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POLLEN GRAIN CHARACTERS OF CERTAIN CACTACEAE

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A study of the pollen grains of cacti native to Arizona shows that the grains are of two forms. Each basic form can be further subdivided by size, sculpturing of exine, and number and position of germ pores, so that the genera, subgenera, and some species may be distinguished by their pollen grains. For this study pollen samples were obtained from plants growing locally, and from herbarium specimens. I am greatly indebted to Dr. F. W. Gould for the use of the University of Arizona Herbarium, Tucson, Arizona, and to R. H. Peebles for the use of the excellent collection of cactus material in the Herbarium at Sacaton, Arizona. I wish also to thank Dr. W. S. Phillips for his kind suggestions and interest in all phases of this study. All pollen was mounted in glycerin jelly and stained either with methyl-green which made the ridge schemes especially clear, or with aqueous fuchsin which brought out the sculpturing of the exine. This method of mounting expanded the grains completely and examination and measurements were made from the expanded grains in polar view. The pollen characters observed are presented in the following keys and discussions.

Grain spheroidal; all grains tricolpate or a mixture of tricolpate and mono-, di-, tetra-, and nonacolpate (*Echinocereus pentalophus* may be dodecacolpate); exine pitted ..... *Cereus, Echinocactus, Mammillaria, Echinocereus.*

Grain dodecacolpate; cube and dodecahedron[1] or a variation of this usually with more than 18 faces, or tending to be a spherical and regular cube and dodecahedron with outline of faces indistinct (*Opuntia*).

Grain spherical, cube and dodecahedron; tetragons and hexagons not distinct; ridges not raised, usually wide; exine pitted; pores circular. *Opuntia* subg. *Cylindropuntia.*

Grain a perfect cube and dodecahedron or a variation of it; ridges raised; tetragons and hexagons distinct; exine reticulate. *Opuntia* subg. *Platyopuntia.*

CEREUS, ECHINOCACTUS, MAMMILLARIA, ECHINOCEREUS

Grain tricolpate; spheroidal; 41–82 μ in diameter; exine finely pitted and in some species, especially *Cereus Schottii,* minutely spiney (spines up to 1.5 μ high). In pollen samples of each species most grains are tricolpate, but many mono-, di-, tetra-, penta-, hexa-, and nonacolpate grains also occur. The furrows of tricolpate grains are long, usually narrow, and approach within 5–10 μ of the poles. As the number of furrows increases the

[1] A cube and dodecahedron is a solid with six squares and twelve hexagons.

furrows become progressively shorter (fig. 3). Of special interest are the grains of *Echinocereus pentalophus* which may be the typical tricolpate type, but many grains are large (67 μ) and dodecacolpate; that is, with twelve short, equally spaced furrows so arranged that their axes converge toward eight triradiate centers. These grains rather closely resemble pollen of *Opuntia leptocaulis* or similar *Opuntia* pollen, and may indicate a possible relationship. Furrow margins of *Cereus, Echinocactus, Mammillaria, Echinocereus* pollen may be distinct or fringed with overlapping exine. Germ pores are not visible. Expansion of grains is accomplished by the evagination of the furrows from the dry state in which the furrows are slightly to deeply invaginated. Germinal furrows may be flecked, granular, or smooth, but this is usually not constant for a species.

Identification of genera and species on the basis of their pollen seems impracticable, although if the genus is previously known, pollen size may be useful in ascertaining the species, as in distinguishing long-spined forms of *Echinocereus coccineus* from *Echinocereus polyacanthus*. Pollen measurements in this group are as follows:

Echinocactus (fig. 3)

48–50 μ—*E. Lecontei* Engelm.
49–51 μ—*E. Wislizenii* Engelm.
50 μ—*E. Covillei* (Britt. & Rose) Berger
50 μ—*E. longihamatus* Galeotti
55 μ—*E. acanthodes* Lemaire
58–59 μ—*E. intertextus* Engelm.
62 μ—*E. Sileri* Engelm.
62–65 μ—*E. polyancistrus* Engelm. & Bigel.
57–65 μ—*E. Whipplei* Engelm. & Bigel.
67 μ—*E. erectocentrus* Coulter
73 μ—*E. Johnsonii* Parry
71–79 μ—*E. horizonthalonius* Lemaire

Mammillaria

43–50 μ—*M. vivipara* Engelm.
52–54 μ—*M. deserti* Engelm.
53–54 μ—*M. microcarpa* Engelm.
58–59 μ—*M. Alversonii* (Coulter) Zeissold
60–63 μ—*M. arizonica* Engelm.

Cereus

50–55 μ, mostly 50 μ—*C. giganteus* Engelm.
58–61 μ—*C. Schottii* Engelm.
65–69 μ—*C. Thurberi* Engelm.
68–82 μ—*C. Greggii* Engelm.

Echinocereus

41–55 μ—*E. mojavensis* (Engelm. & Bigel.) Rumpler
45–60 μ—*E. Ledingii* Peebles
50–55 μ—*E. polyacanthus* Engelm.
50–67 μ, mostly 50–60 μ—*E. pentalophus* (D. C.) Rumpler
52–54 μ—*E. Engelmannii* (Parry) Rumpler
57–59 μ—*E. coccineus* Engelm.
61–62 μ—*E. Bonkerae* Thornber & Bonker
62 μ—*E. rectispinus* Peebles
63–64 μ—*E. Fendleri* (Engelm.) Rumpler
64–65 μ—*E. rigidissimus* (Engelm.) Rose
64–70 μ—*E. rectispinus* var. *robustus* Peebles
65–69 μ—*E. Boyce-Thomsonii* Orcutt

OPUNTIA

Grain dodecacolpate; cube and dodecahedron; 65–130 μ in diameter; exine thick, pitted or reticulate; exine thrown into ridges or ridges not

present; furrows coincide with germ pores; pores flat to convex, smooth, granular or flecked, circular to linear. Usually *Opuntia* grains are cube and dodecahedrons, with a germinal furrow (germ pore) in the center of each of twelve more or less regular hexagons, and six thick, highly reticulate or pitted tetragons (fig. 1). Assuming any two opposite tetragons as poles, three equal polar axes are formed, and the grain appears the same when viewed parallel to each of the three axes. Most samples of pollen of *Opuntia* contain grains of the cube and dodecahedron type, and from few to many grains have more numerous faces (about 30 in *O. gilvescens*), which may be tetragons, triangles, pentagons, hexagons, or in *O. flavescens* regular grains having eight heptagons, six tetragons, and eight hexagons occur (fig. 2). Grains with more than eighteen faces are usually polycolpate with more than the regular number of twelve furrows. The exine in most species is thick except over the hexagons and pores. The ridges are high to low, narrow to wide, depending upon the species. The exine of the tetragons may be pitted or from finely to coarsely reticulate, and the ridges sculptured similarly. The degree of reticulation or pitting is the most consistent character of each species (figs. 4–9). The sculpturing usually becomes granular in the hexagons up to or over the germ pores. If the germ pores are convex in the expanded form they often break through the exine, causing an irregular pore margin. The pores and hexagons evidently act as harmomegathy for the expansion of the grain because in the dry form the hexagons appear as if pushed in, the whole grain assuming a very wrinkled or crumpled form. Upon expansion of the grain the pores may become very prominently protruding or convex, which is especially distinct in *O. fragilis* (fig. 9). It is interesting to note that all grains that possess pitted exine are from plants that belong to the subgenus *Cylindropuntia* or "chollas," whereas all grains that have reticulate exine are from plants of the subgenus *Platyopuntia* or "prickly pears." Comparisons of species in these two groups are as follows.

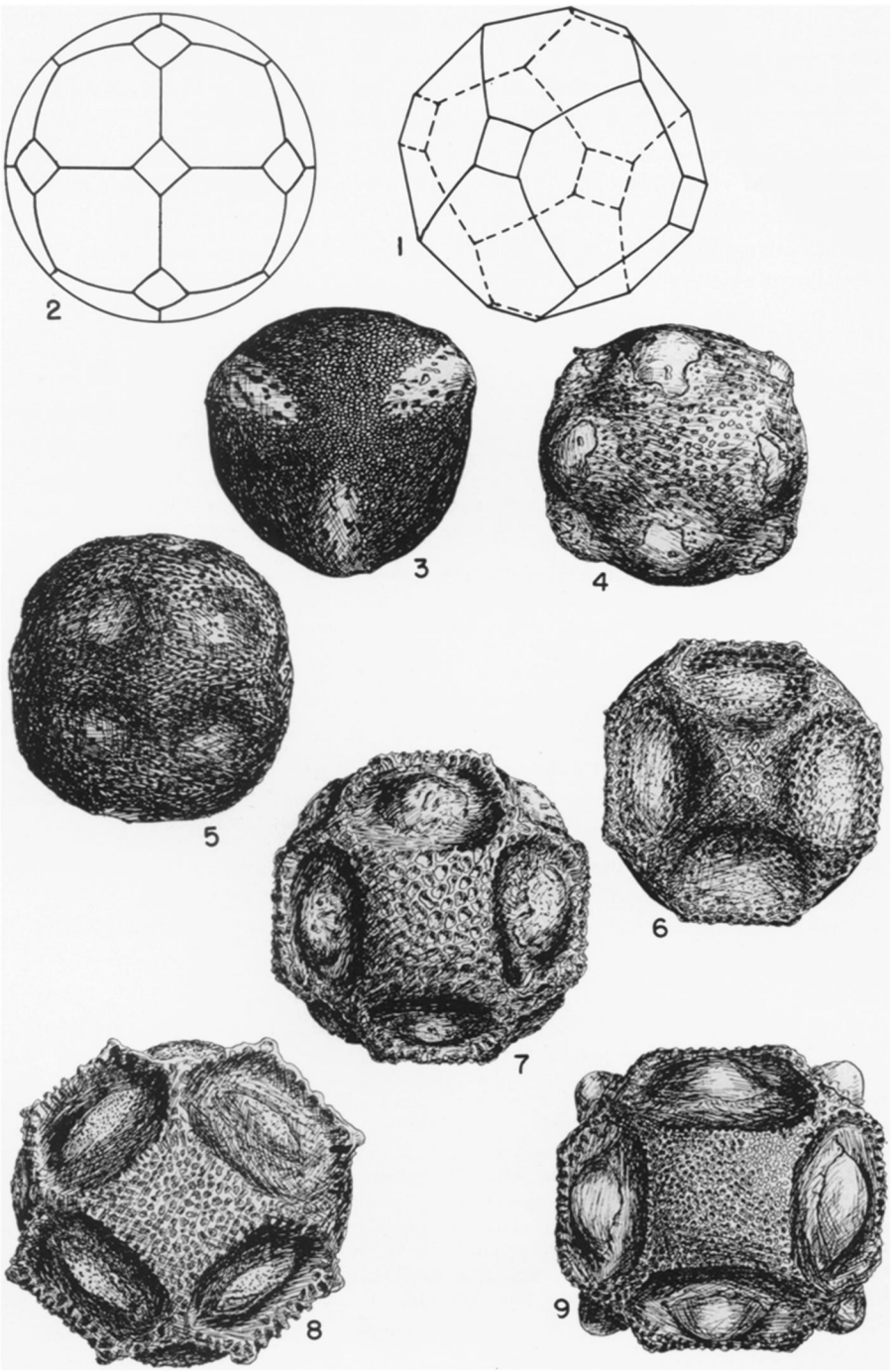
Opuntia subg. *Cylindropuntia*

A. Germ-pores convex (fig. 4)

65–68 μ; pores flecked.	*Opuntia leptocaulis* DC.
73–90 μ, mostly 78–82 μ; pores flecked, flat or mostly convex.	*O. fulgida* Engelm.
76–86 μ; pores flecked.	*O. acanthocarpa* var. *ramosa* Peebles
82–90 μ; pores flecked.	*O. Whipplei* Engelm. & Bigel.
80–120 μ; mostly 98 μ; many irregular.	*O. Bigelovii* Engelm.
93–94 μ; pores flat or convex, granular.	*O. versicolor* Engelm.
98–100 μ; pores granular, flat or convex.	*O. echinocarpa* Engelm. & Bigel.
107 μ; pores flecked, margins irregular.	*O. acanthocarpa* Engelm. & Bigel.

AA. Germ-pores flat, not convex (fig. 5)

73–90 μ, mostly 78–82 μ; pores flecked, flat or mostly convex.	*O. fulgida* Engelm.
73–100 μ, mostly 73–81 μ; pores flecked.	*O. tetracantha* Toumey



78–82 μ; pores flecked.	*O. fulgida* var. *mamillata* (Schott) Coulter
86–94 μ, mostly 90 μ; pores granular.	*O. spinosior* (Engelm.) Toumey
90 μ; pores granular.	*O. Stanlyi* var. *Kunzei* Rose
90 μ; pores granular.	*O. Kunzei* Rose
90–93 μ; pores pitted or granular.	*O. Wrightiana* (Baxter) Peebles
93–94 μ; pores granular.	*O. versicolor* Engelm.
98–100 μ; pores granular.	*O. echinocarpa* Engelm. & Bigel.
100–106 μ; pores granular.	*O. Thornberi* Thornber & Bonker

Opuntia subg. *Platyopuntia*

B. Exine coarsely reticulate

(figs. 6, 7)

94–100 μ; ridges prominent; pores not distinct, convex, may be flecked; tetragons 40–45 μ wide. *O. basilaris* Engelm. & Bigel.

96–100 μ; many irregular; ridges distinct; pores circular, granular. *O. Santa-Rita* (Griffiths & Hare) Rose

98–106 μ; coarsely to medium reticulate; usually regular; ridges distinct, not high; pores linear, reticulate or granular, flat or convex. *O. macrocentra* Engelm.

97–122 μ, mostly 105–110 μ; many irregular; exine finely to coarsely reticulate; ridges distinct; pores circular to linear, convex, flecked; tetragons 48–50 μ wide. *O. Loomisii* Peebles

106–114 μ; mostly irregular; ridges distinct; pores linear, convex, flecked. *O. tenuispina* Engelm.

106–119 μ, mostly 109–114 μ; irregular, some with ridge scheme of heptagons; ridges distinct, narrow; exine finely to coarsely reticulate; pores circular to linear, granular, flat. *O. flavescens* Peebles

110–114 μ; mostly irregular; ridges distinct; pores circular, distinct, convex, granular; tetragons 20 μ wide. *O. laevis* var. *canada* (Griffiths) Peebles

106–130 μ, mostly 114 μ; mostly irregular; exine finely to coarsely reticulate; ridges distinct; pores indistinct, circular to linear, flat to convex, granular. *O. phaeacantha* Engelm.

115–125 μ; mostly irregular; ridges distinct; pores circular, slightly convex, granular. *O. Engelmannii* Salm-Dyck

130 μ; mostly irregular with up to 30 faces; exine finely to coarsely reticulate; ridges distinct; pores indistinct, slightly convex, granular. *O. gilvescens* Griffiths

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Explanation of figures 1–9

FIG. 1. Regular cube and dodecahedron characteristic of *Opuntia pollen.* FIG. 2. Regular atypical ridge scheme of *Opuntia flavescens,* polar view, four of the eight heptagons are visible. FIG. 3. Pollen grain of *Echinocactus acanthodes,* polar view, 52 μ in diameter, exine finely pitted, typical of the pollen of *Cereus, Echinocactus, Mammillaria,* and *Echinocereus.* FIG. 4. Pollen grain of *Opuntia acanthocarpa,* 107 μ in diameter, exine pitted, typical of pollen of subg. *Cylindropuntia* with convex pores. FIG. 5. Pollen grain of *Opuntia fulgida* var. *mamillata,* 80 μ in diameter, exine pitted, typical of pollen of subg. *Cylindropuntia* with flat pores. FIG. 6. Pollen grain of *Opuntia macrocentra,* 98 μ in diameter, exine coarsely reticulate, typical of pollen of subg. *Platyopuntia.* FIG. 7. Pollen grain of *Opuntia basilaris,* 97 μ in diameter, exine coarsely reticulate, pores convex, typical of pollen of subg. *Platyopuntia.* FIG. 8. Pollen grain of *Opuntia ursina,* 100 μ in diameter, exine finely reticulate, pores slightly convex, typical of the pollen of the subgenus *Platyopuntia.* FIG. 9. Pollen grain of *Opuntia fragilis,* 90 μ in diameter, exine finely reticulate, pores very convex.

BB. Exine finely reticulate
(figs. 8, 9)

89–98 μ, mostly 90 μ; ridges distinct; tetragons 32–38 μ wide; pores linear, may be very convex. *O. fragilis* (Nutt.) Haworth.
90–114 μ; some irregular; ridges distinct; pores linear, convex, granular. *O. rhodantha* Schuman
91–113 μ, mostly 98–101 μ; ridges distinct; tetragons 41–48 μ; pores linear, convex, granular. *O. hystricina* Engelm. & Bigel.
81–98 μ, mostly 95–98 μ; some irregular; ridges distinct; tetragons 38–40 μ; pores distinct, circular, convex, granular. *O. polyacantha* var. *trichophora* (Engelm. & Bigel.) Coulter
97–110 μ, mostly 108 μ; many irregular; ridges distinct; pores indistinct, convex, granular, circular. *O. aurea* Baxter
98–102 μ; ridges distinct; tetragons 40 μ; pores linear, convex, flecked. *O. ursina* Weber
98–106 μ, mostly 98–101 μ; some irregular; ridges narrow, distinct; pores linear, convex, granular. *O. erinacea* Engelm.
98–108 μ; exine thick; ridges distinct; pores linear, about 65 μ long, slightly convex, granular. *O. hystricina* var. *rhodantha* Schuman
97–122 μ, mostly 105–110 μ; some irregular; tetragons 48–50 μ wide; exine finely to coarsely reticulate; pores circular to linear, convex, flecked. *O. Loomisii* Peebles
106–122 μ, mostly 109–114 μ; ridges distinct; tetragons 46 μ wide; pores distinct, circular, convex, flecked. *O. polyacantha* Haworth.
106–119 μ, mostly 109–114 μ; mostly irregular with ridge scheme of heptagons; ridges distinct, narrow; exine finely to coarsely reticulate; pores circular to linear, flat, granular. *O. flavescens* Peebles
111–117 μ, mostly 114 μ; mostly irregular; ridges high, 11 μ wide; tetragons 40 μ wide; pores granular or reticulate, circular. *O. tortispina* Engelm. & Bigel.
106–130 μ, mostly 114 μ; mostly irregular; exine finely to coarsely reticulate; ridges distinct; pores indistinct, circular to linear, flat to convex, granular. *O. phaeacantha* Engelm.
130 μ; mostly irregular with up to 30 faces; exine finely to coarsely reticulate; ridges distinct; pores indistinct, slightly convex, granular. *O. gilvescens* Griffiths

SUMMARY

1. A study was made of the pollen of 75 species and varieties of the Cactaceae, mostly native to Arizona.

2. The pollen of species of *Cereus, Echinocereus, Echinocactus,* and *Mammillaria* are usually tricolpate with a finely pitted exine. The diameter range of pollen of these genera is from 41 to 82 μ.

3. Species of *Opuntia* exhibit regular and irregular pollen. Regular grains are cube and dodecahedrons with twelve germ pores (germinal furrows), and the exine is either pitted (subg. *Cylindropuntia*), or from finely to coarsely reticulate (subg. *Platyopuntia*). Irregular grains have more than eighteen faces, and usually a correspondingly increased number of germ pores. Pollen grains of *Opuntia flavescens* are either typical cube and dodecahedrons or regular atypical grains with eight heptagons, six tetra-

gons, and eight hexagons. The diameter range of *Opuntia* pollen is from 65 to 130 μ.

4. Pollen of *Echinocereus pentalophus* is either tricolpate, or large and dodecacolpate, this form closely resembling the smaller pollens of *Opuntia*.

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