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Surface structures of peridial cells of *Gymnosporangium* and *Roestelia* (Uredinales)*

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The surface structures of peridial cell walls (outer, side, and inner walls) of 40 *Gymnosporangium* and 7 *Roestelia* species were examined by scanning electron microscopy. These surface structures were classified into 10 types based on shape, size, and density of the processes. Surface structural types of each wall were stable within a species. Therefore, it is suggested that surface structure types of peridial cell walls could be used as important diagnostic characteristics of *Gymnosporangium* and *Roestelia* species.

Key Words-----Gymnosporangium; peridial cells; Roestelia; rust fungi; Uredinales.

Gymnosporangium and *Roestelia* species are mainly distributed in the northern hemisphere, and 57 and 14 species have been reported, respectively (Kern, 1973; Lee and Kakishima, 1999). Many species have known to produce aecia on species of Rosaceae (Kern, 1973).

Aecia of Gymnosporangium species are characteristically "roestelioid" in most species, but "aecidioid" in a few species (Parmelee, 1965, 1971; Kern, 1973; Littlefield and Heath, 1979). The roestelioid aecium (Roestelia) has a hornlike (or beak-like) structure, which is often 1-3 mm or more long and surrounded by a tubular, onecell-thick peridium (Littlefield and Heath, 1979). Kern (1973) divided roestelioid aecia into five types (roestelioid, fimbriate to base; cornute, horned; balanoid, acorn-shaped; tubular, rupturing at apex; tubular, becoming lacerate) according to shape and rupturing manners. These types have been used as an important taxonomic character (Kern, 1911, 1973; Parmelee, 1965, 1971; Hiratsuka et al., 1992). Peridia of roestelioid aecia have a mechanism to regulate the expulsion of aeciospores in response to changes in ambient humidity (Leppik, 1956, 1977; Pady et al., 1968, 1969; Littlefield and Heath, 1979). However, aeciospores formed in aecidioid aecia are in general forcibly discharged under a highly humid environment (Savile, 1973; Littlefield and Heath, 1979).

Kern (1910) and Leppik (1956) illustrated the articulation of peridial cells by which they are joined together to make up the peridium. Kern (1910) divided sculptures of peridial cell walls (outer, side, and inner walls) into five types (rugose, verruculose, verrucose, spinulose, and smooth) based on the nature of the roughness. Later, in his taxonomic revision of *Gymnosporangium*, Kern (1973) described five types of surface sculpturing of peridial cells: rugose, modified rugose, verrucose, spinulose, and smooth. Although Kern (1910) had declared that surface structures of peridial cells of *Gymnosporangium* species had such complexity that "no single word or even a single phrase will suffice for a description of the markings," surface ornamentation of peridial cells has been treated as an important taxonomic character (Kern, 1911, 1973; Hiratsuka, 1936a-d, 1937; Prince, 1946; Parmelee, 1965, 1971; Ziller, 1974; Peterson, 1982; Wang and Lin, 1985; Hiratsuka et al., 1992).

On the other hand, as reported by Kern (1910) and Parmelee (1965, 1971), peridial cells of many species tend to lie only on their sides or only on their faces when mounted in water or lactophenol solution, as a result of the great disparity between the breadth and thickness of peridial cells. This characteristic mounted-position of peridial cells leads to difficulty in observing and describing structures of outer, side, and inner walls of peridial cells by light microscopy (LM). Though surface structures of peridial cells of several species have been clearly described, those of many species have been described without distinguishing the three walls (Hiratsuka, 1936a-d, 1937; Parmelee, 1965, 1971; Kern, 1973; Ziller, 1974). These descriptions cause difficulty both in understanding of entire surface structure of peridial cells and in diagnostic description of Gymnosporangium and Roestelia species.

Based on shape and size of processes on aeciospores observed by scanning electron microscopy (SEM), Lee and Kakishima (1999) recognized 12 types of surface structures in 40 *Gymnosporangium* species and 7 *Roestelia* species, and these types were used as an important diagnostic character. They also suggested that SEM observation is very useful to distinguish surface structures of aeciospores.

Although the surface structures of peridial cells have

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been treated as an important taxonomic character in *Gymnosporangium* and *Roestelia* species, there are only a few reports on their fine surface structures observed by SEM (Kozar and Netolitzky, 1975; Littlefield and Heath, 1979), Therefore, we observed many specimens of *Gymnosporangium* and *Roestelia* species and clarified the surface structures of their peridial cell walls. These are reported here and their diagnostic significance is discussed.

Materials and Methods

Dry herbarium specimens were used for SEM observation. Most specimens examined were loaned by the following 15 herbaria: the Herbarium, Botanischer Garten und Botanisches Museum Berlin-Dahlem, Germany (B); the National Fungus Collections, United State Department of Agriculture, USA (BPI); the Herbarium, Northern Forestry Centre, Canada (CFB); the National Mycological Herbarium, Biosystematics Research Center, Canada (DAOM); the Mycological Herbarium, the Institute of Microbiology, Academia Sinica, China (HMAS); Rijksherbarium/Hortus Botanicus, Leiden, the Netherlands (L); the University of Michigan Herbarium, USA (MICH); the Herbarium, Botanical Garden and Museum, University of Oslo, Norway (O); the Arthur Herbarium, Purdue University, USA (PUR); the Herbarium, Department of Botany, University of Reading, United Kingdom (RNG); the Herbarium, Swedish Museum of Natural History, Sweden (S); the Herbarium, University of Vienna, Institute of Botany, Austria (WU); the Herbarium, Botanical Institute, Faculty of Agriculture, Hokkaido University, Japan (SAPA); the Herbarium, Forest and Forest Products Research Institute, Japan (TFM:FPH); and the Mycological Herbarium of the Institute of Agriculture and Forestry, University of Tsukuba, Japan (TSH).

A total of 291 specimens in 40 species of *Gymnosporangium* and 7 species of *Roestelia* were observed in relation to host plants and localities (Tables 1, 2). Specimens were re-identified according to Kern (1973), and names of host plants were according to Phipps et al. (1990).

For SEM observation, peridial cells obtained from the specimens were laid down on double-sided adhesive tape on specimen holders, then coated with platinum-palladium using a Hitachi E-1030 lon sputter. Outer, side, and inner walls of the peridial cells were examined by SEM using a Hitachi S-4200 instrument operating at 15 kV.

Results

SEM images of 291 specimens of peridial cells of 40 *Gymnosporangium* and 7 *Roestelia* species exhibited various types of surface structures on their outer, inner, and side walls. Based on the shape, size, and density of the processes, surface structures of peridial cell walls of the 47 species were classified into 10 types. Figure 1 shows a schematic view of these types. Surface structure types of peridial cell walls (outer, side and inner walls) of *Gymnosporangium* and *Roestelia* species are

shown in Tables 1 and 2, respectively. The 10 types are as follows.

1. Type S (smooth): Surfaces are smooth to slightly striate (Figs. 1; 2A, B). Most *Gymnosporangium* and *Roestelia* species have a smooth surface on the outer walls of peridial cells. All wall surfaces of peridial cells of *G. biseptatum* Ell. and *G. hyalinum* Kern ex Cumm. are of this type (Tables 1, 2).

2. Type DE (densely echinulate or spinulose): Processes are echinulate or spinulose and densely distributed. Processes are variable in size and about 2-6 μ m in length (Figs. 1; 2C, D). *Gymnosporangium speciosum* Pk., *G. exiguum* Kern, *G. kernianum* Bethel and *G. vauqueliniae* Long et Goodding had this type of side and/or inner walls of peridial cells (Table 1).

3. Type SE (sparsely echinulate): Process morphology is similar to type DE, but processes of this type are distributed more sparsely than those of type DE. Some processes joined together and produced small papillae of irregular size and shape (Figs. 1; 2E–H). This type was observed on peridial cell walls of six *Gymnosporangium* species and one *Roestelia* species. (Tables 1, 2)

4. Type DV (densely verrucose): Processes are verrucose, granulate, columnate, and tongue-shaped, and densely distributed (Figs. 1; 3A, B). Their size is variable, but smaller than that of types DE and SE (less than 2.5 μ m in height). Three *Gymnosporangium* species and two *Roestelia* species with aecidioid aecia have this type on side and inner walls of peridial cells. *Gymnosporangium miyabei* Yamada et I. Miyake, *G. turkestanicum* Tranz. and *R. nanwutiana* (Tai et Cheo) Jørstad also had this type of inner and/or side walls of peridial cells (Fig. 1; Tables 1, 2).

5. Type SV (sparsely verrucose): Process morphology is similar to type DV, but processes of this type are distributed more sparsely than those of type DV (Figs. 1; 3C). This type was observed on outer walls of peridial cells of two *Gymnosporangium* and one *Roestelia* species having aecidioid aecia (Tables 1, 2).

6. Type SP (small papillate): Small papillae of irregular shape are densely distributed (Figs. 1; 3D). These papillae are much smaller than those of types DV and SV. This type of surface structure was observed on inner walls of peridial cells in 14 *Gymnosporangium* species and 1 *Roestelia* species (Tables 1, 2).

7. Type CP (coralloid projection): Processes are coralloid and morphologically irregular, as shown in Fig. 1. Processes are variable in size but mostly shorter than ca. 4.0 μ m (Figs. 1; 3E–H). This type was observed on side and/or inner walls of peridial cells in *G. inconspicuum* Kern and *G. nootkatense* Arth. (Table 1).

8. Type T (tuberculate): Processes are tuberculate as shown in Fig. 1. These processes are relatively long, 2–3 μ m, and 2–7 μ m or more in width. Heads of processes are usually flat (Figs. 1; 4A, B). This type was observed on side and inner walls of peridial cells of *G. clavipes* (Cke. et Pk.) Cke. et Pk. (Table 1).

9. Type MR (moderately rugose) : Surfaces are made up of ridges which are variable in length but shorter than those of type R. Among these ridges, echinulate or ver-

Species ^{a)}	Host plant	Surface structure of peridial cell walls ^{b)}			
	(No. of specimens examined)	outer	side	inner	
G. amelanchieris	Amelanchier asiatica (4)	S	R	SP	
	A. ovalis (3)	S	R	SP	
	A. vulgaris (2)	S	R	SP	
	Aronia rotundifolia (?) (1)	S	R	SP	
G. asiaticum	Chaenomeles extuscoccine (1)	S	MR	SP	
	C. speciosa (3)	S	MR	SP	
	Cydonia japonica (1)	S	MR	SP	
	C. oblonga (1)	S	MR	SP	
	Photinia villosa (1)	S	MR	SP	
	Pyrus betulaefolia (1)	S	MR	SP	
	P. pyrifolia (2)	S	MR	SP	
	<i>P. pyrifolia</i> var. <i>culta</i> (1)	S	MR	SP	
G. bermudianum	Juniperus virginiana (3)	S	R	R	
	<i>Juniperus</i> sp. (1)	S	R	R	
G. betheli	Crataegus douglasii (2)	S	R	SP	
	Crataegus sp. (2)	S	R	SP	
G. biseptatum	Amelanchier canadensis (3)	S	S	S	
	A. oblongifolia (1)	S	S	S	
	Amelanchier sp. (1)	S	S	S	
G. clavariiforme	Amelanchier alnifolia (2)	S	SE	SE	
	A. bartramiana (1)	S	SE	SE	
	A. wiegandii (2)	S	SE	SE	
	Cotoneaster integerrima (1)	S	SE	SE	
	Crataegus maximowiczii (1)	S	SE	SE	
	C. oxyacantha (2)	S	SE	SE	
	C. sanguinea (1)	S	SE	SE	
	Cydonia vulgaris (1)	S	SE	SE	
G. clavipes	Amelanchier alnifolia (1)	S	Т	т	
	A. bartramiana (1)	S	Т	т	
	Amelanchier sp. (2)	S	т	т	
	Aronia melanocarpa (2)	S	Т	т	
	Crataegus punctata (1)	S	т	т	
	C. lavallei (1)	S	т	т	
	C. oxycantha var. pauli (1)	S	Т	т	
	<i>Crataegus</i> sp. (6)	S	Т	т	
	Cydonia vulgaris (2)	S	т	Т	
	<i>Malus</i> sp. (1)	S	Т	Т	
	Sorbus americana (1)	S	Т	т	
G. confusum	Cotoneaster foveolatus (1)	S	R	R	
	Crataegus altaica (1)	S	R	R	
	C. oxyacantha (1)	S	R	R	
	C. monogynae (1)	S	R	R	
	<i>Crataegus</i> sp. (1)	S	R	R	
	<i>Cydonia</i> sp. (1)	S	R	R	
	Mespilus germanica (1)	S	R	R	
	Pyrus lanata (1)	S	R	R	
G. connersii	Crataegus chrysocarpa (3)	S	R	R	
	C. douglasii (1)	S	R	R	
	C. succulenta (1)	S	R	R	
G. corniculans	Amelanchier alnifolia (2)	S	R	SP	

Table 1. Surface structure types of peridial cells of *Gymnosporangium* species.

a) Asterisks indicate species of which type or isotype specimens were observed.

b) CP: type CP (coralloid projection); DE: type DE (densely echinulate or spinulose); DV: type DV (densely verrucose); MR: type MR (moderately rugose); R: type R (rugose); S: type S (smooth); SE: type SE (sparsely echinulate); SP: type SP (small papillate); SV: type SV (sparsely verrucose); T: type T (tuberculate); --: not determined.

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Table 1. Continued.

Interview outer side interview A. canadensis (1) S R A. canadensis (1) S R A. laevis (1) S R A. laevis (1) S R A. laevis (1) S R Malus diversitolia (1) S MR Pyrus sucuparia (2) S MR S. aucuparia (6) S MR S. bybrida (1) S MR S. bybrida (1) S MR G. cunninghamianum Cotoneaster bacillaris (3) S G. cupressi var. cascadense* Amelanchier pallida (2) S G. davisii Aronia melanocarpa (5) S G. evisii Myrice caroinenesis (3) SV G. evisii Myrice caroinenesis (3) S G. evisii (1) S DE Crataegus travy (2) S DE G. exiguum Crataegus travy (2) S G. exiguum Crataegus travy (2) S G. furiforme Crataegus travy (2) S G. furtificiat (2) S R	Species ^{a)}	Host plant (No. of specimens examined)	Surface structure of peridial cell walls ^{b)}		
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		Pyrus aucuparia (?) (1)	S	MR	SP
$ \begin{array}{c} S. aucuparia (6) & S & MR \\ S. decora (1) & S & MR \\ S. decora (1) & S & MR \\ S. decora (1) & S & MR \\ S. sambucifolia (1) & S & MR \\ Sorbus sp. (1) & S & MR \\ Sorbus sp. (1) & S & MR \\ Cotoneaster bacillaris (3) & S & SE \\ Pyrus pashia (4) & S & SE \\ Pyrus pashia (4) & S & SE \\ Pyrus sp. (1) & S & SE \\ davisi & Aronia melanocarpa (5) & S & MR \\ davisi & Aronia melanocarpa (5) & S & MR \\ d. ettil & Myrica carolinensis (3) & SV & DV \\ M. cerere (2) & S & DE \\ C. viriais (1) & S & DE \\ C. virais (1) & S & DE \\ G. exterum & Gillenia stipulata (2) & S & R \\ G. floriforme & Crataegus racificatios (3) & S & DE \\ G. fratemum & Aronia arbuitfolia (3) & S & R \\ G. floriforme & Crataegus sp. (1) & S & R \\ G. fratemum & Aronia arbuitfolia (4) & S & SE \\ A. atropurpurea (1) & S & SE \\ A. dronia sp. (1) & S & SE \\ A. dronia sp. (1) & S & SE \\ A. dronia sp. (1) & S & SE \\ G. fusisporum & Crataegus beata (1) & S & R \\ C. ceesia (1) & S & R \\ C. ceesia (1) & S & R \\ C. fuscosa (1) & S & R \\ C. fuscosa (1) & S & R \\ C. fuscosa (1) & S & R \\ A. melancheria (2) & S & R \\ A. droja sp. (1) & S & R \\ A. droja sp. (1) & S & R \\ A. droja sp. (1) & S & R \\ C. fuscosa (1) & S & R \\ A. droja (1) & S & R \\ A. droja (1) & S & R \\ A. droja (1) & S & R \\ Anelanchier nervosa (1) & S & R \\ Anelanchier nervosa (1) & S & MR \\ Amelanchier nervosa (1) & S & MR \\ Amelanchier sp. (1) & S & MR \\ Amelanc$		Sobus americana (2)	S	MR	SP
S. decora (1)SMRS. hybrida (1)SMRS. sambucitofia (1)SMRG. cunninghamianumCotoneaster bacillaris (3)SSEPyrus ps. (1)SSEG. cupressi var. cascadense*Amelanchier pallida (2)SMRG. davisiiAronia melanocarpa (5)SMRG. davisiiMyrica carolinensis (3)SVDVG. exiguumCrataegus tracyi (2)SDEC. viridis (1)SDECC. viridis (1)SDEC. viridis (1)SDEG. exiguumCrataegus sp. (1)SDEG. exiguumCrataegus tracyi (2)SDEG. exiguumCrataegus sp. (1)SDEG. foriformeCrataegus sp. (1)SRG. foriformeCrataegus sp. (1)SRG. froiformeCrataegus sp. (1)SRG. fraternumAnonia arbuitfolia (4)SSEA. atropurpurea (1)SSEA. atropurpurea (1)SG. fusisporumCotoneaster integerina (2)SRG. globosumCrataegus beata (1)SRC. caesia (1)SRC. chycocarpa (1)SG. globosumCrataegus beata (1)SRC. fusisporumCotoneaster integerina (2)SRG. fusisporumCrataegus beata (1)SRG. fusisporumCotoneaster integerina (2)SRG.		S. aucuparia (6)	S	MR	SP
$ \begin{array}{c} S. hybrida (1) & S & MR \\ S. sambucitolia (1) & S & MR \\ S. sambucitolia (1) & S & MR \\ Sorbus sp. (1) & S & MR \\ Cotoneaster bacillaris (3) & S & SE \\ Pyrus pashia (4) & S & SE \\ Pyrus ps. (1) & S & SE \\ Pyrus sp. (1) & S & SE \\ G. cupressi var. cascadense* & Amelanchier pallida (2) & S & MR \\ G. advisii & Aronia melanocarpa (5) & S & MR \\ G. advisii & Myrica carolinensis (3) & SV & DV \\ M. cerera (2) & SV & DV \\ M. cerera (2) & SV & DV \\ M. cerera (2) & SV & DV \\ M. gale (1) & SV & DV \\ G. exiguum & Crategus tracyi (2) & S & DE \\ Crataegus sp. (1) & S & DE \\ Crataegus sp. (1) & S & DE \\ Crataegus sp. (1) & S & DE \\ Heteromeles sational (1) & S & DE \\ Crataegus sp. (1) & S & DE \\ G. exterum & Gillenia sitpulata (2) & S & R \\ G. floriforme & Crategy sp. (1) & S & R \\ C. spathulata (2) & S & R \\ G. farternum & Aronia arbuilfolia (4) & S & SE \\ A. melanocarpa (1) & S & SE \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ G. fusisporum & Crategus sp. (1) & S & R \\ C. chrysocarpa (1) & S & R \\ C. thysocarpa (1) & S & R \\ C. trategus sp. (1) & S & R \\ R & Malux sp. (1) & S & R \\ Amelanchier sp. (1) & S & MR \\ Amelanchier sp. (1) &$		S. decora (1)	S	MR	SP
S. sambucifolia (1)SMRSorbus sp. (1)SMRCotoneaster bacillaris (3)SSEPyrus pashia (4)SSEPyrus sp. (1)SSEG. cupressi var. cascadense*Amelanchier pallida (2)SG. davisiiAronia melanocarpa (5)SMRG. davisiiMyrice carolinensis (3)SVDVM. cerera (2)SVDVM. cerera (2)SVDVM. cerera (2)SDEC. viridis (1)SDEC. viridis (1)SDEC. viridis (1)SDEG. exterumGillenia stipulata (2)SG. foriformeCrataegus raleighensis (1)SG. froriformeCrataegus raleighensis (1)SG. fratemumAronia arbuitfolia (4)SA. melanocarpa (1)SSEA. melanocarpa (1)SSEA. melanocarpa (1)SSEG. fusisporumCotoneaster integerima (2)SG. fusisporumCrataegus beate (1)SRG. globosumCrataegus sp. (1)SRC. caesia (1)SRC. caesia (1)SR. diversionalCrataegus sp. (1)SRG. globosumCrataegus sp. (1)SRG. fusisporumCotoneaster integerima (2)SRG. globosumCrataegus sp. (1)SRG. fusisporumCotoneaster integerima (2)SRG. gl		S. hybrida (1)	S	MR	SP
$ \begin{array}{c} Sorbus {\rm sp.} (1) & {\rm S} & {\rm MR} \\ Cotoneaster bacillaris (3) & {\rm S} & {\rm SE} \\ Pyrus pashia (4) & {\rm S} & {\rm SE} \\ Pyrus pashia (4) & {\rm S} & {\rm SE} \\ Pyrus ps. (1) & {\rm S} & {\rm SE} \\ G. cupressi var. cascadense* & Amelanchier pallida (2) & {\rm S} & {\rm MR} \\ G. davisii & Aronia melanccarpa (5) & {\rm S} & {\rm MR} \\ G. davisii & Myrica carolinensis (3) & {\rm SV} & {\rm DV} \\ M. cerera (2) & {\rm SV} & {\rm DV} \\ M. gale (1) & {\rm SV} & {\rm DV} \\ G. exiguum & Crataegus tracyi (2) & {\rm S} & {\rm DE} \\ C. viridis (1) & {\rm S} & {\rm DE} \\ C. viridis (1) & {\rm S} & {\rm DE} \\ C. viridis (1) & {\rm S} & {\rm DE} \\ G. exterum & Gillenia stipulata (2) & {\rm S} & {\rm R} \\ G. floriforme & Crataegus sp. (1) & {\rm S} & {\rm R} \\ G. floriforme & Crataegus sp. (1) & {\rm S} & {\rm R} \\ G. floriforme & Crataegus sp. (1) & {\rm S} & {\rm R} \\ G. fraternum & Gillenia stipulata (2) & {\rm S} & {\rm R} \\ G. fraternum & Aronia arbutifolia (4) & {\rm S} & {\rm SE} \\ A. melanccarpa (1) & {\rm S} & {\rm SE} \\ A. melancoarpa (1) & {\rm S} & {\rm SE} \\ A. melancoarpa (1) & {\rm S} & {\rm SE} \\ A. melancoarpa (1) & {\rm S} & {\rm SE} \\ G. fusisporum & Cotoneaster integerima (2) & {\rm S} & {\rm R} \\ C. caseis (1) & {\rm S} & {\rm R} \\ C. caseis (1) & {\rm S} & {\rm R} \\ C. caseis (1) & {\rm S} & {\rm R} \\ C. caseis (1) & {\rm S} & {\rm R} \\ G. globosum & Crataegus sp. (1) & {\rm S} & {\rm R} \\ G. guatemalianum* & Amelanchier antifolia (3) & {\rm S} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier antifolia (3) & {\rm S} & {\rm C} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier sp. (1) & {\rm S} & {\rm R} \\ Amelanchier sp. (1) & {\rm S} & {\rm MR} \\ Amelanchier sp. (1) & {\rm S} & {\rm MR} \\ Amelanchier sp. (1) & {\rm S} & {\rm MR} \\ Amelanchier sp. (1) & {\rm S} & {\rm MR} \\ Amelanchier sp. (1) & {\rm S} & {\rm MR} \\ Amelanchier sp. (1) & {\rm S} & {\rm MR} \\ Amelanchier sp. (1) & {\rm S} & {\rm MR} \\ Amelanchi$		S. sambucifolia (1)	S	MR	SP
G. cunninghamianumCotoneaster bacillaris (3)SSE $Pyrus pashia (4)$ SSE $Pyrus pashia (4)$ SSE $Pyrus pp. (1)$ SSEG. cupressi var. cascadense*Amelanchier pallida (2)SG. davisiiAronia melanocarpa (5)SMRG. davisiiAronia carolinensis (3)SVDVG. ellisiiMyrica carolinensis (3)SVDVM. cerere (2)SVDVM.G. exiguumCrataegus tracy (2)SDEC. viridis (1)SDECrataegus sp. (1)SG. exiguumCrataegus sp. (1)SDEG. exterumGillenia stipulata (2)SRG. foriformeCrataegus sp. (1)SRG. froiformeCrataegus sp. (1)SRG. fraternumAronia arbutifolia (4)SSEA. atropurpurea (1)SSEAronia arbutifolia (4)SG. fusisporumCotoneaster integerima (2)SRG. fusisporumCotoneaster integerima (2)SRG. globosumCrataegus sp. (1)SRC. caesia (1)SRCC. pedicellatus (1)SRG. guatemalianum*Amelanchier envicea (1)SRC. pedicellatus (1)SRG. fusisporumCotoneaster integerima (2)SRG. fusisporumCotoneaster integerima (2)SRG. guatemalianum*Amelanchier (Sorbus sp. (1)	S	MR	SP
Pyrus pashia (4) S SE Pyrus sp. (1) S SE (a cupressi var. cascadense* Amelanchier pallida (2) S MR (a davisii Aronia melanocarpa (5) S MR (a davisii Myrica carolinensis (3) SV DV M. cerera (2) SV DV M. gale (1) SV DV M. gale (1) SV DV (a exiguum Crataegus tracyi (2) S DE C. viridis (1) S DE Crataegus sp. (1) S DE (c exterum Gillenia stipulata (2) S R G. floriforme Crataegus sp. (1) S R G. foriforme Crataegus sp. (1) S R G. foriforme Crataegus sp. (1) S R G. fraternum Aronia arbuitfolia (4) S SE A. melancarpa (1) S SE Aronia sp. (1) S SE Aronia sp. (1) S SE Aronia sp. (1) S SE Aronia arbuitfolia (4) S SE Aronia sp. (1) S SE G. fuscoum Crataegus betat (1) S R C. crategus sp. (1) S R G. guatemalianum* Amelanchier envosa (1) S R Amelanchier sp. (1) S MR Amelanchier sp. (1) S MR Amelanchier aninfolia (3) S Amelanchier sp. (1) S MR	G. cunninghamianum	Cotoneaster bacillaris (3)	s	SE	SE
Pyrus sp. (1)SSEG. cupressi var. cascadense*Amelanchier pallida (2)SMRG. davisiiAronia melanocarpa (5)SMRG. ellisiiMyrica carolinensis (3)SVDVM. cerera (2)SVDVM. gale (1)SDEC. exiguumCrataegus tracyi (2)SDEC. viridis (1)SDEC. viridis (1)SDEC. viridis (1)SDEC. viridis (1)SDEG. exterumGillenia signalata (2)SRG. floriformeCrataegus sp. (1)SRG. floriformeCrataegus sp. (1)SRG. fraternumAronia arbutifolia (4)SSEA. atropurpure (1)SSEA. melanocarpa (1)SG. fusisporumCotoneaster integerima (2)SRG. fusisporumCrataegus beata (1)SRG. globosumCrataegus sp. (1)SRC. caesia (1)SRRC. caesia (1)SRG. globosumCrataegus beata (1)SRC. fuscosa (1)SRRC. pedicellatus (1)SRG. guatemalianum*Amelanchier sp. (1)SRA. floride (1)SRA. florider sp. (1)SRA. florider sp. (1)SRG. fusisporumCrataegus bp. (1)SRG. fusisporumCrataegus sp. (1)<	C C	Pvrus pashia (4)	s	SE	SE
G. cupressi var. cascadense*Amelanchier pallide (2)SMRG. davisiiAronia melanocarpa (5)SMRG. dilisiiMyrica carolinensis (3)SVDVM. cerera (2)SVDVM. gale (1)SVDVG. exiguumCrataegus tracyi (2)SDEC. viridis (1)SDEC. viridis (1)SDEC. exterumGillenia stipulata (2)SRG. floriformeCrataegus sp. (1)SRG. floriformeCrategus raleighensis (1)SRG. fraternumAronia arbuitfolia (4)SSEA. atopurpurea (1)SSEAronia sp. (1)SG. fusisporumCotoneaster integerima (2)SRG. fusisporumCrataegus beata (1)SSEG. fusisporumCrataegus sp. (1)SSEG. globosumCrataegus beata (1)SRC. caesia (1)SRC. crataegus sp. (1)SG. globosumCrataegus sp. (1)SRC. chrysocarpa (1)SRC. crataegus sp. (1)SG. globosumCrataegus sp. (1)SRC. sup contractic (2)SRRG. globosumCrataegus sp. (1)SRG. fuscarPyrus arbuitfolia (?)SRG. fuscarPyrus arbuitfolia (?)SRG. globosumCrataegus sp. (1)SRG. fusisporumCotoneaster inte		P_{Vrus} sp (1)	S	SE	SE
G. davisiiAronia melanocarpa (5)SMRG. davisiiAronia melanocarpa (5)SMRG. ellisiiMyrica carolinensis (3)SVDVM. cerera (2)SVDVM. gale (1)SVDVG. exiguumCrataegus tracyi (2)SDEC. viridis (1)SDECrataegus sp. (1)SDECrataegus sp. (1)SDEG. exterumGillenia stipulata (2)SRG. floriformeCrataegus raleighensis (1)SRC. spathulata (5)SRCrataegus sp. (1)SRG. fraternumAronia arbutifolia (4)SSEAronia sp. (1)SSEA. atropurpurea (1)SSEAronia sp. (1)SSEA. melanocarpa (1)SSEAronia sp. (1)SSEG. fuscumPyrus arbutifolia (?) (1)SSERG. fuscumCatoneaster integerima (2)SRG. globosumCrataegus sp. (1)SRRC. caesia (1)SRC. caesia (1)SRG. globosumCrataegus sp. (1)SRRG. guotosumCrataegus sp. (1)SRRG. globosumCrataegus sp. (1)SRRG. dussportunCotoneaster integerima (2)SRG. fuscosa (1)SRRRG. globosumCrataegus sp. (1)SRG. fus	G. cupressi var. cascadense*	Amelanchier nallida (2)	S	MR	SP
G. ellisiiMyrica carolinensis (3)SVDV $G. ellisii$ Myrica carolinensis (3)SVDV $M. cerera (2)$ SVDV $M. gale (1)$ SVDV $G. exiguum$ Crataegus tracyi (2)SDE $C. viridis (1)$ SDE $C. viridis (1)$ SDE $C. exterum$ Gillenia stipulata (2)SR $G. trifoliata (2)$ SR $G. trifoliata (2)$ SR $G. fraternum$ Crataegus raleighensis (1)SR $G. fraternum$ Aronia arbutifolia (4)SSE $A. atropurpurea (1)$ SSEAronia sp. (1)S $G. fusisporum$ Cotoneaster integerima (2)SR $G. fusisporum$ Cotoneaster integerima (2)SR $G. globosum$ Crataegus sp. (1)SSE $G. globosum$ Crataegus beata (1)SR $G. globosum$ Crataegus beata (1)SR $G. fusisporum$ Cotoneaster integerima (2)SR $G. globosum$ Crataegus sp. (1)SR $G. fusisporum$ Cotoneaster integerima (2)SR $G. globosum$ Crataegus sp. (1)SR $G. fusisporum$ Cotoneaster integerima (2)SR $G. fusisporum$ Cotoneaster integerima (2)SR $G. globosum$ Crataegus sp. (1)SR $G. fusisporum$ Cotoneaster integerima (2)SR $G. fusisporum$ <td< td=""><td>G davisii</td><td>Aronia melanocarna (5)</td><td>S</td><td>MR</td><td>SP</td></td<>	G davisii	Aronia melanocarna (5)	S	MR	SP
A. endowMyrcle cerver (2)SVDVM. cerver (2)SVDVG. exiguumCrataegus tracyi (2)SDEC. viridis (1)SDEC. viridis (1)SDECrataegus sp. (1)SDEHeteromeles salicifolis (3)SDEG. exterumGillenia stipulata (2)SRG. floriformeCrataegus raleighensis (1)SRC. spathulata (5)SRCG. floriformeCrataegus sp. (1)SRG. fraternumAronia arbutifolia (4)SSEA. atropurpurea (1)SSEA. melanocarpa (1)SG. fuscumPyrus communis (10)SSEG. fuscumCotoneaster integerima (2)SRG. globosumCrataegus sp. (1)SRC. caesia (1)SRC. chrysocarpa (1)SG. globosumCrataegus beata (1)SRC. pedicellatus (1)SRRC. pedicellatus (1)SRG. guatemalianum*Amelanchier nervosa (1)SRG. harknessianumAmelanchier sp. (1)SMRAmelanchier sp. (1)SC-Amelanchier sp. (1)SC-C. patient in the onition (3)S-C. patient in the onition (3)S-C. patient in the onition (3)S-Amelanchier sp. (1)SMRAmelanchier sp. (1) <td< td=""><td>G ellisii</td><td>Myrica carolinensis (3)</td><td>SV</td><td></td><td></td></td<>	G ellisii	Myrica carolinensis (3)	SV		
M. gale (1)SVDVG. exiguum $Crataegus tracyi (2)$ SDEC. viridis (1)SDECrataegus sp. (1)SDEHeteromeles salicitolis (3)SDEG. exterumGillenia stipulata (2)SRG. floriformeCrataegus raleighensis (1)SRCrataegus sp. (1)SRRG. froiformeCrataegus raleighensis (1)SRG. fraternumAronia arbutifolia (4)SSEA. atropurpurea (1)SSEA. melanocarpa (1)SG. fusisporumCotoneaster integerima (2)SRG. fusisporumCotoneaster integerima (2)SRG. globosumCrataegus sp. (1)SRC. caesia (1)SRRC. caesia (1)SRC. fusicosa (1)SRC. fusicosa (1)SRC. fusicosa (1)SRC. fusicosa (1)SRC. fusicosa (1)SRC. fusicosa (1)SRG. guatemalianum*Amelanchier nervosa (1)SMalus sp. (1)SRG. harknessianumAmelanchier sp. (1)SA. florida (1)SCA. florida (1)SCA. florida (1)SCA. florida (1)SCA. florida (1)SCA. florida (1)SCA. florida (1)SC <td>G. 6//0/</td> <td>Myrica caroninensis (5) M. cerera (2)</td> <td>SV SV</td> <td>DV</td> <td></td>	G. 6//0/	Myrica caroninensis (5) M. cerera (2)	SV SV	DV	
G. exiguumCrataegus tracyi (2)SDEC. viridis (1)SDECrataegus sp. (1)SDEHeteromeles salicifolis (3)SDEG. exterumGillenia stipulata (2)SRG. floriformeCrataegus raleighensis (1)SRC. spathulata (2)SRG. floriformeCrataegus raleighensis (1)SRC. spathulata (5)SRG. fraternumAronia arbutifolia (4)SSEA. atropurpurea (1)SSEA. melanocarpa (1)SSEA. melanocarpa (1)SSEG. fuscumPyrus communis (10)SSEG. fuscumCrataegus beata (1)SRG. globosumCrataegus sp. (1)SRG. globosumCrataegus sp. (1)SRG. globosumCrataegus beata (1)SRG. fuscosa (1)SRRG. globosumCrataegus sp. (1)SRG. globosumCrataegus sp. (1)SRG. guatemalianum*Amelanchier enrosa (1)SRG. guatemalianum*Amelanchier sp. (1)SMRAmelanchier anifolia (3)S—A. florida (1)SMRAmelanchier sp. (1)SMRAmelanchier sp. (1)SMRAmelanchier sp. (1)SMR		M_{α} color (2) M_{α} color (1)	SV SV		
$\begin{array}{c} C. viridis (1) & S & DE \\ C. viridis (1) & S & DE \\ Crataegus sp. (1) & S & DE \\ Heteromeles salicifolis (3) & S & DE \\ Heteromeles salicifolis (3) & S & DE \\ \hline \\ G. exterum & Gillenia stipulata (2) & S & R \\ G. floriforme & Crataegus raleighensis (1) & S & R \\ C. spathulata (5) & S & R \\ Crataegus sp. (1) & S & R \\ C. spathulata (5) & S & R \\ Crataegus sp. (1) & S & SE \\ A. atropurpurea (1) & S & SE \\ A. atropurpurea (1) & S & SE \\ A. atropirpurea (1) & S & SE \\ A. melanocarpa (1) & S & SE \\ Pyrus arbutifolia (?) (1) & S & SE \\ Pyrus arbutifolia (?) (1) & S & SE \\ Pyrus arbutifolia (?) (1) & S & SE \\ R. & Crataegus beata (1) & S & SE \\ Pyrus arbutifolia (?) (1) & S & SE \\ R. & C. caesia (1) & S & SE \\ G. flusisporum & Cotoneaster integerima (2) & S & R \\ C. caesia (1) & S & R \\ C. caesia (1) & S & R \\ C. carategus beata (1) & S & R \\ C. fuscosa (1) & $	G exiauum	Crataeque tracvi (2)	5V 6		
$\begin{array}{c} C. virtues (1) \\ Crataegus sp. (1) \\ Heteromeles salicifolis (3) \\ S \\ DE \\ Heteromeles salicifolis (3) \\ S \\ DE \\ \end{array}$	G. exigualit	Crataegus tracyr (2)	5		
$\begin{array}{c c} Crategy b sp. (1) & S & DE \\ Heteromeles salicifolis (3) & S & DE \\ Heteromeles salicifolis (3) & S & DE \\ \hline \\ G. tritoliata (2) & S & R \\ \hline \\ G. tritoliata (2) & S & R \\ \hline \\ G. floriforme & Crataegus raleighensis (1) & S & R \\ \hline \\ C. spathulata (5) & S & R \\ \hline \\ C. spathulata (5) & S & R \\ \hline \\ Crataegus sp. (1) & S & R \\ \hline \\ G. fraternum & Aronia arbutifolia (4) & S & SE \\ \hline \\ A. atropurpurea (1) & S & SE \\ \hline \\ A. atropurpurea (1) & S & SE \\ \hline \\ A. melanocarpa (1) & S & SE \\ \hline \\ A. melanocarpa (1) & S & SE \\ \hline \\ A. melanocarpa (1) & S & SE \\ \hline \\ G. fuscum & Pyrus communis (10) & S & SE \\ \hline \\ G. fusisporum & Cotoneaster integerima (2) & S & R \\ \hline \\ G. globosum & Crataegus beata (1) & S & R \\ \hline \\ C. caesia (1) & S & R \\ \hline \\ C. chrysocarpa (1) & S & R \\ \hline \\ C. fuscosa (1) & S & R \\ \hline \\ R & Crataegus sp. (1) & S & R \\ \hline \\ R & Malus domestica (2) & S & R \\ \hline \\ Malus domestica (2) & S & R \\ \hline \\ Malus sp. (1) & S & R \\ \hline \\ G. guatemalianum* & Amelanchier nervosa (1) & S & MR \\ Amelanchier sp. (1) & S & MR \\ \hline \\ G. harknessianum & Amelanchier anitolia (3) & S \\ \hline \\ A. florida (1) & S & - \\ \hline \end{array}$		Crataogue en (1)	5		
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Crataegus sp. (1)SRG. fraternumAronia arbutifolia (4)SSEA. atropurpurea (1)SSEA. atropurpurea (1)SSEA. melanchier alnifolia (2)SSEPyrus arbutifolia (7) (1)SSEG. fuscumPyrus communis (10)SSEG. fusisporumCotoneaster integerima (2)SRG. globosumCrataegus beata (1)SRC. caesia (1)SRC. chrysocarpa (1)SRC. fuscosa (1)SRC. fuscosa (1)SRC. pedicellatus (1)SRMalus domestica (2)SRMalus sp. (1)SRMalus sp. (1)SRG. guatemalianum*Amelanchier nervosa (1)SG. harknessianumAmelanchier sp. (1)SG. harknessianumAmelanchier sp. (1)SG. harknessianumAmelanchier sp. (1)S		C. spathulata (5)	S	R	R
G. fraternumAronia arbutifolia (4)SSEA. atropurpurea (1)SSEA. melanocarpa (1)SSEAronia sp. (1)SSEPyrus arbutifolia (?) (1)SSEPyrus arbutifolia (?) (1)SSEG. fuscumPyrus communis (10)SSEG. fusisporumCotoneaster integerima (2)SRG. globosumCrataegus beata (1)SRC. caesia (1)SRC. caesia (1)SC. fuscosa (1)SRC. fuscosa (1)SC. fuscosa (1)SRC. fuscosa (1)SC. guatemalianum*Malus domestica (2)SRG. quatemalianum*Amelanchier nervosa (1)SRG. harknessianumAmelanchier alnifolia (3)S-A. florida (1)SMRA. florida (1)SCA. florida (1)SA. florida (1)S- <td></td> <td><i>Crataegus</i> sp. (1)</td> <td>S</td> <td>R</td> <td>R</td>		<i>Crataegus</i> sp. (1)	S	R	R
A. atropurpurea (1)SSEA. melanocarpa (1)SSEAronia sp. (1)SSEPyrus arbutifolia (?) (1)SSEG. fuscumPyrus communis (10)SSEG. fusisporumCotoneaster integerima (2)SRG. globosumCrataegus beata (1)SRC. caesia (1)SRC. caesia (1)SRC. caesia (1)SRC. chrysocarpa (1)SRC. fuscosa (1)SRC. rataegus sp. (1)SRMalus domestica (2)SRMalus sp. (1)SRPyrus americana (1)SRG. guatemalianum*Amelanchier nervosa (1)SMRAmelanchier sp. (1)SMRA. florida (1)S-A.	G. fraternum	Aronia arbutifolia (4)	S	SE	SE
A. melanocarpa (1)SSEAronia sp. (1)SSEAronia sp. (1)SSEPyrus arbutifolia (?) (1)SSEG. fuscumPyrus communis (10)SSEG. fusisporumCotoneaster integerima (2)SRG. globosumCrataegus beata (1)SRC. caesia (1)SRC. caesia (1)SRC. chrysocarpa (1)SRC. fuscosa (1)SRC. fuscosa (1)SRC. fuscosa (1)SRC. pedicellatus (1)SRMalus domestica (2)SRMalus sp. (1)SRMalus sp. (1)SRPyrus americana (1)SRG. guatemalianum*Amelanchier nervosa (1)SMRAmelanchier sp. (1)SMRAmelanchier sp. (1)S-A. florida (1)S-Amelanchier sp. (1)S <td< td=""><td></td><td>A. atropurpurea (1)</td><td>S</td><td>SE</td><td>SE</td></td<>		A. atropurpurea (1)	S	SE	SE
Aronia sp. (1)SSE $Pyrus arbutifolia (?) (1)$ SSE $Pyrus arbutifolia (?) (1)$ SSE $G. fusisporum$ $Pyrus communis (10)$ SSE $G. fusisporum$ $Cotoneaster integerima (2)$ SR $G. globosum$ $Crataegus beata (1)$ SR $C. caesia (1)$ SR $C. caesia (1)$ SR $C. caesia (1)$ SR $C. chrysocarpa (1)$ SR $C. fuscosa (1)$ SR R $C. fuscosa (2)$ S R $Malus domestica (2)$ S $Malus sp. (1)$ SR $Malus sp. (1)$ SR $Pyrus americana (1)$ SR $G. guatemalianum^*$ $Amelanchier nervosa (1)$ S MR $Amelanchier sp. (1)$ SMR $Amelanchier sp. (1)$ S $ A. florida (1)$ S $ A. florida (1)$ S $ Amelanchier sp. (1)$ S $-$		A. melanocarpa (1)	S	SE	SE
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G. fuscum Pyrus communis (10) S SE G. fusisporum Cotoneaster integerima (2) S R G. globosum Crataegus beata (1) S R C. caesia (1) S R R C. caesia (1) S R R C. caesia (1) S R R C. chrysocarpa (1) S R R C. fuscosa (1) S R R C. fuscosa (1) S R R C. pedicellatus (1) S R R Crataegus sp. (1) S R R Malus domestica (2) S R R Malus sp. (1) S R R Pyrus americana (1) S R R G. guatemalianum* Amelanchier nervosa (1) S MR Amelanchier alnifolia (3) S —		Pyrus arbutifolia (?) (1)	S	SE	SE
G. fusisporum Cotoneaster integerima (2) S R G. globosum Crataegus beata (1) S R C. caesia (1) S R C. caesia (1) S R C. caesia (1) S R C. chrysocarpa (1) S R C. fuscosa (1) S R C. fuscosa (1) S R C. pedicellatus (1) S R C. pedicellatus (1) S R Crataegus sp. (1) S R Malus domestica (2) S R Malus sp. (1) S R Pyrus americana (1) S R Sorbus tianschanica (1) S R G. guatemalianum* Amelanchier nervosa (1) S MR Amelanchier alnifolia (3) S - - A. florida (1) S - - Amelanchier sp. (1) S - -	G. fuscum	Pyrus communis (10)	S	SE	SE
G. globosum Crataegus beata (1) S R C. caesia (1) S R C. caesia (1) S R C. chrysocarpa (1) S R C. fuscosa (1) S R C. fuscosa (1) S R C. fuscosa (1) S R C. pedicellatus (1) S R C. pedicellatus (1) S R Malus domestica (2) S R Malus domestica (2) S R Malus sp. (1) S R Pyrus americana (1) S R Sorbus tianschanica (1) S R G. guatemalianum* Amelanchier nervosa (1) S MR Amelanchier sp. (1) S MR A. florida (1) S - A. florida (1) S - Amelanchier sp. (1) S -	G. fusisporum	Cotoneaster integerima (2)	S	R	SP
$ \begin{array}{c c} C.\ caesia\ (1) & S & R \\ C.\ chrysocarpa\ (1) & S & R \\ C.\ chrysocarpa\ (1) & S & R \\ C.\ fuscosa\ (1) & S & R \\ C.\ fuscosa\ (1) & S & R \\ C.\ pedicellatus\ (1) & S & R \\ C.\ pedicellatus\ (1) & S & R \\ Crataegus\ sp.\ (1) & S & R \\ Malus\ domestica\ (2) & S & R \\ Malus\ domestica\ (2) & S & R \\ Malus\ sp.\ (1) & S & R \\ Pyrus\ americana\ (1) & S & R \\ Pyrus\ americana\ (1) & S & R \\ Sorbus\ tianschanica\ (1) & S & R \\ Amelanchier\ nervosa\ (1) & S & MR \\ Amelanchier\ sp.\ (1) & S & MR \\ Amelanchier\ sp.\ (1) & S & - \\ Amelanchier\ sp.\ (1) & S & - \\ Amelanchier\ sp.\ (1) & S & - \\ \end{array} $	G. globosum	Crataegus beata (1)	S	R	SP
$ \begin{array}{c c} C. \ chrysocarpa (1) & S & R \\ C. \ fuscosa (1) & S & R \\ C. \ fuscosa (1) & S & R \\ C. \ pedicellatus (1) & S & R \\ Crataegus sp. (1) & S & R \\ Malus \ domestica (2) & S & R \\ Malus \ domestica (2) & S & R \\ Malus \ sp. (1) & S & R \\ Pyrus \ americana (1) & S & R \\ Pyrus \ americana (1) & S & R \\ Sorbus \ tianschanica (1) & S & R \\ Amelanchier \ nervosa (1) & S & MR \\ Amelanchier \ sp. (1) & S & MR \\ Amelanchier \ sp. (1) & S & - \\ Amelanchier \ sp. (1) & S & - \\ Amelanchier \ sp. (1) & S & - \\ \end{array} $		C. caesia (1)	S	R	SP
C. fuscosa (1) S R C. pedicellatus (1) S R Crataegus sp. (1) S R Malus domestica (2) S R Malus domestica (2) S R Malus sp. (1) S R Pyrus americana (1) S R Sorbus tianschanica (1) S R G. guatemalianum* Amelanchier nervosa (1) S MR Amelanchier sp. (1) S MR A. florida (1) S — A. florida (1) S — Amelanchier sp. (1) S —		C. chrysocarpa (1)	S	R	SP
C. pedicellatus (1) S R Crataegus sp. (1) S R Malus domestica (2) S R Malus domestica (2) S R Malus sp. (1) S R Pyrus americana (1) S R G. guatemalianum* Amelanchier nervosa (1) S MR Amelanchier sp. (1) S MR G. harknessianum Amelanchier alnifolia (3) S — A. florida (1) S — — Amelanchier sp. (1) S — —		C. fuscosa (1)	S	R	SP
Crataegus sp. (1) S R Malus domestica (2) S R M. sylvestris (1) S R Malus sp. (1) S R Pyrus americana (1) S R G. guatemalianum* Amelanchier nervosa (1) S MR Amelanchier sp. (1) S MR G. harknessianum Amelanchier alnifolia (3) S — A. florida (1) S — Amelanchier sp. (1) S —		C. pedicellatus (1)	S	R	SP
Malus domestica (2) S R M. sylvestris (1) S R Malus sp. (1) S R Pyrus americana (1) S R G. guatemalianum* Amelanchier nervosa (1) S MR Amelanchier sp. (1) S MR G. harknessianum Amelanchier alnifolia (3) S — A. florida (1) S — Amelanchier sp. (1) S — Amelanchier sp. (1) S —		<i>Crataegus</i> sp. (1)	S	R	SP
M. sylvestris (1)SRMalus sp. (1)SRPyrus americana (1)SRSorbus tianschanica (1)SRG. guatemalianum*Amelanchier nervosa (1)SMRAmelanchier sp. (1)SMRG. harknessianumAmelanchier alnifolia (3)SA. florida (1)SAmelanchier sp. (1)SAmelanchie		Malus domestica (2)	S	R	SP
Malus sp. (1)SRPyrus americana (1)SRSorbus tianschanica (1)SRG. guatemalianum*Amelanchier nervosa (1)SMRAmelanchier sp. (1)SMRG. harknessianumAmelanchier alnifolia (3)SA. florida (1)SAmelanchier sp. (1)SAmelanc		M. sylvestris (1)	S	R	SP
Pyrus americana (1)SRSorbus tianschanica (1)SRG. guatemalianum*Amelanchier nervosa (1)SMRAmelanchier sp. (1)SMRG. harknessianumAmelanchier alnifolia (3)SA. florida (1)SAmelanchier sp. (1)SAmelanchier sp. (1)SAmelanchier sp. (1)S		Malus sp. (1)	S	R	SP
Sorbus tianschanica (1)SRG. guatemalianum*Amelanchier nervosa (1)SMRAmelanchier sp. (1)SMRG. harknessianumAmelanchier alnifolia (3)SA. florida (1)SAmelanchier sp. (1)SAmelanchier sp. (1)SAmelanchier sp. (1)S		Pyrus americana (1)	S	R	SP
G. guatemalianum* Amelanchier nervosa (1) S MR Amelanchier sp. (1) S MR G. harknessianum Amelanchier alnifolia (3) S — A. florida (1) S — Amelanchier sp. (1) S — A. florida (1) S — Amelanchier sp. (1) S —		Sorbus tianschanica (1)	S	R	SP
Amelanchier sp. (1) S MR G. harknessianum Amelanchier alnifolia (3) S — A. florida (1) S — Amelanchier sp. (1) S —	G. guatemalianum* G. harknessianum	Amelanchier nervosa (1)	s	MB	SP
G. harknessianum Amelanchier alnifolia (3) S — A. florida (1) S — Amelanchier sp. (1) S —		Amelanchier sp. (1)	S	MR	SP
A. florida (1) S — Amelanchier sp. (1) S —		Amelanchier alnifolia (3)	S		SP
Amelanchier sp. (1) S —		A. florida (1)	S	_	CP
		Amelanchier sp. (1)	6		CD
(i hyaliniim Creteorus quesite (1) C C	G hydinym	Cratagous quesite (1)	5	e	or e

Species ^{a)}	Host plant	Surface structure of peridial cell walls ^{b)}			
	(No. of specimens examined)	outer	side	inner	
G. inconspicuum	Amelanchier alnifolia (2)	S	s	СР	
	A. bakeri (2)	S	S	СР	
	A. florida (1)	S	S	СР	
	Amelanchier sp. (1)	S	S	CP	
G. japonicum	Photinia parvifolia (1)	S	SE	SE	
	<i>P. laevis</i> var. <i>villosa</i> (1)	S	SE	SE	
	P. villosa (3)	S	SE	SE	
	<i>Photinia</i> sp. (2)	S	SE	SE	
G. juniperi-virginianae	Malus coronaria (2)	S	R	R	
	M. pumila (1)	S	R	R	
	Malus sp. (4)	S	R	R	
G. kernianum	Amelanchier alnifolia (2)	S	DE	DE	
	Crataegus oxyacantha (1)	S	DE	DE	
G. libocedri	Amelanchier alnifolia (1)	SV	DV	DV	
	A. florida (1)	SV	DV	DV	
	Crataegus douglasii (2)	sv	DV	DV	
G. miyabei	Malus sieboldii (1)	S		DV	
	Malus sp. (1)	5			
	Nicromeiles ainifolia (2)	5			
	Sorbaria (1) japonica (1)	5			
	Sorbus ainifolia (1)	5	DV		
	S. commixta (1)	5			
G nalaani	S. japonica (1)	о с		CD V	
G. Nelsoni	Ameranchier anniona (5) A florida (1)	3 6	R	SP	
	A laevis (1)	5	R	SP	
	Amelanchier sn (2)	ŝ	R	SP	
G nootkatense	Malus fusca (1)	υV		CP	
	Malus sp. (3)	DV	DV	CP	
	Sorbus sitchensis (1)	DV	DV	CP	
	S. sitchensis var. occidentalis (1)	DV	DV	СР	
	Sorbus sp. (2)	DV	DV	CP	
G. speciosum	Fendlera rupicola (5)	DE	sv	DE	
-	Philadelphus microphyllus (1)	DE	sv	DE	
	P. occidentalis (1)	DE	sv	DE	
	P. rugosus (1)	DE	sv	DE	
G. trachysorum	Crataegus marshallii (1)	S	MR	SP	
	Crataegus sp. (1)	S	MR	SP	
G. torminali-juniperinum	Sorbus torminalis (1)	S		SP	
	Sobus sp. (1)	S		SP	
G. tremelloides	Cotoneaster frigidus (?) (1)	S	R	R	
	Malus sylvestris (3)	S	R	R	
	M. domestica (4)	S	R	R	
	<i>Malus</i> sp. (2)	S	R	R	
	Sorbus scopulina (2)	S	R	S	
	S. sitchensis (4)	S	R	S	
G. turkestanicum	Sorbus tianschanica (1)	S	DV	SP	
G. yamadae	Malus asiatica (1)	S	SE	MR	
	M. hallana (1)	S	SE	MR	
	IVI. pumila (2) M. sieboldii (1)	5	SE	MR	
	IVI. SIEDOIAII (1)	5	55	MD	
G vaugueliniae*	W. Speciabilis (1)	3 C	3E DE		
G, vauquemmae	vauquenna canonnea (1)	3		DE	

Table 1. Continued.

Species ^{a)}	Host plant	Surface structure of peridial cell walls ^{b)}			
	(No. of specimens examined)	outer	side	inner	
R. brucensis*	Juniperus horizontalis (7)	S	R	R	
R. distorta*	Cotoneaster bacillaris (5)	S	R	R	
	C. roseus (1)	S	R	R	
R. fenzeliana	Malus kansuensis (1)	S	MR	SP	
	M. kansuensis f. calva (1)				
R. nanwutiana	Cotoneaster soongoricus (2)	S	DV	DV	
R. pourthiaeae	Photinia villosa var. laevis (2)	SV	DV	DV	
R. wenshanensis	Photinia villosa (1)	—	DV	DV	
<i>Roestelia</i> sp.	<i>Sorbus cuspidata</i> (HMAS 67336, 67338)	S	R	SE	
	Sorbus globosa (HMAS 45208)	S	R	SE	
	S. rufopilosa (HMAS 67335)	S	R	SE	
	<i>Sorbus</i> sp. (HMAS 00362, 45209)	S	R	SE	

Table 2. Surface structure types of pridial cells of Roestelia species.

a) Asterisks indicate species of which type or isotype specimens were observed.

b) DV: type DV (densely verrucose); MR: type MR (moderately rugose); R: type R (rugose); S: type S (smooth); SE: type SE (sparsely echinulate); SP: type SP (small papillate); SV: type SV (sparsely verrucose); —: not determined.



Fig. 1. Schematic illustration of surface structure types of peridial cells of *Gymnosporangium* and *Roestelia*.

rucose processes are frequently present (Figs. 1; 4C, D). This type is observed on side or inner walls of peridial cells in 8 *Gymnosporangium* and one *Roestelia* species (Tables 1, 2).

10. Type R (rugose): Surfaces are wrinkled with ridges running along or across the walls. These ridges are variable in length, but longer than those of type MR. (Figs. 1; 4E-G). Papillae are sometimes present among these ridges. This type was observed on inner and/or side walls of 13 *Gymnosporangium* and 3 *Roestelia* species (Tables 1, 2).

As shown Tables 1 and 2, surface structures of peridial cells were stable within each species except for *G. tremelloides* Hartig. Outer wall of peridial cells in 37 *Gymnosporangium* species and 5 *Roestelia* species with roestelioid aecia were of type S, but various other types of surface structures were recognized on their side and inner walls (Tables 1, 2). On the other hand, peridial cells of 5 species with aecidioid aecia were observed to have ornamentation on all walls of peridial cells (Tables 1, 2).

Discussion

Kern (1973) described 5 types of surface sculpturing of peridial cells (rugose, modified rugose, verrucose, spinulose, and smooth). However, we recognized 10 distinct types of surface structures on outer, side, and inner walls of the peridial cells when we examined 40 *Gymnosporangium* species and 7 *Roestelia* species by SEM (Tables 1, 2). In 1 to 19 specimens of each species from different host plants and localities, surface structure types were constant in each wall of peridial cells within each species, except for *G. tremelloides*. Therefore, we consider that these types can be used as an important diagnostic



Fig. 2. Scanning electron micrographs of surface structures of the peridial cells of *Gymnosporangium* species.
A. *G. biseptatum* on *Amelanchier oblongifolia* (type S).
B. *G. hyalinum* on *Crataegus quasita* (Type S).
C, D. *G. exiguum* on *C. tracyi* (type DE).
E. *G. cunninghamianum* Barcl. on *Pyrus pashia*. (type SE).
F. *G. fuscum* Hedw. f. on *P. communis* (type SE).
G. *fraternum* Kern on *Aronia arbutifolia* (type SE).
H. *G. yamadae* Miyabe ex Yamada on *Malus pumila* (type SE).
OW: outer wall, IW: inner wall; SW: side wall.
Scale bars: F=5 µm; C, E, G=10 µm; B, D, H=20 µm; A=40 µm.



Fig. 3. Scanning electron micrographs of surface structures of the peridial cells of *Gymnosporangium* species.
A. *G. miyabei* on *Malus* sp. (type DV). B. *G. ellisii* on *Myrica cerifera* (type DV). C. *G. ellisii* on *M. cerifera* (type SV). D. *G. cornutum* Arth. ex Kern on (type SP). E, F. *G. nootkatense* on *Sorbus* sp. (type CP). G, H. *G. inconspicuum* on *Amelanchier bakeri* (type CP). OW: outer wall; IW: inner wall; SW: side wall. Scale bars: F, H=5 µm; B, C, E=10 µm; A, D, G=20 µm.



Fig. 4. Scanning electron micrographs of surface structures of the peridial cells of *Gymnosporangium* and *Roestelia* species.
A, B. *G. clavipes* on *Amelanchier* sp. (type T). C. *G. trachysorum* Kern on *Crataegus* sp. (type MR). D. *G. guatemalianum* (Crowell) Cumm. on *A. nervosa*. E. *G. tremelloides* on *Malus silvestris* (European specimen, inner walls: type R). F. *G. tremelloides* on *Sorbus scopulina* (North American specimen, inner walls: type S). G, H. *Roestelia* sp. on *S. globosa* (side wall: type R; inner wall: type SE). OW: outer wall, IW: inner wall; SW: side wall. Scale bars: H=5 μm; B, C, G=10 μm; D=20 μm; A, E, F=40 μm.

characteristic of *Gymnosporangium* and *Roestelia* species.

We observed 16 specimens identified as *G. tremelloides* on various host plants collected in North America, Europe, and China (Table 1). Side and inner walls of 10 specimens on *Cotoneaster* spp. and *Malus* spp. collected in Europe and China were both of type R (Table 1; Fig. 4E), but those of 6 North American specimens on *Sorbus* spp. were of type R and S, respectively (Table 1; Fig. 4F). Descriptions of peridial cells and aeciospores in this species also differ among researchers (Parmelee, 1971; Kern, 1973; Ziller, 1974). Taxonomic re-examination of this species is necessary.

Peridial cells of six specimens collected on *Sorbus* spp. in China and labeled as *G. tremelloides* and *G. nipponicum* Yamada ex Hiratsuka, f. have outer walls of type S, inner walls of type SE, and side walls of type R (Table 2; Figs. 4G, H). Surface structures of peridial cells, aeciospore surface structure (type LA), and thickness of aeciospores $(1-2.5 \ \mu m)$ of these specimens did not precisely match the descriptions of *G. tremelloides*, *G. nipponicum*, or other species that have an aecial stage on *Sorbus* (Parmelee, 1971; Kern, 1973; Ziller, 1974; Hiratsuka et al., 1992; Lee and Kakishima, 1999). We have separated these specimens as *Roestelia* sp. (Table 2) and consider that more careful taxonomic examination of them is necessary.

As shown in Tables 1 and 2, most *Gymnosporangium* and *Roestelia* species have peridial cells with type S outer walls, but various types of side and inner walls (Tables 1, 2). All peridial cell walls of *G. hyalinum* and *G. biseptatum* were smooth (type S, Figs. 2A, B), as reported by Kern (1910). These species have exceptionally thick outer walls, whereas most species have thin outer walls and thicker inner walls. It was also recognized that many species examined have the same or similar surface types on side and inner walls of peridial cells (Tables 1, 2). However, no correlation between the surface structure types of peridial cell walls and groups of aecial host plants was recognized in any of the *Gymnosporangium* and *Roestelia* species examined (Tables 1, 2).

On the other hand, three *Gymnosporangium* species and two *Roestelia* species having aecidioid aecia, whose peridial cells are usually rhomboid (Littlefield and Heath, 1979), were ornamented on every wall of peridial cells (Tables 1, 2). With the exception of *G. nootkatense*, these species have side and inner walls of type DV (Tables 1, 2). *G. nootkatense*, the only *Gymnosporangium* species to posses all spore forms (Holm, 1969; Kern, 1973), is unique in the surface structure of its peridial cells, inner walls of type CP and side and inner walls of type DV (Table 1; Figs. 3E, F).

Lee and Kakishima (1999) reported 12 types of aeciospore surface structures in 40 *Gymnosporangium* species and 7 *Roestelia* species. Among 5 species having aecidioid aecia, all except *G. nootkatense*, namely, *G. ellisii* (Berk.) Ell., *G. libocedri* (P. Henn.) Kern, *R. pourthiaeae* (Sydow) Kern, and *R. wenshanensis* (Tai) Kern, have verrucose surface structures both on aeciospores (type RV, verrucose with refractive granules) and on side and inner walls of peridial cells (type DV; Figs. 3A, B; Tables 1, 2). On the other hand, among 42 species having roestelioid aecia, only 2 species, G. miyabei and G. hyalinum, had verrucose aeciospore surface structures (Lee and Kakishima, 1999). Side and inner walls of peridial cells of G. miyabei were of type DV (Fig. 3A), but all walls of peridial cells of G. hyalinum were of type S, as discussed above. As a result, four species having aecidioid aecia, except G. nootkatense, and one species with roestelioid aecia, G. miyabei, have verrucose surface structures both on aeciospores and on side and inner walls of peridial cells (Tables 1, 2). However, no correlation was found between the surface structure types of aeciospores reported by Lee and Kakishima (1999) and those of peridial cells in most Gymnosporangium and Roestelia species examined (Tables 1, 2).

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