

Aeciospore surface structures of *Gymnosporangium* and *Roestelia* (Uredinales)*

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Aeciospore surface structures of 40 *Gymnosporangium* species and 7 *Roestelia* species were investigated with a scanning electron microscope. The surface structures of aeciospores were classified into 12 types on the basis of shape and size of processes. Surface structures of the aeciospores were stable within each species. Therefore, it is suggested that surface structures of aeciospores could be used as an important diagnostic criteria in identifying *Gymnosporangium* and *Roestelia* species.

Key Words—aeciospore; *Gymnosporangium*; *Roestelia*; rust fungi; Uredinales.

The genus *Gymnosporangium* is characterized by typically two-celled teliospores which have one to several germ pores but most often two per cell and long pedicels. These long pedicels swell and then gelatinize when they absorb water. Many species have type 4 spermogonia and roestelioid aecia, although aecidioid aecia are found in some species. Many species have a heteroecious life cycle and produce telia on species of Cupressaceae and aecia with or without spermogonia on species of Rosaceae. *Gymnosporangium* species are mainly distributed in the northern hemisphere, and 57 species have been reported (Kern, 1973). They also cause considerable damage to horticultural plants when both aecial and telial host plants are planted nearby. *Roestelia* is an anamorphic genus of *Gymnosporangium*. However, those that form roestelioid aecia without definite connection to a teleomorph are also treated as *Roestelia*. Fourteen species of *Roestelia* have been reported (Kern, 1973).

Taxonomic studies on *Gymnosporangium* and *Roestelia* had been undertaken mainly by Hiratsuka (1936a–d, 1937), Parmelee (1965, 1971), Kern (1911, 1973), Ziller (1974), Peterson (1982) and Wang and Lin (1985). They used such morphological characteristics as aecial structures, surface structures of peridial cells, and shape, size and color of aeciospores as important taxonomic criteria. Parmelee (1965, 1971) observed the aeciospore surface structures of 16 species collected in Canada by light microscopy (LM) and reported that most species were densely verrucose but some species densely minutely or evenly verrucose. Holm (1971) also examined aeciospore surface ornamentation of 36 species of *Gymnosporangium* by LM and reported that

the standard type of surface structure was finely or densely verrucose. As indicated by Holm (1984), aeciospore surface structures of *Gymnosporangium* species have been described as verrucose or something similar, and one gets the impression that the aeciospores all look much the same in their surface structures.

Many researchers have demonstrated that the fine structures of spore surface clarified by scanning electron microscopy (SEM) are helpful in taxonomy of the Uredinales (Hiratsuka, 1971; Hiratsuka and Kaneko, 1975; Katsuya et al., 1980; Sato and Sato, 1982; Gardner and Hodges, 1985; Lohsomboon et al., 1990; Imazu and Kakishima, 1995). Littlefield and Heath (1979) classified aeciospore ornaments into four categories based on morphology of processes on aeciospores observed by SEM.

The fine aeciospore surface structures of *Gymnosporangium* observed by SEM have been reported in only a few species. Holm et al. (1970) showed that the ornamentation of *G. cornutum* Arth. ex Kern is of a relatively uniform verrucosity. Kozar and Netolitzky (1975) reported that *G. clavipes* (Cke. ex Pk.) Cke. ex Pk. had baculate papillae on the aeciospore surface. Takahashi et al. (1978) observed a coronate structure on the aeciospore surface of *G. asiaticum* Miyabe ex Yamada. Sato and Sato (1982) studied the morphology of aeciospore surface structure of 70 species in 30 rust genera and classified them into eight types based on morphological differences of aeciospore processes. In their study, three types of surface structures, coronate, verrucose, and annulate, were observed in 6 species of *Gymnosporangium*. These observations by SEM showed that *Gymnosporangium* species have variable surface structures, including verrucose, annulate, coronate and baculate processes on their aeciospores. However, aeciospore surface structures of many other species are unknown.

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The present study was carried out to clarify surface structures on aeciospores of the *Gymnosporangium* and *Roestelia* species, and to evaluate their diagnostic significance at the species level.

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 States 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); and 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 288 specimens including 40 species of *Gymnosporangium* and seven species of *Roestelia* were observed in relation to host plants and localities (Tables 1, 2). Specimens were re-identified according to Kern (1973), and the names of host plants were according to Phipps et al. (1990).

For SEM, spores obtained from the specimens were dusted on double-sided adhesive tape on specimen holders, then coated with platinum-palladium with a Hitachi E-1030 Ion Sputter. The spores were examined by SEM with a Hitachi S-4200 instrument operating at 15 kV.

Results

Aeciospore surfaces of the 40 *Gymnosporangium* species and 7 *Roestelia* species observed by SEM exhibited various types of processes. These surface structures were classified into 12 types based on the shapes and sizes of the processes. A schematic view of these types is shown in Fig. 1. Surface structure types of *Gymnosporangium* species and *Roestelia* species are shown in Tables 1 and 2, respectively. The 12 types are as follows.

1. Type LC (large coronate): Basal parts of processes are columnar or cylindrical, and upper parts are divided into several long protuberances. These processes are 0.7–1.2 μm in height. Protuberances are of variable length among species and their tips are round to slightly acute (Figs. 1; 2A–F). This type was found on aecio-

spores of nine *Gymnosporangium* and one *Roestelia* species (Tables 1, 2). Coronate processes of *G. exiguum* Kern, *G. kernianum* Bethel. and *G. vauquelinae* Long ex Gooding showed irregularity in number, size and position of the divided small protuberances; but constancy as a surface structure was recognized because all the processes on an aeciospore exhibited coronate features, and aeciospores from all the specimens showed the same surface structure (Table 1; Figs. 1; 2C–F).

2. Type SC (small coronate): Processes are morphologically similar to type LC but smaller in height, 0.3–0.6(–0.8) μm (Figs. 1; 2G, H). This type was observed on aeciospores of 14 *Gymnosporangium* and 1 *Roestelia* species (Tables 1, 2).

3. Type MC (minutely coronate): Processes are morphologically similar to types LC and SC, but protuberances are very small and sometimes granulate. Variable size of processes (0.2–1.2 μm in height) is observed on the same aeciospore. Small processes of this type are similar to type SV (Figs. 1; 3A, B). Five *Gymnosporangium* species and one *Roestelia* species were of this type (Tables 1, 2).

4. Type M (mountain-shaped): Processes are mountain-shaped and very large, 0.5–1.2 μm in height and 0.6–4 μm in width. Heads of processes are acutely and roughly dentate. This type is similar to type LC, but different in the width of processes and the shape of their heads (Figs. 1; 3C, D). Aeciospores of *G. biseptatum* Ellis have this type of processes (Table 1).

5. Type E (echinulate): Processes of this type are echinulate and large, 0.8–2.0 μm in height. Two or more processes sometimes joined together to exhibit a coronate feature (Figs. 1; 3E–H). However, this type is different from type LC in the size of processes. Aeciospores of *G. clavariiforme* (Pers.) DC., *G. tremelloides* Hartig, and *G. clavipes* are of this type. In the case of *G. clavipes*, 2–10 or more echinulate processes were grouped on a broad frustum-like base on aeciospores (Figs. 1; 3G, H).

6. Type SA (small annulate): Processes are 0.5–1.0 μm in height and have 2–4 annulations. They gradually decrease in size toward the top in a pagoda-like form. Processes are usually connected by reticulate ridges (Figs. 4A, B). Types LC and MC have also annulations on basal parts of their processes. However, heads of their processes are echinulate or granulate whereas those of type SA are smooth. Aeciospores of *G. inconspicuum* Kern and *G. speciosum* Pk. are of this type (Table 1).

7. Type LA (large annulate): Processes are 1.0–2.2(–2.5) μm in height and aciculate or echinulate. Annulations are minutely crenulate or dentate. Minute papillae or verrucae are interspersed among the processes (Figs. 1; 4C–F). This type was observed on aeciospores of *R. distorta* (Arth. ex Cumm.) Kern and one unidentified species (Table 2).

8. Type T (tubulate): Processes are 0.5–0.8 μm in height, thick and tube-like (Figs. 1; 4G, H). This type is identical with the tubulate type of Sato and Sato (1983). Aeciospores of *G. exterum* Arth. ex Kern have this type of processes (Table 1).

Table 1. Aeciospore surface structure types of *Gymnosporangium* species.

Species	Host plant (No. of specimens examined)	Surface structure type ^{a)}	
<i>G. amelanchieris</i>	<i>Amelanchier asiatica</i> (4)	MC	
	<i>A. ovalis</i> (3)	MC	
	<i>A. vulgaris</i> (2)	MC	
	<i>Aronia rotundifolia</i> (?) (1)	MC	
<i>G. asiaticum</i>	<i>Chaenomeles extusoccine</i> (1)	LC	
	<i>C. speciosa</i> (3)	LC	
	<i>Cydonia oblonga</i> (1)	LC	
	<i>C. japonica</i> (1)	LC	
	<i>Pyrus betulaefolia</i> (1)	LC	
	<i>P. pyrifolia</i> (2)	LC	
	<i>P. pyrifolia</i> var. <i>culta</i> (1)	LC	
	<i>Juniperus virginiana</i> (3)	SC	
<i>G. bermudianum</i>	<i>Juniperus</i> sp. (1)	SC	
	<i>Crataegus douglasii</i> (5)	SC	
<i>G. betheli</i>	<i>C. rivularis</i> (1)	SC	
	<i>C. succulenta</i> (1)	SC	
	<i>Crataegus</i> sp. (2)	SC	
<i>G. biseptatum</i>	<i>Amelanchier canadensis</i> (3)	M	
	<i>A. oblongifolia</i> (1)	M	
	<i>Amelanchier</i> sp. (1)	M	
<i>G. clavariiforme</i>	<i>Amelanchier alnifolia</i> (2)	E	
	<i>A. bartramiana</i> (1)	E	
	<i>A. wiegandii</i> (2)	E	
	<i>Cotoneaster integerrima</i> (1)	E	
	<i>Crataegus maximowiczii</i> (1)	E	
	<i>C. oxyacantha</i> (2)	E	
	<i>C. sanguinea</i> (1)	E	
	<i>Cydonia vulgaris</i> (1)	E	
	<i>Amelanchier alnifolia</i> (1)	E	
<i>G. clavipes</i>	<i>A. bartramiana</i> (1)	E	
	<i>Amelanchier</i> sp. (2)	E	
	<i>Aronia melanocarpa</i> (2)	E	
	<i>Crataegus</i> sp. (4)	E	
	<i>Cydonia vulgaris</i> (2)	E	
	<i>Malus</i> sp. (1)	E	
	<i>Sorbus americana</i> (1)	E	
	<i>Crataegus lavalleyi</i> (1)	SA	
	<i>C. oxyacantha</i> var. <i>pauli</i> (1)	SA	
	<i>C. punctata</i> (1)	SA	
	<i>Crataegus</i> sp. (2)	SA	
	<i>G. confusum</i>	<i>Cotoneaster foveolatus</i> (1)	LC
		<i>Crataegus altaica</i> (1)	LC
<i>C. monogyna</i> (1)		LC	
<i>C. oxyacantha</i> (1)		LC	
<i>Crataegus</i> sp (1)		LC	
<i>Cydonia</i> sp. (1)		LC	
<i>Mespilus germanica</i> (1)		LC	
<i>Pyrus lanata</i> (1)		LC	
<i>G. connersii</i>	<i>Crataegus chrysocarpa</i> (4)	SC	
	<i>C. douglasii</i> (1)	SC	
	<i>C. succulenta</i> (1)	SC	
<i>G. corniculans</i>	<i>Amelanchier alnifolia</i> (2)	LC	

a) E: type E (echinulate); LA: type LA (large annulate); LC: type LC (large coronate); LV: type LV (large verrucose); M: type M (mountain-shaped); MC: type MC (minutely coronate); N: type N (nail-headed); RV: type RV (verrucose with refractive granules); SA: type SA (small annulate); SC: type SC (small coronate); SV: type SV (small verrucose); T: type T (tubulate).

Table 1. Continued.

Species	Host plant (No. of specimens examined)	Surface structure type ^{a)}	
<i>G. cornutum</i>	<i>A. canadensis</i> (1)	LC	
	<i>A. laevis</i> (1)	LC	
	<i>Amelanchier</i> sp. (2)	LC	
	<i>Malus diversifolia</i> (1)	MC	
	<i>M. fusca</i> (1)	MC	
	<i>Pyrus aucuparia</i> (?) (1)	MC	
	<i>Sorbus americana</i> (2)	MC	
	<i>S. aucuparia</i> (6)	MC	
	<i>S. decora</i> (1)	MC	
	<i>S. hybrida</i> (1)	MC	
	<i>S. sambucifolia</i> (1)	MC	
	<i>Sorbus</i> sp. (1)	MC	
	<i>G. cunninghamianum</i>	<i>Cotoneaster bacillaris</i> (3)	LC
<i>Pyrus pashia</i> (4)		LC	
<i>Pyrus</i> sp. (1)		LC	
<i>G. cupressi</i> var. <i>cascadense</i>	<i>Amelanchier pallida</i> (2) (Type specimen (PUR 60309) included)	SC	
<i>G. davisii</i>	<i>Aronia melanocarpa</i> (5)	MC	
<i>G. ellisii</i>	<i>Myrica carolinensis</i> (3)	RV	
	<i>M. cerifera</i> (2)	RV	
	<i>M. gale</i> (1)	RV	
<i>G. exiguum</i>	<i>Crataegus tracyi</i> (2)	LC	
	<i>C. viridis</i> (1)	LC	
	<i>Crataegus</i> sp. (1)	LC	
	<i>Heteromeles salicifolia</i> (3)	LC	
<i>G. exterum</i>	<i>Gillenia stipulata</i> (2)	T	
	<i>G. trifoliata</i> (2)	T	
<i>G. floriforme</i>	<i>Crataegus spathulata</i> (5)	SC	
	<i>C. raleighensis</i> (1)	SC	
	<i>Crataegus</i> sp. (1)	SC	
<i>G. fraternum</i>	<i>Aronia arbutifolia</i> (4)	LC	
	<i>A. atropurpurea</i> (1)	LC	
	<i>A. melanocarpa</i> (1)	LC	
	<i>Aronia</i> sp. (1)	LC	
	<i>Pyrus arbutifolia</i> (?) (1)	LC	
<i>G. fuscum</i>	<i>Pyrus communis</i> (10)	SC	
<i>G. fusisporum</i>	<i>Cotoneaster integerrima</i> (2)	MC	
<i>G. globosum</i>	<i>Crataegus beata</i> (1)	SC	
	<i>C. caesia</i> (1)	SC	
	<i>C. chrysocarpa</i> (1)	SC	
	<i>C. fuscosa</i> (1)	SC	
	<i>C. pedicellatus</i> (1)	SC	
	<i>Crataegus</i> sp. (1)	SC	
	<i>Malus domestica</i> (2)	SC	
	<i>M. sylvestris</i> (1)	SC	
	<i>Malus</i> sp. (1)	SC	
	<i>Pyrus americana</i> (1)	SC	
	<i>Sorbus tianschanica</i> (1)	SC	
	<i>G. guatemalianum</i>	<i>Amelanchier nervosa</i> (Type specimen (PUR 49372) included)	SC
		<i>Amelanchier</i> sp. (1)	SC
<i>G. harknessianum</i>	<i>Amelanchier alnifolia</i> (3)	N	
	<i>A. florida</i> (1)	N	
	<i>Amelanchier</i> sp. (1)	N	
<i>G. hyalinum</i>	<i>Crataegus quasita</i> (1)	SV	
<i>G. inconspicuum</i>	<i>Amelanchier alnifolia</i> (2)	SA	

Table 1. Continued.

Species	Host plant (No. of specimens examined)	Surface structure type ^{a)}
	<i>A. bakeri</i> (2)	SA
	<i>A. florida</i> (1)	SA
<i>G. japonicum</i>	<i>Amelanchier</i> sp. (1)	SA
	<i>Photinia parvifolia</i> (1)	SC
	<i>P. laevis</i> var. <i>villosa</i> (1)	SC
	<i>P. villosa</i> (3)	SC
	<i>Photinia</i> sp. (2)	SC
<i>G. juniperi-virginianae</i>	<i>Malus coronaria</i> (3)	SC
	<i>M. pumila</i> (1)	SC
	<i>Malus</i> sp. (4)	SC
<i>G. kernianum</i>	<i>Amelanchier alnifolia</i> (2)	LC
	<i>Crataegus oxyacantha</i> (1)	LC
<i>G. libocedri</i>	<i>Amelanchier alnifolia</i> (1)	RV
	<i>A. florida</i> (1)	RV
	<i>Crataegus douglasii</i> (2)	RV
<i>G. miyabei</i>	<i>Malus sieboldii</i> (1)	LV
	<i>Malus</i> sp. (1)	LV
	<i>Micromelles alnifolia</i> (2)	LV
	<i>Sorbaria</i> (?) <i>japonica</i> (1)	LV
	<i>Sorbus alnifolia</i> (1)	LV
	<i>S. commixta</i> (1)	LV
	<i>S. japonica</i> (1)	LV
<i>G. nelsoni</i>	<i>Amelanchier alnifolia</i> (5)	LC
	<i>A. florida</i> (1)	LC
	<i>A. laevis</i> (1)	LC
	<i>Amelanchier</i> sp. (2)	LC
<i>G. nootkatense</i>	<i>Malus fusca</i> (1)	N
	<i>Malus</i> sp. (3)	N
	<i>Sorbus sitchensis</i> (1)	N
	<i>S. sitchensis</i> var. <i>occidentalis</i> (1)	N
	<i>Sorbus</i> sp. (2)	N
<i>G. speciosum</i>	<i>Fendlera rupicola</i> (5)	SA
	<i>Philadelphus microphyllus</i> (1)	SA
	<i>P. occidentalis</i> (1)	SA
	<i>P. rugosus</i> (1)	SA
<i>G. torminali-juniperinum</i>	<i>Sorbus torminalis</i> (1)	MC
	<i>Sorbus</i> sp. (1)	MC
<i>G. trachysorum</i>	<i>Crataegus marshallii</i> (1)	SC
	<i>Crataegus</i> sp. (1)	SC
<i>G. tremelloides</i>	<i>Cotoneaster frigidus</i> (?) (1)	E
	<i>Malus sylvestris</i> (3)	E
	<i>M. domestica</i> (4)	E
	<i>Malus</i> sp. (2)	E
	<i>Sorbus scopulina</i> (2)	E
	<i>S. sitchensis</i> (4)	E
<i>G. turkestanicum</i>	<i>Sorbus tianschanica</i> (1)	SC
<i>G. vauqueliniae</i>	<i>Vauquelinia californica</i> (1) (Type specimen (PUR 48928) included)	LC
<i>G. yamadae</i>	<i>Malus asiatica</i> (1)	SC
	<i>M. halliana</i> (1)	SC
	<i>M. pumila</i> (2)	SC
	<i>M. sieboldii</i> (1)	SC
	<i>M. spectabilis</i> (1)	SC

Table 2. Aeciospore surface structure types of *Roestelia* species.

Species	Host plant (No. of specimens examined)	Surface structure type ^{b)}
<i>R. brucensis</i>	<i>Juniperus horizontalis</i> (7) (Isotype specimen (DAOM 91910) included)	SC
<i>R. distorta</i>	<i>Cotoneaster bacillaris</i> (5) (Type specimen (PURF 1890) included)	LA
	<i>C. roseus</i> (1)	LA
<i>R. fenzeliana</i>	<i>Malus kansuensis</i> (1)	LC
	<i>M. kansuensis</i> f. <i>calva</i> (1)	LC
<i>R. pourthiaeeae</i>	<i>Photinia villosa</i> var. <i>laevis</i> (2)	RV
<i>R. nanwutiana</i>	<i>Cotoneaster soongoricus</i> (2)	MC
<i>R. wenshanensis</i>	<i>Photinia villosa</i> var. <i>laevis</i> (1)	RV
<i>Roestelia</i> sp. ^{a)}	<i>Sorbus</i> sp. (HMAS 00362)	LA
	<i>S. cuspidata</i> (HMAS 67336, 67338)	LA
	<i>S. rufopilosa</i> (HMAS 67335)	LA

a) Species collected in China and labelled as *G. tremelloides*.

b) LA: type LA (large annulate); LC: type LC (large coronate); MC: type MC (minutely coronate); RV: type RV (verrucose with refractive granules); SC: type SC (small coronate).

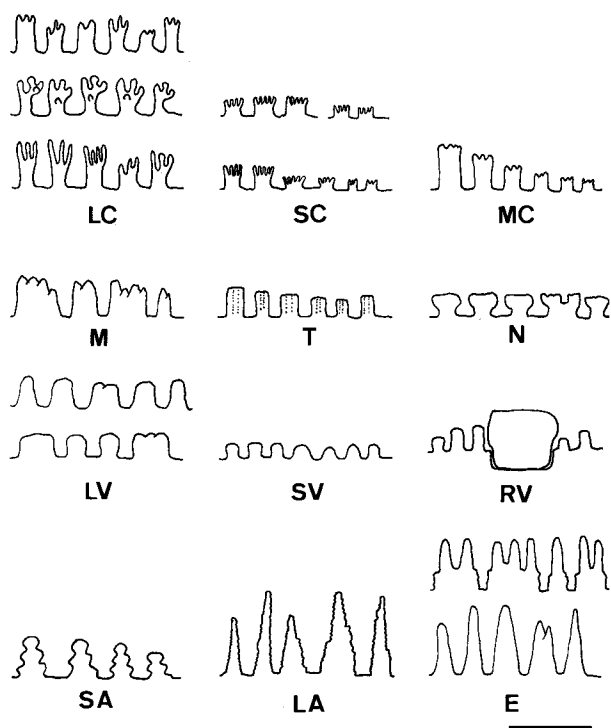


Fig. 1. Schematic view of processes of aeciospore surface structure types.

Type LC (large coronate), type SC (small coronate), type MC (minutely coronate), type M (mountain-shaped), type T (tubulate), type N (nail-headed), type LV (large verrucose), type SV (small verrucose), type RV (verrucose with refractive granules), type SA (small annulate), type LA (large annulate), type E (echinulate). Bar = 2 μ m.

9. Type N (nail-headed): Processes are 0.5–0.8 μ m in height, nail-headed, and peltate. Heads of processes are granulate with small papillae. Basal parts of processes

are cylindrical and connected by narrow reticulate ridges (Figs. 1; 5A, B). This type is similar to the nail-headed type of Sato and Sato (1982) and was observed on aeciospores of *G. nootkatense* Arth. and *G. harknessianum* Arth. (Table 1).

10. Type LV (large verrucose): Processes are large, 0.6–1.3 μ m in height, and verrucose, papillate, columnate, granulate, or sometimes conical. Two or more processes frequently joined together to show sinuate or crenate features (Figs. 1; 5C). Type LV was observed on aeciospores of *G. miyabei* Yamada ex I. Miyake (Table 1).

11. Type SV (small verrucose): Processes are morphologically similar to type LV but smaller in size and uniform, 0.3–0.6 μ m in height (Figs. 1; 5D). *Gymnosporangium hyalinum* Kern ex Cummins have this type of aeciospores (Table 1).

12. Type RV (verrucose with refractive granules): Processes are morphologically similar to type SV, but refractive granules are present among them (Fig. 5E). Four species that have acidoid aecia, *G. ellisii* (Berk.) Ell., *G. libocedri* (P. Henn.) Kern, *R. pourthiaeeae* (Sydow) Kern, and *R. wenshanensis* (Tai) Kern, are of this type (Tables 1, 2).

One to 15 specimens collected on various host plants were observed for each of 47 species. Aeciospore surface structures were found to be stable within each species (Tables 1, 2), except for *G. clavipes*. Types LC, SC, and MC were observed on 28 *Gymnosporangium* species and 2 *Roestelia* species, and the other nine types were observed in a few species each (Tables 1, 2).

Discussion

Sato and Sato (1982) studied aeciospore surface structures on 70 species of 30 rust genera with SEM and classified them into 8 types (verrucose, aciculate, nail-headed, echinulate, coronate, tubulate, annulate and reticu-

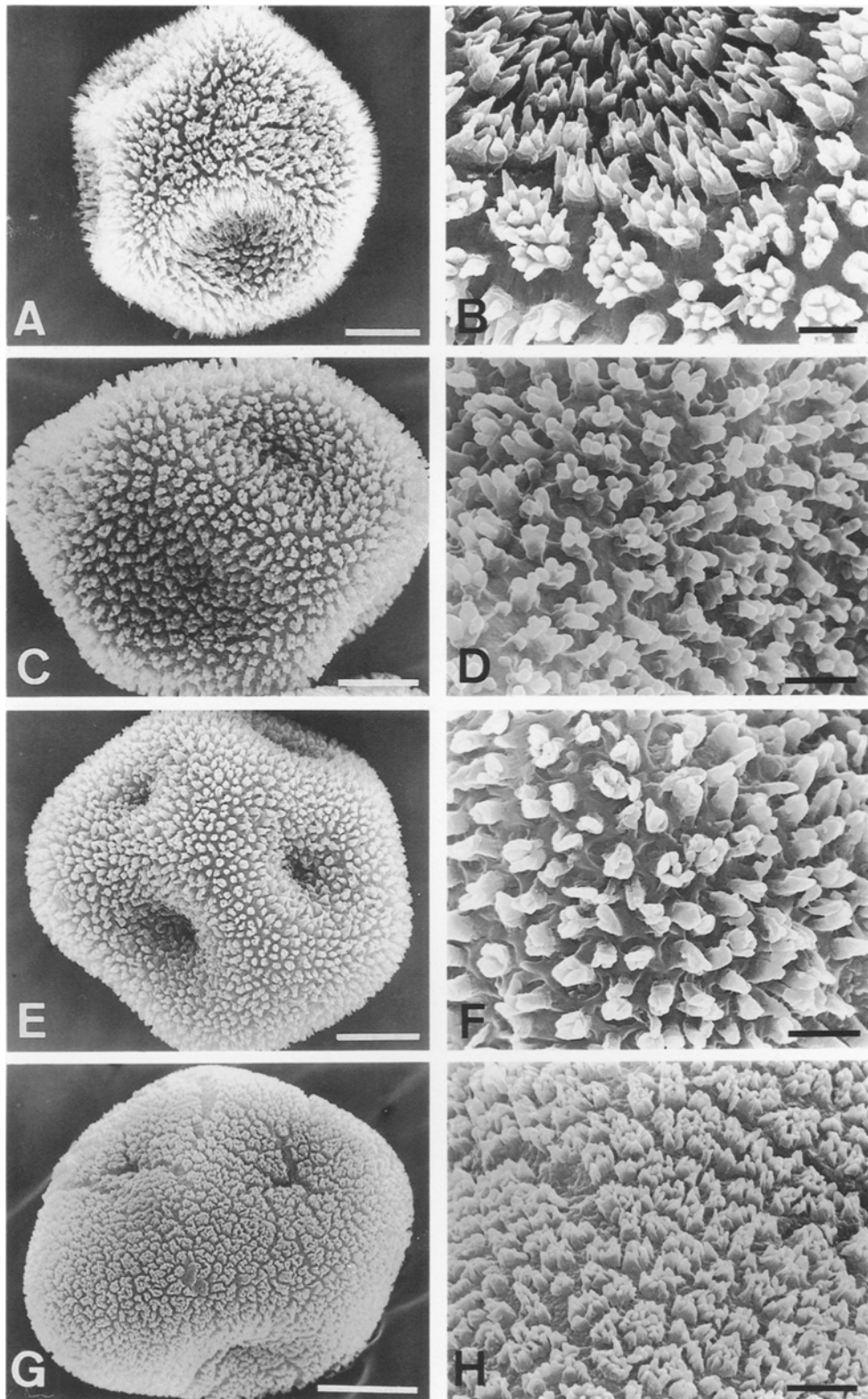


Fig. 2. Scanning electron micrographs of aeciospores of *Gymnosporangium* species.

A, B. *G. cunninghamianum* on *Pyrus pashia* (type LC). C, D. *G. exiguum* on *Crataegus tracyi* (type LC). E, F. *G. nelsoni* Arth. on *Amelanchier alnifolia* (type LC). G, H. *G. trachysorum* Kern on *Crataegus* sp. (type SC). Bar = 5 μ m in Figs. A, C, E, G; 1 μ m in Figs. B, D, F, H.

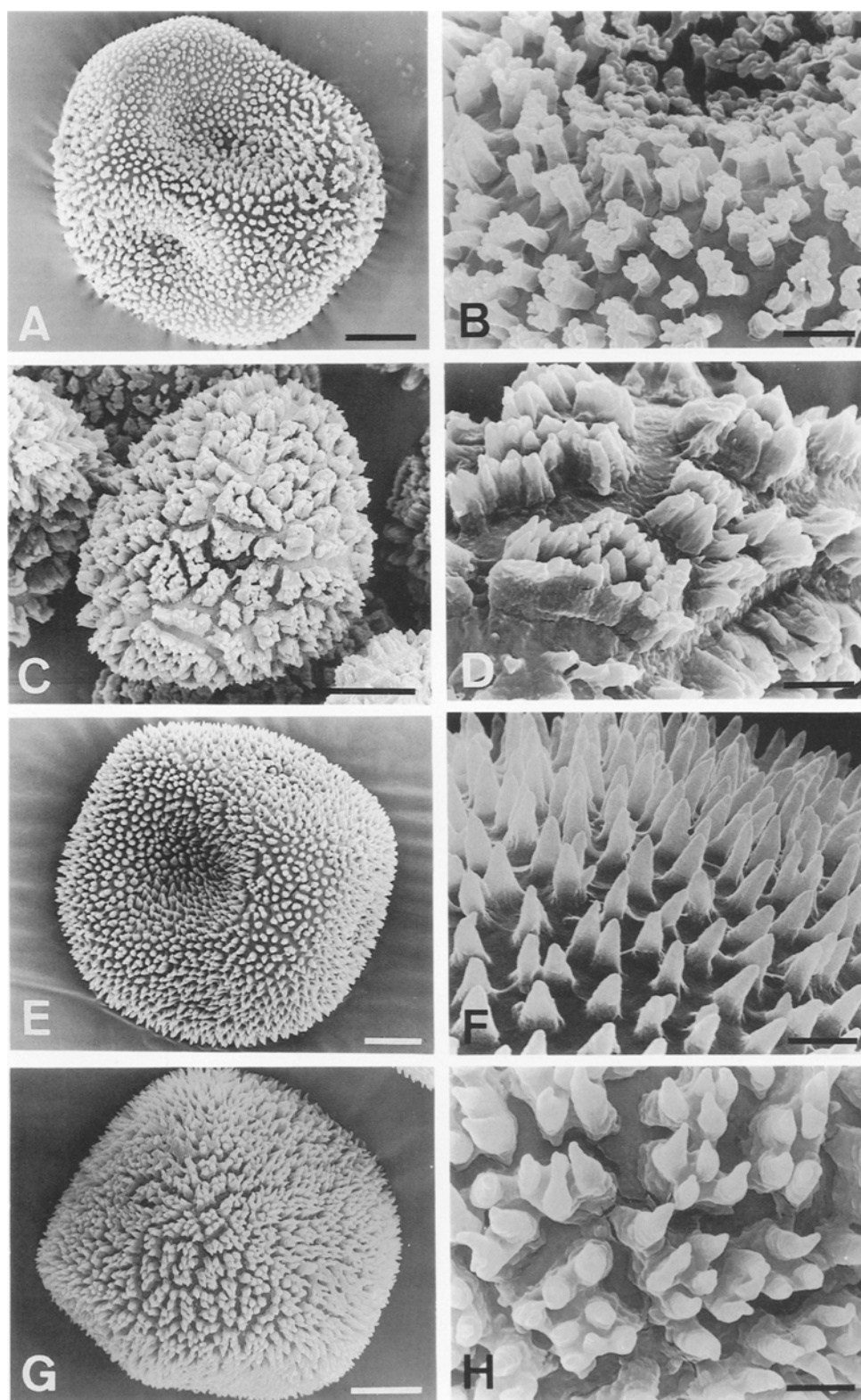


Fig. 3. Scanning electron micrographs of aeciospores of *Gymnosporangium* species. A, B. *G. amelanchieris* Ed. Fisch. ex Kern on *Amelanchier vulgaris* (type MC). C, D. *G. biseptatum* on *Amelanchier oblongifolia* (type M). E, F. *G. tremelloides* on *Sorbus scopulina* (type E). G, H. *G. clavipes* on *Amelanchier alnifolia* (type E). Bar = 5 μm in Figs. A, C, E, G; 1 μm in Figs. B, D, F, H.

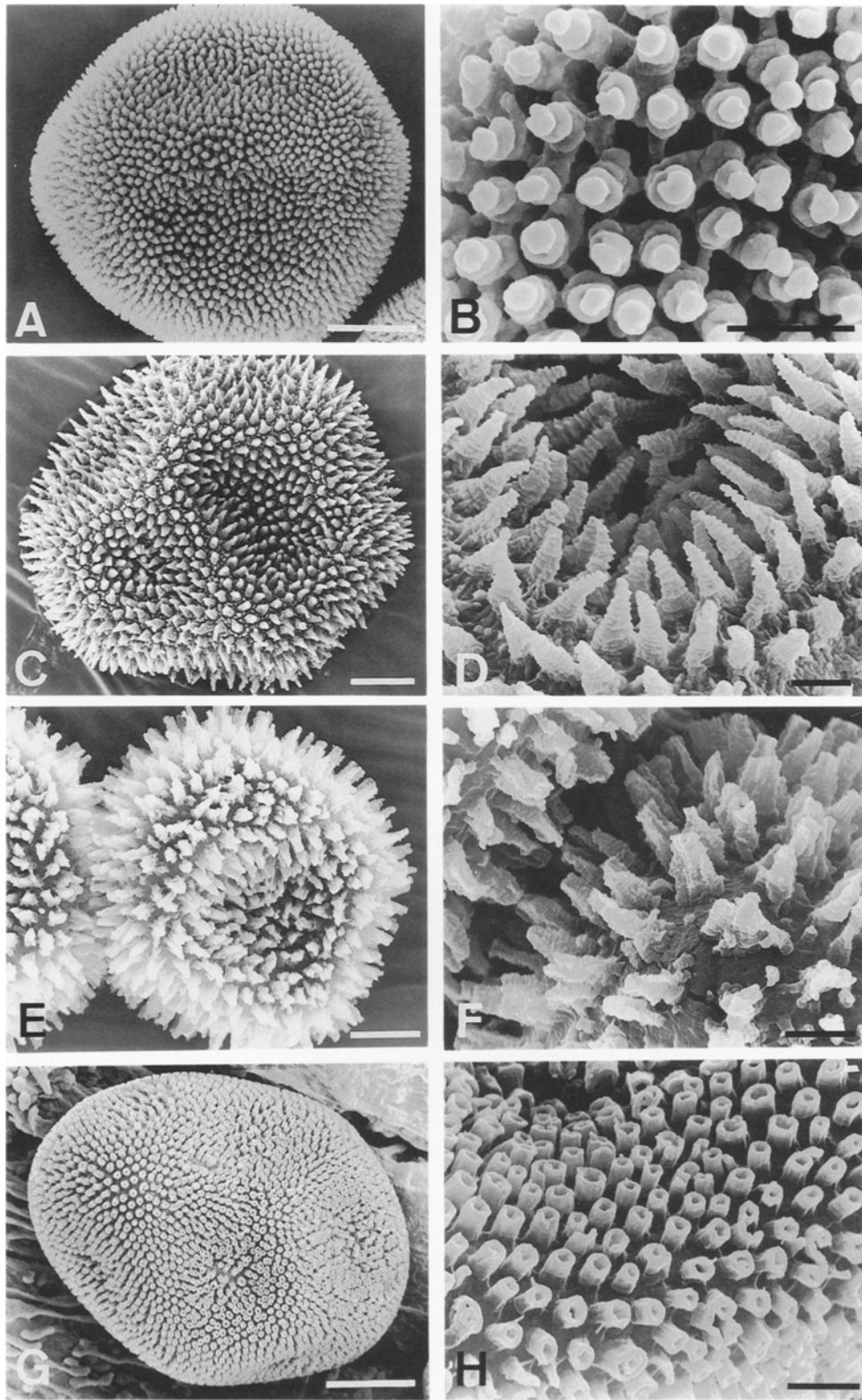


Fig. 4. Scanning electron micrographs of aeciospores of *Gymnosporangium* and *Roestelia* species. A, B. *G. speciosum* on *Philadelphus rugosus* (type SA). C, D. *Roestelia* sp. on *Sorbus* sp. (type LA). E, F. *R. distorta* on *Cotoneaster bacillaris* (type LA). G, H. *G. exterum* on *Gillenia trifoliata* (type T). Bar = 5 μ m in Figs. A, C, E, G; 1 μ m in Figs. B, D, F, H.

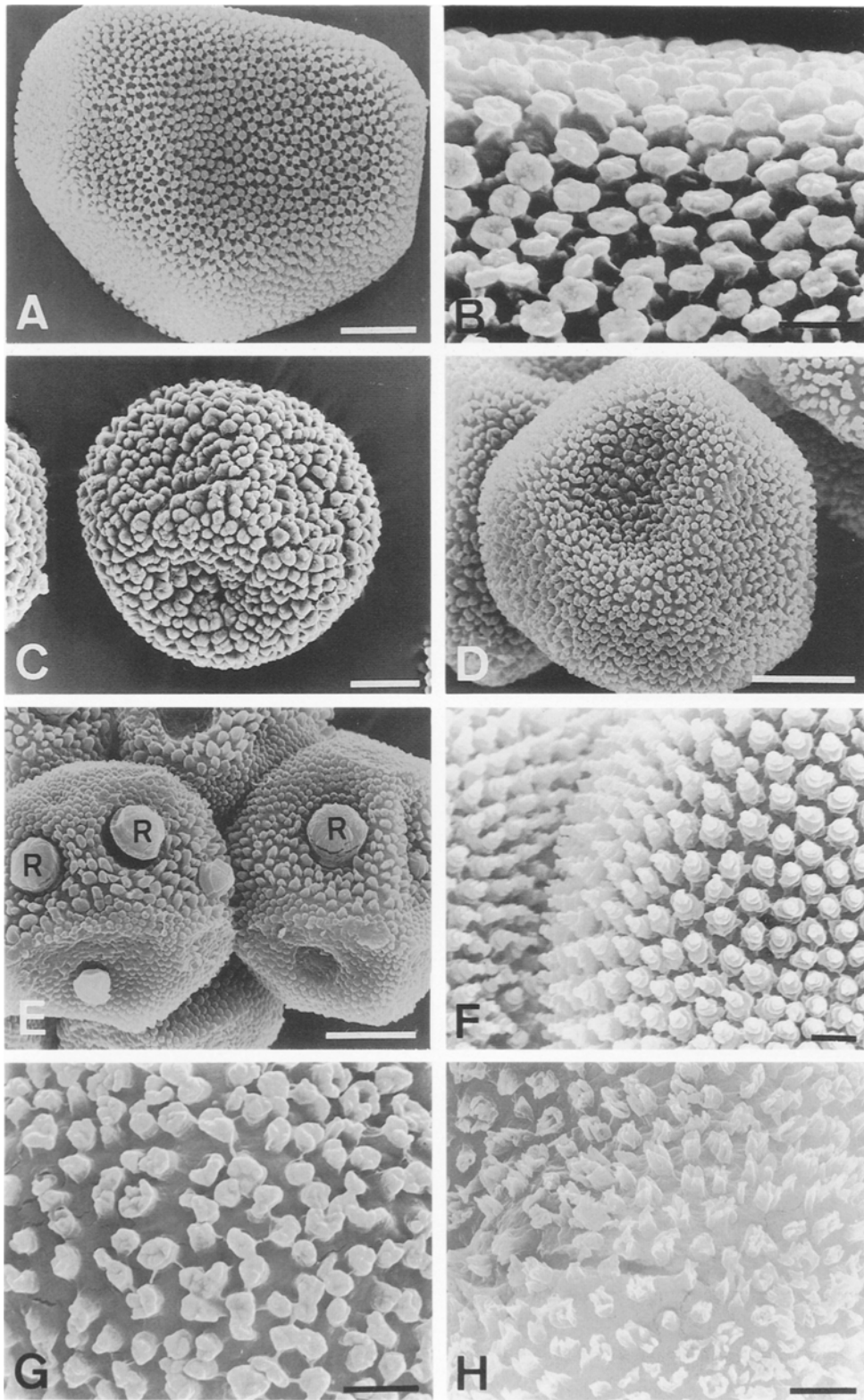


Fig. 5. Scanning electron micrographs of aeciospores of *Gymnosporangium* species.

A, B. *G. nootkatense* on *Pyrus fusca* (type N). C. *G. miyabei* on *Micromeles alnifolia* (type LV). D. *G. hyalinum* on *Crataegus quasita* (type SV). E. *G. libocedri* on *Amelanchier florida* (type RV), R=refractive granules. F. *G. clavipes* on *Crataegus* sp. (type SA). G. *G. cupressi* var. *cascadense*. H. *G. guatemalianum*. Bar=5 μm in Figs. A, C, D, E; 1 μm in Figs. B, F, G, H.

Table 3. Relationship between aeciospore surface structure types of Sato and Sato (1982) and those of the present study.

Type of Sato and Sato (1982)	Type of the present study
Coronate	LC, SC, MC, M
Verrucose	LV, SV, RV
Annulate	LA, SA
Echinulate	E
Nailheaded	N
Tubulate	T
Reticulate	— ^{a)}
Aciculate	—

a) —: not observed in the present study.

late types) based on morphological differences of aeciospore processes. As shown in Table 3, six of the types reported by Sato and Sato (1982), all except the aciculate and reticulate types, were observed in 40 *Gymnosporangium* species and 7 *Roestelia* species (Tables 1–3). Based on the shape and size of processes, the coronate, verrucose, and annulate types of Sato and Sato (1982) were subdivided into several types (Table 3). Types LC, SC, MC, and M were included in the coronate type of Sato and Sato (1982), being distinguished from each other by the shape and size of processes. The annulate type of Sato and Sato (1982) was divided into two types, SA and LA. Processes of type LA are ca. 2 times larger than those of type SA. Although types LC and MC have sometimes annulations on basal parts of their processes, types LA and SA are clearly different from types LC and MC in the shape of upper parts of the processes. The verrucose type of Sato and Sato (1982) was divided into three types, LV, SV, and RV, based on the size of processes and the presence or absence of refractive granules (Fig. 5E). Aeciospore surface structures of types E, N, and T were similar to the echinulate, nailheaded, and tubulate types of Sato and Sato (1982), respectively (Table 3).

Sato and Sato (1982) suggested that the coronate surface structure may be the principal type among *Gymnosporangium* species. The present SEM observation supports this suggestion, because coronate types including types LC, SC, MC, and M were observed in 30 species (ca. 64%) among the 47 species of *Gymnosporangium* and *Roestelia* (Tables 1, 2). Types LC and SC were most frequently observed among the coronate types, appearing in 10 and 14 species, respectively (Tables 1, 2). Most of the species having coronate aeciospore surface structures produce aecia on species of the subfamily Maloideae in the Rosaceae (Tables 1, 2), the principal aecial host plants of *Gymnosporangium* species (Kern, 1973). Some species produce aecia on species of Spiraeoideae (subfamily of the Rosaceae), Myricaceae, Hydrangiaceae, and Cupressaceae (Kern, 1973; Tables 1, 2). However, no correlation between the aeciospore surface structure types and the groups of aecial host plants was recognized.

It has been suggested that fungal species belonging to the same genus generally have the same or similar spore surface structures (Kukkonen, 1969; Hiratsuka and Kaneko, 1975; Kakishima, 1980; Udagawa and Horie, 1973; Sato and Sato, 1982; Holm, 1984). However, 12 types of surface structures were recognized in *Gymnosporangium*. Therefore, aeciospores of *Gymnosporangium* species are morphologically variable, as reported by Holm (1980, 1984) and Cummins and Hiratsuka (1983).

Holm et al. (1970) observed aeciospore ornamentation of *G. cornutum* on *Sorbus aucuparia* L. collected in Sweden by SEM and reported that it is a relatively uniform in verrucosity. However, aeciospores of type MC were observed in 15 specimens of *G. cornutum* on nine host plants belonging to *Malus*, *Pyrus* (?), and *Sorbus* collected in Europe, Asia, and North America (Table 1). Therefore, reidentification of the specimen used by Holm et al. (1970) will be required to clarify these differences.

Kozar and Netolitzky (1975) reported that aeciospores of *G. clavipes* on leaves and fruits of *Amelanchier* sp. collected in Alberta, Canada had surface structures characterized by “a dense covering of baculate projections.” We examined aeciospore surface structures of 19 specimens of *G. clavipes* on different host plants in six genera collected in North America. Among 19 specimens, aeciospore surface structures of 14 specimens were of type E (Table 2; Figs. 3G, H), and those of 5 specimens on *Crataegus* spp. collected in USA were of type SA (Table 2; Fig. 5F). From the morphological observation, it was also recognized that peridial cells of specimens of type E are more linear than those of specimens of type SA, and aeciospore walls of specimens of type E are thicker than those of type SA. Therefore, taxonomic re-examination of this species is necessary.

Aeciospore surface structure of *G. tremelloides* on *Malus* and *Sorbus* collected in Europe and North America is type E (Table 1; Figs. 3E, F). However, aeciospores of four specimens on *Sorbus* spp. collected in China and labeled as *G. tremelloides* were of type LA (Table 2; Figs. 4C, D). These four specimens have peridial cells with smooth outer walls, rugose side walls and echinulate inner walls. These surface structures of peridial cells are different from the descriptions of *G. tremelloides* by Kern (1973). The specimens also have thinner aeciospore walls (1–2.5 μm) than *G. tremelloides* (3–5 μm) (Kern, 1973). Therefore, we have treated these specimens as *Roestelia* sp. (Table 2).

Peterson (1982) reported that four *Gymnosporangium* species, *G. cupressi* Long ex Goodding, *G. cupressi* var. *cascadense* R. Pete., *G. guatemalianum* (Crowell) Cumm., and *G. meridissimum* (aecial stage not reported), were reduced to synonyms of *G. cunninghamianum* Barcl. mainly based on surface structures of peridial cells. However, the aeciospore surface structure of *G. cunninghamianum* (type LC; Figs. 1A, B) differed from those of *G. cupressi* var. *cascadense* and *G. guatemalianum* in the process morphology (type SC; Figs. 5G, H) (Table 1). Therefore, Peterson's taxonomic treatment should be

reconsidered.

We observed 1 to 15 specimens of each species from different host plants and localities. However, aeciospore surface structure type is constant within each species, as shown in Tables 1 and 2. Therefore, we conclude that these types can be used as an important taxonomic character of *Gymnosporangium* and *Roestelia* species.

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