POLLEN MORPHOLOGY OF THE PLANTAGO SPECIES OF THE COLOMBIAN ANDES AND ITS APPLICATION TO FOSSIL MATERIAL

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ABSTRACT

The pollen morphology of recent pollen grains of the genus *Plantago (Plantaginaceae)* occurring in the Colombian Andes is described on the basis of light and scanning electron microscopy. The results were found to be applicable to the determination of fossil pollen types found in lake sediments of the same area.

INTRODUCTION

Whilst analysing lake sediments of the Sabana de Bogotá (Colombia) striking differences in size and sculture of pollen grains of the genus *Plantago (Plantaginaceae)* became apparent. In palynological studies of Colombia and Venezuela no differentiation is made between these types. As the ecology of the different *Plantago* species differs widely *(Cleef,* 1978 and *Rahn,* 1974) a pollen key to the different types will allow a more complete interpretation of pollen diagrams of this area.

Therefore, an attempt was made to define the morphological differences and enable identification, combining both light and scanning electron microscopy methods.

Rahn (1974) studied the pollen morphology of *Plantago* sect. *Virginica* but found no taxonimically useful characters. He found considerable differences in size between different collections of the same species; the absolute diameter of the verrucae varied depending on the size of the anthers and no correlation appeared to exist between the number of pores and the size of the pollen, verrucae or anthers.

Basser & Crompton (1968) studied North American species of *Plantago* and were able to produce a key to the *Plantaginaceae* in North America base on pollen morphology. However, the pollen morphological characters they use are sometimes questionable, especially when applied to fossil pollen grains. This study gives a pollen key, based on morphological characters visible by the light microscope, for the relevant *Plantago* species of the Colombian and Venezuelan Andes.

MATERIAL AND METHODS

The pollen studied was taken from plants in the herbaria of Utrecht (U) and Copenhagen (C). See list of specimens examined. Pollen removed from flowers of dried herbarium material was acetolyzed according to *Erdtman* (1952).

Boil the pollen with 5% KOH for 5 min., pass throught a sieve, wash twice with aqua dest., wash once with acetic acid, boil for 5 min. in an acetolyse mixture (acetic anhydride: H_2SO_4/9:1), wash twice with aqua dest., wash 3 times with alcohol (96%, 100%, 100%), (specimens are now ready for S.E.M. technique), wash once with xylol, wash once with cyclohesaan, add a drop of silicone oil and place the residue for one night in a warm stove, (specimens are now ready for pollen slides for light microscopy).

For several months the pollen was kept in 100% alcohol during which period the S.E.M. micrographs were made. Finally the pollen was mounted in silicone oil to measure pollen diameters and to make light microscope photographs. To avoid size aberrations *(Reitsma,* 1969) measurements were

carried out inmediately after the preparation of the pollen slides with a Leitz Orthoplan microscope. The light microscope photographs were taken with a Leitz Orthomat photomicroscope.

In the S.E.M. preparation technique some drops of a pollen suspension were placed on a S.E.M. stubholder, covered with a thin layer of mixed carbon powder and rubber cement and allowed to dry. A thin layer of gold was applied by evaporation in vacuum, prior to observation. The vacuum coating unit is a S.E.M. coating unit E5000 (Polaron Equipment Ltd.). The Scanning Electron Microscope used was a Cambrigde Mark II stereoscan. The best results were obtained with an accelerating voltage of 10 kV. The magnifications used were 2000 x, 5000 x, 10,000 x, 20,000 x.

Almost all botanical collections from *Plantago* species used were recently determinated or revised by Dr. K. Rahn (C).

SPECIMENS EXAMINED

(sect. *Gnaphaloides):*

HdV 4247 *P. sericea* HBK ssp. *argyrophylla* (Decne) Rahn

(HdV 2880) Colombia, Dep. Boyacá: páramo NW of Belén, pathway S. José de la Montaña, Alto de las Cruces and surroundings.
Alt. 3850m, 24-02-1972, A.M. Cleef 1784 A (U)

HdV 4250 *P. sericea* HBK ssp. *argyrophylla* (Decne.) Rahn
Colombia, Dep. Boyacá: Sierra Nevada del Cocuy, Alto Valle Lagunillas.
Alt. 4000m, 02-10-1972, A.M. Cleef 5734 (U)

HdV 3096 *P. sericea* HBK ssp. *argyrophylla* (Decne.) Rahn
Colombia, Dep. Boyacá: Sierra Nevada del Cocuy, La Pintada, dry páramo.
Alt. 3950 m, A.M. Cleef 5503 (U).

HdV 4418 *P. sericea* Ruiz & Pavón ssp. *sericans* (Pilger) Rahn
Argentina, Prov, La Rioja: Sierra Famatina, La Encrucijada.
Alt. 3250 m, 04-02-1966, Hawkes, Hjerting & Rahn 3395 (C)

HdV 4370 *P. sericea* Ruiz & Pavón ssp. *perreymondii* (Barn.) Rahn
Colombia, Magdalena: E. of Manaure.
Alt. 3530-3450 m, 08-11-1959, Cuatrecasas *et al.* 25138 (C).

HdV 4417 *P. sericea* Ruiz & Pavón ssp. *sericea* var. *lanuginosa* Griseb.
Argentina, Prov. Salta, Dep. Santa Victoria: 29.5 km from Santa Victoria.
Alt. 4150 m, 15-03-1966, Hawkes, Hjerting & Rahn 3885 (C).

HdV 4419 *P. sericea* Ruiz & Pavón ssp. *sericea* var. *sericea*
Perú, Dep. Ancash, Prov. Bolognesi: Chiquián.
Alt. 3540 m, 08-04- 1949, Cerrato 60 (C)

HdV 4252 *P. sericea* Ruiz & Pavón ssp. *sericea* var. *sericea*
Colombia, Dep. Boyacá: Cucaita.
Alt. 2950m, 30-04-1975, Breure B90 (U)

HdV 4376 *P. linearis* HBK
Colombia, Dep. Cundinamarca: municipio Soacha, Est. Exp. San Jorge (I.C.A.).
Alt. 3150 m, 23-04-1974, Hjerting 5933 (C).

HdV 4248 *P. linearis* HBK
Colombia, Dep. Cundinamarca: Usaquén subpáramo. Alt. 3100 m, 30-05-1972, A.M. Cleef 3904 (U).

HdV 4416 *P. linearis* HBK var. *agrostophylla* (Decne.) Pilg.
Colombia, Dep. Valle: Cord. Central, W slope, basin of Río Bugalagrande, Barragán, páramo de Baraya, Corrales.
Alt. 3450-3520 m, 03-1946, Cuatrecasas 20182 (U).

(sect. *Oliganthos*):

HdV 4421 *P. rigida* HBK
Colombia, Dep. Caldas: Cord. Central, Nevado del Ruiz. Alt. 4100-4500 m, 31-10-1952, H. Humbert, J. Idrobo, R. Jaramillo & E. Pérez Arbeláez 27074 (U).

HdV 4249 *P. rigida* HBK
Colombia, Dep. Boyacá: páramo de la Rusia. Alt. 3720 m, 16-12-1972, A.M. Cleef 7309 (U).

HdV 4420 *P. rigida* HBK
Colombia, Dep. Boyacá: páramo de la Sarna NE of Laguna de Tota, small valley with peat. Alt. 3390 m, 05-04-1973, A.M. Cleef 9399 (U).

HdV 3741 *P. rigida* HBK
(HdV 3097)
Colombia, Dep. Meta: páramo de Sumapáz, Cerro Nevado de Sumapaz, superpáramo on NE side, humid stony slope, very much exposed to wind, calcareous soil.
Alt. 4130 m, 16-01-1973, A.M. Cleef 7921 (U).

(sect. *Virginica*):

HdV 4251 *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
(HdV 2838)
Colombia, Dep. Cundinamarca: páramo Cruz Verde. Alt. 3335 m, 24-04-1972, A.M. Cleef 3071 (U).

HdV 4411 *P. australis* Lam. ssp. *oreades* Decne.) Rahn

Colombia, Dep. Boyacá: páramo de Pisba, highroad Socha-La Punta km 72, S side of the Cerro El Bizcocho.
Alt. 3510 m, 09-06-1972, A.M. Cleef 4273 (U).

HdV 4412 *P. australis* Lam. ssp. *oreades* (Decne.) Rahn

Colombia, Dep. Boyacá: Sierra Nevada del Cocuy, Alto Valle Lagunillas, 500 m NNW of Laguna Pintada. Alt. 3985 m 03-10-1972, A.M. Cleef 5759 (U).

HdV 4414 *P. australis* Lam. ssp. *oreades* (Decne.) Rahn

Colombia, Dep. Boyacá: Sierra Nevada del Cocuy, Alto Valle Lagunillas, Laguna Pintada. Alt. 3950 m, 02-10-1972, A.M. Cleef 5720 (U).

HdV 4098 *P. australis* Lam. ssp. *oreades* (Decne.) Rahn

Colombia, Dep. Cundinamarca: páramo de Palacio, W side km 6 of the highroad, subpáramo marsh. Alt 3100 m, 12-05-1972, A.M. Cleef 3709 (U).

HdV 4369 *P. australis* Lam. ssp. *sodiroana* (Pilger) Rahn

Colombia, Magdalena: Sierra de Perijá, E of Manaure, Quebrada de Floridablanca.
Alt. 2700-2800 m, Cuatrecasas 25202 (C).

HdV 4415 *P. australis* Lam. ssp. *hirtella* (HBK) Rahn

Colombia, Dep. Valle: Cord. Occidental, E slope, basin of Río Cali, Río Pichindé.
Alt. 2070-2260 m, 07-08-1946, Cuatrecasas 21988 (U).

HdV 4377 *P. australis* Lam. ssp. *hirtella* (HBK) Rahn

Colombia, Dep. Antioquia.
Alt. 700 m, 26-03-1949, Scolnik *et al.* 593 (C).

POLLEN MORPHOLOGY, DISTRIBUTION AND HABITAT

The pollen morphology terminology is taken after *Iversen & Troels-Smith* (1950). Descriptions are made on the basis of both light microscopical and S.E.M. photos. Diameters are based on measurements in silicone oil of 50 pollen grains. For the taxa not occurring in Colombia concise data are given for the habitat.

P. sericea HBK ssp. *argyrophylla* (Decne.) Rahn

Grains spheroidal, occasionally ovoidal or irregular, diameter (27-)32-44(-48)μm, av. 38 μm; 3-5 pores, irregular in shape with jagged margins, diameter about 2-3.5 μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 1 μm thick; verrucae variable: irregular in shape and size with microspines, occasionally with granules and microspines in between the verrucae. Number of microspines 4-7 per μm^2.

Present distribution

Northern part of Cordillera Oriental in Colombia (6-10°N), and Cordillera de Mérida in Venezuela, alt. 3300-4200 m (**Rahn**, in preparation).

Habitat

Dry páramo on undeep stony soils, apparently replacing the zonal *Calamagrostis effusa* tussocks in unfavourable habitats. This species spans the upper subpáramo and grass páramo. Well developed zonal vegetation dominated by *P. sericea* ssp. *argyrophylla* was observed on the southern dry side of the Páramo del Almorazadero (*Cleef*, in press).

Notes

Produces much pollen.

Illustrations

Plate I: 1-3; Plate IV: 33-34; Plate VII: 53-61.

P. sericea Ruiz & Pavón ssp. *sericans* (Pilger) Rahn

Grains spheroidal, occasionally ovoidal, diameter (27-) 33-40(-46)μm, av. 37μm; 3-5 pores, irregular in shape with jagged margins, diameter about 2.5-3.5 μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 1.5μ m thick; verrucae irregular in shape and zise with 3-6 microspines per $\mu\ m^2$.

Present distribution

Along the Andes from Perú to Argentine (13-30°S), alt. 2800-4500 m (*Rahn*, in prep.).

Habitat

Puna

Illustrations

Plate I: 4-5; Plate IV: 35; Plate VII: 62-65.

P. sericea Ruiz & Pavón ssp. *sericea* var. *sericea*

Grains spheroidal, occasionally irregular, diameter (32-)34-38(-42)μm, av. 36 μm 3-5 pores, irregular in shape with jagged margins, diameter about 3 μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 1 μm thick; verrucae irregular in shape and size with 3-7 microspines per $\mu\ m^2$.

Present distribution

Perú: Cordillera Occidental 8-13°S and (?) Colombia: Cordillera Oriental 4-6°N, alt. 2600-3800 m, (*Rahn*, in prep.).

Habitat

Peruvian puna element. The isolated Colombian

populations occur as dwarf shrubs in xerophytic *Dodonea viscosa* vegetation, on dry hills bordering the Sabana de Bogotá and was observed constituting a true low shrubby vegetation at about 3000 m alt. between Tunja and Villa de Leiva (Dep. Boyacá) (*Cleef*, in press). The presence of an isolated Colombian *P. sericea* ssp. *sericea* vegetation may be a relict of a former more extensive distribution of xerophytic elements throughout the northern tropical Andes during the driest stadials of maximum glaciation (see *Van der Hammen*, 1974).

Notes

Two collections north of Bogotá, ca. 2600 m alt. are rather similar to *P. sericea* var. *sericea* from Perú (Rahn, pers. comm.).

Illustrations

Plate I: 11; Plate IV: 39; Plate VII: 74-76.

P. sericea Ruiz & Pavón ssp. *sericea* var. *lanuginosa*

Grains spheroidal, occasionally irregular, diameter (36-)37-43(-46)μm, av. 40 μm; 3-5 pores, irregular in shape with jagged margins, diameter about 3-4 μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 1.5 μm thick; verrucae irregular in shape and size with 3-7 microspines per μm^2.

Present distribution

Mountains in Perú, Bolivia and NW Argentine, alt. 2100-4250 m (*Rahn*, in prep.).

Habitat

In Argentine and S Bolivia in pajonales or wet puna vegetation, often on rocky slopes, in C Bolivia and Peru also in dryer places. Altitudinal range 2100-4150 m, corresponding to mean temperatures of January 6-20°C and July -5-16°C. Precipitation 400-1000 mm per year, dry season (2-)4-8(-11) months during winter (*Rahn*, in prep.).

Illustrations

Plate I: 8,10; Plate IV: 37-38; Plate VII 70-73.

P. sericea Ruiz & Pavón ssp. *perreymondii* (Barn,) Rahn.

Grains spheroidal, occasionally irregular, diameter (31-)38-45(-51)μm, av. 42 μm; 3-5 pores, very irregular in shape with jagged margins, diameter about 5 μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 1 μm thick; verrucae irregular in shape and size more or less melted together with 3-7 microspines per μm^2.

Present distribution

Mountains in Venezuela and northern Colombia, alt. 2600-4200 m (*Rahn*, in prep.).

Habitat

Often forming large colonies in páramo vegetation. Mean yearly temperature probably between 5°C and 13°C (*Rahn*, in prep.).

Illustrations

Plate I: 6-7, 9: Plate IV: 36; Plate VII: 66-69.

P. linearis HBK

Grains spheroidal, occasionally irregular, diameter (26-)28-33(-35)μm, av. 30 μm; 3-5 pores, irregular in shape with jagged margins, diameter about 2-3μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 1μm thick; verrucae irregular in shape and size with (3-)4-7 microspines per μ m^2.

Present distribution

Mountains of Venezuela, Colombia, Ecuador, N and C Perú, a single collection from México, alt. 2500-4400 m (*Rhan*, in prep.).

Habitat

P. linearis HBK occurs in the Colombian páramos mainly between 3100 and 4000 m alt., frequently found along mule tracks, mostly in the subpáramo on the dry side of the mountains (*Cleef*, in press). Mean yearly temperature probably between 4°C and 16°C with insignificant seasonal variation. Precipitation between about 500 and 1000mm per year (*Rahn*, in prep.).

Illustrations

Plate II: 12-14; Plate V: 40-42; Plate VIII: 77-81.

P. linearis HBK var. *agrostophylla* (Decne.) Pilg.

Grain spheroidal, occasionally irregular or ovoidal, diameter (40-)45-47(-53) μm, av. 46μm; 3-5 pores, irregular in shape and size with jagged margins, diameter about 5-7μm, pore membrane with granules and microspines no operculum, no annulus; exine and intine about 1.0-1,5 μm thick; verrucae ± isodiametric with 3-5 microspines per μm^2.

Notes

Rahn does not recognize any subspecies or variety of *P. linearis* HBK Specimens referred to it by Pilger and others are large specimens of *P. linearis* HBK found throughout the area. The largest variation regarding size is found in Ecuador. *Pilger* (1973) cites *P. linearis* var. *agrostophylla* from both Ecuador and Colombia (Rahn, pers. comm.).

Illustrations

Plate II: 15-16; Plate V: 43; Plate VIII: 82-83.

P. rigida HBK

Grains spheroidal, occasionally irregular, diameter (20-)23-46(-50) μm, av. 35 μm; 8-15 pores, very irregular in shape and size with jagged margins, diameter about 3-5 μm, pore membrane with

granules and microspines, no operculum, no annulus; exine and intine about 0.7-1.4 μm thick; sculpture very variable: verrucae hard to distinguish with microspines and microperforations (pseudo-scabrate) to clear verrucae, irregular in shape and size with microspines, more or less protruding with granules and microspines in between the verrucae to with joining verrucae. Number of microspines 8-16 μm^2.

Present distribution

Along the Andes from Mérida (Venezuela) to the Cordillera Real (Bolivia) (*Cleef*, 1978).

Habitat

P. rigida HBK constitutes virtual cushion bogs at high elevation (3000–5200 m alt.) in the puna and páramo. According to *Cleef* (1978, and in press) *P. rigida* cushion bogs are common in the grass páramo (± 3600-4200 m alt.) of the Colombian Andes and occur in boggy valleys, on former lakes or even float on glacial lakes in the humid bamboo páramo.

Notes

Produces large quantities of pollen.

Illustrations

Plate II: 17-21; Plate III: 22-23; Plate V: 44-47; Plate VIII: 84-91.

P. australis Lam. ssp. *oreades* (Decne.) Rahn

Grains spheroidal, occasionally irregular, diameter (20-)24-37(-40) μm, av. 30 μm; 8-12 pores, circular, occasionally irregular with jagged margins, diameter about 2.0-4.5 μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 1.0-1.5 μm thick; verrucae more or less swollen, irregular in shape and size with microspines, occasionally with granules and microspines in between the verrucae. Number of microspines (4-)6-9(-10)μm^2.

Present distribution

Sierra Nevada de Mérida (Venezuela) and the Cordillera Oriental (Colombia), alt. 2600-4000 m, but mainly above 3400 m alt. (*Rahn*, 1974).

Habitat

P. australis ssp. oreades is a common element in wet subpáramo and grass páramo vegetations. In the Colombian Eastern Cordillera this subspecies was recorded with low cover in different azonal moist páramo communities: e.g., *Lupinus alopecuroides-Mimulus glabratus* peat in small subpáramo valleys, dense *Blechnum loxense-Espeletia* div. spec. subpáramo bog, *Calamagrostis ligulata* grass mires, also in lake hydrosere succession, humid *Hypericum laricifolium* ssp. *laricoides* shrub and dense *Espeletia* stands on boggy glacial valley floors (*Cleef*, in press).

Notes

Produces large quantities of pollen.

Illustrations

Plate III: 24, 26-30; Plte VI: 48-51; Plate VIII: 92-101.

P. australis Lam. ssp. *sodiroana* (Pilger) Rahn

Grains spheroidal, occasionally ovoidal or irregular, diameter (19-)22-41(-48) μm; 9-14 pores, circular or slightly irregular in shape with jagged margins, diameter about 2 μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 0.8 μm thick; verrucae variable; very small (0.8 μm in diameter, pseudo-scabrate) to 2.5 μm in dimeter with 7-11 microspines per μm^2.

Present distribution

Along the Andes from central Peru to Venezuela (*Rahn*, 1984).

Habitat

According to *Rahn* (1974): "In the mountains from 1300-3700 m but mainly between 2500-3600 m. Little is known about its ecology: it occurs in wet places but no doubt it is also found elsewhere".

Notes

Both semi-cleistogamous and chasmogamous flowers. The latter have larger anthers with many pollen grains which are smaller than those from semi-cleistogamous flowers (*Rahn*, 1974). The sculpture of the pollen grains studied in this paper (diameter verrucae 0.8 mm; pseudo-scabrate) differs from the results obtained by *Rahn* (1974) (diameter verrucae 2,5 μm; verrucate). It should be regarded as exemplifying the limits of variability in the sculpture of this subspecies. The pollen diameters provided by *Rahn* (1974) are incorporated in the description here presented. Illustrations are given of both sculpture types.

Illustrations

Plate III: 31-32; Plate VI: 52; Plate VIII: 102-106.

P. australis Lam. ssp. *hirtella* (HBK) Rahn

Grains spheroidal, occasionally irregular, diameter (22-)26-30(-34) μm; 8-12 pores, irregular in shape with jagged margins, diameter about 3 μm, pore membrane with granules and microspines, no operculum, no annulus; exine and intine about 1.0-1.5 μm thick; verrucae irregular in shape and size with ± 8 microspines per μm^2.

Present distribution

According to *Rahn* (1974): "Two probably separate areas. One in S Brazil, S Paraguay and NE Argentine mostly below 1000 m; the other exten-

	SPECIES	RESIDU	$\bar{x}$	s
subgen.Psyllium sect. Gnaphaloides	P.sericea ssp.argyrophylla	HdV 4247	35,8	3,99
		HdV 4250	40,2	4,15
		HdV 3096	32,7	1,78
	P.sericea ssp.sericans	HdV 4418	36,7	3,73
	P.sericea ssp.perreymondii	HdV 4370	41,7	3,45
	P.sericea ssp.sericea var.lanuginosa	HdV 4417	39,9	2,75
	P.sericea ssp.sericea var.sericea	HdV 4419	35,8	2,04
		HdV 4252	31,7	2,55
	P.linearis	HdV 4376	30,5	1,93
		HdV 4248	30,1	1,57
	P.linearis var.agrostophylla	HdV 4416	46,1	3,17
subgen.Plantago sect. Oliganthos	P.rigida	HdV 4421	42,0	4,28
		HdV 4249	26,7	3,57
		HdV 4420	28,7	3,94
		HdV 3741	27,2	1,75
sect. Virginica	P.australis ssp.oreades	HdV 4251	28,0	2,37
		HdV 4411	32,3	2,29
		HdV 4412	26,6	2,85
		HdV 4414	34,5	2,81
		HdV 4098	25,6	1,99
		R		
	P.australis ssp.sodiroana	HdV 4369	24,3	2,19
		R	36,8	4,13
		R	29,6	2,03
	P.australis ssp.hirtella	HdV 4415		
		R		
		R		
		R		

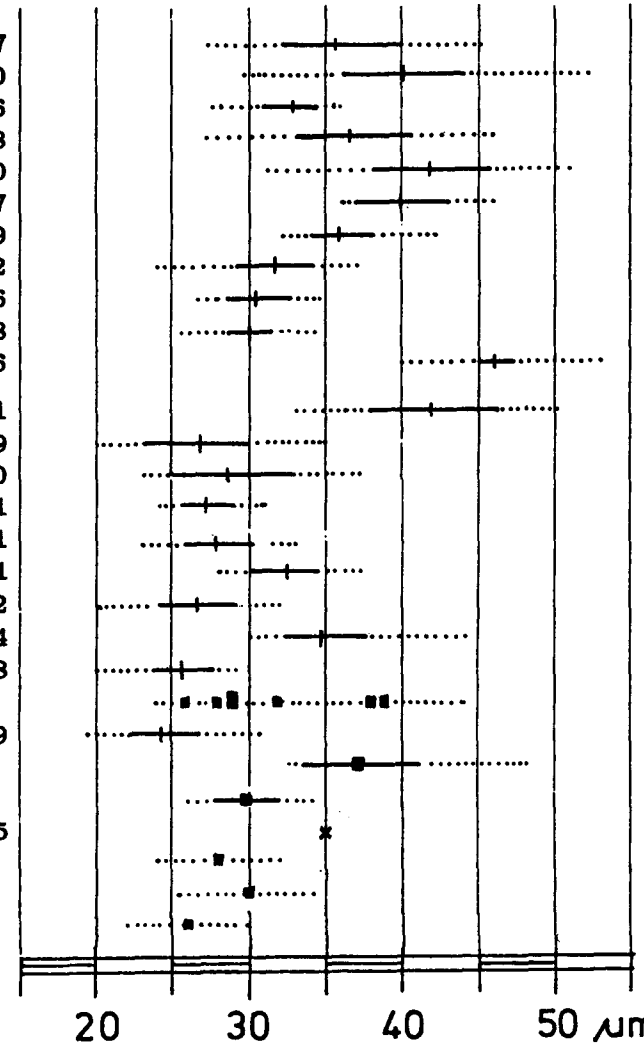

Table I. Pollen sizes of the Colombian Plantago species. Diameters are based on the measurements in silicone oil of 50 pollen. The horizontal lines represent the standard deviation of the mean pollen size. The dotted lines represent the range of diameters measured. The short vertical lines indicate the mean size. Blocks indicate the mean size of the collections studied by Rahn (1974). HdV 4415 provided only one pollen grain. Each residue number corresponds with a botanical collection mentioned in the list of specimens examined.

ding from S Arizona, through México, C. América and the Andes to NW Argentine, mostly between 100 and 3000 m. On both sides of the Cordillera from Mexico to Ecuador, but further south (i.e., in Perú, Bolivia and NW Argentine) only on the eastern side".

Habitat

Mainly in open places in subtropical forest, e.g., along roads, with rainfall mainly during the summer (**Rahn**, 1974).

Notes

The flowers are semi-cleistogamous with small anthers which produce very few pollen grains (*Rahn*, pers. comm.). Data about pollen diameter copied from *Rahn* (1974). This taxon is of no importance for pollen analysis and is not incorporate in the pollen key.

Illustrations

Plate III: 25.

POLLEN KEY TO THE SPECIES OF THE GENUS PLANTAGO IN COLOMBIA AND VENEZUELA

a	Number of pores 3-6	b
aa	Number of pores 8-14	c
b	Pores irregular in shape with jagged margins, diameter 2-3.5 μm. Pore membrane with granules and microspines. Verrucae variable: irregular in shape and size with microspines, joined together or occasionally with granules and microspines in between the verrucae (3-7 microspines per μm^2). Grains (24-)29-45(-51) μm in diameter.	*P. sericea* group or *P. linearis* HBK (subgen. *Psyllium* sect. *Gnaphaloides*)
bb	Pores irregular in shape and size with jagged margins, diameter 5-7 μm. Pore membrane with granules and microspines. Verrucae more or less isodiametric, with microspines (3-5 μm^2). Grains (40-)45-47(-53) μm in diameter.	*P. linearis* HBK var. *agrostophylla* (Decne.) Pilger (subten. *Psyllium* sect. *Gnaphaloides*)
c	Pores circular, occasionally irregular, with jagged margins. Diameter 2.0-4.5 μm. Pore membrane with granules and microspines. Verrucae more or less swollen, irregular in shape and size with microspines, occasionally with granules and microspines in between the verrucae ((4-)6-9(-11) microspines μm^2). Grains (20-)23-37(-40) μm in diameter, av. 30 μm.	*P. australis* Lam. ssp. *oreades* (Decne.) Rahn or *P. australis* Lam. ssp. *sodiroana* (Pilger) Rahn (Subgen. *Plantago*, sect. *Virginica*)
cc	Pores very irregular in shape and size with jagged margins, occasionally pores to circular. Diameter (2.5-)3-6 μm. Pore membrane with granules and microspines. Verrucae very variable: verrucae from difficult to distinguish, with microspines (pseudo-scabrate), to clear verrucae, irregular in shape and size with microspines, close together or at some distance with granules and microspines in between (8-16 microspines per μm^2). Grains (20-)23-46(-50) μm in diameter, av. 35μm.	*P. rigida* HBK (subgen. *Plantago* sect. *Oliganthos*)

DISCUSSION

On the basis of the descriptions given pollen grains of the subgenus *Psyllium*, sect. *Gnaphaloides (P. sericea* and *P. linearis)* and subgenus *Plantago*, sect. *Oliganthos (P. rigida)* and sect. *Virginica (P. australis)* can be distinguished.

The variability in pollen diameter, pore diameter and shape and size of the verrucae in each section is great. Many transitional forms exist between distinct taxa recognised at first sight. Thus in the section *Gnaphaloides* it is impossible to distinguish between the different subspecies of *P. sericea* and the very similar *P. linearis* with certainty. *P. linearis* HBK var. *agrostophylla* (Decne.) Pilg. can be isolated in the section *Gnaphaloides* mainly because of the very large pore diameter and pollen size. These quantitative kinds of morpholigical characters correspond with the opinion of Rahn that *P. linearis* var. *agrostophylla* represents the large specimens of *P. linearis* HBK. Isolation of this taxon, therefore, appears ungrounded, moreover because no typical ecological information is available.

A remarkable discrepancy appears between the pollen of *P. rigida* of the Cordillera Oriental and the Cordillera Central. The material of the Cordillera Oriental (HdV 4249, HdV 4420, HdV 3741) is very homogeneous in pollen diameter and sculpture. The material of the Cordillera Central (HdV 4421) is different in pollen diameter (see Table I) and sculpture (see Plate II: 17, 20; Plate III: 22) and is very similar to the fossil pollen grains of *P. rigida* of the Laguna Otún (Cordillera Central). This may point to and evolutionary differentiation in the two separated populations or ecotype differentiation.

Although the S.E.M. micrographs did not provide us with more useful taxonomical characters they do give additional information on the light microscope photos, e.g., the great variability in shape and size of the verrucae and the distance between them.

When dealing with fossil pollen grains in lake sediments one has to consider the different amounts of pollen produced by different taxa.

According to present-day distribution in the Cordillera Oriental, the sequence of the most common species in lake sediment is as follows (from high to low pollen producers): *P. rigida, P. australis* ssp. *oreades, P. sericea* ssp. *argyrophylla* and more rarely *P. linearis, P. australis* ssp. *sodiroana, P. australis* ssp. *hirtella* and *P. sericea* ssp. *sericea.*

The pollen key provided has also been applied to fossil pollen grains of Plantago from lake deposits. In the lake sediment of Funza, Sabana de Bogotá, Cordillera Oriental (*Hooghiemstra,* in prep.) fossil *Plantago* pollen could be identifies ad mainly *P. australis* Lam. ssp. *oreades* (Pilger) Rahn. The age of the identified fossil pollen grains varies from about 1,2, to 2,5 million years.

Fossil pollen grains of Plantago of the lake sediment of the Laguna Otún, Cordillera Central (*Kuhry,* in prep.) of Holocene age, could be identified as corresponding to *P. rigida* HBK exclusively. *Plantago rigida* cushion bogs are at present still very common near the Laguna Otún.

Acknowledgements

The author wishes to thank the Netherlands Foundation for the Advancement of Tropical Research WOTRO, which sponsored this study. He is also much indebted to Drs. A.M. Cleef of the Institute of Systematic Bobany, State University of Utrecht and Dr. Knud Rahn of the Botanical Museum University of Copenhagen for supplying him the pollen samples and with whom he had some very helpful discussions. He also thanks Dr. R.A. Wijmstra for his valuable advice. The assistance of Mr. G.W. Noldus, who prepared the pollen material, of Mr. G. Oomen, who assisted in the photographic work, Ms J. dos Santos, who typed the manuscript and Mr. C. Bakker, technician of the Research Group for Scanning Electron Microscopy of the University of Amsterdam, is gratefully acknowledged. He thanks Dr. C.A.N. van Oorschot for revising the English text.

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PLATE I

1. *P. sericea* HBK ssp. *argyrophylla* (Decne.) Rahn* x 2000, HdV 4247

2., 3. *P. sericea* HBK ssp. *argyrophylla* (Decne.) Rahn* x 2000, HdV 4250

4., 5. *P. sericea* Ruiz & Pavón ssp. *sericans* (Pilger) Rahn** x 2000, HdV 4418

6., 7., 9. *P. sericea* Ruiz & Pavón ssp. *perreymondii* (Barn.) Rahn x 2000, HdV 4370

8., 10. *P. sericea* Ruiz & Pavón ssp. *sericea* var. *lanuginosa* Griseb. x 2000, HdV 4417

11. *P. sericea* Ruiz & Pavón ssp. *sericea* var. *sericea* x 2000, HdV 4419

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* Previously erroneously identified as *P. nubigena* HBK

** Previously erroneously identified as *P. monticola* Decne.

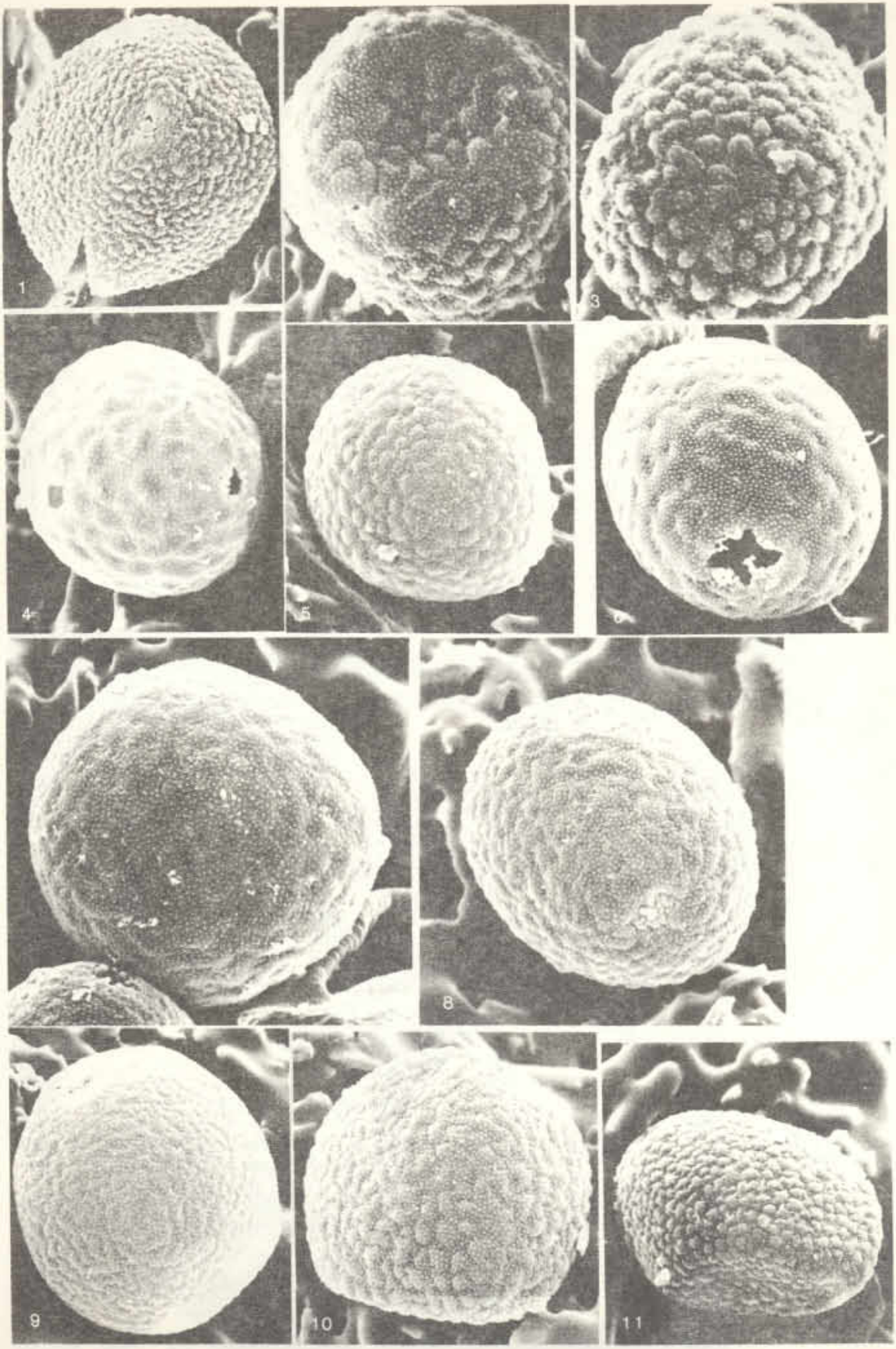
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PLATE II

12., 13. *P. linearis* HBK
x 2000, HdV 4376

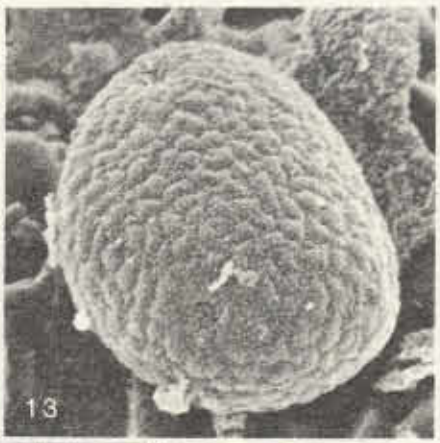
14. *P. linearis* HBK
x 2000, HdV 4248

15., 16. *P. linearis* HBK var. *agrostophylla* (Decne.) Pilger
x 2000, HdV 4416

17., 20. *P. rigida* HBK
x 2000, HdV 4421

18.,19.,20. *P. rigida* HBK
21 x 2000, HdV 4420


12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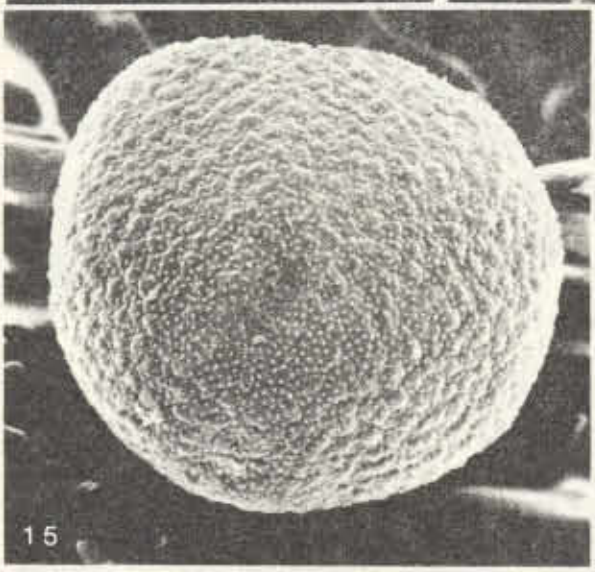
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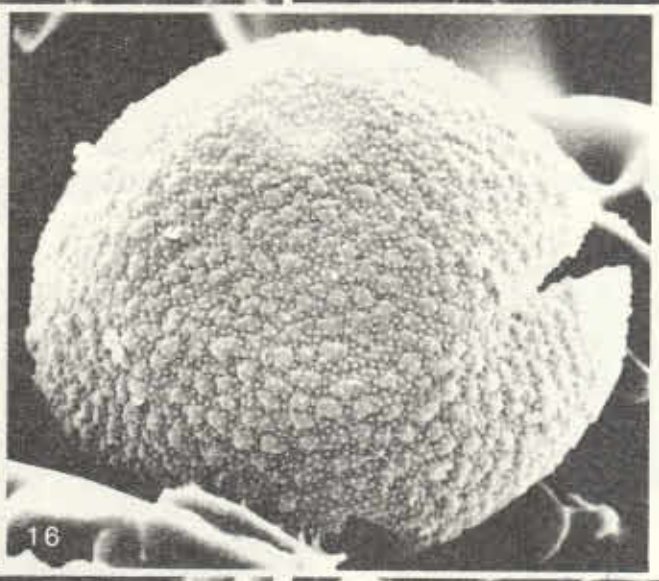
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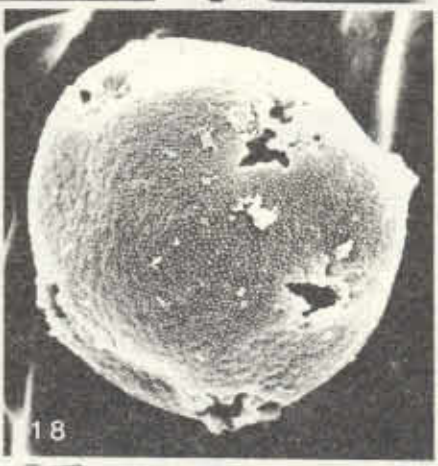
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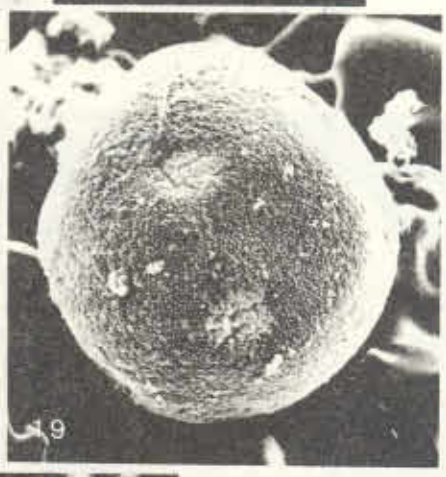
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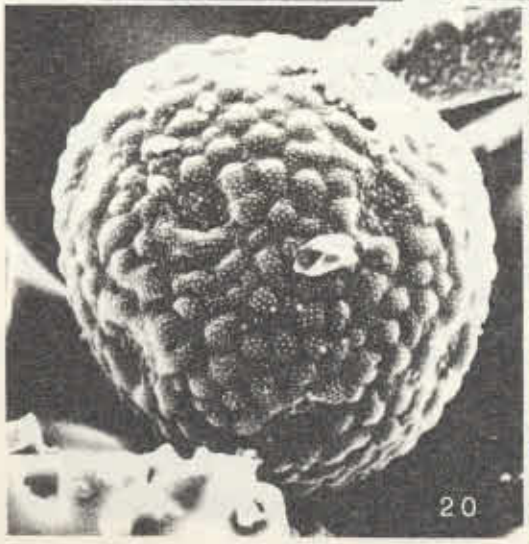
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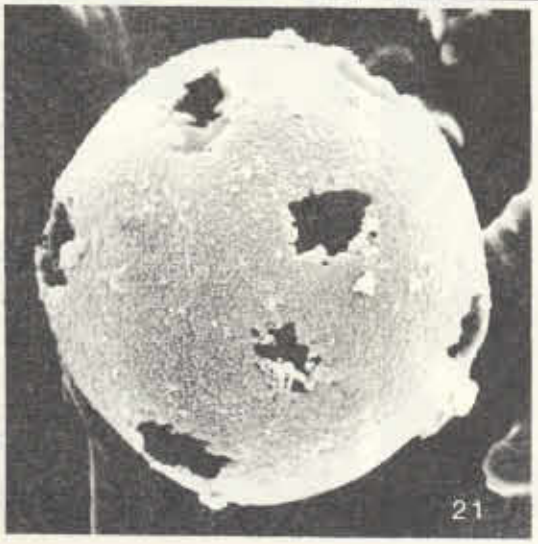
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PLATE III

22. *P. rigida* HBK
x 2000, HdV 4421

23. *P. rigida* HBK
x 2000, HdV 4420

24. 27. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 2000, HdV 4414

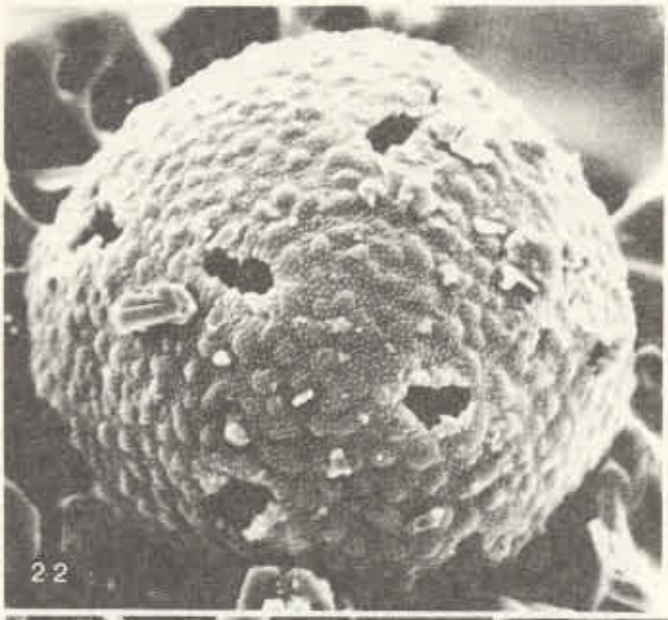
25. *P. australis* Lam. ssp. *hirtella* (HBK) Rahn
x 2000, HdV 4415

26. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 2000, HdV 4251

28., 29. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 2000, HdV 4411

30. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 2000, HdV 4412

31.,32. *P. australis* Lam. ssp. *sodiroana* (Pilger) Rahn
x 2000, HdV 4369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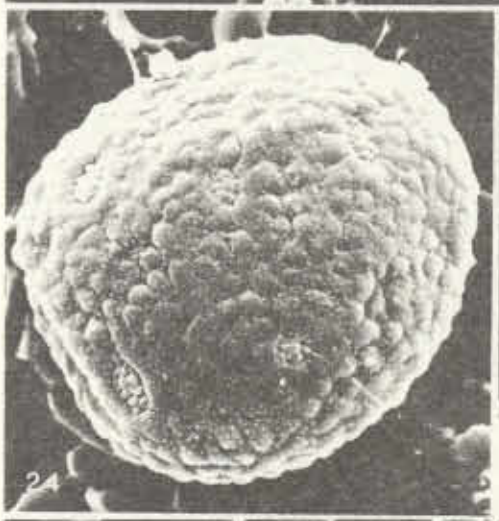
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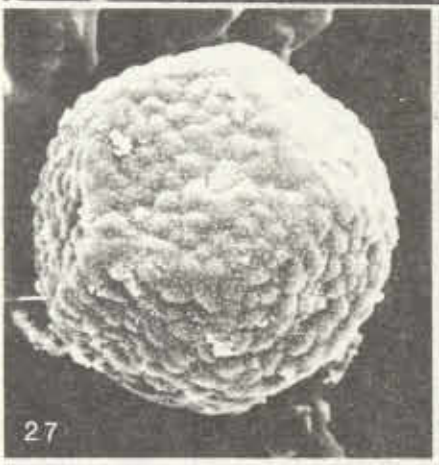
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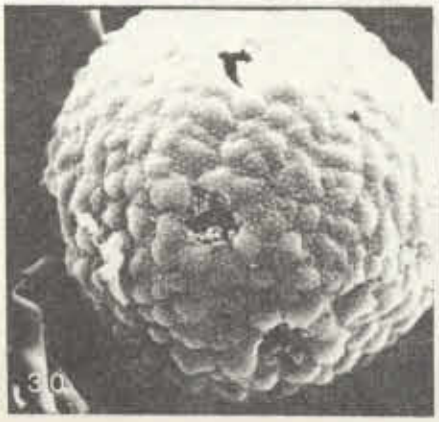
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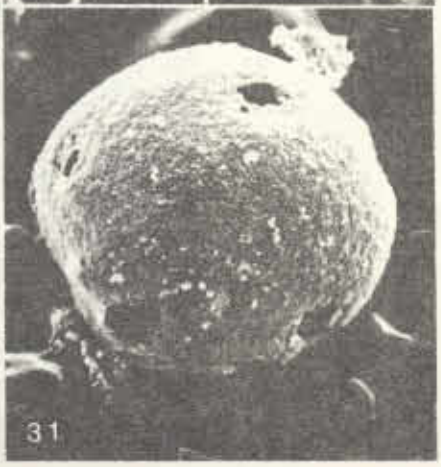
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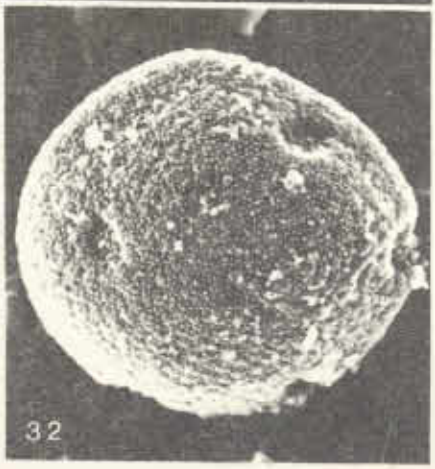
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PLATE IV

33. *P. sericea* HBK ssp. *argyrophylla* (Decne.) Rahn* x 10,000, HdV 4247

34. *P. sericea* HBK ssp. *argyrophylla* (Decne.) Rahn* x 10,000, HdV 4250

35. *P. sericea* Ruiz & Pavón ssp. *sericans* (Pilger) Rahn** x 10,000, HdV 4418

36. *P. sericea* Ruiz & Pavón ssp. *perreymondii* (Barn.) Rahn x 10,000, HdV 4370

37., 38. *P. sericea* Ruiz y Pavón ssp. *sericea* var. *lanuginosa* Griseb. x 2000, HdV 4417

39. *P. sericea* Ruiz & Pavón ssp. *sericea* var. *sericea* x 10,000, HdV 4419

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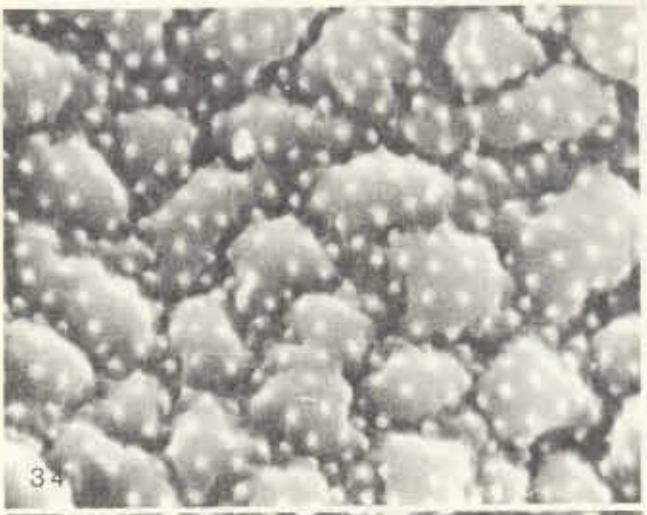
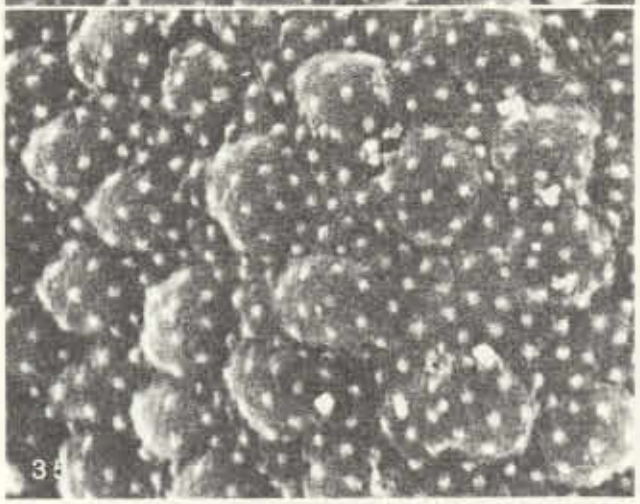
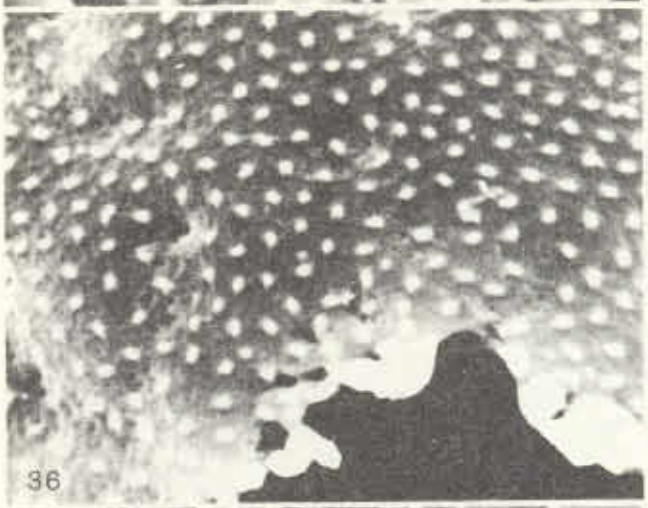
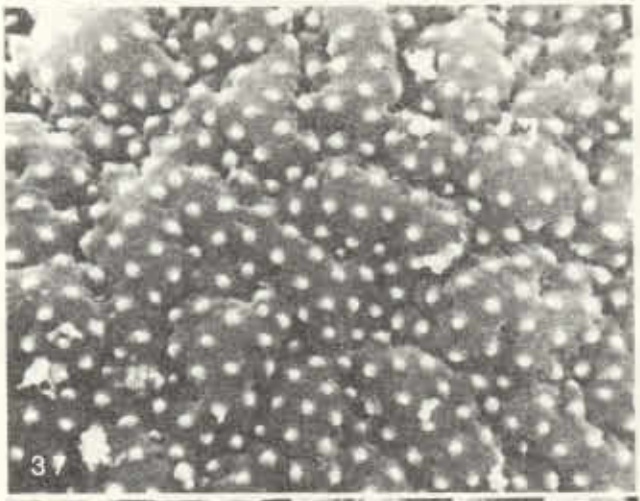
* Previously erroneously identified as *P. nubigena* HBK

** Previously erroneously identified as *P. monticola* Decne.









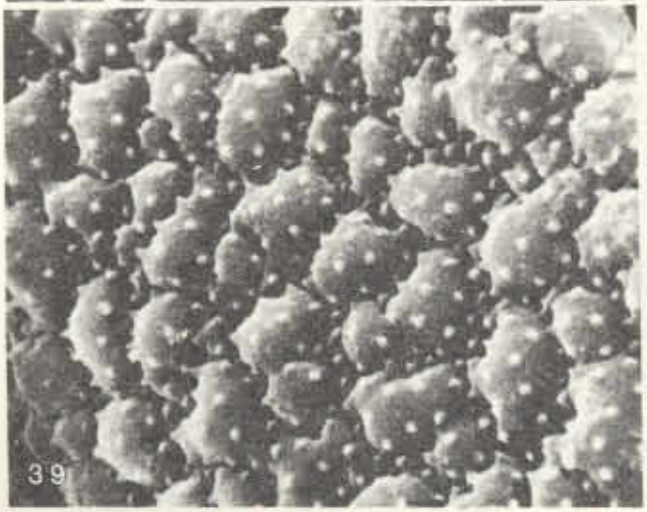


PLATE V

40., 41. *P. linearis* HBK
x 10,000, x 5000, HdV 4376

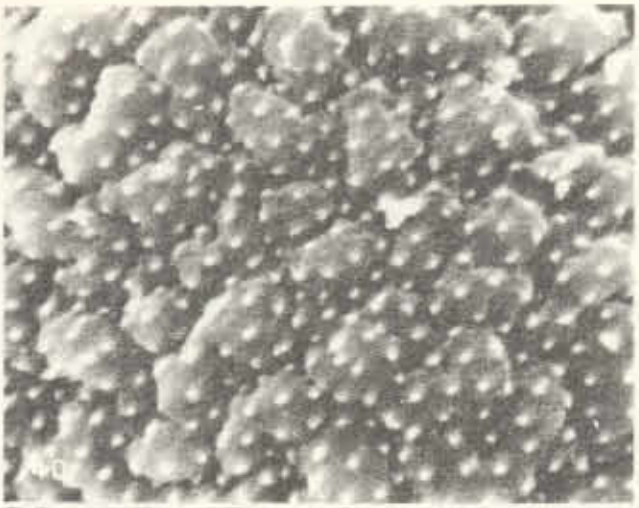
42. *P. linearis* HBK
x 10,000, HdV 4248

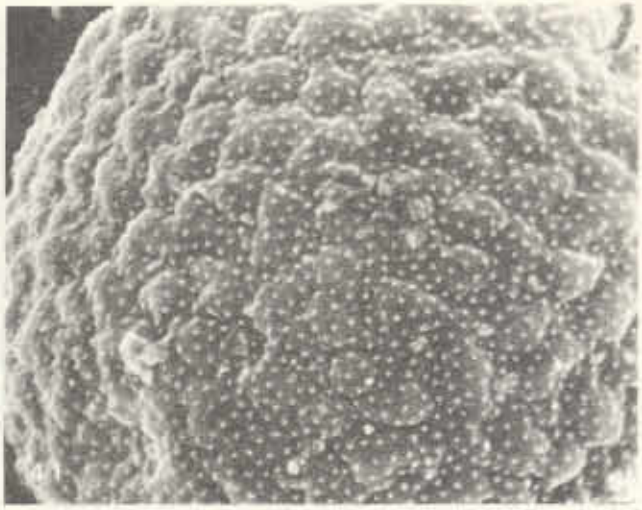
43. *P. linearis* HBK var. *agrostophylla* (Decne.) Pilger
x 5000, HdV 4416

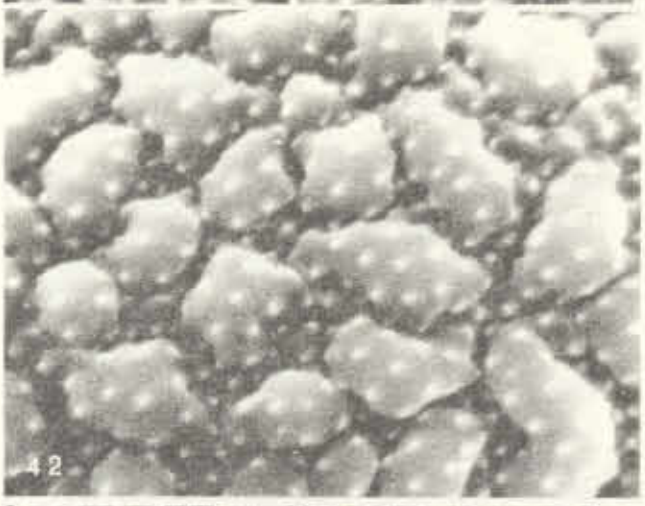
44. *P. rigida* HBK
x 10,000, HdV 4421

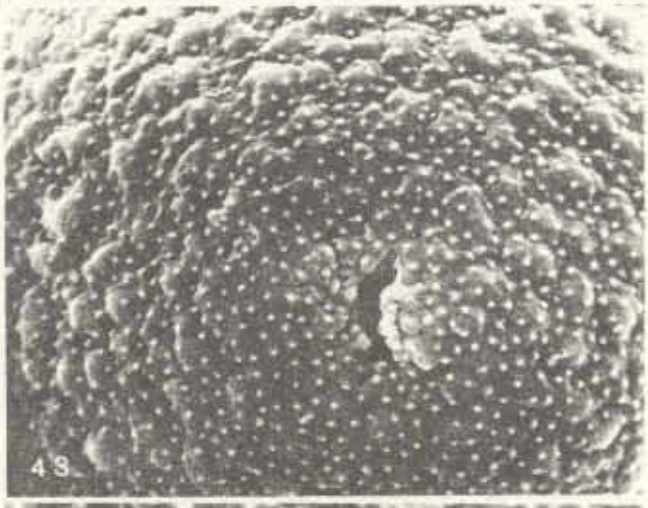
45. *P. rigida* HBK
x 10,000, HdV 4249

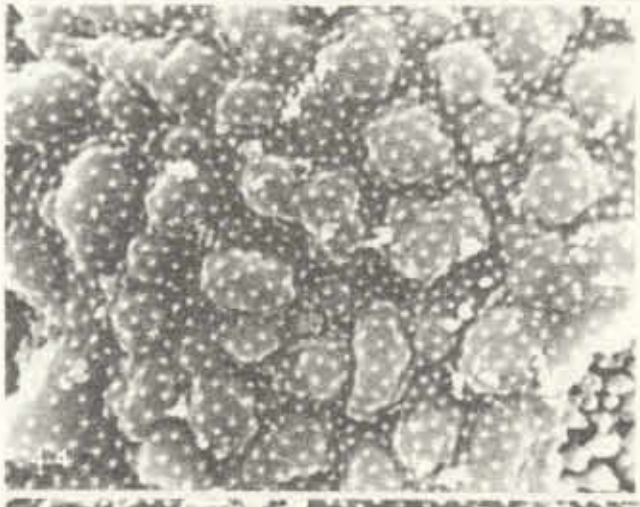
46., 47. *P. rigida* HBK
x 10,000, HdV 4420

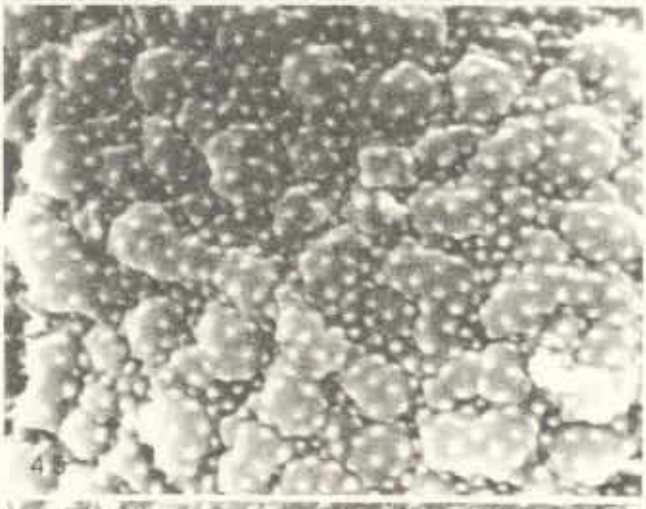


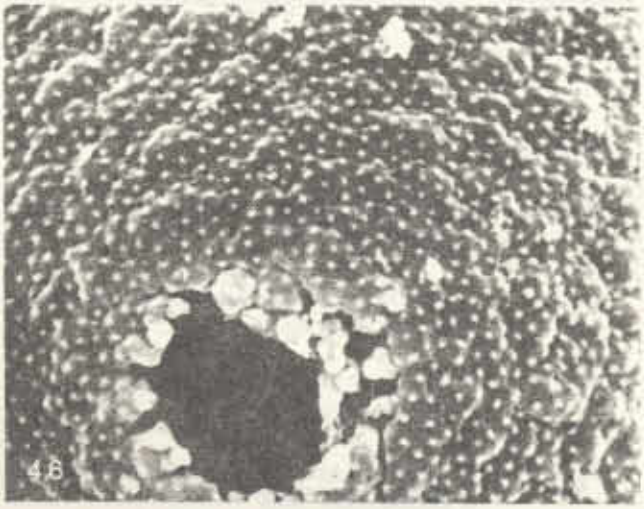












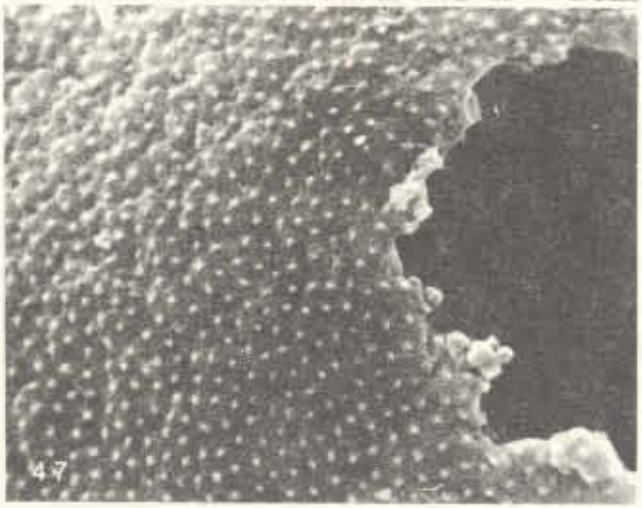


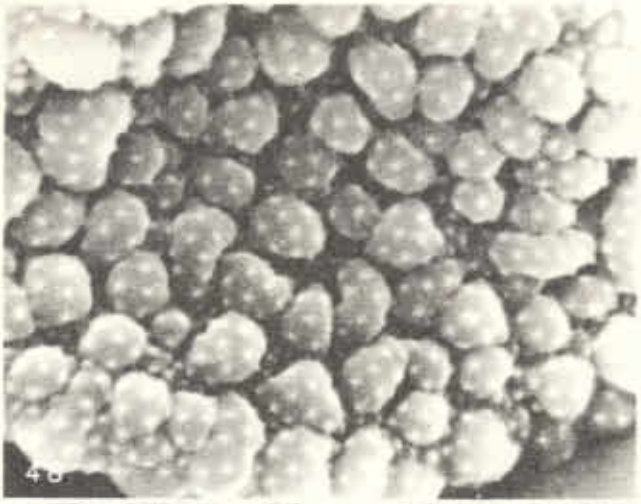
PLATE VI

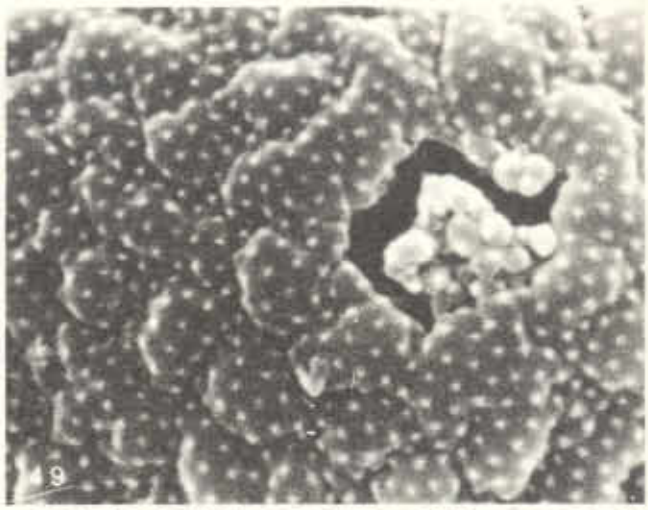
48., 49. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 10,000, HdV 4251

50. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 10,000, HdV 4412

51. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 10,000, HdV 4411

52. *P. australis* Lam. ssp. *sodiroana* (Pilger) Rahn
x 10,000, HdV 4369



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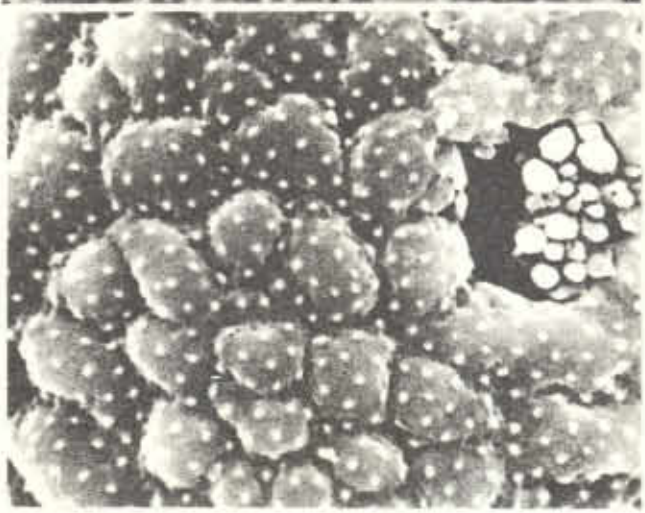

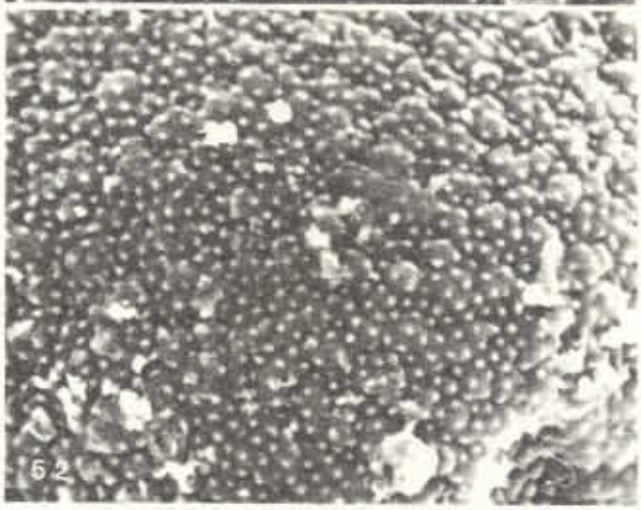
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PLATE VII

53., 56. *P. sericea* HBK ssp. *argyrophylla* (Decne.) Rahn* x 1000, HdV 2880

57., 61. *P. sericea* HBK ssp. *argyrophylla* (Decne.) Rahn* x 1000, HdV 3096

62., 65. *P. sericea* Ruiz & Pavón ssp. *sericans* (Pilger) Rahn** x 1000, HdV 4418

66., 69. *P. sericea* Ruiz & Pavón ssp. *perreymondii* (Barn.) Rahn x 1000, HdV 4370

70., 73. *P. sericea* Ruiz & Pavón ssp. *sericea* var. *lanuginosa* Griseb. x 1000, HdV 4417

74.,76. *P. sericea* Ruiz & Pavón ssp. *sericea* var. *sericea* x 1000, HdV 4419

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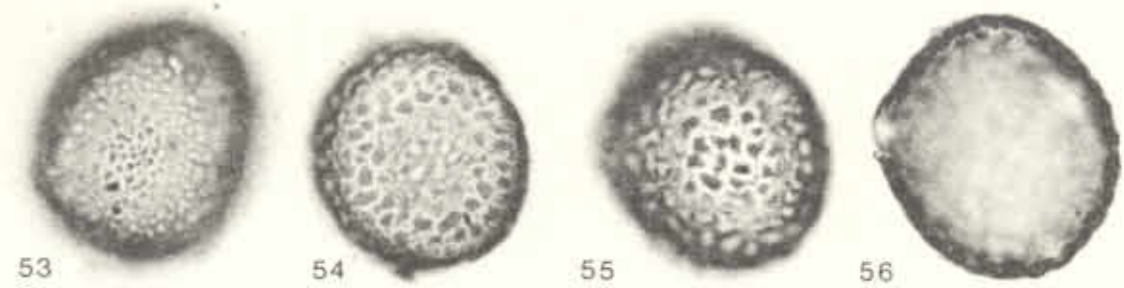
* Previously erroneously identified as *P. nubigena* HBK

** Previously erroneously identified as *P. monticola* Decne.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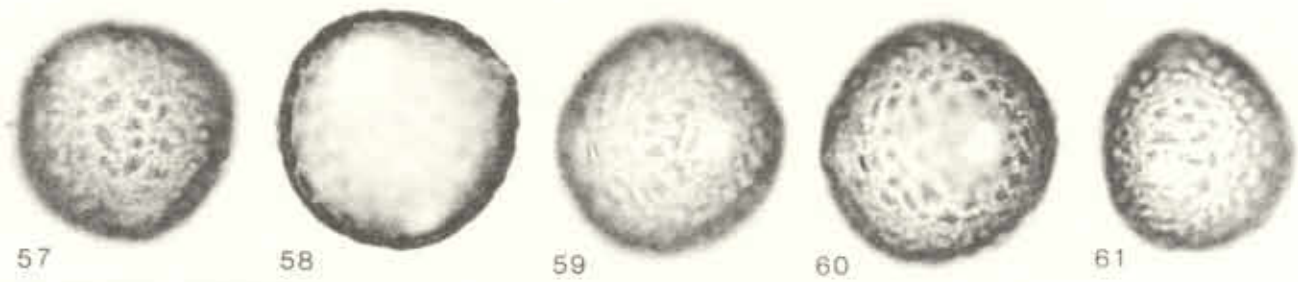
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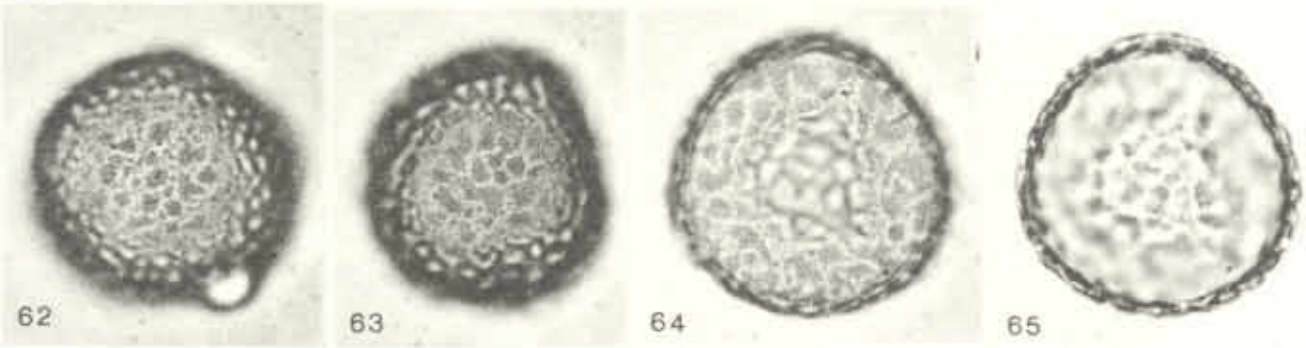
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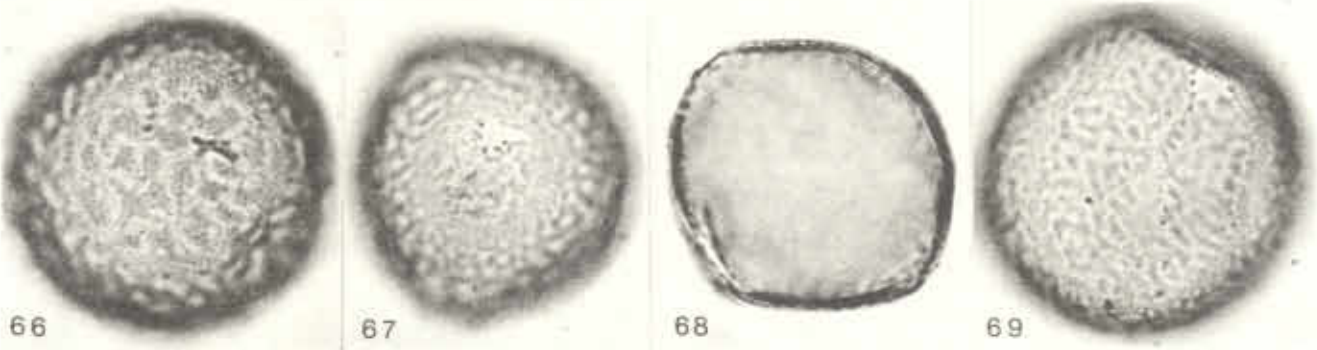
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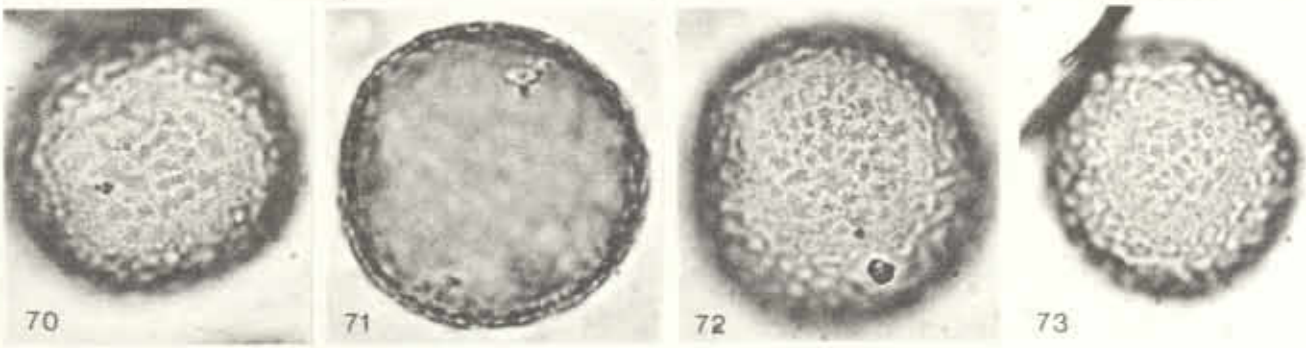
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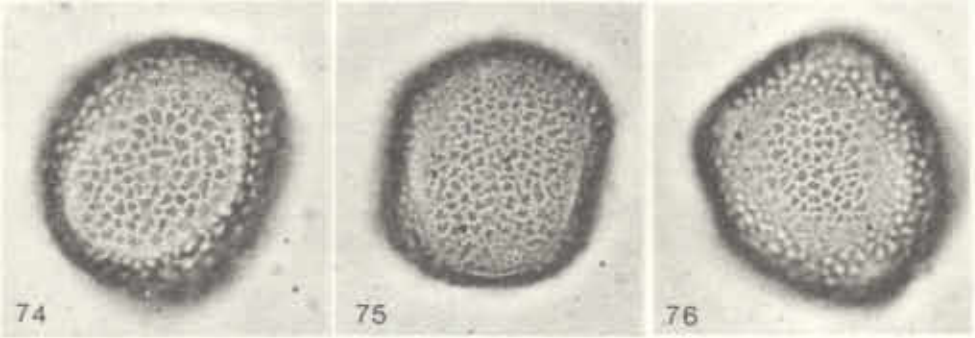
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PLATE VIII

77., 79. *P. linearis* HBK
x 1000, HdV 4376

80., 81. *P. linearis* HBK
x 1000, HdV 4248

82., 83. *P. linearis* HBK var. *agrostophylla* (Decne.) Pilger
x 1000, HdV 4416

84., 88. *P. rigida* HBK
x 1000, HdV 3097

89., 91. *P. rigida* HBK
x 1000, HdV 3741

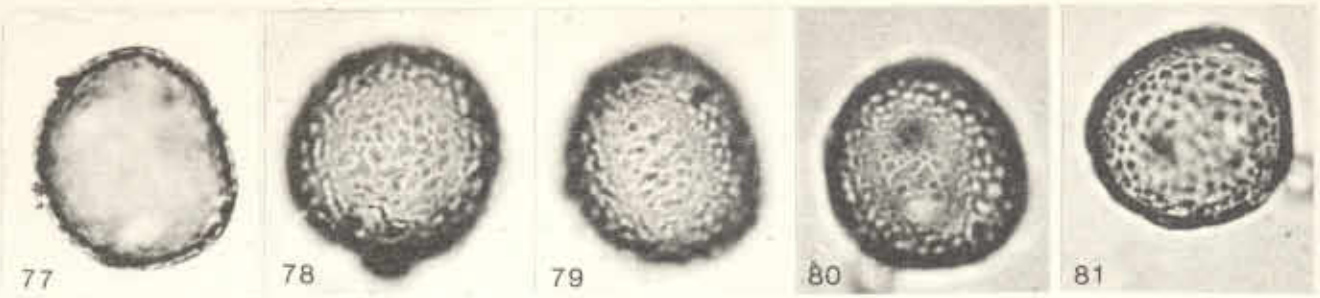
92., 96. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 1000, HdV 2838

97., 100. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 1000, HdV 4098

101. *P. australis* Lam. ssp. *oreades* (Decne.) Rahn
x 1000, HdV 4411

102,104. *P. australis* Lam. ssp. *sodiroana* (Pilger) Rahn
x 1000, Rahn, cult. R 418

105,106. *P. australis* Lam. ssp. *sodiroana* (Pilger) Rahn
x 1000, HdV 4369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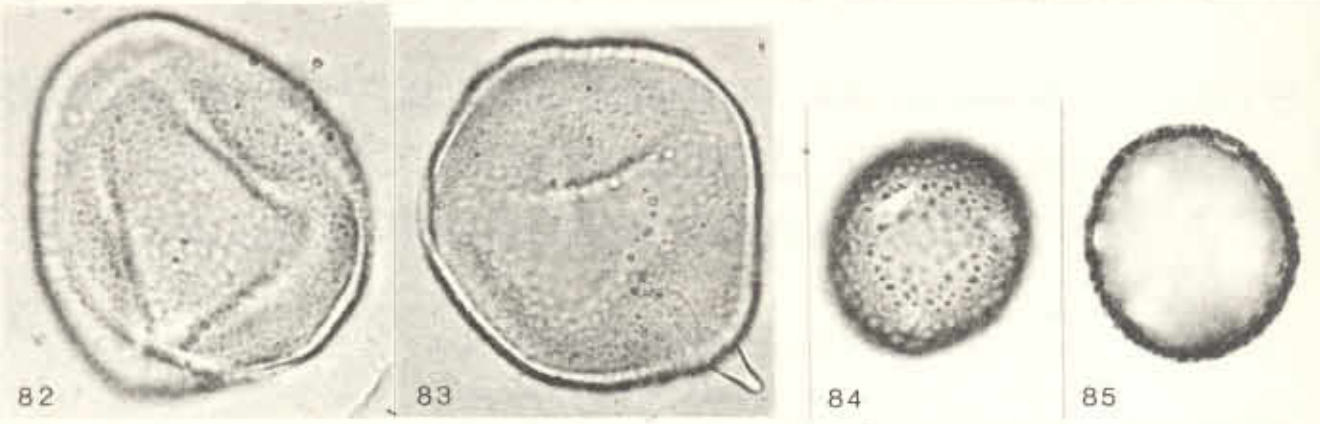
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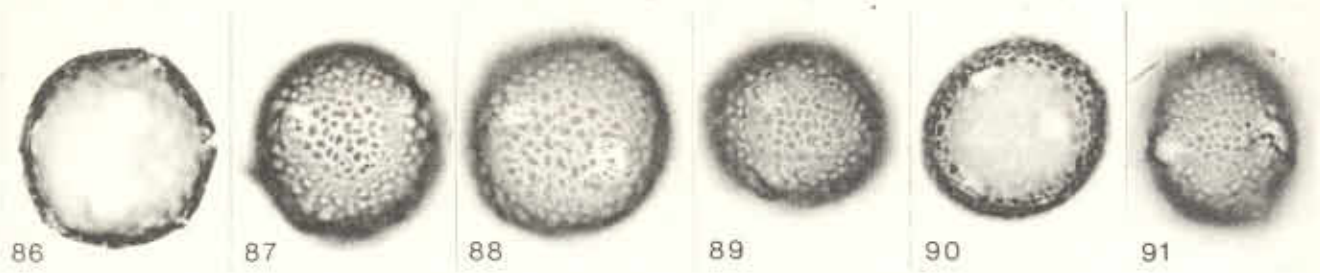
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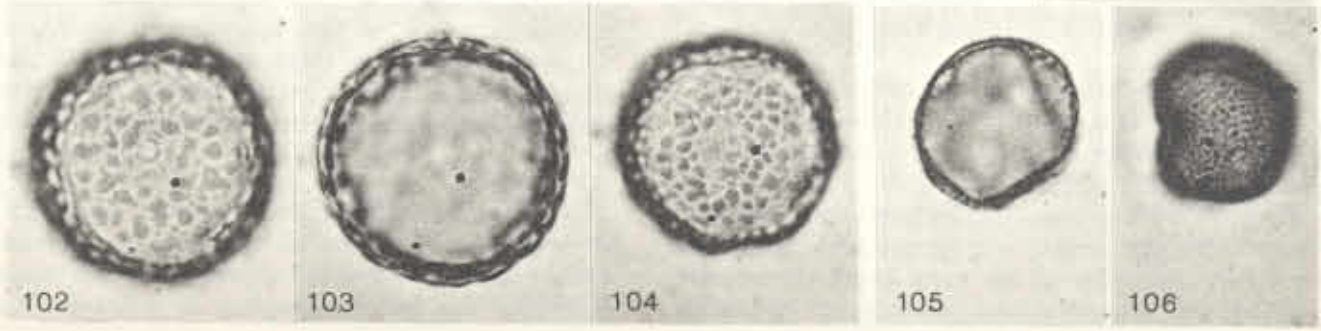
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