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# **An overview of pollen morphology and its systematic significance in *Vaccinium* L. (Ericaceae)**

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The extend of general palynological diversity in the permanent tetrads of *Vaccinium* pollen was studied by investigating the pollen of 37 species, representing 18 of the approximately 30 sections of *Vaccinium* currently recognized. Light (LM), scanning electron (SEM) and transmission electron microscopy (TEM) were used. The variation in apocolpial exine sculptures revealed by SEM, combined with the overall characteristics of the pollen tetrads as observed with LM, were used to assess the present sectional position of each species. Apocolpial exine sculpture of the pollen tetrad varied from finely verrucate through rugulate to psilate; the rugulae have “secondary sculptures”, this ranges from faint to fine to clear striate, and the lirae sometimes have beads-like sculpture. Seven main types (Types 1 – 7) as well as twelve subtypes, within Types 1 – 3, were recognized for exine sculpture. Although the palynological characters do not appear to correlate very clearly with current sectional classification of *Vaccinium*, they do provide useful information on taxonomic relationships and allow an insight into some of the taxonomic problems within this genus. Pollen tetrads of *V. japonicum* sect. *Oxycoccoides* are the smallest, and have a very distinctive, finely verrucate exine sculpture (Type 6); pollen data support the separation of this species from the genus *Vaccinium*. Slight differences in tetrad size and exine sculpture were found corresponding to geographical distribution. In general the pollen of the New World species of *Vaccinium* was relatively larger in

size than the Old World species, with coarsely rugulate to coarsely rugulate-psilate exine sculpture. Pollen of the Old World species tends to be smaller, has wider variation in exine sculpture, ranging from finely verrucate through rugulate to psilate.

**Key words:** pollen morphology, sectional classification, *Vaccinium*

## Introduction

The genus *Vaccinium* L. with about 450 species, is the third largest genus after *Rhododendron* (850 spp.) and *Erica* (600 spp.) in the Ericaceae <sup>(1)</sup>. It is a morphologically diverse and polyphyletic genus <sup>(2-4)</sup> distributed in temperate and subtropical or tropical montane regions of most continents except Antarctica, New Zealand, Australia, and most of Africa. Approximately two thirds of the species occur in Malaysia and other 70 species in Southeast Asia <sup>(5)</sup>. Drude <sup>(6)</sup> divided *Vaccinium* into 5 subgenera; *Batodendron*, *Cyanococcus*, *Oxycoccus*, *Eu-Vaccinium* and *Epigynium*. Thereafter, Sleumer <sup>(7)</sup> divided this genus into 33 sections based on overall similarities and a few selected characters. Since then, the species composition of a section and phylogenetic relationships among these sections in *Vaccinium* have been the subject of much debate <sup>(3, 4, 8-17)</sup>.

Scanning electron microscopic (SEM) study on the pollen morphology provides a useful plant identification tool for distinguishing between closely related species and even clones <sup>(18-19)</sup>, and is valuable for determining the systematic relationships at generic and specific levels in the Ericaceae <sup>(20-23)</sup>. Pollen morphology of the *Vaccinium* species under both light microscope (LM) and/or SEM has been studied numerously, and it has also been fragmentally mentioned in many regional pollen floras <sup>(24-54)</sup>. However, the number of species reported in these works is still limited, and especially the pollen morphology of some taxa: e.g., *V. angustifolium*, *V. corymbosum*, *V. myrtilus*, *V. uliginosum*, *V. vitis-idaea* etc., has been described many times. Palynological characters have not been used for delimiting the sections in *Vaccinium*. Sometimes the measurements of only one or two palynological characters e.g. tetrad diameter, were used for classification of few individual sections <sup>(5, 13, 16, 55)</sup>.

Phylogenetic analysis using both morphological and molecular data for all the sections of this genus has yet to be elaborated. Kron et al. <sup>(3)</sup> suggested the necessity of more detailed phylogenetic analyses within *Vaccinium* including the assessment of sectional monophyly. The present research is a general palynological survey on *Vaccinium* in order to clarify the infrageneric diversity and to assess the systematic significance of the pollen morphological characters.

### Materials and Methods

Pollen morphology of 37 species of *Vaccinium* was investigated representing 18 of about 30 sections of the genus *Vaccinium* which generally follow Sleumer <sup>(7)</sup> with modifications by Airy Shaw <sup>(8)</sup>, Stevens <sup>(9-10)</sup>, Vander Kloet <sup>(5)</sup>, Vander Kloet and Dickinson <sup>(15-16)</sup>, and Vander Kloet et al. <sup>(17)</sup> (Table 1). Sections and species examined are cited alphabetically both in the text and tables. Pollen grains were examined in LM and SEM for most specimens, and in transmission electron microscope (TEM) for *V. smallii*. Polliniferous materials used in this investigation were taken from the dried herbarium specimens deposited in the herbaria C, GB, KYO, SAPS, and TUS. Abbreviation of the herbarium names are according to the Index Herbariorum <sup>(56)</sup>.

Preparation of pollen grains follows Sarwar et al. <sup>(57)</sup>. 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 <sup>(45)</sup>, and the D/d, P/E and 2f/D ratios were calculated. The measurements given in Table 3 are based on at least 10 grains from each specimen. Pollen slides of all collections are deposited in the Hokkaido University Museum, Sapporo, Japan.

Descriptive terminology follows Punt et al. <sup>(58)</sup>. Quantitative data gained from LM observations were used for calculating correlations among different pollen morphological features by using the XLSTAT-Pro computer package.

## Results

### General pollen morphology of *Vaccinium*

Pollen grains are commonly united at both lobed and compact tetrahedral tetrad (Figs. 1O and C, respectively); other configurations (e.g. Fig. 4B) are also found in some species too, and sometimes one grain of the tetrad is poorly developed. Abnormal pollen tetrads: only one grain of tetrad has developed and/or whole tetrads are shrunk or deformed or broken, are observed in one specimen of *V. corymbosum* (Meyer and Mazzeo 13278). Viscin threads absent. In the range of average values of the specimen, tetrad diameter (D) 32.5 – 49.2  $\mu\text{m}$ , polar length (P) 15.7 – 26.1  $\mu\text{m}$ , equatorial diameter (E) 24.5 – 37.2  $\mu\text{m}$ , P/E 0.62 – 0.83, shape generally oblate but sometimes suboblate. Ratio of tetrad diameter to individual grain diameter (D/d) 1.24 – 1.43, 3-aperturate, apertures arranged according to “Fischer’s Law”, rarely 4-aperturate. Colpor(oid)ate, colpi distinct, 14.0 – 29.0  $\mu\text{m}$  long, width 0.9 – 3.0  $\mu\text{m}$ , ratio of colpus length to tetrad diameter (2f/D) 0.35 – 0.70, significantly wider at middle, generally acute, sometimes tapering towards ends, colpus margin distinct. Ora distinct, but indistinct in some species; shape of ora commonly lalongate, but also circular or sometimes not clear. Costae usually present, though in *V. uliginosum* not clear. Exine tectate, apocolpial exine 1.5 – 3.3  $\mu\text{m}$  thick, septum thickness 0.5 – 2.4  $\mu\text{m}$ .

In SEM, apocolpial exine sculpture varies from finely verrucate to coarsely rugulate-psilate; the rugulae with secondary sculptures, from faintly to finely and clearly striate, and lirae sometimes beads-like sculptured (Figs. 1 – 5). Exine sculpture along the colpi similar to that appearing at distal pole, but the mesocolpial exine has a tendency to decrease in lateral extension of the rugulae with more distinct units. Colpus membrane is commonly granular, but has sometimes a tendency towards smooth or granuloid.

In TEM for *V. smallii*, the apocolpial exine is composed of ektexine; tectum, columellae (rod-like elements distinct) and foot layer, and endexine with electron density (Fig. 6B). Ektexine is ca. 1.1  $\mu\text{m}$  and a total exine is ca. 1.4 – 1.7  $\mu\text{m}$  in thickness (Fig. 6). In the septum, tectum is lacking and two foot layers of adjacent grains are connected by columellae (Fig. 6C); a total exine (septum) is ca. 1.2 – 1.5  $\mu\text{m}$  in thickness. The exine in LM appears about 2 times thicker than in TEM.

Some significant correlations among different palynological features with LM were found viz. D showed correlation with P, E, apocolpial exine thickness and 2f ( $r = 0.91, 0.93, 0.45$  and  $0.49$  respectively), P correlated with E and apocolpial exine thickness ( $r = 0.82$  and  $0.42$ , respectively), E correlated with 2f and apocolpial exine thickness ( $r = 0.49$  and  $0.47$ , respectively), D/d correlated with P/E ( $r = 0.67$ ), both D/d and P/E correlated with septum thickness ( $r = 0.47$  and  $0.52$ , respectively) etc. and of course D/d and P/E has a strong correlation and directly depend upon the individual values of D, P and E.

### **Variation of palynological characters based on LM**

The palynological features are divided into smaller groups (classes) and summarized in Table 2, and all the palynological characters studied with LM are listed in Table 3. Among the species studied, pollen of *V. cubense* showed the highest values of D, E and 2f ( $49.2 \mu\text{m}$ ,  $37.2 \mu\text{m}$  and  $29.0 \mu\text{m}$ , respectively), and the longest P ( $26.1 \mu\text{m}$ ) was observed in *V. corymbosum* (Spon. & Bouf. 1764). On the other hand, pollen of *V. japonicum* showed all the lowest values ( $32.5 \mu\text{m}$ ,  $24.5 \mu\text{m}$  and  $15.7 \mu\text{m}$ , respectively) except 2f ( $14.0 \mu\text{m}$ ) in *V. caespitosum*. Both the lowest values of D/d and P/E ( $1.24$  and  $0.62$ , respectively) were observed in the grains of *V. sprengelii*, but the highest values ( $1.43$  and  $0.83$ , respectively) in *V. oldhamii* and *V. crassifolium*, respectively (Table 3). Moreover, parameters with same value were also observed in different taxa, e.g. the D/d value  $1.43$  was found in *V. oldhamii*, *V. caespitosum* and *V. oxycoccus* (Table 3). The highest value of ectoaperture width, 2f/D, apocolpial exine and septum thickness ( $3.0 \mu\text{m}$ ,  $0.70$ ,  $3.3 \mu\text{m}$  and  $2.4 \mu\text{m}$ , respectively) was found in the grains of *V. corymbosum* (Utech et al. 83-050), *V. macrocarpon*, *V. consanguineum* and *V. bracteatum*, respectively. On the other hand, the lowest value of ectoaperture width, 2f/D, apocolpial exine and septum thickness ( $0.9 \mu\text{m}$ ,  $0.35$ ,  $1.5 \mu\text{m}$  and  $0.5 \mu\text{m}$ , respectively) was found in the grains of *V. floribundum* var. *floribundum*, *V. corymbosum* (Spon. & Bouf. 1764), *V. myrsinites* and *V. uliginosum* (Takahashi 9908), respectively.

### **Variation of exine sculpture based on SEM**

The variation in exine sculpture is shown in Figs. 1 – 4. Most exine sculptures in the genus

*Vaccinium* were classified into 12 subtypes within Types 1 – 3 (see Fig. 5) based on tendency from narrow and wavy rugulate to wide and flat rugulate, and from indistinct to distinct in the secondary sculpture on rugulae. However, four other distinct types (Types 4 – 7) of exine sculpture were recognized. *Vaccinium emarginatum* of sect. *Conchophyllum* shows a peculiarity among the species. Pollen surface of this species is somewhat flat, and exine consists of irregularly-shaped elements, surrounded by deep clear grooves. Elements are clearly, deeply and tangentially striate (Type 4, Fig. 1J). Pollen surface of *V. vacciniaceum* of sect. *Epigynium* is mostly even, and exine sculpture is coarsely rugulate-psilate (Fig. 2G) to mostly psilate (Fig. 2H); secondary sculpture beaded striate (Type 5). Exine sculpture of *V. japonicum* of sect. *Oxycoccoides* is very peculiar and finely verrucate (Type 6, Fig. 3M). Pollen surface of *V. stamineum* of sect. *Polycodium* is uneven and rugged, and exine sculpture is very coarsely rugulate with the rugulae clearly beaded striate and loosely arranged (Type 7, Fig. 4D). As seen in Figs. 1 – 4, the exine sculpture sometimes varies to a certain extent even within a species; e.g. in *V. wrightii* surface uneven and rugged, the rugulae finely striate (Fig. 1F) to surface relatively flat, the rugulae more finely and clearly striate (Fig. 1G), but a more or less continuous and serial variation in the exine sculpture was observed among the *Vaccinium* species.

## Discussion

### Variation of palynological characters

The rare occurrences (less than 5% of total observed grains) of unusual 4-aperturate pollen grains are observed in two species of *Vaccinium*; *V. myrtillus* and *V. oxycoccus* (Table 2). This might be due to abnormality in the microsporogenesis stage of pollen development, or related to ploidy level and/or pollen size<sup>(21, 59)</sup>. The shape of tetrahedral tetrads with 4-aperturate grains was little different from that of tetrahedral tetrads with 3-aperturate grains. A slight infraspecific variation in palynological characters has been found in *V. corymbosum* and *V. uliginosum* (Tables 2 & 3), but the difference was very distinct between two specimens (Takahashi 24491 and Kikuchi s.n.) of *V. smallii* (Tables 2 and 3; Figs. 2K – L and 3A). Morphological variation of the leaf shape and hairiness within

*V. smallii* is also very wide (Takahashi personal observation). A study of infraspecific morphological and palynological variations should be a subject for future research.

The relative globularity of the tetrad (D/d) is correlated with septum thickness ( $r = 0.47$ ). It indicates that septum is relatively thicker at lobed tetrad compared to that of compact tetrad. Again, the D/d and septum thickness both are correlated with pollen shape (P/E) index ( $r = 0.69$  and  $0.51$ , respectively). These might indicate that tetrad shape (lobed or compact) and septum thickness directly depend upon the size and shape of individual pollen grain. The apocolpial exine thickness also correlates with both tetrad diameter or size and shape of individual pollen grain. Along with D, P and E, the apocolpium exine ( $1.5 - 3.3 \mu\text{m}$ ) and septum thickness ( $0.5 - 2.4 \mu\text{m}$ ) also showed a wide variation (Table 3). Usually the former is thicker than the latter. But septum thicker than apocolpial exine was also noticed in different species viz. *V. oldhamii*, one specimen of *V. smallii* (Kikuchi s.n.), *V. ovalifolium* and *V. stamineum* (Table 3).

The SEM observations within the genus *Vaccinium* show a variation in the exine sculpture (Figs. 1 – 4). The common feature for this genus is rugulae with secondary sculptures; faintly to finely and clearly striate. This might be a synapomorphic palynological character of *Vaccinium* within Ericaceae. Seven types of exine sculpture (additional subtypes recognized in the Types 1 – 3) have been recognized within the *Vaccinium* species (Table 2). The following exine sculptural types might be derived from different subtypes of Types 1 – 3: viz., exine sculpture of *V. emarginatum* (Type 4, Fig. 1J) from that of *V. oldhamii* (Type 3b, Fig. 1H), *V. vacciniaceum* (Type 5, Fig. 2G – H) from *V. floribundum* var. *floribundum* (Type 2d, Fig. 4G) and/or *V. sprengelii* (Type 3d, Fig. 2F), and *V. stamineum* (Type 7, Fig. 4D) from *V. scoparium* (Type 2a, Fig. 3K) and/or *V. vitis-idaea* (Type 2a, Figs. 4K). Type 6 is very distinct from other types. A more or less continuous and serial variation in the apocolpial exine sculpture was also observed in other genera of the family Ericaceae<sup>(20–23)</sup>.

Variation in exine sculpture within the same specimen of *V. wrightii* (Figs 1 F and G) might indicate the “morphological connection” between uneven, rugged pollen surface with the rugulae finely striate and more flat surface with the rugulae more finely and clearly striate. The similar variation of exine sculpture in *V. vacciniaceum* of sect. *Epigynium* might also indicate the “morphological connection” between coarsely rugulate-psilate and mostly psilate (Figs. 2G – H).

### Palynological comments on infrageneric systems

Vander Kloet and Bohm <sup>(55)</sup> regarded *V. randaiense* Hayata as a synonym of *V. erythrocarpum* of sect. *Oxycoccoides*, but, later other scientists did not agree with their opinion <sup>(60–61)</sup>. Palynologically *V. randaiense* was distinctly different from the other member of sect. *Oxycoccoides*, *V. japonicum* (Table 3, Figs. 1E and 3M). On the other hand, *V. randaiense* showed closer similarity with the other two members, *V. bracteatum* and *V. wrightii* of the sect. *Bracteata* (Tables 2 and 3; Figs. 1D – F). Thus, it might be better to recognize the individual specific status of *V. randaiense* under the sect. *Bracteata*. Powell and Kron <sup>(4)</sup> reported that *V. oldhamii* of sect. *Ciliata* is intermediate and sister to both *Bracteata* and *Cyanococcus* clade. Palynological observations viz. D, P, E, exine sculptures etc., of this study agreed with this opinion (Tables 2 and 3; Figs. 1C – I, 1K – O and 2A – C).

Abnormal pollen tetrads: e.g. only one grain of tetrad developed and/or whole tetrads were shrunk or deformed, have occurred in one specimen of *V. corymbosum* (Meyer and Mazzeo 13278) under both LM and SEM. Odell and Vander Kloet <sup>(62)</sup> also reported similar exceptions for other morphological characters. In their studies, they found one specimen of *V. corymbosum* which shared common characters with *V. hirsutum*. This type of variation might be expected to occur time to time due to the hybrid origin of *V. corymbosum* <sup>(62)</sup>. Due to shrinkage and/or breakdown of grains, we could not study the pollen of *V. angustifolium* of sect. *Cyanococcus* in detail by LM or SEM except for coarsely rugulate exine sculpture. The pollen grains of this specimen might be susceptible to acetolysis treatment. Vander Kloet <sup>(13)</sup> reported that the pollen tetrads of *V. angustifolium* and *V. hirsutum* were 38.0 and 41.0  $\mu\text{m}$  in diameter, respectively.

The taxonomic position of the northeast Asian *V. hirtum* and *V. smallii*, from sect. *Hemimyrtillus* has been subject of much debate <sup>(4, 13, 15)</sup>. Recently, Powell and Kron <sup>(4)</sup> showed that sect. *Hemimyrtillus* is polyphyletic and the northeast Asian taxa are neither closely related to species from sect. *Cyanococcus* nor sect. *Hemimyrtillus* of Sleumer <sup>(7)</sup>, but rather are sister to a clade that includes sections *Oxycoccoides* and *Praestantia*. They suggested that the northeast Asian species should be removed from sect. *Hemimyrtillus* and the Tethyan species of this section may be the sister to rest of tribe Vaccinieae. Results of the present studies showed that *V. hirtum* has a similarity in many

palynological characters with *V. praestans* of the sect. *Praestantia* (Table 3), and no specimen of sect. *Hemimyrtillus* from Tethyan region has been included in our study. So, we were not able to make any specific comments on this issue from our palynological results.

The P/E ratio and septum thickness showed two distinct groups (0.64 – 0.68 and 1.3 – 1.4  $\mu\text{m}$  vs. 0.75 – 0.80 and 2.0  $\mu\text{m}$ ) within the sect. *Myrtillus* (Table 3). This might be due to variation in ploidy level among the species. As the karyological studies revealed that *V. myrtillus* and *V. ovalifolium* had both diploid ( $2n = 24$ ) and tetraploid ( $2n = 48$ ) populations, and *V. caespitosum* only diploid<sup>(63, 16)</sup>. Generally tetraploids have larger values in all morphological traits compared to those of the diploids. Cockerham and Galletta<sup>(64)</sup> found that the mean pollen diameter was 11% larger in the tetraploids compared to that in the diploids in certain *Vaccinium* species. There is a possibility that our specimen of *V. myrtillus* is also diploid. But we are not sure as we did not perform any karyological test. One grain of the pollen tetrad shrinks a little bit or breaks among the members of this section except *V. myrtillus* under LM. This character was also found in *V. bracteatum* of sect. *Bracteata* and in one specimen of *V. corymbosum* (Spon. & Bouf. 1764) of sect. *Cyanococcus*. This might be due to poor development in one grain of the tetrads. Cockerham and Galletta<sup>(64)</sup> also observed frequent pollen irregularities viz. empty pollen grains, granular and unstained grains or distorted and partially stained grains in certain *Vaccinium* species. They concluded these irregularities as the indication of possibility of early post-meiotic abortions.

Powell and Kron<sup>(4)</sup> indicated that Hawaiian blueberries, *V. calycinum*, *V. reticulatum*, and *V. dentatum* are monophyletic and should be transferred from the sect. *Macropelma* to the sect. *Myrtillus*. The wood anatomical study of blueberry tribe by Lens et al.<sup>(65)</sup> supported the transfer of *V. calycinum* to sect. *Myrtillus*. Palynological characteristics of *V. calycinum* f. *glabreccens* showed similarities in many aspects viz. medium in size, coarsely rugulate exine sculptures etc. with the members of the sect. *Myrtillus* (Tables 2 and 3; Figs. 3C – G, 3I, and 3K), and also agreed with the transfer of this species from the sect. *Macropelma* to the sect. *Myrtillus*.

Section *Oxycoccooides* has a southeastern North American and eastern Asian distribution<sup>(5)</sup>. Vander Kloet<sup>(5)</sup> was doubtful about their individual specific status between the North American *V. erythrocarpum*, and the Asian *V. japonicum*. Latter species was described as a subspecies of the

former; as *V. erythrocarpum* subsp. *japonicum* by Vander Kloet and Bohm <sup>(55)</sup>. However, Yamazaki <sup>(66)</sup> did not agree with this opinion and indicated the individual specific identity. Pollen of *V. japonicum* has many distinct characters with the lowest values viz. tetrad diameter, polar and equatorial length of pollen (32.5, 15.7 and 24.5  $\mu\text{m}$ , respectively) among the *Vaccinium* species examined in this study (Table 3). This species showed a very distinct and exceptional type of exine sculpture, finely verrucate (Type 6) within *Vaccinium* (Fig. 3L). Taking pollen morphology into account, *V. japonicum* appears to be more differentiated than other species of *Vaccinium*. Sometimes *V. japonicum* was treated under a distinct genus *Hugeria*; as *H. japonica* (Miq.) Nakai <sup>(67)</sup>. Palynological evidence supports the separation of *V. japonicum* from the genus *Vaccinium*. Although Powell and Kron <sup>(4)</sup> regarded *V. erythrocarpum* and *V. japonicum* of sect. *Oxycoccoides* as being sister to *V. praestans* of sect. *Praestantia*. The exine sculpture is distinctly different between the two sections, the exine sculptures of *V. japonicum* (Type 6, Fig. 3M) and *V. praestans* (Type 1d, Fig. 4E).

Pollen grains of *V. macrocarpon* and *V. oxycoccus* of sect. *Oxycoccus* are very clearly differentiated in most palynological characters on LM (Tables 2 and 3). Pollen size of *V. macrocarpon* is smaller than that of *V. oxycoccus*. This might also be due to variation in ploidy level between the species. According to Camp <sup>(68)</sup>, both species were entirely diploid initially, but later through autopolyploidy, *V. oxycoccus* became locally a tetraploid ( $2n = 48$ ) or a hexaploid ( $2n = 72$ ) <sup>(68, 5)</sup>.

The coarsely rugulate exine sculptures with wide rugulae and more linear edge in *V. consanguineum* and *V. ovatum* of sect. *Pyxothamnus* (Type 2c, Figs. 4F and H), were very distinct compared to the other species of *Vaccinium* except *V. meridionale* (Type 2c, Fig. 2E) of sect. *Eococcus*. Kron et al. <sup>(3)</sup> first reported the sister relationship between sects. *Eococcus* and *Pyxothamnus* and their relationship was also supported in the wood anatomical studies of Lens et al. <sup>(65)</sup>. But, Vander Kloet et al. <sup>(17)</sup> opinioned that *V. meridionale* should be transferred from sect. *Eococcus* to sect. *Pyxothamnus* as *V. meridionale* produced a common clade with *V. consanguineum*. They also reported that the other two members *V. floribundum* and *V. ovatum*, of sect. *Pyxothamnus* produced a clade which was comparatively distantly positioned from the earlier clade. So, it is more probable that the sister relationship exists between these two sections. It was very interesting that the

apocolpial exine thickness of *V. consanguineum* (3.3  $\mu\text{m}$ ) was nearly about to double compare to other two species (1.7  $\mu\text{m}$ ) studied from this section (Tables 2 and 3).

Both Stevens<sup>(9)</sup> and Vander Kloet<sup>(5)</sup> placed the monotypic sect. *Vitis-Idaea* as closely related to the Neotropical sect. *Pyxothammus*. But, the recent cladistic analyses showed that *V. vitis-idaea* is sister and make a common clade with the North American species *V. macrocarpon* of sect. *Oxycoccus*<sup>(3-4)</sup>. Results of our palynological studies agreed with the recent opinion (Tables 2 and 3; Figs. 3O and 4K).

### **Taxonomic significance of pollen morphology**

The palynological characters alone were sufficient to distinguish only two sections; *Oxycoccoides* and *Polycodium* from eighteen sections of *Vaccinium* (Figs. 3M and 4D, respectively). Some infra- and inter-sectional variations and/or overlaps were observed in all quantitative and qualitative palynological characters (Tables 2 and 3). Similar result was also found for other genera of Ericaceae<sup>(20, 22 - 23)</sup>. Differences in palynological characters corresponding to the geographical distribution were also found. Generally pollen grains of the new world *Vaccinium* species were relatively larger in size with exine sculptures coarse rugulate to coarse rugulate-psilate (Table 2, Figs. 1 - 4). And those of the old world species were relatively smaller in size with a wider variation in exine sculptures from fine verrucate through rugulate to psilate. Variation of D in the old world species is wider, and the smallest class I (20.1 - 30.0  $\mu\text{m}$ ) is only found in old world species and the largest class IV (50.1 - 60.0  $\mu\text{m}$ ) is found in only one species (Table 2). On the other hand, the new world species do not possess any pollen tetrad of class I, although four species having class IV tetrad. Higher number of species<sup>(5)</sup>, and a wide variation in D and exine sculptures of the old world species might be an indication to the centre of origin and/or diversity of *Vaccinium* lies in this area. Croizat<sup>(69)</sup> suggested that the centre of origin of *Vaccinium* was near Madagascar. Palynological characters give some useful information regarding taxonomic relationships as discussed above and helped to give an insight into some taxonomic problems/ambiguity within this genus. Goldy et al.<sup>(31)</sup> also concluded that exine sculpture patterning may provide useful information on taxonomic relationships of *Vaccinium*. Although subdivision in pollen grain types could not be found correlating with a

subdivision based on macromorphology, morphological trends were noticed in pollen, concerning size, shape and exine sculpture. The psilate exine sculpture situated at the end of a serial variation of exine sculpturing might be the most specialized character state within this genus. The major morphological evolutionary trends of exine sculpture is postulated within *Vaccinium*; i) from rugulae narrow and wavy surface to psilate/flat surface and/or vice versa, and ii) striate secondary sculpture indistinct to distinct and/or vice versa (Fig. 5).

In the recent phylogenetic studies using molecular data, it is reported that the members of the *Vaccinium* sect. *Conchophyllum* made a common clade with the species of the genus *Agapetes*<sup>(3-4)</sup>, and *V. crassifolium* of sect. *Herpothamnus* made a common clade with *Gaylussacia dumosa* and sister to *Orthaea/Notoropa* clade<sup>(3)</sup>. Palynological features support both the relationships. Exine sculpture of *V. emarginatum* of sect. *Conchophyllum* is similar to that of some *Agapetes* species e.g. *A. lobbii* and *A. oblonga*, and also it is similar between *V. crassifolium* and *G. dumosa* (Sarwar personal observations). Kron et al.<sup>(3)</sup> opinioned that genus *Vaccinium* needs to be enlarged to include all species of the tribe Vaccinieae, or to be broken up, with some groups of species given different names. Our palynological observations support the latter opinion, as discussed in case of *V. japonicum*. However, these changes await more complete morphological, palynological and molecular data with larger number of specimens. An intensive sampling of *Gaylussacia* and representatives of pseudo-ten-locular *Vaccinium* is suggested to resolve the relationship of *Gaylussacia* to other temperate *Vaccinium*<sup>(3)</sup>.

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**Table 1:** Specimens examined in *Vaccinium* (sections and species in alphabetical order).

Section and Species	Collector and No.	Voucher information (Herbarium acronym)
<i>Batodendron</i> (Nutt.) A. Gray [1/3] <sup>1)</sup>		
<i>V. cubense</i> (A. Rich.) Griseb.	Ekman 5294 (L, S) <sup>2)</sup>	Cuba: Prov. Oriente, Sierra Maestra, 07.04.1915 (S)
<i>Bracteata</i> Nakai [3/16]		
<i>V. bracteatum</i> Th.	Oka s.n. (L, S)	Japan: Nagasaki Pref., Nagasaki-shi, Mt. Inasa-yama, 13.07.1896 (SAPS)
<i>V. randaiense</i> Hayata	Kikuchi s.n. (L, S)	Taiwan: Baibara, 15.06.1925 (SAPS)
<i>V. wrightii</i> A. Gray	Collector unknown (L, S)	Japan: Okinawa, Hachiyama, no day.03.1888 (SAPS)
<i>Ciliata</i> Nakai [1/5]		
<i>V. oldhamii</i> Miq.	Takahashi 232 (L, S)	Japan: Hokkaido, Prov. Hidaka, Mt Apoi, 05.07.1978 (SAPS)
<i>Conchophyllum</i> Sleum. [1/9]		
<i>V. emarginatum</i> Hayata	Wang 1022 (L, S)	Taiwan: Pingtung Hsien, Wutai Hsiang, Wutoushan nature prot. area, 23.04.1995 (KYO)
<i>Cyanococcus</i> A. Gray [6/9]		
<i>V. angustifolium</i> Ait.	Laferriere 233 (grains shrink)	USA: Wisconsin, Columbia Co., 10.05.1960 (SAPS)
<i>V. corymbosum</i> L.	Meyer & Mazzeo 13278 (L, S)	USA: Georgia, Wayne Co. edge of Jessup, 27.03.1973 (TUS 75346)
	Spongberg & Boufford 1764 (L, S)	USA: North Carolina, Transylvania Co., 09.05.1982 (TUS 117140)
	Utech et al. 83-050 (L, S)	USA: Alabama, Sumter Co., 28, 23.03.1983 (TUS 96720)
<i>V. hirsutum</i> Buckley	Boufford & Wood 23586 (S)	USA: Tennessee, Polk Co. NE of the town of Parksville, 16.05.1985 (TUS 127189)
<i>V. myrsinites</i> Lam.	Moldenke 948 (L, S)	USA: Florida, Lee Co., Fort Myers, 12.04.1930 (GB)
<i>V. myrtilloides</i> Michx.	Turesson & Alm 146 (L, S)	USA: Maine, Washington Co., Columbia Falls, 13.06.1938 (GB)
<i>V. pallidum</i> Ait.	Setchell s.n. (L, S)	USA: California, Norwich Co., no day.05.1883 (SAPS)
<i>Eococcus</i> Sleum. [3/12]		
<i>V. leucanthum</i> Cham. & Schlecht.	Luteyn & Luteyn 11574 (L, S)	Mexico: Chapas, Sierra Madre de Chiapas, 18.06.1985 (GB)
<i>V. meridionale</i> Sw.	Luteyn 6031 (L, S)	Venezuela: Edo Tachira, Paramo de Portachuelo, 23.10.1978 (S)
<i>V. sprengelii</i> (Don.) Sleum.	Larsen et al. 2016 (L, S)	Thailand: Northern, 30 km S of Bo Luang along the Om Koi trail, 03.07.1968. (C)
<i>Epigynium</i> (Klotzch) Hook. f. [1/8]		
<i>V. vacciniaceum</i> (Roxbgh.) Sleum.	Nishioka 1211 (L, S)	Nepal: Eastern, near Marimajua, 23.04.1962 (KYO)
<i>Hemimyrtillus</i> Sleum. [2/6]		
<i>V. hirtum</i> Thunb.	Takahashi 7153 (L, S)	Japan: Hokkaido, Kawakami-sicho, Kawakami-cho, Asahidake spa, 15.07.1987 (SAPS)
<i>V. smallii</i> A. Gray	Takahashi 24491 (L, S)	Japan: Hokkaido, Hiyama-sicho, Imakane-cho, Mt Kanikan-dake, 21.05.1998 (SAPS)
	Kikuchi s.n. (L, S)	Japan: Yamagata Pref., Nishimurayama-gun, Hongo-mura, 23.5.1932 (SAPS)
	Sarwar & Takahashi s.n. (T)	Japan: Hokkaido, Sapporo, cult., Bot. Gard. Hokkaido University, 02.06.2004 (SAPS)
<i>Herpothamnus</i> (Small) Sleum. [1/1]		
<i>V. crassifolium</i> Andr.	Iltis and Botany 16 23116 (L, S)	USA: South Carolina, Sumter Co., about 3 mi. S of Conway, 21.04.1965 (KYO)
<i>Macropelma</i> (Klotz.) Hook. f. [1/4]		
<i>V. calycinum</i> Sm. f. <i>glabreccens</i> Sk.	Skottsberg 1132 (L, S)	USA: Hawaii, Kauai, Waimea, 29.10.1922 (GB)
<i>Myrtillus</i> Dumort. [5/7]		
<i>V. caespitosum</i> Michx.	Churchill s.n. (L, S)	USA: N. H., Mt. Washington, White Mountains, 08.07.1895 (SAPS)
<i>V. myrtillus</i> L.	Willoline s.n. (L, S)	No locality, 06.05.1882 (SAPS)
<i>V. ovalifolium</i> Sm.	Takahashi et al. 27579 (L, S)	Japan: SW Hokkaido, Mt Kariba-yama, 05.07.2000 (SAPS)
<i>V. parvifolium</i> Sm.	Allen 71 (L, S)	USA: Casade Mountain, upper valley of the Nesqually, 28.05.1894, 21.08.1894 (SAPS)
<i>V. scoparium</i> Leiberg	Porsild & Breitung 12504 (S)	Canada: Alberta, Mt. Redoubt, in timberline forest, 4-14.07.1945 (SAPS)

**Table 1:** (concluded).

Section and Species	Collector and No.	Voucher information (Herbarium acronym)
<i>Oxycoccoides</i> Hook. f. [1/2]		
<i>V. japonicum</i> Mig.	Takahashi 1544 (L, S)	Japan: Hokkaido, Prov. Ishikari, Sapporo-shi, Jyozankei, 26.07.1981 (SAPS)
<i>Oxycoccus</i> (Hill) Koch [3/3]		
<i>V. macrocarpon</i> Ait.	Ernest & LeBlanc 61141 (L, S)	Canada: Quebec, Gaspesie, Barrachois, 23.07.1961, (GB)
<i>V. microcarpum</i> (Turcz.) Schmalh.	Takahashi 9873 (S)	Sweden: Torne Lappmark, Abisco, 19.07.1989 (SAPS)
<i>V. oxycoccus</i> L.	Furuse 8915 (L, S)	Japan: Hokkaido, Prov. Teshio, Shimo-Sarobetsu moor, 25.06.1975 (TUS 112787)
<i>Polycodium</i> (Raf.) Rehder [1/1]		
<i>V. stamineum</i> L.	Unknown s.n. (L, S)	North America, no locality (Herb. Arboretum, Harvard Univ.), 07.06.1892. (SAPS)
<i>Praestantia</i> Nakai [1/1]		
<i>V. praestans</i> Lamb.	Takahashi et al. 27575 (L, S)	Japan: SW Hokkaido, Mt Kariba-yama, 05.07.2000 (SAPS)
<i>Pyxothamnus</i> (Nut.) Sleum. [3/5]		
<i>V. consanguineum</i> Kl.	Allen 4768 (L, S)	Panama: Prov. Chiriqui, forested ridges south of Finca Lerida, 26.07.1947 (S)
<i>V. floribundum</i> H.B.K. var. <i>floribundum</i>	Larsson s.n. (L, S)	Colombia: Cundinamarca, Bogota, Paramo de Guerrero, 05.1962 (S)
<i>V. ovatum</i> Pursh.	Unknown 26 (L, S)	USA: Contra Cota Co., head of San Leandro canyon, 25.03.1916 (SAPS)
<i>Uliginosa</i> Nakai [1/1]		
<i>V. uliginosum</i> L.	Takahashi 9864 (L, S)	Sweden: Torne Lappmark, Abisco, 19.07.1989 (SAPS)
	Takahashi 9908 (L, S)	Sweden: Torne Lappmark, Abisco, 20.07.1989 (SAPS)
<i>Vitis-Idaea</i> (Moench) Koch [1/1]		
<i>V. vitis-idaea</i> L.	Takahashi 9856 (L, S)	Sweden: Torne Lappmark, Abisco, 19.07.1989 (SAPS)
section not known		
<i>V. donianum</i> Wight.	Alsterlund 100 (L, S)	Burma: West Central region, Southern Chin hills, Mt. Victoria region, 19.03.1956 (GB)

## Explanation of symbols:

<sup>1)</sup> [Number of species examined/ species number of the section].

<sup>2)</sup> Specimens were studied by light microscopy (L), scanning electron microscopy (S) or transmission electron microscopy (T).

**Table 2:** Morphological data of *Vaccinium* pollen based on light microscopic investigation D tetrad diameter, P polar axis, E equatorial diameter, Apo.

Apocolpial.

Name of Section* and Species	Tetrad	D**	D/d***	P/E****	Apo. Exine thickness <sup>†</sup>	Septum thickness <sup>††</sup>	Ornamentation <sup>†††</sup>	Figure(s)	Remarks <sup>††††</sup>
Section <i>Batodendron</i> [3]									
<i>V. cubense</i> (N)	Lobed	IV	II	II	II	IV	3a	Figs. 1A – B	1
Section <i>Bracteata</i> [16]									
<i>V. bracteatum</i> (O)	Compact	I	III	III	III	IV	2d	Figs. 1C – D	1, 2, 3
<i>V. randaiense</i> (O)	Lobed	II	II	III	II	III	2a	Fig. 1E	1, 5
<i>V. wrightii</i> (O)	Lobed	II	II	II	II	III	3b	Figs. 1F – G	1, 4, 6
Section <i>Ciliata</i> [5]									
<i>V. oldhamii</i> (O)	Lobed	III	IV	III	I	IV	3b	Figs. 1H – I	1, 2
Section <i>Conchophyllum</i> [9]									
<i>V. emarginatum</i> (O)	Lobed	III	III	IV	II	III	4	Fig. 1J	1, 2, sometimes 4
Section <i>Cyanococcus</i> [9]									
<i>V. corymbosum</i> (N) Spon. & Bouf. 1764	Lobed	IV	II	III	II	III	2b	Fig. 1K	2, 3
Utech et al. 83-050	Compact	III	II	III	III	III	2b	Fig. 1M	
<i>V. myrsinites</i> (N)	Lobed	III	III	II	I	I	2d	Fig. 1N	
<i>V. myrtilloides</i> (N)	Lobed	II	II	III	II	I	2b	Figs. 1O, 2A – B	
<i>V. pallidum</i> (N)	Lobed	III	II	III	II	III	2d	Fig. 2C	1, 5
Section <i>Eococcus</i> [12]									
<i>V. leucanthum</i> (N)	Lobed	III	II	I	II	II	2d	Fig. 2D	3, 6
<i>V. meridionale</i> (N)	Lobed	IV	I	II	III	II	2c	Fig. 2E	4
<i>V. sprengelii</i> (O)	Compact	II	I	I	II	I	3d	Fig. 2F	

**Table 2:** (continued).

Name of Section and Species	Tetrad	D	D/d	P/E	Apo. Exine thickness <sup>†</sup>	Septum thickness <sup>††</sup>	Orname-ntation <sup>†††</sup>	Figure(s)	Remarks <sup>††††</sup>
Section <i>Epigynium</i> [8]									
<i>V. vacciniaceum</i> (O)	Compact	III	IV	IV	II	II	5	Figs. 2G – H	2
Section <i>Hemimyrtillus</i> [6]									
<i>V. hirtum</i> (O)	Lobed	I	III	II	I	III	2d	Figs 2I – J	1, 6
<i>V. smallii</i> (O)	Takahashi 24491	Compact	III	I	II	II	1d	Figs. 2K – L	1, 5, 6
	Kikuchi s.n.	Compact	II	III	II	IV	1b	Fig. 3A	1, 4, 6
Section <i>Herpothamnus</i> [1]									
<i>V. crassifolium</i> (N)	Lobed	II	IV	V	II	III	1b	Fig. 3B	2, 3
Section <i>Macropelma</i> [4]									
<i>V. calycinum</i> f. <i>glabreccens</i> (N)	Lobed	III	III	III	I	I	2d	Figs. 3C – D	4
Section <i>Myrtillus</i> [7]									
<i>V. caespitosum</i> (N)	Lobed	II	IV	I	II	II	1b	Fig. 3E	3, 4
<i>V. myrtillus</i> (O)	Lobed	II	III	II	II	II	2a	Fig. 3F	7
<i>V. ovalifolium</i> (O)	Lobed	II	IV	III	I	IV	2d	Fig. 3G	2, 4
<i>V. parvifolium</i> (N)	Lobed	III	IV	IV	III	IV	2d	Figs. 3H – I	1, 2, 4
Section <i>Oxycoccoides</i> [2]									
<i>V. japonicum</i> (O)	Compact	I	II	II	II	III	6	Figs. 3L – M	
Section <i>Oxycoccus</i> [3]									
<i>V. macrocarpon</i> (N)	Compact	II	II	II	I	I	2a	Figs. 3O, 4A	
<i>V. oxycoccus</i> (O)	Lobed	IV	IV	IV	IV	IV	1c	Figs. 4B – C	2, 6, 7
Section <i>Polycodium</i> [1]									
<i>V. stamineum</i> (N)	Lobed	III	III	IV	II	IV	7	Fig. 4D	1, 2, 4, 6

**Table 2:** (concluded).

Name of Section and Species	Tetrad	D	D/d	P/E	Apo. Exine thickness <sup>†</sup>	Septum thickness <sup>††</sup>	Ornamentation <sup>†††</sup>	Figure(s)	Remarks <sup>††††</sup>	
Section <i>Praestantia</i> [1]										
<i>V. praestans</i> (O)	Lobed	I	III	III	II	II	1d	Fig. 4E	6	
Section <i>Pyxothamnus</i> [5]										
<i>V. consanguineum</i> (N)	Lobed	IV	I	II	IV	II	2c	Fig. 4F		
<i>V. floribundum</i> var. <i>floribundum</i> (N)	Lobed	II	II	II	I	I	2d	Fig. 4G		
<i>V. ovatum</i> (N)	Lobed	II	II	II	I	II	2c	Fig. 4H	1	
Section <i>Uliginosa</i> [1]										
<i>V. uliginosum</i> (O)	Takahashi 9864	Lobed	II	II	III	I	I	1a	Fig. 4I	Costae not clear
	Takahashi 9908	Lobed	III	II	II	I	I	2a	Fig. 4J	Costae not clear
Section <i>Vitis-Idaea</i> [1]										
<i>V. vitis-idaea</i> (O)	Compact	II	II	II	II	I	2a	Fig. 4K		
Section <i>not known</i>										
<i>V. donianum</i> (O)	Lobed	II	I	I	I	II	2a	Fig. 4L		

Explanation of symbols:

\* [Number of species in this section], O Old World , N New World

<sup>††</sup> I: 0.5 – 0.9  $\mu\text{m}$ , II: 1.0 – 1.4  $\mu\text{m}$ , III: 1.5 – 1.9  $\mu\text{m}$ , IV: 2.0 – 2.4  $\mu\text{m}$

\*\* I: 30.1 – 35.0  $\mu\text{m}$ , II: 35.1 – 40.0  $\mu\text{m}$ , III: 40.1 – 45.0  $\mu\text{m}$ , IV: 45.1 – 50.0  $\mu\text{m}$

<sup>†††</sup> Types of exine ornamentation by SEM corresponding to Fig. 1 – 5.

\*\*\* I: – 1.30, II: 1.31 – 1.35, III: 1.36 – 1.40, IV: 1.41 –

<sup>††††</sup> 1: Other configurations found, 2: Pollen shape suboblate, 3: Colpus tapering

\*\*\*\* I: 0.61 – 0.65, II: 0.66 – 0.70, III: 0.71 – 0.75, IV: 0.76 – 0.80, V: 0.81 –

towards end, 4: Ora indistinct, 5: Ora circular, 6: Colpus membrane smooth

<sup>†</sup> I: 1.1 – 1.5  $\mu\text{m}$ , II: 1.6 – 2.0  $\mu\text{m}$ , III: 2.1 – 2.5  $\mu\text{m}$ , IV: 2.6 – 3.0  $\mu\text{m}$

to granuloid, 7: rarely 4-colpor(oid)ate.

**Table 3:** Variation in pollen characters of *Vaccinium* showing mean value in  $\mu\text{m}$  and standard deviation D tetrad diameter, P polar axis, E equatorial diameter.

Name of Species	D	P	E	D/d	P/E	Ectoaperture		2f/D	Apocolpial exine thickness	Septum thickness	
						Length (2f)	Width				
Section <i>Batodendron</i>											
<i>V. cubense</i>	49.2±2.4	26.0±1.4	37.2±1.7	1.32	0.70	29.0±2.3	1.5±0.5	0.59	2.3±0.4	2.0	
Section <i>Bracteata</i>											
<i>V. bracteatum</i>	34.3±2.7	19.1±1.8	25.3±3.3	1.36	0.75	15.4±2.0	1.6±0.7	0.45	2.5±0.2	2.4±0.7	
<i>V. randaiense</i>	39.0±1.8	20.8±1.7	29.2±1.2	1.34	0.71	18.4±2.5	2.4±0.4	0.47	2.3±0.5	1.6±0.5	
<i>V. wrightii</i>	40.2±2.0	21.2±1.9	30.8±1.3	1.31	0.69	17.5±1.3	2.1±0.5	0.44	2.3±0.3	1.8±0.3	
Section <i>Ciliata</i>											
<i>V. oldhamii</i>	43.3±3.2	22.5±4.0	30.2±3.0	1.43	0.75	21.3±4.8	2.7±1.0	0.49	1.9±0.4	2.4±0.5	
Section <i>Conchophyllum</i>											
<i>V. emarginatum</i>	42.5±2.5	24.5±4.3	31.2±3.6	1.36	0.79	19.5±2.2	1.7±0.6	0.46	2.3±0.3	1.5±0.4	
Section <i>Cyanococcus</i>											
<i>V. corymbosum</i>	Spon. & Bouf. 1764	45.7±2.5	26.1±2.4	34.9±3.0	1.31	0.75	16.2±3.3	2.0±0.5	0.35	2.3±0.3	1.9±0.4
	Utech et al. 83-050	43.3±2.9	22.6±0.8	31.3±1.4	1.38	0.72	21.0±5.1	3.0±0.9	0.48	2.8±0.5	1.9±0.3
<i>V. myrsinites</i>		41.2±2.5	21.7±2.2	31.1±1.1	1.32	0.70	20.7±2.1	2.4±0.6	0.50	1.5±0.2	0.8±0.3
<i>V. myrtilloides</i>		38.4±2.4	20.5±1.2	28.7±1.3	1.34	0.71	21.3±2.4	1.3±0.3	0.55	2.0±0.3	0.7±0.2
<i>V. pallidum</i>		42.4±1.9	22.8±1.7	31.7±1.6	1.34	0.72	17.3±3.4	2.3±0.6	0.41	2.3±0.5	1.5±0.4
Section <i>Eococcus</i>											
<i>V. leucanthum</i>		44.8±4.2	21.3±2.4	33.3±3.2	1.34	0.64	19.0±2.1	1.8±0.4	0.42	2.3±0.5	1.3±0.2
<i>V. meridionale</i>		45.5±2.2	24.1±2.5	35.4±1.9	1.29	0.68	24.4±1.9	1.1±0.8	0.54	2.6±0.5	1.1±0.2
<i>V. sprengelii</i>		40.1±1.0	20.0±1.5	32.4±0.9	1.24	0.62	18.9±1.5	1.3±0.8	0.47	2.4±0.3	0.9±0.4

**Table 3:** (continued).

Name of Species	D	P	E	D/d	P/E	Ectoaperture		2f/D	Apocolpial exine thickness	Septum thickness	
						Length (2f)	Width				
Section <i>Epigynium</i>											
<i>V. vacciniaceum</i>	42.6±1.9	23.4±2.7	30.1±2.3	1.42	0.78	22.8±3.9	2.0±0.4	0.54	2.0±0.4	1.4±0.3	
Section <i>Hemimyrtillus</i>											
<i>V. hirtum</i>	33.1±2.0	17.1±2.7	24.3±2.2	1.36	0.70	18.6±2.8	2.1±0.5	0.56	1.8±0.4	1.7±0.4	
<i>V. smallii</i>	Takahashi 24491	43.9±1.6	23.1±1.4	35.0±1.9	1.25	0.66	22.1±3.8	2.3±0.4	0.50	2.2±0.3	1.3±0.3
	Kikuchii s.n.	36.3±2.2	18.6±1.5	26.5±2.0	1.37	0.70	21.1±3.0	1.4±0.4	0.58	2.1±0.4	2.2±0.3
Section <i>Herpothamnus</i>											
<i>V. crassifolium</i>	35.7±2.3	20.5±2.6	25.1±2.3	1.42	0.83	14.5±1.9	1.7±0.3	0.41	2.1±0.3	1.8±0.6	
Section <i>Macropelma</i>											
<i>V. calycinum f. glabreccens</i>	42.1±1.3	21.7±0.8	30.6±1.5	1.38	0.71	23.0±1.7	1.5±0.4	0.54	1.9±0.2	0.7±0.3	
Section <i>Myrtillus</i>											
<i>V. caespitosum</i>	36.4±4.2	16.4±4.5	25.5±1.7	1.43	0.64	14.0±1.8	2.0±0.1	0.38	2.2±0.3	1.4±0.1	
<i>V. myrtillus</i>	38.4±2.5	19.1±2.7	28.1±2.6	1.37	0.68	18.3±1.2	2.6±0.5	0.48	2.2±0.4	1.3±0.3	
<i>V. ovalifolium</i>	39.0±4.5	21.8±2.3	29.1±1.4	1.34	0.75	17.1±1.8	2.2±0.6	0.44	1.9±0.3	2.0±0.4	
<i>V. parvifolium</i>	44.1±2.9	24.7±2.3	31.0±1.4	1.42	0.80	18.7±2.8	2.3±0.2	0.42	2.6±0.3	2.0±0.4	
Section <i>Oxycoccoides</i>											
<i>V. japonicum</i>	32.5±1.2	15.7±1.6	24.5±1.3	1.33	0.70	20.2±3.0	2.3±0.7	0.62	2.2±0.3	1.9±0.3	
Section <i>Oxycoccus</i>											
<i>V. macrocarpon</i>	37.0±1.7	18.7±0.9	27.5±1.1	1.35	0.68	26.0±2.1	1.6±0.3	0.70	1.9±0.2	0.9±0.4	
<i>V. oxycoccus</i>	46.1±2.5	24.9±3.4	32.3±2.2	1.43	0.77	20.7±3.5	2.0±0.3	0.45	3.0±0.5	2.2±0.3	

**Table 3:** (continued).

Name of Species	D	P	E	D/d	P/E	Ecto-aperture		2f/D	Apocolpial exine thickness	Septum thickness	
						Length (2f)	Width				
Section <i>Polycodium</i>											
<i>V. stamineum</i>	42.6±2.4	23.3±1.9	30.4±1.5	1.40	0.77	21.9±0.9	2.3±0.3	0.51	2.1±0.3	2.4±0.6	
Section <i>Praestantia</i>											
<i>V. praestans</i>	34.3±1.7	17.9±2.7	25.1±1.6	1.37	0.71	16.4±2.7	1.7±0.8	0.48	2.0±0.3	1.2±0.3	
Section <i>Pyxothamnus</i>											
<i>V. consanguineum</i>	46.6±1.2	23.5±1.4	35.8±0.6	1.30	0.66	25.9±2.3	2.4±0.8	0.55	3.3±0.4	1.0±0.4	
<i>V. floribundum</i> var. <i>floribundum</i>	38.3±1.3	20.0±0.7	28.5±1.3	1.34	0.70	21.9±3.3	0.9±0.3	0.57	1.7±0.3	0.9±0.3	
<i>V. ovatum</i>	36.9±2.1	18.8±1.8	28.1±1.8	1.31	0.67	18.0±1.8	2.3±0.8	0.49	1.7±0.2	1.2±0.3	
Section <i>Uliginosa</i>											
<i>V. uliginosum</i>	Takahashi 9864	35.7±2.1	19.9±1.1	26.8±1.1	1.33	0.74	22.2±2.3	2.2±0.6	0.62	1.7±0.3	0.6±0.1
	Takahashi 9908	41.2±1.2	21.2±1.5	30.6±1.0	1.35	0.69	23.4±2.5	2.0±0.7	0.57	1.7±0.2	0.5±0.1
Section <i>Vitis-Idaea</i>											
<i>V. vitis-idaea.</i>	35.9±1.6	18.0±1.0	27.0±1.2	1.33	0.67	21.9±1.5	1.3±0.3	0.61	2.0±0.2	0.6±0.2	
Section not known											
<i>V. donianum</i>	37.5±1.6	18.9±1.3	29.5±0.9	1.27	0.64	20.4±1.9	2.0±0.9	0.54	1.9±0.2	1.1±0.3	

**Figure captions:**

Fig. 1. Scanning electron micrographs of *Vaccinium* pollen (apocolpial exine if not otherwise noted). Sect. *Batodendron* A – B. *V. cubense*; Sect. *Bracteata* (C – G): C – D. *V. bracteatum*, E. *V. randaiense*, F – G. *V. wrightii* Sect. *Ciliata* H – I. *V. oldhamii*; Sect. *Concophyllum* J. *V. emarginatum*; Sect. *Cyanococcus* (K – O): K – M. *V. corymbosum* (Spon. & Bouf. 1764, Meyer & Mazzeo 13278 and Utech et al. 83-050, respectively), N. *V. myrsinites*, O. *V. myrtilloides*. (C & O whole tetrad showing apocolpium)

Fig. 2. Scanning electron micrographs of *Vaccinium* pollen (apocolpial exine if not otherwise noted). Sect. *Cyanococcus* (A – C): A – B. *V. myrtilloides*, C. *V. pallidum*; Sect. *Eococcus* (D – F): D. *V. leucanthum*, E. *V. meridionale*, F. *V. sprengelii*; Sect. *Epigynium* G – H. *V. vacciniaceum*; Sect. *Hemimyrtillus* (I – L): I – J. *V. hirtum*, K – L. *V. smallii* (Takahashi 24491). (I whole tetrad showing colpi)

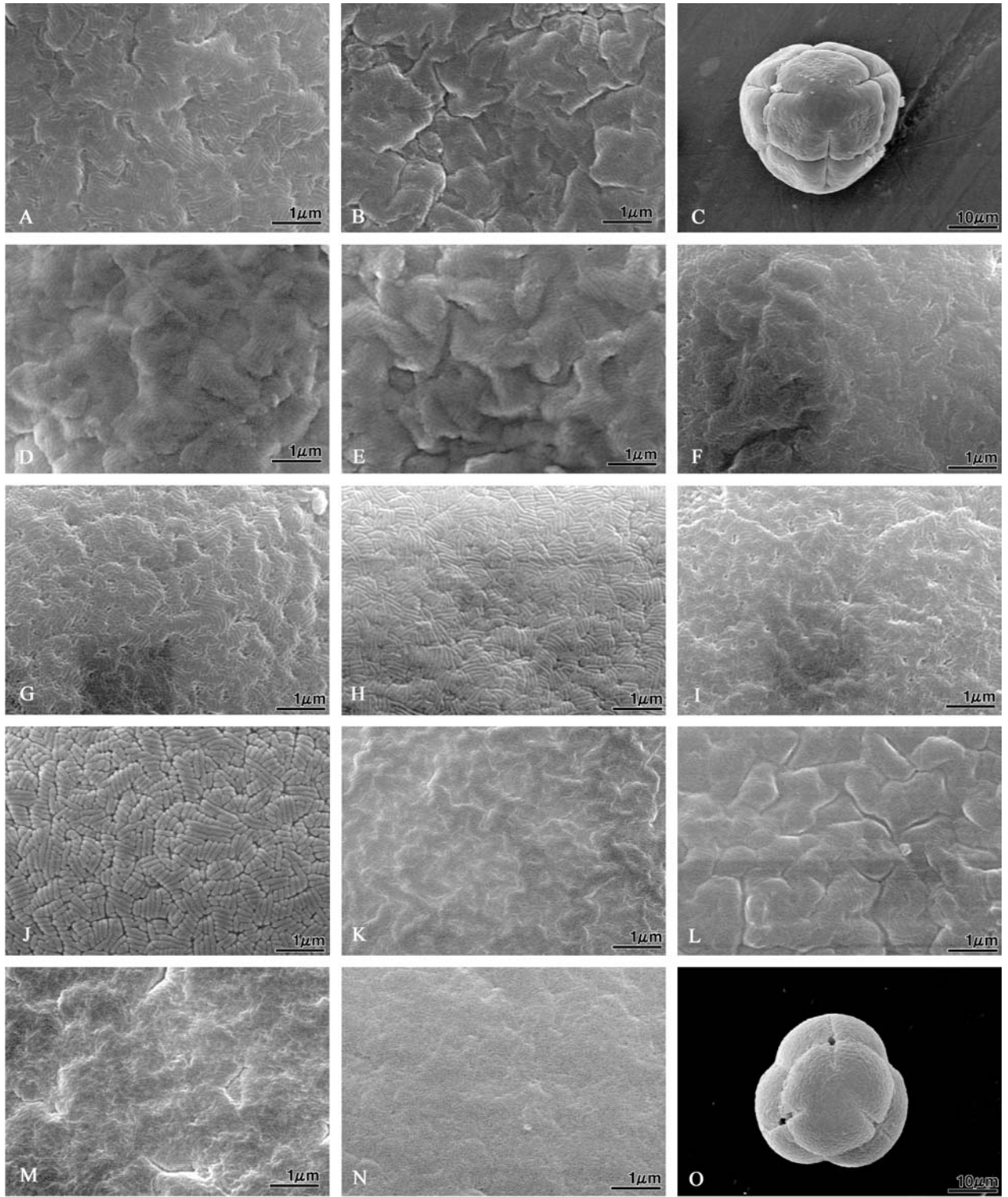
Fig. 3. Scanning electron micrographs of *Vaccinium* pollen (apocolpial exine if not otherwise noted). Sect. *Hemimyrtillus* A. *V. smallii* (Kikuchi s.n.); Sect. *Herpothamnus* B. *V. crassifolium*; Sect. *Macropelma* C – D. *V. calycinum* f. *glabreccens*; Sect. *Myrtillus* (E – K): E. *V. caespitosum*, F. *V. myrtillus*, G. *V. ovalifolium*, H – I. *V. parvifolium*, J – K. *V. scoparium*; Sect. *Oxycoccoides* L – M. *V. japonicum*; Sect. *Oxycoccus* (N – O): N. *V. microcarpum*, O. *V. macrocarpon*. (L whole tetrad showing mesocolpium)

Fig. 4. Scanning electron micrographs of *Vaccinium* pollen (apocolpial exine if not otherwise noted). Sect. *Oxycoccus* (A – C): A. *V. macrocarpon*, B – C. *V. oxycoccus*; Sect. *Polycodium* D. *V. stamineum*; Sect. *Praestantia* E. *V. praestans*; Sect. *Pyxothamnus* (F – H). F. *V. consanguineum*, G. *V. floribundum* var. *floribundum*, H. *V. ovatum*; Sect. *Uliginosa* I – J. *V. uliginosum* (Takahashi 9864 and 9908, respectively); Sect. *Vitis-Idaea* K. *V. vitis-idaea*; Sect. not known L. *V. donianum*. (B whole tetrad with a plane configuration)

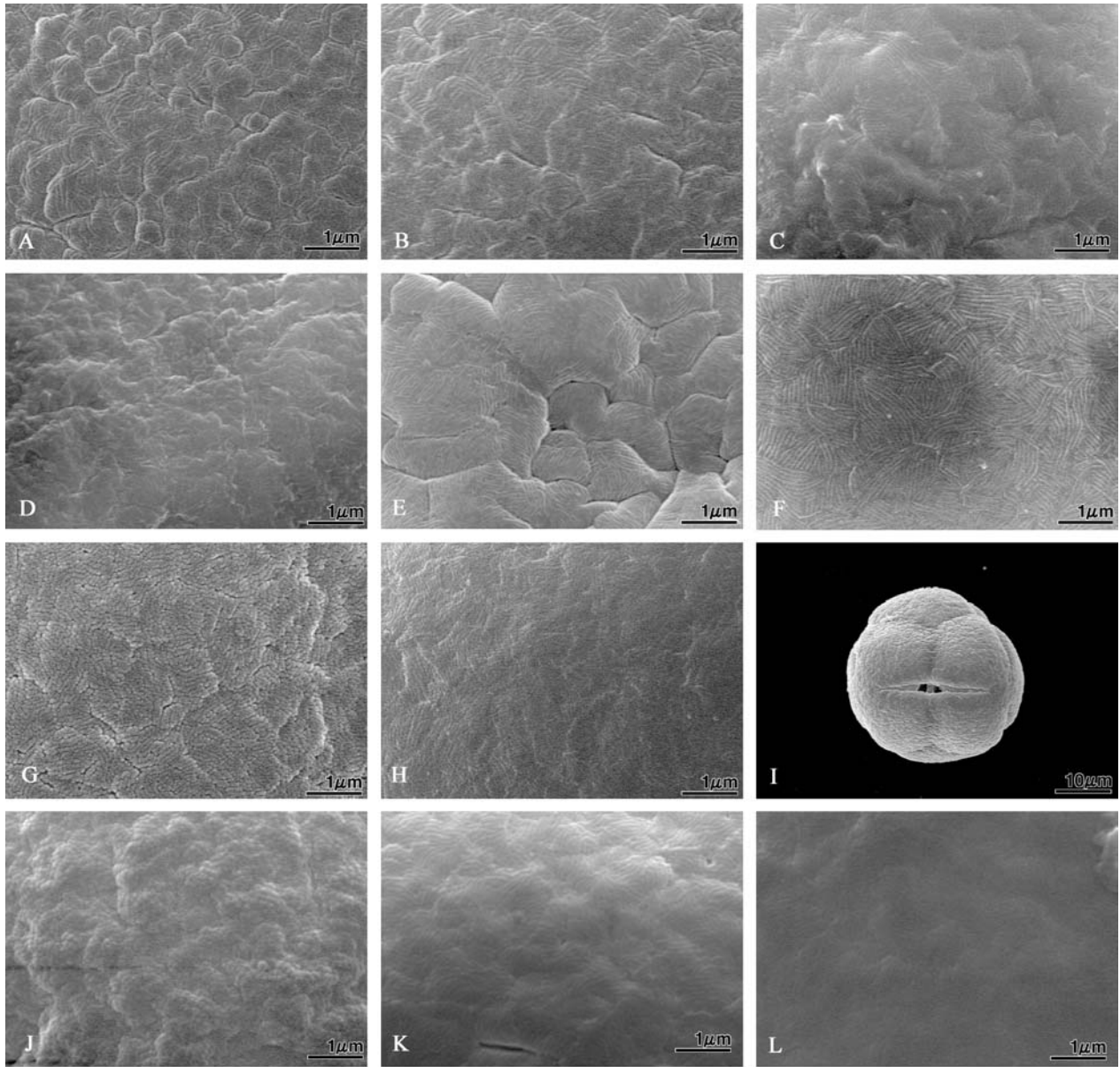
**Figure captions:** (concluded)

Fig. 5. A morphological relationship and variation of apocolpial exine sculpture in *Vaccinium*. From Type 1 to Type 3, a tendency in secondary sculpture: from faintly striate to clearly striate. From a to d, a tendency in pollen surface: from uneven and rugged to flat.

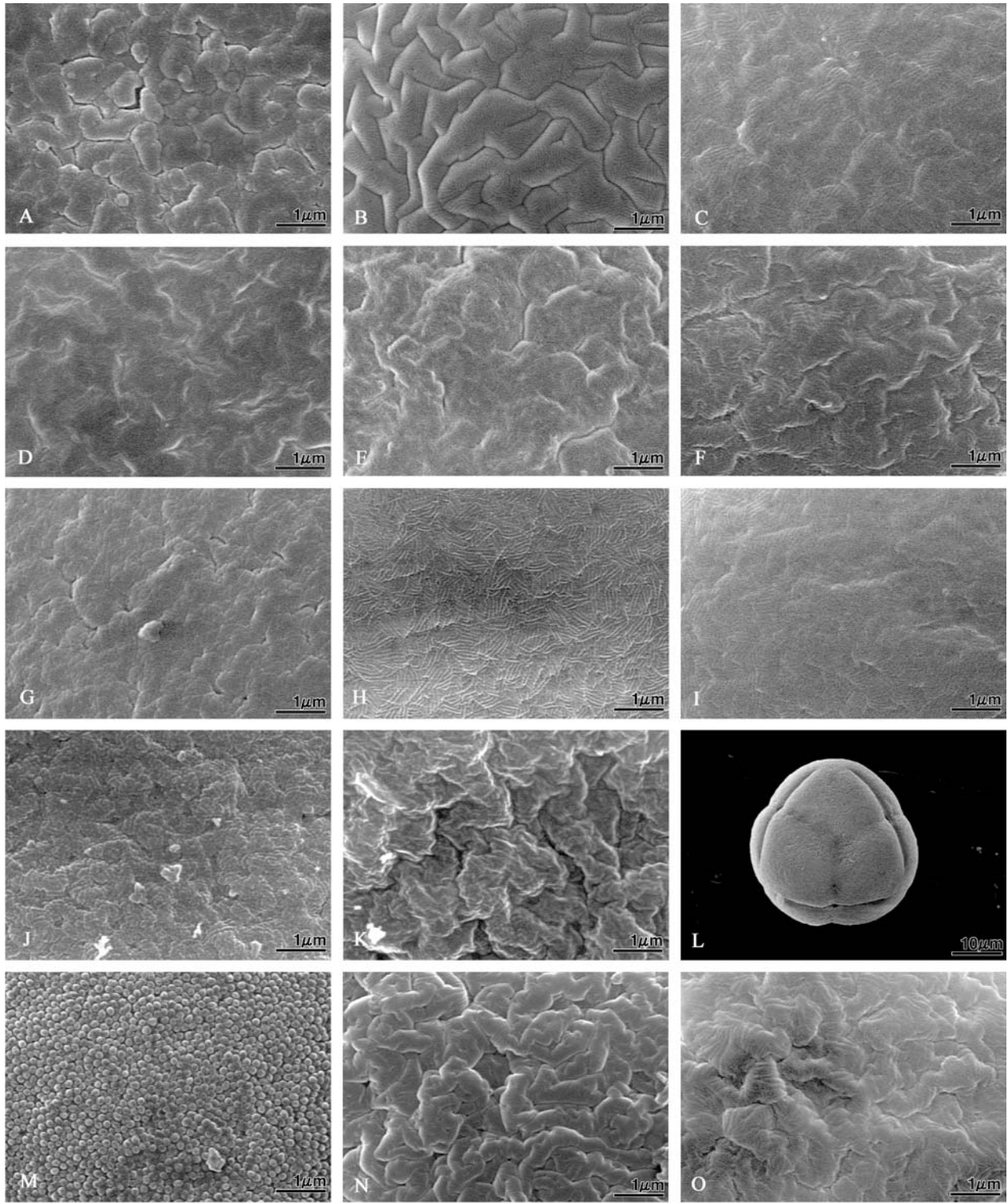
Fig. 6. TEM micrograph of *V. smallii* (Sarwar & Takahashi s.n.). A. whole tetrad, B. apocolpial exine composed of tectum, columellea, foot layer and endexine, C. septum (the thickness of ectexine reduced).



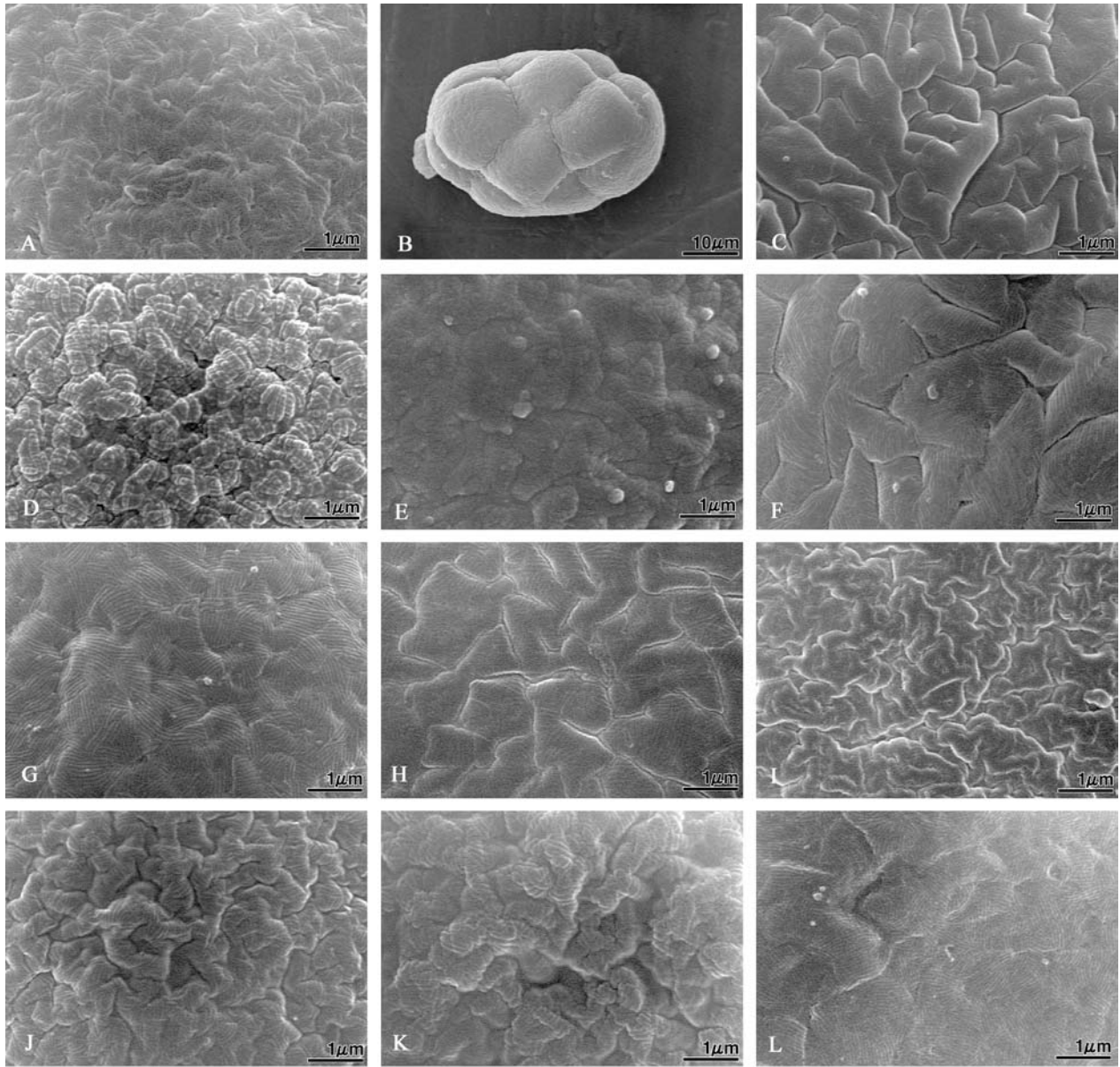
*Fig. 1.*



*Fig. 2.*



*Fig. 3.*



*Fig. 4.*

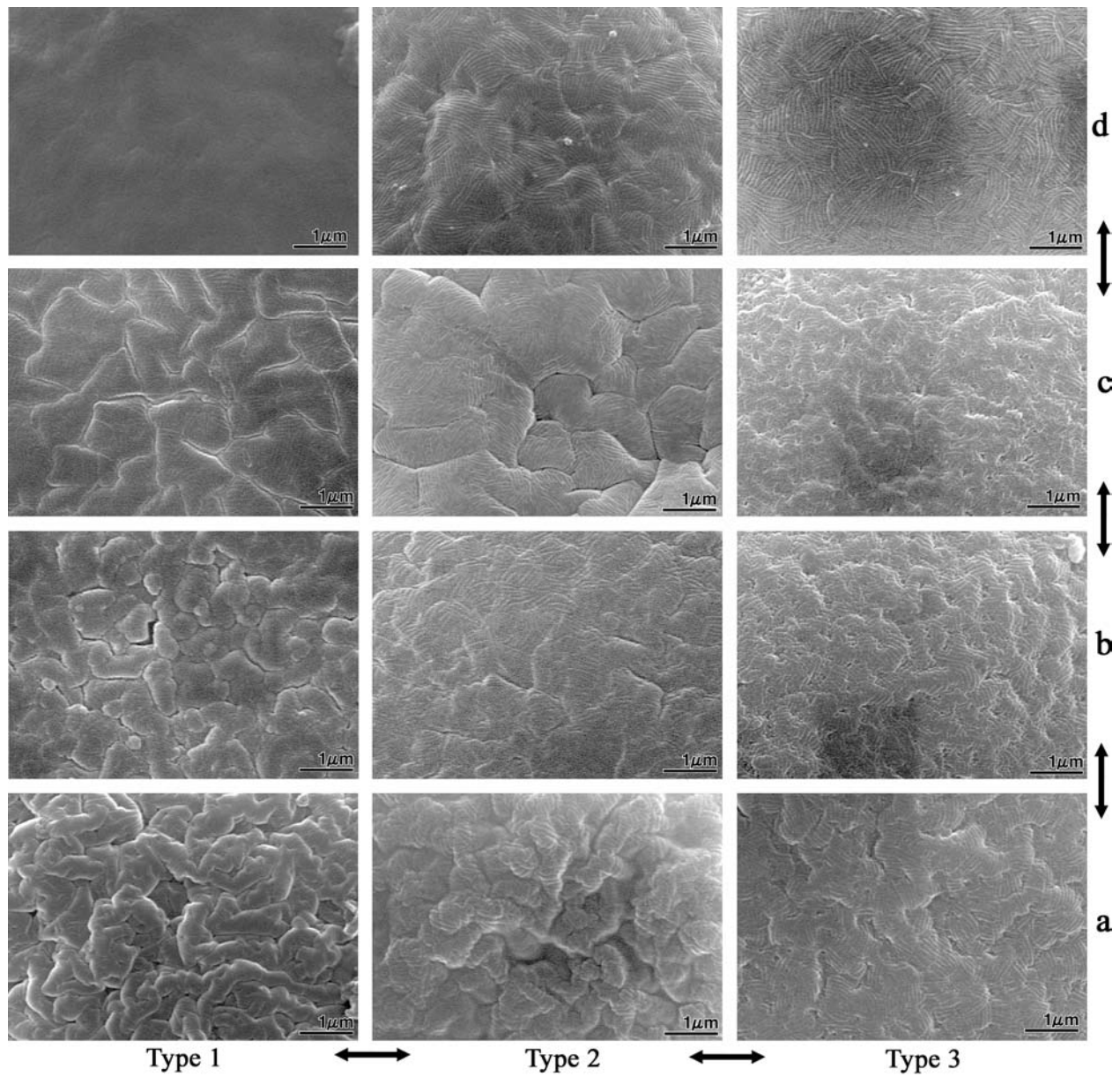


Fig. 5.

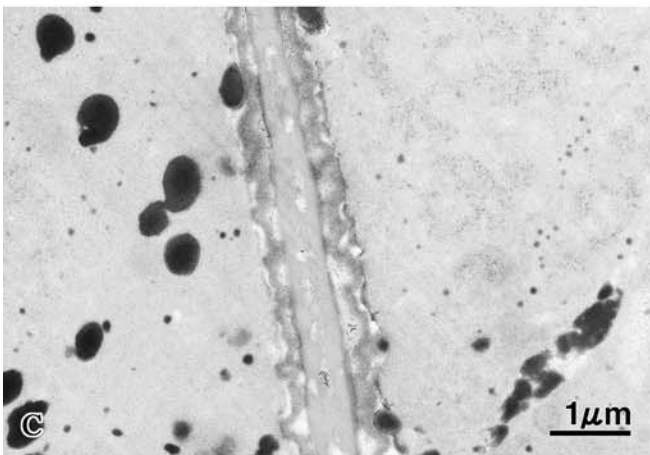
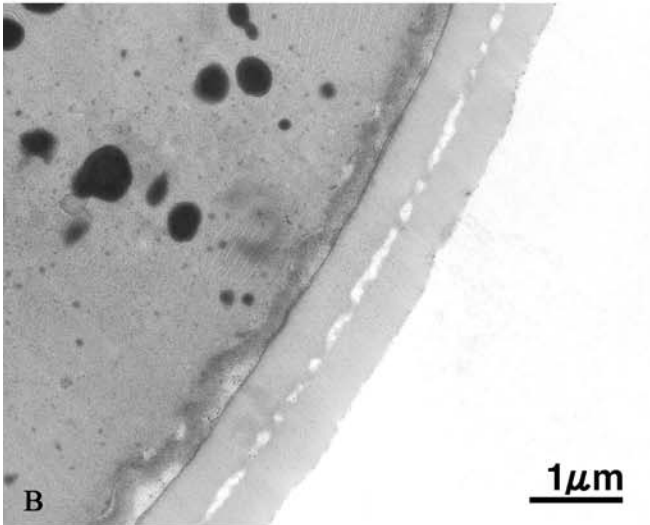
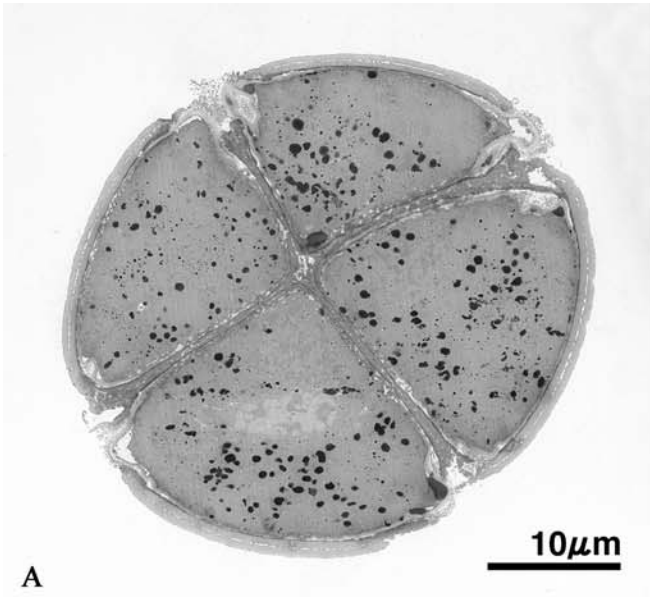


Fig. 6.