An overview of pollen morphology and its systematic significance in the subfamily Arbutoideae of the Ericaceae

Subfamily Arbutoideae (Ericaceae) comprises four genera (*Arbutus*, *Arctostaphylos*, *Comarostaphylos* and *Ornithostaphylos*) and 81 species. We have examined the pollen morphology of 17 species from three of these genera: *Arbutus*, *Arctostaphylos*, *Comarostaphylos* representing using light microscopy (LM) and scanning electron microscopy (SEM) and also, for selected species, transmission electron microscopy (TEM). The Arbutoideae are generally stenopalynous; the four 3-colpor(-oid)ate grains are united in compact rounded permanent tetrads. No pollen morphological characters or character combinations distinguish Arbutoideae within the Ericaceae. However, within the subfamily, *Arctostaphylos* and *Comarostaphylos* commonly have smaller pollen tetrads with a thin perforated septum, while *Arbutus* pollen tetrads are usually larger and characterized by thicker septum without distinct perforations. The rugulate apocolpial exine sculpture of *Arctostaphylos* is usually less distinct than the coarser rugulate ectexine often observed for the pollen of *Arbutus* and *Comarostaphylos*.

Key words: stenopalynous, permanent tetrads, exine sculpture, light microscopy, scanning electron microscopy, transmissionelectron microscopy

Introduction

The cosmopolitan Ericaceae comprises eight subfamilies, some 124 genera and 4100 species [1, 2, 3]. The Arbutoideae Nied. is a small subfamily of Ericaceae. It comprises four genera: *Arbutus* (10 spp.), *Arctostaphylos* (60 spp.: including *Arctous* and *Xylococcus*), *Comarostaphylos* ("*Comarostaphylis*" in Diggs [4]; 10 spp.) and monotypic *Ornithostaphylos* [1, 2, 3, 5]. This subfamily was previously recognized as the tribe Arbuteae within the five tribes of the subfamily Vaccinioideae *sensu* Stevens [6, 7]. Genera included in the subfamily Arbutoideae form a distinct and natural group within the Ericaceae, characterized by a drupe or drupe-like berry with only 1 to few seeds per locule, flowers with

long unicellular hairs on the inside of calyx, and strongly dilated basal parts of filaments. Circumscription of the Arbutoideae is also supported by anatomy, phytochemistry and molecular data [2, 6, 8]. The Arbutoideae is a subfamily of commonly shrubs or small trees, including many dry adapted sclerophyllous taxa. It occurs in Mediterranean regions of Europe, North Africa, the Middle East, and the Canary Islands, and most of the diversity in the subfamily is found in the regions of Mediterranean climate in western North America [5]. *Arctostaphylos* has also circumarctic *A. alpina* and circumboreal *A. uva-ursi*.

Pollen morphology of some species of *Arbutus* (e.g., *A. andrachne*, *A. menziesii* and *A. unedo*) and of *Arctostaphylos* (e.g., *A. alpina*, *A. columbiana*, *A. rubra* and *A. uva-ursi*) has been repeatedly described and illustrated in regional pollen floristic studies in the Northern Hemisphere under LM or SEM e.g., Canada [9, 10], Europe [11], European part of Russia [12], Ireland [13], N. America [14], Spain [15, 16], W. Europe [17]. Sørensen [18] reported the preliminary SEM image of pollen tetrads for four *Arbutus* species occurring in the Neotropics, and recently Zhang and Anderberg [19] showed the detailed SEM images of *Arctostaphylos alpina* pollen. Rosatti [20] clarified the infraspecific variation of the pollen morphology of *Arctostaphylos uva-ursi* using SEM. But the data from pollen morphology has not been used significantly for the purpose of the classification of these two genera. The only pollen morphological study of *Comarostaphylos*; *C. longifolia*, indicated few differences that would be useful in distinguishing this genus within Ericaceae [4].

Among eight subfamilies of the Ericaceae, we have already reported the pollen morphology of the subfamilies; Enkianthoideae [21], Monotropoideae [22, 23] and Vaccinioideae [24, 25, 26, 27]. This study is part of the study on "Pollen morphology and its systematic significance in the family Ericaceae". We investigated the pollen morphology of the subfamily Arbutoideae with the combination of LM, SEM and TEM observations, so we discuss new pollen morphological data in light of the recent classification of the subfamily [1, 2, 3].

MATERIALS AND METHODS

Pollen morphology of 19 specimens of 17 species representing 3 genera out of 81 species and 4 genera constituting the subfamily Arbutoideae, was examined with LM and SEM (Table 1). Pollen of *Arctostaphylos andersonii* and *Comarostaphylos glaucescens* was investigated especially with TEM. The

number of specimens examined and the coverage of their geographical distribution mainly depend on the availability of specimens in the herbaria consulted. But we tried to consider the pollen morphological data of the previous studies cited in Introduction.

Pollen morphological characters studied and measured with LM are listed in Table 2, and the pollen morphological features including SEM data and the previous studies are summarized in Table 3. Polliniferous materials used in this study were taken from dried specimens available from the herbaria C, GB, S, SAPT and TUS. Abbreviations of the herbarium names except for SAPT are according to the Index Herbariorum [(28)]. SAPT indicates the Herbarium, the Botanic Garden of Hokkaido University, Sapporo, Japan.

Preparation of pollen grains follows Sarwar et al. [(29)]. Pollen sample was acetolysed, and after the dehydration in an ethanol series, acetolysed pollen was embedded in silicone oil for LM observations. But the preparation for LM in some taxa followed the glycelin jelly embedment. The following measurements were carried out with LM within one week after the preparation making. The main dimensions “D”, “P”, “d (E)” and “2f” corresponding to the tetrad diameter, polar length and equatorial diameter of the single pollen grain within the tetrad, and total length of two concurrent colpi were measured, and the ratios of D/d, P/E and 2f/D were calculated. Furthermore width (W) of colpi (ectoapertures) and length and width of endoapertures (ora), thickness of apocolpial exine and septum (inner wall) were also measured. The measurements given in Table 2 are based on at least 10 grains from each specimen. Pollen slides of all collections are deposited in the Hokkaido University Museum, Sapporo, and in part in the Palynological Laboratory of Swedish Museum of Natural History, Stockholm. Descriptive terminology follows Oldfield [(17)], Punt et al. [(30)], and Zhang and Anderberg [(19)]. Common exine wall which binds the adjoining pollen grains and is situated internally within the pollen tetrad, has been termed as partition wall [(31)]; inner wall [(10, 17)]; internal wall [(32)]; interior wall [(33)] or septum [(24, 34, 35, 36)]. But any pollen morphological terms for the common exine wall situated internally within the pollen tetrad have not been adopted in the latest glossary [(30)], and so we use the term ‘septum’ in the present study as in our previous studies [(24, 25, 26, 27, 29)].

RESULTS

General pollen morphology

In LM observations, pollen grains are united in normal and compact tetrahedral tetrad (Figs. 1A, 1K, 3A); grains oblate, viscin threads absent. In range of average values of the specimen, D 38.8 – 54.4 µm, P 19.0 – 28.5 µm, E 31.7 – 44.1 µm, D/d 1.12 – 1.29, P/E 0.59 – 0.67 (Table 2). Three aperturate, apertures arranged according to "Fischer's law"; apertures colpor(oid)ate, colpi distinct, 2f 22.1 – 34.3 µm, W 0.5 – 2.8 µm, 2f/W 7.89 – 64.80, 2f/D 0.44 – 0.68 (Table 2); colpus wider at middle, tip generally acute, sometimes tapering towards ends or bifurcated, colpus margin distinct. Costae usually present and distinct, but indistinct in some species of *Arctostaphylos*, endocracks absent or indistinct, but sometimes distinct in some species of *Arctostaphylos* and *Comarostaphylos* (Table 3). Endoaperture distinct, but indistinct in some species of *Arctostaphylos* (Table 3), 0.7 – 2.9 µm long, 5.8 – 14.9 µm wide (Table 2). Exine tectate, apocolpial exine appearing 1.6 – 3.8 µm thick; septum 0.6 – 1.9 µm thick (Table 2); septum usually with perforations in *Arctostaphylos* and *Comarostaphylos*, at the former genus with two exceptions (micro-pits in *A. viscida* and no distinct perforations in one collection of *A. nummularia*), but constantly without perforations in *Arbutus* (Table 3).

Among the species examined, pollen of *Arctostaphylos crustacea* showed the highest values of D, P, E and 2f/W (54.4 µm, 28.5 µm, 44.1 µm, and 64.80, respectively) and also the lowest values of ectoaperture width, endoaperture length and septum thickness (0.5 µm, 0.7 µm and 0.6 µm, respectively). On the other hand, pollen of *Arctostaphylos viscida* showed the lowest values of D, P, 2f and 2f/W (38.8 µm, 19.0 µm, 22.1 µm and 7.89, respectively) and the widest ectoaperture (2.8 µm). The highest values of D/d, P/E, 2f, 2f/D, length and width of endoaperture, apocolpial exine and septum thickness (1.29, 0.67, 34.3 µm, 0.68, 2.9 µm, 14.9 µm, 3.8 µm and 1.9 µm, respectively), and the lowest values of E, D/d, P/E, 2f/D, length and width of endoaperture (31. 7 µm, 1.12, 0.59, 0.44, 0.7 µm, 5.8 µm, 1.6 µm and 0.6 µm, respectively) were found in different taxa (Table 2). The ratio of ectoaperture length to tetrad diameter (2f/D) in pollen tetrads is relatively large (0.44-0.68), resulting the smaller apocolpial region in most of the species (Table 3).

In SEM observations, pollen surface varied from rugged to somewhat flat, and the exine sculpture was moderate to coarse rugulate at apocolpial region (Figs. 1D–J, 1M–O, 2A–L, 3C–F). Furthermore three

secondary sculpture types on the rugulae were recognized: (1) the rugulae with secondary sculpture of transversely striate (Type RS); (2) the rugulae with minute (diam. < 0.2 µm) granules (Type RG); (3) the rugulae without any distinct secondary sculpture (Type R). But intermediate types (Types R-RG, R-RS, RG-RS) very often occur also. Exine sculpture along the colpi is similar to that appearing at distal pole (apocolpial exine). Sculpture of the mesocolpial exine is usually not so different from that of the apocolpial exine. Colpus membrane is commonly granular, sometimes with large granules or a tendency towards granuloid (Table 3).

TEM study of *Arctostaphylos andersonii* and *Comarostaphylos glaucescens* has shown that the apocolpial exine is composed of ectexine; tectum, columellae and foot layer, and endexine with higher electron density (Figs. 2M–N, 3G–H). Sexine (tectum + columellae) is about 0.7 – 1.0 µm thick and a total exine at distal surface is about 1.5 – 2.0 µm thick. Baculate structure in the columellae is not distinct at distal region (Figs. 2N, 3H). The septal exine is composed of two foot layers of adjacent grains and vestigial thin columellae (Figs. 2O, 3I); septum is about 0.5 – 1.0 µm thick in total. As revealed by LM (Figs. 1K, 3A), characteristic perforations in septum were also confirmed by TEM observations (Figs. 2O, 3I). Intine shows lower electron density than the endexine. At ectoaperture regions (colpi), tectum and columellae are lacking and the endexine becomes thick (Figs. 2M, 3G). At endoaperture regions (ora), exine is lacking and only intine is present (Fig. 3G).

Arbutus

(4 spp. examined / 10 spp.)

Pollen grains are in compact tetrahedral tetrad, rarely somewhat lobed tetrads in *A. canariensis* (Figs. 1A–C, Table 3), sometimes pollen grains broken along the colpi in *A. menziesii*; D 45.0 – 52.5 µm, P 22.6 – 26.8 µm, E 36.4 – 41.4 µm, D/d 1.23 – 1.29, P/E 0.62 – 0.67, grains oblate; 3-colporate, 2f 23.3 – 34.3 µm, W 0.9 – 2.0 µm, 2f/W 11.65 – 36.78, 2f/D 0.44 – 0.68 (Table 2); colpi acute toward ends, costae present and distinct, colpus margin distinct; endocracks absent or indistinct; endoaperture lalongate, 1.6 – 2.9 µm long, 7.5 – 14.9 µm wide; apocolpial exine 1.8 – 2.8 µm thick, tectate, exine sculpture appears verrucate to rugulate; septum 1.1 – 1.9 µm thick.

In SEM, the apocolpial exine sculpture was medium to coarse rugulate. The secondary sculpture type RG and the intermediates between RG and RS or R, were found on rugulae (Table 3). Colpus membrane large granulate, granulate, rarely granuloid (Table 3).

Arctostaphylos

(11 spp. examined / 60 spp.)

Pollen grains are constantly in compact tetrahedral tetrad, many grains somewhat shrink in *A. nevadensis*; D 38.8 – 54.4 µm, P 19.0 – 28.5 µm, E 31.7 – 44.1 µm, D/d 1.17 – 1.23, P/E 0. 59 – 0.64, grains oblate; 3-colpor(oid)ate, 2f 22.1 – 34.2 µm, W 0.5 – 2.8 µm, 2f/W 7.89 – 64.80, 2f/D 0.51 – 0.66 (Table 2), colpi acute toward ends, narrow (2f/W class VII) and elongate in *A. crustacea*, costae present and distinct, but sometimes indistinct, colpus margin distinct; endocracks commonly absent or indistinct, but distinct in some species; endoaperture lalongate, 0.7 – 2.1 µm long, 5.8 – 10.9 µm wide; apocolpial exine 1.6 – 3.8 µm thick, tectate, exine sculpture appears verrucate to rugulate or psilate; septum 0.6 – 1.9 µm thick, perforated, micro-pits present at periphery of thick septum in *A. viscida*, and thick septum without distinct perforations in one collection of *A. nummularia*.

In SEM, the apocolpial exine sculpture was mainly medium rugulate, but rarely coarse rugulate in *A. nevadensis* (Table 3). All three secondary sculpture types (RS, RG, and R) and those intermediates, were found. Colpus membrane generally with large granules to granules, but granules sometimes not discerned (Table 3).

In TEM for *A. andersonii*, the apocolpial exine is composed of ectexine and endexine (Figs. 2M–O). Endexine with high electron density becomes thick at colpus regions. Sexine (tectum + columellae) is about 0.7 µm thick and a total exine is about 1.4 µm thick. The perforated septum is thin and about 0.6 µm thick in total (Fig. 2O). Perforations of the septa are filled with intine. The exine in LM appears thicker than in TEM.

Comarostaphylos

(2 spp. examined / 10 spp.)

Pollen grains are in compact tetrahedral tetrad; D 39.0 – 46.5 µm, P 19.6 – 23.3 µm, E 32.9 – 37.7 µm, D/d 1.12 – 1.19, P/E 0.61 – 0.62, grains oblate; 3-colporate, 2f 22.9 – 30.8 µm, W 1.0 – 2.3 µm, 2f/W 13.30 – 22.90, 2f/D 0.59 – 0.66, colpi acute toward ends, costae present and distinct, colpus margin distinct; endocracks absent or indistinct in *C. discolor* ssp. *discolor*, but distinct in *C. glaucescens*; endoaperture lalongate, 0.8 – 1.8 µm long, 7.2 – 13.4 µm wide; apocolpial exine 1.8 – 2.3 µm thick, tectate, exine sculpture appears verrucate to rugulate; septum 0.8 – 1.0 µm thick, perforated (Fig. 3A).

In SEM, pollen surface is somewhat flat, apocolpial exine sculpture commonly coarse rugulate (Figs. 3C–F; Table 3). Granulate secondary sculpture type (RG) and the intermediates between RG and RS or R, were found (Table 3). Colpus membrane with granules to large granules.

In TEM for *C. glaucescens*, the apocolpial exine is composed of ectexine and endexine (Figs. 3G–H). Sexine (tectum + columellae) is about 1.0 µm thick and total exine is about 2.1 µm thick. Endocracks, irregular grooves occurring in the inner surface of the endexine with high electron density, are distinct (Fig. 3G – H). The septum is about 1.0 µm thick in total, with perforations (Figs. 3G, I). At one perforation, cytoplasm was connected between the adjoining grains (Fig. 3I).

DISCUSSION

Pollen morphological comments on taxonomy

The subfamily Arbutoideae

There is currently no disagreement on the demarcation of the subfamily Arbutoideae [1, 2, 3, 5] and this subfamily has been recently regarded as being composed of the four genera; *Arbutus*, *Arctostaphylos*, *Comarostaphylos* and *Ornithostaphylos* [1, 3]. In the present study we could not get the pollen samples of monotypic *Ornithostaphylos* endemic to S and Baja California.

The subfamily Arbutoideae are stenopalynous, characterized by medium, oblate, and 3-colpor(oid)ate pollen grains united in compact tetrahedral tetrads. Comparatively long colpi result in the smaller apocolpial region. But, there are no pollen morphological features which distinguish the only subfamily Arbutoideae among eight subfamilies within Ericaceae.

Even so, compactness of pollen tetrads in most species and perforated septum in most species of *Arctostaphylos* and all specimens examined of *Comarostaphylos* should be noticed. Imperforated thick septum of *Arbutus* pollen tetrads is distinguished from the perforated thin septum found usually in *Arctostaphylos* and *Comarostaphylos*. *Arbutus* pollen has a tendency of larger tetrad diameter than those of *Arctostaphylos* and *Comarostaphylos* (Table 3). *Arbutus* and many species of *Arctostaphylos* have more lobed pollen tetrads than those of *Comarostaphylos*.

Pollen tetrads of *Comarostaphylos* show constantly more compact and globular shape. The compactness or globularity of pollen tetrads is indicated by low ratios of D/d and P/E (Tables 2 – 3).

Compact pollen tetrads with similar low ratios of D/d and P/E occur sporadically at least within the subfamily Vaccinioideae in the Ericaceae [24, 25, 26]. Septum with distinct perforations has been found commonly in the tribe Andromedeae of the subfamily Vaccinioideae [25]. Considering the phylogenetic relationships clarified by the combined analysis of morphological and molecular data [2], these pollen morphological similarities between the Arbutoideae and a part of the Vaccinioideae may be regarded as the result of the convergent evolution.

Arbutus

Molecular sequence data from the ITS region and part of the 28s region of nuclear rDNA did not support the monophyly of the genus *Arbutus* [5]. Rather, Mediterranean Basin species of *Arbutus* are more closely related to the other North American genera; *Arctostaphylos* and *Comarostaphylos*, than to the western North American species of *Arbutus*. The paraphyletic relationship of *Arbutus* species implies that characters formerly used to diagnose the genus may be plesiomorphic for the Arbutoideae, or the result of convergent evolution [5]. The pollen morphological characters could not show a distinct difference between the two lineages of *Arbutus* species; western North American and the Mediterranean Basin species (Table 3).

Arctostaphylos

In the most recent classification study of Ericaceae [1, 2, 3], the genus *Arctostaphylos* is delimited as including *Arctous* and *Xylococcus*. But *Arctous* and *Xylococcus* have been often segregated [5, 37, 38], and thus the generic limit of *Arctostaphylos* has not been necessarily settled yet. The quantitative palynological

characters of the two species of *Arctous*; *A. alpina* and *A. rubra*, are similar to those of *Arctostaphylos* species (e.g., Moriya [39], Comtois and Larouche [9]), and the exine sculpture of *Arctous alpina*; verrucose-rugulate with large irregularly-shaped warts (as *Arctostaphylos*; Fig. 9G in Zhang and Anderberg [19]), is somewhat similar to that of *Arctostaphylos densiflora* (Fig. 2E) and *A. nevadensis* (Figs. 2F–G). Pollen morphology does not indicate the distinct difference between *Arctostaphylos* s.str. and *Arctous*.

The wide variation of morphological characters in *Arctostaphylos* was well supported by our pollen morphological observations (Tables 2 – 3). But palynological data did not support the infrageneric classification of *Arctostaphylos* [40]. Among the pollen tetrads of *Arctostaphylos* examined, the occurrence of thick septum of *A. viscida* and one specimen *of A. nummularia* is distinct. Such pollen morphological difference is possibly due to the aberrant pollen development or hybridization. An interesting variation in pollen morphology from North American populations of *Arctostaphylos uva-ursi* has been reported by Rosatti [20]. He considered that variation of pollen tetrad size, aperturation, exine sculpturing and grain distinctiveness in the pollen tetrad is of little taxonomic significance within this species.

Hileman et al. [5] confirmed the monophyly of *Arctostaphylos* (including *Arctous*) and *Comarostaphylos* based on their molecular data. The septum with perforations found at both genera might be an indication to the close relationship between *Arctostaphylos* and *Comarostaphylos.* Perforated septum has been already noticed for *Arctostaphylos* species. *Arctostaphylos alpina* pollen has been reported as densely perforate and *A. uva-ursi* pollen as with few perforations by Faegri and Iversen [33]. Furthermore the pollen of *Arctostaphylos alpina and A. rubra* has been described as with numerous perforations and that of *A. uva-ursi* and *A. columbiana* as with less numerous perforations by Warner and Chinnappa [10].

Comarostaphylos

The genus *Comarostaphylos* is a homogenous and natural group [4]. Pollen morphology of *Comarostaphylos* is characterized by the compact pollen tetrads with thin perforated septum and coarse rugulate exine sculpture (Table 3). Although the number of specimens examined for *Comarostaphylos* was limited in the present study, the same thin perforated septum is found in most species of *Arctostaphylos* and the same coarse rugulate sculpture is found in some species of *Arbutus*.

Septum with perforations

Perforated septum is also found in the pollen tetrads of other families (e.g., Winteraceae [34], Periplocaceae [41]). That is found also in the polyads. These perforations which contain common cytoplasm may form to complete intercommunications between the grains to act as single harmomegathic unit [17]; but these perforations may be results from the cytoplasmic channels in the early developmental stage of tetrads [42, 43]. Guinet [44] considered them to ultimately function in tetrad separation. Although we are not sure about the reason of this type of special feature, it may have a taxonomic importance in the Arbutoideae as well as Ericaceae and may be an apomorphic pollen character state for this subfamily as described for Sarcolaneaceae [45].

Exine sculpturing

Although the variation in exine sculpture from verrucate through rugulate to psilate has been observed in the subfamily Enkianthoideae [21] and Monotropoideae [22, 46, 47, 48], apomorphic state of exine sculpture is not clear for the subfamily Arbutoideae. Like other genera of the family Ericaceae [21, 22, 27, 47], a more or less continuous and serial variation of the apocolpial exine sculpture was found in the three genera. (Table 3; Figs. 1 – 3). Even so coarse rugulate sculpture at distal area occured in some species of *Arbutus* and all specimens examined of *Comarostaphylos*, and medium rugulate sculpture was mostly common in the *Arctostaphylos* species. Thus, the size of rugulae might also be used as character of some taxonomic importance within this subfamily. Some specimens of *Arctostaphylos* is also characterized by colpus membrane without distinct granules.

The evolutionary trend in the secondary exine sculpture (between type RG and RS) is not clear in the Arbutoideae. The secondary sculpture types are not valuable to distinguish the genera in this subfamily because the intermediate secondary sculptures were found in most species. But the exine sculpture with secondary sculpture may be more specialized morphological character state situated at the end of a serial variation of exine sculpturing in the subfamily Arbutoideae as well as in the subfamily Vaccinioideae.

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和文要旨

ツツジ科アルブトゥス亜科の花粉形態の大要とその体系学的意義

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広義のツツジ科全体の花粉形態を観察し, その体系学的意義をあきらかにする目的で, これまで科に含まれる８亜科のうちドウダンツツジ亜科, シャクジョウソウ亜科, スノキ亜科の３亜科について報告してきた,.本研究ではアルブトゥス亜科の花粉形態について報告した,.本亜科を構成する 4 属 81 種のうち 3 属 17 種の花粉サンプルを得て, その花粉形態を光学顕微鏡, 走査型電子顕微鏡, 透過型電子顕微鏡で観察し, 先行研究の結果と併せて花粉形態の体系学的意義について検討した,. 本亜科の花粉形態は均一で, ３溝孔（類孔）の花粉粒４個が合着した緊密で球状の花粉四集粒を形成する,.ツツジ科の中でアルブトゥス亜科のみを特徴づけるような花粉形態形質やその組み合わせはなかった,.ウラシマツツジ属とコマロスタフィロス属の花粉サイズは小さく四集粒内隔壁は薄く穿孔があるのが普通であるが, アルブトゥス属の花粉サイズは通常大きく, 四集粒内隔壁はより厚く明確な穿孔がなかった,.溝粒極域の花粉表面模様において, ウラシマツツジ属では通常は中程度の細かさのしわ模様だが, コマロスタフィロス属とアルブトゥス属ではしばしばより粗いしわ模様となる点でやや異なっていた,.

Legends

Fig. 1. LM and SEM micrographs of *Arbutus* (A-J) and *Arctostaphylos* (K-O) pollen. (A) *Arbutus menziesii*, compact pollen tetrad ; (B) *A. canariensis*, somewhat lobed pollen tetrad showing short colpi; (C) *A. menziesii*, compact pollen tetrad showing long colpi; (D) *A. andrachne*, apocolpial exine (type R-RG); (E) *A. canariensis*, apocolpial exine (type RG); (F) *A. canariensis*, mesocolial exine (type R-RG); (G) *A. menziesii*, apocolpial exine (type RG); (H) *A. menziesii*, mesocolpial exine (type R-RG); (I) *A. xalapensis*, apocolpial exine (type R-RG); (J) *A. xalapensis*, mescolpial exine (type R-RG). (K) *Arctostaphylos glauca*, compact pollen tetrad showing thin septum with perforations (arrows); (L) *A. viscida*, compact pollen tetrad showing long colpi with granulate membrane. (M) *A. andersonii* , apocolpial exine (type RS); (N) *A. auriculata*, apocolpial exine sculpture (type RG-RS); (O) A. *crustacea*, apocolpial exine sculpture (type R-RG-RS).

Fig. 2. SEM (A-L) and TEM (M-O) micrographs of *Arctostaphylos* pollen. (A) *Arctostaphylos crustacea*, mesocolpial exine (type RG-RS); (B) *A. glauca*, apocolpial exine (type R); (C) *A. bakeri*, apocolpial exine (type RG-RS); (D) *A. bakeri*, mesocolpial exine (type RG-RS); (E) *A. densiflora*, apocolpial exine (type R-RG); (F) *A. nevadensis*, apocopial exine (type R-RG-RS); (G) *A. nevadensis*, meocolpial exine (type R); (H) *A. viscida*, apocolpial exine (type R-RG-RS); (I) *A. viscida*, mesocolpial exine (type R); (J) *A. nummularia* (Rose s.n.), apocolpial exine (type RG); (K) *A. nummularia* (Rose 61009), apocolpial exine (type R-RG-RS); (L) *A. nummularia* (Rose 61009), mesocolpial exine (type RS). (M) *A. andersonii*, whole tetrad showing relatively thicker endexine at aperture regions; (N) *A. andersonii*, apocolpial exine showing tectum, columellae, foot layer and endexine; (O) *A. andersonii*, septum composed of two thin endexines and foot layers of the adjacent grains and thin vestigial columellae. Perforation is filled with intine between two adjacent grains.

Fig. 3. A-F. LM (A), SEM (B-F) and TEM (G-I) micrographs of *Comarostaphylos* pollen. (A) *Comarostaphylos glaucescens*; compact pollen tetrad with thin septum with perforations (arrows); (B) *C. discolor* ssp. *discolor* (Pringle 6815), compact pollen tetrad showing long colpi; (C) *C. discolor* ssp. *discolor* (Pringle 6815), apocolpial exine (type RG-RS), (D) *C. discolor* ssp. *discolor* (Pringle 6815), mesocolpial exine (type RG); (E) *C. glaucescens*, apocolpial exine (type RG); (F) *C.*

glaucescens, mesocolpial exine (type R-RG-RS).. (G) *C. glaucescens*, whole tetrad showing relatively thicker endexine at aperture regions; (H) *C. glaucescens*, apocolpial exine showing tectum, columellae, foot layer and endexine with endocracks; (I) *C. glaucescens*, perforated septum showing an cytoplasmic connection between two adjacent grains.

Table 1. Specimens examined in the subfamily Arbutoideae

Taxon	Collector & No. (Herb. acronym)	Voucher information (LM & SEM No.)
Arbutus andrachne L.	I. Segelberg s.n. (S)	GREECE: Rhodes, Petalondes, 06.03.1959. (LM no. 21.046, SEM no. 213)
A. canariensis Veill.	E. & R. Wahlstom s.n. (C)	CANARY ISLANDS: Tenerif, in vicin peg, cult., no day.01.1933. (LM no. 21.184, SEM no. 214)
A. menziesii Pursh	J.M. Grant s.n. (S)	USA: Washington, Marysville, sea shore, no day.04.1927. (LM no. 21.047, SEM no. 215)
A. xalapensis Kunth*	P.D. Sorensen, T. Huton & J. Irager 7310E (C)	USA: Texas, Jeff Davis Co., Davis Mount Resort, 7500ft alt., 18.04.1973. (LM sno. 21.155, SEM no. 216)
Arctostaphylos andersonii Gray	L.S. Rose 47029 (GB)	USA: California, Santa Cruz Co., Brookdate, 11.03.1947. (LM no. 21.222, SEM no. 219)
A. auriculata Eastwood	L.S. Rose 49004 (GB)	USA: California, Contra Costa Co., Mt. Diablo, above Rock city, 1700ft alt., 06.03.1949. (LM no. 21.221, SEM no. 220)
A. bakeri Eastw.	L.S. Rose 55031 (GB)	USA: California, S Sonoma Co., 2 mi. NE of Occidental, serpentine hills, 700ft alt., 21.03.1955. (LM no. 21.220, SEM no. 221)
A. crustacea Eastw.	L.S. Rose 42007 (C)	USA: California, San Mateo Co., Kings Mt. Rocky brushy hills, 30.03.1942. (LM no. 21.154, SEM no. 222)
A. densiflora M.S.Baker	L.S. Rose 55005 (GB)	USA: California, Sonoma Co., Vine hill, 9 mi. W of Santa Rosa, 28.02.1955. (LM no. 21.219, SEM no. 223)
A. glauca Lindl.	C. Skottsberg s.n. (GB)	USA: California, Contra Costa Co., Mt. Diablo, 2000ft alt., 09.01.1949. (LM no. 21.218, SEM no. 224)
A. nevadensis Gray	O.D. Allen 110 (C)	USA: Washington, Cascade Mts., upper valley of the Nesqually, 27. 04.1895. (LM no. 21.153, SEM no. 225)
A. nummularia Gray	L.S. Rose s.n. (S)	USA: California, Santa Cruz Co., N entrance to the Bis Basin hill slopes, 1900ft alt., 05.05.1937. (LM no. 21.001, SEM no. 230)
	L.S. Rose 61009 (GB)	USA: California, Marin Co., S slope of Mt. Tamalpais, 1000ft alt., 17.02.1961. (LM no. 21.217, SEM no. 226)
A. patula Greene	R.F. Thorne & C.W. Tilforth 39693 (SAPT)	USA: California, Shaver Lake campground, 5450ft alt., 25.05.1971. (LM no. 21.086, SEM no. 227)
A. pungens Kunth	J. Gray s.n. (TUS 7321)	USA: Arizona, Mt. Lemmon, 06.03.1960. (SEM no. 227a)
A. viscida Parry	L.S. Rose 60006 (S)	USA: California, Toulumne Co. Confidence, dry slopes, 4200ft alt., 01.05.1962. (LM no. 21.010, SEM no. 229)
Comarostaphylos discolor (Hook.) Diggs ssp. *discolor*	C.G. Pringle 6815 (C)	MEXICO: State of Mexico, Sierra de las Cruces, 1000ft alt., 20.04.1898. (LM no. 21.150, SEM no. 217)
	J.A. Steyermark 5059b (S)	GUATEMALA: Dept. Huehuenango, Cerro Pixpix, above San Ildefonso Ixtahuacan, 1600-2800m alt., 15.08.1945. (LM no. 21.114, SEM no. 228)
C. glaucescens (Kunth) Zucc.	C.G. Pringle 13762 (C)	MEXICO: State of Oaxaca, Hills above Oaxaca city, 70000ft alt., 22.05.1906. LM no. 21.149, SEM no. 218)

* *A. texana* Buckley was treated as *A. xalapensis* Kunth according to the opinion of Sørensen [18].

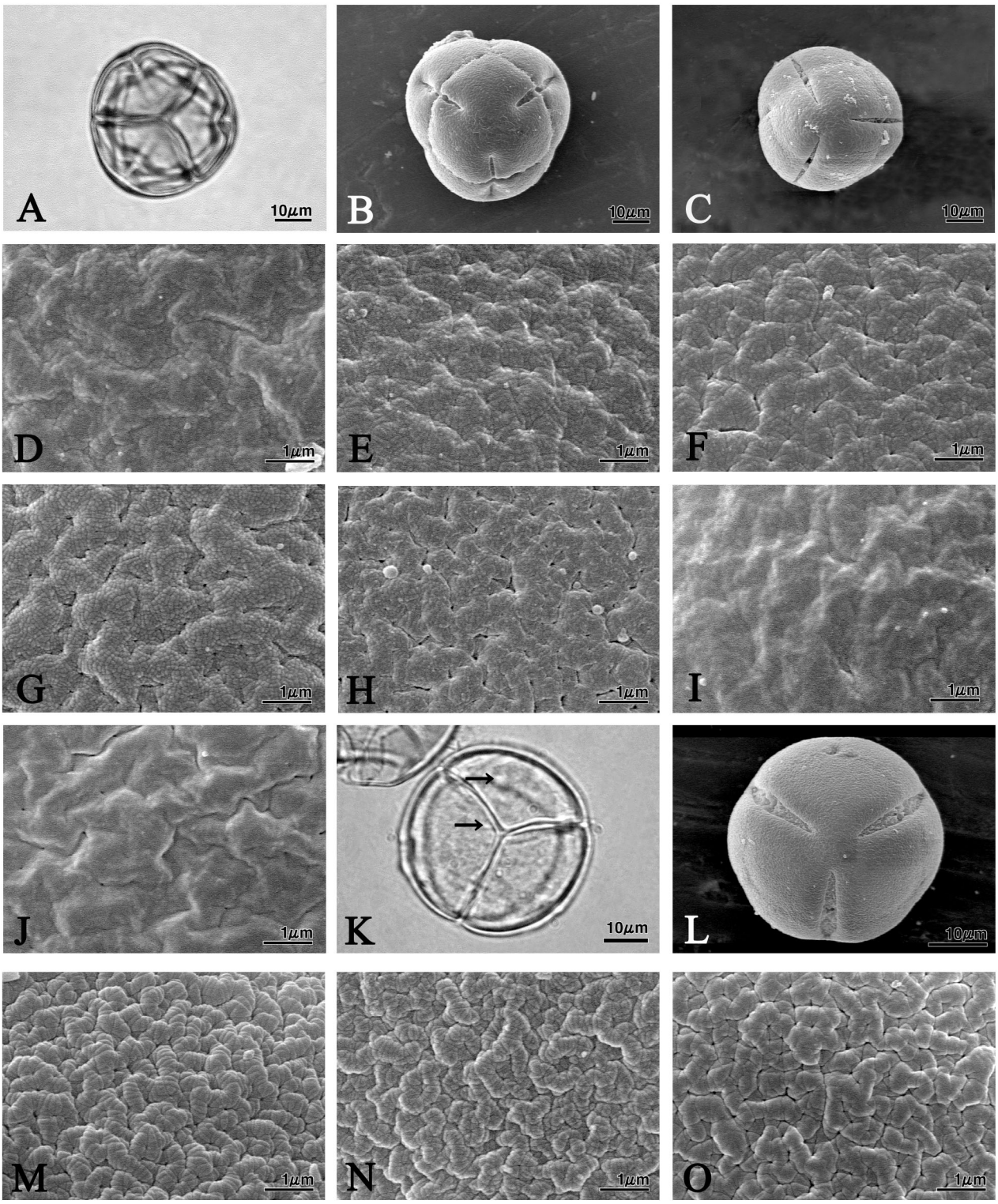
Table 2. Variation in pollen characters of subfamily Arbutoideae showing mean value in µm and standard deviation. minimum–maximum values in µm in parenthesis, D Tetrad diameter, P Polar length, d(E) Equatorial diameter, Apo. Apocolpial.

Taxon	D	P	d (E)	D/d	P/E	Ectoaperture			2f/D	Endoaperture		Apo. exine thickness	Septum thickness
						Length (2f)	Width (W)	2f/W		Length	Width		
Arbutus andrachne	51.1±2.4	26.8±2.1	41.4±1.9	1.23	0.65	33.1±2.3	0.9±0.3	36.78	0.65	2.9±0.8	7.5±1.8	2.8±0.2	1.9±0.2
	(48.7-56.1)	(23.1-29.7)	(38.0-44.6)			(31.4-38.0)	(0.5-1.3)			(2.0-4.1)	(5.0-9.9)	(2.5-3.0)	(1.7-2.1)
A. canariensis	52.5±1.6	26.1±1.2	40.7±1.7	1.29	0.64	23.3±1.7	2.0±0.3	11.65	0.44	1.6±0.4	14.7±2.3	2.2±0.5	1.1±0.2
	(50.2-56.0)	(24.1-27.7)	(38.8-44.6)			(19.8-24.8)	(1.3-2.5)			(0.7-2.0)	(11.6-18.2)	(1.7-3.1)	(0.7-1.3)
A. menziesii	45.0±1.6	22.6±1.5	36.4±1.7	1.24	0.62	28.5±1.8	1.7±0.4	16.76	0.67	2.0±0.7	11.6±1.9	2.7±0.4	1.5±0.3
	(42.1-46.2)	(20.1-24.4)	(33.8-39.3)			(26.4-31.4)	(0.7-2.4)			(0.5-2.5)	(8.3-14.9)	(2.1-3.3)	(1.2-2.0)
A. xalapensis	50.8±2.3	26.3±2	39.1±2	1.29	0.67	34.3±4.7	1.8±1.4	19.06	0.68	2.5±0.7	14.9±5.2	1.8±0.2	1.1±0.3
	(47.9-54.1)	(25.1-29.7)	(36.3-42.9)			(28.1-42.3)	(0.3-3.1)			(1.3-3.3)	(8.3-24.8)	(1.7-2.3)	(0.5-1.5)
Arctostaphylos andersonii	43.3±1.3	22.3±1.5	36.2±0. 9	1.19	0.61	25.7±1.5	1.3±0.7	19.77	0.59	1.4±0.7	7.4±2.1	2.3±0.4	0.9±0.4
	(41.6-44.9)	(20.3-24.6)	(35.5-38.0)			(23.1-28.1)	(0.5-2.3)			(0.8-2.6)	(4.1-9.9)	(2.0-3.0)	(0.5-1.3)
A. auriculata	40.5±0.9	20.4±1.8	34.5±1.5	1.17	0.59	25.6±2.1	1.9±0.9	13.47	0.63	1.4±0.5	7.5±2.0	1.9±0.1	0.9±0.3
	(39.6-41.7)	(18.6-22.8)	(33.0-36.6)			(21.5-28.9)	(0.5-3.0)			(0.5-2.0)	(5.0-11.6)	(1.7-2.0)	(0.5-1.3)
A. bakeri	42.9±1.4	22.0±1.1	35.6±1.6	1.20	0.61	28.3±1.0	0.7±0.2	40.43	0.66	1.9±1.0	5.8±1.8	2.6±0.5	0.8±0.4
	(41.1-45.9)	(19.8-24.0)	(33.5-38.3)			(26.4-29.7)	(0.5-1.2)			(0.7-3.3)	(3.3-8.3)	(1.7-3.1)	(0.3-1.3)
A. crustacea	54.4±4.0	28.5±3.1	44.1±3.0	1.23	0.64	34.2±1.6	0.5±0.2	64.80	0.63	0.7±0.4	7.2±2.3	2.5±0.5	0.6±0.3
	(47.9-59.4)	(23.4-32.7)	(39.6-47.9)			(31.3-36.3)	(0.3-0.8)			(0.3-1.2)	(5.0-9.9)	(1.8-3.0)	(0.3-1.3)
A. densiflora	42.3±1.3	21.3±0.6	35.1±1.7	1.20	0.61	24.2±1.9	2.0±0.4	12.10	0.57	1.7±0.6	8.3±2.4	1.7±0.2	0.9±0.3
	(39.6-44.1)	(19.8-21.8)	(33.0-38.0)			(19.8-26.4)	(1.7-3.0)			(0.7-2.6)	(4.1-13.2)	(1.5-2.0)	(0.7-1.2)
A. glauca	47.4±2.9	24.8±1.5	38.9±1.3	1.21	0.64	27.5±1.7	1.7±0.5	16.18	0.58	1.7±0.7	9.2±1.2	2.5±0.4	0.7±0.2
	(42.9-53.6)	(22.8-26.1)	(36.3-40.4)			(25.6-29.7)	(1.2-3.0)			(1.0-3.3)	(8.3-11.6)	(2.1-3.3)	(0.3-1.0)
A. nevadensis	49.1±2.7	25.3±1.1	40.4±2.2	1.22	0.63	25.1±2.7	1.8±0.8	13.94	0.51	2.1±0.9	10.1±1.6	3.8±0.4	1.0±0.4
	(44.6-52.8)	(23.6-26.4)	(36.3-43.7)			(21.5-28.1)	(1.2-3.3)			(0.8-3.3)	(8.3-13.2)	(3.3-4.6)	(0.5-1.7)
A. nummularia Rose s.n.	45.2±1.3	22.0±1.2	37.3±1.9	1.21	0.59	24.2±1.3	2.4±0.8	10.08	0.54	1.3±0.6	10.9±3.8	2.1±0.2	1.9±0.4
	(43.4-47.9)	(19.8-24.4)	(34.7-40.9)			(21.5-26.4)	(1.2-3.6)			(0.5-2.0)	(6.6-16.5)	(2.0-2.5)	(1.7-2.6)
Rose 61009	43.0±1.2	21.7±0.6	35.3±1.6	1.22	0.61	24.7±2.7	2.1±0.9	11.76	0.57	1.5±0.8	8.5±2.2	2.2±0.2	1.0±0.3
	(41.3-44.6)	(21.1-22.8)	(33.0-38.8)			(19.8-27.2)	(0.7-3.3)			(0.5-3.3)	(6.6-13.2)	(2.0-2.6)	(0.5-1.3)
A. patula	38.8±1.4	19.7±0.6	33.1±1.5	1.17	0.59	22.9±1.4	1.4±0.7	16.36	0.59	1.5±0.9	8.4±2.9	1.6±0.2	0.9±0.4
	(37.1-41.3)	(18.8-20.8)	(30.2-36.3)			(20.6-24.8)	(0.7-2.8)			(0.3-3.3)	(5.0-13.2)	(1.5-2.0)	(0.5-1.5)
A. viscida	38.8±1.1	19.0±1.6	31.7±1.2	1.22	0.60	22.1±0.8	2.8±0.4	7.89	0.57	0.9±0.4	7.2±0.7	1.9±0.4	1.6±0.4
	(37.5-39.6)	(17.3-22.8)	(29.7-33.8)			(20.6-23.1)	(2.1-3.3)			(0.7-1.7)	(6.6-8.3)	(1.3-2.8)	(1.3-2.0)
Comarostaphylos discolor subsp. *discolor* Pringle 6815	41.0±2.0	21.4±1.3	34.4±2.0	1.19	0.62	26.6±1.8	2.0±0.6	13.30	0.64	1.8±0.8	7.9±1.8	1.8±0.2	0.8±0.3
	(36.6-44.6)	(19.5-23.1)	(31.4-36.3)			(24.8-29.7)	(0.8-3.3)			(0.8-3.3)	(5.8-9.9)	(1.3-2.0)	(0.3-1.3)
Steyermark 5059b	39.0±1.2	19.6±0.6	32.9±1.4	1.19	0.62	22.9±1.8	1.0±0.4	22.90	0.59	0.8±0.3	7.2±1.8	2.3±0.3	1.0±0.3
	(37.3-41.3)	(18.2-20.1)	(30.5-34.7)			(19.8-24.8)	(0.5-1.7)			(0.5-1.3)	(5.0-9.9)	(2.0-3.0)	(0.5-1.5)
C. glaucescens	46.5±2.2	23.3±1.8	37.7±2.3	1.12	0.61	30.8±2.9	2.3±0.9	13.39	0.66	1.7±0.7	13.4±2.7	2.1±0.4	0.9±0.3
	(44.6-50.5)	(20.1-26.1)	(33.8-41.3)			(28.1-36.3)	(0.7-3.6)			(0.7-3.0)	(9.9-16.5)	(1.7-2.8)	(0.3-1.3)

Table 3. Summary of pollen morphological characters of subfamily Arbutoideae including the previous studies. D Tetrad diameter, P Polar length, d(E) Equatorial diameter, 2f Ectoaperture length, W Ectoaperture width, Apo. Apocolpial, Orn. Ornamentation, Memb. Membrane.

Taxon	Config-uration[1)]	D[2)]	P[3)]	D/d[4)]	P/E[5)]	2f[6)]	2f/W[7)]	2f/D[8)]	Apo. Exine thickness[9)]	Septum thickness[10)]	Orn.[11)]	Figs.	Colpus Memb. [12)]	Remarks and References[13)]
Arbutus andrachne	CT	IV	IV	II	I	III	IV	V	IV	III	R-RG	1D	G/Gr	2
A. canariensis	T-CT	IV	IV	II	I	II	II	III	III	II	RG	1B, 1E-F	Gr/LG	
A. menziesii	CT	III	III	II	I	II	II	V	IV	II	RG	1A, 1C, 1G-H	G	1
A. unedo	CT	IV-V	—	II-III	—	II	—	IV	—	—	RG-RS	—	—	D & F, F & D, O
A. xalapensis	CT	IV	IV	II	II	III	II	V	II	II	R-RG	1I-J	G	
Arctostaphylos alpina	CT	III	—	II	—	II	—	IV	—	P	—	—	—	O, W & C
A. andersonii	CT	III	III	I	I	II	II	IV	III	I P	RS	1M. 2M-O	G	4
A. auriculata	CT	III	III	I	I	II	II	V	II	I P	RG-RS	1N	n.d.	3
A. bakeri	CT	III	III	II	I	II	V	V	IV	I P	RG-RS	2C-D	G	4, 5
A. columbiana	CT	III	—	—	—	II	—	IV	—	P (few)	—	—	—	W & C
A. crustacea	CT	IV	IV	II	I	III	VII	V	III	I P	R-RG-RS	1O, 2A	G	5
A. densiflora	CT	III	III	II	I	II	II	IV	II	I P	R-RG	2E	LG	
A. glauca	CT	III	III	II	I	II	II	IV	III	I P	R	1K, 2B	G	3, 4
A. nevadensis	CT	III	IV	II	I	II	II	IV	V	I P	R-RG-RS	2F-G	G	3, 6
A .nummularia Rose s.n.	CT	III	III	II	I	II	II	IV	III	III	RG	2J	n.d.	
Rose 61009	CT	III	III	II	I	II	II	IV	III	I P	R-RG-RS	2K-L	G	3
A. patula	CT	II	II	I	I	II	II	IV	II	I P	—	—	n.d.	3
A. rubra	CT	III	—	—	—	II	—	IV	—	P	—	—	—	W & C
A. uva-ursi	T-CT	II-IV	II-III	II-IV	I-III	II	—	V	—	P (few)	—	—	—	D & F, F & D, O, R
A. viscida	CT	II	II	II	I	II	I	IV	II	III (P)	R-RG-RS	1L, 2H-I	G	
Comarostaphylos discolor														
ssp. *discolor* Pringle 6815	CT	III	III	I	I	II	II	V	II	I P	RG-RS	3B-D	LG	
Steyermark 5059b	CT	II	II	I	I	II	III	IV	III	I P	—	—	G	
C. glaucescens	CT	III	III	I	I	III	II	V	III	I P	RG	3A, 3E-I	LG	1, 4
C. longifolia	CT	II	II	II	I	—	—	—	—	—	—	—	—	D

1) T: Tetrahedral tetrad, CT: Compact tetrahedral tetrad
2) II: 30.1 – 40.0, III: 40.1 – 50.0, IV: 50.1 – 60.0 µm
3) II: 15.1– 20.0, III: 20.1 – 25.0, IV: 25.1 – 30.0 µm
4) I: – 1.19, II: 1.20 – 1.29
5) I: – 0.65, II: 0.66 – 0.70
6) II: 20.1 – 30.0, III: 30.1 – 40.0 µm
7) I: – 10.0, II: 10.1 – 20.0, III: 20.1 – 30.0, IV: 30.1 – 40.0, V: 40.1 – 50.0, VI: 50.1 – 60.0, VII: 60.1 –
8) III: 0.41 – 0.50, IV: 0.51 – 0.60, V: 0.61 – 0.70
9) II: 1.6 – 2.0, III: 2.1 – 2.5, IV: 2.6 – 3.0, V: 3.1 – µm
10) I: 0.5 – 1.0, II: 1.1 – 1.5, III: 1.6 – 2.0 µm, P: Perforated
11) Apocolpial exine ornamentation types by SEM corresponding to Figs. Coarse rugulate underlined. For abbreviations of sculpture, see 'General pollen morphology' of RESULTS.
12) G: Granulate, LG: Large granulate, Gr: Granuloid, n.d.: Not discerned
13) 1: Sometimes broken along colpi, 2: Costae thick, 3: Costae indistinct, 4: Endocracks distinct, 5: Endoaperture indistinct, 6: Many grains somewhat shrink
D: Diggs (1995)(4), D & F: Diez and Fernandez (1989)(16), F & D: Foss and Doyle (1988)(13), O: Oldfield (1959)(17), R: Rosatti (1988)(20)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C
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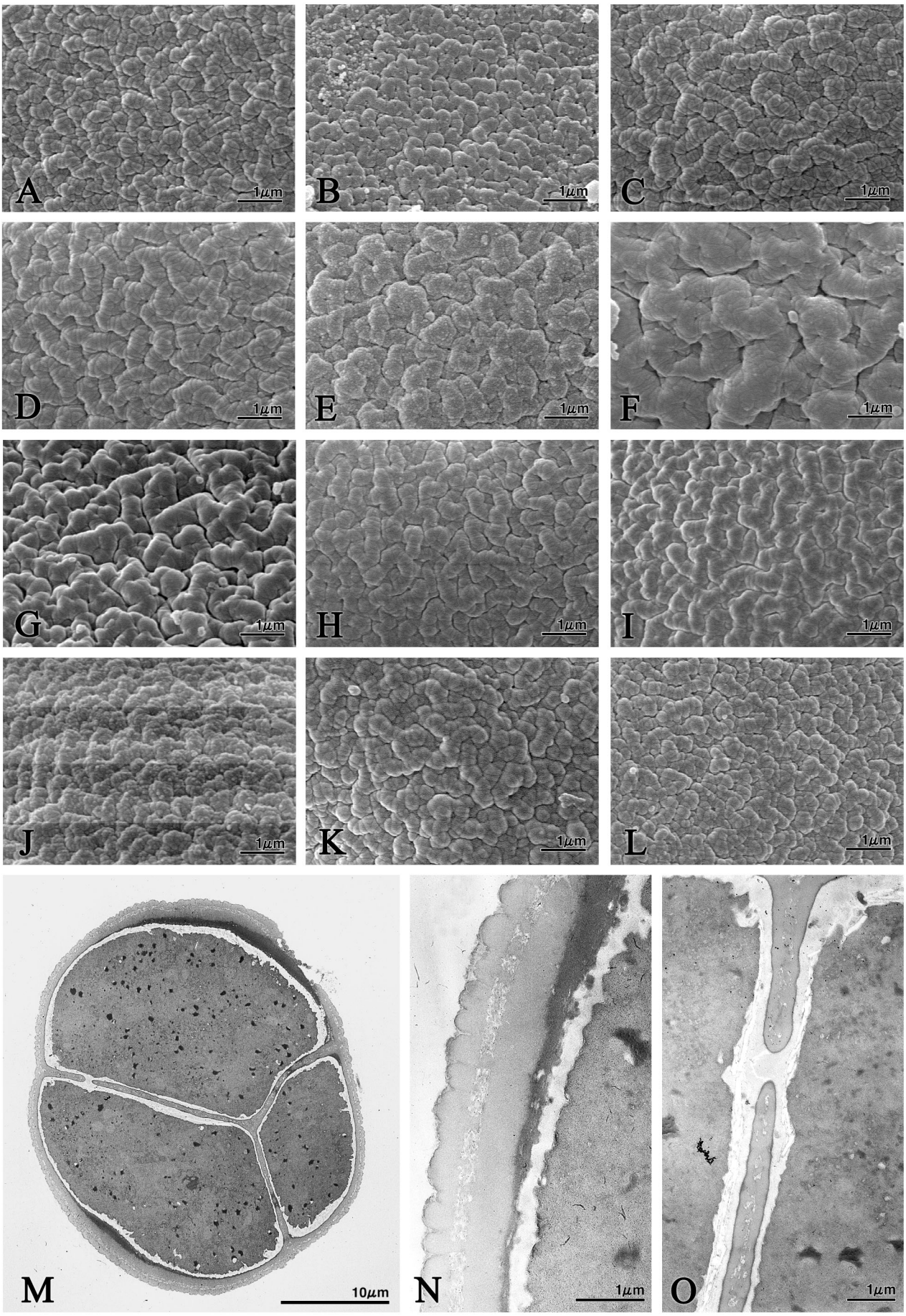
Fig. 1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K
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1μm

Fig. 2

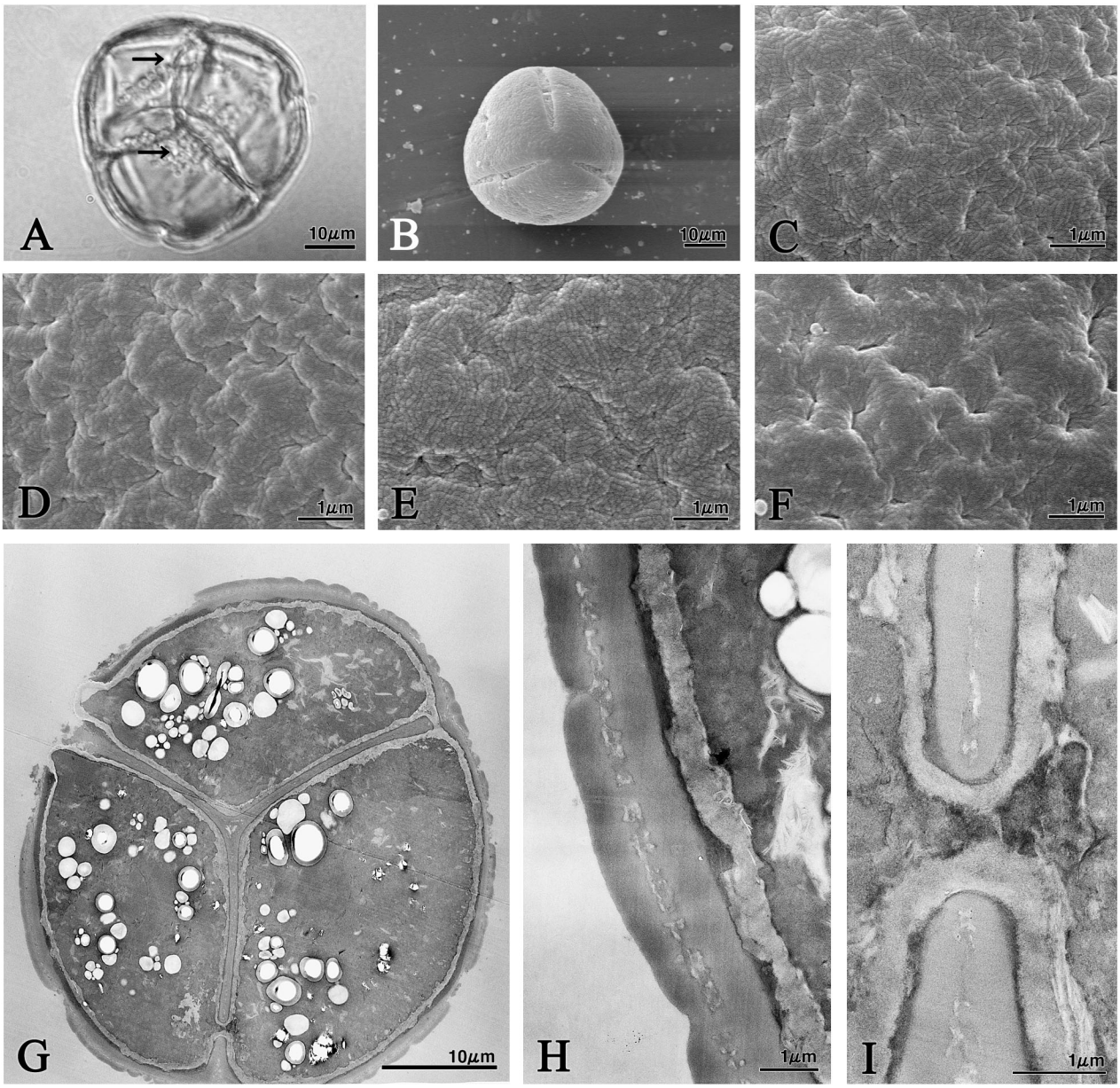

Fig. 3.