The taxonomic significance of pollen morphology in Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae (Ericaceae: Vaccinioideae)

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The pollen morphology of 41 species in 12 of the 13 genera constituting tribes Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae of Ericaceae, subfamily Vaccinioideae, was investigated with light (LM) and scanning electron microscopy (SEM). The pollen of the species included in these tribes is stenopalynous: 3-colopor(oid)ate grains in oblate permanent tetrads. Pollen characteristics do not show notable correlation with the tribal classification, although it is observed that the pollen tetrads tend to be compact in Andromedeae s.s., Gaultherieae and Oxydendreae, but usually lobed in Lyonieae, especially in Lyonia. The compact tetrads of tribe Andromedeae are characterized by a thin, perforated septum. Apocolpial exine sculpture of individual grains within the pollen tetrad varies from psilate to coarsely rugulate, the rugulae have a 'secondary sculpture' of faint to well-defined fine or coarse striae. Two main R and S types, six subtypes and seven sub-subtypes of exine are recognized based on the primary sculpture and distinctness of secondary sculpture on the rugulae. A continuous series of variation in both qualitative and quantitative characters of the pollen was observed within all four tribes. Sometimes exine sculpture shows little variation in some genera within these tribes; e.g. Leucothoë (S2 and S2**) within the tribe Gaultherieae, and Agarista (R2-3 and R4) and Lyonia (R3, R3* and R3**) within the tribe Lyonieae. Exine sculpture, degree of tetrad compactness, tetrad size and septum thickness proved to be the most useful characters for helping to clarify the infrageneric classification in Gaultheria, Agarista and Lyonia. An exine surface

with secondary striate sculpture is apparently characteristic of subfamily Vaccinioideae, based on our general palynological survey of the Ericaceae.

Key words: Andromedeae *s.s.*, Gaultherieae, Lyonieae, Oxydendreae, pollen morphology, taxonomic significance

Introduction

The cosmopolitan family Ericaceae comprises about 130 genera and 2700 species [1]. The most recent classification of the family [2] recognizes eight subfamilies and twenty tribes. The subfamily Vaccinioideae which is characterized by the presence of disintegration tissue on the back of anther and a base chromosome number of twelve, includes five tribes viz., Andromedeae *s.s.*, Gaultherieae, Lyonieae, Oxydendreae and Vaccinieae. And the monotypic tribe Oxydendreae is sister to the rest of Vaccinioideae. As a part of our comprehensive pollen morphological study on the Ericaceae, the subfamilies Enkianthoideae [3] and Monotropoideae [4 – 6], and part of the tribe Vaccinieae of the subfamily Vaccinioideae [7 – 9] were already studied. In the present study, we report the pollen morphology of the remaining four tribes of the subfamily Vaccinioideae.

The tribes Andromedeae *s.s.*, Gaultherieae, Lyonieae and Oxydendreae are composed of 13 genera and more than 325 species. Plants are evergreen shrubs or small trees, which occur in a wide range of geographical areas, ranging from arctic and temperate regions of the Northern Hemisphere to the tropical regions of the Old and New World. The genera included in these four tribes were previously grouped in the tribe Andromedeae *sensu* Stevens [10] and he classified them into two well-defined groups within Andromedeae, namely the *Lyonia*-group and *Gaultheria*-group, on the basis of the indumentum, stamen morphology, seed and phloem anatomy, type of stomata and cytological features. The remaining three other genera (*Andromeda*, *Chamaedaphne* and *Oxydendrum*) were isolated within the tribe [10]. However, in the recent phylogenetic classification of Ericaceae based on

morphological and molecular data [2], the members of Andromedeae *sensu* Stevens are recognized as those of four distinct tribes viz., Andromedeae *s.s.*, Gaultherieae, Lyonieae and Oxydendreae.

Previous studies on the pollen morphology of these tribes were mainly based on LM studies of some selected taxa, or incorporated in the regional pollen floras [11 – 45]. The pollen morphology of some taxa viz., *Andromeda polifolia, Chamaedaphne calyculata* etc., has been numerously described, but little is known about palynological features for systematic/taxonomic purpose [36, 43].

Therefore, a general pollen survey on these four tribes of the subfamily Vaccinioideae was carried out with both LM and SEM, and the taxonomic significance of the pollen morphology is discussed in light of the recent classification of Ericaceae [2]. The variation of palynological characters and their evolutionary trends are also discussed.

MATERIALS AND METHODS

Pollen morphology of 41 species representing 12 genera from 13 genera constituting the tribes Andromedeae *s.s.*, Gaultherieae, Lyonieae and Oxydendreae, was investigated using LM and SEM (Table 1). Polliniferous materials used in this investigation were taken from dried specimens from the Herbaria C, GB, S, SAPS, SAPT and TUS. Abbreviations of the herbarium names except for SAPT (the Botanic Garden, Hokkaido University, Sapporo) are according to the Index Herbariorum [46]. Infrageneric classifications of *Gaultheria*, *Agarista* and *Lyonia* by Middleton [47], Judd [48] and Judd [49], respectively are followed.

Preparation of pollen grains follows Sarwar et al. [7]. The dimensions “D”, “P”, “E (d)” and “2f”, corresponding to the tetrad diameter, polar length and equatorial diameter of pollen grain and total length of two concurrent colpi were measured [31], 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 Oldfield [31], Punt et al. [50], and Zang and Anderberg [51].

RESULTS

General pollen morphology

In LM, pollen grains are commonly united in tetrahedral tetrads (Figs. 1A – B), rarely in other configurations; e.g. decussate tetrad (Fig. 1C), tetragonal tetrad and so on, viscin threads absent, shape oblate (Table 2). In range of average values of the specimen, tetrad diameter (D) 24.8 – 59.6 μm, P 12.5 – 30.5 μm, E (d) 19.0 – 44.9 μm, D/d 1.19 – 1.42, P/E 0.61 – 0.75. Among the species studied, pollen grains of *Tepuia venusta* showed the highest values of D, P and E (59.6, 30.5 and 44.9 μm, respectively) and those of *Gaultheria oppositifolia* had the lowest values (24.8, 12.5 and 19.0 μm, respectively) (Table 3). Three aperturate, spatial position of the colpi according to Fischer's law, rarely 4-aperturate in *Leucothoë grayana* var. *oblongifolia*, colpor(oid)ate, colpi distinct, the concurrent colpi (2f) 12.5 – 28.3 μm long, 0.4 – 5.1 μm wide, 2f/D 0.38 – 0.67, significantly wider at middle, acute or rarely tapering towards end, rarely tip of colpi bifurcated, costae present but sometimes not clear; endoaperture present and distinct, but in some species indistinct, lalongate, 0.4 – 3.5 μm long, 5.0 – 17.2 μm wide; exine tectate, apocolpial exine 1.4 – 3.1 μm thick, septum 0.6 – 2.5 μm thick, very thin (or may be absent) in *Lyonia lingustrina*. Generally apocolpial exine is thicker than the septum, with exceptions in *Craibiodendron yunnanensis*, *Lyonia lucida* and *Pieris floribunda* which have thicker septum (Tables 2 – 3).

In SEM, apocolpial exine sculpture varies from coarsely rugulate to psilate, the rugulae with "secondary sculptures"; faintly to clearly and finely to coarsely striate (Figs. 2 – 5). Exine sculptures were classified into two main types; Type R and S (Fig. 2). Type R is characterized by rugulate to rugulate-psilate primary exine sculpture, primary sculpture unit clear, with faintly, indistinct striate secondary sculpture and is divided into four subtypes (R1, R2, R3 and R4) by the tendency to psilate primary sculpture and further sub-subtypes (R1*, R1**, R2*, R3* and R3**) as the derivatives by the tendency to clear striate secondary sculpture (Fig. 2). Type S is characterized by mostly rugulate-psilate to psilate primary exine sculpture with clearly striate secondary sculpture and thus, both primary and secondary sculpture units are not distinctly discerned each other. This type is divided into two subtypes (S1 and S2) by the width of secondary lirae and two sub-subtype (S2* and S2**) as the

derivatives by the tendency to more granulate-like striate secondary sculpture (Fig. 2). Exine sculpture along the colpi is similar to that appearing near the distal pole, but mesocolpial exine has a tendency to decrease in lateral extension of the rugulae with more distinct units; colpus membrane is granular to granuloid or smooth.

Pollen morphology of tribes

Andromedeae (genera studied: *Andromeda* and *Zenobia*)

Septum thin and perforated (Fig. 1E) in both genera, tip of colpi sometimes bifurcated in *Z. pulverulenta* (Table 2). In SEM, pollen surface somewhat flat, primary exine sculpture coarsely rugulate, the rugulae faintly and finely striate (Types R2, R2-3; Figs. 3 A, B). The exine sculpture of *A. polifolia* var. *glaucophylla* couldn't be studied due to unavailability of grains on SEM stub, but it was similar to that of *A. polifolia* by LM.

Gaultherieae (genera studied: *Chamaedaphne, Diplycosia, Gaultheria, Leucothoë* and *Tepuia*)

Tip of colpi sometimes or often bifurcated in *C. calyculata* and *T. venusta*, pollen sometimes at decussate (Fig. 1C) and/or tetragonal tetrads in *G. appressa* and *G. prostrate*, tetrads circular in *G. insane* and often shrink in *G. itatiaiae,* endoaperture sometimes H-shaped in *G. erecta*, grains often broken along colpi and rarely 4-aperturate in *L. grayana var. oblongifolia*.

In SEM, pollen surface somewhat flat, primary exine sculpture coarsely rugulate to coarsely rugulate-psilate, the rugulae faintly and finely striate (Types R 2 – 4; Figs. 3 C, G – H, J – L, 4 B – C, E – G) for *C. calyculata*, *G. prostrate*, *G. bracteata*, *G. rigida*, *G. eriophylla* var. *eriophylla*, *G. tomentosa*, *G. anastomosans*, *G. buxifolia*, *G. itatiaiae*, *G. myrtilloides* var. *myrtilloides* and *G. insane*; or surface uneven and rugged, primary exine sculpture coarsely rugulate, the rugulae coarsely but faintly striate (Type R1; Fig. 3E) for *G. adenothrix*, or clearly striate (Types R1*, R1**, R3*; Figs. 3 F, I, 4 A, D, J) for *G. miqueliana*, *G. erecta*, *G. procumbens*, *G. foliolosa* and *T. venusta*; or surface flat, primary exine sculpture psilate with clearly striate secondary sculpture (Types S2*, S2; Figs. 3D, 4H) for *D. heterophylla* and *L. grayana* var. *oblongifolia*, or granulate-striate (Type S2**; Fig. 4I) for *L. keiskei*.

Lyonieae (genera studied: *Agarista, Craibiodendron*, *Lyonia* and *Pieris*)

Often 1 – 2 grains in each tetrad shrink in *A. salicifolia* and *L. buchii*, costae thick in *A. populifolia* and short in *A. salicifolia*, endoaperture very lalongate and colpi margin psilate in *C. yunnanensis*.

In SEM, pollen surface somewhat flat, primary exine sculpture coarsely rugulate to coarsely rugulate-psilate to psilate, the rugulae faintly and finely striate (Types R4, R2-3; Figs. 4 K – L, 5 A – C, G) for *Agarista spp.* and *L. lucida*; or surface uneven to somewhat flat and rugged, primary exine sculpture coarsely rugulate to coarsely rugulate-psilate, the rugulae clearly striate (Types R3**, R3*; Figs. 5 D – F, H) for *C. yunnanensis*, *L. ligustrina*, *L. buchii* and *L. ovalifolia* var. *elliptica*, or psilate primary sculpture with clearly striate secondary sculpture (Type S1; Fig. 5I) for *P. floribunda*.

Oxydendreae (monotypic, studied genus: *Oxydendrum*)

Compact tetrahedral tetrads circular in shape, apocolpial exine sculpture finely verrucate to finely rugulate. We were not able to study the pollen of *O. arboreum* under SEM due to either shrinkage and/or break down of all grains on SEM stub.

Pollen morphology of selected genera

Gaultheria

Gaultheria adenthrix of sect. *Amblyandra* is characterized by compact pollen tetrads with exine sculpture Type R1 (Fig. 3E).

Members of the sect. *Brossaea* have both types of pollen tetrads; lobed and compact, and exine sculpture commonly varies from Type R2 to Type R3 (Figs. 3 G – H, J – L). However, in the same section *G. miquelina* of subsect. *Botryphoros* and *G. erecta* of subsect. *Dasyphyta* possess exine sculpture Type R1* (Table 2, Figs. 3 F, I).

Pollen of *G. procumbens* of monotypic sect. *Gaultheria* is characterized by exine sculpture Type R1** (Fig. 4A).

Pollen grains of sect. *Monoanthemona* are characterized by compact tetrads (Table 2), and exine sculpture Types R3 and R4 (Figs. 4 B – C, E – F), except in *G. foliolosa* (Type R3*; Figs. 4D).

The pollen tetrads of *G. insane* of monotypic sect. *Pseudogaultheria* are somewhat large (Class III, D 44.3 µm), compact and circular in shape, septum thicker than that of apocolpial exine thickness (Tables 2 – 3), and exine sculpture Type R4 (Fig. 4G).

Agarista

Agarista salicifolia of monotypic sect. *Agauria* possesses many exceptional palynological characters within the genus; viz., lobed, significantly smaller pollen tetrads (D 30.5 µm), minute grains (P16.3 µm X E22.9 µm), smaller 2f (12.5 µm) and exine sculpture Type R2-3 (Tables 2 – 3, Fig. 5C).

Members of the sect. *Agarista* show a variation in the palynological characters viz. both compact and lobed tetrads, relatively lager (D 35.8 – 43.1 µm), medium grains (P19.6 - 22.9 µm X E27.1 – 33.3 µm), larger 2f (16.5 – 27.3 µm) and exine sculpture Type 4 except in *A. eucalyptoides* exine sculpture of Type R2-3 (Tables 2 – 3, Fig. 4 K – L, 5 A – B).

Lyonia

Section *Arsenococcus* is characterized by exine sculpture Type R3** (Fig. 5E). Members of the sect. *Lyonia* showed wide variability palynological characters. Pollen grains are united in both lobed and compact tetrads and exine sculpture Type R3* (Tables 2 – 3; Fig. 5F). *Lyonia lucida* of Sect. *Maria* is distinctly characterized by pollen with thick septum (Class IV) which is also thicker than its apocolpial exine (Table 2), and exine sculpture Type R3 (Fig. 5G); sect. *Pieridopsis* by exine sculpture Type R3* (Fig. 5H).

Discussion

Variation of palynological characters and evolutionary trend

All taxa studied have 3-colpor(oid)ate and oblate pollen tetrads having similar rugulate to rugulate-psilate (rarely psilate) exine with secondary striate sculpture, which suggest that the taxa included in this study are closely related. Although a wide more or less continuous and serial variation

was found in both quantitative and qualitative pollen features at both tribal and generic level (Table 3, Figs. 3 – 5), the morphological and anatomical distinctness of some genera studied could be supported and/or defined well by palynological features, and they provide useful information in confirming or denying already proposed relationships within the tribes or genera.

Both types, lobed and compact, of pollen tetrad are found within the members of these tribes. The round and compact tetrads, which characterize the family Empetraceae and most members of subfamily Vaccinioideae, were considered as primitive within the Ericaceae by Warner and Chinnappa [43]. In the most recent classification of Ericaceae [2], tribe Vaccinieae of the subfamily Vaccinioideae is regarded as the most advanced tribe within the family Ericaceae, and Empetraceae was included as a tribe Empetreae in the subfamily Ericoideae. The pollen of the tribe Vaccinieae is characterized by lobed (normal) tetrads ([8], Sarwar and Takahashi unpublished data). Our palynological observations support and confirm the opinion of Warner and Chinnappa [43]. The compact tetrads found at most of the taxa might be symplesiomorphic pollen characters within these tribes and reverse independently to apomorphic state, lobed tetrads in different taxa (Table 2).

Accordingly, medium size pollen grains found in most of the taxa could be a synapomorphic pollen character state and reverse independently to plesiomorphic minute grains in different taxa viz., *Chamaedaphne cacyculata*, *Gaultheria spp*., *Agarista salicifolia* and *Lyonia spp*. (Table 3). The primitive state of angiosperm pollen is large grains, and two different evolutionary trends are found in pollen size; towards even larger or gigantic grains, or towards smaller grains [52]. They also reported the easy reversibility of this character.

An exceptional palynological feature; pollen tetrads with very thin or (may be) without septum is found in *Lyonia lingustrina* under LM. Pollen tetrad without septa is a very rare character, and has been previously reported for only two species of the genus *Ceratostema* of the tribe Vaccinieae, Ericaceae as well as any other angiosperm families [9]. So, a transmission electron microscopic (TEM) study of pollen is necessary to confirm whether the septum is very thin or absent also in *L. ligustrina*.

In SEM, apocolpial exine sculpture varies from coarsely rugulate to psilate, the rugulae with secondary sculptures; faintly and finely to clearly striate (Figs. 2 – 5). But, the synapomorphic state of

exine sculpture for these tribes is not clear as the exine sculpture very often evolved parallely. If we accept the same evolutionary trend of the exine sculpture as that suggested in *Enkianthus* of the Ericaceae [3], the major morphological trends of the primary exine sculpture are postulated within these tribes from coarsely rugulate through coarsely rugulate-psilate to psilate with faintly and finely striate secondary sculptures (Fig. 2, Type R1 → Type R2 → Type R3 → Type R4).

Taxonomic significances of palynological characters

Tribal/generic palynological characteristics

Pollen tetrads of tribes Andromedeae *s.s.*, Gaultherieae and Oxydendreae are commonly compact and those of the tribe Lyonieae relatively lobed, especially *Lyonia* (Table 2). The close relationship between the tribes Andromedeae *s.s.* and Gaultherieae, as identified by morphological and molecular data [2], is mostly supported by both quantitative and qualitative palynological characters (Table 2). However, the palynological features of other tribes Lyonieae and Oxydendreae are not clearly differentiated from those of Andromedeae *s.s.* and Gaultherieae (Table 2). The tribe Andromedeae including *Andromeda* and *Zenobia*, is clearly characterized by relatively thinner (Class I) and perforated septum (Table 2).

Based on exine sculpture, two distinct groups are identified among the genera of the tribe Gaultherieae. Group one composed of *Diplycosia* and *Leucothoë*, is characterized by exine sculpture Type S2 and its derivatives (S2* and S2**) (Table 2). And the other group composed of *Chamaedaphne*, *Gaultheria* and *Tepuia*, is characterized by exine sculpture of Type R and its derivatives (Table2). The palynological close relationship between *Gaultheria* and *Tepuia* is well supported by morphological and molecular data, but *Chamaedaphne* is situated at relatively distant position [53]. In this combined analysis [53], *G. procumbens* is also emerged as sister to *G. cumingiana* + the *Diplycosia* clade. Although we did not study *G. cumingiana*, the distinctness of secondary striate sculpture may give additional support to the close relationship between *G. procumbens* (R1**) and *D. heterophylla* (S2*) (Figs.3D, 4A).

Among the taxa of the tribe Lyonieae, *Pieris floribunda* is easily distinguishable by its exceptional exine sculpture (Type S1) (Table 2, Fig. 2). But pollen of the genus *Pieris* has actually

different types of exine sculpture (Types R3, R3* and S1) revealed by us already [36]. The combined analysis of morphological and molecular data [54], *Craibiodendron* was closely related to *Lyonia* than to *Pieris* and *Agarista*. This close relationship between *Craibiodendron* and *Lyonia* is also supported by the present palynological features (Tables 2 – 3, Fig. 5). The range of variation found in the exine sculptures of some genera; e.g. *Gaultheria*, *Agarista* and *Lyonia* (Table 2, Figs. 3 – 5), possessed taxonomic importance and has been used to add additional insights on the infrageneric classifications for these genera based on morphological and anatomical observations.

Exine sculptures of *Vaccinium*, the largest genus of the subfamily Vaccinioideae, have many similarities to those of the members of these four tribes [8]. However, the exine sculpture of *V. japonicum* is very distinct even within the subfamily Vaccinioideae ([7–9, 36], Sarwar and Takahashi unpublished data), which may support the separation of *V. japonicum* from the genus *Vaccinium* as we advocated before [8]. The rugulae with secondary sculpture; faintly and finely to clearly striate, is a common feature for these tribes [36]. Similar feature of rugulae was also observed in the tribe Vaccinieae ([8, 9], Sarwar and Takahashi unpublished data). So, the exine surface with secondary striate sculptures seems to characterize the subfamily Vaccinioideae.

Infrageneric classifications

The infrageneric classifications based on morphological and anatomical characters for the genera; *Gaultheria* [47], *Agarista* [48] and *Lyonia* [49], are generally supported and/or confirmed by the palynological characters (Table 2 – 3, Figs. 3 – 5). Palynological features of the genus *Pieris* have also supported Judd's [55] infrageneric classification for this genus as discussed in our earlier study [36].

Gaultheria

Members of sect. *Amblyandra* are characterized by campanulate flowers, exaristate and basally dilated stamens and large leaves for solitary flowered species [47] and compact pollen tetrads with exine sculpture Type R1 (Fig. 3E). The exine sculpture of *G. adenothrix* showed some similarities to *G. miqueliana* and *G. erecta* (Type R1*) (Figs. 3 F, I) but clearly different from other species (Table 2, Figs. 3 G, H, J – L, 4 A – G).

Section *Brossaea* the largest section of *Gaultheria*, contains extremely variable species and is characterized by racemose flower, but rarely (only) solitary species [47]. The wide morphological variability is also found and supported by the palynological characters (Tables 2 – 3). Within the Sect. *Brossaea*, pollen tetrads of subsect. *Botryphoros* is characterized by minute grains (E ≤ 23.4 µm) and subsect. *Dasyphyta* by relatively larger grains (E ≥ 24.7 µm) (Table 3). The close relationship among members of ser. *Domingenses* and ser. *Tomentosae* of subsect. *Dasyphyta* [47] is also supported by palynological observations (Tables 2 – 3, Figs. 3 H – L).

Most species of *Gaultheria* are characterized by the Type R1 – Type R4, the relatively exceptional exine sculpture (Type R1**) may support recognition of *G. procumbens* as a member of monotypic sect. *Gaultheria* (Table 2). Moreover, the exine sculptures of *G. procumbens* (Type R1**, Fig. 4A) and *G. maqueliana* (Type R1*, Fig. 3F) may also support the close relationship between these two species as reported by Airy-Shaw [56].

Section *Monoanthemona*, one of the large sections of *Gaultheria*, contains most of the solitary flowered species without apical bracteoles, and the monotypic sect. *Pseudogaultheria* primarily characterized by racemose type of inflorescence and temperate South American distribution [47]. Palynological characters of both these two taxa have some distinctions, which support their systematic position as different sections within the genus *Gaultheria* (Tables 2 – 3, Figs. 4 B – G).

Agarista

The genus *Agarista* includes 31 species and is divided into two sections; monotypic sect. *Agauria* (including *A. salicifolia*) and sect. *Agarista* (including the remaining 30 species) [48]. The placement of *A. salicifolia* in the monotypic sect. *Agauria* is supported by many exceptional palynological characters of this taxon within the genus *Agarista* viz., lobed, significantly smaller pollen tetrads (D 30.5 µm), minute grains (P16.3 µm X E22.9 µm) and exine sculpture Type R2-3 (Tables 2 – 3, Fig. 5C).

Based on the palynological features, two distinct pollen morphological groups were identified among the members of sect. *Agarista*. One group composed of *A. chlorantha* and *A. coriifolia* var. *coriifolia*, is characterized by relatively larger pollen tetrads (D Class III), thicker apocolpial exine

(Class III – IV), but smaller D/d (Class II) and P/E (Class II) values. And the other composed of *A. eucalyptoides* and *A. populifolia*, is characterized by relatively larger D/d (Class III – IV) and P/E (Class III) values, but smaller pollen tetrads (D Class II – III) and thinner apocolpial exine (Class II) (Tables 2 – 3). Previously, the cladistic analysis of morphological and anatomical data also produced six more or less weakly diagnosed clades within the species of this section [57]. So, combined analyses of morphological, anatomical, palynological and molecular data are suggested for better understanding of the relationships among the members of *Agarista* sect. *Agarista*.

Lyonia

Lyonia, a genus of 36 species, is divided into four sections mainly based on structure of multicellular hairs, inflorescence type and several anatomical characters [49]. The palynological features of different sections support the infrageneric classification of *Lyonia* (Tables 2 – 3; Fig. 5 E – H). The sister relationship between *Lyonia ligustrina* and *L. ovalifolia* as identified by combined analysis morphological and molecular data [54], may also be supported and confirmed by palynological data (Tables 2 – 3, Figs. 5 E, H).

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Table 1: Taxa examined (tribes, genera, sections, series and species in alphabetical order).

Name of Taxa	Collector and No.	Voucher information (Herbarium acronym)
Tribe Andromedeae [2/2][1)]		
Andromeda polifolia L.	Takahashi & Fujita 9753 [2)]	Japan: Hokkaido, Kushiro-sicho, Kushiro-sitsugen, 17.06.1989. (SAPS)
A. polifolia L. var. *glaucophylla* (Link) DC.	Moore s.n. (LM)	USA: Wisconsin, Rusk Co., bog on S edge of two bear Lake, 22.05.1971. (C)
Zenobia pulverulenta (Bart.) Pollard.	Britt 3109	USA: North Carolina, Robeson Co., 23.05.1965. (C)
Tribe Gaultherieae [5/6]		
Chamaedaphne calyculata (L.) Moench.	Takahashi & Fujita 9755	Japan: Hokkaido, Kushiro-sicho, Kushiro-sitsugen, 17.06.1989. (SAPS)
Diplycosia heterophylla Bl.	Kjellberg s.n.	Indonesia: Java, Papandajan, 2000m, no day.03.1930. (S)
Gaultheria		
Section *Amblyandra*		
G. adenothrix (Miq.) Maxim.	Takahashi et al. 7574	Japan: Hokkaido, Sorachi-sicho, Mt. Yubari-dake, 29.07.1987. (SAPS)
Section *Brossaea*		
Subsection *Botryphoros*		
Series *Hispidae*		
G. appressa A.W. Hill	Constable 4081 (LM)	Australia: N.S.W., Werong Range, Mount Werong. 26.11.1962. (S)
Series *Leucothoides*		
G. miqueliana Takeda	Endo et al. 2505	Japan: Honshu, Fukusima Pref., Mt. Bandaisan, 08.07.1985. (SAPT)
G. prostrata W.W. Smith	Webster et al. 11395	Mexico: Pineland 4 miles below (west of) Paso de Cortez, 16.06.1962. (S)
Series *Ruprestres*		
G. oppositifolia Hook.f.	Skottsberg s.n. (LM)	New Zealand: N.J. Rotorna District, Maunga Kakaramea, 21.10,1938. (GB)
Subsection *Dasyphyta*		
Series *Domingenses*		
G. bracteata (Cav.) G. Don.	Asplund 13613	Peru: Dep. Huánuco, Prov. Pachitea, Pano, 11.09.1940. (S)
G. erecta Ventenat	Pringle 8896	Mexico: State of Puebla, Pine forests near Honey Station, 22.04.1904. (S)
G. gracilis Small	Burger & Leisner 6470 (LM)	Costa Rica: Prov. San José and Cartago, 27.11.1969. (S)
G. rigida H.B.K.	Meyer 9490	Chile: Juan Fernandez Islands, Mas Atierra, 09.12.1965. (S)
Series *Tomentosae*		
G. eriophylla (Pers.) Sleum. ex Burtt var. *eriophylla*	Dusén 57	Brazil: Itatinga, alt. 1850m, 21.05.1902. (S)
G. tomentosa H.B.K.	Harling et al. 14981	Ecuador: Canar, paramo and mountain scrub, 04.11.1977. (GB)
Section *Gaultheria*		
G. procumbens L.	Miyabe s.n. (SEM)	USA: Shelburne, n.b., no day.07.1887. (SAPS)
Section *Monoanthemona*		
Series *Antipodae*		
G. anastomosans (L.F.) H.B.K.	Killip & Smith 17683	Columbia: Eastern Cordillera, Dept. Statander, Parmo Rico, 18.01.1927. (S)
G. buxifolia Willd.	Alston 7959	Colombia: Piendamor, alt. 1700m, 11.04.1939. (S)
G. foliolosa Benth.	Harling & Andersson 23657	Ecuador: Zamora-Chinchipe, Nudo de Sabanilla, 04.04.1985. (GB)
G. vaccinoides Weddel	Asplund 12874 (LM)	Peru: Dep Huánco, Prov. Huánco, Carpis, 06.08.1940. (S)
Series *Itatiaiae*		
G. itatiaiae Wawra	Hatschbach 1756	Brazil: Est. Paraná, Mun. Morretes, Pico Olimpo, 15.01.1950. (S)
Series *Myrtilloideae*		
G. myrtilloides Cham. & Schl. var. *myrtilloides*	Barba 1639	Argentina: Gob. Neuquén, Ladera Co., Belveder, 15.01.1947. (S)

Table 1: (concluded).

Name of Taxa	Collector and No.	Voucher information (Herbarium acronym)
Section *Pseudogaultheria*		
G. insane (Molina) Middleton	Valentin s.n.	Chile: Prov. Concepcion, Talcahuano, 17.10.1921. (S)
Leucothoë grayana Maxim. var. *oblongifolia* (Miq.) Ohwi	Takahashi 165	Japan: Prov. Mutsu, Shimokita pen., 28.06.1978. (SAPS)
L. keiskei Miq.	Ohwi s.n.	Japan: Wakayama Pref., Mt. Nachi, (Ex Herb. J. O.), 29.07.1883. (SAPS)
Tepuia venusta Camp.	Luteyn & Steyermark 9578	Venezuela: Bolivar, Parq. Nac Canaima, Auyantepui, 18.02.1984. (GB)
Tribe Lyonieae [4/4]		
Agarista		
Section *Agarista*		
Agarista chlorantha (Cham.) G. Don.	Hatschbach & Guimaraes 24777	Brazil: Rio Jeronimo (mm. s. Jeronimo de Serra) Parana, 26.09.1970. (C)
A. coriifolia (Thunb.) Hook.f. var. *coriifolia*	Macedo 3757	Brazil: Serra de Cipo, Vermelhas, 05.09.1952. (S)
A. eucalyptoides (Cham. & Schlecht.) G. Don.	Dusen 2011	Brazil: Serra de Itatiaia, in compo, alt. 2100m, 18.10.1903. (S)
A. populifolia (Lam.) Judd	Biltmore Herbarium 2656a	USA: North Carolina, Buncombe Co., 11.06.1898. (S)
Section *Agauria*		
A. salicifolia (Comm. Ex Lam.) G. Don	Schlieben 1160A (LM)	Tanzania: Strogabiet des oberen Ruhudje, no date.1931. (S)
	Dorr & Barnett 3156 (SEM)	Madagascar: Antananarivo Prov., Parc de Isimbazaza 21.10.1984. (S)
Craibiodendron yunnanensis W.W. Sm.	Forrest 8218	China: NW of Tengyueh, Flanks of volcanic mountain, no day.06.1912. (S)
Lyonia		
Section *Arsenococcus*		
L. ligustrina DC.	DeSimone 420	USA: Conneticut, Litchfield Co., 24.06.1983. (SAPT)
Section *Lyonia*		
Lyonia buchii Urban	Ekman (Pl. Idn. Occ. 3236)	Haiti: Massif de la Selle, Foureg. 13.02.1925. (S)
L. jamaicensis (Swatrz) D. Don	Harris s.n. (LM)	Jamaica: Blue Mountains, 12.06.1894. (S)
L. macrophylla (Britton) Ekman ex Urban	Ekman (Pl. It. Reg. 9702) (LM)	Cuba: Prov. Orienta, Sierra de Nipe, alt. 725m, 11.07.1919. (S)
Section *Maria*		
L. lucida (Lam.) K. Koch	Ekman 12150	Cuba: Isla de Pinos, Los Fridios, 08.11.1920. (S)
Section *Pieridopsis*		
L. ovalifolia (Wall.) Drude var. *elliptica* (Sieb. & Zucc.) Hand-Mazz.	Takahashi 1887	Japan: Shikoku, Kagawa Pref., Ohkawa-gun, Nagao-cho, 01.06.1984. (SAPT)
Pieris floribunda (Pursh) B. & H.	Boufford & Wood 21058	USA: West Virginia, Pendleton Co., 19.05.1979. (TUS 90950)
Tribe Oxydendreae [1/1]		
Oxydendrum arboreum DC.	Small & Heller 113 (LM)	USA: WN Carolina, Caldwell Co., 31.07.1891. (S)

Explanation of symbols:

[1)] [Number of genera examined / total number of genera in the tribe].

[2)] Specimens were examined by both light microscopy (LM) and scanning electron microscopy (SEM), if not otherwise stated.

Table 2: Pollen morphological data based on light microscopic investigation. D Tetrad diameter, P Polar axis, E Equatorial diameter, Apo. Apocolpial. Ornamentation based on SEM observation (types corresponding to Fig. 2).

Name of Species	Shape of tetrads	D*	D/d**	P/E***	Apo. Exine thickness†	Septum Thickness ††	Orname-ntation	Figure(s)	Remarks†††
Tribe Andromedeae (2/2)									
Andromeda polifolia	Compact	III	III	II	III	I P	R2	1E, 3A	
A. polifolia var. *glaucophylla*	Compact	III	III	II	III	I P	–		
Zenobia pulverulenta	Compact	II	III	I	II	I P	R2-3	3B	Sometimes tip of colpi bifurc.
Tribe Gaultherieae (5/6)									
Chamaedaphne calyculata	Compact	II	III	II	II	I	R2-3	3C	Sometimes tip of colpi bifurc.
Diplycosia heterophylla	Lobed	III	IV	III	III	II	S2*	3D	Endoaperture indist.
Gaultheria									
Section *Amblyandra*									
G. adenothrix	Compact	II	III	II	III	II	R1	3E	
Section *Brossaea*									
Subsection *Botryphoros*									
Series *Hispidae*									
G. appressa	Lobed	II	III	II	II	II	–		Other tetrad config.
Series *Leucothoides*									
G. miqueliana	Compact	II	III	II	I	I	R1*	3F	Endoaperture indist.
G. prostrate	Lobed	II	III	II	II	II	R3	1C, 3G	Other tetrad config., endoaperture indist.
Series *Ruprestres*									
G. oppositifolia.	Compact	I	III	II	II	II	–		Costae indist.

Table 2: (Continued).

Name of Species	Shape of tetrads	D*	D/d**	P/E***	Apo. Exine thickness†	Septum Thickness ††	Orname-ntation	Figure(s)	Remarks†††
Subsection *Dasyphyta*									
Series *Domingenses*									
G. bracteata	Compact	II	III	II	II	II	R2	3H	
G. erecta	Compact	II	III	II	II	II	R1*	3I	Endoaperture sometimes H-shaped
G. gracilis	Compact	II	I	I	II	I	–		Costae indistinct
G. rigida	Compact	II	II	I	II	I	R3	3J	Other tetrad config., costae indist.
Series *Tomentosae*									
G. eriophylla var. *eriophylla*	Lobed	II	III	II	II	I	R2	3K	
G. tomentosa	Compact	II	III	II	II	I	R3	3L	
Section *Gaultheria*									
G. procumbens	Compact	-	-	-	-	-	R1**	4A	
Section *Monoanthemona*									
Series *Antipodae*									
G. anastomosans	Compact	II	II	II	II	I	R3	4B	Costae indist.
G. buxifolia	Compact	II	III	II	II	I	R3	4C	Endoaperture indist.
G. foliolosa	Compact	II	III	III	III	II	R3*	4D	
G. vaccinoides	Compact	II	III	II	II	I	–		Costae indist.
Series *Itatiaiae*									
G. itatiaiae	Compact	II	II	I	III	I	R3	4E	Grains often shrink, costae indist.

Table 2: (Continued).

Name of Species	Shape of tetrads	D*	D/d**	P/E***	Apo. Exine thickness†	Septum Thickness ††	Orname-ntation	Figure(s)	Remarks†††
Series *Myrtilloideae*									
G. myrtilloides var. *myrtilloides*	Compact	I	III	III	II	I	R4	4F	
Section *Pseudogaultheria*									
G. insane	Compact	III	II	I	II	III	R4	4G	Tetrad circular in shape
Leucothoë grayana var. *oblongifolia*	Compact	III	II	I	II	I	S2	4H	Grains often broken along colpi, rarely 4-aperturate, endoaperture indist.
L. keiskei	Lobed	III	III	III	III	III	S2**	4I	
Tepuia venusta	Lobed	IV	III	II	V	II	R3*	4J	Often tip of colpi bifurc.
Tribe Lyonieae (4/4)									
Agarista									
Section *Agarista*									
Agarista chlorantha	Compact	III	II	II	III	II	R4	4K	
A. coriifolia var. coriifolia	Compact	III	II	II	IV	I	R4	4L	
A. eucalyptoides	Compact	II	III	III	II	I	R2-3	5A	Costae indist.
A. populifolia	Lobed	III	IV	III	II	I	R4	5B	Costae thick
Section *Agauria*									
A. salicifolia Schlieben 1160A	Lobed	II	III	III	II	II	-		Often 1 – 2 grains in tetrad shrink, costae short
Dorr & Barnett 3156	Lobed	-	-	-	-	-	R2-3	5C	
Craibiodendron yunnanensis	Compact	II	III	III	III	V	R3**	5D	Endoaperture very lalongate, colpi margin psilate

Table 2: (Concluded).

Name of Species	Shape of tetrads	D*	D/d**	P/E***	Apo. Exine thickness†	Septum Thickness ††	Orname-ntation	Figure(s)	Remarks†††
Lyonia									
Section *Arsenococcus*									
L. ligustrina	Lobed	II	III	II	I	0	R3**	5E	
Section *Lyonia*									
Lyonia buchii	Lobed	II	III	II	II	I	R3*	5F	Often 1 – 2 grains in tetrad shrink, costae indist.
L. jamaicensis	Compact	I	II	II	II	I	–		Costae indist.
L. macrophylla	Lobed	II	III	III	II	I	–		Costae indist.
Section *Maria*									
L. lucida	Lobed	II	III	III	II	IV	R3	5G	Endoaperture indist.
Section *Pieridopsis*									
L. ovalifolia var. *elliptica*	Lobed	II	III	II	II	I	R3*	1A, 5H	
Pieris floribunda	Lobed	III	III	III	I	III	S1	5I	
Tribe Oxydendreae (1/1)									
Oxydendrum arboreum	Compact	II	II	I	II	II	–	1 B, D	Tetrad circular in shape, exine sculpture finely verrucate to finely rugulate

Explanation of symbols:

* I: 20.1–30.0 µm, II: 30.1–40.0 µm, III: 40.1–50.0 µm, IV: 50.1–60.0 µm.

** I: –1.19, II: 1.20–1.29, III: 1.30–1.39, IV: 1.40– .

*** I: 0.61–0.65, II: 0.66–0.70, III: 0.71–0.75, IV: 0.76– .

† I: 1.1–1.5 µm, II: 1.6–2.0 µm, III: 2.1–2.5 µm, IV: 2.6–3.0 µm, V: 3.5 µm– .

†† 0: Very thin or absent, I: 0.5–0.9 µm, II: 1.0–1.4 µm, III: 1.5–1.9 µm, IV: 2.0– 2.4 µm, V: 2.5 µm– , P: Septum with perforations.

††† bifurc.: bifurcated, indist.: indistinct, config.: configurations

Table 3: Variation in palynological characters showing mean value in µm and standard deviation, highest – lowest value in µm in parenthesis, D Tetrad diameter, P Polar axis, E Equatorial diameter, Apo. Apocolpium, n.d. not discerned.

Name of Species	D	P	E	D/d	P/E	Ectoaperture		2f/D	Endoaperture		Apo. exine thickness	Septum thickness
						Length (2f)	Width		Length	Width		
Tribe Andomedeae												
Andromeda polifolia	43.3±1.6 (42.3-46.2)	21.9±1.5 (19.5-24.8)	33.3±1.7 (30.5-35.5)	1.30 (1.26-1.35)	0.66 (0.61-0.70)	22.0±1.9 (19.8-24.8)	3.0±0.6 (2.5-4.0)	0.51 (0.43-0.58)	1.7±0.4 (1.3-2.5)	8.7±1.6 (6.6-9.9)	2.1±0.4 (1.7-3.0)	0.7±0.3 (0.3-1.2)
A. polifolia var. *glaucophylla*	43.5±1.2 (41.9-44.4)	22.4±1.0 (21.1-24.1)	33.1±1.2 (30.7-34.7)	1.32 (1.26-1.39)	0.68 (0.62-0.75)	21.3±2.0 (18.2-24.8)	2.9±0.7 (1.7-3.6)	0.49 (0.43-0.58)	1.9±0.7 (0.8-3.0)	9.9±1.6 (8.3-13.2)	2.3±0.4 (1.7-3.0)	0.9±0.4 (0.2-1.7)
Zenobia pulverulenta	35.5±1.3 (33.2-37.1)	17.9±1.0 (16.5-19.8)	27.4±1.5 (24.8-29.7)	1.30 (1.18-1.40)	0.65 (0.60-0.73)	23.3±1.9 (20.6-26.4)	2.2±0.7 (1.3-3.3)	0.66 (0.59-0.75)	1.5±0.6 (0.8-2.5)	7.7±0.8 (6.6-8.3)	1.7±0.1 (1.5-2.0)	0.9±0.3 (0.3-1.5)
Tribe Gaultherieae												
Chamaedaphne calyculata	30.6±1.5 (28.9-33.3)	15.9±1.6 (13.2-17.8)	23.0±1.0 (21.5-25.1)	1.33 (1.25-1.38)	0.69 (0.57-0.82)	19.2±1.4 (16.5-21.5)	1.4±0.7 (0.8-3.3)	0.63 (0.57-0.67)	1.4±0.5 (0.5-2.5)	7.2±2.5 (5.0-13.2)	1.6±0.3 (1.2-2.0)	0.8± 0.3 (0.3-1.2)
Diplycosia heterophylla	41.9±2.6 (36.9-47.5)	21.5±0.7 (20.1-23.1)	29.5±2.1 (28.1-34.7)	1.42 (1.28-1.53)	0.73 (0.62-0.77)	28.0±1.6 (25.6-31.4)	2.1±0.7 (1.3-3.3)	0.67 (0.63-0.75)	2.4±0.6 (1.7-3.3)	9.1±3.0 (3.0-13.2)	2.2±0.3 (1.7-2.6)	1.2±0.4 (0.7-1.7)
Gaultheria												
Section *Amblyandra*												
G. adenothrix	33.3±1.3 (31.3-34.7)	16.8±1.1 (14.9-18.3)	25.0±1.2 (22.8-26.4)	1.34 (1.28-1.40)	0.67 (0.61-0.71)	20.5±1.9 (18.5-23.1)	1.2±0.5 (0.7-2.1)	0.61 (0.57-0.71)	1.0±0.5 (0.3-1.7)	7.2±2.0 (5.0-9.9)	2.1±0.7 (1.8-2.4)	1.2±0.3 (0.7-1.5)
Section *Brossaea*												
Subsection *Botryphoros*												
Series *Hispidae*												
G. appressa	30.4±2.3 (28.1-35.0)	15.1±1.3 (13.2-17.2)	21.9±1.9 (19.8-25.1)	1.39 (1.27-1.50)	0.69 (0.66-0.78)	17.2±1.0 (15.7-18.2)	0.6±0.3 (0.3-1.3)	0.57 (0.48-0.65)	0.6±0.4 (0.3-1.7)	5.2±1.0 (3.3-6.6)	1.9±0.2 (1.7-2.0)	1.2±0.5 (0.5-2.3)
Series *Leucothoides*												
G. miqueliana	30.8±1.7 (29.0-34.2)	15.8±1.0 (14.5-17.7)	22.7±1.0 (21.5-24.8)	1.36 (1.29-1.47)	0.70 (0.64-0.76)	18.8±1.5 (16.5-21.5)	0.9±0.6 (0.3-1.3)	0.61 (0.51-0.67)	0.6±0.5 (0.3-1.7)	9.9±3.1 (6.6-14.9)	1.4±0.2 (1.2-1.7)	0.8±0.3 (0.3-1.3)
G. prostrate	32.4±2.1 (29.7-36.3)	16.4±0.8 (15.3-18.2)	23.4±1.5 (21.5-26.4)	1.38 (1.32-1.43)	0.70 (0.63-0.75)	19.2±1.1 (18.2-21.5)	1.4±0.6 (0.5-2.5)	0.60 (0.55-0.67)	0.4±0.1 (0.3-0.5)	6.1±1.9 (5.0-8.2)	1.7±0.1 (1.5-2.0)	1.4±0.2 (1.2-1.7)

Table 3: (Continued).

Name of Species	D	P	E	D/d	P/E	Ectoaperture		2f/D	Endoaperture		Apo. exine thickness	Septum thickness
						Length (2f)	Width		Length	Width		
Series *Ruprestres*												
G. oppositifolia	24.8±1.7 (23.0-28.5)	12.5±1.0 (11.6-14.9)	19.0±1.0 (18.2-20.6)	1.31 (1.21-1.42)	0.66 (0.58-0.75)	14.5±0.7 (13.2-14.9)	0.9±0.4 (0.3-1.3)	0.59 (0.53-0.65)	0.7±0.1 (0.7-0.8)	7.2±1.0 (6.6-8.3)	1.8±0.1 (1.7-2.0)	1.0±0.2 (0.8-1.3)
Subsection *Dasyphyta*												
Series *Domingenses*												
G. bracteata	35.4±1.4 (32.7-37.5)	18.3±0.7 (17.3-19.5)	26.5±1.3 (24.8-28.1)	1.34 (1.22-1.42)	0.69 (0.62-0.74)	17.2±1.1 (14.9-18.2)	1.3±0.2 (1.0-1.7)	0.49 (0.41-0.53)	1.4±0.4 (0.8-1.7)	8.3±3.0 (5.0-13.2)	2.0±0.3 (1.7-2.5)	1.0±0.2 (0.5-1.3)
G. erecta	38.2±1.5 (36.0-40.4)	19.0±0.7 (18.2-19.8)	28.1±1.0 (26.4-29.7)	1.36 (1.29-1.44)	0.68 (0.61-0.71)	21.0±1.0 (19.8-22.3)	1.1±0.4 (0.5-1.7)	0.55 (0.49-0.61)	1.2±0.5 (0.3-1.7)	8.0±1.1 (6.6-9.9)	1.8±0.2 (1.5-2.0)	1.1±0.5 (0.5-1.7)
G. gracilis	32.9±1.4 (31.7-36.0)	16.9±1.0 (15.7-18.5)	27.5±1.1 (26.1-29.4)	1.19 (1.10-1.28)	0.61 (0.56-0.67)	15.3±1.6 (13.2-16.5)	1.4±0.2 (1.2-1.7)	0.46 (0.40-0.51)	0.9±0.1 (0.8-0.9)	6.6±4.7 (3.3-9.9)	1.9±0.1 (1.7-2.0)	0.9±0.2 (0.5-1.3)
G. rigida	31.0±1.0 (29.7-32.3)	15.5±0.9 (14.0-16.5)	24.7±1.1 (23.1-26.4)	1.26 (1.17-1.31)	0.63 (0.57-0.67)	18.6±1.2 (16.5-19.8)	3.0±0.4 (2.0-3.6)	0.60 (0.51-0.66)	1.7±0.6 (0.7-2.5)	7.8±0.8 (6.6-8.3)	1.8±0.2 (1.3-2.1)	0.6±0.3 (0.5-1.3)
Series *Tomentosae*												
G. eriophylla var. *eriophylla*	35.4±1.5 (33.0-37.5)	18.2±0.5 (17.8-19.3)	26.6±1.0 (24.8-27.7)	1.33 (1.25-1.40)	0.68 (0.65-0.71)	17.7±1.7 (14.9-20.6)	1.3±0.4 (0.7-1.7)	0.50 (0.40-0.59)	1.9±0.8 (0.7-3.3)	7.0±1.4 (5.0-8.3)	1.9±0.1 (1.8-2.1)	0.8±0.4 (0.3-1.3)
G. tomentosa	33.3±1.0 (32.0-35.1)	17.0±0.6 (16.5-18.2)	25.3±1.0 (23.4-26.4)	1.32 (1.27-1.37)	0.67 (0.64-0.73)	17.1±2.9 (14.9-24.8)	1.3±0.4 (0.7-1.8)	0.51 (o.45-0.74)	2.0±0.7 (1.2-3.0)	9.0±1.6 (6.6-11.6)	1.8±0.1 (1.7-2.1)	0.8±0.4 (0.3-1.3)
Section *Monoanthemona*												
Series *Antipodae*												
G. anastomosans	36.5±0.9 (35.0-38.0)	19.2±1.3 (16.8-21.1)	28.3±1.7 (25.6-29.7)	1.29 (1.19-1.39)	0.68 (0.58-0.80)	23.3±1.3 (21.1-25.6)	2.2±0.6 (1.3-3.0)	0.64 (0.58-0.69)	1.8±0.8 (0.8-3.6)	10.0±2.4 (5.8-13.2)	2.0±0.1 (1.8-2.1)	0.9±0.4 (0.3-1.7)
G. buxifolia	34.4±1.6 (32.2-36.5)	17.5±1.6 (15.8-20.5)	26.4±1.8 (23.4-28.9)	1.31 (1.20-1.51)	0.66 (0.58-0.80)	19.6±2.0 (17.3-23.1)	2.2±0.6 (1.2-3.0)	0.57 (0.48-0.69)	1.8±0.9 (0.5-2.5)	8.0±2.4 (3.3-11.6)	1.9±0.3 (1.7-2.5)	0.9±0.3 (0.5-1.3)
G. foliolosa	34.0±1.0 (32.7-35.3)	17.9±0.9 (16.5-19.3)	25.3±1.2 (23.9-27.7)	1.35 (1.26-1.41)	0.71 (0.67-0.81)	18.3±0.9 (17.3-19.8)	1.4±0.6 (0.5-3.0)	0.54 (0.50-0.60)	1.1±0.4 (0.5-1.7)	7.7±1.1 (6.6-9.9)	2.3±0.3 (2.0-3.0)	1.1±0.4 (0.5-1.7)
G. vaccinoides	31.7±1.9 (29.7-34.7)	17.0±1.2 (15.3-19.3)	24.2±1.0 (22.3-25.6)	1.31 (1.20-1.40)	0.70 (0.63-0.75)	18.9±1.6 (16.5-21.5)	1.1±0.8 (0.3-3.0)	0.60 (0.52-0.67)	1.4±0.8 (0.3-2.5)	7.9±1.4 (5.0-9.9)	1.8±0.2 (1.7-2.1)	0.6±0.3 (0.3-1.0)
Series *Itatiaiae*												
G. itatiaiae	38.3±1.8 (36.1-41.3)	19.4±1.3 (17.0-21.5)	30.3±1.8 (26.4-32.2)	1.26 (1.18-1.37)	0.64 (0.60-0.70)	20.3±1.5 (17.3-23.1)	2.1±0.6 (1.3-3.1)	0.53 (0.48-0.59)	1.2±0.5 (0.5-2.1)	10.7±2.6 (8.3-16.5)	2.3±0.3 (2.0-2.8)	0.6±0.3 (0.2-1.3)

Table 3: (Continued).

Name of Species	D	P	E	D/d	P/E	Ectoaperture		2f/D	Endoaperture		Apo. exine	Septum
						Length (2f)	Width		Length	Width	thickness	thickness
Series *Myrtilloideae*												
G. myrtilloides var. *myrtilloides*	27.8±1.3 (26.4-30.9)	14.6±0.7 (13.5-15.5)	20.3±0.7 (19.5-21.5)	1.37 (1.33-1.46)	0.72 (0.66-0.78)	17.4±0.8 (16.5-18.2)	0.7±0.2 (0.5-1.0)	0.63 (0.53-0.68)	0.8±0.4 (0.5-1.7)	8.2±3.9 (3.3-14.9)	1.7±0.2 (1.5-2.0)	0.9±0.2 (0.7-1.3)
Section *Pseudogaultheria*												
G. insane	44.3±2.4 (41.3-46.2)	22.7±1.3 (21.5-24.8)	35.8±3.1 (31.4-37.1)	1.24 (1.16-1.32)	0.64 (.59-0.73)	23.0±2.5 (19.8-26.4)	1.2±0.3 (0.7-1.7)	0.53 (0.43-0.63)	1.1±0.2 (0.7-1.3)	10.8±2.8 (8.3-16.5)	2.0±0.4 (1.7-2.6)	1.7±0.5 (1.3-2.0)
Leucothoë grayana var. *oblongifolia*	41.5±1.0 (39.6-42.9)	21.0±1.1 (19.5-22.8)	32.4±1.4 (31.4-34.7)	1.28 (1.1-1.37)	0.65 (0.59-0.73)	22.2±1.4 (21.5-24.8)	2.0±1.1 (0.5-3.3)	0.54 (0.50-0.60)	1.5±1.2 (0.5-3.3)	6.9±2.7 (5.0-9.9)	1.9±0.2 (1.7-2.3)	0.8±0.3 (0.5-1.3)
L. keiskei	40.3±3.3 (35.5-47.5)	21.9±1.3 (18.7-24.0)	29.2±1.9 (25.9-31.7)	1.38 (1.22-1.50)	0.75 (0.65-0.85)	17.3±1.6 (14.4-19.2)	2.3±0.5 (1.2-2.9)	0.43 (0.33-9.51)	n.d.	n.d.	2.5±0.4 (1.9-2.9)	1.8±0.4 (1.0-2.4)
Tepuia venusta	59.6±2.2 (55.6-63.5)	30.5±1.5 (28.1-32.7)	44.9±2.2 (42.6-48.7)	1.33 (1.28-1.39)	0.68 (0.59-0.76)	28.3±2.3 (26.4-33.0)	5.1±0.6 (4.3-5.8)	0.47 (0.41-0.55)	3.5±1.2 (1.7-5.0)	17.2±3.7 (11.6-23.1)	3.1±0.4 (2.3-3.6)	1.1±0.4 (0.7-1.8)
Tribe Lyonieae												
Agarista												
Section *Agarista*												
A. chlorantha	40.9±1.7 (38.0–42.9)	21.0±1.2 (19.8–22.9)	31.8±1.0 (29.7–33.0)	1.28 (1.20-1.34)	0.66 (0.59-0.71)	19.7±3.0 (15.7-26.4)	1.1±0.9 (0.3-3.0)	0.48 (0.37-0.64)	1.5±0.4 (0.5-2.0)	13.3±4.9 (6.6-19.8)	2.4±0.5 (1.8-3.0)	1.2±0.3 (0.5-1.7)
A. coriifolia var. coriifolia	43.1±3.7 (39.6-49.5)	22.9±2.8 (19.5-27.1)	33.3±2.8 (31.3-38.0)	1.29 (1.21-1.37)	0.69 (0.62-0.78)	16.5±2.3 (14.9-18.2)	2.1±1.3 (1.2-3.0)	0.31 (0.36-0.46)	2.0±0.5 (1.7-2.3)	17.3±1.2 (16.5-18.2)	2.6±0.3 (2.1-3.0)	0.9±0.4 (0.5-1.3)
A. eucalyptoides	35.8±1.6 (33.5-38.0)	19.6±0.7 (18.2-20.1)	27.1±1.1 (25.1-28.1	1.32 (1.19-1.41)	0.72 (0.71-0.75)	18.8±2.7 (13.2-21.5)	0.9±0.4 (0.5-1.7)	0.53 (0.35-0.64)	1.1±0.4 (0.5-1.7)	12.7±2.6 (8.3-16.5)	1.8±0.2 (1.7-2.1)	0.9±0.4 (0.5-1.7)
A. populifolia	41.0±1.4 (39.6-43.2)	21.4±1.3 (19.3-23.1)	28.9±0.5 (28.1-29.7)	1.42 (1.37-1.49)	0.74 (0.66-0.80)	27.3±2.8 (24.8-34.7)	2.4±0.9 (1.7-3.3)	0.49 (0.40-0.56)	2.2±0.8 (1.3-3.6)	7.8±2.3 (5.0-11.6)	1.8±0.2 (1.3-2.1)	0.7±0.3 (0.2-1.2)
Section *Agauria*												
A. salicifolia	30.5±1.5 (27.7-33.0)	16.3±1.9 (12.9-18.2)	22.9±0.9 (21.5-24.8)	1.33 (1.27-1.43)	0.71 (0.59-0.79)	12.5±1.3 (11.6-15.7)	0.4±0.1 (0.3-0.7)	0.41 (0.36-0.52)	0.8±0.6 (0.3-1.7)	7.9±2.4 (5.0-11.6)	2.0±0.2 (1.7-2.1)	1.3±0.4 (0.7-1.7)
Craibiodendron yunnanensis	32.3±1.5 (29.7-35.3)	17.1±0.6 (16.0-18.2)	23.7±1.1 (21.5-25.1)	1.36 (1.26-1.48)	0.72 (0.66-0.77)	18.9±1.8 (17.3-23.1)	1.6±0.5 (0.7-2.0)	0.59 (0.53-0.71)	0.7±0.2 (0.5-1.0)	9.9±3.6 (6.6-14.9)	2.3±0.2 (2.0-2.8)	2.5±0.9 (1.0-3.6)

Table 3: (Concluded).

Name of Species	D	P	E	D/d	P/E	Ectoaperture		2f/D	Endoaperture		Apo. exine thickness	Septum thickness
						Length (2f)	Width		Length	Width		
Lyonia												
Section *Arsenococcus*												
L. ligustrina	33.1±2.0 (31.3-36.3)	16.2±1.0 (14.9-17.3)	25.0±1.3 (23.1-26.4)	1.32 (1.27-1.36)	0.65 (0.59-0.75)	17.9±0.5 (17.3-18.2)	1.4±1.3 (0.3-2.8)	0.55 (0.53-0.58)	1.1±0.8 (0.5-1.7)	5.0±2.3 (3.3-6.6)	1.4±0.1 (1.3-1.9)	0
Section *Lyonia*												
L. buchii	37.0±2.2 (33.3-40.1)	19.0±1.2 (17.8-21.8)	28.6±1.9 (25.6-32.7)	1.30 (1.21-1.40)	0.67 (0.65-0.70)	19.0±1.9 (16.5-21.5)	0.9±0.3 (0.5-1.3)	0.51 (0.43-0.57)	1.1±0.5 (0.7-2.0)	6.8±1.3 (5.0-8.3)	2.0±0.2 (1.7-2.5)	0.9±0.4 (0.3-1.5)
L. jamaicensis	28.0±1.4 (25.1-29.7)	15.1±0.7 (14.0-16.3)	22.0±1.2 (19.5-23.3)	1.27 (1.22-1.36)	0.69 (0.63-0.76)	14.1±2.1 (9.1-16.5)	0.5±0.1 (0.3-0.8)	0.50 (0.34-0.56)	0.5±0.4 (0.3-1.7)	5.0±1.1 (3.3-6.6)	1.9±0.1 (1.8-2.1)	0.9±0.3 (0.3-1.3)
L. macrophylla	30.9±1.2 (28.4-33.0)	16.2±1.0 (14.7-17.5)	22.3±1.0 (21.5-24.1)	1.39 (1.29-1.54)	0.73 (0.64-0.82)	17.7±0.6 (16.5-18.2)	0.7±0.3 (0.5-1.2)	0.57 (0.53-0.61)	0.8±0.4 (0.5-1.7)	6.9±1.1 (5.0-8.3)	1.7±0.2 (1.5-2.1)	0.7±0.3 (0.3-1.3)
Section *Maria*												
L. lucida	33.8±0.9 (32.2-34.7)	17.8±1.2 (15.7-19.8)	24.6±0.5 (23.1-25.1)	1.37 (1.30-1.50)	0.72 (0.63-0.80)	19.2±2.8 (16.5-25.6)	0.8±0.3 (0.5-1.3)	0.56 (0.49-0.74)	1.1±0.6 (0.5-1.7)	5.6±1.9 (3.3-8.3)	1.9±0.3 (1.3-2.3)	2.0±0.7 (1.3-3.3)
Section *Pieridopsis*												
L. ovalifolia var. *elliptica*	32.5±1.5 (30.4-35.5)	16.8±0.8 (15.3-17.8)	24.8±1.5 (22.3-26.4)	1.31 (1.17-1.44)	0.68 (0.62-0.74)	15.3±1.4 (13.2-18.2)	1.3±0.6 (0.5-2.5)	0.47 (0.42-0.54)	1.1±0.7 (0.3-2.0)	6.1±1.7 (3.3-8.3)	1.7±0.2 (1.3-2.0)	0.7±0.2 (0.5-1.2)
Pieris floribunda	40.9±1.8 (38.0-43.7)	22.3±1.6 (18.2-23.5)	30.8±1.6 (28.3-32.6)	1.33 (1.26-1.40)	0.73 (0.61-0.81)	21.5±2.4 (16.3-24.5)	1.7±0.2 (1.4-1.9)	0.52 (0.42-0.58)	1.5±0.3 (1.2-1.9)	8.0±1.1 (5.8-9.1)	1.4±0.3 (1.0-1.9)	1.7±0.4 (1.0-1.9)
Tribe Oxydendreae												
Oxydendrum arboreum	33.4±1.1 (32.2–35.3)	16.5±1.2 (13.7–18.0)	26.5±1.2 (24.8–28.1)	1.26 (1.21-1.32)	0.62 (0.54-0.69)	17.3±0.8 (16.5–18.2)	0.7±0.3 (0.5–1.3)	0.52 (0.48-0.56)	0.9±0.4 (0.5-1.7)	9.4±2.3 (6.6-13.2)	2.0±0.2 (1.7–2.2)	1.2±0.5 (0.3-1.7)

Figure captions:

Fig. 1. Morphological features of pollen tetrads. A. Lobed tetrahedral tetrad (*Lyonia ovalifolia* var. *elliptica*), B. Compact tetrahedral tetrad (*Oxydendrum arboreum*), C. Decussate tetrad (*Gaultheria prostrate*), D. Normal septum (septal exine) (*Oxydendrum arboreum*), E. Septum with perforations (arrow) (*Andromeda polifolia*).

Fig. 2. Different types of apocolpial exine sculptures found in tribes Andromedeae *s.s.*, Gaultherieae, Lyonieae and Oxydendreae (by SEM).

Fig. 3. Scanning electron micrographs of apocolpial exine sculptures. Tribe Andromedeae (A – B): A. *Andromeda polifolia*, B. *Zenobia pulverulenta*; Tribe Gaultherieae (C – L): C. *Chamaedaphne calyculata*, D. *Diplycosia heterophylla*, E. *Gaultheria adenothrix*, F. *G. miqueliana*, G. *G. prostrate*, H. *G. bracteata*, I. *G. erecta,* J. *G. rigida*, K. *G. eriophylla* var. *eriophylla*, L. *G. tomentosa.*

Fig. 4. Scanning electron micrographs of apocolpial exine sculptures. Tribe Gaultherieae (A – J): A. *Gaultheria procumbens*, B. *G. anastomosans*, C. *G. buxifolia*, D. *G. foliolosa*, E. *G. itatiaiae*, F. *G. myrtilloides* var. *myrtilloides*, G. *G. insane*, H. *Leucothoë grayana* var. *oblongifolia*, I. *L. keiskei*, J. *Tepuia venusta*; Tribe Lyonieae (K – L): K. *Agarista chlorantha*, L. *A. coriifolia var. coriifolia*.

Fig. 5. Scanning electron micrographs of apocolpial exine sculptures. Tribe Lyonieae (A – I): A. *Agarista eucalyptoides*, B. *A. populifolia*, C. *A. salicifolia*, D. *Craibiodendron yunnanensis*, E. *Lyonia ligustrina*, F. *L. buchii*, G. *L. lucida*, H. *L. ovalifolia* var. *elliptica*, I. *Pieris floribunda.*

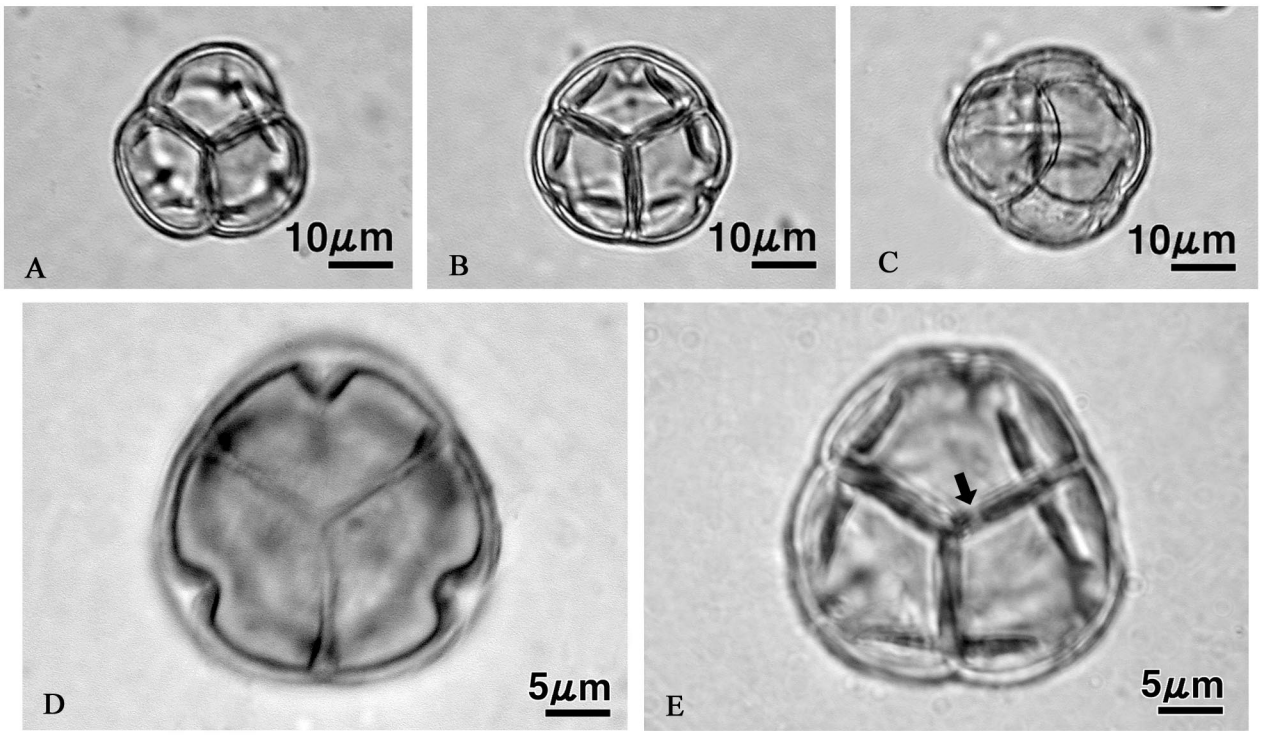

Fig. 1.

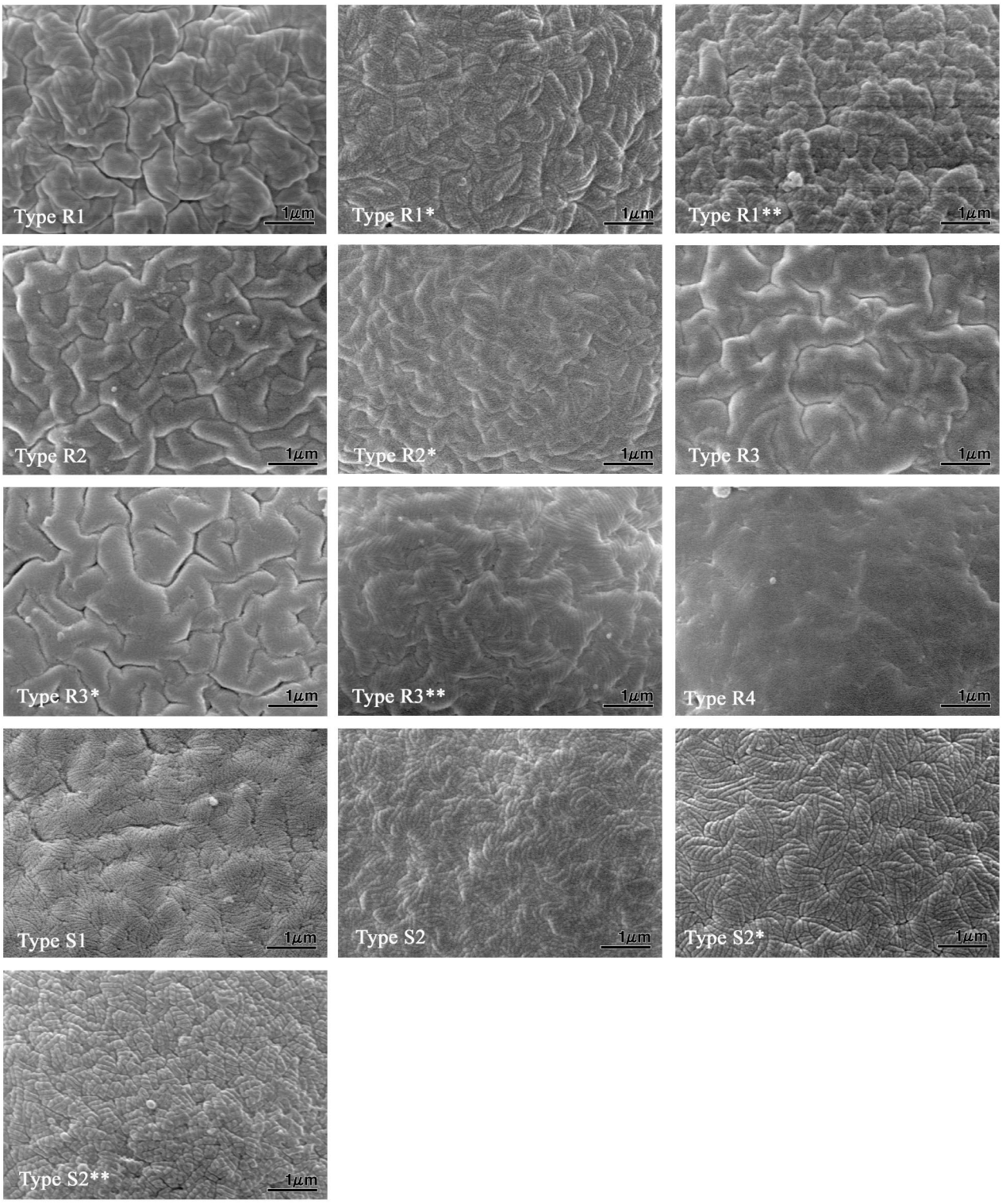
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Fig. 2.

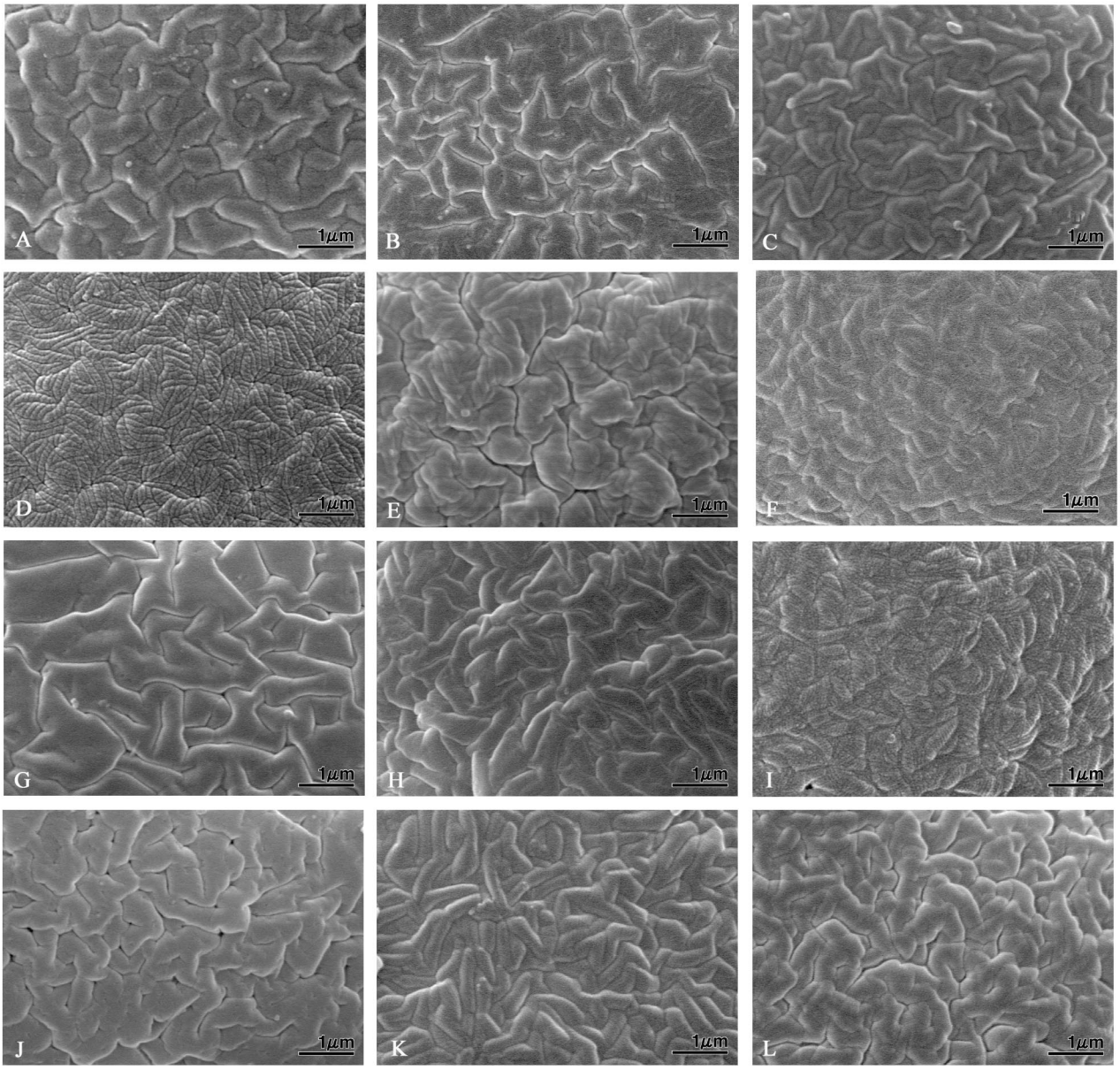

Fig. 3.

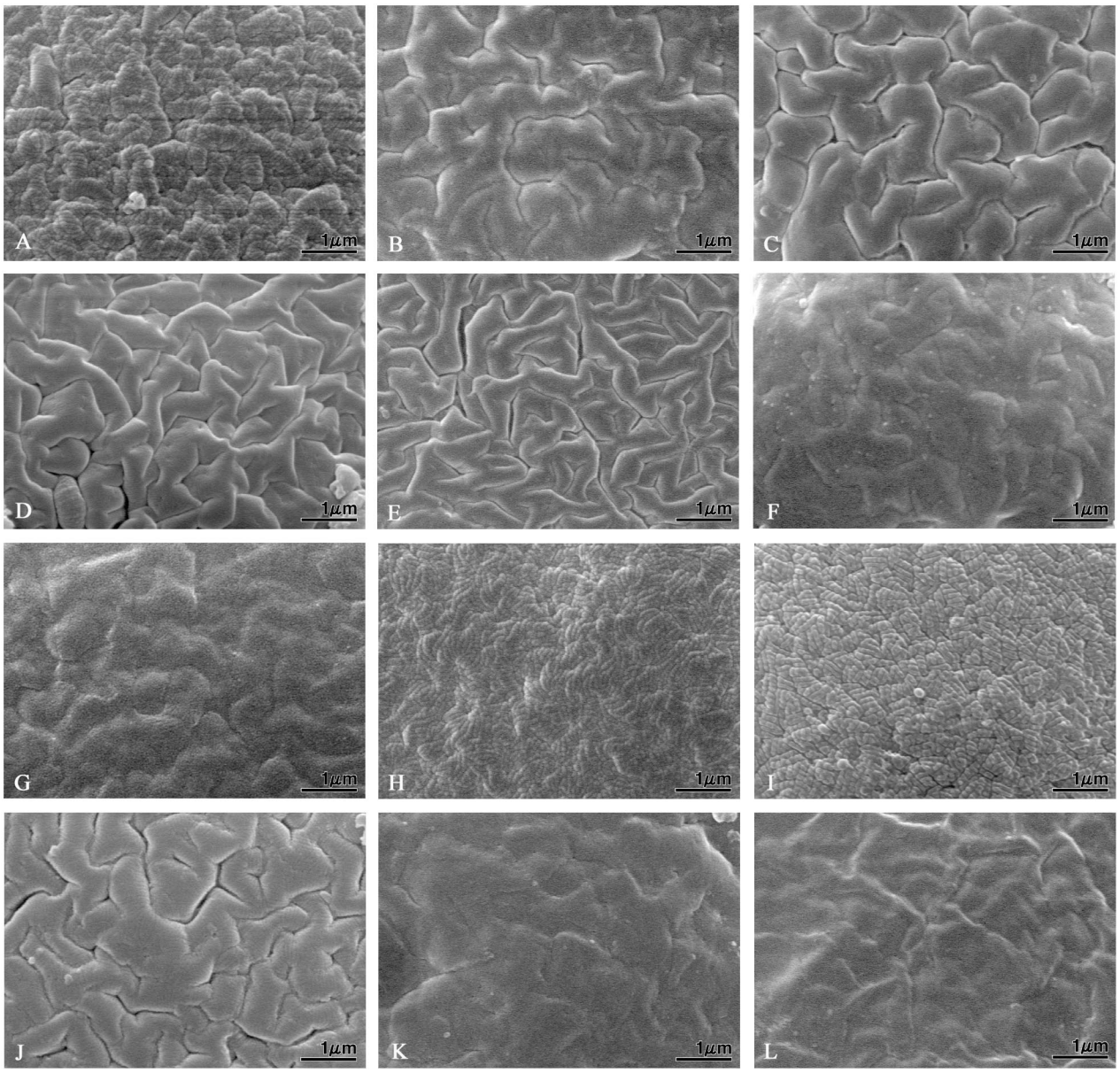

Fig. 4.

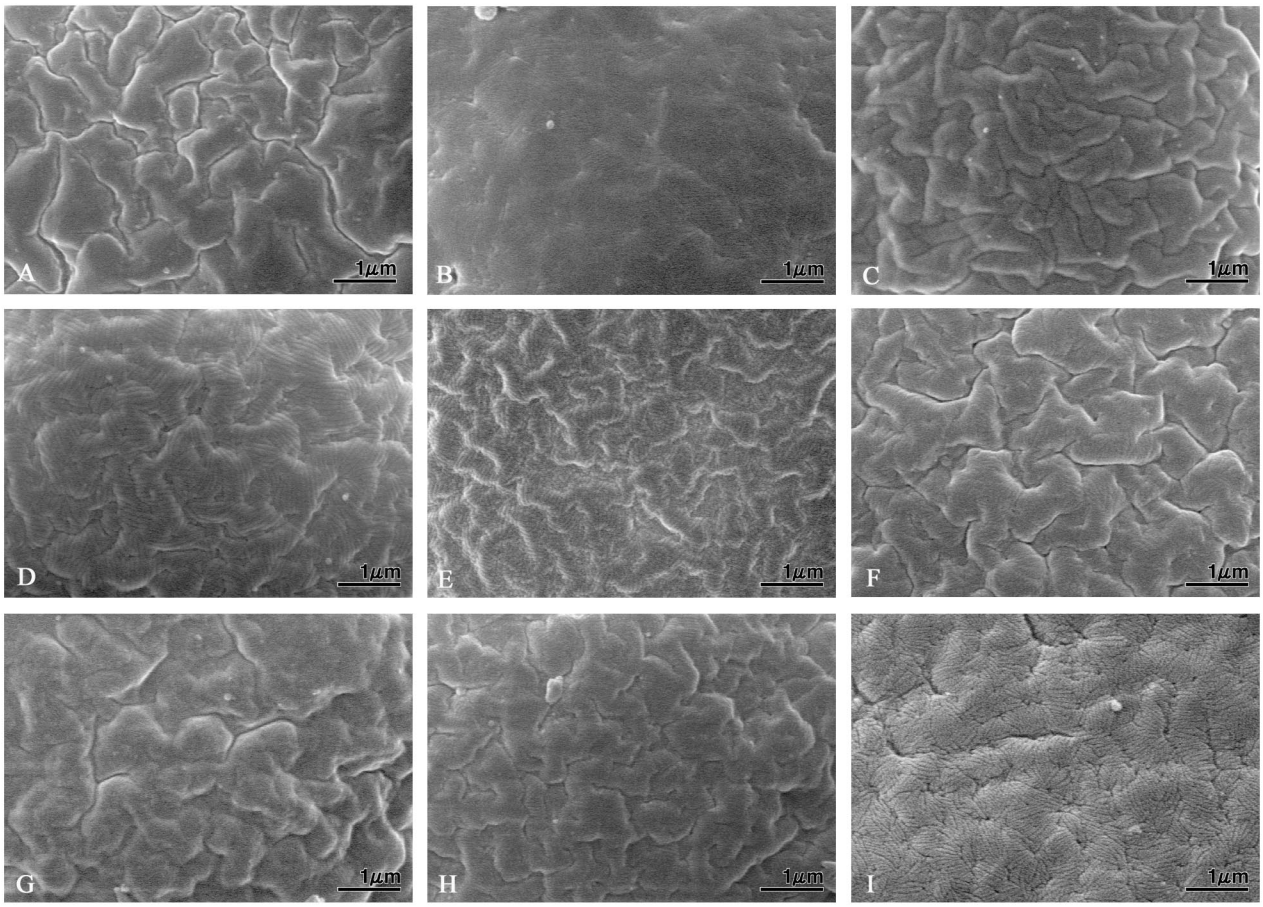

Fig. 5.

ツツジ科スノキ亜科のヒメシャクナゲ連、シラタマノキ連、ネジキ連、オキシデンドラム連における花粉形態の分類学的意義

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ヒメシャクナゲ連、シラタマノキ連、ネジキ連、オキシデンドラム連を構成する 13 属のうち 12 属・41 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た。これら４連の花粉は３溝孔（類孔）型・偏球形の花粉粒からなる四集粒という点で共通し、ステノパリナス（狭範花粉型）であった。花粉形態形質はこれら連のレベルでの分類システムと明瞭に対応しているという訳ではなかったが、ヒメシャクナゲ連、シラタマノキ連、オキシデンドラム連の四集粒においては、各花粉粒は通常密に合着しているが、ネジキ連（特にネジキ属）の四集粒では各花粉粒が遠心極側に突出している種が多い。密に合着しているヒメシャクナゲ連の四集粒はセプタム（隣接する４花粉粒間の壁）が薄く穿孔がある点で特徴づけられる。各連の遠心極域の外壁表面模様は粗いしわ模様型から平滑型まで変異し、しわにある「二次模様」は縞模様で、その縞模様は不明瞭から明瞭なものまで、微細なものから粗いものまである。表面模様全体と二次模様の明瞭さに基づいて、外壁は２つの主型：Ｒ型とＳ型、６亜型、さらに７つのより下の型に分けられた。しかし、各連の中においてはこれら外壁表面模様や定量的な花粉形質は連続的につながって変異していた。それでも時に外壁表面模様はある属でほとんど変化がなく安定している：イワナンテン属（S2 と S2**型)、アガリスタ属（R2-3 と R4 型）やネジキ属（R3、R3*、R3**型)。外壁表面模様とともに、四集粒の合着程度やサイズ、セプタムの厚さ等の花粉形態形質は、シラタマノキ属、アガリスタ属、ネジキ属などの属内分類体系を明らかにする上で有効な形質であることが分かった。これまでのツツジ科全体の花粉形態研究を基にすると、二次的な縞模様を持った外壁表面はスノキ亜科全体を特徴づける花粉形質と思われる。