

Spore studies in the genus *Gymnocarpium*

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Scanning electron microscopy was used to examine the variation in perispore characters within and between six currently recognized taxa of the genus *Gymnocarpium* Newm. in North America. Representative scanning electron micrographs are presented and depict the perispore features observed. Spores of those taxa studied here do not each possess a distinctive morphology providing practical species discrimination, rather they all exhibit similar patterns of variation. Spore size was also examined and shown to be correlated to ploidy level, permitting positive identification of the diploid taxon *G. dryopteris* ssp. *disjunctum* from the tetraploid *G. dryopteris* ssp. *dryopteris*.

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La microscopie électronique à balayage a été utilisée pour étudier la variation des caractères de la périspore dans six taxons du genre *Gymnocarpium* Newm. en Amérique du Nord. Des micrographies au MEB sont présentées et illustrent les caractéristiques observées sur les périspores. Les taxons étudiés ici ne possèdent pas tous, au niveau de la périspore, des caractères morphologiques distinctifs permettant une séparation pratique des espèces, mais ils montrent plutôt des patrons de variation semblables. La dimension des spores a également été examinée; elle est corrélée avec le niveau de pléidie et elle permet donc de séparer le taxon diploïde *G. dryopteris* ssp. *disjunctum* du tétraploïde *G. dryopteris* ssp. *dryopteris*.

[Traduit par le journal]

Introduction

In his study of Fennoscandian fern species, Sorsa (1964) surveyed the spores of two species of *Gymnocarpium*, *G. dryopteris* (L.) Newm. and *G. robertianum* (Hoffm.) Newm., with light microscopy and provided measurements for the spores as well as descriptions of the perine sculpture. According to his study, the spores of *G. dryopteris* were saccate (the sacchi sometimes lengthened into folds), and the perine surface was foveo-reticulate. The perine sculpture of *G. robertianum* was also saccate and the surface was described as psilate to punctate-foveolate or irregularly foveo-reticulate. These two species were again included in a pteridophyte spore study by Erdtman and Sorsa (1971) and the perine surface descriptions given for these two taxa closely matched those by Sorsa (1964).

At the same time as the present investigation, a parallel study of the spore morphology and spore sizes of *Gymnocarpium* was being conducted in Finland by Sorsa (1980), a colleague of J. Sarvela who has recently revised the genus (1978) on the basis of European, Asiatic, and American material. Using both light and scanning electron microscopy, the exospore and perispore characters of the spores of 8 of the 11 taxa recognized by Sarvela were studied. On the basis of perispore characters, Sorsa divided the taxa into two groups which corresponded with Sarvela's groupings of the genus based on gross vegetative morphology. In

addition, Sorsa considered perispore characters to be of diagnostic value at the specific and subspecific level.

The genus *Gymnocarpium* in North America has recently been the subject of systematic study (Pryer 1981). In this treatment six taxa are recognized as follows: *G. dryopteris* (L.) Newm. ssp. *dryopteris*; *G. dryopteris* (L.) Newm. ssp. *disjunctum* (Rupr.) Sarvela; *G. robertianum* (Hoffm.) Newm.; *G. jessoense* (Koidz.) Koidz. ssp. *parvulum* Sarvela; *G. dryopteris* (L.) Newm. ssp. \times *brittonianum* Sarvela, and *G. \times intermedium* Sarvela. With an emphasis on North American material, the spore characteristics of these taxa were considered in detail using scanning electron microscopy (SEM). The variation in perispore patterns was examined critically within and between all taxa with a view to assessing its taxonomic significance, particularly in the light of the claims made by Sorsa (1980).

Spore size has been shown to be significantly correlated to ploidy level in several fern genera (Manton 1950; Lovis 1964; Wagner and Chen 1965; Whittier 1970). Brown (1964) and Britton (1968), however, working on *Woodsia* and *Dryopteris*, respectively, were unable to show any size differences between spores of some tetraploid taxa and those of closely related diploid species.

Different ploidy levels are known to occur in *Gymnocarpium*. Chromosome counts of $n = 80$ for the tetraploid taxa, *G. dryopteris* ssp. *dryopteris* and *G. robertianum*, and $n = 40$ for the diploid *G. dryopteris* ssp. *disjunctum* and *G. jessoense* (Koidz.) Koidz. ssp.

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TABLE 1. Herbarium specimens of *Gymnocarpium* used in spore morphology studies (S) and for spore measurements (M)

Taxon	Collection location		Voucher
<i>G. dryopteris</i> ssp. <i>dryopteris</i>	Ontario	S	Parry Sound Distr., Grundy Prov. Park, <i>Britton 6760</i> (OAC)
		S M	Thunder Bay Distr., Crooks Twp., Pine Bay, <i>Garton 19097</i> (OAC)
		S M	Thunder Bay Distr., Gorham Twp., Bentley Creek, <i>Garton 18947</i> (OAC)
		M	Thunder Bay Distr., Sibley Peninsula, <i>Britton 6836</i> (OAC)
		S M	Thunder Bay Distr., Squaw Bay, <i>Britton 6853</i> (OAC)
		M	Wellington Co., Drew Bog, <i>Britton & von Aderkas 5794</i> (OAC)
		S M	Wellington Co., Guelph Twp., Speed River, <i>Britton 6794</i> (OAC)
		M	Wellington Co., Guelph Twp., Little Tract, <i>Pryer 613</i> (OAC)
		M	Wellington Co., Irish Creek, <i>Anderson 314</i> (OAC)
		M	Wellington Co., Pilkington Twp., Conc. VI, <i>Pryer 610</i> (OAC)
		M	Wellington Co., West Garafraxa Twp., <i>Britton 6895</i> (OAC)
		M	Montcalm Co., St. Calixte, <i>Jolicoeur 3559</i> (MT)
		M	Nouveau Québec, Schefferville, Aries Bog, <i>Pryer 490</i> (OAC)
	S M	Nouveau Québec, Schefferville, Dyke Lake, <i>Pryer 502</i> (OAC)	
	M	Nouveau Québec, Schefferville, Osprey Lake, <i>Pryer 530</i> (OAC)	
	M	Rimouski Co., Le Bic, <i>Coiteaux 188</i> (MT)	
	M	Vaudreuil Co., Rigaud Mtn., <i>Pryer 341</i> (OAC)	
	Japan	S	Kai, Hondo, <i>Sugimoto 1486</i> (A)
		S	Kashiho Karafuto, <i>Kakuo Uno 20837</i> (GH)
		S	Kitami-Fuji Hokkaido, <i>Kakuo Uno 16273</i> (A)
U.S.S.R.	S	Prov. Rjasan, Elatjma Distr., 23 July 1968, <i>Novikov et al. s.n.</i> (A)	
<i>G. dryopteris</i> ssp. <i>× brittonianum</i>	Ontario	S	Wellington Co., West Garafraxa Twp., Belwood, <i>Pryer 612</i> (OAC)
		S	Wellington Co., Pilkington Twp., Conc. VI, <i>Pryer 611</i> (OAC)
<i>G. dryopteris</i> ssp. <i>disjunctum</i>	British Columbia	S M	Cariboo Distr., Azu Village, John Hart Hwy, <i>Barclay 2047</i> (V)
		S M	Cariboo Distr., Timothy Mountain, 2 May 1970, <i>Barneveld s.n.</i> (UVIC)
		S M	Vancouver Island, Cathedral Grove, 13 July 1962, <i>Ashlee s.n.</i> (UVIC)
		S M	Vancouver Island, Forbidden Plateau, 26 July 1951, <i>Hardy s.n.</i> (V)
		S M	Vancouver Island, Golden Hind Mountain, 16 August 1965, <i>Davies & Davies s.n.</i> (UVIC)
	Idaho	S M	Vancouver Island, MacMillan Memorial Grove, <i>Britton 8092</i> (OAC)
		M	Shoshone Co., Clarkia, <i>Cronquist & Jones 6018</i> (MT)
	Washington	M	Clearwater Co., Potlatch Creek, Bovil, <i>Cronquist & Jones 5980</i> (MT)
		M	Whatcom Co., Skyline Ridge, Mt. Baker, <i>Thompson 8079</i> (MT)
	<i>G. intermedium</i>	U.S.A.	S
Japan		S	Yumoto, Nikko, <i>Matsumura s.n.</i> (GH)
<i>G. jessoense</i> ssp. <i>jessoense</i>	Japan	M	Nagano Pref., Mt. Toyoguchi, <i>Mitsui s.n.</i> (OAC)
		M	Sinano, Hondo, <i>Shiota 7282</i> (A)
	U.S.S.R.	M	Terezovo?, <i>G. N. Nepin? s.n.</i> (A)

TABLE 1 (Concluded)

Taxon	Collection location	Voucher	
<i>G. jessoense</i> ssp. <i>parvulum</i>	Manitoba	M Herb Lake, <i>Scoggan 6584</i> (MT)	
	New Brunswick	S M Restigouche Co., Restigouche River, 19 July 1888, <i>Brittain s.n.</i> (GH)	
	Ontario	S Algoma Distr., Wawa, 23 July 1938, <i>R. C. Hosie s.n.</i> (LKHD)	
		M Rainy River Distr., Quetico Prov. Park, <i>Walshe 76-179</i> (OAC)	
		S M Thunder Bay Distr., Kaministiquia River, <i>Britton 6811</i> (OAC)	
		S M Thunder Bay Distr., Kaministiquia River, <i>Garton 19075</i> (2 colls.) (OAC)	
		M Thunder Bay Distr., Kaministiquia River, <i>Garton 19076</i> (OAC)	
		S M Thunder Bay Distr., Lybster Twp., The Palisades, <i>Pryer 588</i> (OAC)	
		S M Thunder Bay Distr., Sibley Peninsula, <i>Garton 18960</i> (2 colls.) (OAC)	
		M Thunder Bay Distr., Wolf River, <i>Garton 18906</i> (OAC)	
		S M Thunder Bay Distr., Wolf River, <i>Garton 18908</i> (OAC)	
		S Thunder Bay Distr., Wolf River, <i>Pryer 583</i> (OAC)	
		M Cook Co., Mountain Lake, <i>Butters, Burns & Hendrickson s.n.</i> (MT)	
	<i>G. robertianum</i>	Newfoundland	S St. Barbe Distr., Bonne Bay, <i>Fernald, Long, Fogg 1131</i> (GH)
			M St. Barbe Distr., Bonne Bay, <i>Rouleau 3345</i> (MT)
		S Stanleyville, <i>Fernald, Long, Fogg 1130</i> (GH)	
Ontario		M Bruce Co., Bruce Peninsula, <i>Pryer 483</i> (OAC)	
		S M Bruce Co., Bruce Peninsula, <i>Britton 7128</i> (2 colls.) (OAC)	
		S M Frontenac Co., Palmerston Twp., <i>Britton 6902</i> (3 colls.) (OAC)	
		S Frontenac Co., Palmerston Twp., <i>Pryer 386</i> (OAC)	
		M Frontenac Co., Palmerston Twp., <i>Brunton 1644</i> (OAC)	
		S Manitoulin Island, Fossil Hill, <i>Kott 906</i> (OAC)	
		S Thunder Bay Distr., Kitto Twp., Blackwater River, <i>Garton 7738</i> (LKHD)	
		M Timiskaming Distr., New Liskeard, <i>Britton 3257</i> (OAC)	
		S Timiskaming Distr., New Liskeard, <i>Pryer 616</i> and <i>Pryer 617</i> (OAC)	
Quebec		S Anticosti Island, Betsie River, 3 September 1883, <i>Macoun s.n.</i> (MTMG)	
		S M Anticosti Island, Rivière Vaureal, <i>Victorin et Rolland-Germain 27-047</i> (GH)	
		S M Bonaventure Co., Baie des Chaleurs, 5, 6, 8 August 1904, <i>Collins, Fernald & Pease s.n.</i> (GH)	
	S M Bonaventure Co., Bonaventure River, 8 August 1904, <i>Collins, Fernald & Pease s.n.</i> (GH)		
Iowa	S M Alamakee Co., Decorah, <i>Holway s.n.</i> (GH)		
Michigan	S M Delta Co., Burnt Bluff, <i>Fernald & Pease 3044</i> (GH)		
Norway	S M Opland Biri, 20 July 1937, <i>Holmboe s.n.</i> (A)		
Scandinavia	S M No location, 28 July 1923, <i>Nilsson s.n.</i> (GH)		

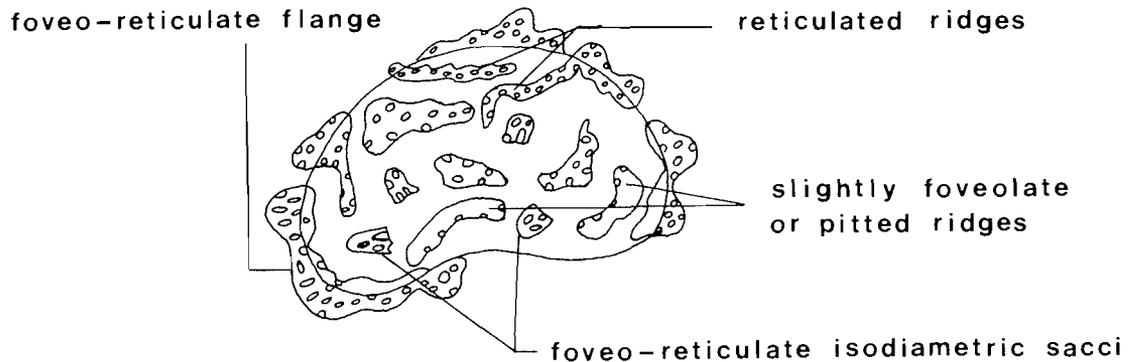


FIG. 1. Schematic diagram of *Gymnocarpium* perispore sculpture.

jessoense (an Asiatic subspecies) have been well documented in the literature and are summarized in Löve et al. (1977). In addition, a chromosome number of $n = 80$ has recently been reported for *G. jessoense* ssp. *parvulum* (Sarvela et al. 1981).

Wagner (1966), in reporting $n = 40$ for *G. dryopteris* ssp. *disjunctum*, determined that its spore size averages were distinctly lower than those for the tetraploid *G. dryopteris* ssp. *dryopteris*. A comparison of the spore sizes of all the North American species of *Gymnocarpium* was carried out to determine if the diploid taxa could be distinguished from the tetraploids on the basis of spore size alone.

Materials and methods

Spores used in this investigation were obtained directly from herbarium specimens selected from a broad geographical area (Table 1).

The spores used in the morphological studies were mounted on aluminum SEM stubs with double-stick adhesive tape and coated with gold-palladium alloy (6 min at 15 mA) in a Technics Hummer V sputter-coater. Stubs were viewed with an ETEC Autoscan scanning electron microscope at 20 kV. Over 370 photographs were taken in all, from which representative pictures of spores were chosen.

Spores that were used for size determinations were mounted directly in Euparal on glass slides. Between 20 and 50 mature spores per herbarium specimen were drawn at $480\times$ magnification using a camera lucida device (Britton 1968). Only the outer exospore walls, as seen through the transparent perispore, were drawn. Measurements of exospore length were made on the drawings at the largest diameter. This method eliminated the variability that would result if the irregular folds of the perispore were included in the measurements.

Observations and discussion

Spore morphology

A generalized diagram of a spore of *Gymnocarpium*, indicating the terminology used in discussing perispore sculpture, is shown in Fig. 1. The spores are reniform in outline and are monolete.

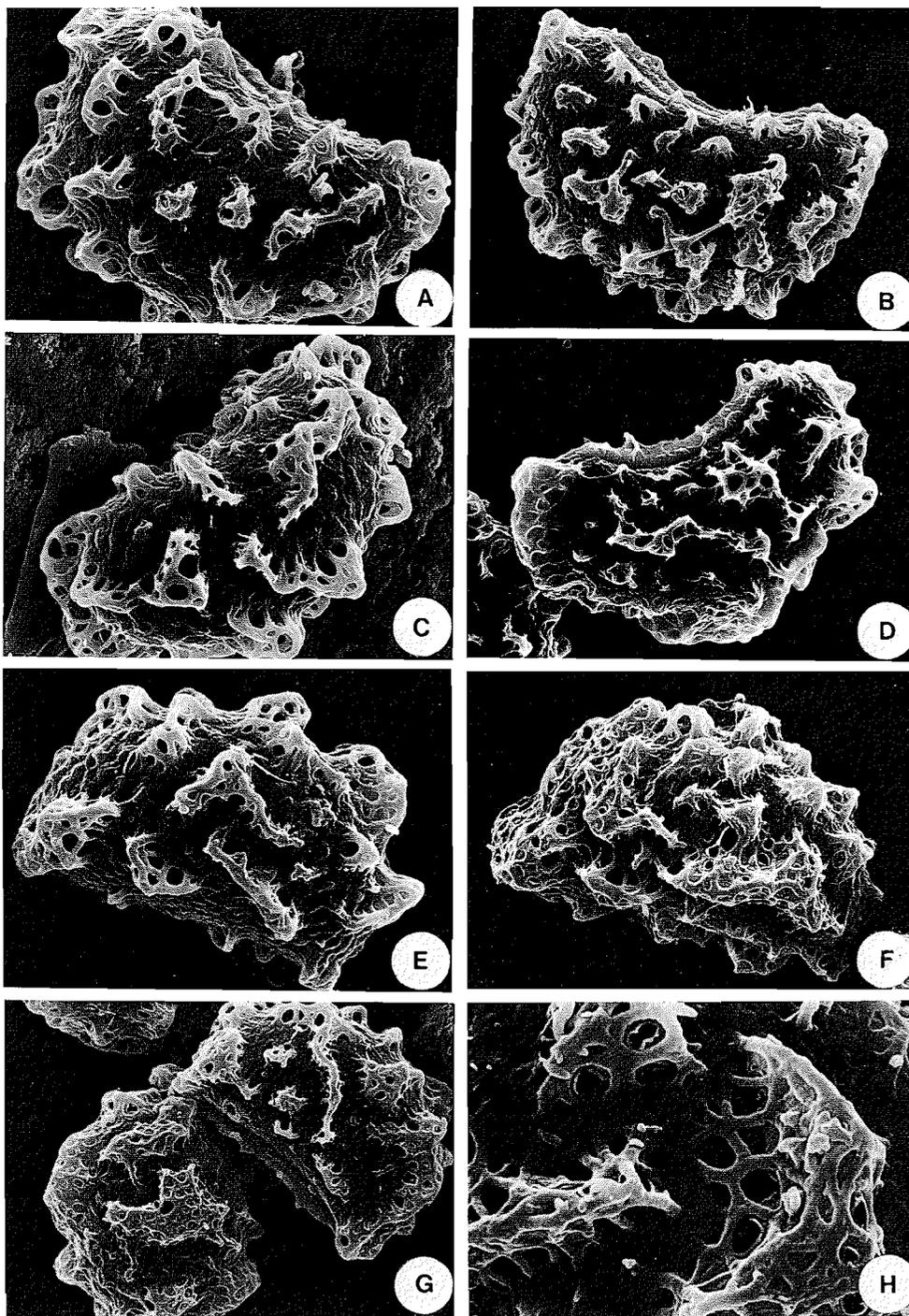
Representative scanning electron micrographs of the spores for each taxon surveyed are presented in Figs. 2–6. The photographs were selected so as to best depict the perispore pattern variations observed within each of the taxa.

An initial cursory glance at Figs. 2–6 shows that there are no striking differences in spore sculpturing among the taxa. Indeed, spore morphological studies indicate the close relationship of all the taxa of *Gymnocarpium* studied.

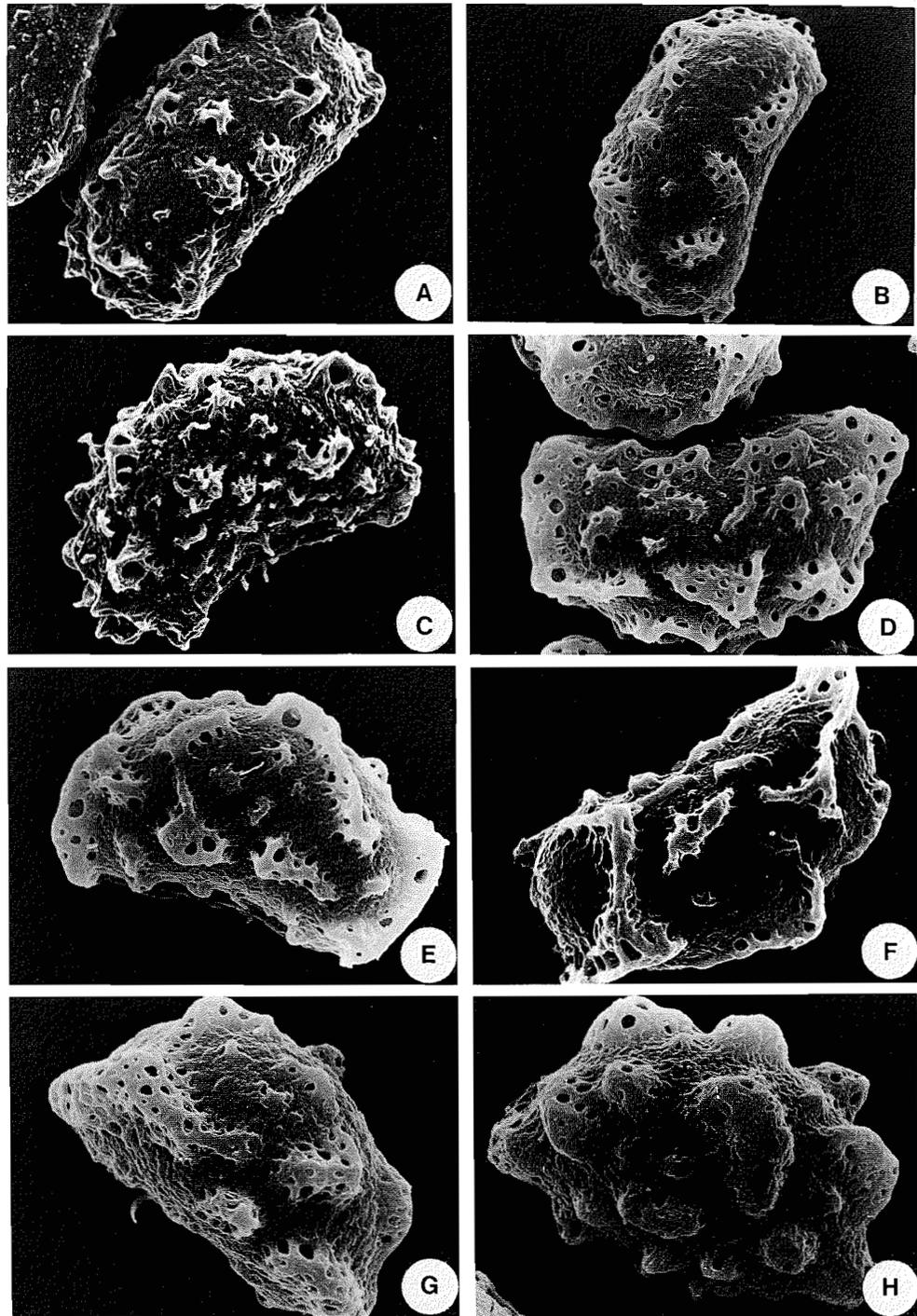
The perispore variation observed for spores of *G. dryopteris* ssp. *dryopteris* ranged over the following patterns: spores with discrete, foveo-reticulate, isodiametric sacci (Figs. 2A, 2B); spores with sacci forming well-defined, relatively short and narrow reticulate ridges along the faces of the spores (Figs. 2C–2E), and occasionally with reticulate flanges at the polar ends and across the dorsal margin (Figs. 2C, 2D); spores with interconnected, relatively broad, reticulate sacci or folds (Figs. 2F, 2G, lower spore, 2H). The latter pattern tends to give the spores a convoluted appearance (Fig. 2F).

The development of the reticulumlake pattern of the sacci or folds was observed at various stages for all taxa. Often the impressions of the perforations were evident, yet the actual perforation had not taken place and a thin layer of perispore material covered the area much like a windowpane. In Fig. 2H, a close-up of one of the sacci shows several of these “windowpanes” deteriorating to form the lumen.

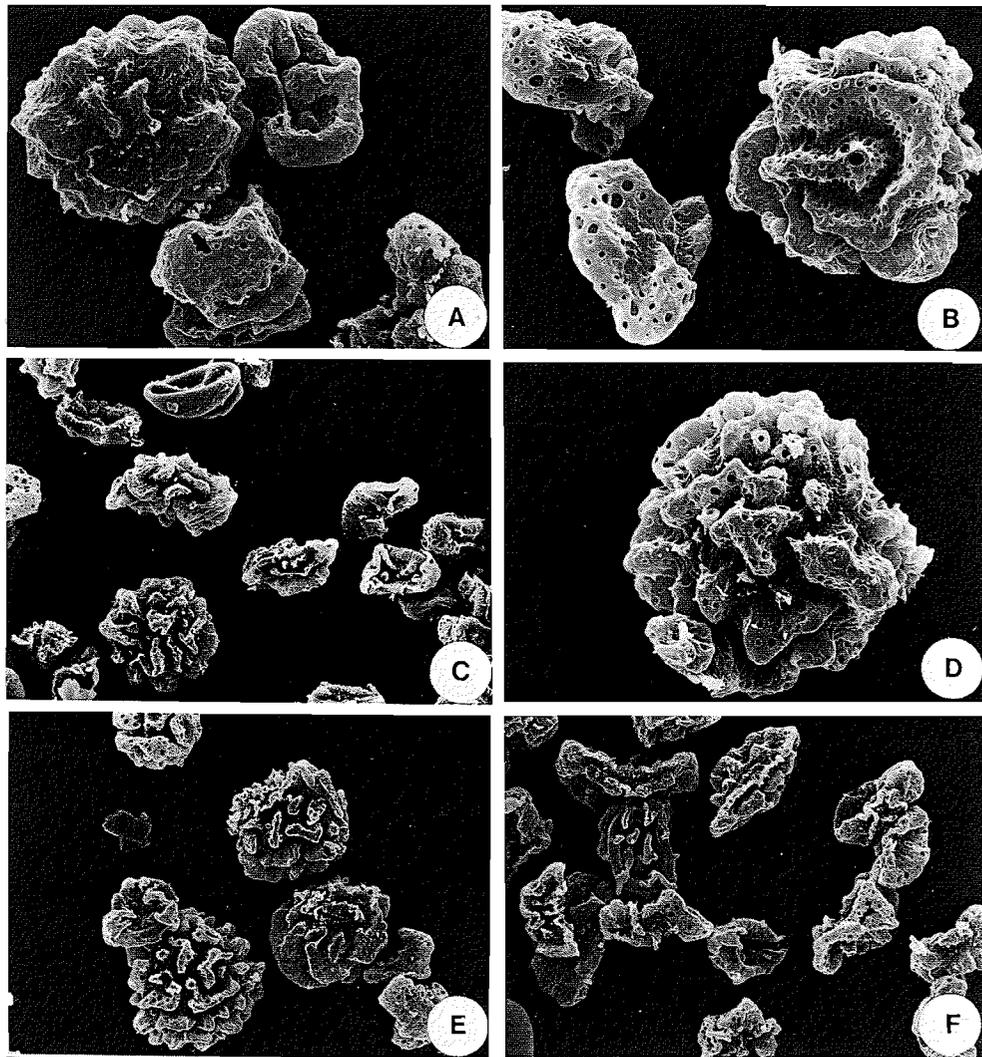
The perispore patterns of *G. dryopteris* ssp. *disjunctum* exhibit very similar variation to that seen in *G. dryopteris* ssp. *dryopteris*. Spores with discrete, foveo-reticulate, isodiametric sacci were frequently observed (Figs. 3A–3C). These sacci usually appeared to be fewer in number and more well spaced than in *G. dryopteris* ssp. *dryopteris*. The sacci were also often interconnected to form well-defined, narrow reticulate ridges of varying lengths across the face of the spore



FIGS. 2A–2H. Scanning electron micrographs of spores of *Gymnocarpium dryopteris* ssp. *dryopteris*. (A, B) Spores with discrete, foveo-reticulate, isodiametric sacci. (A) *Pryer 610* (OAC). $\times 1870$. (B) *Sugimoto 1486* (A). $\times 1595$. (C–E) Spores with relatively narrow and short, reticulate ridges and reticulate polar flanges. This is best seen in C and D. C. *Britton 6760* (OAC). $\times 1790$. D. *Pryer 502* (OAC). $\times 1295$. E. *Kakuo Uno 16273* (A). $\times 1630$. (F) Spore with broad, reticulate folds and flanges. *Pryer 613* (OAC). $\times 1570$. (G) Two spores are illustrated, the lower with broad, reticulate folds and flanges and the upper with long and narrow, reticulate ridges and foveo-reticulate sacci. *Pryer 610* (OAC). $\times 1360$. (H) Close-up of a broad saccus, showing perforations at various stages of formation. *Pryer 610* (OAC). $\times 4420$.



FIGS. 3A–3H. Scanning electron micrographs of spores of *Gymnocarpium dryopteris* ssp. *disjunctum*. (A–C) Spores with discrete, foveo-reticulate, isodiametric sacci. (A) *Ashlee* s.n. (UVIC). $\times 1800$. (B) *Barclay 2047* (V). $\times 1980$. (C) *Barneveld* s.n. (UVIC). $\times 1680$. (D–F) Spores with both short and long reticulate ridges; D–E with reticulate flanges. (D) *Britton 8092* (OAC). $\times 2020$. (E) *Britton 8092* (OAC). $\times 1925$. (F) *Britton 8092* (OAC). $\times 2400$. (G–H) Spores with rounded and broad, reticulate sacci. (G) *Barclay 2047* (V). $\times 1980$. (H) *Hardy* s.n. (V). $\times 2160$.



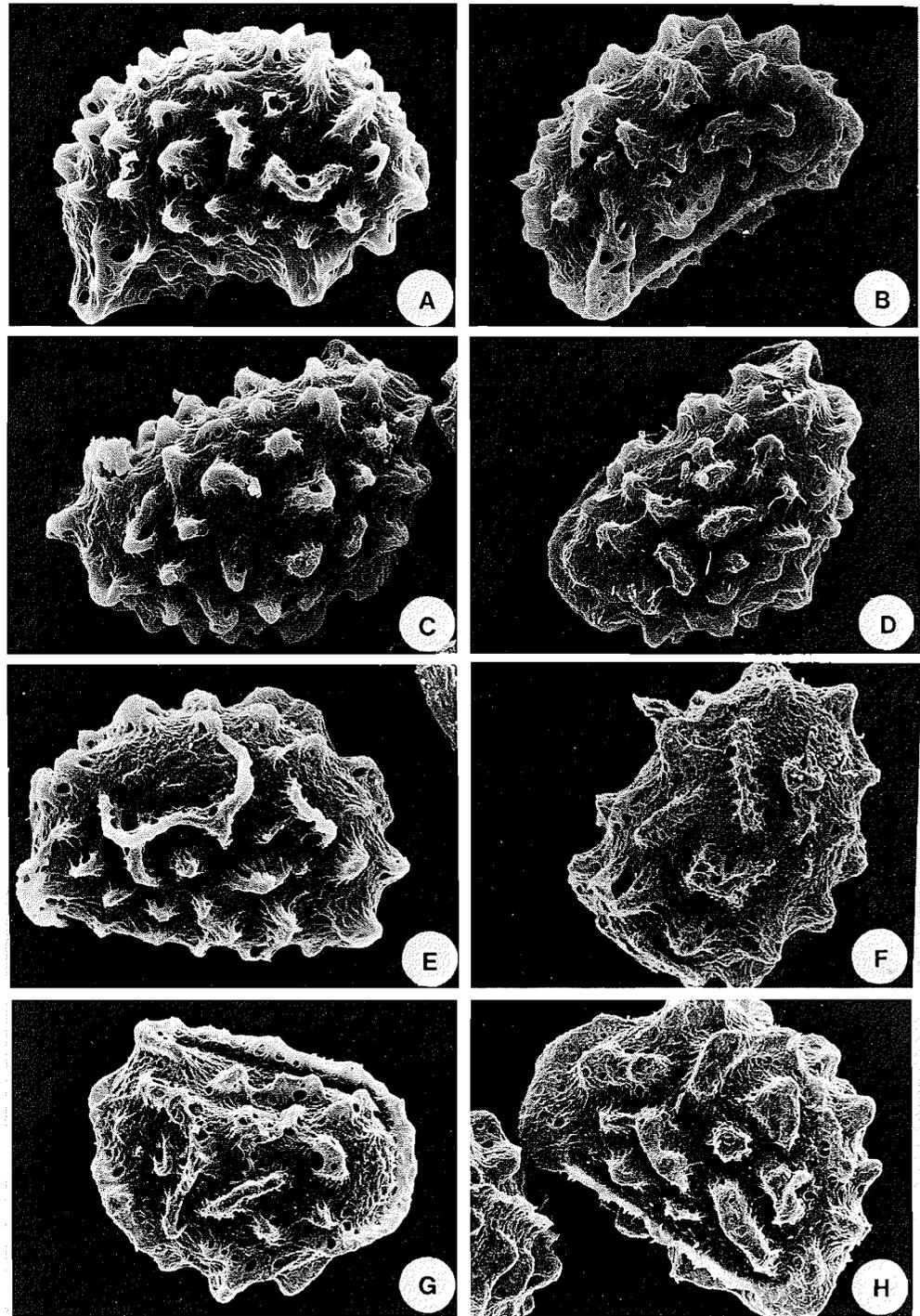
FIGS. 4A–4C. Scanning electron micrographs of spores of *Gymnocarpium dryopteris* ssp. \times *brittonianum*. (A) Round unreduced spore with extensive reticulate perispore and four small distorted, aborted spores. *Pryer 611* (OAC). $\times 884$. (B) Three aborted spores with very elaborate and exaggerated perispores. *Pryer 611* (OAC). $\times 952$. (C) Round unreduced spore with extensive reticulate ridges, surrounded by a variety of irregular aborted spores. *Pryer 612* (OAC). $\times 455$. (D–F) Scanning electron micrographs of spores of *Gymnocarpium* \times *intermedium*. (D) Round unreduced spore with broad reticulate ridges. *Tryon 4154* (GH). $\times 1120$. (E) Mixture of round unreduced spores and twisted aborted spores. *Tryon 4154* (GH). $\times 448$. (F) A variety of aborted spores with elaborate laticelike perispores. *Tryon 4154* (GH). $\times 480$.

(Figs. 3D–3F), and reticulate flanges at the polar ends of the spores (Figs. 3D, 3E). As with *G. dryopteris* ssp. *dryopteris*, spores with rounded and broad, reticulate sacci or folds were also observed (Figs. 3G, 3H).

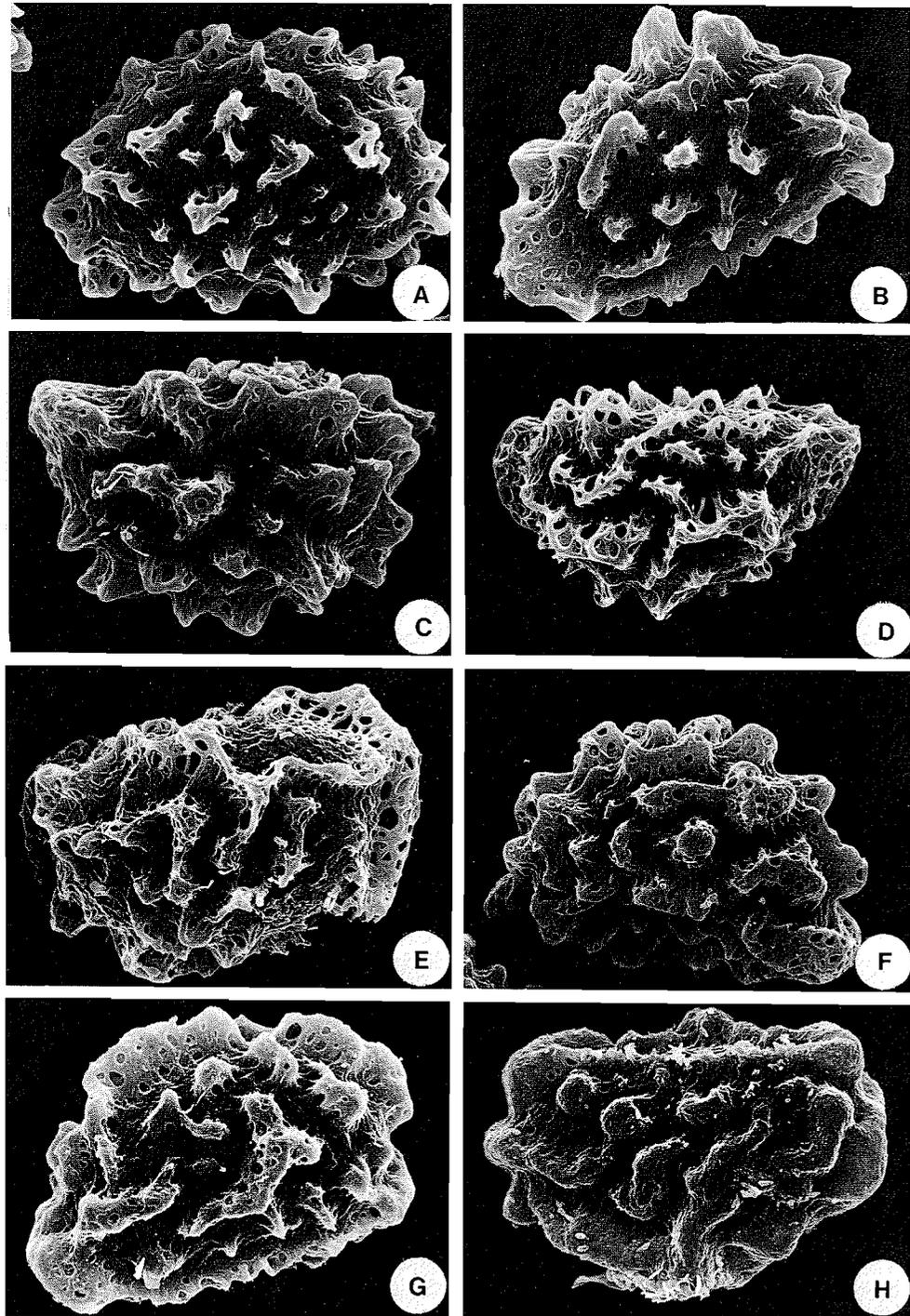
Two types of spores were noted for the hybrids, *G. dryopteris* ssp. \times *brittonianum* Sarvela and *G.* \times *intermedium* Sarvela. The majority of spores were aborted and unusually small in size. These were not typically reniform but were twisted into a variety of irregular and distorted shapes (Figs. 4B, 4C, 4F).

The perispores were often much more elaborate and irregularly crested than usual. Devi (1980) has reported seeing several cases of highly developed perispore matter over shrunken or sterile spores, especially in *Polystichum* and *Dryopteris*.

In addition to these misshapen spores, there were spores which were considerably larger than the normal meiospore and round instead of bilateral. The perispore of these spores was extensive and predominantly composed of reticulate sacci of various lengths and



FIGS. 5A–5H. Scanning electron micrographs of spores of *Gymnocarpium jessoense* ssp. *parvulum*. (A–D) Spores with discrete, foveo-reticulate, isodiametric sacci. (A) *Brittain s.n.* (GH). $\times 1630$. (B) *Pryer 583* (OAC). $\times 1430$. (C) *Brittain s.n.* (GH). $\times 1760$. (D) *Hosie s.n.* (LKHD). $\times 1460$. (E–G) Spores with both foveo-reticulate, isodiametric sacci and narrow, reticulate ridges. (E) *Pryer 583* (OAC). $\times 1560$. (F) *Garton 18908* (OAC). $\times 1560$. (G) *Garton 18960* (OAC). $\times 1430$. (H) Spore with broad foveo-reticulate sacci and foveo-reticulate flanges. *Garton 18960* (OAC). $\times 1430$.



FIGS. 6A-6H. Scanning electron micrographs of spores of *Gymnocarpium robertianum*. (A) Spores with discrete foveo-reticulate, isodiametric sacci. *Victorin et Rolland-Germain 27-047* (GH). $\times 1920$. (B-E) Spores with narrow reticulate ridges and reticulate flanges at the polar ends of B, D, and E. (B) *Collins, Fernald and Pease s.n.* (GH). $\times 1680$. (C) *Collins, Fernald and Pease s.n.* (GH). $\times 1740$. (D) *Pryer 617* (OAC). $\times 1500$. (E) *Garton 7738* (LKHD). $\times 1680$. (F and G) Spores with broad reticulate sacci and reticulate ridges. (F) *Fernald and Pease 3044* (GH). $\times 1900$. (G) *Holway s.n.* (GH). $\times 1800$. (H) Spores with mostly long and broad sacci which are only slightly foveolate or pitted. *Nilsson s.n.* (GH). $\times 1920$.

TABLE 2. Comparison of data for *Gymnocarpium* exospore lengths

	Overall \bar{x} (μm)	SD (μm)	SE	Range of \bar{x} (μm)	Range of lengths (μm)
<i>G. robertianum</i> (4 \times)	36.6	2.6	0.12	33.8–38.6	29–44
<i>G. dryopteris</i> ssp. <i>dryopteris</i> (4 \times)	36.2	2.8	0.14	33.9–38.9	28–44
<i>G. jessoense</i> ssp. <i>parvulum</i> (4 \times)	34.2	2.7	0.13	32.2–37.1	27–44
<i>G. dryopteris</i> ssp. <i>disjunctum</i> (2 \times)	29.5	2.5	0.15	27.1–31.5	23–42
<i>G. jessoense</i> ssp. <i>jessoense</i> (2 \times)	29.9	2.4	0.32	29.2–30.5	24–34

widths (Figs. 4A, 4C, 4E). These spores conform with DeBenedictis' (1969) description of unreduced spores in fern hybrids.

The perispore patterns observed for specimens of *G. jessoense* ssp. *parvulum* were somewhat more consistent and uniform than those for the other taxa studied. The majority of spores had well-defined, foveo-reticulate, isodiametric sacci (Figs. 5A–5D). In combination with these sacci, short and narrow, reticulate ridges were commonly observed (Figs. 5E–5G). Occasionally, the sacci and ridges appeared rather broad and formed reticulate flanges at the polar ends (Fig. 5H). Nevertheless, the sacci always appeared as discrete units.

In *G. robertianum*, perispore patterns covered the range of variation observed for all other taxa. The spores of this taxon occasionally showed discrete foveo-reticulate, isodiametric sacci (Fig. 6A). More commonly, however, the spores were overlain with narrow, reticulate ridges (Figs. 6B–6E), with occasional extensive reticulate flanges at the polar ends (Fig. 6E). These ridges were often quite broad and markedly convoluted over the entire spore surface (Figs. 6F–6H). All North American specimens studied with the latter type of spore sculpture were highly foveo-reticulate. The spores of the European specimens of *G. robertianum* were convoluted with broad ridges; these ridges, however, were only slightly foveolate or pitted at the base (Fig. 6H).

Sorsa (1980) acknowledges that there is little intra-generic variation in the spores of the genus *Gymnocarpium* on the one hand, while insisting on the other, that the two subspecies of *G. dryopteris* can be clearly separated on the basis of perispore characters and spore size. As shown in the following section, spore size is indeed useful in separating these two subspecies, but as demonstrated here in Figs. 2 and 3, perispore characters are not clearly distinguishable between *G. dryopteris* ssp. *dryopteris* and *G. dryopteris* ssp. *disjunctum*.

Sorsa (1980) grouped *G. dryopteris* ssp. *dryopteris*, *G. dryopteris* ssp. *disjunctum*, and *G. jessoense* ssp. *parvulum* together on the basis of having mostly a

foveolate or foveo-reticulate perispore. He did not include *G. robertianum* with these taxa because the six specimens he studied had a less foveolate perispore which was smooth or with minute widely spaced holes. Only two of his specimens showed a foveolate to foveo-reticulate perispore, one being the only North American specimen studied.

Of the 16 specimens of *G. robertianum* examined in this study, 14 were from North American localities and all showed a foveolate to foveo-reticulate perispore of one kind or another. The two European specimens studied here, however, had spores which fit in well with Sorsa's (1980) perispore description for the species. It is therefore concluded that specimens of North American *G. robertianum* cannot be as successfully distinguished from the other taxa on the basis of spore morphology, as perhaps can the European specimens of this taxon.

The principal conclusion drawn from the present investigation of spore morphology in the genus *Gymnocarpium* is that the spores of those taxa studied here do not possess a distinctive morphology providing species discrimination but rather are all closely similar in their patterns of variation. Moreover, Sorsa's recognition of two perispore-type groups is not borne out in that the range of variation in spore morphology in *G. robertianum* covers that said to be characteristic of each group.

Spore size

Spore size determinations are given in Table 2. The overall mean exospore lengths for the three tetraploid taxa are very close and they share the same range of variation. The diploid *G. dryopteris* ssp. *disjunctum* has a distinctly lower overall mean, and as illustrated by Fig. 7, its range of means shows no overlap with those for the tetraploids.

The Asian diploid taxon *G. jessoense* ssp. *jessoense* is included here for comparative purposes only. Its overall mean and range of means are very close to that of diploid *G. dryopteris* ssp. *disjunctum* (Table 2).

TABLE 3. Comparison of mean exospore length of *Gymnocarpium* and range of means (μm) as determined by various workers

Reference	<i>G. robertianum</i>	<i>G. dryopteris</i>	<i>G. jessoense</i> ssp. <i>parvulum</i>	<i>G. dryopteris</i> ssp. <i>disjunctum</i>
Sorsa (1964)	35(32-40)	36(32-39)		
Wagner (1966)	33(28-38)	33(28-37)		28(25-32)
Erdtman and Sorsa (1971)	33(35-40)	—(35-42)		
Sorsa (1980)	43.3(41-46)	41.9(40-43)	40.1(34-43)	34.2(33-35)
Pryer (1981)	36.6(34-39)	36.2(34-39)	34.2(32-37)	29.5(27-31)

Frequency histograms of exospore lengths (Fig. 8) show that for all taxa the spore sizes tend to approximate rather steep normal curves of variation with the majority of spores close to the numerical mean. Although there is an overlap in the range of diploid and tetraploid exospore lengths in *G. dryopteris* (Fig. 8B), the frequency with which this occurs is quite low. From this and the results shown in Fig. 7, it is clear that the calculation of the mean spore size from examination of a relatively small number of spores will permit accurate discrimination of diploid from tetraploid taxa.

The results of this study are compared with those of previous workers in Table 3. The figures given by Sorsa (1964, 1980) and Erdtman and Sorsa (1971) appear to be the means of 10-20 spore measurements. Wagner's

work is based on a considerable number of spore measurements, a 10-spore sample from each of more than 30 collections (1966). In each of these studies, the relative sizes are very similar; the tetraploids share the same range of variation and relatively close means

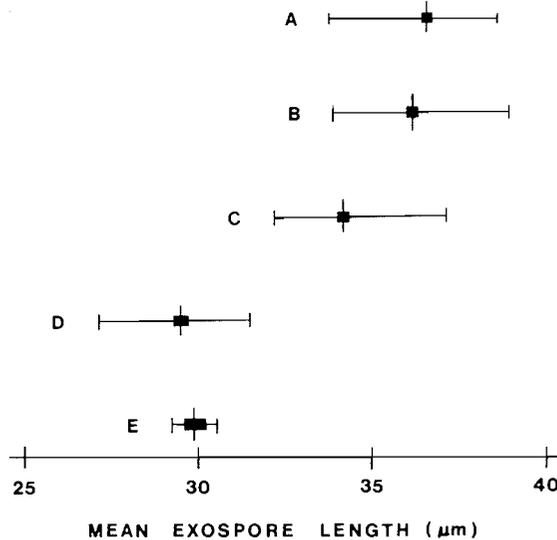


FIG. 7. Comparison of *Gymnocarpium* mean exposure lengths. Terminal cross lines equal range of mean exospore lengths. Central cross line equals overall mean exospore length. ■, standard error. A, *G. robertianum*; B, *G. dryopteris* ssp. *dryopteris*; C, *G. jessoense* ssp. *parvulum*; D, *G. dryopteris* ssp. *disjunctum*; E, *G. jessoense* ssp. *jessoense*.

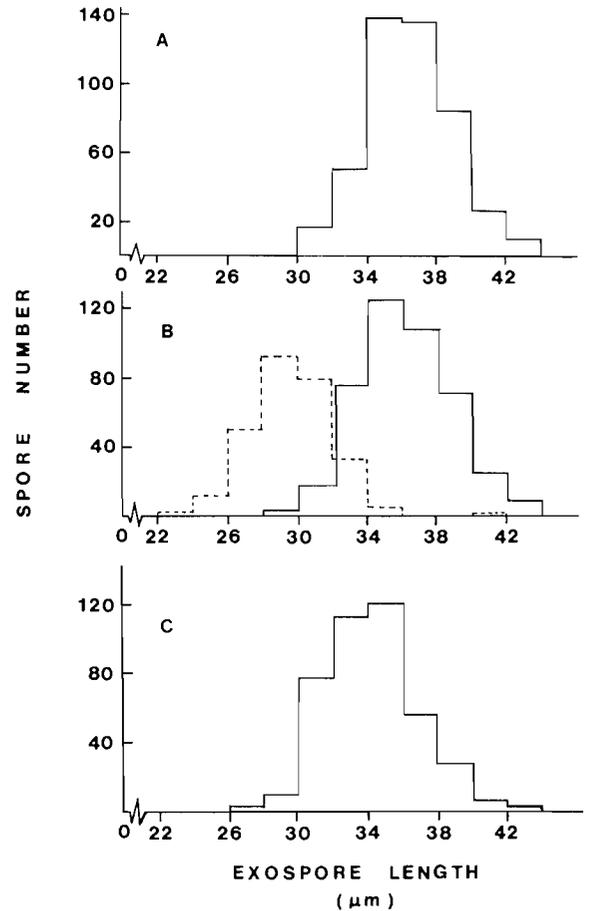


FIG. 8. Frequency histograms of *Gymnocarpium* exospore lengths. Fig. 8A. *G. robertianum*. Fig. 8B. Broken line represents *G. dryopteris* ssp. *disjunctum*. Solid line represents *G. dryopteris* ssp. *dryopteris*. Fig. 8C. *G. jessoense* ssp. *parvulum*.

and the diploids occupy a lower range of variation and a distinctly lower mean. Nevertheless, there are differences in the absolute sizes reported.

The degree of discrepancy between the spore sizes given by the three earlier studies and those of this study is less than 10%. By comparison, the 1980 measurements given by Sorsa are considered to be high, as the degree of discrepancy here is of the order of 15–20%. The source of the difference may be in the mountant used. It has been reported that spores mounted in glycerine jelly (Sorsa's mountant) tend to swell (Brown 1960; Lovis 1964). Sorsa's spores were also acetolyzed. The acetolysis mixture has been shown to over expand pollen grains from 2–17% and sometimes 43% (Brown 1960).

In conclusion, the positive relationship between spore size and ploidy level in ferns, as documented by a number of earlier studies, is clearly supported here by the examination of spore sizes of diploid and tetraploid taxa in the genus *Gymnocarpium*.

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