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POLLEN MORPHOLOGY OF THE TRIBE PHYLLODOCEAE (ERICOIDEAE, ERICACEAE) AND ITS TAXONOMIC SIGNIFICANCE¹

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Keywords: Pollen morphology; Exine sculpture; Phyllodoceae; Taxonomic significance.

Abstract

Pollen morphology of 13 taxa belonging to 5 genera of the tribe Phyllodoceae (Ericaceae) was examined by means of light and scanning electron microscopy (LM and SEM, respectively), or SEM alone. In Phyllodoceae, 3-colpor(oid)ate, minute to medium, oblate pollen grains are united usually in tetrahedral tetrads. Pollen tetrads are generally characterized by the presence of viscin threads except *Elliottia pyroliflora*, *Epigaea asiatica* and *Phyllodoce caerulea*. The absence of viscin threads might indicate to a secondary loss, since these are present at least in some species within all the genera of Phyllodoceae. The pollen morphological data confirm the infra- and inter-generic relationships as identified by molecular phylogeny of Phyllodoceae and/or vice-versa. Although various palynological characters were found to be taxonomically important at different taxonomic levels, the apocolpial exine sculpture is emerged as one of the most important palynological features of systematic importance. The rugulate apocolpial exine with striate secondary sculpture and a reduced colpus might be apomorphic palynological character states for this tribe and Ericaceae as well. Hitherto, it is the first SEM study of *Rhodothamnus* pollen.

Introduction

The Phyllodoceae Drude is one of the most morphologically heterogeneous group that apparently has no morphological synapomorphy (Kron, 1997). Moreover, the inclusion of *Epigaea* in the tribe Phyllodoceae might increase the morphological heterogeneity of this group and the monophyly of this group is not well supported by morphology. Nearly all descriptions of the tribe have diagnosed the group based upon suites of characters that are homoplasious within the broader Ericoideae, rather than recognizing any particular potentially synapomorphic character (Kron *et al.*, 2002). Gillespie and Kron (2010) used molecular data to clarify tribe-level relationships within the Ericoideae and to propose a new classification that includes five tribes, namely Rhodoreae, Empetreae, Ericaceae, Bryanthaeae and Phyllodoceae; the Phyllodoceae is sister to a clade comprised of the other four tribes. Most members of Phyllodoceae are native to temperate-boreal regions of the Northern Hemisphere. The flowers are variable in shape, size and colour. Some species have pollen dispersed by curved stamens that spring out from the flower centre, explosively. Many species in this group are also poisonous, e.g., *Kalmia*, both to livestock and people. The molecular analyses indicated two strongly supported clades: *Kalmia s.l.* (including *Leiophyllum* and *Loiseleuria*) and a *Phyllodoce* clade (including *Epigaea*, *Kalmiopsis* and *Rhodothamnus*), and *Elliottia* is sister to *Kalmia* + *Phyllodoce* clade (Kron *et al.*, 2002; Gillespie and Kron, 2013). In addition, at least one taxon from all currently recognized tribes within the Ericoideae have at some point been classified within the Phyllodoceae, illustrating the difficulty in determining relationships of these taxa based on morphological or anatomical evidence alone (Gillespie and Kron, 2013).

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Pollen of the family Ericaceae is very diverse – monads vs. tetrads, or as polyads of indefinite number of tetrads; and its phylogenetic importance have been well documented (Kron *et al.*, 2002; Sarwar, 2007). Among the genera of Phyllodoceae, the pollen morphology of *Kalmia* has already been reported (Sarwar and Takahashi, 2012), but fragmentary palynological information is only available for other genera of this tribe (Sladkov, 1954; Oldfield, 1959; Stevens, 1971; Bohm *et al.*, 1978; Comtois and Larouche, 1981; Clements, 1995; Kron *et al.*, 2002; Radcliffe *et al.*, 2010). Light microscopy (LM) was mainly employed in these studies; and scanning electron microscopy (SEM) was employed in a few cases. The aims of the present study are to provide the palynological data of the genera of Phyllodoceae in addition to *Kalmia*, by using both LM and SEM, and to discuss its systematic significance in light of the recent molecular phylogenetic relationship of this tribe.

Materials and Methods

Pollen morphology of 13 taxa belonging to 5 (out of 7) genera of the tribe Phyllodoceae, was examined by means of light microscopy (LM) and scanning electron microscopy (SEM), or SEM alone (Table 1). Pollen morphology of the genus *Kalmia* has been studied in details (Sarwar and Takahashi, 2012) and the data has been included in discussion. The remaining genus *Kalmiopsis* is endemic to Oregon State, USA and could not be included due to unavailability of pollen samples. Polliniferous materials used in this investigation were taken from the dried specimens of the herbaria GB, S and SAPS. Abbreviations of names of the herbaria are according to the Index Herbariorum (Holmgren *et al.*, 1990).

Table 1. List of Phyllodoceae taxa used in this study along with their voucher specimens.

No.	Name of the taxa	Voucher specimens
1.	<i>Bejaria aestuans</i> Mutis ex L.	Venezuela: Edo, Tachira Hwy. 9, 37 km south of Delicias, 28.01.1978, J.L. Luteyn <i>et al.</i> 5296 (S)
2.	<i>B. racemosa</i> Vent.	USA: Florida, Dade Co., west of Fulford, 10.02.1930, H.N. Moldenke 601 (S)
3.	<i>B. resinosa</i> Mutis ex L. f.	Colombia: District Cauca, El Tambo, 08.11.1936, K. von Sneidern 1069 (S)
4.	<i>B. subsessilis</i> Benth.	Ecuador: Prov. Loja-Zamora road, 17.06.1979, B. Lójtant & U. Molau 15010 (GB)
5.	<i>Elliottia bracteata</i> (Maxim.) Benth. <i>et</i> Hook. f.	Japan: Hokkaido, Prov. Teshio, Masike-gun, Masike-cho, Mt. Shokanbetsu, 28.07.1983, H. Takahashi 4500 (SAPS)
6.	<i>E. paniculata</i> (Sieb. <i>et</i> Zucc.) Benth. <i>et</i> Hook. f.	Japan: Hokkaido, Hiyama-sicho, Kudoo-gun, Taisei-cho, Mt. Ohta-san, 06.08.1987, H. Takahashi 7802 (SAPS)
7.	<i>E. pyroliflora</i> (Bong.) Brim & Stevens	USA: Alaska, Juneau Quadrangle, Mt. Roberts behind, August 1967, L.A. Viereck 8624 (S)
8.	<i>Epigaea asiatica</i> Maxim.	Japan: Hokkaido, Hiyama-shicho, Kaminokuni-cho, 18.04.1982, M. Hara 5212 (SAPS)
9.	<i>E. repens</i> L.	USA: New York, Tomplins Co., slopes on east side of valley of Cayuga Intel, 13.04.1935, R.I. Clausen 19207 (S)
10.	<i>Phyllodoce aleutica</i> (Spreng.) A. Heller	Japan: Hokkaido, Jyozankei, Mt. Yoici-dake, 02.09.1982, H. Takahashi <i>et al.</i> 3666 (SAPS)
11.	<i>P. caerulea</i> (L.) Bab.	Japan: Hokkaido, the Hidaka range, Mt. Poroshiri – Mt. Tottabetsu, 01.08.1983, H. Takahashi 4569 (SAPS)
12.	<i>P. nipponica</i> Makino var. <i>oblong-ovata</i> (Tatew.) Toyokuni	Japan: Hokkaido, Hidaka range, Mt. Poroshiri – Mt. Tottabetsu, 01.08.1983, H. Takahashi 4568 (SAPS)
13.	<i>Rhodothamnus chamaecistus</i> (L.) Rchb.	Austria: Kärnten, Loibl-pass, 28.05.1960, I. Segelberg <i>s.n.</i> (S)

The preparation of pollen grains for LM and SEM, and pollen parameter studied follow Sarwar and Takahashi (2012). Pollen slides of all collection are deposited at the Hokkaido University Museum, Sapporo, Japan. Pollen size and shape classes were made following Erdtman (1986) and descriptive terminology follows Punt *et al.* (2007). The infrageneric classifications of *Bejaria* and *Phyllodoce* follow Clements (1995) and Good (1926 cf. Gillespie and Kron, 2013), respectively.

Results and Discussion

Pollen grains are united usually in tetrahedral tetrads, sometimes compact tetrahedral tetrads and/or with other configurations (Table 2). Viscin threads are usually present, sometime swelling at base in *Bejaria aestuans*, or absent in *Elliottia pyroliflora*, *Epigaea asiatica*, and *Phyllodoce caerulea*. The shape of the pollen grains varies from oblate to suboblate. Costae are usually distinct, but indistinct in *Bejaria*, 3-colpor(oid)ate (Fig. 1B), rarely 4-colporate in *Rhodothamnus chamaecistus* (Fig. 2K), ectoaperture (colpus) margins are distinct in all species. Endoapertures are usually distinct, but indistinct or absent in *Bejaria subsessilis* and *Phyllodoce aleutica*, lalongate, sometimes H-shaped in *Epigaea repens*; and endocracks are usually indistinct or absent in *Phyllodoce* and *Rhodothamnus*. Septum perforations are only observed in *Phyllodoce nipponica* var. *oblong-ovata*. The Phyllodoceae pollen ranges in mean values: D 30.0-53.3 μm , P 15.8-26.9 μm , E 22.0-38.7 μm , D/d 1.31-1.39, P/E 0.66-0.76, 2f 11.5-21.5 μm , W 0.9-2.3 μm , 2f/D 0.26-0.56, endoaperture length 0.8-2.0 μm , width 7.4-13.4 μm , apocolpial exine 1.7-3.0 μm thick, and septum 0.9-2.8 μm thick; tectate, apocolpial exine sculpture from verrucate to rugulate (Table 2).

In SEM, apocolpial exine sculptures mainly constitute two distinct groups, viz. i) primary exine sculpture indistinct, secondary sculpture gemmate-pilate (Figs 1C, E, G-H, L) or intermediate type (Fig. 1M); ii) primary exine sculpture moderately to coarsely rugulate or rugulate-psilate or intermediate types (Figs 2B, C, D, G-I, L); colpus membrane largely granulate or granuloid.

The genera of the Phyllodoceae employed in the present study reveal variation in SEM. In *Bejaria*, pollen surface is somewhat flat, primary apocolpial exine sculpture indistinct, secondary sculpture finely (diam. < 0.5 μm) gemmate-pilate (Type FG; Figs 1C, E, G, H); colpus membrane largely granulate or granuloid.

In *Elliottia*, pollen surface is uneven to somewhat flat, primary apocolpial exine sculpture indistinct, secondary sculpture unit moderately (diam. > 0.5 μm) gemmate-pilate (Type MG; Fig. 1L), or intermediate type (MG/R; Fig. 1M); colpus sometimes narrow and elongate, membrane granulate. The pollen surface of *Epigaea* is somewhat flat, apocolpial exine sculpture coarsely rugulate, the rugulae transversely striate and intermediate type (RS/R; Fig. 2B), or coarsely rugulate-psilate and intermediate type (R/P; Fig. 2C); colpus membrane granulate. Pollen surface in *Phyllodoce* is uneven and rugged, apocolpial exine sculpture intermediate type (R/FG; Fig. 2G); or the surface is somewhat flat, exine sculpture moderately to coarsely rugulate (Type R; Figs 2H-I); colpus membrane granulate or smooth. In *Rhodothamnus*, pollen surface is somewhat flat, apocolpial exine sculpture coarsely rugulate-psilate, the rugulae loosely arranged and clearly striate (Type RS; Fig. 2L); colpus membrane granuloid.

The present study reveals that in Phyllodoceae, both medium or minute and oblate pollen grains are united usually in tetrahedral tetrads (Table 2; Sarwar and Takahashi, 2012). Pollen tetrads of this tribe are generally characterized by the presence of viscin threads except in some species (Table 2; Sarwar and Takahashi, 2012). Results of the present study, in general, support previous palynological observations, however, in several instances, marked differences among the observations are apparent e.g., viscin threads on pollen tetrads of *Epigaea*. We did not observe any

Table 2. Variation in pollen characters of the tribe Phyllodoceae showing mean value in μm and standard deviation. D tetrad diameter, P polar length, P polar length, d(E) equatorial diameter, Apo. apocolpium, n.d. not discerned.

Name of Species	Config-uration ¹	D	P	d	D/d	P/E	Ectoperture		2f/D	Endoperture		Apo. exine thickness	Septum thickness	Ornamentation ²	Remarks ³	
							Length (2f)	Width (W)		Length	Width					
<i>Bejaria</i>																
Section <i>Bejaria</i>																
<i>B. aestuans</i>	T(+V)	39.7±2.3	21.2±1.5	29.0±1.7	1.37	0.73	15.4±1.6	1.4±0.8	11.00	0.39	1.4±1.0	13.2±3.3	3.0±0.3	2.8±0.8	FG	1
<i>B. resinosa</i>	T(+V)	45.3±2.1	25.0±1.3	32.7±1.2	1.39	0.76	11.8±1.3	1.7±1.0	6.94	0.26	1.0±0.4	12.9±3.2	2.4±0.5	1.1±0.5	FG	1
<i>B. subsessilis</i>	T(+V)	48.4±2.4	25.0±0.7	35.7±1.7	1.36	0.70	13.4±1.2	1.5±0.4	8.93	0.28	1.3±0.7	13.4±3.5	2.6±0.5	1.7±0.6	FG	1, 2
Section <i>Racemosae</i>																
<i>B. racemosa</i>	T(+V)	40.4±2.1	20.9±1.5	30.8±1.2	1.31	0.68	15.0±1.6	1.3±0.6	11.54	0.37	1.2±1.0	12.8±4.4	2.3±0.3	1.6±0.3	FG	1, 3
<i>Ellioitia bracteata</i>	T(+V)	52.1±3.1	26.9±1.8	37.5±2.1	1.39	0.72	20.0±3.4	1.0±0.4	20.00	0.38	2.0±1.1	11.6±2.0	1.8±0.2	1.2±0.4	MG	
<i>E. paniculata</i>	T(+V)	45.7±1.4	24.4±1.6	33.7±1.4	1.36	0.72	19.2±3.1	1.7±0.2	11.29	0.42	1.6±0.5	8.6±1.0	1.8±0.2	1.2±0.4	MG/R	4
<i>E. pyroliflora</i>	(T)	53.3±1.6	26.7±2.1	38.7±1.8	1.38	0.69	20.7±2.8	2.3±0.8	9.00	0.39	1.7±1.1	10.8±1.6	2.1±0.2	1.5±0.3	-	
<i>Epigaea asiatica</i>	T	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	RS/R	
<i>E. repens</i>	CT(+V)	38.5±1.5	19.8±1.2	29.0±1.0	1.33	0.68	21.5±1.9	2.1±0.3	10.24	0.56	0.8±0.4	8.1±2.3	2.5±0.4	1.4±0.1	R/P	
<i>Phyllodoce</i>																
Subgen. <i>Eu-Phyllodoce</i>																
<i>P. alenica</i>	T(+V)	33.0±1.7	15.8±2.0	24.1±1.1	1.37	0.66	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	1.7±0.1	1.0±0.3	R/FG	4
<i>P. caerulea</i>	(T)	30.0±1.7	16.1±1.2	22.0±1.3	1.36	0.73	15.8±1.2	0.9±0.3	17.56	0.53	1.3±0.6	7.6±2.9	1.9±0.3	0.9±0.3	R	
Subgen. <i>Parabryanthus</i>																
<i>P. nipponica</i> var. <i>oblong-ovata</i>	(T)(+V)	33.7±2.7	17.2±1.6	25.2±1.0	1.34	0.68	11.5±1.4	2.3±0.7	5.00	0.34	0.9±0.5	7.4±1.7	1.7±0.1	1.1±0.3	R	2, 4, P
<i>Rhodothammus chamaecistus</i>	T(+V)	42.4±1.8	22.3±1.1	31.5±1.3	1.35	0.70	17.7±1.6	1.6±0.4	11.06	0.42	1.4±0.8	10.4±1.2	1.8±0.3	1.5±0.6	RS	4, 5

¹ T: Tetrahedral tetrads, (+V): Viscin threads present, (T): Tetrahedral tetrads with other configurations, CT: Compact tetrahedral tetrads

² Exine ornamentation type by SEM. FG: Finely gemmate-pilate, MG: Moderately gemmate-pilate, R: Moderately to coarsely rugulate, RS: Coarsely rugulate-psilate with clearly striate rugulae, MG/R or RS/R or R/P or R/FG: Intermediates. For details please consult with the text.

³ 1: Costae indistinct, 2: Endoperture indistinct, 3: Apocolpial region small, 4: Endocracks absent/indistinct, 5: Rarely 4-aperturate, P: Perforated septum

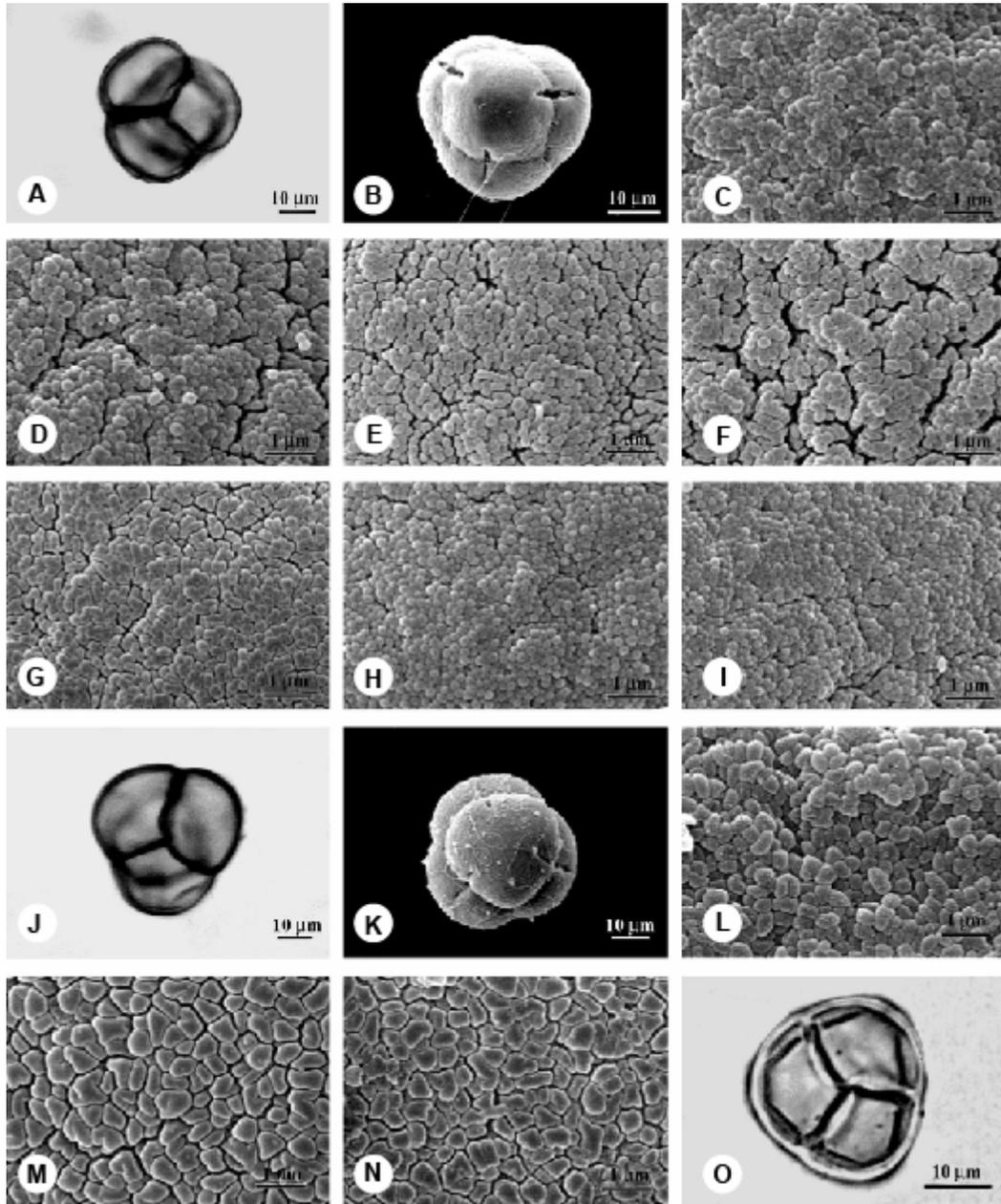


Fig. 1. LM and SEM pollen micrographs. A. *Bejaria aestuans* (Lutyen *et al.* 5296); B. *B. subsessilis* (Lójtant & Molau 15010); C–D. *B. aestuans* (Lutyen *et al.* 5296); E–F. *B. resinosa* (Sneidern 1069); G. *B. subsessilis* (Lójtant & Molau 15010); H–I. *B. racemosa* (Moldenke 601); J–K. *Elliottia paniculata* (Takahashi 7802); L. *E. bracteata* (Takahashi 4500); M–N. *E. paniculata* (Takahashi 7802); O. *Epigaea repens* (Clausen 19207). Pollen tetrads at polar view (A–B, J–K, O); pollen tetrad with viscin threads (B, K); micrographs with apocolpial exine sculpture details (C, E, G, H, L, M); micrographs with mesocolpial exine sculpture details (D, F, I, N). Scale bars = 1 μm (C–I, L–N), 10 μm (A, B, J, K, O).

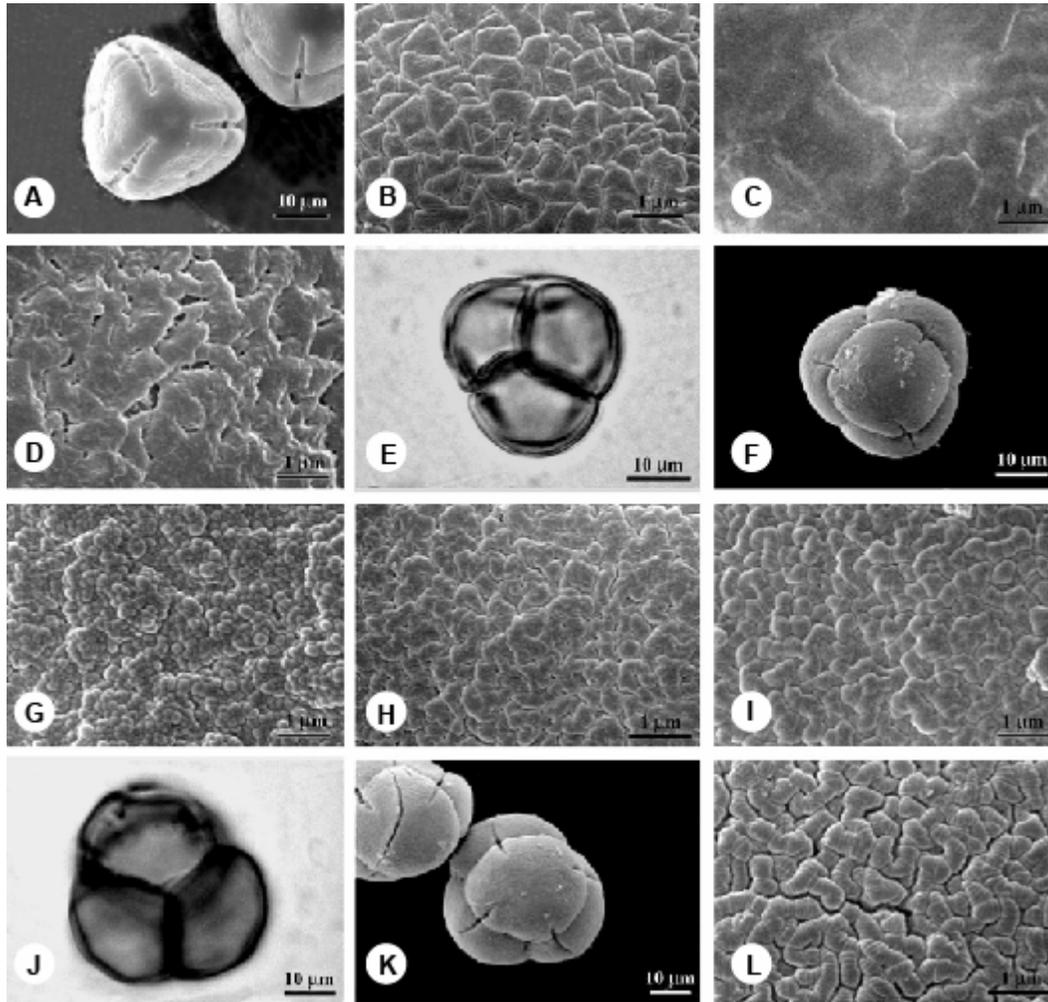


Fig. 2. LM and SEM pollen micrographs. A. *Epigaea repens* (Clausen 19207); B. *E. asiatica* (Hara 5212); C–D. *E. repens* (Clausen 19207); E. *Phyllodoce caerulea* (Takahashi 4569); F–G. *P. aleutica* (Takahashi et al. 3666); H. *P. caerulea* (Takahashi 4569); I. *P. nipponica* var. *oblong-ovata* (Takahashi 4568); J–L. *Rhodothamnus chamaecistus* (Segelberg s.n.). Pollen tetrads at polar view (A, E–F, J–K); tetrad with viscin threads (A, F, K); micrographs with apocolpial exine sculpture details (B–C, G–I, L); micrographs with mesocolpial exine sculpture details (D). Scale bars—1 μm (B–D, G–I, L), 10 μm (A, E, F, J, K).

viscin threads on the pollen tetrads of *E. asiatica* (Table 2), although it was reported that all three species of *Epigaea* have viscin threads with their pollen (Stevens, 1971).

Pollen tetrads with viscin threads are often regarded as indicating to entomophilous mode of pollination in the Ericaceae (Waha, 1984; Gillespie and Kron, 2013); however, there are many entomophilous taxa in Ericaceae without viscin threads on their pollen tetrads (Buchmann, 1983). High seed-set success was reported for *Phyllodoce aleutica* whose pollen tetrads have viscin threads, on the other hand, co-occurring *P. caerulea* whose pollen tetrads do not have viscin threads shown the lower seed-set success (Kasagi and Kudo, 2003). The presence or absence of

viscin threads may possibly affect the crossing and selfing ability of these two *Phyllodoce* species. Viscin threads might be anticipated in all species with open-campanulate inflorescence, since these are associated with insect pollination. The absence of viscin threads in *P. caerulea* might indicate to a secondary loss (Table 2), since viscin threads are present at least in some species within some genera of the Phyllodoceae (Gillespie and Kron, 2013).

The genera *Epigaea*, *Rhodothamnus*, *Phyllodoce* and *Kalmiopsis*, are consistently made a clade in all molecular analyses (Kron *et al.*, 2002; Gillespie and Kron, 2010, 2013); the close relationship within these four genera also represented in their palynological features. For example, all these genera possess apocolpial exine sculptures rugulate and/or its derivatives (Table 2; Figs 2B, C, G–I, L). The exine sculpture has also been proven as a useful taxonomic tool at the infrageneric level (Sarwar and Takahashi, 2006, 2012), although various palynological characters have been found to be important at different taxonomic levels. For example, *Elliottia bracteata* and *E. paniculata* are sister taxa in all molecular analyses (Gillespie and Kron, 2013) and are characterised by the similar value (0.72) of P/E ratio (Table 2).

The exine sculpture of *Rhodothamnus chamaecistus*, with clearly striate secondary sculpture on the rugulae (Type RS; Fig. 2L), is significantly different than that of other members of this tribe except *Epigaea asiatica* (RS/R; Fig. 2B), and very much similar to exine sculpture of members of the tribe Vaccinieae of subfamily Vaccinioideae (Sarwar and Takahashi, 2007). Hitherto, it is the first SEM study of *Rhodothamnus* pollen. In combined analyses of morphological and molecular data, *Epigaea repens* is strongly supported as sister to a clade of both *Rhodothamnus* species (Gillespie and Kron, 2013). The similarity in exine sculpture may be one of the indications of closeness of these two genera (Sarwar, 2007). The apocolpial exine with striate secondary sculpture may be an apomorphic palynological character state for this tribe, and Ericaceae as well (Kron *et al.*, 2002; Sarwar and Takahashi, 2007).

The apocolpial exine sculpture types vary often within a single genus. For example, the exine sculptures in *Epigaea asiatica* and *E. repens*, are distinctly different (Type RS/R vs. R/P; Figs 2B, D). The other (external) morphological features of *E. asiatica* also differ considerably from those of *E. repens* (Stevens, 1969), which might be due to disjunct geographic distribution. The infrageneric variation in palynological features due to geographic distribution has also been reported for some other genera of Ericaceae e.g., *Pyrola* (Takahashi, 1986) and *Enkianthus* (Sarwar and Takahashi, 2006).

The generic circumscription of the tribe Bejarieae (Kron *et al.*, 2002) and the systematic position of *Bejaria* was a matter of debate for long time (Gillespie and Kron, 2010). Based on palynological, both quantitative and qualitative features it was reported that the monotypic genus *Bryanthus* is clearly distinguished from other members of the tribe Bejarieae - *Bejaria* and *Ledothamnus* (Sarwar, 2007). The molecular phylogenetic studies later confirmed the above finding and transferred the genus *Bejaria* to the tribe Phyllodoceae and construct a new tribe Bryantheae (includes *Bryanthus* and *Ledothamnus*) (Bush and Kron, 2008; Gillespie and Kron, 2010, 2013). Between two sections, *Bejaria* sec. *Bejaria* is characterized by larger values of P, D/d, P/E and thicker apocolpial exine compared to those of *Bejaria* sec. *Racemosae* (Table 2). The close relationship between *B. aestuans* and *B. subsessilis* is supported by values of D/d, ecto- and endo-aperture length and apocolpial exine thickness (Table 2; Bush and Kron, 2008). Moreover, the monophyly of *Bejaria* may be supported by apocolpial exine sculpture (Table 2; Figs 1C, E, G–H). The pollen tetrads of *Bejaria* are similar to those of some *Rhododendron* species of the tribe Rhodoreae. But these similarities may be due to homoplasy. Indistinct costae and lower 2f/D in *Bejaria* are stable and distinct palynological characters within the Ericoideae except for some species of *Rhododendron* and *Therorhodion* (Sarwar, 2007). These palynological features might imply an evolutionary tendency to a reduced (smaller) ectoaperture (Warner and Chinnappa,

1986), and might be an apomorphic pollen character state for this genus as well as the family Ericaceae (Sarwar, 2007). Among the other genera of the tribe Phyllodoceae, the systematic significances of pollen morphological features of *Kalmia* have previously been discussed in details (Sarwar and Takahashi, 2012).

The pollen morphological data confirm the infra- and inter-generic relationships as identified by molecular phylogeny of Phyllodoceae (Gillespie and Kron, 2013) and/or vice-versa. Although various palynological characters were found to be taxonomically important at different taxonomic levels, the apocolpial exine sculpture is emerged as one of the most important palynological features of systematic importance. The rugulate apocolpial exine with striate secondary sculpture, and a reduced colpus might be apomorphic palynological character states for the tribe Phyllodoceae and the family Ericaceae.

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