

POLLEN MORPHOLOGY OF THE GENUS *ECHINOPEPON* (CUCURBITACEAE)

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ABSTRACT

Pollen descriptions of *Echinopepon* species and a palynological key are presented. Data on apertures, exine, polarity, shape, and size of pollen grains are included. Pollen morphology is distinctive for the species of *Echinopepon* and *Echinocystis* and in some *Marah* species. The main features of each taxon are illustrated by photographs.

RESUMEN

Se presenta la descripción del polen de las especies de *Echinopepon*. Se incluyen datos de la apertura, exina, polaridad, forma y tamaño de los granos, así como una clave palinológica para su identificación. La morfología polínica es característica en *Echinopepon* y distintiva de *Echinocystis* y de algunas especies de *Marah*. Se ilustra con fotografías las características principales de cada taxon.

Echinopepon is an American genus, whose distribution extends from southeastern United States to Argentina. It has seven species (Rodríguez, in press): *E. cirrhopedunculatus* Rose, *E. coulteri* (A. Gray) Rose, *E. gemellus* (Ser.) Rodríguez, *E. minimus* (Kellogg) S. Watson, *E. pubescens* (Benth.) Rose, *E. racemosus* (Steud.) C. Jeffrey, and *E. wrightii* (A. Gray) S. Watson (Table 1); the first four are endemic to Mexico. All species are herbaceous, generally with an annual life cycle; have characteristic capsular, echinate, rostrate, and operculate fruit; and white or white-green pentamerous flowers, five stamens with filaments joined and anthers forming heads.

Jeffrey (1978) placed *Echinopepon* in the tribe Cyclanthereae. He later (Jeffrey 1990) placed it in tribe Sicyeae subtribe Cyclantherinae, showing its close relationship to the genera *Marah* and *Echinocystis* as demonstrated by the large number of morphologic characteristics which it shares with these genera. They are distinguished from *Echinopepon* by two or three stamens and globose fruits with apical and irregular dehiscence. *Marah* is distinguished also by its perennial habit and swollen seeds.

Palynologically the tribe Cyclanthereae (Jeffrey 1964) is characterized

by 4–8-colporate and punctitegillate pollen grains (Jeffrey 1964), the same as the subtribe Cyclantherinae (Jeffrey 1990). This tribe was also described by Marticorena (1963) as having 4 to polycolporate pollen grains except, *Echinopepon wrightii* (A. Gray) S. Watson (as *Echinocystis wrightii* A. Gray) which has only polycolporate pollen grains. In a palynological classification of Cucurbitaceae from India (Shridar & Sing 1990), subtribe Cyclantherinae was described as having multizonocolporate pollen grains.

The pollen morphology of *Echinopepon* species has been little studied. Dieterle (1974) found similarities between *Apatzingania arachioidea* Dieterle pollen grains (asymmetrical polycolpate, spinulose and exquisitely foveolate-reticulate) and those of *Echinopepon cirrhopedunculatus* and *E. ge*

TABLE 1. The species of *Echinopepon*.

Accepted name	Synonyms
<i>E. cirrhopedunculatus</i> Rose <i>E. coulteri</i> (A. Gray) Rose	<i>Echinocystis coulteri</i> (A. Gray) Cogn., 1877; <i>Echinopepon confusus</i> Rose, 1897; <i>Echinopepon parvifolius</i> Rose, 1897.
<i>E. gemellus</i> (Ser.) C. Rodríguez	<i>Echinopepon milleflorus</i> Naudin, 1866; <i>Echinopepon quinquelobatus</i> Naudin, 1866; <i>Echinocystis gemella</i> (Ser.) Cogn., 1877; <i>Echinocystis milleflora</i> (Naudin) Cogn., 1877; <i>Echinocystis torquata</i> (Ser.) Cogn., 1877; <i>Echinocystis torquata</i> var. <i>brevispina</i> Cogn., 1881; <i>Echinopepon torquatus</i> (Ser.) Rose, 1897.
<i>E. minimus</i> (Kellogg) S. Watson	<i>Echinocystis minima</i> (S. Watson) Cogn., 1881; <i>Echinopepon peninsularis</i> H.S. Gentry, 1949; <i>Echinopepon minimus</i> (Kell.) S. Watson var. <i>peninsularis</i> (H.S. Gentry) K.M. Stocking, 1955.
<i>E. pubescens</i> (Benth.) Rose	<i>Echinocystis floribunda</i> Cogn., 1877; <i>Echinocystis pubescens</i> (Benth.) Cogn., 1877; <i>Echinopepon floribundus</i> (Cogn.) Rose, 1897.
<i>E. racemosus</i> (Steud.) C. Jeffrey	<i>Echinopepon horridus</i> Naudin, 1866; <i>Echinocystis lanata</i> Cogn., 1877; <i>Echinocystis polycarpa</i> Cogn., 1877; <i>Echinocystis muricata</i> Cogn., 1878; <i>Echinocystis araneosa</i> Griseb., 1879; <i>Echinocystis macrocarpa</i> Britton, 1890; <i>Echinopepon jaliscanus</i> Rose, 1897; <i>Echinopepon lanatus</i> (Cogn.) Rose, 1897; <i>Echinopepon pringlei</i> Rose, 1897; <i>Echinopepon racemosus</i> (Steud.) Martínez, Crov., 1955.
<i>E. wrightii</i> (A. Gray) S. Watson	<i>Echinocystis glutinosa</i> Cogn., 1877; <i>Echinocystis longispina</i> Cogn., 1877; <i>Echinocystis paniculata</i> Cogn., 1877; <i>Echinocystis wrightii</i> (A. Gray) Cogn., 1877; <i>Echinopepon longispina</i> (Cogn.) Rose, 1897; <i>Echinopepon nelsoni</i> Rose, 1897; <i>Echinopepon paniculatus</i> (Cogn.) J.V. Dieterle, 1976.

mellus (as *Echinocystis gemella*). Dieterle (1976) also found that different types of apertures in pollen grains seemed to be associated with thecae form, replicate thecae occurring with non-colpate grains and U-shaped thecae occurring with multicolpate grains. Stafford and Sutton (1992, 1994) indicated that certain species of *Echinopepon* had pantozonocolporate pollen grains, corroborating Dieterle's idea about palynological similarities between the genera *Apatzingania* and *Echinopepon*, however, there are enough macromorphological differences to distinguish *Apatzingania* from *Echinopepon*. Palacios-Chavez et al. (1995) described *Echinopepon coulteri* pollen the valley of Mexico as 7-colpate, perreticulate and suboblate grains and *E. gemellus* pollen (as *Echinopepon milleflorus*) as 14-colpate, punctitegillate and suboblate.

MATERIALS AND METHODS

Pollen samples of the seven taxa of *Echinopepon* and the relatives *Echinocystis* and *Marah* were taken from herbarium specimens at: Escuela Nacional de Ciencias Biológicas, IPN, México (ENCB); Herbario Nacional of México, UNAM, México (MEXU); Instituto de Ecología, Bajío, México (IEB) and Field Museum (F). The samples were prepared using the standard acetolysis method of Erdtman (1943) and mounted in glycerine jelly. The samples were examined by the light microscope. The slides are deposited in the pollen collections of the Palynology Laboratory, Department of Botany, ENCB, Mexico.

RESULTS

Palynological key to the species *Echinopepon*

1. Grains stephanocolpate, 7–16-colpate or 7–17-colporoidate, reticulate or punctitegillate.
 2. Grains 7-colpate or colporoidate.
 3. Grains 7-colpate, reticulate *E. coulteri* (Figs. 6–11)
 3. Grains 7-colporoidate, punctitegillate *E. pubescens* (Figs. 22–27)
 2. Grains 14–16-colpate or 9–10-colporoidate.
 4. Grains 9–10-colporoidate *E. minimus* (Figs. 16–21)
 4. Grains 14–16-colpate.
 5. Grains 14-colpate, punctitegillate *E. gemellus* (Figs. 12–15)
 5. Grains 16-colpate, reticulate *E. cirrhopedunculatus* (Figs. 1–5)
1. Grains 10–12-perirrugate or 7–8-pericolpate, punctitegillate-echinulate or perreticulate.
 6. Grains perirrugate, 10–12 rugas, echinulate *E. racemosus* (Figs. 28–34)
 6. Grains pericolpate, perreticulate *E. wrightii* (Figs. 35–41)

Descriptions of pollen grains

***Echinopepon cirrhopedunculatus* Rose (Figs. 1–5).** MEXICO. MORELOS: Zacatepec, C. Rodríguez et al. 1856 (ENCB).

Grains usually stephanocolpate, 16-colpate (sometimes with 15 or 17 colpi), semitectate, spheroidal, $(88-)72-104 \times 77-104(-82) \mu\text{m}$ P/E 1.07. Polar view circular, $(103-)92-114 \mu\text{m}$ in diameter. Exine $5.6 \mu\text{m}$, thick, sexine $4 \mu\text{m}$ and nexine $1.6 \mu\text{m}$, thick reticulate, with colpus thin; membrane smooth.

Echinopepon coulteri (A. Gray) Rose (Figs. 6–11). MEXICO. HIDALGO: Cerro Gordo, 5 km W of Pachuca, *J. Rzedowski* 33524 (ENCB).

Grains usually stephanocolpate, 7-colpate, sometimes 8-colpate, semitectate, suboblate, $(104-)83-117 \times 87-142(-126) \mu\text{m}$. P/E 0.82. Polar view circular $(118-)77-154 \mu\text{m}$ in diameter. Exine $4 \mu\text{m}$, thick sexine $3.2 \mu\text{m}$ and nexine $0.8 \mu\text{m}$, thick, reticulate superficially, colpus shallow, membrane smooth.

Echinopepon gemellus (Ser.) C. Rodríguez (Figs. 12–15). MEXICO. VERACRUZ: Camino a Tatatila, Las Vigas, *F. Ventura* 17716 (ENCB).

Grains stephanocolpate, 14-colpate, tectate, suboblate, $(76-)66-97 \times 66-106(-90) \mu\text{m}$. P/E 0.84. Polar view circular $(88-)70-112 \mu\text{m}$ in diameter. Exine $4 \mu\text{m}$, thick, sexine $3.2 \mu\text{m}$ and nexine $0.8 \mu\text{m}$, thick, punctitegillate superficially, colpus thin; membrane smooth.

Echinopepon minimus (Kellogg) S. Watson (Figs. 16–21). MEXICO. BAJA CALIFORNIA: Sierra de Plateros, Mulege, *D. Breedlove* 60907 (ENCB).

Grains usually stephanocolporoidate, 10-colporoidate, sometimes 9-colporoidate, semitectate, spheroidal, $(71-)60-85.6 \times 74-84(-80) \mu\text{m}$. P/E 0.95. Polar view circular, $(85-)80-96 \mu\text{m}$ in diameter. Exine $5 \mu\text{m}$, thick, sexine $3.2 \mu\text{m}$ and nexine $1.8 \mu\text{m}$, thick, reticulate superficially, colpus with smooth membrane. Pores diffuse.

Echinopepon pubescens (Benth.) Rose (Figs. 22–27). MEXICO. OAXACA: Chilapa, Tamazulapa, *J. Rzedowski* 34498 (ENCB).

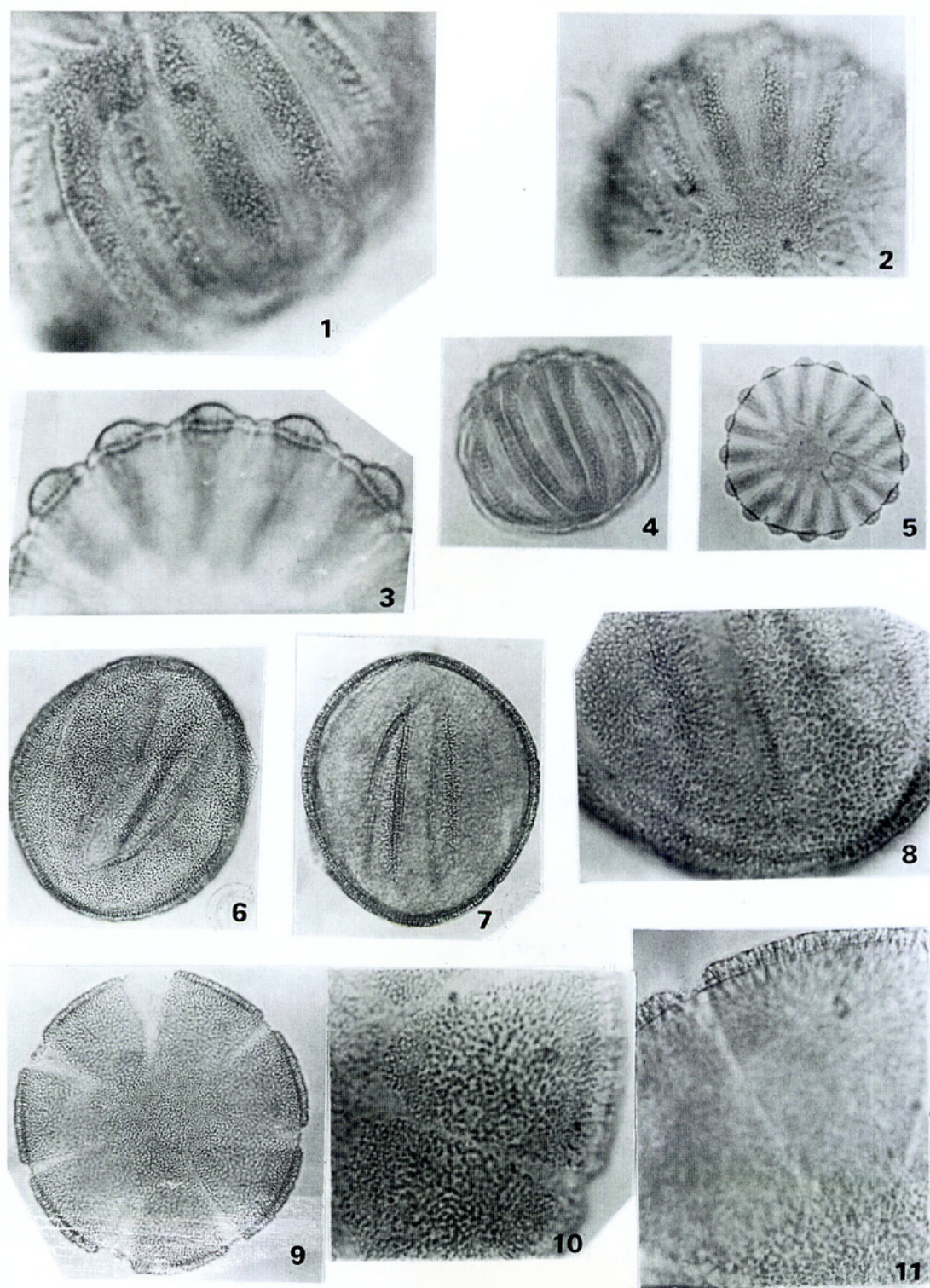
Grains stephanocolporoidate, 7-colporoidate some times 6-colporoidate, tectate, spheroidal, $(94-)81-110 \times 81-103(-94) \mu\text{m}$. P/E 1.0. Polar view circular $(102-)91-112 \mu\text{m}$ in diameter. Exine $4 \mu\text{m}$, thick, sexine as thick as nexine, punctitegillate superficially, thin colpus, smooth membrane, bordered with margin $2-3 \mu\text{m}$ wide.

Echinopepon racemosus (Steud.) C. Jeffrey (Figs. 28–34). MEXICO. OAXACA: Ojitlán, Buena Vista, *F. Ventura* 15539 (ENCB).

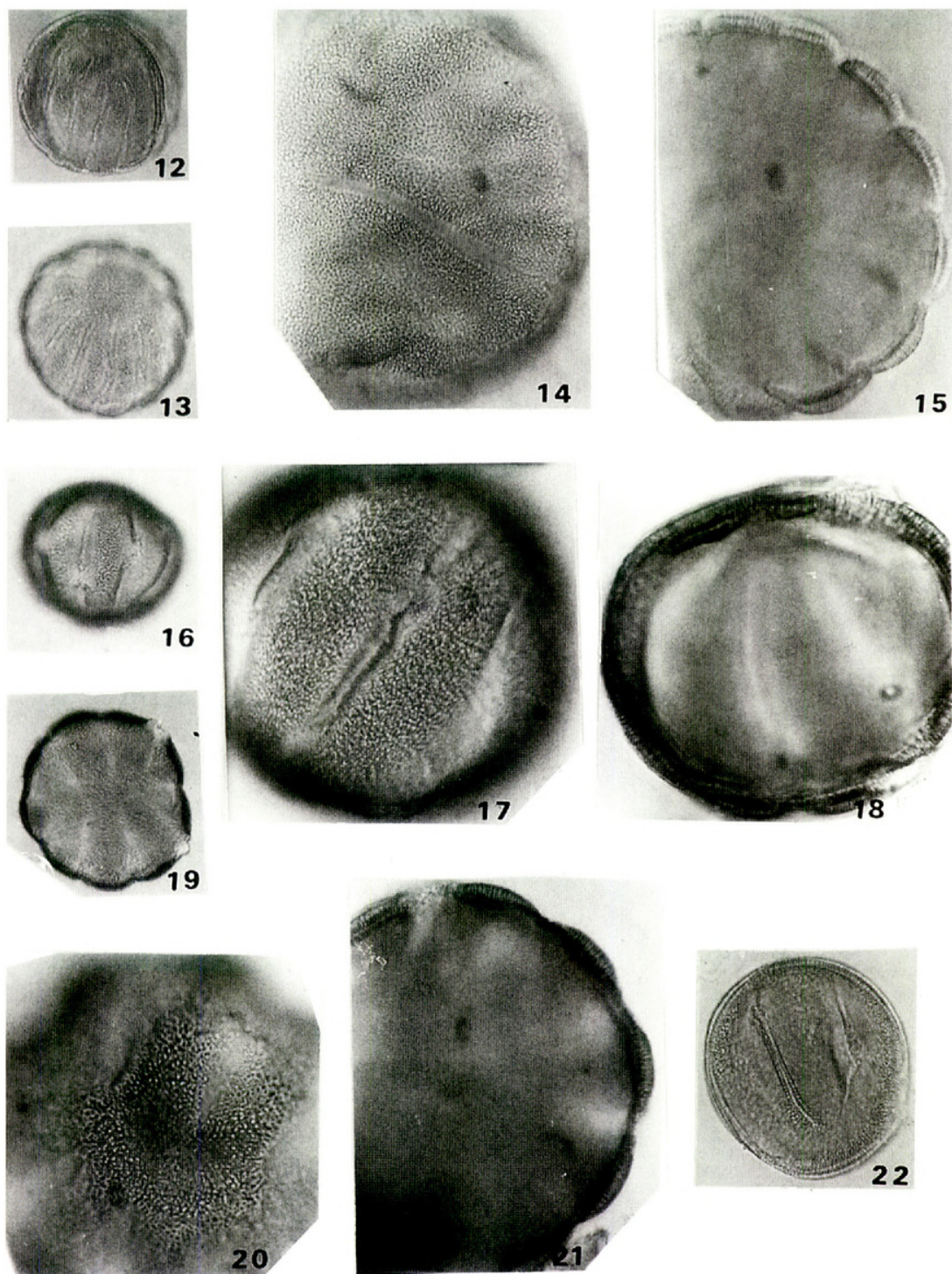
Grains perirrugate, tectate, apolar, spheroidal, $(94-)81-110 \times 91-112(-102) \mu\text{m}$ in diameter. Exine $5.6 \mu\text{m}$, thick, sexine as thick as nexine, echinulate superficially. Rugas 10 or 12 of $16 \mu\text{m}$ long, situated superficially, with verrucate membranes. Some grains have a triradiate colpus.

Echinopepon wrightii (A. Gray) S. Watson (Figs. 35–41). MEXICO. MICHOACÁN: 3 km NW of Eréndira Carácuaro, *J. Rzedowski* 35510 (ENCB).

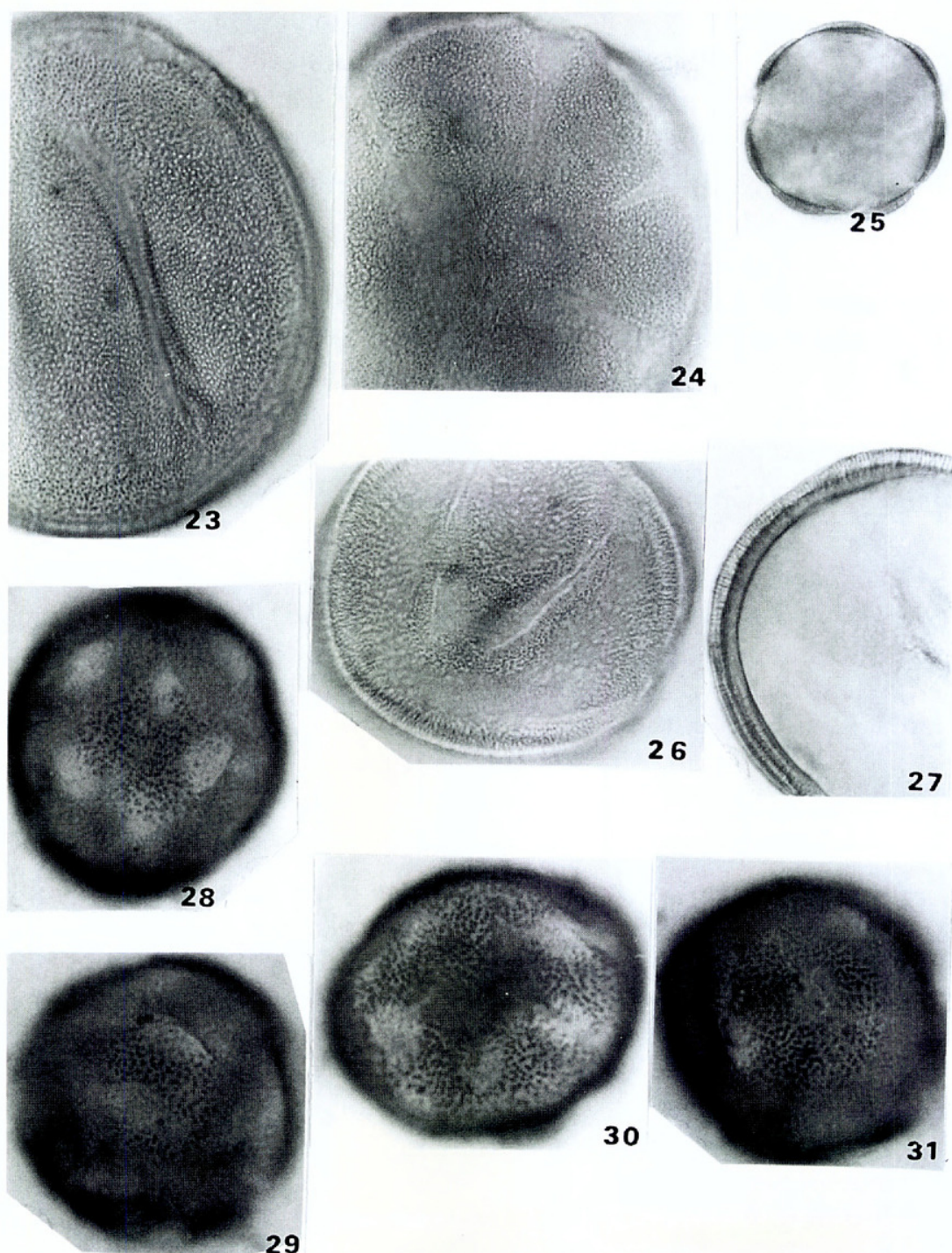
Grains stephanocolpate, usually 7-colpate, sometimes 8-colpate, semitectate,



FIGS. 1-11.—*Echinopepon cirrhopedunculatus*. Fig. 1. Equatorial view; Fig. 2. Polar view; Fig. 3. Optical section exine ($\times 1000$); Fig. 4. Equatorial view ($\times 800$); Fig. 5. Polar view ($\times 800$). *Echinopepon coulteri*. FIG. 6. Transversal section exine; Fig. 7. Polar view surface $\times 800$; Fig. 8. Polar view optical section ($\times 800$); Fig. 9. Equatorial view surface ($\times 800$); Fig. 10. Reticulate surface; Fig. 11. Optical section ($\times 1000$).



FIGS. 12–22.—*Echinopepon gemellus*. Fig. 12. Equatorial view ($\times 800$); Fig. 13. Polar view ($\times 800$); Fig. 14. Polar view, punctitegillate surface; Fig. 15. Optical section. ($\times 1000$). *Echinopepon minimus*. Fig. 16. Equatorial view ($\times 800$); Fig. 17. Equatorial view, reticulate surface; Fig. 18. Optical section ($\times 1000$); Fig. 19. Polar view ($\times 800$); Fig. 20. Echinulate apocalpium; Fig. 21. Optical section ($\times 1000$). Fig. 22. *E. pubescens*. Equatorial view ($\times 800$)



FIGS. 23–31.—*Echinopepon pubescens*. Fig. 23. Punctitegillate surface; Fig. 24. Polar view ($\times 1000$); Fig. 25. Polar view, optical section ($\times 800$); Fig. 26. Colpi and punctitegillate surface; Fig. 27. Exine thick. Figs. 28–31. *Echinopepon racemosus*. ($\times 800$). Fig. 28. Perirugate; Fig. 29. Ruga aequatorialis; Fig. 30. Ruga and echinulate surface; Fig. 31. Echinulate surface.

spheroidal, (81–)71–90 $\times$ 86–94(–89) μm . P/E 0.94. Polar view circular, (94–)80–108 μm in diameter. Exine 5 μm , thick, sexine and nexine with the same thickness, perreticulate superficially, 7 colpi in equatorial position but 8-colpate where one colpus is over a pole.

Echinocystis lobata (Michx.) Torr. & A. Gray (Figs. 42–49). U.S.A. OHIO. DARKE CO.: *M.A. Vincent* 1372 (MEXU).

Grains stephanocolporate, usually 5-colporate, often 6-colporate, tectate, suboblate, (60–)53–68 $\times$ 64–77(–70) μm . P/E 0.85. Polar view pentagonal or circular of (69–)64–72 μm in diameter. Exine 4.8 μm , thick, sexine and nexine the same thickness, punctitegillate. Colpi with scabrate membranes, margocolpate. Pores lalongate, (17–)12–20 $\mu\text{m} \times$ (7.6–)4–9 μm , with granulate opercula.

Marah gilensis (Greene) Greene (Figs. 50–53). U.S.A. ARIZONA: 1968, *P. Stewart s.n.* (MEXU).

Grains stephanocolporate, usually 4-colporate, often 5-colporate, semitectate, spheroidal, (60–)56–63 $\times$ 47–60(–56) μm . P/E 1.07. Polar view quadrangular, (56–)53–63 μm in diameter. Exine 4 μm , thick, sexine thicker than nexine, reticulate (clava forming a reticulum). Colpi with smooth membranes, acute ends, with broad margin 3 μm wide. Transversal colpi (18–)14–21 $\times$ 3–5(–4) μm , with scabrate opercula.

Marah macrocarpa (Greene) Greene (Figs. 54–57). MÉXICO. BAJA CALIFORNIA: *R. Moran* 29109 (ENCB).

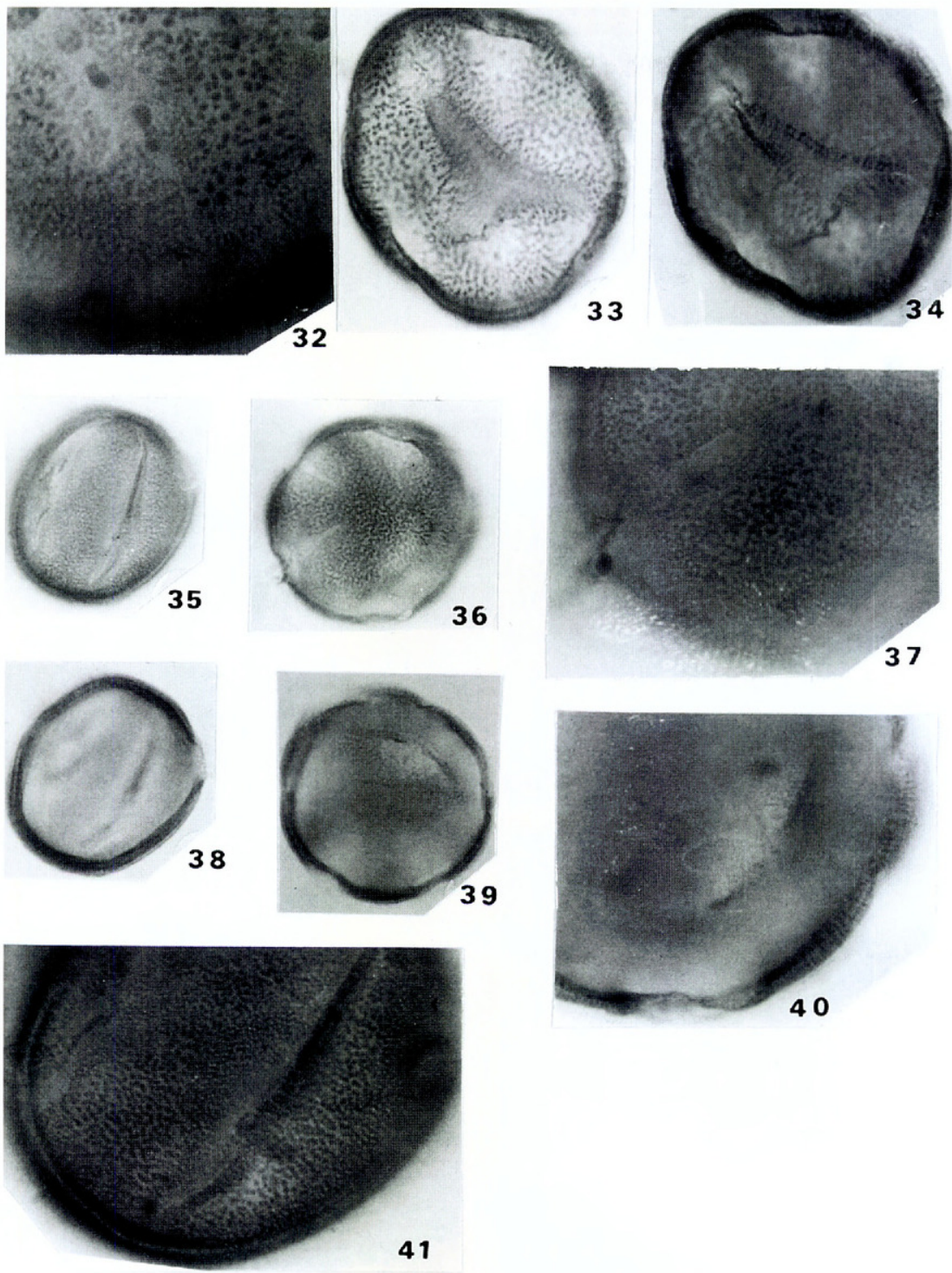
Grains stephanocolporate, 4-colporate, semitectate, subprolate, (69–)65–76 $\times$ 50–62(–57) μm . P/E 1.2. Polar view circular (64–)50–73 μm in diameter. Exine 3 μm , thick, sexine and nexine the same thickness retipilate. Colpi with acute ends, with broad margin 3 μm wide, syncolpate at a pole, membranes smooth. Circular pores (7–)5–10 μm in diameter.

DISCUSSION

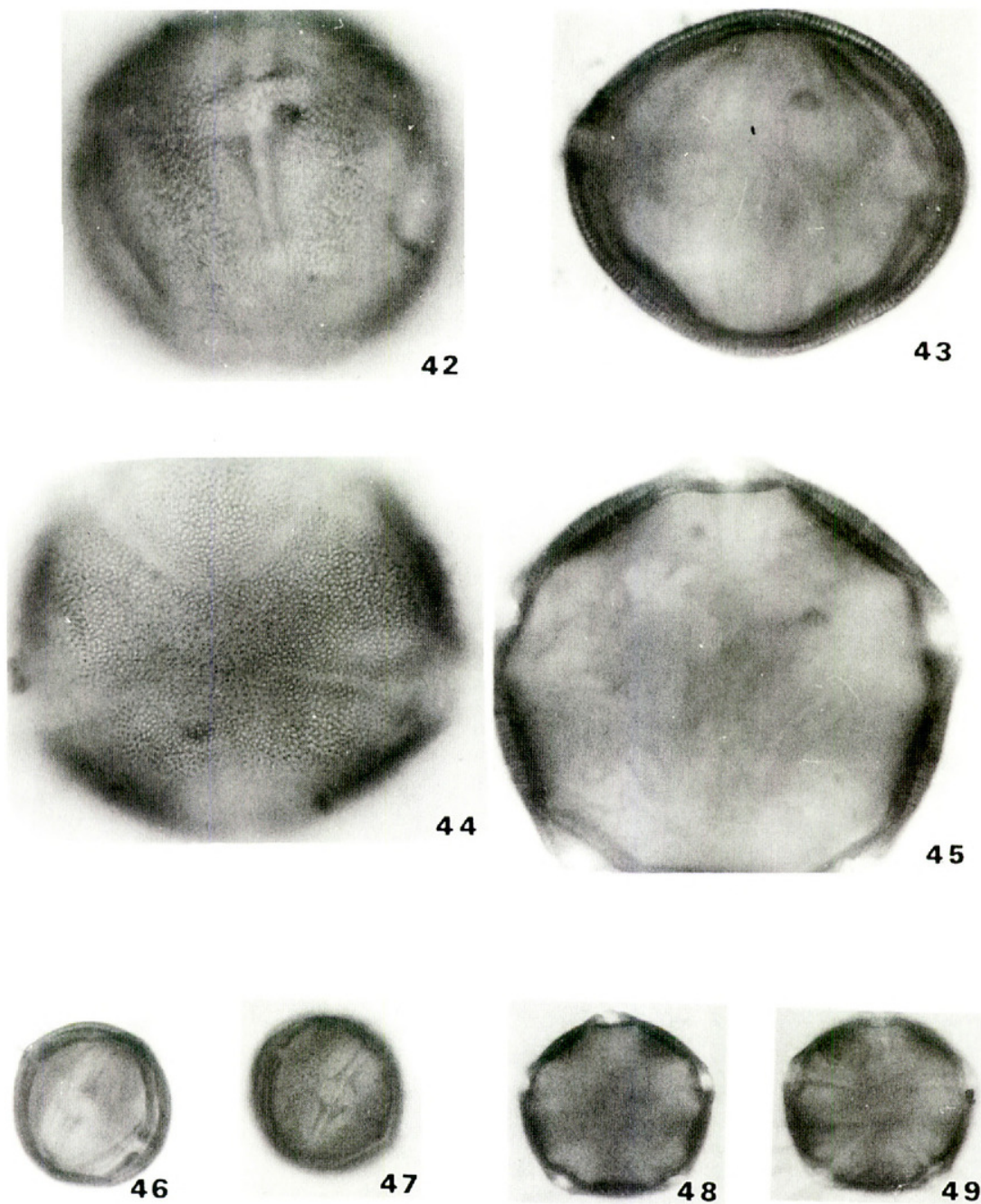
Pollen morphology is characteristic for *Echinopepon* and *Echinocystis* and for some species of *Marah*.

Pollen from *Echinopepon* species was found to be variable between species, especially in the number of openings and in their ornamentation. The highest number of colpi was sixteen (Table 2) and contrasts with Jeffrey's data (4–8-colporate) for tribe Cyclanthereae (1964) and subtribe Cyclantherinae (Jeffrey 1990).

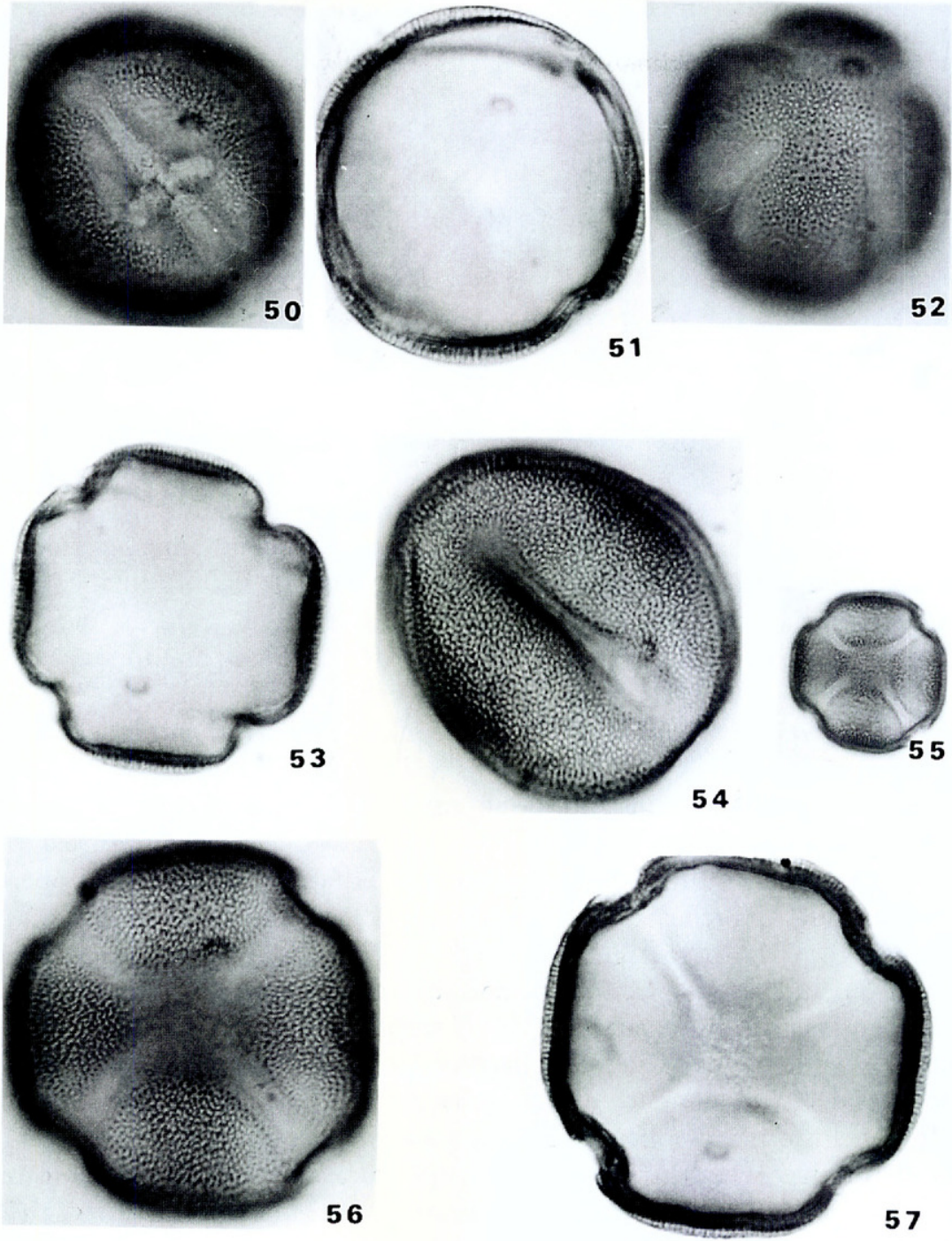
The pollen ornamentation was found to be reticulate (R), echinate (E), perreticulate (PR) and punctitegillate (PT) in different species (Table 2). The punctitegillate type was reported by Jeffrey (1964, 1990) and Stafford and Sutton (1994) for *Echinopepon coulteri*, *E. racemosus* and *Echinocystis lobata*.



FIGS. 32–41.—*Echinopepon racemosus*. Fig. 32. Echinulate surface; Figs. 33, 34. Triradiate colpi ($\times 1000$). *Echinopepon wrightii*. Fig. 35. Equatorial view ($\times 800$); Fig. 36. Polar view ($\times 800$). 37. Perreticulate surface; Fig. 38. Equatorial view; Fig. 39. Polar view, optical section ($\times 800$); Fig. 40. Colpus over a pole; Fig. 41. Perreticulate surface ($\times 1000$).



FIGS. 42–49.—*Echinocystis lobata*. Fig. 42. Equatorial view, punctitegillate surface; Fig. 43. Optical section; Fig. 44. Polar view ($\times 1000$); Figs. 45–49. Optical section ($\times 800$).



FIGS. 50–57.—*Marab gilensis*. Fig. 50. Equatorial view; Fig. 51. Optical section; Fig. 52. Polar view surface; Fig. 53. Optical section ($\times 1000$); *M. macrocarpa*. Fig. 54. Equatorial view surface ($\times 1000$); Fig. 55. Syncolpate grain; Fig. 56. Polar view syncolpate ($\times 800$); Fig. 57. Optical section ($\times 1000$).

TABLE 2. Palynological characteristics *Echinopepon* species.

	P (µm) X	E (µm) X	P/E	Ornam.	Nº Colpi	Exine	Thecae Type
<i>E. cirrhopedunculatus</i>	88	82	1.07	R	16	5.6	U
<i>E. coulteri</i>	104	126	0.82	R	7	4.0	U
<i>E. gemellus</i>	76	90	0.84	PT	14	4.0	U
<i>E. minimus</i>	71	80	0.95	R	10 por.	5.0	U
<i>E. pubescens</i>	94	94	1.00	PT	7 por.	4.0	Replicate
<i>E. racemosus</i>	94	102		E		5.6	Replicate
<i>E. wrightii</i>	81	89	0.94	PR	7	5.0	Straight or Arched

P. Polar Axis E. Equatorial Axis P/E. Relation between polar axis and equatorial axis.

Echinopepon cirrhopedunculatus, *E. coulteri*, *E. gemellus* and *E. minimus* have U-shaped thecae and colpate or colpoidate pollen grains, while *E. racemosus* has replicate thecae and its pollen grains lack longitudinal colpi. *E. pubescens* has replicate thecae and colpoidate pollen grains, while the thecae of *E. wrightii* are straight or arched with a 7–8 colpate pollen. The results presented in Table 2 agree with those reported by Dieterle (1976) for *E. gemellus* (as *E. torquatus*), *E. racemosus* (as *E. horridus*) and *E. wrightii* (as *E. paniculatum*).

The tectate pollen grains and the absence of longitudinal colpi observed in *E. racemosus* may suggest that it is the most advanced species of the genus. This taxon is quite variable regarding the shape of its leaves, number of tendrils and branches, degree of pubescence and wide geographical distribution from Mexico to Argentina. On the other hand, *E. cirrhopedunculatus*, *E. gemellus* and *E. minimus* may be considered less advanced because their pollen grains are semitectate and 10–17 colpate-colpoidate; they are reported as endemic to Mexico (Rodríguez 1995). Although *E. pubescens* is also considered endemic to México, it has 6–7-colpoidate pollen grains.

In conclusion, the pollen of *Echinopepon*, *Echinocystis* and *Marah* is often distinctive, which in some cases helps in taxonomic determination. *Echinopepon* pollen characters have diagnostic value in identification of the seven accepted species.

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