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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, one-cell-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 Ion 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 μm 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 μm 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 μm (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 μm, and 2–7 μm 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-

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

Species[a]	Host plant (No. of specimens examined)	Surface structure of peridial cell walls[b]		
		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
	P. pyrifolia var. *culta* (1)	S	MR	SP
G. bermudianum	*Juniperus virginiana* (3)	S	R	R
	Juniperus 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	T	T
	A. bartramiana (1)	S	T	T
	Amelanchier sp. (2)	S	T	T
	Aronia melanocarpa (2)	S	T	T
	Crataegus punctata (1)	S	T	T
	C. lavallei (1)	S	T	T
	C. oxycantha var. *pauli* (1)	S	T	T
	Crataegus sp. (6)	S	T	T
	Cydonia vulgaris (2)	S	T	T
	Malus sp. (1)	S	T	T
	Sorbus americana (1)	S	T	T
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
	Crataegus sp. (1)	S	R	R
	Cydonia 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

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.

Table 1. Continued.

Species[a]	Host plant (No. of specimens examined)	Surface structure of peridial cell walls[b]		
		outer	side	inner
	A. canadensis (1)	S	R	SP
	A. laevis (1)	S	R	SP
	Amelanchier sp. (2)	S	R	SP
G. cornutum	*Malus diversifolia* (1)	S	MR	SP
	M. fusca (1)	S	MR	SP
	Pyrus aucuparia (?) (1)	S	MR	SP
	Sobus americana (2)	S	MR	SP
	S. aucuparia (6)	S	MR	SP
	S. decora (1)	S	MR	SP
	S. hybrida (1)	S	MR	SP
	S. sambucifolia (1)	S	MR	SP
	Sorbus sp. (1)	S	MR	SP
G. cunninghamianum	*Cotoneaster bacillaris* (3)	S	SE	SE
	Pyrus pashia (4)	S	SE	SE
	Pyrus sp. (1)	S	SE	SE
G. cupressi var. *cascadense**	*Amelanchier pallida* (2)	S	MR	SP
G. davisii	*Aronia melanocarpa* (5)	S	MR	SP
G. ellisii	*Myrica carolinensis* (3)	SV	DV	DV
	M. cerera (2)	SV	DV	DV
	M. gale (1)	SV	DV	DV
G. exiguum	*Crataegus tracyi* (2)	S	DE	DE
	C. viridis (1)	S	DE	DE
	Crataegus sp. (1)	S	DE	DE
	Heteromeles salicifolis (3)	S	DE	DE
G. exterum	*Gillenia stipulata* (2)	S	R	R
	G. trifoliata (2)	S	R	R
G. floriforme	*Crataegus raleighensis* (1)	S	R	R
	C. spathulata (5)	S	R	R
	Crataegus sp. (1)	S	R	R
G. fraternum	*Aronia arbutifolia* (4)	S	SE	SE
	A. atropurpurea (1)	S	SE	SE
	A. melanocarpa (1)	S	SE	SE
	Aronia sp. (1)	S	SE	SE
	Pyrus arbutifolia (?) (1)	S	SE	SE
G. fuscum	*Pyrus communis* (10)	S	SE	SE
G. fusisporum	*Cotoneaster integerima* (2)	S	R	SP
G. globosum	*Crataegus beata* (1)	S	R	SP
	C. caesia (1)	S	R	SP
	C. chrysocarpa (1)	S	R	SP
	C. fuscosa (1)	S	R	SP
	C. pedicellatus (1)	S	R	SP
	Crataegus sp. (1)	S	R	SP
	Malus domestica (2)	S	R	SP
	M. sylvestris (1)	S	R	SP
	Malus sp. (1)	S	R	SP
	Pyrus americana (1)	S	R	SP
	Sorbus tianschanica (1)	S	R	SP
*G. guatemalianum**	*Amelanchier nervosa* (1)	S	MR	SP
	Amelanchier sp. (1)	S	MR	SP
G. harknessianum	*Amelanchier alnifolia* (3)	S	—	SP
	A. florida (1)	S	—	SP
	Amelanchier sp. (1)	S	—	SP
G. hyalinum	*Crataegus quasita* (1)	S	S	S

Table 1. Continued.

Species[a]	Host plant (No. of specimens examined)	Surface structure of peridial cell walls[b]		
		outer	side	inner
G. inconspicuum	*Amelanchier alnifolia* (2)	S	S	CP
	A. bakeri (2)	S	S	CP
	A. florida (1)	S	S	CP
	Amelanchier sp. (1)	S	S	CP
G. japonicum	*Photinia parvifolia* (1)	S	SE	SE
	P. laevis var. *villosa* (1)	S	SE	SE
	P. villosa (3)	S	SE	SE
	Photinia 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	DV
	Malus sp. (1)	S	DV	DV
	Micromelles alnifolia (2)	S	DV	DV
	Sorbaria (?) *japonica* (1)	S	DV	DV
	Sorbus alnifolia (1)	S	DV	DV
	S. commixta (1)	S	DV	DV
	S. japonica (1)	S	DV	DV
G. nelsoni	*Amelanchier alnifolia* (5)	S	R	SP
	A. florida (1)	S	R	SP
	A. laevis (1)	S	R	SP
	Amelanchier sp. (2)	S	R	SP
G. nootkatense	*Malus fusca* (1)	DV	DV	CP
	Malus sp. (3)	DV	DV	CP
	Sorbus sitchensis (1)	DV	DV	CP
	S. sitchensis var. occidentalis (1)	DV	DV	CP
	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
	Malus 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. halliana (1)	S	SE	MR
	M. pumila (2)	S	SE	MR
	M. sieboldii (1)	S	SE	MR
	M. spectabilis (1)	S	SE	MR
*G. vauqueliniae**	*Vauquelinia californica* (1)	S	DE	DE

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

Species[a]	Host plant (No. of specimens examined)	Surface structure of peridial cell walls[b]		
		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
Roestelia sp.	*Sorbus cuspidata* (HMAS 67336, 67338)	S	R	SE
	Sorbus globosa (HMAS 45208)	S	R	SE
	S. rufopilosa (HMAS 67335)	S	R	SE
	Sorbus sp. (HMAS 00362, 45209)	S	R	SE

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.

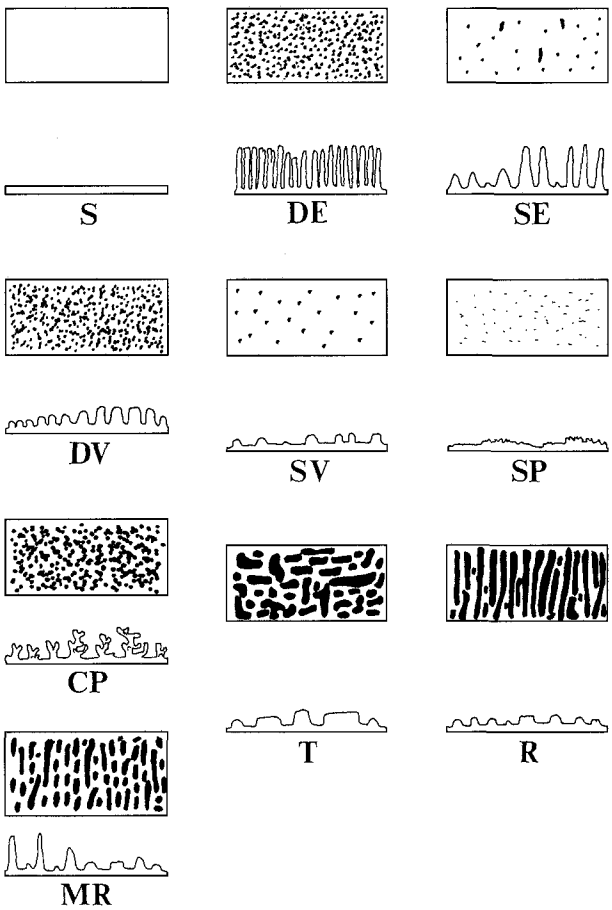

Fig. 1. Schematic illustration of surface structure types of peridial cells of *Gymnosporangium* and *Roestelia*.

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

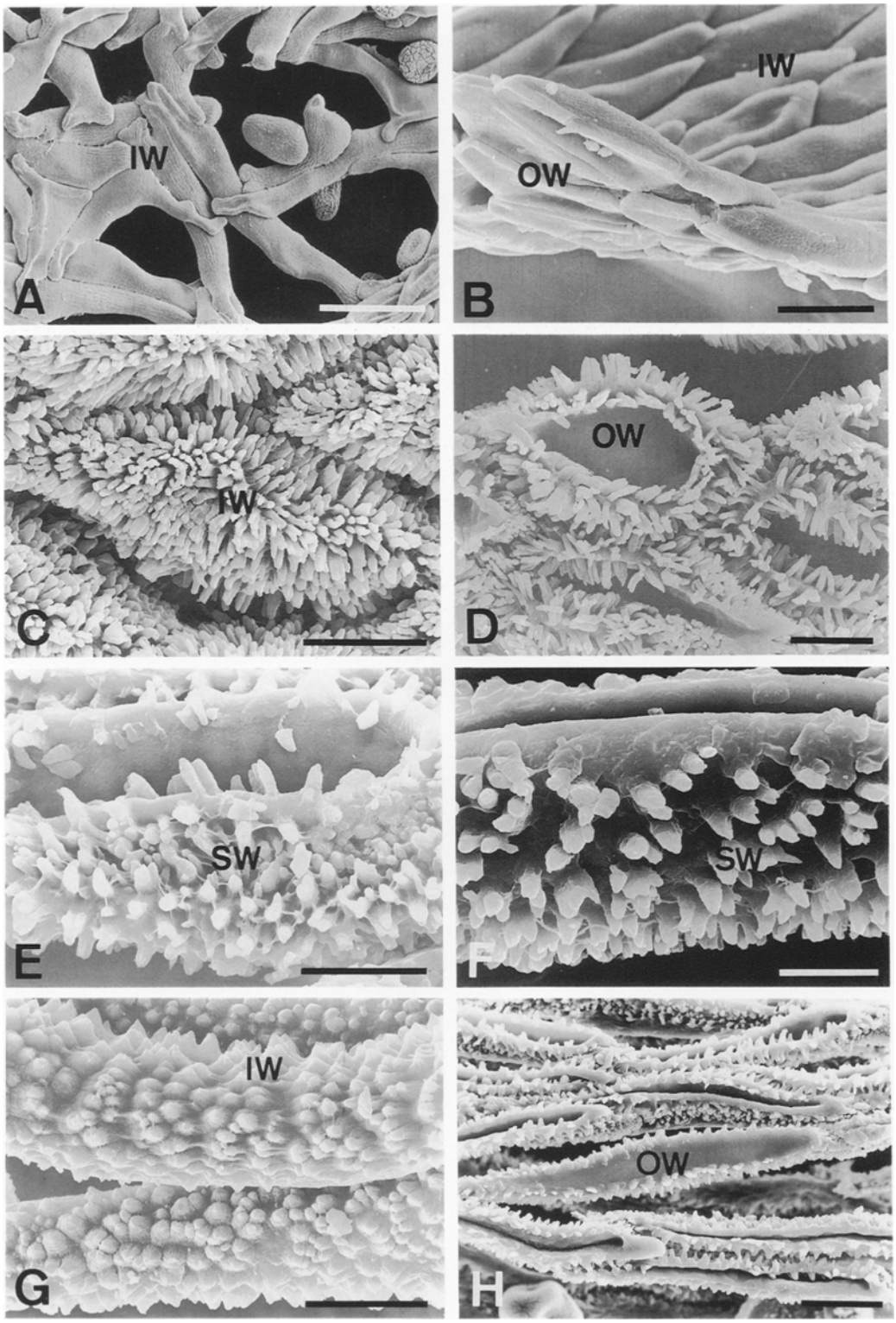

Fig. 2. Scanning electron micrographs of surface structures of the peridial cells of *Gymnosporangium* species.
A. *G. biseptatum* on *Amelanchier oblongifolia* (type S). B. *G. hyalinum* on *Crataegus quasita* (Type S). C, D. *G. exiguum* on *C. tracyi* (type DE). E. *G. cunninghamianum* Barcl. on *Pyrus pashia*. (type SE). F. *G. fuscum* Hedw. f. on *P. communis* (type SE). G. *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.

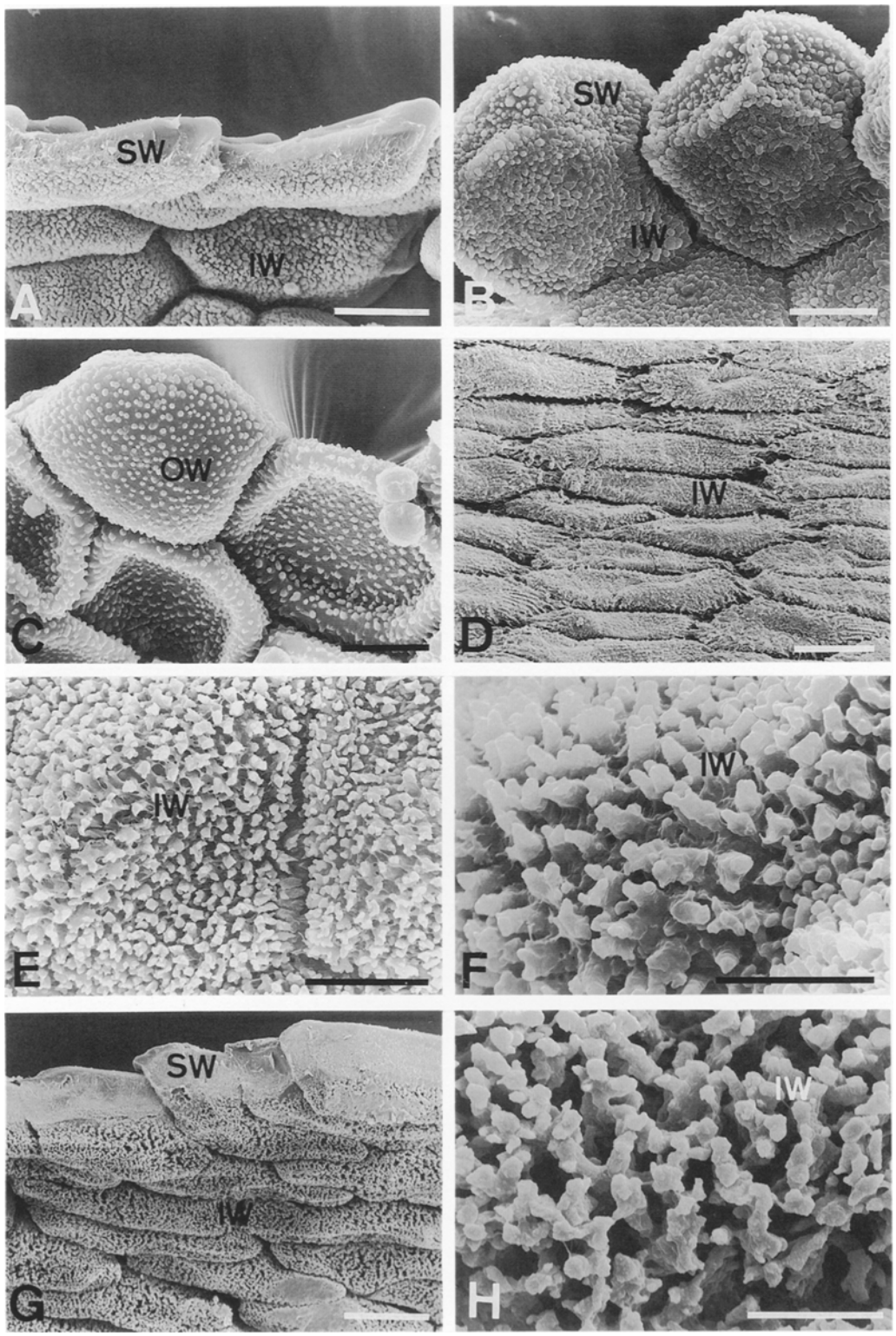

Fig. 3. Scanning electron micrographs of surface structures of the peridial cells of *Gymnosporangium* species.
A. *G. miyabei* on *Malus* sp. (type DV). B. *G. ellisii* on *Myrica cerifera* (type DV). C. *G. ellisii* on *M. cerifera* (type SV). D. *G. cornutum* Arth. ex Kern on (type SP). E, F. *G. 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.

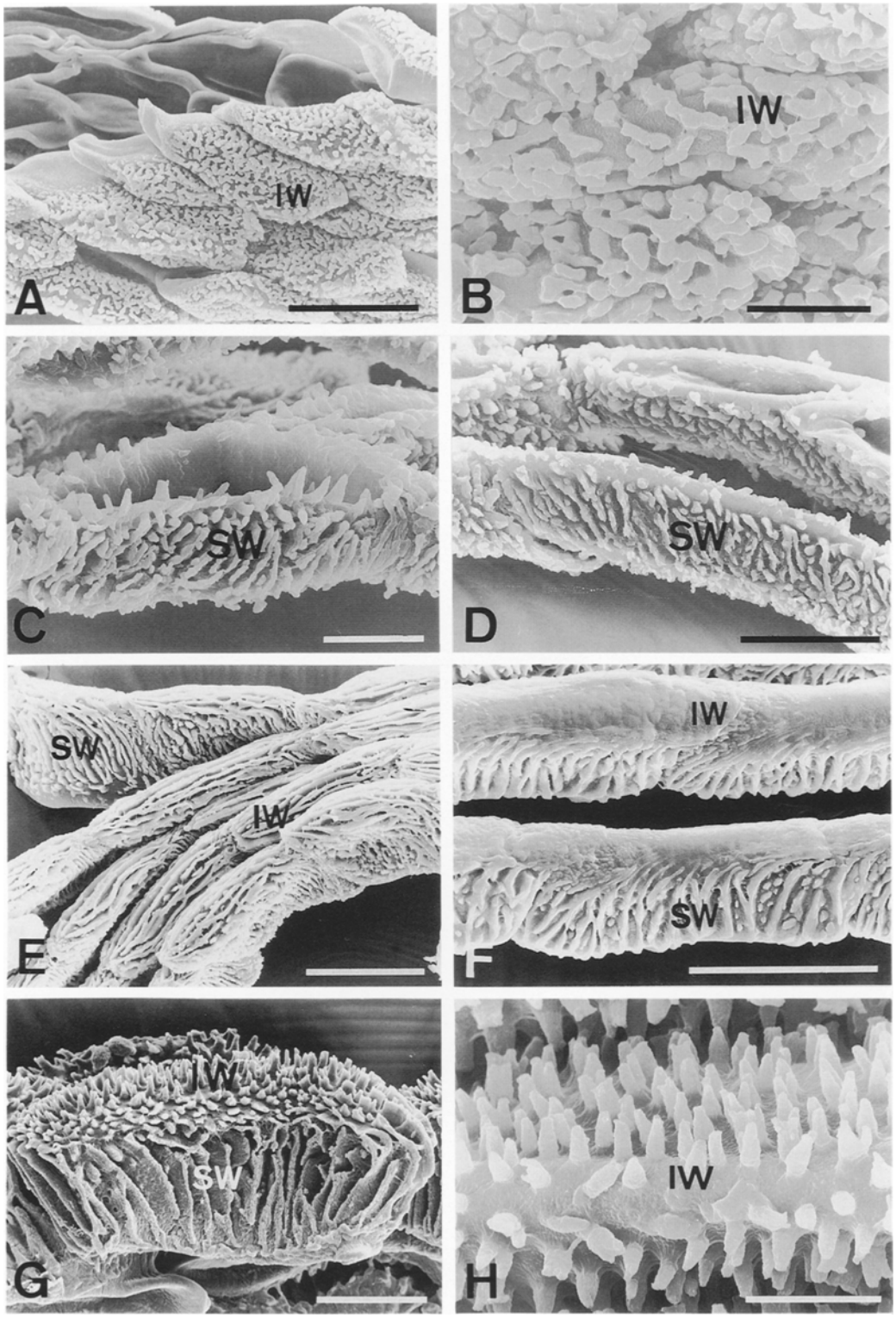

Fig. 4. Scanning electron micrographs of surface structures of the peridial cells of *Gymnosporangium* and *Roestelia* species. A, B. *G. clavipes* on *Amelanchier* sp. (type T). C. *G. trachysorum* Kern on *Crataegus* sp. (type MR). D. *G. guatemalianum* (Crowell) Cumm. on *A. nervosa*. E. *G. tremelloides* 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 μm) 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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