, *P. formosa*, and *P. floribunda*), and sect. Phillyreoides Benth. & Hook. f. (including *P. phillyreifolia*, *P. cubensis*, and *P. swinhoei*). Recent combined phylogenetic analysis of phenotypic and molecular data shows that subgenus Arcterica composed of *P. nana* is sister to the other monophyletic subgenus Pieris including *P. formosa*, *P. floribunda* and *P. phillyreifolia* (Kron et al. 1999). But the monophyly of sect. Pieris is not supported in the combined analysis, thus subgenus Pieris needs further study.

Mainly light microscopic (LM) observations on pollen grains of *Pieris* have been carried out previously (Yang 1952, Ikuse 1956, 2001, Ueno 1962, Nair 1965, Huang 1972, Shimakura 1973, Nakamura 1980, Wang et al. 1995, Wei 2003). Scanning electron microscopic (SEM) observation of pollen grains has been made for only a single species, *P. japonica* (Kurosawa 1991). Therefore, the present study examines the pollen morphology of the genus in detail with the help of both LM and SEM to discuss and review the present infrageneric classification.

Materials and Methods

The pollen of six species from the seven on so species in the genus *Pieris* was examined by using LM and SEM (Table 1). Polliniferous material used in this investigation was taken from dried herbarium specimens from the herbaria; KYO, S, SAPS and

Table 1. Voucher specimens for the palynological studies of *Pieris*. LM: light microscope; SEM: scanning electron microscope. Infrageneric classification follows Judd (1982)

Taxon	Collector and number	Voucher information
Subgenus **Arcterica**		
P. nana (Maxim.) Makino	Fukuda 180, 181 (LM, SEM)	Japan: Honshu, Rikuchu, Mt. Hayachine, 19 June 1932 (KYO)
	Takahashi & al. 2571 (SEM)	Japan: Hokkaido, Prov. Kitami, Monbetsu-gun, Shirataki-mura, Mt. Hirayama, alt. 1770 m, 29 June 1982 (SAPS)
Subgenus **Pieris**		
Sect. **Pieris**		
P. japonica (Thunb.) D. Don	Takahashi 457 (LM, SEM)	Japan: Tokyo, Koishikawa Bot. Gard., cult., petals pink, 23 March 1980 (SAPS)
	Sasao s. n. (SEM)	Taiwan: Prov. Taichû, Kantojum, 20 November 1931 (SAPS)
P. koidzumiana Ohwi	Sonohara 10 (LM, SEM)	Japan: Okinawa Islands, Kunigami, Hendona, no date (KYO)
P. formosa (Wall.) D. Don	McLaren 32F (LM, SEM)	China: Yunnan, Pai-ching, 13 April 1936 (ex Herb. Hort. Bot. Reg. Edin.) (KYO)
Sect. **Phillyreoides**		
P. phillyreifolia (Hook.) DC.	Newcombe 267 (LM, SEM)	USA: Georgia, Charlton Co., Okefenokee National Wildlife Refuge, 13 Sept. 1982 (SAPT)
P. cubensis (Griseb.) Small	Ekman (Pl. Ind. Occ. 16387) (LM, SEM)	Cuba: Prov. Pinar del Rio, Sierra de los Organos, 31 March 1923 (S)

Table 2. Variation in pollen characters of *Pieris* showing value (μm) and standard deviation. D: Tetrad diameter; P: Polar axis; E: Equatorial axis; minimum – maximum values in parenthesis. Sculpture by SEM. CR: Coarsely rugulate; CRP: Coarsely rugulate-psilate; P: Psilate. Parentheses mean indistinctness

Name of Subgenus/ Section/Species	D	P	E(d)	D/d	P/E	Colpus		2f/D	Apocolpial exine thickness	Septum thickness	Sculpture by SEM
						Length (2f)	Width				
Subgenus **Arcterica**											
P. nana	31.9±1.4 (30.0–34.6)	17.1±1.9 (14.9–20.6)	24.3±2.5 (21.1–30.0)	1.31 (1.15–1.42)	0.70 (0.64–0.78)	17.3±2.8 (13.9–21.6)	2.0±0.3 (1.7–2.4)	0.54 (0.45–0.63)	2.2±0.2 (1.9–2.4)	1.6±0.3 (1.2–1.9)	CR* –CR(P)(*)–*
Subgenus **Pieris**											
Sect. **Pieris**											
P. japonica	42.8±2.4 (39.3–46.2)	22.0±1.5 (19.5–24.4)	33.1±1.4 (31.4–36.0)	1.29 (1.14–1.41)	0.66 (0.60–0.74)	20.2±2.5 (16.5–24.8)	1.6±0.6 (0.7–2.5)	0.47 (0.36–0.58)	2.4±0.3 (2.1–3.0)	1.1±0.3 (0.7–1.5)	CR–CR(P)(*)
P. koidzumiana	39.3±2.1 (37.4–42.7)	21.4±1.6 (19.0–23.5)	29.7±1.5 (27.1–31.2)	1.32 (1.23–1.40)	0.72 (0.65–0.78)	16.9±2.8 (13.4–20.6)	1.6±0.5 (0.7–1.9)	0.43 (0.36–0.54)	2.6±0.3 (2.2–2.9)	1.7±0.2 (1.4–2.2)	CR–CRP(*)
P. formosa	41.5±2.6 (37.2–45.6)	22.1±1.4 (19.9–27.7)	30.5±2.5 (27.8–34.8)	1.36 (1.28–1.45)	0.72 (0.65–0.81)	13.8±1.2 (12.5–16.8)	2.0±0.3 (1.4–2.4)	0.33 (0.27–0.45)	2.1±0.2 (1.9–2.4)	2.2±0.2 (1.9–2.4)	P*
Sect. **Phillyreoides**											
P. phillyreifolia	48.6±1.6 (47.0–51.2)	24.3±2.0 (20.8–27.7)	35.6±2.2 (32.2–39.6)	1.37 (1.26–1.49)	0.68 (0.62–0.74)	29.0±2.8 (24.8–33.0)	0.7±0.3 (0.5–1.5)	0.6 (0.53–0.64)	1.9±0.5 (1.3–2.8)	1.0±0.4 (0.5–1.7)	CRP*
P. cubensis	39.3±1.2 (38.0–41.3)	20.8±1.0 (19.8–22.8)	30.7±1.2 (29.4–33.0)	1.28 (1.24–1.33)	0.68 (0.63–0.72)	18.6±1.4 (17.3–21.4)	0.6±0.1 (0.5–0.8)	0.47 (0.42–0.52)	2.3±0.3 (2.0–2.8)	0.7±0.2 (0.5–1.2)	CRP*

*Secondary striate sculpture distinct

Table 3. Cumulative variance and eigen vectors of principal component analysis (PCA) using ten palynological characters based on LM for six species of *Pieris*. Character abbreviations corresponding to Table 2

Principal component axis	1	2	3
Cumulative variance (%)	39.926	60.622	76.138
Characters		Eigen vectors	
D	0.417	0.336	–0.030
P	0.355	0.437	–0.149
E (d)	0.432	0.186	–0.297
D/d	–0.024	0.337	0.579
P/E	–0.155	0.460	0.230
Colpus length (2f)	0.416	–0.118	0.364
Colpus width	–0.363	0.067	0.110
2f/D	0.228	–0.378	0.465
Apocolpial exine thickness	–0.185	0.032	–0.353
Septum thickness	–0.312	0.416	0.126

SAPT (the Botanic Garden, Hokkaido University, Sapporo).

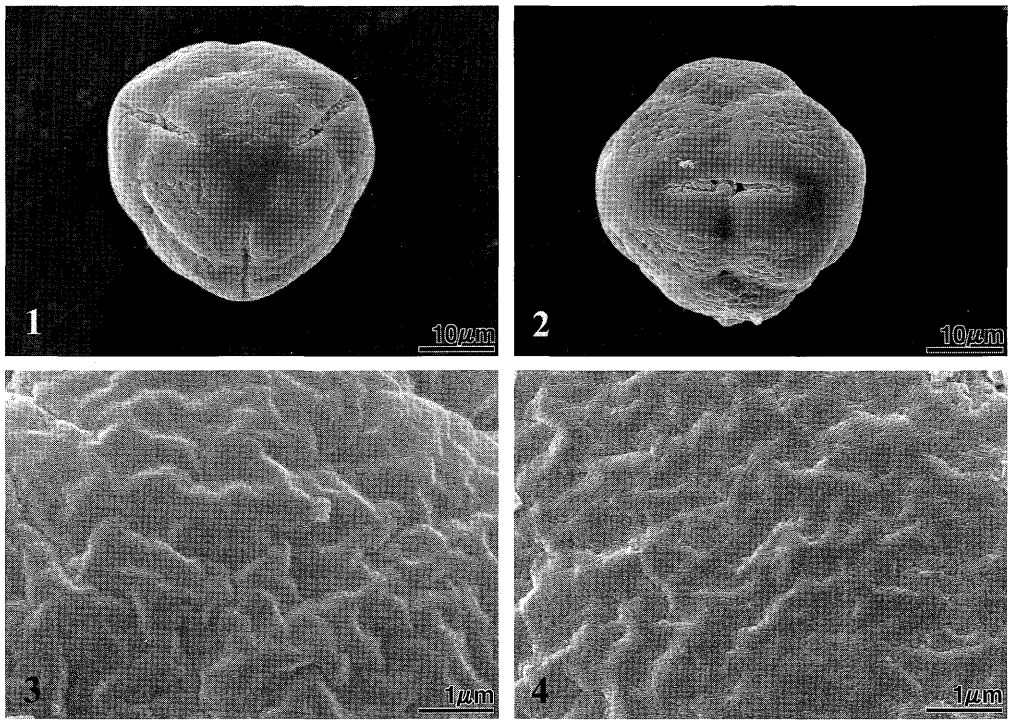
Pollen was acetolysed following the technique of Erdtman (1960) modified by Takahashi (1987). For LM, the pollen was mounted in silicone oil (viscosity 3000 cs), and examined and measured with a Nikon Eclipse E 200 microscope. The dimensions "D", "P", "E (d)" and "2f", corresponding to the tetrad diameter, polar length, equatorial diameter and colpus length of pollen grain, were measured, and the D/d, P/E and 2f/D ratios were calculated (see Oldfield 1959). The measurements given in Table 2 are based on at least 10 grains from each specimen. Pollen size and shape classes follow Erdtman (1986). Pollen slides of all collections are deposited at the Hokkaido University Museum, Sapporo, Japan. For SEM, the acetolysed pollen samples were dehydrated in an ethanol series, and mounted and air dried on aluminum stubs from 70 % ethanol, and sputter coated with Platinum-Palladium or Gold-Palladium by a HITACHI E102 ion sputter. Subsequently the prepared pollen was examined and photographed with a JEOL JSM-5310LV scanning electron microscope operated at 15 KV. Descriptive terminology follows Punt et al. (1994).

Quantitative data of pollen morphological features (first ten characters shown in Table 2) were used for statistical calculations of total similarities between the pollen grains of six species with principal component analysis (PCA) using the Excel Stat computer package.

Results

General pollen morphology of *Pieris*

Light microscopy observations: pollen grains united at tetrahedral tetrad (Fig. 1), rarely other configurations, viscin threads absent, size medium, or minute in *P. nana*, D 31.9–48.6 μm, P 17.1–24.3 μm, E 24.3–35.6 μm, P/E 0.66 –0.72, oblate in shape, ratio of tetrad diameter to individual grain diameter (D/d) 1.28–1.37, 3-aperturate, apertures arranged according to "Fischer's Law", colporate, colpi distinct (Fig. 2), 13.8–29.0 μm long, width 0.6–2.0 μm, ratio of colpus length to tetrad diameter (2f/D) 0.33–0.60, wider at middle, somewhat obtuse to acute towards ends, colpus margin distinct, ora distinct, lalongate, 1.0–3.0 μm long, width 6.4–11.0 μm, costae present but not clear in *P. phillyreifolia* and *P. japonica*, exine tectate, apocolpial exine 1.9–2.6 μm thick, septum thickness 0.7–2.2 μm, apocolpial exine com-



Figs. 1–4. SEM micrographs of pollen grains in *Pieris* species. 1: Pollen tetrad at polar view (*P. formosa*). 2: Pollen tetrad at equatorial view showing aperture (*P. formosa*). 3–4: Apocolpial exine sculpture of *P. nana* (Takahashi & al. 2571 and Fukuda 180, respectively).

monly thicker than septum except *P. formosa* with thicker septum. Exine sculpture commonly verrucate to finely rugulate or rugulate in *P. cubensis, P. phillyreifolia* and *P japonica*, or coarsely verrucate to coarsely rugulate in *P. formosa, P. koidzumiana* and *P. nana*.

SEM Observations: apocolpial exine sculpture various from coarsely rugulate to psilate, the rugulae with secondary sculptures; faintly to finely and clearly striate (Figs. 3–10). Exine sculpture along the colpi similar to that appearing at distal pole, but mesocolpial exine having a tendency to decrease in lateral extension of the rugulae with more distinct units, colpus membrane granular to granuloid.

In principal component analysis (PCA) using the LM characters, dots from each species occupy each distinct range, so we can generally compare the palynological features of six *Pieris* species in this analysis (Fig. 11).

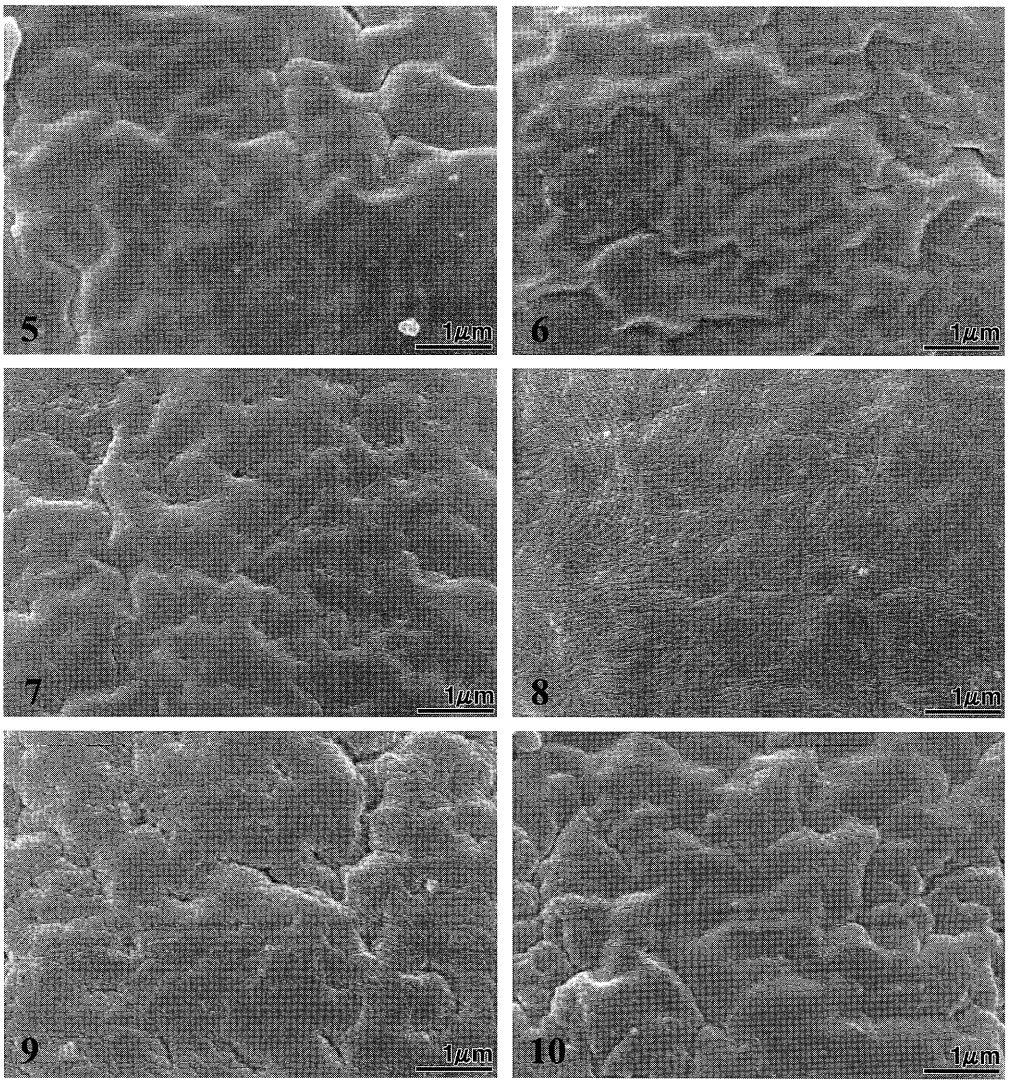
Pollen characteristics of *Pieris*

Subgenus Arcterica (monotypic, species examined: *P. nana*)

Pollen grains few in number at both LM slide and SEM stub. Pollen surface uneven and rugged, exine sculpture coarsely rugulate, the rugulae faintly (Fig. 3) to finely striate (Fig. 4). In PCA, *P. nana* is situated at the lower left edge of total variation of the *Pieris* pollen (Fig. 11).

Subgenus Pieris

Section Pieris (species examined: *P. japonica, P. koidzumiana* and *P. formosa*)



Figs. 5–10. SEM micrographs of apocolpial exine sculpture in *Pieris* species. 5–6: *P. japonica* (Takahashi 457 and Sasao s. n., respectively). 7: *P. koidzumiana*. 8: *P. formosa*. 9: *P. phillyreifolia*. 10: *P. cubensis*.

Colpus membrane coarsely granulate in *P. japonica*. Pollen surface uneven to somewhat flat and rugged, exine sculpture coarsely rugulate, the rugulae faintly to finely striate in *P. japonica* and *P. koidzumiana* (Figs. 5–7) to psilate with clearly striate sculpture in *P. formosa* (Fig. 8). In PCA, members of this section fall in the middle of total variation, along with *P. cubensis* of Sect. Phillyreifolia. Among the species *P. formosa* shows the highest value in the second component (Fig. 11).

Section Phillyreoides (species examined: *P. phillyreifolia* and *P. cubensis*)

Most grains shrink somewhat in *P.*

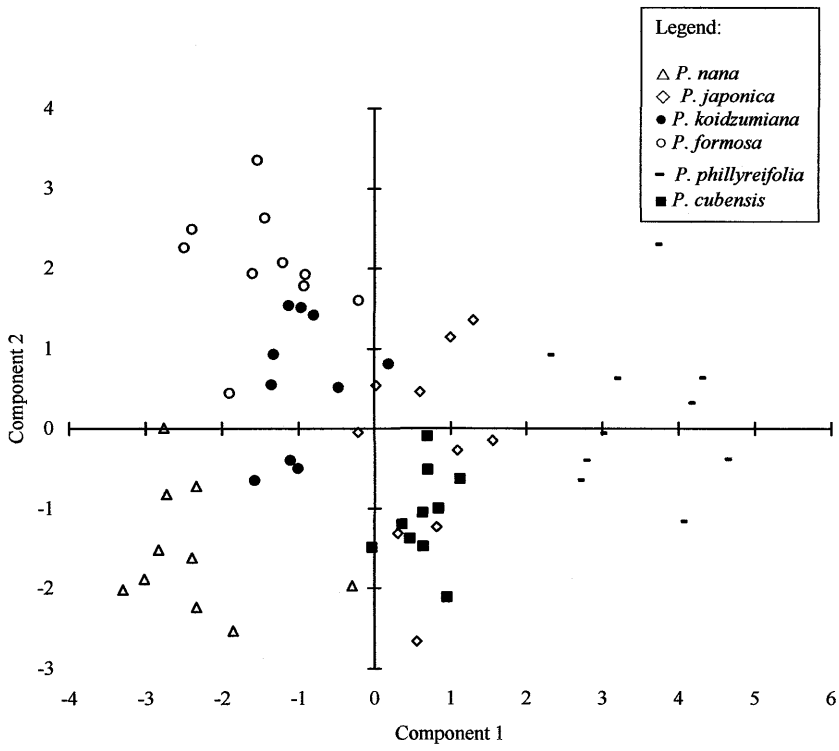


Fig. 11. Two dimensional diagram of component 1 and 2 of pollen grains of six *Pieris* species based on principal component analysis using ten palynological characters.

phillyreifolia. Pollen surface uneven and rugged, exine sculpture coarsely rugulate (-psilate), the rugulae loosely arranged, and finely and clearly granulate-striate in *P. phillyreifolia* (Fig. 9) or striate in *P. cubensis* (Fig. 10). In PCA, *P. phillyreifolia* is situated at the right edge of total variation of the *Pieris* pollen which shows the highest value of the first component and *P. cubensis* pollen could not be separated from *P. japonica* pollen (Fig. 11).

Discussion

All species of *Pieris* examined in this study have 3-colporate and oblate pollen tetrads having similar rugulate to rugulate-psilate (rarely psilate) exine with secondary striate sculpture, which suggests that the genus including *P. nana* is, as a whole a group of closely related entities. However, SEM observations show a variation in exine sculpture within the genus (Figs. 3–10). There is a more or less continuous and serial variation in the exine sculpture from coarsely rugulate through coarsely rugulate-psilate to psilate, among the *Pieris* species.

Pieris nana has the smallest pollen tetrad (D = 31.9 μm) and the smallest rugulae in size (compare Figs. 3–4 and 5–10). This species has also very distinctive morphological characters viz. low shrub with small, entire and usually whorled leaves, roughened-papillose filament, and anthers with poorly developed disintegration tissue etc., differing from the other species of the genus (Judd 1982). The low number of pollen grains in both LM slide and SEM stub might be due to the presence of poorly developed disintegra-

tion tissue in anthers, or all specimens might have been collected at very late flowering stage. The distinctiveness of the *P. nana* pollen is also supported by PCA (lower left edge of total variation) using 10 palynological characters based on LM observations (Fig. 11). The PCA also indicates that among the remaining five species, *P. japonica, P. koidzumiana*, *P. formosa* and *P. cubensis* are relatively closer together and situated at the middle of total variation, and *P. phillyreifolia* also has a distinct (right-hand most) position (Fig. 11). This results of PCA support the division of the genus *Pieris* into two subgenera; the monotypic subgenus Arcterica (including *P. nana*) and the other subgenus Pieris composed of the remaining species. The infrageneric classification of *Pieris* proposed by Judd (1982) is generally supported by the palynological characters, with some exceptions viz. *P. cubensis* of sect. Phillyreoides shows a closer relationship with the members of sect. Pieris (especially *P. japonica*) (Fig. 11).

Within subgenus Pieris, P/E ratio shows a difference between the two sections (Table 2). Section Pieris possesses a relatively larger value (0.72) of P/E, and sect. Phillyreoides possesses the smaller value (0.68), except for *P. japonica* of sect. Pieris that has the P/E value 0.66, even lower than sect. Phillyreoides. Colpus length, width and ratio of colpus length to tetrad diameter (2f/D) show distinct differences among the species (Table 2). Pollen grains of the sect. Pieris possess comparatively smaller but wider colpus (13.8–20.2 μm and 1.6–2.0 μm, respectively) compared to those of the sect. Phillyreoides (18.6–29.0 μm and 0.6–0.7 μm, respectively). The 2f/D value is relatively smaller (0.33–0.47) in the sect. Pieris, and larger (0.47–0.60) in the sect. Phillyreoides. Distinct differences in P/E and 2f/D ratios were also reported previously among the sections of the genus *Enkianthus* (Sarwar and Takahashi 2005) and different subfamilies of Ericaceae (Warner and Chinappa 1986). These two palynological characters might be of special taxonomic importance in Ericaceae. Distinct differences have also been found in apocolpial exine and septum thickness between the two sections (Table 2): sect. Pieris have comparatively thicker apocolpial exine and septum (2.1–2.6 μm and 1.1–2.2 μm, respectively) than those of the sect. Phillyreoides (1.9–2.3 μm and 0.7–1.0 μm, respectively).

Judd (1982) considered *P. japonica* as a variable species; it includes a number of synonyms at the species level, e. g., *P. popowi* Palibin, *P. taiwanensis* Hayata, *P. polita* W. W. Sm. & Jeffrey, *P. koidzumiana* Ohwi. *Pieris koidzumiana* occupies the intermediate space between *P. japonica* and *P. formosa* in PCA (Fig. 11). But in exine sculpture *P. koidzumiana* (Fig. 7) is more similar to *P. japonica* (Figs. 5–6) than *P. formosa* (Fig. 8). Thus palynological characters do not positively support the separation of *P. koidzumiana* from *P. japonica*. Judd (1982) also did not confirm the species status of *P. koidzumiana*, because he did not find any clear gap between *P. koidzumiana* and *P. japonica* in leaf shape or marginal dentation, although he recognized some distinct morphological differences between them. However, considering other distinctions in the morphological characters of *P. koidzumiana*: e. g. the leaves oblanceolate with more blunt tip, rachis densely puberulous, flowers longer etc. compared to those of *P. japonica* (Yamazaki 1993), it is better to separate *P. koidzumiana* from *P. japonica* as a distinct species, endemic to the Ryukyu Islands, Japan.

Neither the close relationships between *P. japonica* and *P. formosa*, nor *P. phillyreifolia* with *P. cubensis* and *P. japonica*, which were found in morphological and anatomical characters (Judd 1982), is supported by our palynological observations (Figs. 5–11). However, *P. japonica* pollen

can not be separated from that of *P. cubensis* in PCA (Fig. 11), and the exine sculpture is also similar between the two species (Figs. 5–6 , 10). *Pieris japonica* and *P. cubensis* act as a bridge between the two sections Pieris and Phillyreoides. A close relationship between *P. formosa* and *P. phillyreifolia* suggested by Kron et al. (1999) was not supported by PCA (Fig. 11), but the distinctness of secondary striate sculpture is common palynological feature between these two species (Figs. 8–9). Under SEM, *P. formosa* is readily distinguished by its psilate exine with clear secondary striate sculpture (Fig. 8) among *Pieris* species. Other species have a serial variation in the coarsely rugulate-psilate exine sculpture (rugulae faintly to finely striate). Further research including the study of more specimens and combined analysis of morphological and molecular data from other regions is needed to clarify the relationships among the *Pieris* species.

Key to the species of *Pieris* based on pollen morphology

1a. Pollen grains minute, pollen surface uneven and rugged, exine sculpture coarsely rugulate, the rugulae smallest ..... *P. nana*

1b. Pollen grains medial, pollen surface uneven and rugged to somewhat flat, exine sculpture coarsely rugulate to psilate, the rugulae relatively larger 2

2a. 2f/D 0.33–0.47, colpus width 1.6–2.0 μm, septum relatively thicker (1.1–2.2 μm) 3

3a. D/d 1.29–1.32, 2f/D 0.43–0.47, distal exine thicker than septum, septum thickness 1.1–1.7 μm, pollen surface uneven and rugged, exine sculpture coarsely rugulate, the rugulae faintly to finely striate 4

4a. D/d 1.29, P/E 0.66, 2f/D 0.47, septum thickness 1.1 μm .... *P. japonica*

4b. D/d 1.32, P/E 0.72, 2f/D 0.43, septum thickness 1.7 μm ..... *P. koidzumiana*

3b. D/d 1.36, 2f/D 0.33, septum thicker than distal exine, septum thickness 2.2 μm, pollen surface somewhat flat, exine sculpture psilate with clearly secondarily striate ..... *P. formosa*

2b. 2f/D 0.47–0.60, colpus width 0.6–0.7 μm, septum relatively thinner (0.7–1.0 μm) 5

5a. D/d 1.37, 2f/D 0.60, septum thickness 1.0 μm, the rugulae finely and clearly granulate-striate ..... *P. phillyreifolia*

5b. D/d 1.28, 2f/D 0.47, septum thickness 0.7 μm, the rugulae finely and clearly striate ..... *P. cubensis*

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A. K. M. ゴラム サルワル[a], 高橋英樹[b]：アセビ属（ツツジ科ネジキ連）の花粉形態と分類学的意義

アセビ属 *Pieris* 約7種のうち6種の花粉形態を光学顕微鏡と走査型電子顕微鏡で観察し，Judd の属内分類体系を花粉形態形質から再検討した．アセビ属はステノパリナス（花粉の形態変異幅が狭いこと）で，偏球形の3溝孔粒からなる四集粒花粉であった．それでも属内には，花粉壁の彫刻紋様，四集粒径，極軸・赤道軸長，遠心極域の壁厚において連続的な変異があった．この中でコメバツガザクラ *P. nana* は最も小さいサイズの花粉粒を持ち，花粉壁のしわ紋様の単位も最小で，他の明瞭な外部形態形質を考えあわせると，本種1種からなる単型のコメバツガザクラ亜属 Arcterica を認めることを支持する．残りのアセビ亜属 Pieris 内の，Pieris 節と Phillyreoides 節とは溝の幅，四集粒内の花粉粒間壁厚，四集粒径に対する溝長の比率で微妙な差がある．*P. formosa* は明瞭な二次的縞模様を持った平滑型の花粉彫刻模様により識別される．アセビ *P. japonica* と *P. cubensis* とは花粉形質では十分に区別することができず，Pieris 節と Phillyreoides 節とを結ぶ位置を占めている．花粉形態形質によるこれら分類群の検索表を作成した．

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