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Pollen morphology of the Boraginaceae from Santa Catarina State (southern Brazil), with comments on the taxonomy of the family

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The pollen morphology of 30 Boraginaceae taxa native to the Santa Catarina State was investigated by both light and scanning electron microscopy. The species were classified into nine pollen types on the basis of aperture characteristics and surface ornamentation. Sub-types were defined with regard to differences in shape, surface ornamentation and the number of apertures. The general agreement of these pollen types with taxonomic classifications was verified, with a few exceptions. An extensive re-evaluation of the systematics of the subfamily Heliotropioideae, especially of the genus *Heliotropium*, is suggested.

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The family Boraginaceae occurs worldwide, especially in the tropics and subtropics. It comprises about 100 genera and 2000 species, of which only 10 genera are native to Brazil. The majority of these occur in the southern part of the country. Most representatives of this family are herbaceous, but lianas, shrubs and trees also occur (Barroso 1986). Boraginaceae is one of the more eurypalynous families; not only is there a wide range of morphological types, but also a large proportion of species which can be recognized from their pollen grains (Clarke 1977). Pollen morphology, therefore, has great potential as a means of classification, and is frequently utilized to clarify taxonomic questions (Nowicke & Ridgway 1973, Nowicke & Skvarla 1974, Nowicke & Miller 1990, Taroda & Gibbs 1986 *a*, Díez et al. 1986, Miller & Nowicke 1989, Díez & Valdés 1991).

The pollen morphology of native species of Boraginaceae from Santa Catarina State (southern Brazil) is described here. This provides both important data on the characterization of taxa for taxonomists, and reference material for studies in other areas of palynology, especially those concerned with the Quaternary. Pollen grains from this family are frequently found in sediments (Van der Hammen & Gonzalez 1960, Graham & Jarzen 1969, Graham 1976, Gruas-Cavagnetto et al. 1988, Hooghiemstra 1984, Muller 1984, Behling 1993), but species identifications are not always in accordance with the morphological aspects presented here (Behling 1993).

MATERIAL AND METHODS

Twenty-nine native species of the family Boraginaceae from Santa Catarina State were studied; one of these has two varieties. The botanical material was collected from the following herbaria: Barbosa Rodrigues (HBR), Per Karl Dusèn (PKDC), Cia. Vale do Rio Doce Reserve (CVRD), Department of Botany, USP (SPF), Institute of Botany, São Paulo (SP), Rio de Janeiro Botanical Garden (RB) and National Museum (R). Measurements and photomicrographs refer to the first exsiccata cited in the list of investigated specimens, except where otherwise noted.

The pollen samples were acetolysed and permanent slides were made with the material mounted in glycerin jelly and sealed with paraffin. Acetolysed samples for SEM were stored in 70% ethyl alcohol; drops of the pollen suspension were left to dry on the surface of SEM stubs and sputter coated with gold.

The polar axis and equatorial diameter of 25 pollen grains were measured; other measurements (apocolpia, sexine, nexine thickness, apertures and ornamentation) were taken from 10 pollen grains. For the results based on the 25 pollen grain sample, the arithmetic mean, 95% confidence intervals, and amplitude (minimum and maximum values) are given. Otherwise, only the arithmetic mean and amplitude are presented. The ratio of polar to equatorial axis (P/E) based on the mean was calculated, as well as the extreme values. The relation of 3- to 4-colporate pollen grains in specimens of *Cordia trichotoma* was obtained by counting all the pollen grains found in equatorial view in three slides.

Pollen measurements are presented in Table I.

Abbreviations.—P = polar axis, E = equatorial axis, P/E = polar to equatorial diameter ratio, Apo = apocolpium, Sex = sexine, Nex = nexine, ∧Po = pore length, > Po = pore width, ∧En = endoaperture length, > En = endoaperture width, ∧Sp = spine length, > Sp = spine width (at the base), ∧Gm = gemma length, > Gm = gemma width, Lum = lumen, Mur = murus, LM = light microscopy, SEM = scanning electron microscopy.

A. = *Antiphytum*, *C.* = *Cordia*, *H.* = *Heliotropium*, *M.* = *Moritzia*, *P.* = *Patagonula*, *T.* = *Tournefortia*.

RESULTS

All species studied here have isopolar, radially symmetrical pollen grains. The species were grouped into nine pollen types on the basis of aperture characteristics and surface ornamentation. Sub-types were defined with reference to differences in the shape, surface ornamentation and number of apertures of the pollen grains. The distribution of the species in terms of the different pollen types is generally in agreement with current taxonomic classification, with a few exceptions.

It must be pointed out that the definition of the sub-types is based upon characters which may present polymorphism. Nevertheless, we have chosen to present it in this way, because we believe that they can be useful in suggesting phylogenetic relationships between species. We are also aware that these taxa may present even greater variability, when other geographical regions are considered.

Description of pollen types

1. TRIPORATE-RETICULATE (Figs. 1. A–M, 2. A–L, 3. A–H)
Pollen grains 3-porate, rarely 4-porate; (36-) 53 (-80) × (42-) 58 (-85) µm; suboblate to oblate spheroidal; amb rounded.
Pores 3–12 µm in diameter, rounded to broadly elliptical.
Sexine about twice as thick as nexine, reticulate, lumina elliptical to angular, muri microechinate (spinules only visible in SEM).

Comments. – Reticulate lumina are particularly large in *C. verbenacea*. The spinules of the reticulum muri are larger in *C. verbenacea*; they are smaller, more numerous and more evenly dispersed in *C. axillaris* and *C. guaranitica*; they tend to be concentrated in the muri angles in *C. verbenacea* and in *C. monosperma*. Pollen grains of *C. guaranitica* and *C. paucidentata* are distinctly larger, with small pores. Tetraporate pollen grains were only observed in *C. verbenacea* (Fig. 3. E).

Species included: Cordia axillaris, C. guaranitica, C. monosperma, C. paucidentata, C. verbenacea.

2. TRIPORATE-GEMMATE (Fig. 5. H–M)
Pollen grains 3-porate; (12-) 15 (-16) × (16-) 18 (-21) µm; suboblate to oblate spheroidal; amb rounded to subtriangular.
Sexine slightly thicker than nexine, gemmate.

Comments. – Ornamentation of gemmae and granules, irregular and densely distributed over the surface, which makes the observation of the apertures very difficult.

Species included: Tournefortia bicolor.

3. TRICOLPORATE-PSILATE (Fig. 7. A–D)
Pollen grains 3-colporate; (14-) 17 (-25) × (9-) 14 (-18) µm; oblate spheroidal to perprolate; apocolpium large; amb triangular.
Colpi narrow, endoapertures lalongate, oval-shaped.
Sexine slightly thicker than nexine, nexine thicker at endoaperture margins, sexine psilate.

Species included: Moritzia dasyantha.

4. TRICOLPORATE-SCABRATE (Fig. 6. X–AA)
Pollen grains 3-colporate; (42-) 46 (-54) × (23-) 27 (-32) µm; subprolate to prolate.
Colpi very narrow, endoapertures lolongate, annulate, broadly elliptical.
Sexine and nexine about the same thickness, nexine with endocracks, sexine scabrate.

Comments. – Pollen grains particularly rare in polar view.

Species included: Heliotropium indicum.

5. TRICOLPORATE-RUGULATE (Fig. 5. A–G)
Pollen grains 3-colporate; (22-) 25 (-27) × (17-) 19 (-21) µm; subprolate to prolate; apocolpium small; amb rounded.
Colpi long, endoapertures lalongate, oval-shaped.
Sexine and nexine about the same thickness, sexine rugulate.

Species included: Patagonula americana.

6. TRICOLPORATE-MICRORETICULATE
Subtype-a: tricolporate-microreticulate (Fig. 7. k–t)
Pollen grains 3-colporate; (20-) 23 (-26) × (17-) 19 (-21) µm; prolate spheroidal to subprolate; apocolpium medium to large; amb triangular.
Colpi narrow, endoapertures lalongate, oval-shaped.
Nexine slightly thicker than sexine, nexine thicker at endoaperture margins, sexine microreticulate, lumina rounded.

Comments. – *M. tetraquetra* pollen grains are very fragile, and crush easily when acetolysed.

Species included: Moritzia ciliata, M. tetraquetra.

Subtype-b: tricolporate-microreticulate to finely reticulate (Fig. 7. E–J)
Pollen grains 3-colporate; (24-) 26 (-30) × (21-) 24 (-27) µm; oblate spheroidal to prolate; apocolpium medium to large; amb triangular.
Colpi narrow, endoapertures lalongate, oval-shaped.
Sexine and nexine about the same thickness, nexine thicker at endoaperture margins, sexine microreticulate or finely reticulate, lumina rounded.

Species included: Moritzia dusenii.

7. TRICOLPORATE-PERFORATE (Fig. 7. U–AG)
Pollen grains 3-colporate; (12-) 14 (-16) × (11-) 12 (-13) µm; prolate spheroidal to subprolate; apocolpium small; amb subtriangular.
Colpi narrow, endoapertures lolongate, broadly elliptical, particularly large in relation to pollen size.
Sexine and nexine with variable relative thickness, sexine perforate, undulate in SEM.

Comments. – Apertures with a granulate operculum forming a well marked protuberance in optical section (Fig. 7. W, Z).

Species included: Antiphytum cruciatum.

Table I. *Pollen measurements (in µm) of the different pollen types*

*only 15 grains measured, **measure taken from Pirani 1745.

	P	E	P/E	Apocolp
TRIPORATE-RETICULATE				
Cordia axillans	43.9±0.2 (39.4–48.4)	48.3±0.2 (45.9–51.8)	0.9 (0.85–0.99)	—
C. guaranitica	62.4±0.2 (59.0–66.9)	67.1±0.2 (63.6–72.6)	0.93 (0.88–0.99)	—
C. monosperma	41.8±0.3 (36.4–47.2)	46.0±0.3 (41.8–51.3)	0.9 (0.81–0.98)	—
C. paucidentata	70.4 (59.0–80.4)	76.8 (63.2–84.5)*	0.92 (0.80–0.98)	—
C. verbenacea	47.4±0.4 (40.5–54.1)	51.1±0.4 (42.2–58.2)	0.93 (0.85–0.99)	—
TRICOLPORATE-ECHINATE				
C. ecalyculata	35.8±0.3 (30.8–40.5)	41.0±0.2 (37.1–44.9)	0.87 (0.83–0.94)	21.1 (17.8–24.5)
C. sellowiana	33.1±0.2 (30.4–36.4)	36.0±0.2 (32.9–39.0)	0.92 (0.82–0.99)	21.6 (17.8–24.7)
C. silvestris	28.7±0.1 (26.2–32.2)	32.2±0.1 (30.0–34.7)	0.89 (0.82–0.98)	21.2 (17.6–24.7)
C. trichotoma	47.2±0.2 (42.0–50.5)	45.4±0.2 (39.8–48.9)	1.04 (0.91–1.16)	20.5 (17.6–25.6)
TRICOLPORATE-RUGULATE				
Patagonula americana	24.7±0.1 (22.6–26.9)	18.9±0.1 (17.2–20.8)	1.3 (1.10–1.55)	6.2 (4.1–7.9)
TRIPORATE-GEMMATE				
Tournefortia bicolor	15.5±0.1 (12.4–16.5)	18.1±0.1 (15.7–20.7)	0.85 (0.68–0.95)	—
HETEROCOLPATE-PSILATE				
Heliotropium amplexicaule	33.5±0.2 (28.7–39.0)	20.1±0.2 (16.9–24.3)	1.67 (1.50–1.94)	8.2 (6.8–13.6)
H. elongatum	33.2±0.2 (29.2–37.9)	19.2±0.2 (16.5–24.0)	1.73 (1.38–2.06)	—
H. leiocarpum	28.5±0.1 (25.4–30.5)	19.3±0.1 (16.7–21.3)	1.48 (1.30–1.74)	8.5 (6.3–10.7)
H. procumbens	26.2±0.3 (22.5–32.2)	19.1±0.3 (15.0–26.1)	1.37 (1.00–1.62)	—
H. salicoides	34.9±0.2 (30.5–38.7)	25.4±0.2 (20.1–29.7)	1.37 (1.13–1.81)	6.8 (4.6–8.8)**
H. transalpinum	29.5±0.2 (26.0–32.8)	18.4±0.2 (14.0–21.2)	1.6 (1.38–2.07)	7.7 (4.9–11.7)
H. trans. var *tiaridioides*	29.0±0.2 (25.9–36.1)	16.4±0.1 (14.4–18.7)	1.77 (1.61–2.12)	8.7 (6.5–12.8)
Tournefortia breviflora	26.1±0.2 (21.3–29.2)	17.6±0.1 (14.9–20.7)	1.48 (1.23–1.78)	6.3 (3.5–8.3)
T. gardneri	28.3±0.2 (24.9–32.3)	22.6±0.2 (19.2–26.2)	1.25 (1.04–1.51)	7.5 (6.3–8.7)
T. membranacea	16.1±0.1 (13.7–18.1)	11.3±0.2 (9.4–13.7)	1.42 (1.19–1.71)	6.3 (4.0–7.8)
T. paniculata	27.8±0.2 (23.3–33.3)	23.7±0.2 (21.0–27.6)	1.17 (1.05–1.35)	9.1 (7.0–10.9)
T. rubicunda	26.9±0.2 (22.3–30.2)	19.8±0.2 (16.5–24.4)	1.36 (1.14–1.80)	11.5 (7.7–12.4)
T. villosa	28.2±0.1 (26.2–29.8)	22.2±0.2 (19.2–25.0)	1.27 (1.14–1.48)	13.6 (12.8–17.1)
TRICOLPORATE-SCABRATE				
Heliotropium indicum	46.1±0.3 (42.2–54.3)	26.9±0.2 (23.1–32.3)	1.71 (1.46–1.99)	—
TRICOLPORATE-MICRORETICULATE				
Moritzia ciliata	23.6±0.1 (20.5–25.6)	18.9±0.1 (17.9–20.7)	1.24 (1.07–1.32)	10.6 (9.4–12.6)
M. dusenii	26.5±0.2 (24.0–29.8)	23.7±0.2 (21.0–27.1)	1.12 (0.90–1.4)	11.9 (10.1–15.3)
M. tetraquetra	21.9±0.1 (19.8–24.0)	19.2±0.1 (17.7–20.8)	1.14 (1.04–1.25)	12.2 (9.8–15.0)
TRICOLPORATE-PSILATE				
M. dasyantha	17.3±0.3 (14.5–24.8)	13.6±0.2 (9.1–17.8)	1.27 (1.03–2.07)	11.2 (8.6–15.0)
TRICOLPORATE-PERFORATE				
Antiphytom cruciatum	13.9±0.0 (12.4–15.8)	11.9±0.0 (10.9–13.3)	1.16 (1.08–1.33)	4.7 (3.7–5.6)

8. TRICOLPORATE-ECHINATE

Subtype-a: tricolporate-echinate suboblate to oblate spheroidal (Fig. 3. I–M, Fig. 4. A–I, N)

Pollen grains 3-colporate; (26-) 32 (-40) × (30-) 36 (-45) µm; suboblate to oblate spheroidal; apocolpium large; amb rounded to subtriangular.

Colpi narrow, endoapertures lolongate, broadly elliptical.

Sexine and nexine about the same thickness, sexine thicker at aperture margins, echinate with scattered spines interspersed with irregular granules.

Comments. – The surface granules are more apparent in *C. sellowiana* and *C. silvestris*. In SEM observations the tectum is always undulate. The pollen grains are very fragile and crush very easily when acetolysed.

Species included: Cordia ecalyculata, C. sellowiana, C. silvestris.

Subtype-b: tricolporate-echinate subprolate (Fig. 4. J–M, O–P)

Pollen grains 3- or 4-colporate; (42-) 47 (-50) × (40-) 45 (-49) µm; subprolate to prolate spheroidal (mainly subprolate), rarely oblate spheroidal; apocolpium large; amb rounded to subtriangular.

Colpi narrow, endoapertures broadly elliptical variably-shaped.

Sexine much thicker than nexine, sexine thicker at aperture margins, echinate with scattered spines interspersed with a few irregular granules.

Comments. – In SEM observations the tectum is always undulate. The pollen grains are very fragile and crush very easily when acetolysed. On the basis of the specimens examined, 3- and 4-colporate pollen grains may occur in proportions of up to 53 and 47 per cent, respectively.

Species included: Cordia trichotoma.

Sexine	Nexine	^Po/^Eh	>Po/>En	Lum/^Sp/^Gm	Mur/>Sp/>Gm
2.6 (2.2–2.8)	1.4 (1.1–1.7)	6.5 (4.6–8.3)	5.5 (4.5–6.3)	1.7 (1.1–2.3)	1.3 (1.0–1.6)
2.6 (2.1–3.2)	1.0 (1.0–1.1)	6.5 (4.8–7.9)	6.0 (4.0–8.4)	2.2 (1.6–2.9)	1.4 (1.0–1.8)
2.7 (2.3–3.2)	0.8 (0.6–1.1)	5.7 (4.3–7.1)	4.6 (3.1–5.8)	1.3 (1.0–1.4)	1.1 (1.0–1.4)
2.4 (1.8–2.8)	1.2 (1.0–1.6)	6.9 (5.2–10.2)	4.7 (3.5–5.5)	2.4 (1.1–3.2)	1.4 (1.1–1.8)
2.3 (1.8–2.8)	1.2 (1.0–1.6)	6.5 (4.8–7.9)	10.1 (8.0–12.3)	2.7 (1.4–3.5)	1.3 (1.0–1.7)
1.1 (1.1–1.3)	0.8 (0.7–0.8)	6.5 (5.5–7.7)	3.9 (3.0–6.3)	1.8 (1.4–2.3)	1.0 (0.6–1.4)
1.0 (0.8–1.1)	0.8 (0.7–1.0)	6.2 (5.2–7.0)	5.6 (4.4–6.6)	1.5 (1.0–1.8)	—
0.9 (0.8–1.0)	0.8 (0.7–1.0)	6.9 (5.2–8.4)	—	1.8 (1.4–2.1)	1.8 (1.4–2.4)
1.4 (1.3–1.6)	0.8 (0.7–1.0)	4.5 (3.7–6.2)	3.4 (2.2–4.3)	1.9 (1.6–2.3)	1.3 (1.0–1.8)
1.0 (0.7–1.0)	0.9 (0.7–1.0)	3.2 (1.9–3.5)	–	—	—
0.7 (0.6–0.8)	0.6 (0.4–0.7)	—	—	2.4 (1.6–3.2)	2.8 (2.3–3.5)
0.7 (0.6–0.8)	0.6 (0.4–0.7)	3.5 (2.7–4.5)	—	—	—
0.6 (0.6–0.8)	0.6 (0.6–0.7)	3.5 (2.2–4.8)	—	—	—
0.6 (0.6–0.7)	0.6 (0.6–0.6)	3.3 (2.4–4.2)	—	—	—
0.5 (0.4–0.6)	0.5 (0.4–0.6)	2.5 (2.1–3.3)	—	—	—
0.8 (0.7–1.0)	0.7 (0.6–0.7)	4.2 (3.5–5.0)	3.1 (2.5–3.5)	—	—
0.6 (0.4–0.6)	0.6 (0.4–0.6)	2.4 (1.8–3.2)	—	—	—
0.6 (0.6–0.6)	0.6 (0.4–0.6)	3.2 (2.7–4.2)	—	—	—
0.6 (0.4–0.7)	0.6 (0.6–0.7)	3.1 (2.1–4.6)	—	—	—
0.7 (0.6–0.8)	0.6 (0.6–0.8)	3.5 (2.6–6.0)	—	—	—
0.7 (0.6–0.9)	0.6 (0.5–0.6)	1.8 (1.6–2.1)	—	—	—
0.8 (0.6–1.0)	0.6 (0.5–0.8)	3.0 (2.6–3.2)	—	—	—
0.6 (0.6–0.8)	0.6 (0.4–0.7)	3.0 (2.1–4.2)	—	—	—
0.6 (0.6–0.7)	0.6 (0.6–0.7)	2.7 (2.2–3.4)	—	—	—
0.9 (0.7–1.1)	0.9 (0.7–1.0)	5.4 (3.4–6.6)	—	—	—
0.6 (0.4–0.6)	0.8 (0.6–0.8)	2.9 (2.4–3.5)	5.6 (3.5–7.4)	0.6 (0.3–0.7)	0.6 (0.4–0.8)
0.8 (0.6–1.0)	0.7 (0.6–1.0)	3.3 (2.5–4.0)	6.7 (5.3–7.9)	1.0 (0.6–1.0)	0.9 (0.4–1.3)
0.6 (0.6–0.8)	0.8 (0.7–1.0)	3.9 (2.9–5.0)	4.4 (3.2–6.2)	0.6 (0.3–0.7)	0.6 (0.3–1.0)
0.6 (0.6–0.8)	0.6 (0.4–0.7)	2.7 (2.0–4.0)	4.3 (4.2–5.2)	—	—
0.6 (0.4–0.7)	0.5 (0.4–0.6)	1.9 (1.5–2.4)	1.4 (1.0–1.8)	0.4 (0.2–0.6)	0.5 (0.3–0.6)

9. HETEROCOLPATE-PSILATE

Subtype-a: tricolporate and tri-pseudo-colpate-psilate (Fig. 5. N–AD; Fig. 6. A–W)

Pollen grains 3-colporate and 3-pseudocolpate, rarely 4-colporate and 4-pseudocolpate; (14-) 28 (-39) × (9-) 19 (-28) µm; prolate spheroidal to perprolate; apocolpium usually small; amb 6-lobate.

Colpi narrow, generally long, endoapertures usually lalongate, elliptical, more or less elongate according to species, rarely rounded.

Sexine and nexine about the same thickness, sexine psilate.

Comments. – In SEM observations the tectum is always undulate, the degree of undulation depending upon the species. In *T. paniculata* the endoaperture is particularly elongated. Four-colporate and 4-pseudocolpate pollen grains were found in low abundance in *T. villosa* and *T. breviflora*, as well as tricolporate pollen grains in *H. elongatum*. In the latter species pollen grains rarely occur in polar view. In *H. procumbens* the pollen grains are frequently inflated and the pseudocolpi are sometimes difficult to discern; the apocolpium is slightly lobate or almost round.

Species included: Heliotropium amplexicaule, H. leiocarpum, H. elongatum, H. transalpinum var. *transalpinum, H. transalpinum* var. *tiaridioides, H. procumbens, Tournefortia breviflora, T. gardneri, T. membranacea, T. paniculata, T. rubicunda, T. villosa.*

Subtype-b: tetracolporate and tetra-pseudo-colpate-psilate (Fig. 6. AB)

Pollen grains 4-colporate and 4-pseudocolpate; (30-) 35 (-39) × (20-) 25 (-30) µm; subprolate to perprolate.

Colpi narrow, of medium length, endoapertures lolongate, broadly elliptical.

Sexine and nexine about the same thickness, sexine psilate.

Comments. – Pollen grains particularly rare in polar view.

Species included: Heliotropium salicoides.

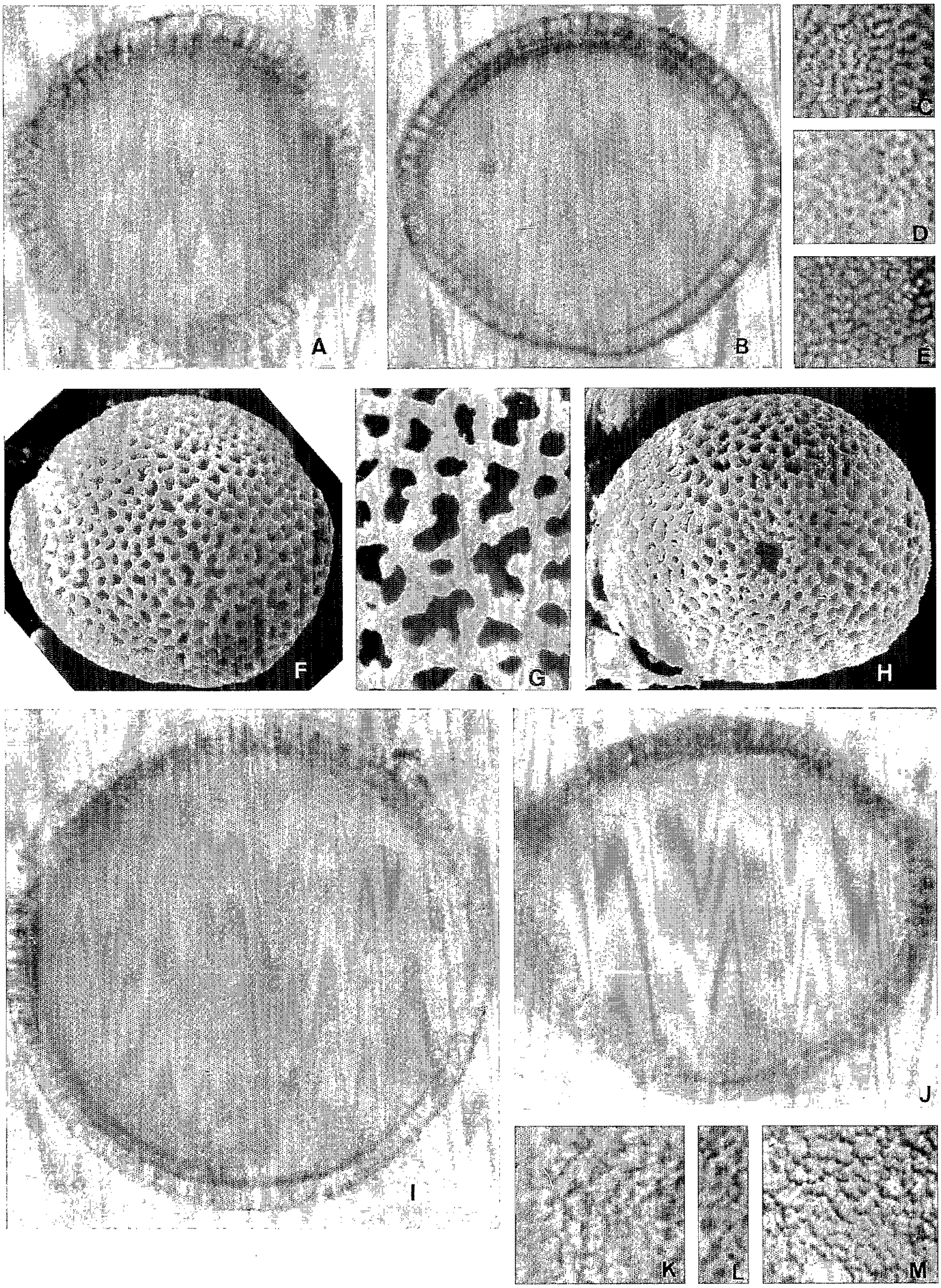


Fig. 1. A–H. *Cordia axillaris.* (A) polar view, optical section, (B) equatorial view, optical section, (C–E) surface L-O analysis (LM, ×1000), (F) polar view (SEM, ×1000), (G) surface ornamentation (SEM, ×3000), (H) equatorial view (SEM, ×1000). I–M. *Cordia guaranitica.* (I) polar view, optical section, (J) equatorial view, optical section, (K–M) surface L-O analysis (LM, ×1000).

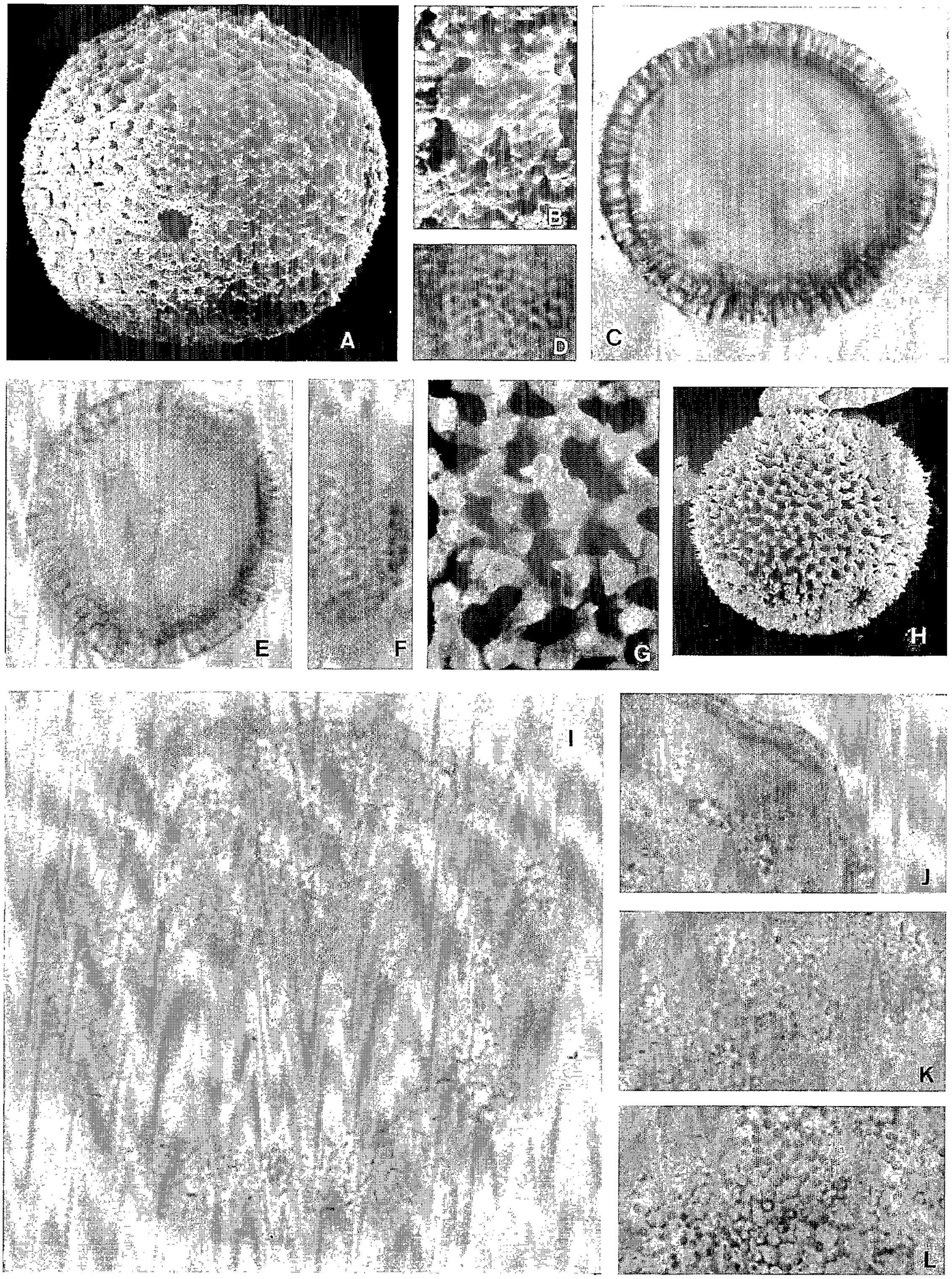


Fig. 2. A–B. *Cordia guaranitica.* (A) equatorial view (SEM, ×750), (B) surface ornamentation (SEM, ×3000). C–H. *Cordia monosperma.* (C) equatorial view, optical section, (D) surface ornamentation, equatorial view, (E) polar view, optical section, (F) surface ornamentation, polar view (LM, ×1000), (G) surface ornamentation (SEM, ×3000), (H) polar view (SEM, ×750). I–L. *Cordia paucidentata.* (I) polar view, (J) polar view, optical section. detail, (K–L) surface L–O analysis (LM, ×1000).

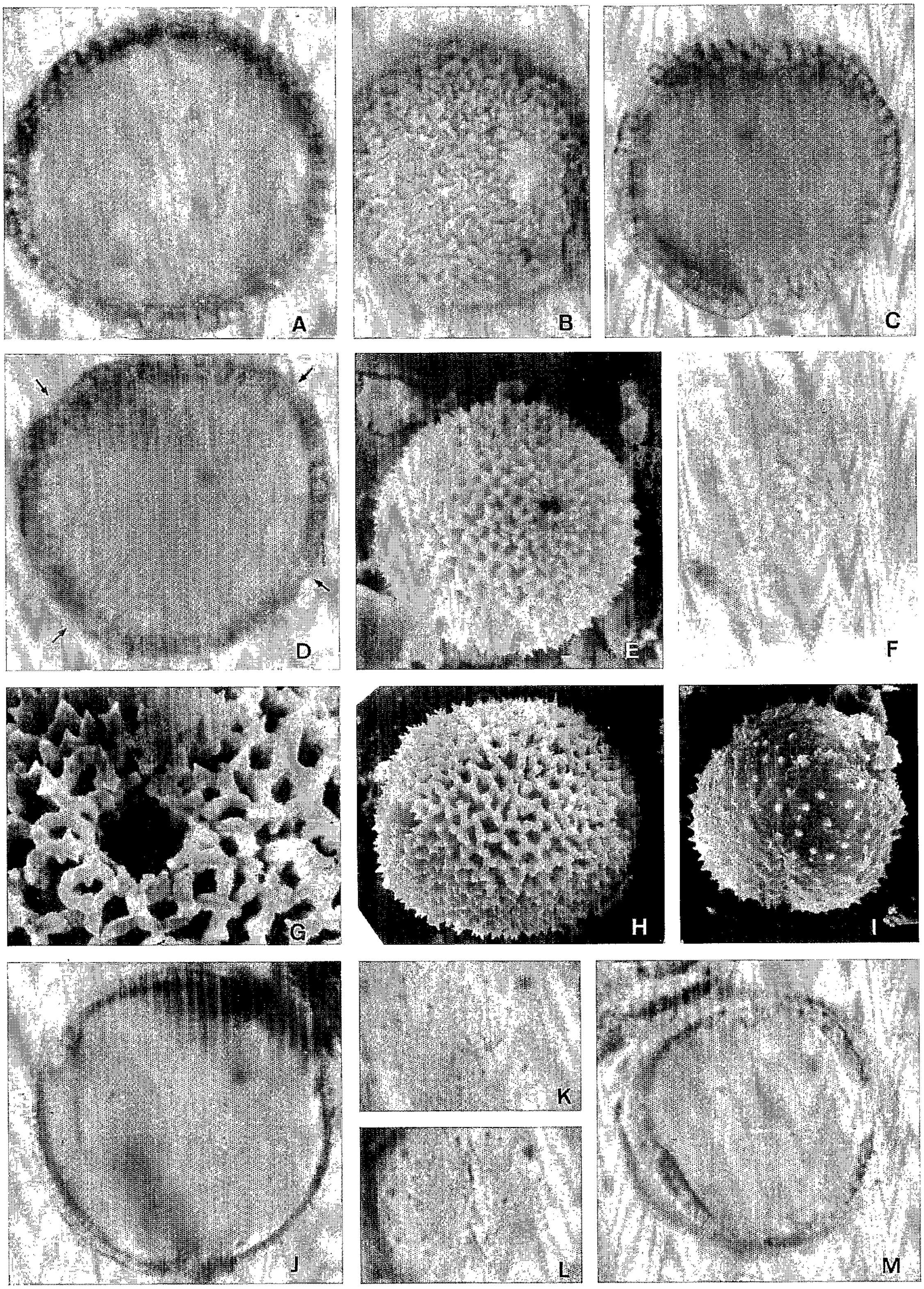


Fig. 3. A–H. *Cordia verbenacea.* (A) equatorial view, optical section, (B) equatorial view, (C) polar view, optical section, (D) polar view, optical section, tetracolporate pollen grain (LM, ×1000), (E) sub-equatorial view (SEM, ×750), (F) polar view (LM, ×1000), (G) surface ornamentation and pore (SEM, ×3000), (H) equatorial view (SEM, ×750). I–M. *Cordia ecalyculata.* (I) polar view (SEM, ×750), (J) polar view, optical section, (K) surface ornamentation, polar view, (L) surface ornamentation, equatorial view, (M) equatorial view, optical section (LM, ×1000).

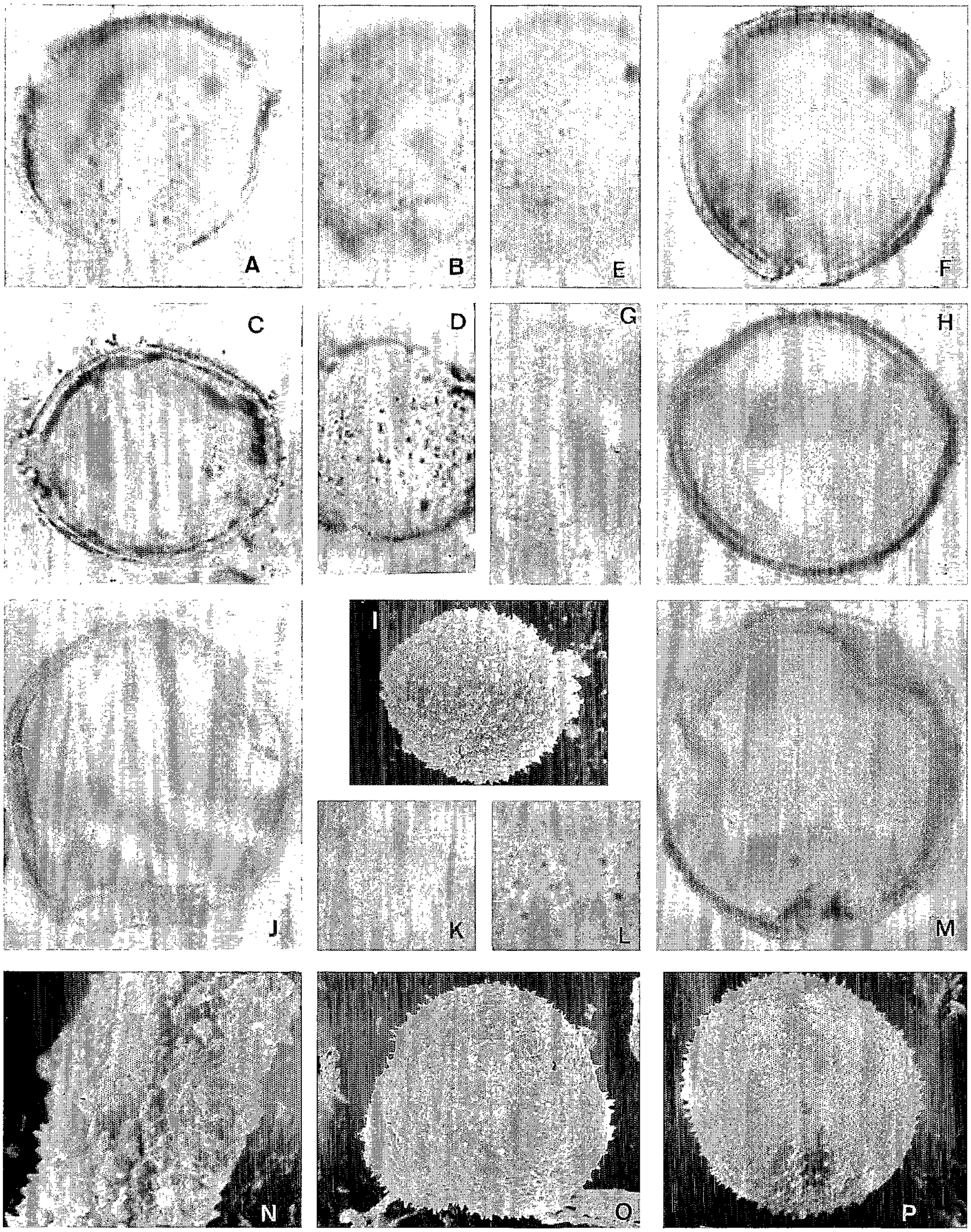
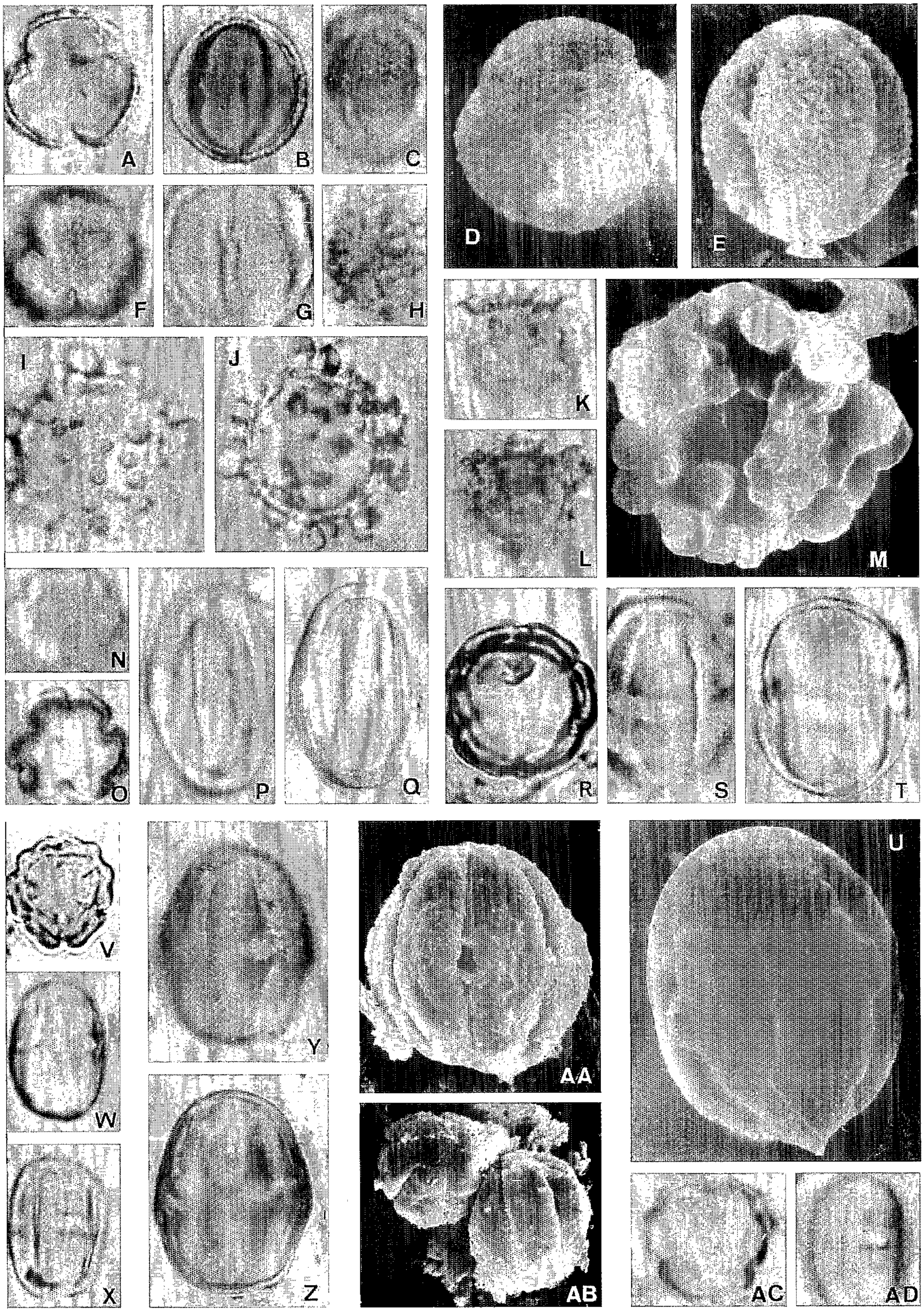


Fig. 4. A–D&N. *Cordia sellowiana.* (A) polar view, optical section, (B) surface ornamentation, polar view, (C) equatorial view, optical section, (D) surface ornamentation, polar view (LM, × 1000), (N) surface ornamentation (SEM, × 3000). E–I. *Cordia silvestris.* (E) surface ornamentation, polar view, (F) polar view, optical section, (G) surface ornamentation, equatorial view, (H) equatorial view, optical section (LM, × 1000), (I) polar view (SEM, × 750). J–M, O&P. *Cordia trichotoma.* (J) equatorial view, optical section, (K) surface ornamentation, equatorial view, (L) surface ornamentation, polar view, (M) polar view, optical section (LM, × 1000), (O) polar view, (P) equatorial view (SEM, × 750).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Key to the taxa

1. Pollen grains porate
   2. Sexine reticulate ....*Cordia* subg. *Varronia* (*C. axillaris, C. guaranitica, C. monosperma, C. paucidentata, C. verbenacea*): Cordioideae
   2′. Sexine gemmate ......*Tournefortia* sect. *Eutournefortia* (*T. bicolor*): Heliotropioideae
1′. Pollen grains colporate or heterocolporate
   3. Pollen grains tricolporate
      4. Sexine ornated
         5. Sexine echinate
            6. Pollen grains suboblate to oblate spheroidal.. *Cordia* subg. *Myxa* sect. *Myxa* (*C. ecalyculata, C. sellowiana, C. silvestris*): Cordioideae
            6′. Pollen grains subprolate ....*Cordia* subg. *Myxa* sect. *Gerascanthus* (*C. trichotoma*): Cordioideae
         5′. sexine not echinate
            7. Sexine rugulate ......*Patagonula americana*: Cordioideae
            7′. Sexine not rugulate
               8. Sexine scabrate ....*Heliotropium indicum* (sect. *Tiaridium*): Heliotropioideae
               8′. Sexine not scabrate
                  9. Sexine microreticulate
                     10. Lumina always less than 1 μm ..... *Moritzia ciliata, M. tetraquetra*
                     10′. Lumina often equal to 1 μm....... *M. dusenii*: Boraginoideae
                  9′. Sexine perforate.....*Antiphytum cruciatum*: Boraginoideae
      4′. Sexine psilate .... *Moritzia dasyantha*: Boraginoideae

Pollen grains heterocolpate

11. Pollen grains 3-colporate and 3-pseudocolpate .... *Tournefortia* sect. *Cyphocyema* (*T. breviflora, T. gardneri, T. membranacea, T. paniculata, T. rubicunda, T. villosa*), *Heliotropium* sect. *Heliophytum* (*H. amplexicaule, H. leiocarpum*), *H.* sect. *Coeloma* (*H. transalpinum*), *H.* sect. *Orthostachys* subsect. *Ebracteata* (*H. procumbens*), *H.* sect. *Tiaridium* (*H. elongatum*): Heliotropioideae
11′. Pollen grains 4-colporate and 4-pseudocolpate .... *Heliotropium* sect. *Orthostachys* subsect. *Bracteata* (*H. salicoides*): Heliotropioideae

DISCUSSION

Among the Boraginaceae represented in Santa Catarina State, *Cordia* is the best studied genus; it was in this genus that pollen morphology was first consistently associated with the taxonomy of the family. Nowicke & Ridgway (1973) defined three pollen types in *Cordia* which are well correlated with flower and inflorescence characteristics, and which could be associated with the different sections proposed by Johnston (1930, 1935, 1940, 1949 & 1950). The former authors associated section *Varronia* with "pollen type I, three-porate grains with a reticulate sexine", section *Cordia* to "pollen type II, three-colpate or 3-colporoidate grains with a striato-reticulate sexine" and sections *Gerascanthus, Myxa, Physoclada* and *Rhabdocalyx* to "pollen type III, three-colpate or 3-colporate grains with a spinulose sexine". On the basis of the pollen morphology, they suggested that section *Varronia* should be raised to the genus level.

Taroda & Gibbs (1986 *b*) analyzed this division of the genus *Cordia*, arguing that "whilst it is possible to 'draw lines' around such groups by employing a single character such as pollen, it is difficult to find two still less more characters which are uniformly correlated and which would readily allow one to recognize members of each group at generic level". Also taking into consideration the difficulties this division would bring to the stability of nomenclature, due to the fact that the type-species corresponds to a very small section, these authors decided to elevate the three principal groups defined by pollen morphology to subgenus level. So, "pollen type I" referred to above would correspond to subgenus *Varronia*, "pollen type II", to subgenus *Cordia*, and "pollen type III" to subgenus *Myxa*. These same pollen types, associated with the same taxonomic groups, were also found by Palacios-Chávez & Quiroz-Garcia (1985) and Moncada & Herrera-Oliver (1989) for species of the genus *Cordia* occurring in Mexico and Cuba, respectively. None of the species that we examined belongs to the subgenus *Cordia*. The pollen types that we described for the species of the other two subgenera and the resulting groups agree with the associations given above. The distinct pollen types that we found in this genus clearly show that it is a heterogeneous group of species without a close phylogenetic relationship. This agrees with the opinions of Nowicke & Ridgway (1973).

In the tricolporate-echinate pollen type, the species are more uniform. However, two sub-types were defined based on differences in shape, which is essentially suboblate in subtype-A and subprolate in subtype-B. However, it must be stated that *C. trichotoma* (subtype-B) presents a few oblate spheroidal pollen grains, which could be easily confused with

Fig. 5. A–G. *Patagonula americana.* (A) polar view, optical section, (B) equatorial view, optical section, (C) surface ornamentation, equatorial view (LM, ×1000), (D) polar view, (E) equatorial view (SEM, ×1500), (F) polar view, (G) surface ornamentation, equatorial view (LM, ×1000). H–M. *Tournefortia bicolor.* (H) surface ornamentation and aperture, (I) equatorial view, (J) equatorial view, optical section, (K) polar view, (L) polar view, optical section (LM, ×1000), (M) equatorial view and aperture (SEM, ×2000). N–Q. *Tournefortia breviflora.* (N) polar view, (O) polar view, optical section, (P) equatorial view, (Q) equatorial view, optical section (LM, ×1000). R–U. *Tournefortia paniculata.* (R) polar view, optical section, (S) equatorial view, (T) equatorial view, optical section (LM, ×1000), (U) equatorial view (SEM, ×1500). V–X. *Tournefortia membranacea.* (V) polar view, optical section. (W) equatorial view, optical section, (X) equatorial view (LM, ×1000). Y,Z & AA, AB. *Tournefortia gardneri.* (Y) equatorial view, (Z) equatorial view, optical section (LM, ×1000), (AA) equatorial view (SEM, ×1000), (AB) polar and equatorial views (SEM, ×750). AC & AD. *Heliotropium leiocarpum.* (AC) polar view, optical section, (AD) equatorial view (LM, ×1000).

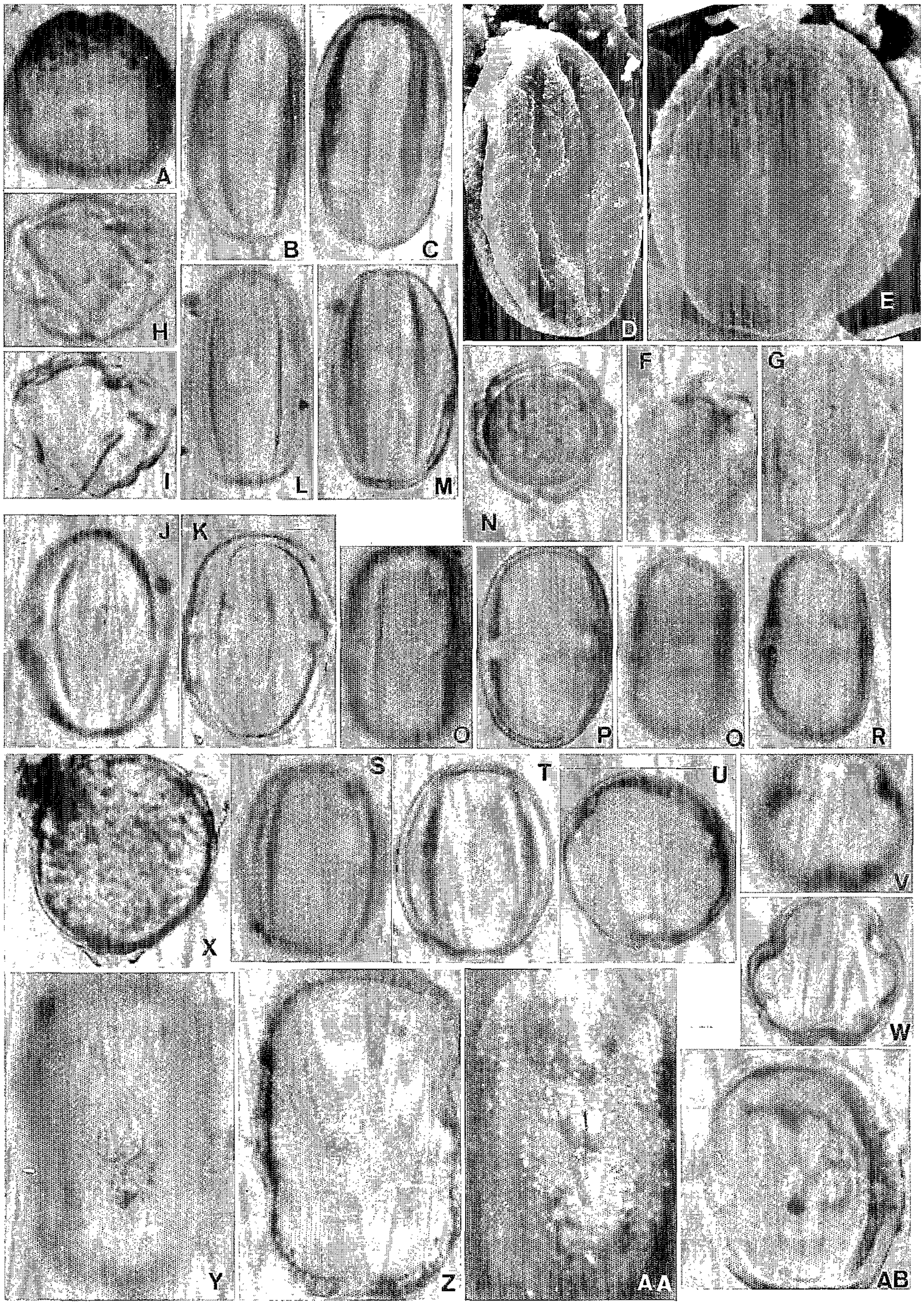

Fig. 6. A–D. *Heliotropium amplexicaule.* (A) polar view, (B) equatorial view, (C) equatorial view, optical section (LM, ×1000), (D) equatorial view (SEM, ×1000). E–G. *Tournefortia rubicunda.* (E) equatorial view (SEM, ×1500), (F) polar view, (G) equatorial view (LM, ×1000). H–K. *Tournefortia villosa.* (H) polar view, (I) polar view, optical section, (J) equatorial view, (K) equatorial view, optical section (LM, ×1000). L–N. *Heliotropium transalpinum* var. *transalpinum.* (L) equatorial view, (M) equatorial view, optical section, (N) polar view, optical section (LM, ×1000). O–P. *Heliotropium transalpinum* var. *tiaridioides.* (O) equatorial view, (P) equatorial view, optical section (LM, ×1000). Q–R. *Heliotropium elongatum.* (Q) equatorial view, (R) equatorial view, optical section (LM, ×1000). S–W. *Heliotropium procumbens.* (S) equatorial view, (T) equatorial view, optical section, (U) polar view, optical section, (V) polar view, (W) polar view, optical section (LM, ×1000). X–Z & AA. *Heliotropium indicum.* (X) polar view, optical section, (Y) equatorial view, (Z) equatorial view, optical section (LM, ×1000), (AA) equatorial view (SEM, ×1000). (AB) *Heliotropium salicoides*, equatorial view, optical section (LM, ×1000).

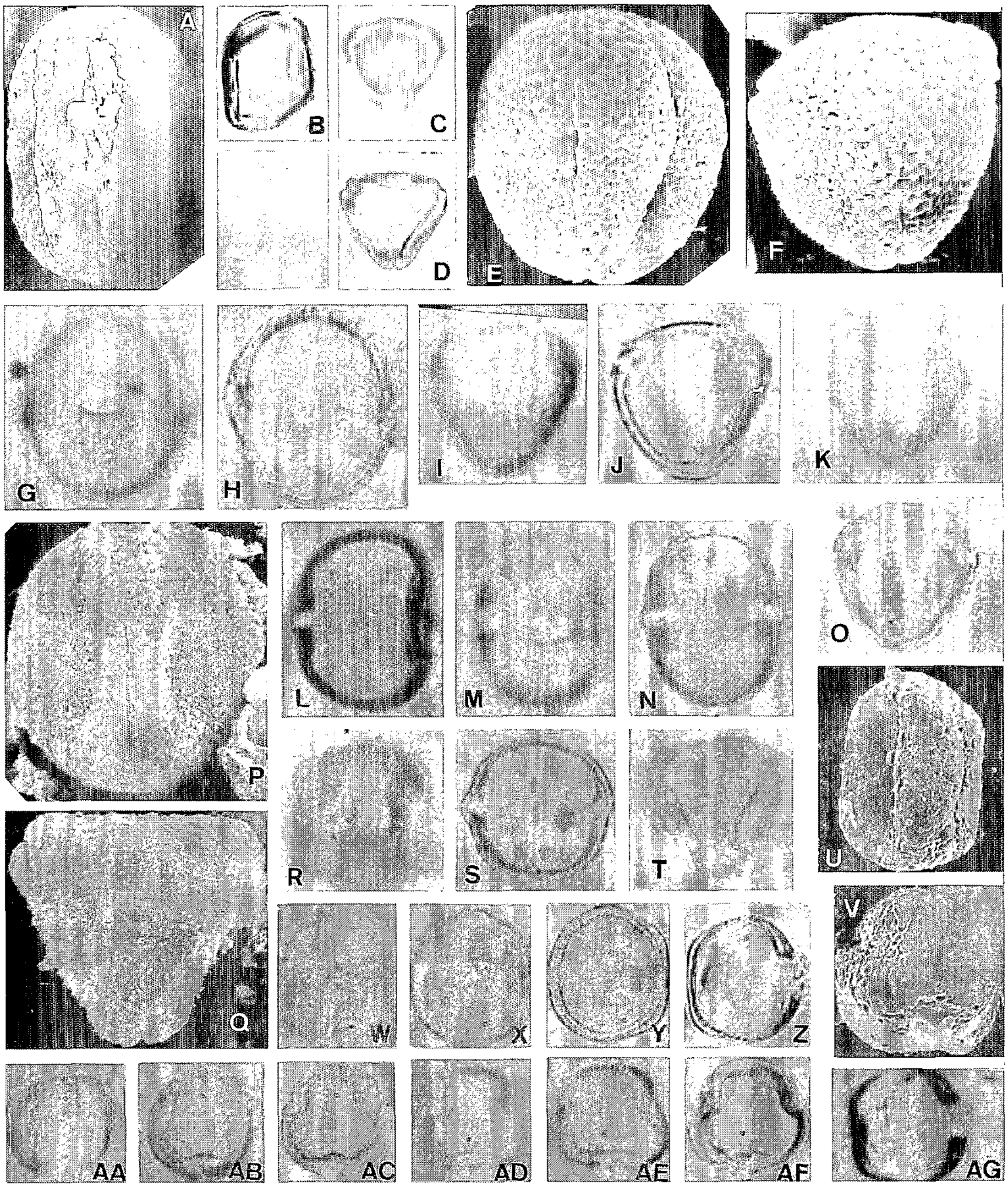

Fig. 7. A–D. *Moritzia dasyantha.* (A) equatorial view (SEM, ×2000), (B) equatorial view, optical section (LM, ×1000), (C) polar view, (D) polar view, optical section (LM, ×1000). E–J. *Moritzia dusenii.* (E) equatorial view, (F) polar view (SEM, ×2000), (G) equatorial view, (H) equatorial view, optical section, (I) polar view, (J) polar view, optical section (LM, ×1000). K–O. *Moritzia ciliata.* (K) polar view, (L, N) equatorial view, optical section, (M) equatorial view, (O) polar view, optical section (LM, ×1000). P–T. *Moritzia tetraquetra.* (P) equatorial view, (Q) polar view (SEM, ×2000), (R) equatorial view, (S) equatorial view, optical section, (T) polar view (LM, ×1000). U–Z & *AA, AA-AG Antiphytum cruciatum.* (U) equatorial view, (V) polar view (SEM, ×1500), (W–Y) equatorial view. operculum, aperture and optical section, respectively, (Z) equatorial view, optical section. operculum, (AA–AB) polar view, (AC) polar view, optical section, (AD–AE) polar view, (AF) polar view, optical section, (AG) equatorial view (LM, ×1000).

the pollen grains of subtype-A, particularly if found in a mixed pollen assemblage, e.g. in samples from soil or honey.

Pollen grains of *C. trichotoma*, *C. ecalyculata* and *C. verbenacea* were described by Nowicke & Ridgway (1973). Although the descriptions of these authors correspond to those presented here, their measurements in general indicate smaller grains. There is also a small discordance in the description of *C. trichotoma*, defined as "colpate or slightly colporoidate". Taroda & Gibbs (1987) described the pollen grains of *C. ecalyculata* and *C. sellowiana* as "3-colpate or 3-colporoidate", and those of *C. trichotoma* as "3-colpate or 3-colporate". We have generally verified the presence of well-defined endoapertures for all these species, although in some instances they can be rather difficult to distinguish. Miranda et al. (1980) stated that *C. trichotoma* pollen grains are "tricolporate with granulate surface", and Miranda & Andrade (1990) described a "pollen type *Cordia*, inaperturate reticulate", while presenting an illustration of echinate pollen grains from the former species. Pollen grains of *C. sellowiana* from Santa Catarina State described by Barth & Silva (1963, Barth 1964: Addendum) have the same morphology as that presented here, but their measurements indicate slightly smaller grains. The authors refer to the extreme fragility of these pollen grains, a characteristic that we remarked in every species of this pollen type.

The other genus from the subfamily Cordioideae in Santa Catarina, *Patagonula*, is represented there by a single species, *P. americana*, whose pollen grains correspond to the tricolporate-rugulate pollen type. The description of the pollen grains of this species by Nowicke & Miller (1990) agrees entirely with what is presented here. Markgraf & D'Antoni (1978) defined the pollen type of this species as "heterocolpate, per-reticulate", while Erdtman (1952: 78) described it as "3-colporate, oblate spheroidal, with vestigial spines". Both are strongly contradicted by our results, and we believe they probably examined incorrectly identified plant specimens.

In the genus *Tournefortia* we found two distinctly different pollen types: triporate-gemmate in *T. bicolor*, the only representative of section *Eutournefortia* in the studied area, and heterocolpate-psilate in the other species, from section *Cyphocyema*. Although Nowicke & Skvarla (1974) found a great variety of pollen types in *Tournefortia* not directly correlated to section delimitations in this group, the two pollen types here described correspond very well to the sectional distribution of the species. Nowicke & Skvarla (1974) characterized pollen grains from *T. bicolor* as "spheroidal, 3-porate, the ectexine conspicuously clavate", but in our results they appeared to be tectate. Pollen grain diameters presented by these authors are in accordance with our polar and equatorial axis measurements. In spite of the density of the gemmae, which makes observation of the apertures very difficult, the triaperturate character is clearly recognised in polar view, particularly in those pollen grains where the cytoplasm has not been completely eliminated by acetolysis. It is also confirmed by SEM observations.

The heterocolpate-psilate pollen type, which is found in all species of *Tournefortia* sect. *Cyphocyema*, is quite homogeneous. Although there is some variety of size, shape, and sometimes also of endoaperture characteristics, the definition of pollen sub-types is impossible because of the superposition of extreme values between the species. Pollen morphology in these species corresponds to one of the pollen types defined by Nowicke & Skvarla (1974) for the genus *Tournefortia*, whose description agrees entirely with our results, and in which the authors included pollen of *T. breviflora*, *T. membranacea*, *T. paniculata*, *T. rubicunda* and *T. villosa* (among others). The measurements given for the first three are equivalent to ours or only slightly different, while no numerical results were presented for the latter two species.

Most *Heliotropium* species also correspond to the heterocolpate-psilate pollen type. It is not possible to distinguish them from the *Tournefortia* species included here. Interestingly enough, on the basis of pollen morphology, *Tournefortia* sect. *Cyphocyema* species are more closely related to these *Heliotropium* species than to *T.* sect. *Eutournefortia*, confirming what was suggested by Johnston (1930) using other taxonomic characters. Nowicke & Skvarla (1974) stated that "the generic boundary between *Tournefortia* and *Heliotropium* is difficult to define and in the past the two genera have been separated on the basis of habit, woody versus herbaceous, and the condition of mesocarp, fleshy versus dry". In spite of this *Heliotropium* is the only genus among those studied which presents important discrepancies between taxonomy and pollen morphology. Although most sections are stenopalynous, sect. *Tiaridium* has two very distinct pollen types: heterocolpate-psilate in *H. elongatum* (like the pollen grains referred to above), and tricolporate-scabrate in *H. indicum*. Besides these significant differences in the number of apertures and surface ornamentation, pollen grains of the latter species are considerably larger and the exine is clearly distinguished by the presence of endocracks, an aspect that has not been mentioned for this family until now. This characteristic was recorded by Oldfield (1959), Lobreau (1969) and Nilsson (1986), referring respectively to the orders Ericales, Celastrales and Gentianales.

Most descriptions of *H. indicum* found in the literature diverge from our observations, but this divergence can often be attributed to a disagreement on terminology. Quiroz-Garcia & Palacios-Chávez (1985) described tricolporate pollen grains with a tectate exine, seen as microreticulate in light microscopy and scabrate in SEM. Bonnefille & Riollet (1980) described tricolporate pollen grains with a rugulate ectexine and equatorial axis slightly larger than our measurements. Pal (1963) described tricolporate pollen grains with a tegillate sexine, the measurements being significantly smaller than ours. Huang (1972 – In: Quiroz-Garcia & Palacios-Chávez 1985), on the other hand, described the pollen of this species as "heterocolpate with psilate tectum and reticulate sexine", which would place it in a pollen type completely different from what we found. Although Johnston (1928) declared that *H. elongatum* is the only species closely related to *H. indicum* and described a variety of the former that could be an intermediate form between them, our palynological observations show that this species group is entirely artificial.

In the section *Orthostachys*, the trimerous apertures in pollen grains of *H. procumbens* (subsect. *Ebracteata*) differ from those of *H. salicoides* (subsect. *Bracteata*), which are exclusively tetramerous. However, it is important to notice that this difference in the number of apertures sets *H. salicoides* aside from all the other species of the genus. Several authors, referring to pollen grains of *Heliotropium* species, reported a pollen morphology resembling what we found in the psilate-heterocolpate pollen type (Erdtman 1952, Pal 1963, Marticorena 1968, Clarke 1977, Markgraf & D'Antoni 1978, Quiroz-Garcia & Palacios-Chávez 1985).

A rather interesting character observed in this family is the occurrence, in three genera (*Cordia*, *Tournefortia* and *Heliotropium*), of species with both trimerous and tetramerous pollen grains. References to tetramerous species have been found only for the last two genera (Nowicke & Skvarla 1974, Quiroz-Garcia & Palacios-Chávez 1985), but the only reference to both pollen types occurring in the same species was made by Clarke (1977) for *H. europaeum*. Van Campo (1966), on the other hand, included Boraginaceae in a group of families of dicotyledons where pollen dimorphism or polymorphism has been observed.

Finally, the subfamily Boraginoideae is represented in Santa Catarina by two small genera of the tribe Lithospermae, *Moritzia* and *Antiphytum*. Johnston (1927) referred to *Moritzia* as "a very natural genus of Colombia and Venezuela and of southern Brazil". Even though we found variations in pollen morphology in this genus, they are relatively small and do not presuppose a greater phylogenetic distance between the species. *Moritzia* has four species in this State, three of which are included in the tricolporate-microreticulate pollen type, and the other in the tricolporate-psilate pollen type. *M. dasyantha* is clearly distinguished from the other species by its psilate surface and distinctly smaller pollen grains. The rather wide range of shape observed in this species is remarkable. The other species, *M. ciliata*, *M. tetraquetra* and *M. dusenii*, are quite similar in pollen morphology, although the microreticulum in the last one is rougher than in the first two, allowing the establishment of pollen sub-types. Johnston (1927) stated that *M. dusenii* is a very distinct species, somewhat intermediate between *M. ciliata* and *M. lindenii*, but clearly more related to the former. On the basis of our results and on the description of *M. lindenii* presented by Hooghiemstra (1984) of scabrate, 4-aperturate pollen grains, we confirm this affirmation based on pollen morphology.

Pollen grains of the genus *Antiphytum*, represented in Santa Catarina only by *A. cruciatum*, are not very different from those of the genus *Moritzia* in their morphology, although the tricolporate-perforate pollen type is readily identifiable, its especially large endoaperture with a granulate operculum being particularly noteworthy. No references to the pollen grains of this genus were found in the literature.

CONCLUSIONS

1. The study of 30 native taxa, of six genera, from Santa Catarina State, resulted in the definition of nine pollen types on the basis of apertures and surface ornamentation, which correspond in general to taxonomic groups.
2. Subfamily Cordioideae: The nine species of the genus *Cordia* are classified into two pollen types each one associated with a different subgenus, *Varronia* (pollen type triporate-reticulate) and *Myxa* (pollen type tricolporate-echinate). These clear differences in pollen morphology, which have been extensively discussed in the literature, suggest that it is a heterogeneous group of species without a close phylogenetic connection.
3. *Patagonula americana* is readily identifiable by its pollen morphology (pollen type tricolporate-rugulate).
4. Subfamily Heliotropioideae: All the species of *Tournefortia* sect. *Cyphocyema* and most of *Heliotropium* are grouped in a single pollen type with rather uniform characteristics (heterocolpate-psilate). This is interpreted as a sign of a close phylogenetic relationship.
5. *Heliotropium salicoides* (sect. *Orthostachys*, pollen type heterocolpate-psilate) is the only one of the species studied with exclusively 4-aperturate pollen grains, which sets it a little aside from the rest of the genus and led us to classify it in a different pollen sub-type.
6. *Tournefortia bicolor* (sect. *Eutournefortia*, pollen type triporate-gemmate) presents a remarkably distinct pollen morphology, suggesting a more distant phylogenetical relationship with all the rest of the subfamily.
7. *Heliotropium indicum* (sect. *Tiaridium*, pollen type tricolporate-scabrate) is the species with the most differentiated pollen morphology in this genus. The presence of endocracks is recorded here for the first time in the family Boraginaceae.
8. In *Heliotropium* sect. *Tiaridium* the results of palynological analysis clearly disagree with the taxonomic classification, while a less important disagreement is also verified in the section *Orthostachys*.
9. An extensive re-evaluation of the systematics of the genus *Heliotropium*, possibly of all the subfamily Heliotropioideae, is suggested, in order to verify if there are also other taxonomic characters that may confirm these palynological results.
10. Subfamily Boraginoideae: The pollen grains of the species of the genera *Moritzia* and *Antiphytum* (pollen types tricolporate-microreticulate, tricolporate-psilate and tricolporate-perforate), even though presenting some variability, are quite similar, suggesting that this subfamily is a more natural group than the ones referred to above.

ACKNOWLEDGEMENTS

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SPECIMENS INVESTIGATED

Antiphytum cruciatum (Cham.) DC. BRASIL: Rio Grande do Sul. B. Rambo 48956 (HBR); BRASIL: Rio Grande do Sul. B. Rambo 51510 (HBR).

Cordia axillaris I. M. Johnston. BRASIL: Rio de Janeiro, Teresópolis. Luiz Emygdio de Mello Filho (X.1941), det E. Guimarães (R); BRASIL: Rio de Janeiro, prox. Passa Três. Z. A. Trinta 850 det. E. Guimarães et C. L. Ichaso (R); BRASIL: Rio de Janeiro, Itatiaia. Altamiro et Walter 18, det. Brade (RB); BRASIL: Rio de Janeiro, Tandiá. Kuhlmann (08.XI.1938), det. E. F. Guimarães (RB); BRASIL: Rio de Janeiro, Petrópolis. O. C. Góes et Dionisio 1036, det. E. F. Guimarães (RB).

C. ecalyculata Vell. BRASIL: Santa Catarina, S. Miguel D'Oeste. L. B. Smith et R. M. Klein 14142, det. L. B. Smith (R). BRASIL: Santa Catarina, Alfredo Wagner. Reitz 6716, det. L. B. Smith (HBR); BRASIL: Santa Catarina, Nova Teutônia. F. Ploumann 259, det. Brade (RB); BRASIL: Pará, Peixeboi. A. Ducke

(24.III.1927) (RB); BRASIL: Paraná. J. C. Lindeman et J. Hihaas 3607, det. L. Mautone (RB).
C. guaranitica Chodat et Hassler. BRASIL: Rio Grande. Riedel 634, det. Brade (R).
C. monosperma (Jacq.) R. et S. BRASIL: Paraná, São Mateus do Sul. R. M. Britez 1295 det. R. M. Britez (PKDC); BRASIL: Paraná, São Mateus do Sul. E. de Melo 33, det. R. M. Britez (PKDC).
C. paucidentata Fresen. BRASIL: Mato Grosso, Rio Brilhante. G. Hatschbach 26095, det. Hatschbach (RB).
C. sellowiana Cham. BRASIL: Santa Catarina, Araraquari. Reitz et Klein 1498, det. L. B. Smith (HBR); BRASIL: Rio de Janeiro, Petrópolis. O. C. Góes 86, det. Brade (RB); BRASIL: Rio de Janeiro, Petrópolis. Otavia (28.III.1941) (RB); A. Frazão, det. Brade (RB); BRASIL: Minas Gerais, São João del Rei. E. Pereira 3130, det. E. Pereira (RB); BRASIL: Espírito Santo, Reserva Florestal CVRD. D. A. Folli 16, det. A. L. Peixoto (CVRD).
C. silvestris Fresen. BRASIL: Santa Catarina, Itajaí. Klein 1005, det. L. B. Smith (HBR); BRASIL: Bahia, Agua Preta. G. Bondar (20.X.1937), det. F. C. Hoehne (SP); BRASIL: Paraná, Morreto. G. Hatschbach 33779, det. Hatschbach (SP).
C. trichotoma (Vell.) Arrab. ex Steud. BRASIL: Santa Catarina, Canoinhas. Reitz et Klein 12490, det. L. B. Smith (HBR); BRASIL: Santa Catarina, S. Miguel d'Oeste. A. Castellanos 24837, det. E. F. Guimarães (RB); BRASIL: Santa Catarina, Mondaí. A. Castellanos 24850, det. E. F. Guimarães (RB); BRASIL: Espírito Santo, Reserva Florestal CVRD. J.S. 045/78, det. A. L. Peixoto (CVRD); BRASIL: Espírito Santo, Reserva Florestal CVRD. J.S. 187/73, det. R. M. de Jesus (CVRD); BRASIL: Espírito Santo, Reserva Florestal CVRD. D. A. Folli 204/80, det. R. M. de Jesus (CVRD).
C. verbenacea DC. BRASIL: Santa Catarina, Araraquari. Pe.R.Reitz 112, det. Brade (RB); BRASIL: Rio de Janeiro, Quinta da Boa Vista. Freire et Vidal 193, det. Brade (R); BRASIL: Minas Gerais, Serra do Cipó. J. Vidal V-44, det. J. Augusto (R); BRASIL: Santa Catarina, Florianópolis. F. A. Silva F. et J. Cardoso 07, det. F. A. Silva F. (R); BRASIL: Santa Catarina, Florianópolis. J. G. Kuhlmann (18.IX.1950), det. E. Guimarães (RB).
Heliotropium amplexicaule Vahl. BRASIL/ARGENTINA: Corcovado. det. I. M. Johnston (SP); UNITED STATES: Queensland, Leichhardt Distr. S. L. Everist 21, det. R. W. Johnston (SP); UNITED STATES: North Carolina, Brunswick County. S. W. Leonard 2487, det. D. B. Russ (SP); BRASIL: Rio de Janeiro, Restinga do Leblon. A. Machado (20.III.1948), det. G. M. Barroso et E. Guimarães (RB).
H. elongatum Hoffm. ex R. et S. BRASIL: Rio Grande do Sul, Guaíba. B. C. Teixeira et A. R. Teixeira 49 (SP); BRASIL: Minas Gerais, Pouso Alegre. F. C. Hoehne (27.IV.1927), det. I. M. Johnston (SP).
H. indicum L. BRASIL: Santa Catarina, Doradina. R. Braga et R. Lange 69, det. L. B. Smith (RB); BRASIL: São Paulo, Cidade Jardim. W. Hoehne et M. Kuhlmann (11.IV.1935), det. comp. W. Hoehne (SPF); BRASIL: Maranhão. Viana O. de Carvalho (14.X.1919), det. F. C. Hoehne (SP); BRASIL: São Paulo, S. Manoel. H. Luederwaldt (XI.1913), det. I. M. Johnston (SP); BRASIL: Goiás, Caiaponia/Aragarças. D. R. Hunt et J. F. Ramos 6163, det. R. M. Harley (SP).
H. leiocarpum Morong. BRASIL: Santa Catarina, Rio Iracema. Smith et Klein 13116, det. Smith (R); BRASIL: Santa Catarina, Riqueza. Smith et Reitz 12593, det. Smith (R); BRASIL: Santa Catarina, Dionísio Cerqueira. Smith, Reitz et Pereira 9678, det. Smith (R).
H. procumbens Mill. BRASIL: São Paulo, Porto Tibiriçá. J. E. Rombouts (08.X.1938), det. comp. A. Gehrt (SP); BRASIL: Serra do Jatobá, Milagres/Jequié. R. M. Harley 22019, det. K. G. Shawe (SPF); BRASIL: Minas Gerais, Ouro Preto. Glaziou 14137, det. E. Guimarães (R); BRASIL: Minas Gerais, Lagoa Santa. Mello Barreto 2133, det. Field Museum (R); BRASIL: Minas Gerais, Viçosa. Irwin 2173, det. Smith (R); BOLIVIA: Amazonia boliviana, State of Pando. G. T. Prance 6119, det. Prance (R); BRASIL: Boca do Acre: rios Purus and Acre. G. T. Prance 2544, det. Prance (R).
H. salicoides Cham. BRASIL: Minas Gerais, Serra do Espinhaço. H. S. Irwin 28645, det. S. R. Hill (SP); BRASIL: Goiás, Parque Nacional da Chapada dos Veadeiros. J. R. Pirani 1745 (SPF); BRASIL: Minas Gerais, Várzea da Palma. A. P. Duarte 7415, det. G. Barroso et E. Guimarães (RB); BRASIL: Goiás, Palmital/Amoreira. Glaziou 21774, det. E. Guimarães (R); BRASIL: Paraná, Ponta Grossa. G. Hatschbach (21.XII.1952), det. I. M. Johnston (PKDC).
H. transalpinum Vell. var. *transalpinum*. BRASIL: Santa Catarina, S. Carlos. L. B. Smith et Pe.R.Reitz 12574, det. L. B. Smith (R); BRASIL: Santa Catarina, Águas de Chapecó. Smith et Klein 13101, det. Smith (R); ARGENTINA: Prov. Corrientes, Dep. Santo Tomé. A. Krapovickas 17038, det. R. Perez-Moreau (PKDC); PARAGUAI: Ponte Sertoni. C. Stellfeld 1242, det. I. M. Johnston (PKDC).
H. transalpinum var. *tiaridioides* (Cham.) I. M. Johnston. BRASIL: São Paulo,Ribeira. J. R. Pirani, I. Cordeiro et D. C. Zappi 969, det. D. C. Zappi (SPF); BRASIL: Pernambuco, Serra Talhada/Petrolina. E. P. Heringer 22, det. Andrade-Lima (R).
Moritzia ciliata (Cham.) DC. BRASIL: Rio Grande do Sul, Porto Alegre. B. Rambo 49 (SP).
M. dasyantha (Cham.) Fresen. BRASIL: Santa Catarina, Lajes. L. B. Smith et R. M. Klein 8110, det. L. B. Smith (R); BRASIL: Santa Catarina, Estação Experimental de Chapecó. E. Santos 3657 (R); BRASIL: Santa Catarina, Curitibanos. Smith et Klein 11095, det. Smith (R).
M. dusenii I. M. Johnston-BRASIL: Santa Catarina, Abelardo Luz. L. B. Smith et R. M. Klein 13306, det. L. B. Smith (R); BRASIL: Santa Catarina, Abelardo Luz. Smith et Reitz 12826, det. Smith (R); BRASIL: Paraná, Araucaria. L. Th. Dombrowski 3027, det. L. Th. Dombrowski (PKDC).
M. tetraquetra (Cham.) Brand. BRASIL: Santa Catarina, Ponte Alta do Norte. Reitz et Klein 13384, det. L. B. Smith (RB).
Patagonula americana L. BRASIL: Santa Catarina, Herval Velho. Smith et Reitz 12414, det. L. B. Smith (HBR); BRASIL: Santa Catarina, Nova Teutônia. F. Ploumann 163 (RB); BRASIL: São Paulo, Penápolis. J. R. Pirani 128, det. J. R. Pirani (SPF); BRASIL: Santa Catarina, S. Miguel d'Oeste. L. B. Smith et Pe. R. Reitz 12763, det. L. B. Smith (SP).
T. bicolor Sw. BRASIL: Santa Catarina, Joinville. E. Pereira 8805, det. G. M. Barroso (RB); BRASIL: Santa Catarina, Brusque. Reitz 5862, det. L. B. Smith (HBR); BRASIL: Paraná, Ipiranga/Volta Redonda. P. Dúsèn 3622 (R); ECUADOR: Prov. Napo-Pastaza, Borja. G. Harling 15/26, det. E. Asplund (R); BRASIL: São Paulo, Vila Cerqueira Cesar. W. Hoehne (24.IV.1933), det. comp. W. Hoehne (SPF); BRASIL: São Paulo, Estação Ecológica da Juréia. I. Cordeiro 819, det. M. P. Costa (SP); BRASIL: Minas Gerais, Paraisópolis. F. C. Hoehne (16.IV.1927), det. I. M. Johnston (SP).
T. breviflora DC. BRASIL: Rio de Janeiro, Alto da Boa Vista. Brade 10560, det. Brade (R); BRASIL: Bahia, Ilhéus. H. Velloso 1045, det. H. Velloso (R); BRASIL: Rio de Janeiro, Parque Nacional Itatiaia. D. Sucre 5184, det. E. F. Guimarães (RB); BRASIL: Mato Grosso, Corumbá. E. Pereira, W. Egler et G. Barroso 355 (RB).
T. gardneri A.DC. BRASIL: Santa Catarina, Reserva Florestal dos Piões. A. P. Duarte et J. Falcão 3136, det. E. Guimarães (RB); BRASIL: Rio de Janeiro, Teresópolis. Luiz Emygdio et H. P. Velloso (17.IX.1942), det. E. Guimarães (R).
T. membranacea (Gardn.) DC. BRASIL: Santa Catarina, Florianópolis. Klein, Souza et Bresolin 6444, det. L. B. Smith (HBR); BRASIL: Rio de Janeiro, Restinga da Marambaia. D. Sucre, E. Pereira et Cordelia 1262, det. E. Guimarães (RB); BRASIL: Rio de Janeiro, Restinga de Cabo Frio. D. Sucre 1921, det. Borgeth et Cordelia (RB); BRASIL: Bahia, Porto Seguro. A. P. Duarte 6033, det. E. Guimarães (RB).
T. paniculata Cham. BRASIL: Santa Catarina, Monte Castelo. Klein 3980, det. L. B. Smith (HBR); BRASIL: São Paulo, Banhado de Butantã. A. B. Joly (03.XII.1946), det. A. B. Joly (SPF); BRASIL: Santa Catarina, Nova Teutônia. F. Ploumann 222, det. Brade (RB).

T. rubicunda Salzm. BRASIL: Pernambuco, Olinda. B. Pickel 935, det. I. M. Johnston (SP); BRASIL: Rio Grande do Sul, Ilha dos Marinheiros. G. A. Malme 360 (R); BRASIL: Mato Grosso, Cuiabá. G. O. A. Malme 2538 (R).

Tournefortia villosa Salzm. BRASIL: Minas Gerais, Viçosa. H. S. Irwin 2030, det. L. B. Smith (R); BRASIL: Espírito Santo, prox. Vitória. Z. A. Trinta 1057 et E. Fromm 2133 (R); BRASIL: Paraná, Ilha do Mel. R. M. Britez 1015 (PKDC).

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