Pollen morphology of the subtribe Cuspariinae (Rutaceae)

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Morton, Cynthia M. and Jacquelyn A. Kallunki (New York Botanical Garden, Bronx, NY 10458-5126 U.S.A.). Pollen morphology of the subtribe Cuspariinae (Rutaceae). Brittonia 45: 286–314. 1993.—The neotropical subtribe Cuspariinae (Rutaceae) comprises as many as 26 genera and over 125 species. Pollen grains from 111 collections representing 71 species and 24 genera were examined by LM, SEM, and TEM. The pollen morphology of this subtribe is very diverse. Grains are mostly 3–6-aperturate and colporate, rarely porate (*Spiranthera*) or pantocolporate (*Almeidea*). Exine sculpturing is most commonly reticulate, sometimes perforate, foveolate-perforate, foveolate, foveolate-reticulate, reticulate, striate-reticulate, echinate, clavate, or baculate. The exine structure is columellate and tectate-perforate, columellate and semitectate, or intectate and is stratified into ektexine and endexine. The exine of *Leptothyrsa* is distinctive in that the ektexine of the mesocolpium is longitudinally deeply ridged. The pollen of *Hortia*, characterized by a psilate exine with rare perforations, a very thick foot-layer, and reduced columellae, is unlike that of any member of the Cuspariinae and offers no support for the transfer of this genus from the Toddalioideae. The pollen data correlate with macromorphological characters and are taxonomically useful.

Key words: Rutaceae, Cuspariinae, *Hortia*, *Rutaneblina*, pollen morphology.

Cuspariinae Engl. and Pilocarpinae Engl. are the only two subtribes in the tribe Cusparieae DC. of the subfamily Rutoideae of the Rutaceae. The subtribe Cuspariinae is composed of about 26 neotropical genera with about 125 described species. Most genera are monotypic or represented by fewer than 10 species. The largest are *Angostura* with more than 35 species and *Raveniopsis* with 19 species. Most are small trees and shrubs with dehiscent fruit (as all Rutoideae), derived from either an apocarpous or syncarpous gynoecium. The Cuspariinae differ from the rest of the subfamily by several tendencies: zygomorphic flowers, union of petals into a tubular corolla, union of the filaments with the corolla, reduction in number of fertile stamens from five to two by sterilization, basally appendaged anthers, loss of endosperm, and plicate cotyledons.

The most recent treatment of the subtribe, that of Engler (1931) in which he recognized 16 genera, is outdated. The second author's study of the Cuspariinae is resulting in modifications of Engler's system (Kallunki, 1990, 1992, unpubl.). For purposes of the present study, 26 genera are recognized (Table I), differing from Engler in the following cases. 1) *Angostura* includes *A. trifoliata* (the type of the genus), the apocarpous species of *Galipea* (e.g., *G. longiflora*), and some undescribed species. In addition to apocarpous ovaries, these share connate petals, anthers with free basal appendages, tuberculate seeds, and branched trichomes. 2) All other species described in *Angostura* are here called "Angostura-1." This "genus" is a collection of species without a distinct combination of characters. Although all species have alternate leaves, the genus is polymorphic for all other characters examined so far. Most species have free carpels, free petals, free stamens, two fertile stamens, no anther appendages, and curved embryos, but others have various combi-

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TABLE I

A COMPARISON OF THE GENERA OF CUSPARIINAE RECOGNIZED FOR THE PRESENT STUDY WITH THOSE RECOGNIZED BY ENGLER (1931)

Present study	Engler's circumscription
Achuaria Gereau[a,b]	
Adiscanthus Ducke	same
Almeidea A. St.-Hil.	same
Angostura Roem. & Schult. [including *Angostura trifoliata* (Willd.) T. S. Elias and apocarpous *Galipea*, e.g., *G. longiflora* K. Krause[c]]	as *Cusparia* Humb., composed of *A. trifoliata* and "Angostura-1"
"Angostura-1"[a] (including all *Angostura* except *A. trifoliata*)	included in *Cusparia*
Apocaulon R. S. Cowan[a]	
Decagonocarpus Engl.	same
Desmotes Kallunki[a]	
Ertela Adans.	as *Monnieria* L.
Erythrochiton Nees & Mart. (excluding *Toxosiphon* and *Desmotes*)	including *Toxosiphon*
Euxylophora Huber	same
Galipea Aubl. (including only syncarpous species of *Galipea* and excluding the apocarpous species, e.g., *G. longiflora*)	including both syncarpous and apocarpous species
Leptothyrsa Hook. f.	same
Lubaria Pittier	same
Naudinia Planch. & Linden[b]	same
Neoraputia Emmerich	included in *Raputia*
Nycticalanthus Ducke[a]	
Raputia Aubl. (including *Ravenia amazonica* Huber and *Lubaria szczerbanii* Steyerm.[a])[c]	including *Neoraputia, Raputiarana, Sigmatanthus*
Raputiarana Emmerich (including *Raputia heptaphylla* Pittier)[c]	included in *Raputia*
Rauia Nees & Mart.	same
Ravenia Vell. (excluding *Ravenia amazonica*)	± same, but including *R. ruellioides* Oliv. (now included in *Raveniopsis*) and *R. amazonica*
Raveniopsis Gleason[a]	
Sigmatanthus Emmerich	included in *Raputia*
Spiranthera A. St.-Hil.	same
Ticorea Aubl.	same
Toxosiphon Baill.	included in *Erythrochiton*

[a] These taxa were described after 1931 (or not yet in the case of "Angostura-1") and were not treated by Engler.

[b] Pollen of these genera was not included in this study.

[c] The nomenclatural transfers will be published elsewhere (Kallunki, unpubl.).

nations of connate carpels (at least axially), coherent or connate petals, connate filaments, connate anthers, three or five fertile stamens, anther appendages, and straight embryos. Whether or not the species in "Angostura-1" form a coherent genus is not yet resolved. 3) *Erythrochiton* is recognized in a restricted sense by the segregation of *Toxosiphon* and *Desmotes* (Kallunki, 1992). 4) *Galipea* includes the syncarpous species, which share connate anthers with a gland-dotted dorsum, a sterilized base (above the point of attachment of the filament), and connate appendages; connate carpels (and consequently a capsular fruit); smooth seeds; and simple, if any, trichomes. 5) *Raputia* is recognized with the exclusion of *Neoraputia, Raputiarana,* and *Sigmatanthus* (Emmerich, 1978) and of *Raputia heptaphylla* Pittier (Kallunki, 1990) and with the inclusion of *Ravenia amazonica* Huber and *Lubaria szczerbanii* Steyerm. *Raputia heptaphylla* differs from the other species assigned to the genus by, for example, its alternate (vs. opposite) leaves, free (vs. connate) anthers, tuberculate (vs. smooth) seeds, and

conduplicate and plicate (vs. merely conduplicate) cotyledons. It resembles *Raputiarana* in these characters and, therefore, is considered as a member of that genus. *Ravenia amazonica* differs from most species of *Ravenia* in its smooth (vs. tuberculate) seeds and leathery (vs. succulent) cotyledons. *Lubaria szczerbanii* differs from the other species of *Lubaria* in its five connate (vs. four connate and one free) petals and no connate filaments (vs. the two fertile filaments connate). Both share with *Raputia* five connate petals, no connate filaments, smooth seeds, and leathery cotyledons and, therefore, are considered to belong in *Raputia.*

Because pollen morphology proved to be useful in distinguishing *Toxosiphon* from *Erythrochiton* (Kallunki, 1992), pollen of other Cuspariinae was examined to assess whether the pollen characters are taxonomically useful and whether they support the reorganization of the subtribe outlined above and in Table I.

In this study, pollen was examined also of some possibly related genera: *Rutaneblina* Steyerm. & Luteyn, a genus of uncertain subtribal affinity, and *Hortia,* whose transfer from Engler's drupaceous-fruited subfamily Toddalioideae to the Cusparieae was suggested recently because of chemical similarities (Fernandes da Silva et al., 1988).

Materials and Methods

Pollen from 71 species (111 specimens), representing all but two of the 26 genera of the Cuspariinae were studied by light microscopy (LM) and scanning electron microscopy (SEM). Some species, chosen to represent the range of pollen types, were examined also with transmission electron microscopy (TEM). Pollen was obtained from the dried herbarium specimens and the few pickled specimens listed in Appendix I.

For light microscopy, pollen was mounted in glycerine jelly on glass slides sealed with paraffin. Slides were studied with a Nikon Optiphot microscope, and measurements of pollen grains were made with a computerized morphometric unit and Neurolucida software. The size classes used in the descriptions are based on the measurement of the longest axis of the pollen grain, exclusive of any spines (Erdtman, 1969). Shape was determined by the ratio of the mean length of the polar axis and the mean length of the equatorial axis (Erdtman, 1969). Photomicrographs were taken with a Nikon AFM automatic photomicrograph attachment. Glass slides of all specimens examined are deposited at the New York Botanical Garden.

Pollen samples for SEM study were mounted on stubs to which double-adhesive tape had been attached and were coated with gold-palladium in a sputter-coater for approximately 90 seconds. Observations were made on a JSM-T300 scanning electron microscope. All SEM micrographs were taken using Polaroid Type 665 P/N film with 0 tilt and an accelerating voltage of 15 KV.

For TEM, acetolyzed pollen was washed in distilled water, suspended in agar, fixed with osmium tetroxide for 2 hours, stained with uranyl acetate for one hour, dehydrated in a graded ethyl alcohol series, and embedded in LR White at 60°C. Pollen was sectioned using an RMC MT6000 ultramicrotome with a DuPont diamond knife, and sections were stained with lead citrate and examined and photographed with a JEOL 1200EX TEM. Measurements of the exine thickness were obtained from only a single individual for all sampled taxa except from two each for *Adiscanthus fusciflorus* and *Spiranthera odoratissima.*

The terminology used here for morphological characters follows, with few exceptions, Walker and Doyle (1975). "Pantocolporate" and "mesocolpium" are used in the sense of Erdtman (1971) and "endoapertures" and "ectoapertures" in the sense of van der Ham (1990). The ratio of colpus length to polar axis length (CL/PL) is introduced in this paper to describe the length of the colpus. These ratios were arbitrarily divided into classes of: short (0.01–0.35), medium (0.36–0.65), long (0.66–0.9), and very long (0.91–1). When used to describe the frequency of infratectal rod-like structures, "dense" means that the surface of the

foot-layer is obscured by the closely packed structures, "less dense" means that the surface can be seen between the structures, and "occasional" means that only a few structures are present.

Results

The observations of the pollen samples in Table II and in Figures 1 through 12 were used as the basis of the following descriptions. To facilitate discussion and comparison, the pollen was divided into 12 types based on sculpture pattern and aperture type (Table III).

Pollen of the subtribe Cusparinae

Pollen grains are solitary, radially symmetrical, isopolar or rarely apolar (*Almeidea*), usually oblate-spheroidal, sometimes euprolate, subprolate, prolate-spheroidal, or spherical, rarely suboblate (*Nycticalanthus*) or perprolate (*Leptothyrsa*), usually large, sometimes medium, or infrequently very large (*Erythrochiton brasiliensis, E. gymnanthus,* and *Ticorea longiflora*). Mean grain size ranges from 32.9 μm (P) × 18.8 μm (E), in "Angostura-1" sp. 4, to 107.6 μm (P) × 114.1 μm (E), in *Ticorea longiflora.* Grains are 3–6-colporate or rarely 3-porate (*Spiranthera*) or pantocolporate (*Almeidea*). Ectoapertures are meridionally aligned or rarely evenly distributed (*Almeidea*). Colpi are short, medium, or long. Endoapertures are lalongate, circular, or inconspicuous. Exine sculpturing is most commonly reticulate, sometimes perforate, foveolate-perforate, foveolate, foveolate-reticulate, reticulate, striate-reticulate, echinate, clavate, or baculate. The exine structure is columellate and tectate-perforate, columellate and semitectate, or intectate, stratified into ektexine and endexine, with the ektexine composed either of a distinct tectum, columellae, and a foot-layer or of columellae and a foot-layer. Nonapertural exine thickness ranges from 1.29 μm (in "Angostura-1" *ucayalina*) to 9.4 μm (in *Leptothyrsa sprucei*). The endexine is thin to absent in the mesocolpium and thicker, or rarely equal (*Angostura*), along the margins of and/or under the colpi.

Pollen of the genera of the Cusparinae

Adiscanthus Ducke (Fig. 1A–D)

Pollen grains 3-colporate, euprolate, large. Ectoapertures long (ave. CL/PL 0.8), narrow, with sparse small granules covering the surface. Endoapertures lalongate. Exine sculpturing reticulate, the lumina irregular in outline, small to medium, the reticulum forming a solid tectum along the colpi margins. Exine structure columellate, semitectate, with a nonapertural exine ca. 2.8 μm thick, stratified into a distinguishable ektexine and endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well developed, ca. 37% of the total exine thickness, the columellae reduced, ca. 6.5% of the total exine thickness, the foot-layer very prominent, ca. 56.5% of the total exine thickness. Endexine thin in the mesocolpium and slightly thicker under and along the margins of the colpi.

Almeidea A. St.-Hil. (Fig. 1E)

Pollen grains pantocolporate, medium. Ectoapertures ca. 10 μm long, narrow to wide, with sparse polymorphic granules covering the surface. Endoapertures circular. Exine sculpturing foveolate-perforate, the lumina circular to irregular in outline and small. Exine structure columellate, tectate-perforate.

Angostura Roem. & Schult. (Fig. 2A–D)

Pollen grains 5- or 6-colporate, oblate-spheroidal, large. Ectoapertures short (ave. CL/PL 0.2), wide, with dense polymorphic granules covering the surface. Endoapertures inconspicuous. Exine sculpturing baculate, with small rod-like structures between bacula, the sculpturing elements more abundant surrounding the apertures. Exine structure intectate, with a nonapertural exine ca. 3.6 μm thick, stratified into a distinguishable ektexine and a reduced or absent endexine. Ektexine composed of columellae and foot-layer, the columellae distinct, ca. 67% of the total exine thickness, the foot-layer prominent, ca. 33% of the total exine thickness. Endexine thin to absent in the

TABLE II

MORPHOLOGICAL CHARACTERS OBSERVED BY SEM AND LM OF GENERA OF THE CUSPARIINAE AND ALSO OF *Rutaneblina* AND *Hortia*. THE TAXA ARE LISTED IN THE GENERA IN WHICH THEY ARE RECOGNIZED IN THIS STUDY (CF. TABLE I). SUCH LISTINGS ARE NOT NOMENCLATURAL TRANSFERS. FOR SPECIES OF WHICH MORE THAN ONE SAMPLE WAS STUDIED, THE SAMPLE NUMBER CORRESPONDING TO THE VOUCHER SPECIMEN IN APPENDIX I IS GIVEN IN PARENTHESES FOLLOWING THE SPECIFIC EPITHET.

	n[a]	Polar axis (μm)[b]	Equatorial[b] axis (μm)	P/E[c] (x̄)	Aperture	Sculpture pattern[d]
ADISCANTHUS (1 sp.)						
fusciflorus (2)	3	53.0–(54.2)–56.7	24.3–(29.4)–33.0	1.84	3-colporate	R
fusciflorus (3)	25	45.3–(55.4)–59.7	29.5–(31.4)–34.5	1.76	3-colporate	R
ALMEIDEA (5 spp.)						
limae	25	42.6–(45.3)–47.2	38.0–(41.5)–45.0		pantocolporate	F-P
rubra (1)	25	42.3–(47.0)–52.0	37.9–(42.8)–47.1		pantocolporate	F-P
rubra (2)	20	45.0–(48.5)–52.0	39.7–(43.9)–50.0		pantocolporate	F-P
ANGOSTURA (ca. 6 spp.)						
Galipea longiflora	25	77.1–(83.6)–94.5	79.2–(87.5)–100.1	0.96	5–6-short-colporate	B
sp. nov.	25	81.0–(91.2)–97.1	75.2–(94.4)–105.0	0.97	6-short-colporate	B
trifoliata (1)	24	66.1–(71.3)–78.5	70.1–(75.5)–83.1	0.94	5–6-short-colporate	B
"ANGOSTURA-1" (ca. 35 spp.)						
Angostura larensis					3-colporate	P
A. macrophylla (2)	25	34.9–(37.3)–39.6	33.8–(37.5)–40.0	0.99	4-colporate	P
A. pentagyna (1)	11	29.6–(36.1)–42.3	31.3–(39.2)–43.4	0.92	5–6-colporate	F
A. ramiflora (2)	14	56.9–(60.9)–64.8	58.4–(63.7)–68.3	0.96	6-colporate	R
A. silvestris (2)	25	38.9–(43.8)–47.3	41.6–(45.7)–51.7	0.96	4–5-colporate	F
sp. 1	25	34.2–(36.6)–39.4	25.0–(27.0)–29.1	1.36	4-colporate	F
sp. 2					4-colporate	R
sp. 3	25	37.5–(40.3)–43.0	27.6–(30.9)–34.9	1.30	3-colporate	R
sp. 4	25	30.8–(32.9)–34.4	17.6–(18.8)–20.9	1.75	4-colporate	F
A. cf. *transitionalis*	14	58.2–(63.8)–68.8	38.0–(40.9)–44.5	1.56	3-colporate	P
A. ucayalina (2)	25	42.4–(44.4)–47.7	28.4–(31.0)–33.1	1.43	3-colporate	F-R
APOCAULON (1 sp.)						
carnosum	17	49.7–(53.2)–55.6	39.7–(44.9)–52.0	1.18	4-colporate	S-R
DECAGONOCARPUS (2 spp.)						
cornutus					3-colporate	R
oppositifolius (1)	25	52.8–(70.1)–78.4	44.4–(53.0)–58.5	1.32	3-colporate	R
oppositifolius (2)	12	81.9–(85.0)–88.0	59.8–(66.7)–72.2	1.27	3-colporate	R
DESMOTES (1 sp.)						
incomparabilis						E

TABLE II
CONTINUED

	n[a]	Polar axis (μm)[b]	Equatorial[b] axis (μm)	P/E[c] (ε)	Aperture	Sculpture pattern[d]
ERTELA (2 spp.)						
trifolia					3-colporate	R
ERYTHROCHITON (7 spp.)						
brasiliensis (2)	25	98.8–(103.3)–114.5	97.6–(106.0)–117.1	0.97	3-short-colporate	B
brasiliensis (5)	6	73.4–(75.6)–80.3	76.2–(80.8)–88.1	0.94	3-short-colporate	B
fallax (1)	25	72.2–(76.5)–79.9	71.5–(80.4)–83.9	0.95	3-short-colporate	E
fallax (2)	25	71.4–(77.9)–81.6	71.4–(79.6)–85.0	0.98	3-short-colporate	E
fallax (3)	25	66.6–(74.4)–86.4	71.1–(76.2)–85.1	0.98	3-short-colporate	E
gymnanthus (2)	25	82.5–(102.3)–112.5	82.5–(104.5)–117.5	0.98	3–4-short-colporate	C
EUXYLOPHORA (1 sp.)						
paraensis (2)	25	46.6–(50.2)–53.3	29.9–(33.1)–36.4	1.52	3-colporate	P
GALIPEA (ca. 12 spp.)						
davisii	25	70.2–(78.8)–85.4	66.0–(73.4)–80.3	1.07	3-short-colporate	R
jasminiflora (1)	10	53.3–(61.2)–68.2	67.2–(69.5)–72.8	0.88	3-4-short-colporate	R
jasminiflora (2)	25	58.5–(63.7)–67.6	66.3–(71.5)–75.4	0.89	3–4-short-colporate	R
jasminiflora (4)	11	60.7–(65.2)–71.4	67.7–(71.9)–75.1	0.91	3–4-short-colporate	R
sp. nov. 1 (1)	13	69.8–(73.4)–76.9	66.0–(69.7)–74.0	1.05	3-short-colporate	R
sp. nov. 1 (2)	25	63.9–(67.1)–70.9	69.7–(73.0)–76.4	0.92	3–4-short-colporate	R
LEPTOTHYRSA (1 sp.)						
sprucei (1)	25	72.7–(77.5)–83.5	30.6–(33.9)–37.2	2.29	3-colporate	S-R
sprucei (2)	25	72.8–(79.7)–83.6	29.4–(34.5)–39.9	2.31	3-colporate	S-R
LUBARIA (1 sp.)						
aroensis (2)					5–6-colporate	R
NEORAPUTIA (5 spp.)						
alba	25	72.3–(81.0)–88.2	80.9–(86.0)–93.8	0.94	3-colporate	R
paraensis	5	68.1–(68.9)–70.8	72.6–(76.6)–80.7	0.90	3-colporate	R
trifoliata	25	54.3–(59.5)–65.8	53.7–(59.7)–62.5	1.00	3-colporate	R
NYCTICALANTHUS (1 sp.)						
speciosus	4	66.6–(73.0)–76.8	84.2–(88.6)–90.8	0.82	4-short-colporate	B
RAPUTIA (ca. 9 spp.)						
maroana						R
sp. nov. 1					5–6-colporate	R

TABLE II
CONTINUED

	n[a]	Polar axis (μm)[b]	Equatorial[b] axis (μm)	P/E[c] (ℰ)	Aperture	Sculpture pattern[d]
sp. nov. 2	22	68.6–(72.7)–77.5	67.2–(72.4)–78.4	1.00	5–6-colporate	R
Lubaria szczerbanii	17	62.0–(65.8)–70.4	62.1–(64.9)–68.1	1.01	5-colporate	R
ulei					5-colporate	R
RAPUTIARANA (2 spp.)						
subsigmoidea (1)	25	85.5–(92.5)–97.8	82.7–(87.7)–93.7	1.05	3-colporate	R
subsigmoidea (2)	25	82.7–(88.7)–94.7	83.0–(86.7)–91.7	1.02	3-colporate	R
Raputia heptaphylla					3-colporate	R
RAUIA (ca. 10 spp.)						
resinosa (1)	25	46.8–(54.6)–58.5	31.2–(33.8)–36.4	1.62	3-colporate	P
sp. nov. 1					3-colporate	P
spicata	22	64.1–(68.4)–73.8	43.0–(48.1)–51.6	1.42	3-colporate	P
subtruncata					3-colporate	P
RAVENIA (11 spp.)						
biramosa	25	85.9–(95.6)–105.4	74.3–(88.2)–97.6	1.08	5–6-colporate	R
leonis					6-colporate	R
rosea	8	67.7–(70.1)–74.7	72.4–(75.5)–80.0	0.93	5-colporate	R
urbanii	25	71.5–(74.6)–79.1	76.7–(79.7)–83.7	0.94	6-colporate	R
RAVENIOPSIS (19 spp.)						
breweri					6-colporate	R
fraterna (2)	25	27.2–(31.6)–37.3	19.1–(24.4)–28.0	1.30	3-colporate	R
linearis					3-colporate	R
peduncularis (2)	25	61.9–(66.8)–70.7	55.5–(59.3)–62.4	1.13	5–6-colporate	R
ruellioides (3)	25	74.9–(87.1)–94.6	56.1–(60.8)–64.8	1.43	3-colporate	R
sericea					5-colporate	R
stelligera					5-colporate	R
steyermarkii					5-colporate	R
SIGMATANTHUS (1 sp.)						
trifoliatus (1)	5	73.6–(79.4)–82.2	81.0–(83.4)–85.7	0.95	5–6-short-colporate	R
SPIRANTHERA (3 spp.)						
odoratissima (2)	25	54.0–(61.5)–65.6	59.4–(65.6)–70.7	0.94	3-porate	E
parviflora					3-porate	E

TABLE II
CONTINUED

	n[a]	Polar axis (μm)[b]	Equatorial[b] axis (μm)	P/E[c] (x̄)	Aperture	Sculpture pattern[d]
TICOREA (3 spp.)						
foetida	25	85.0–(89.5)–94.9	89.8–(95.4)–102.3	0.94	6-short-colporate	R
longiflora	21	97.0–(107.6)–120.4	105.6–(114.1)–124.4	0.94	6-short-colporate	R
cf. *longiflora*					6-short-colporate	R
TOXOSIPHON (4 spp.)						
carinatus					3-colporate	R
lindenii	25	79.3–(83.7)–89.7	80.9–(88.3)–94.4	0.95	3-colporate	R
trifoliatus (1)	25	73.7–(83.5)–88.7	77.3–(89.0)–97.3	0.94	3-colporate	R
trifoliatus (2)	25	53.9–(68.6)–77.4	59.2–(70.3)–76.3	0.98	3-colporate	R
HORTIA (ca. 9 spp.)						
arborea	16	31.4–(34.4)–37.7	24.1–(26.6)–28.6	1.29	3-colporate	Ps-P
brasiliana (1)	25	29.3–(32.8)–34.8	23.3–(26.3)–28.4	1.25	3-colporate	Ps-P
brasiliana (2)	6	30.0–(34.1)–35.1	25.2–(26.9)–28.4	1.27	3-colporate	Ps-P
excelsa	25	36.7–(40.1)–42.8	23.9–(28.6)–31.7	1.40	3-colporate	Ps-P
RUTANEBLINA (1 sp.)						
pusilla (2)	11	25.8–(28.1)–30.0	20.1–(21.6)–23.9	1.30	3-colporate	R

[a] The number of grains upon which the measurements, if any, of the axes were made.
[b] These measurements represent the range and, in parentheses, the mean.
[c] P/E = ratio of the length of the polar axis to that of the equatorial axis. Because the pantocolporate grains of *Almeidea,* by definition, have no polar axis, the measurements in the "polar axis" column refer to another equatorial axis.
[d] B = baculate, C = clavate, E = echinate, F = foveolate, P = perforate, Ps = psilate, R = recticulate, S = striate (as used by Walker and Doyle, 1975).

TABLE III
POLLEN TYPES OF THE CUSPARIINAE[a]

Pollen type[b]	Taxon
1. Perforate, 3- or 4-colporate	"Angostura-1" *larensis*, "A.-1" *macrophylla*, "A.-1" cf. *transitionalis* *Euxylophora* *Rauia*
2. Foveolate-perforate, pantocolporate	*Almeidea*
3. Foveolate, 4–6-colporate	"Angostura-1" sp. 1, "A.-1" *pentagyna*, "A.-1" *silvestris*, "A.-1" sp. 4
4. Foveolate-reticulate, 3-colporate	"Angostura-1" *ucayalina*
5. Reticulate, 3- or 4-colporate	*Adiscanthus* "Angostura-1" sp. 2, "A.-1" sp. 3 *Decagonocarpus* *Ertela* *Galipea* *Neoraputia* *Raputiarana* *Raveniopsis fraterna*, *R. linearis*, *R. ruellioides* *Toxosiphon*
6. Reticulate, 5- or 6-colporate	"Angostura-1" *ramiflora* *Lubaria* *Raputia* *Ravenia* *Raveniopsis breweri*, *R. peduncularis*, *R. sericea*, *R. stelligera*, *R. steyermarkii* *Sigmatanthus* *Ticorea*
7. Striate-reticulate, 3-colporate	*Leptothyrsa*
8. Striate-reticulate, 4-colporate	*Apocaulon*
9. Echinate, 3-porate	*Spiranthera*
10. Baculate, echinate, or clavate, 3(4)-colporate	*Erythrochiton*
11. Baculate, 4-colporate	*Nycticalanthus*
12. Baculate, 5- or 6-colporate	*Angostura*

[a] Not examined: *Achuaria*, *Naudinia*.
[b] Of uncertain type: *Desmotes* (echinate, but apertures unknown).

mesocolpium and thin under and along the margins of the colpi.

"Angostura-1" (Figs. 2E–G, 3)

Pollen grains 3–6-colporate, euprolate, subprolate, or oblate-spheroidal, medium or large. Ectoapertures of some grains medium (ave. CL/PL 0.38), of others long (ave. CL/PL 0.83), narrow to wide, with sparse or dense polymorphic granules covering the surface. Endoapertures lalongate. Exine sculpturing perforate, foveolate, reticulate, or rarely foveolate-reticulate (*A. ucayalina*), the lumina circular to irregular in outline, small to medium, either smooth or with occasional infratectal rod-like structures. Exine structure columellate, tectate-perforate or semitectate, with a nonapertural exine ca. 1.29 μm thick, stratified into a distinguishable ektexine and a reduced or absent endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well developed, ca. 54% of the total exine thickness, the columellae reduced or granular, ca. 2% of the total exine thickness, the foot-

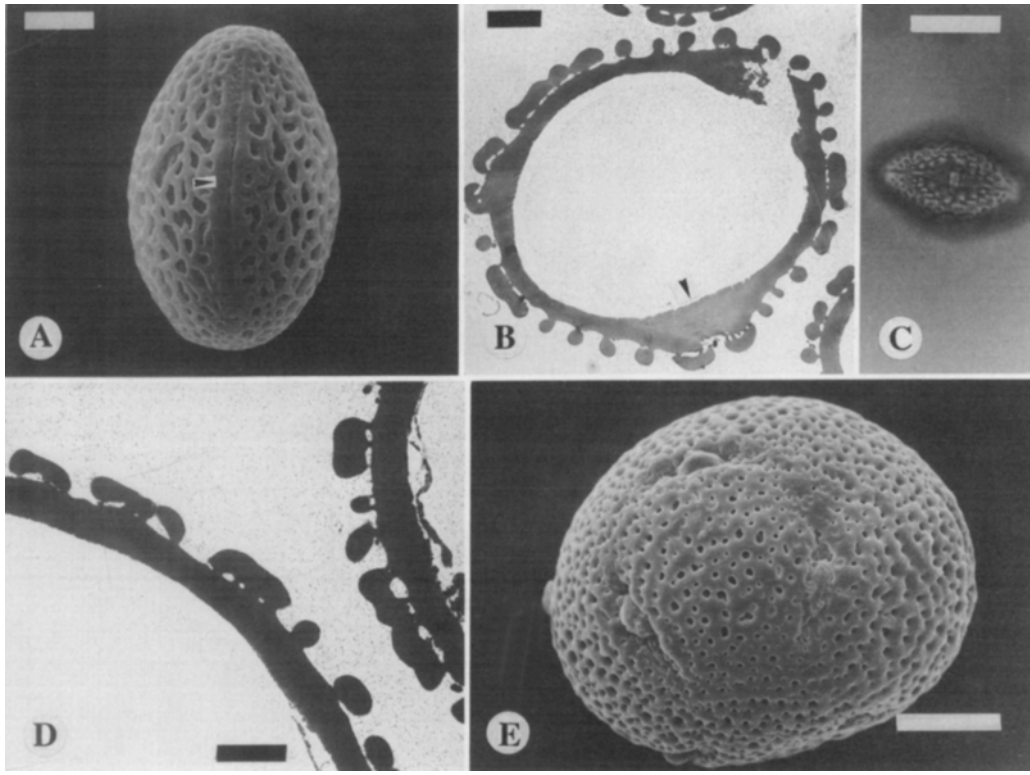

FIG. 1. Pollen of Cuspariinae. **A–D.** *Adiscanthus fusciflorus* (A, *Daly et al. 5722*; B–D, *Ducke 234*). **A.** Equatorial view showing long, narrow ectoaperture and reticulate sculpturing with the sculpturing forming a solid tectum along the colpus margin (arrow). **B.** Radial section of whole grain showing thicker endexine under and along the aperture (arrow). **C.** Equatorial view showing lalongate endoaperture. **D.** Radial section through mesocolpium showing reduced columellae and prominent foot-layer. **E.** *Almeidea rubra* (*Farias 118*). Pollen grains with foveolate-perforate sculpturing and pantocolporate apertures. (Scale bars: A, E = 10 μm; B, D = 4 μm; C = 30 μm.)

layer ca. 44% of the total exine thickness. Endexine thin to absent in the mesocolpium and thicker under and along the margins of the colpi.

Apocaulon R. S. Cowan (Fig. 4A–D)

Pollen grains 4-colporate, subprolate, large. Ectoapertures long (ave. CL/PL 0.85), narrow, with sparse small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing striate-reticulate, the lumina irregular in outline, small to medium, with occasional infratectal rod-like structures. Exine structure columellate, semitectate, with a nonapertural exine ca. 2.0 μm thick, stratified into a distinguishable ektexine and endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well developed, ca. 30% of the total exine thickness, the columellae distinct, ca. 36% of the total exine thickness, the foot-layer ca. 34% of the total exine thickness. Endexine thin in the mesocolpium and thicker under and along the margins of the colpi.

Decagonocarpus Engl. (Fig. 4E, F)

Pollen grains 3-colporate, subprolate, large. Ectoapertures very long (ave. CL/PL 0.91), narrow, with either sparse or no small granules covering the surface. Endoapertures short-lalongate. Exine sculpturing reticulate, the lumina irregular in outline, medium, with occasional infratectal rod-like structures. Exine structure columellate, semitectate.

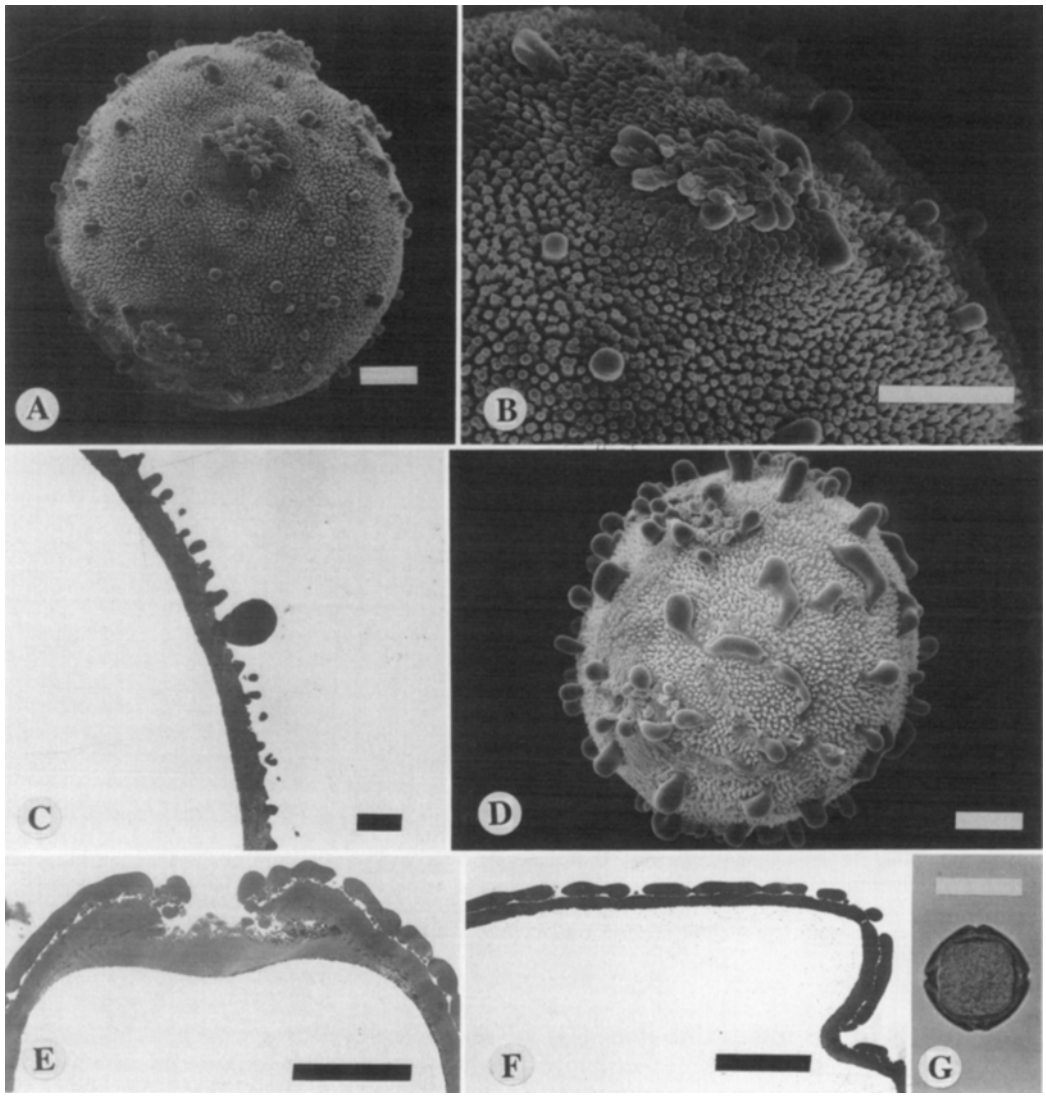

FIG. 2. Pollen of Cuspariinae. **A-C.** *Angostura trifoliata* (*Stergios et al. 5909*). **A.** Oblique equatorial view showing short-colporate apertures. **B.** Surface view showing baculate sculpturing with rod-like structures. **C.** Radial section through mesocolpium showing intectate exine. Note sizes of bacula and rod-like structures. **D.** *Galipea longiflora* (= *Angostura*) (*Daly 6382*). Oblique equatorial view showing baculate sculpturing with rod-like structures and short-colporate apertures. **E, F.** *Angostura ucayalina* (= "Angostura-1") (*Schunke 5635*). **E.** Radial section showing thickened endexine under and along the margin of the aperture. **F.** Radial section showing reduced and granular columellae. **G.** *Angostura macrophylla* (= "Angostura-1") (*Thomas et al. 6817*). Polar view showing 4 apertures. (Scale bars: A, B, D = 10 μm; C, E, F = 4 μm; G = 30 μm.)

Desmotes Kallunki

(One collapsed sample was observed.) Pollen solitary. Exine sculpturing echinate, with rod-like structures between the spines. Exine structure intectate.

Ertela Adans. (Fig. 4G)

Pollen grains 3-colporate, medium. Ectoapertures short, narrow, with sparse small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing re-

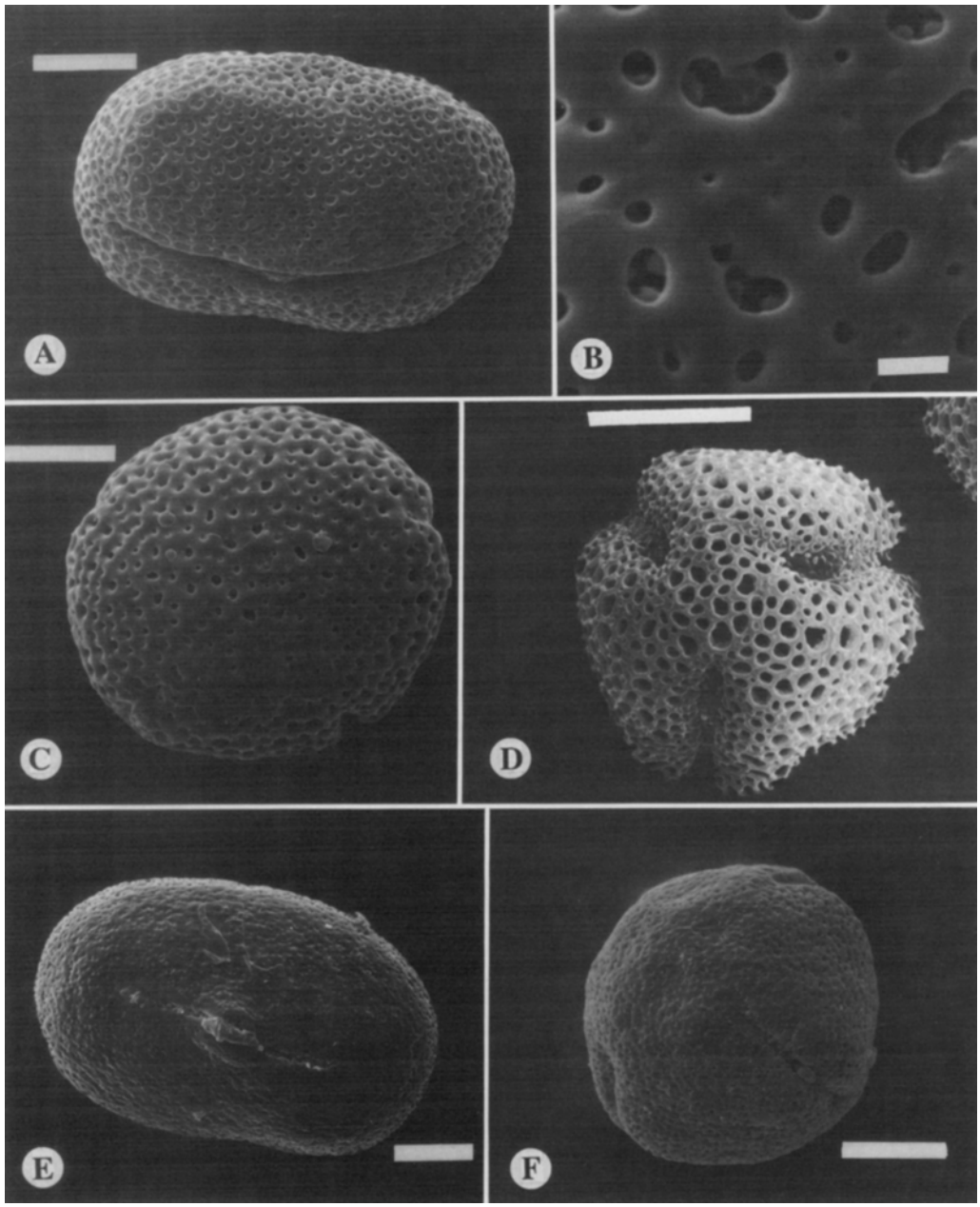

FIG. 3. Pollen of Cuspariinae. **A, B.** *Angostura ucayalina* (= "Angostura-1") (*Schunke 5635*). **A.** Oblique equatorial view showing foveolate-reticulate sculpturing. **B.** Surface view showing irregularly shaped lumina. **C.** *Angostura pentagyna* (= "Angostura-1") (*Sousa 453*). Polar view showing foveolate sculpturing. **D.** "Angostura-1" sp. 3 (*Mattos Silva et al. 1822*). Polar view showing reticulate sculpturing and 3 apertures. **E.** *Angostura* cf. *transitionalis* (= "Angostura-1") (*Pinard 860*). Equatorial view showing perforate sculpturing. **F.** *Angostura macrophylla* (= "Angostura-1") (*Thomas 6817*). Oblique polar view showing perforate sculpturing and 3 of the 4 apertures. (Scale bars: A, B, D, F = 10 μm; C = 15 μm; E = 11 μm.)

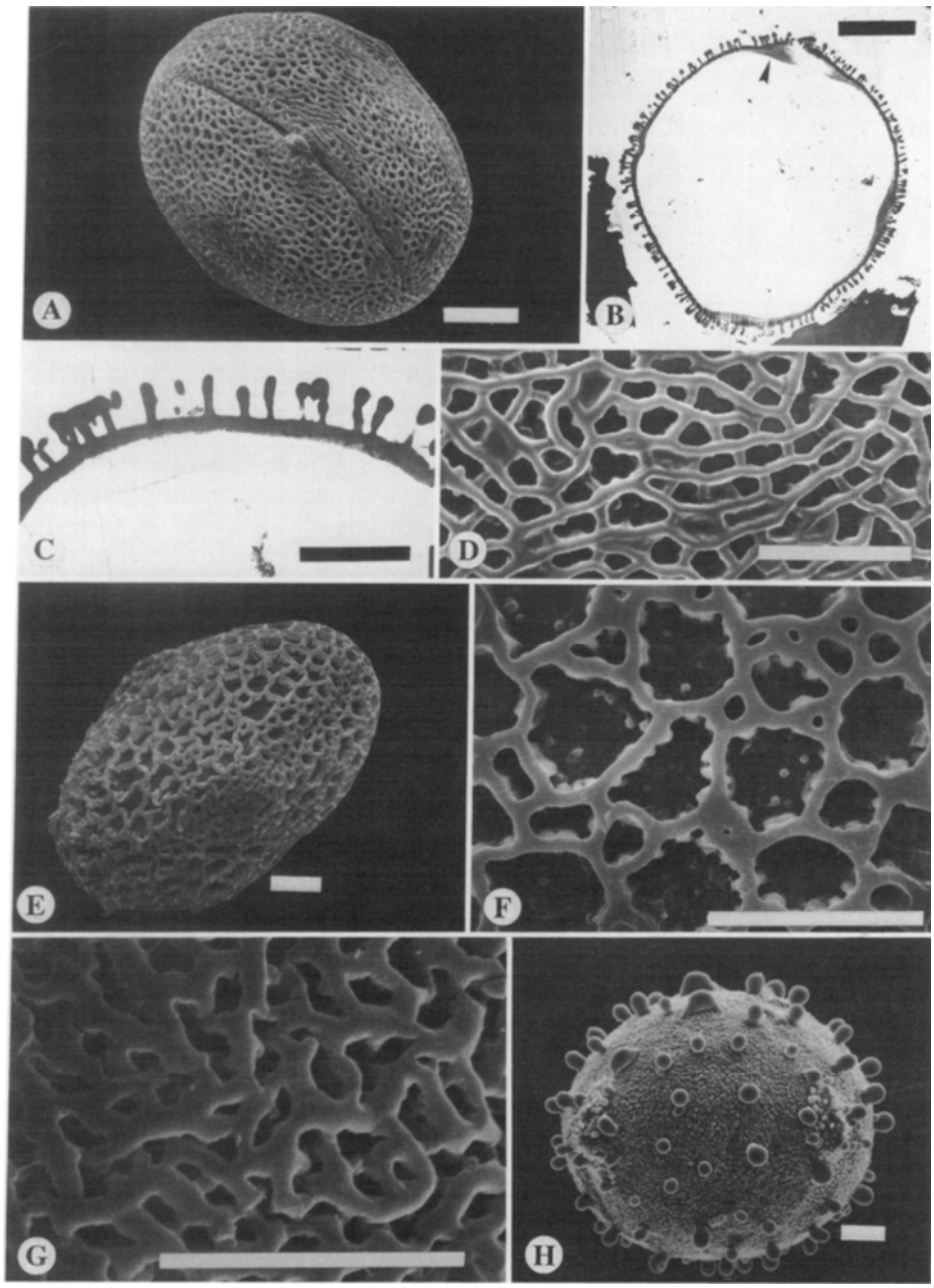

FIG. 4. Pollen of Cuspariinae. **A–D.** *Apocaulon carnosum* (*Maguire & Maguire 29188*). **A.** Equatorial view showing striate-reticulate sculpturing and long, narrow ectoaperture. **B.** Radial section of whole pollen grain. Note increased thickness of endexine under and along the aperture (arrow). **C.** Radial section through mesocolpium showing thin endexine. **D.** Surface view showing lumina with occasional infratectal rod-like structures. **E, F.** *Decagnocarpus oppositifolius* (E, *Maguire et al. 37493*; F, *Maguire et al. 42618*). **E.** Equatorial view showing reticulate sculpturing and ectoaperture. **F.** Surface view showing lumina with occasional infratectal rod-like structures. **G.** *Ertela trifolia* (*H. T. Beck et al. 321*). Surface view showing reticulate sculpturing. **H.** *Erythrochiton gymnanthus* (*Kallunki 309*). Equatorial view showing short-colporate apertures and clavate sculpturing. (Scale bars: A, B, E, F = 10 μm; C = 4 μm; D, G = 20 μm; H = 15 μm.)

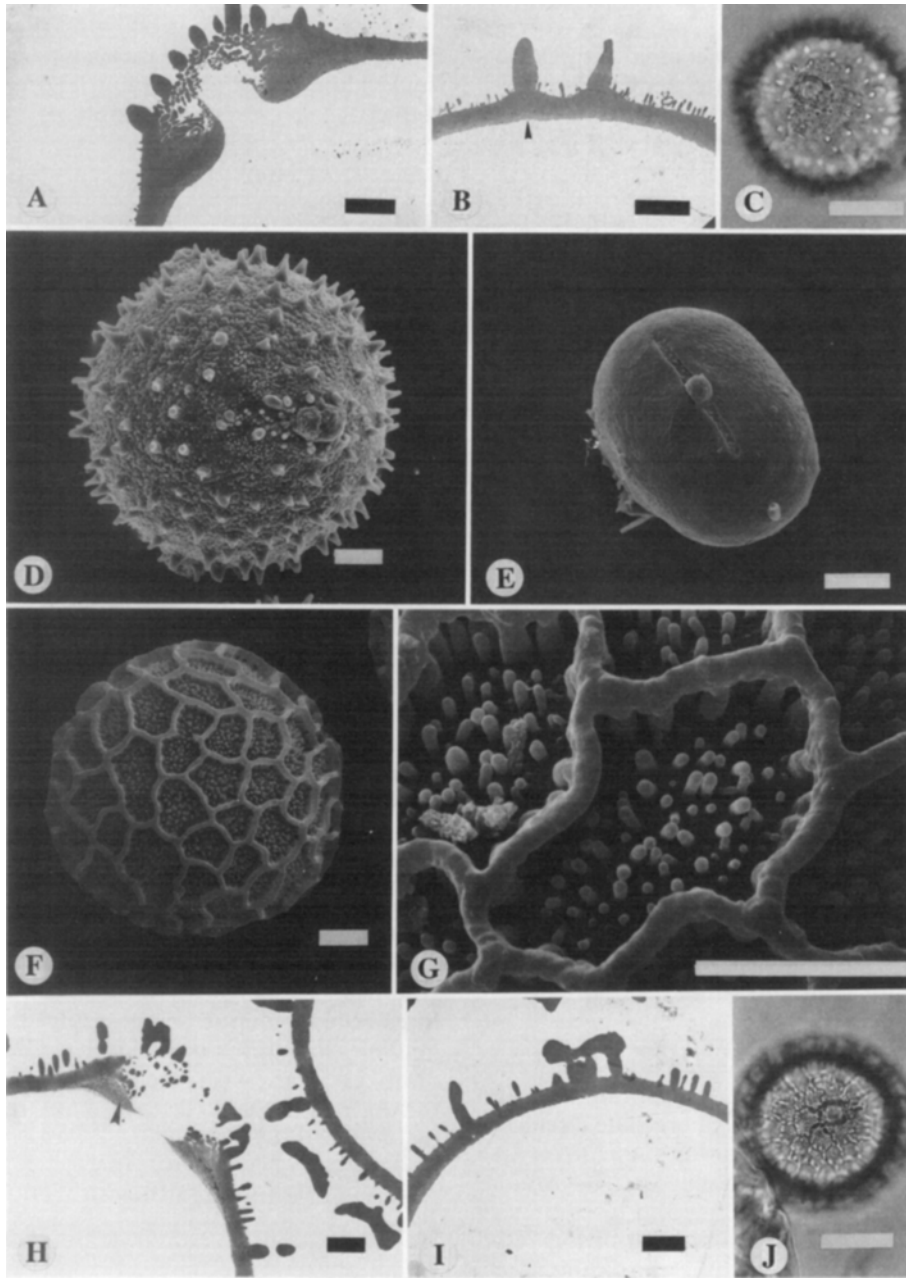

FIG. 5. Pollen of Cuspariinae. **A–D.** *Erythrochiton fallax* (A, B, *Idrobo & Schultes* 830; C, D, *Daly et al. 6445*). **A.** Radial section showing abundant spines near the aperture. **B.** Radial section through mesocolpium showing spines and reduced rod-like structures. Note thin endexine in the mesocolpium (arrow). **C.** Equatorial view. **D.** Oblique equatorial view showing short-colporate aperture and echinate sculpturing. **E.** *Euxylophora paraensis* (*Rosa & Santos 2227*). Equatorial view showing perforate sculpturing. **F.** *Galipea* sp. nov. 1 (*Daly et al. 1891*). Polar view showing reticulate sculpturing. **G–I.** *Galipea jasminiflora* (*Anderson 12331*). **G.** Surface view showing large lumina with rod-like structures. **H.** Radial section showing thickened endexine near the aperture (arrow). **I.** Radial section through mesocolpium showing semitectate exine with rod-like structures. **J.** *Galipea davisii* (*Ducke RB-35598*). Equatorial view. (Scale bars: A, B, H, I = 4 μm; C, J = 30 μm; D, F, G = 10 μm; E = 13 μm.)

ticulate, the lumina irregular in outline, small to medium, either smooth or with occasional infratectal rod-like structures. Exine structure columellate, semitectate.

Erythrochiton Nees & Mart. (Figs. 4H, 5A–D)

Pollen grains 3(4)-colporate, oblate-spheroidal, large or very large. Ectoapertures of some grains short (ave. CL/PL 0.35), of others medium (ave. CL/PL 0.45), wide, with dense polymorphic granules covering the surface. Endoapertures circular or inconspicuous. Exine sculpturing baculate, echinate, or clavate, with small rod-like structures between projections, the sculpturing elements more abundant around the apertures. Exine structure intectate, with a nonapertural exine ca. 6 μm thick, stratified into a distinguishable ektexine and endexine. Ektexine composed of columellae and foot-layer, the columellae distinct, ca. 64.5% of the total exine thickness, the foot-layer ca. 35.5% of the total exine thickness. Endexine thin in the mesocolpium and thicker under and along the margins of the colpi.

Euxylophora Huber (Fig. 5E)

Pollen grains 3-colporate, euprolate, large. Ectoapertures of medium length (ave. CL/PL 0.55), narrow, with sparse granules covering the surface. Endoapertures lalongate. Exine sculpturing perforate, the lumina circular in outline and small.

Galipea Aubl. (Fig. 5F–J)

Pollen grains 3- or 4-colporate, prolate-spheroidal or oblate-spheroidal, large. Ectoapertures inconspicuous, short (ave. CL/PL 0.28), narrow, with sparse small granules covering the surface. Endoapertures circular or inconspicuous. Exine sculpturing reticulate, the lumina irregular in outline, large, with less dense infratectal rod-like structures. Exine structure semi-tectate, with a nonapertural exine ca. 5.5 μm thick, stratified into a distinguishable ektexine and endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well developed, ca. 36% of the total exine thickness, the columellae distinct, ca. 32% of the total exine thickness, the foot-layer prominent, ca. 32% of the total exine thickness. Endexine thin in the mesocolpium and thicker under and along the margins of the colpi.

Leptothyrsa Hook. f. (Fig. 6)

Pollen grains 3-colporate, perprolate, large. Ectoapertures long (ave. CL/PL 0.86), narrow, with sparse polymorphic granules covering the surface. Endoapertures lalongate. Exine sculpturing striate-reticulate, the lumina irregular in outline, small to medium, with occasional infratectal rod-like structures, the reticulum forming a solid tectum along the colpi margins. Exine structure columellate, semitectate, with a nonapertural exine 3.0–9.4 μm thick, stratified into a distinguishable ektexine and endexine. Ektexine of the ridged mesocolpium, composed of tectum, columellae, and foot-layer, the tectum well-developed, 10–23% of the total exine thickness, the columellae distinct, 11–27% of the total exine thickness, the foot-layer very prominent, 50–79% of the total exine thickness. Endexine thin and granular in the mesocolpium and thicker under and along the margin of the colpi.

Lubaria Pittier (Fig. 7A, B)

Pollen grains 5- or 6-colporate. Ectoapertures inconspicuous, long (ave. CL/PL 0.73), narrow, with either sparse or no small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with occasional infratectal rod-like structures. Exine structure columellate, semitectate.

Neoraputia Emmerich (Fig. 7C, D)

Pollen grains 3-colporate, oblate-spheroidal or spherical, large. Ectoapertures of medium length (ave. CL/PL 0.65), narrow, with sparse to dense polymorphic granules covering the surface. Endoapertures circular to short lalongate. Exine sculpturing reticulate, the lumina irregular in outline, medium, with less dense infratectal rod-like structures. Exine structure columellate, semitectate.

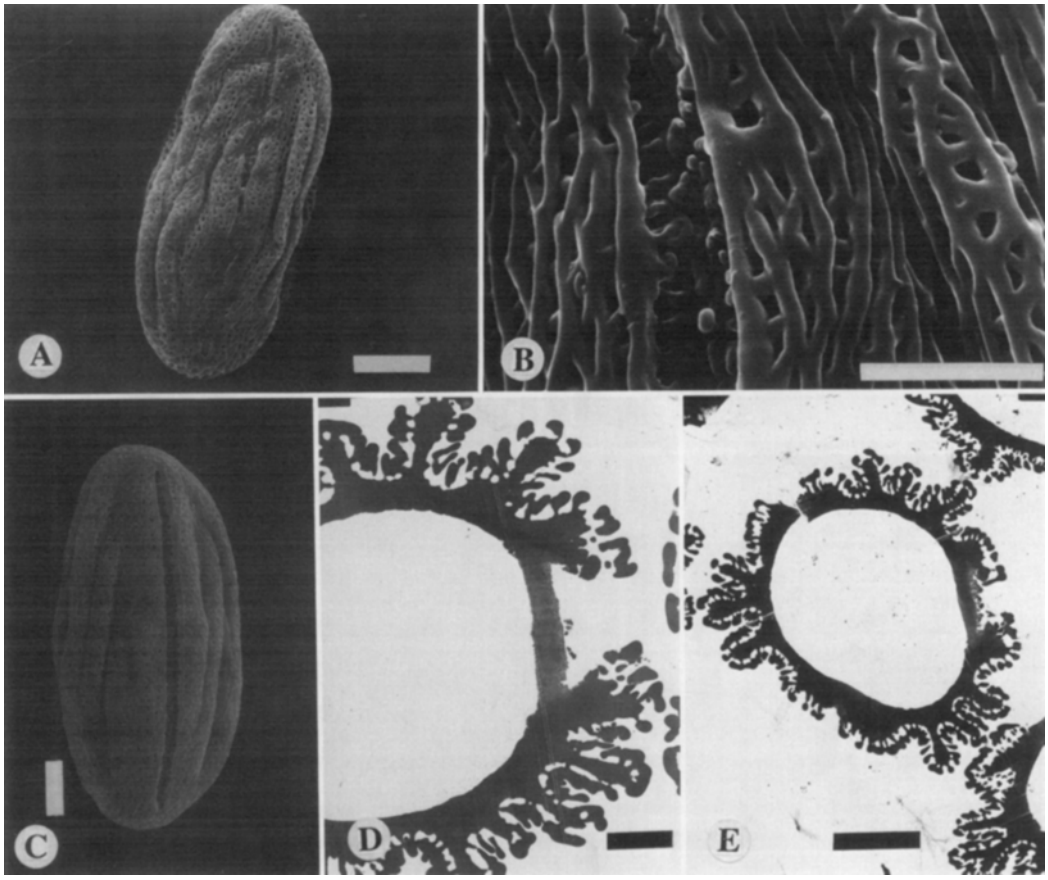

FIG. 6. Pollen of Cuspariinae. **A–E.** *Leptothyrsa sprucei* (A–C, *Killip & Smith 29844*; D, E, *McDaniel & Rimachi Y. 29660*). **A.** Equatorial view showing striate-reticulate sculpturing with ridged walls of the mesocolpium. **B.** Surface view showing striate-reticulate sculpturing with the sculpturing forming a solid tectum along the colpus margin. **C.** Equatorial view showing the ridged walls of the mesocolpium. **D.** Radial section showing the presence of endexine under and along the margins of the aperture. **E.** Radial section of whole grain showing ridged walls of the mesocolpium. (Scale bars: A, C = 12 μm; B = 20 μm; D = 4 μm; E = 8 μm.)

Nycticalanthus Ducke (Fig. 7E–G)

Pollen grains 4-short-colporate, suboblate, large. Ectoapertures short (ave. CL/PL 0.2), wide, with sparse to dense polymorphic granules covering the surface. Endoaperture inconspicuous. Exine structure columellate, tectate-perforate. Exine sculpturing baculate, with small rod-like structures (1.5 μm) between bacula, the sculpturing elements more abundant around the apertures. Exine structure intectate, with a nonapertural exine ca. 6.4 μm thick, stratified into a distinguishable ektexine and a reduced or absent endexine. Ektexine composed of columellae and foot-layer, the columellae distinct, ca. 70% of the total exine thickness, the foot-layer prominent, ca. 30% of the total exine thickness. Endexine absent in the mesocolpium and thin under and along the margins of the colpi.

Raputia Aubl. (Fig. 8A)

Pollen grains 5- or 6-colporate, spherical or prolate-spheroidal, large. Ectoapertures long (ave. CL/PL 0.88), narrow, with sparse small granules covering the surface. Endoapertures lalongate. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with less dense infratectal

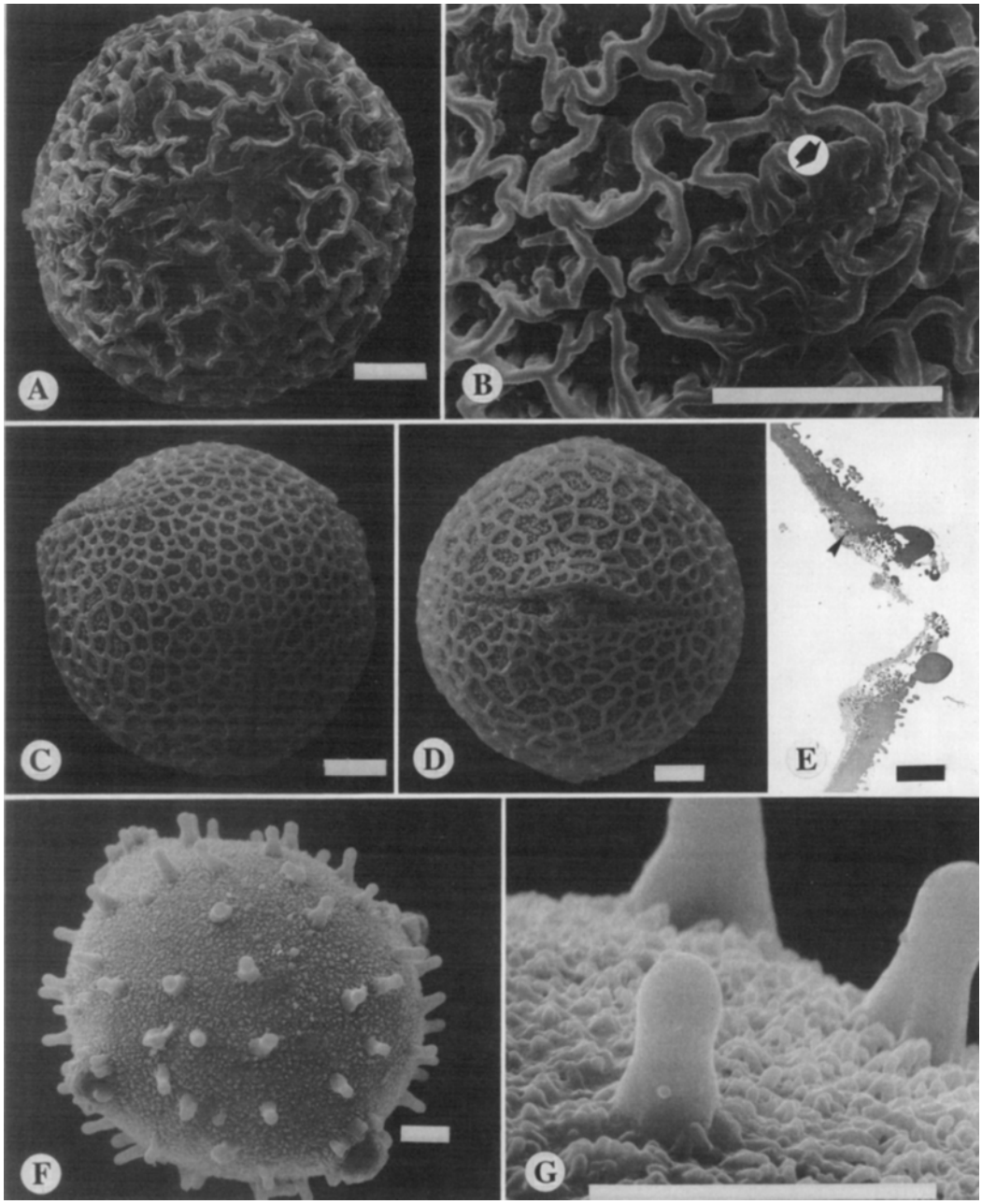

FIG. 7. Pollen of Cuspariinae. **A, B.** *Lubaria aroensis* (*Bernardi 5824*). **A.** Oblique polar view showing reticulate sculpturing and inconspicuous aperture. **B.** Surface view showing lumina with occasional rod-like structures. Note aperture (arrow). **C, D.** *Neoraputia alba* (*Pirani et al. 2489*). **C.** Polar view showing reticulate sculpturing, lumina with rod-like structures, and 3 apertures. **D.** Equatorial view showing colporate aperture. **E-G.** *Nycticalanthus speciosus* (*Duke 99*). **E.** Radial view showing endexine (arrow) and ektexinous bacula near the aperture. **F.** Slightly oblique polar view showing baculate sculpturing and 4 apertures. **G.** Surface view showing rod-like structures between bacula. (Scale bars: A, B, F, G = 10 μm; C = 14 μm; D = 12 μm; E = 4 μm.)

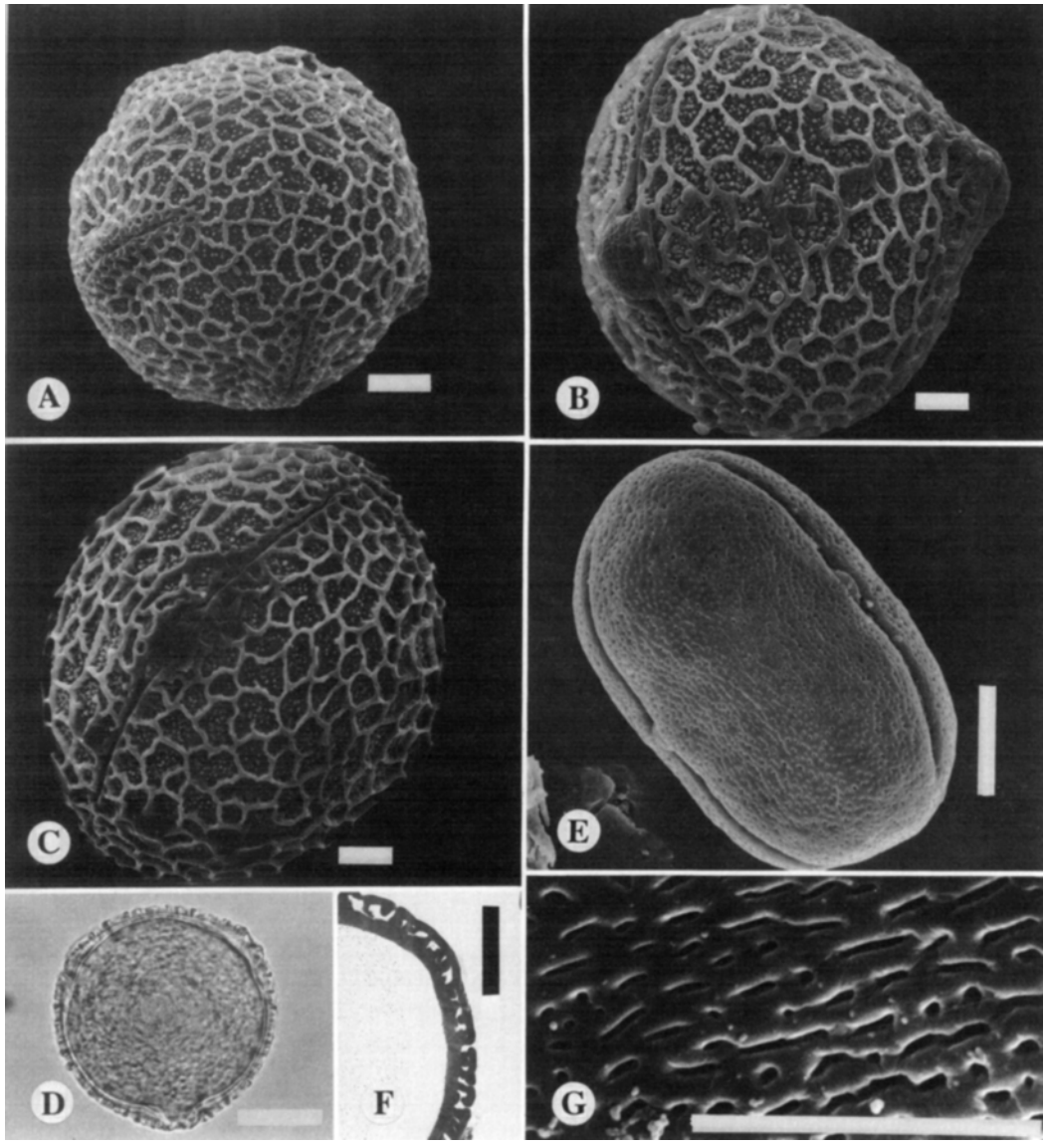

FIG. 8. Pollen of Cuspariinae. **A.** *Raputia ulei* (*Maas & Maas 490*). Oblique polar view showing reticulate sculpturing and lumina with occasional infratectal rod-like structures. **B.** *Raputia heptaphylla* (= *Raputiarana*) (*Steyermark 91443*). Oblique equatorial view showing meridionally aligned, long, narrow ectoapertures. **C, D.** *Raputiarana subsigmoidea* (C, *Davidson 5209*; D, *Rimachi Y. 2728*). **C.** Equatorial view showing reticulate sculpturing and irregular lumina with occasional infratectal rod-like structures. **D.** Polar view showing 3 apertures. **E–G.** *Rauia resinosa* (E, *Mori et al. 11540*; F, G, *Duarte 6291*). **E.** Equatorial view showing perforate sculpturing and 2 of 3 apertures. **F.** Radial view through mesocolpium showing tectate-perforate exine. **G.** Surface view showing elongate and circular perforations. (Scale bars: A, B, C = 10 μm; D = 30 μm; E = 13 μm; F = 4 μm; G = 20 μm.)

rod-like structures. Exine structure columellate, semitectate.

Raputiarana Emmerich (Fig. 8B–D)

Pollen grains 3-colporate, prolate-spheroidal, large. Ectoapertures long (ave. CL/PL 0.8), narrow, with sparse to dense small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with less dense infratectal rod-like structures. Exine structure columellate, semitectate.

Rauia Nees & Mart. (Fig. 8E–G)

Pollen grains 3-colporate, euprolate, large. Ectoapertures long (ave. CL/PL 0.79), narrow, with sparse small granules covering the surface. Endoapertures lalongate. Exine sculpturing perforate, lumina circular or elongate in outline, small. Exine structure columellate, tectate-perforate, with a nonapertural exine ca. 1.75 μm thick, stratified into a distinguishable ektexine and endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well-developed, ca. 39% of the total exine thickness, the columellae reduced, ca. 14% of the total exine thickness, the foot-layer prominent, ca. 47% of the total exine thickness. Endexine thin in the mesocolpium and thicker under and along the margins of the colpi.

Ravenia Vell. (Fig. 9A)

Pollen grains 5- or 6-colporate, oblate-spheroidal or prolate-spheroidal, large. Ectoapertures of medium length (ave. CL/PL 0.5), narrow, with sparse small granules covering the surface. Endoapertures circular. Exine sculpturing reticulate, lumina irregular in outline, medium to large, smooth or with occasional infratectal rod-like structures. Exine structure columellate, tectate-perforate or semitectate.

Raveniopsis Gleason (Fig. 9B–G)

Pollen grains 3-colporate or 5- or 6-colporate, euprolate, prolate-spheroidal, or subprolate, medium or large. Ectoapertures of some grains medium (ave. CL/PL 0.64), of others long (ave. CL/PL 0.84), narrow, with sparse small granules covering the surface. Endoapertures circular. Exine sculpturing reticulate, the lumina irregular in outline, medium, either smooth or with occasional infratectal rod-like structures. Exine structure columellate, tectate-perforate or semitectate, with a nonapertural exine ca. 2.75 μm thick, stratified into a distinguishable ektexine and endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well-developed, ca. 23% of the total exine thickness, the columellae reduced, ca. 32% of the total exine thickness, the foot-layer prominent, ca. 45% of the total exine thickness. Endexine thin to absent in the mesocolpium and thicker under and along the margins of the colpi.

Sigmatanthus Emmerich (Fig. 10A)

Pollen grains 5-/or 6-colporate, oblate-spheroidal, large. Ectoapertures inconspicuous, short (ave. CL/PL 0.31), narrow, with sparse to dense small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing reticulate, the lumina very irregular in outline, medium to large, with less dense infratectal rod-like structures. Exine structure columellate, semitectate.

Spiranthera A. St.-Hil. (Fig. 10B–E)

Pollen grains 3-porate, oblate-spheroidal, large. Ectoapertures porate (ave. 4 μm in diam.). Endoapertures circular. Exine sculpturing echinate, with a dense infratectal rod-like structures between spines, the sculpturing elements more abundant around the apertures. Exine structure intectate, with a nonapertural exine ca. 3.9 μm thick. Exine stratified into a distinguishable ektexine and a reduced or absent endexine. Ektexine composed of columellae and foot-layer, the columellae distinct, ca. 53% of the total exine thickness, the foot-layer prominent, ca. 47% of the total exine thickness. Endexine absent in the mesocolpium and thin under and along the margins of the colpi.

Ticorea Aubl. (Fig. 10F–I)

Pollen grains 6-short-colporate, oblate-spheroidal, large or very large. Ectoapertures sometimes inconspicuous, short (ave. CL/PL 0.12), narrow, with either sparse or

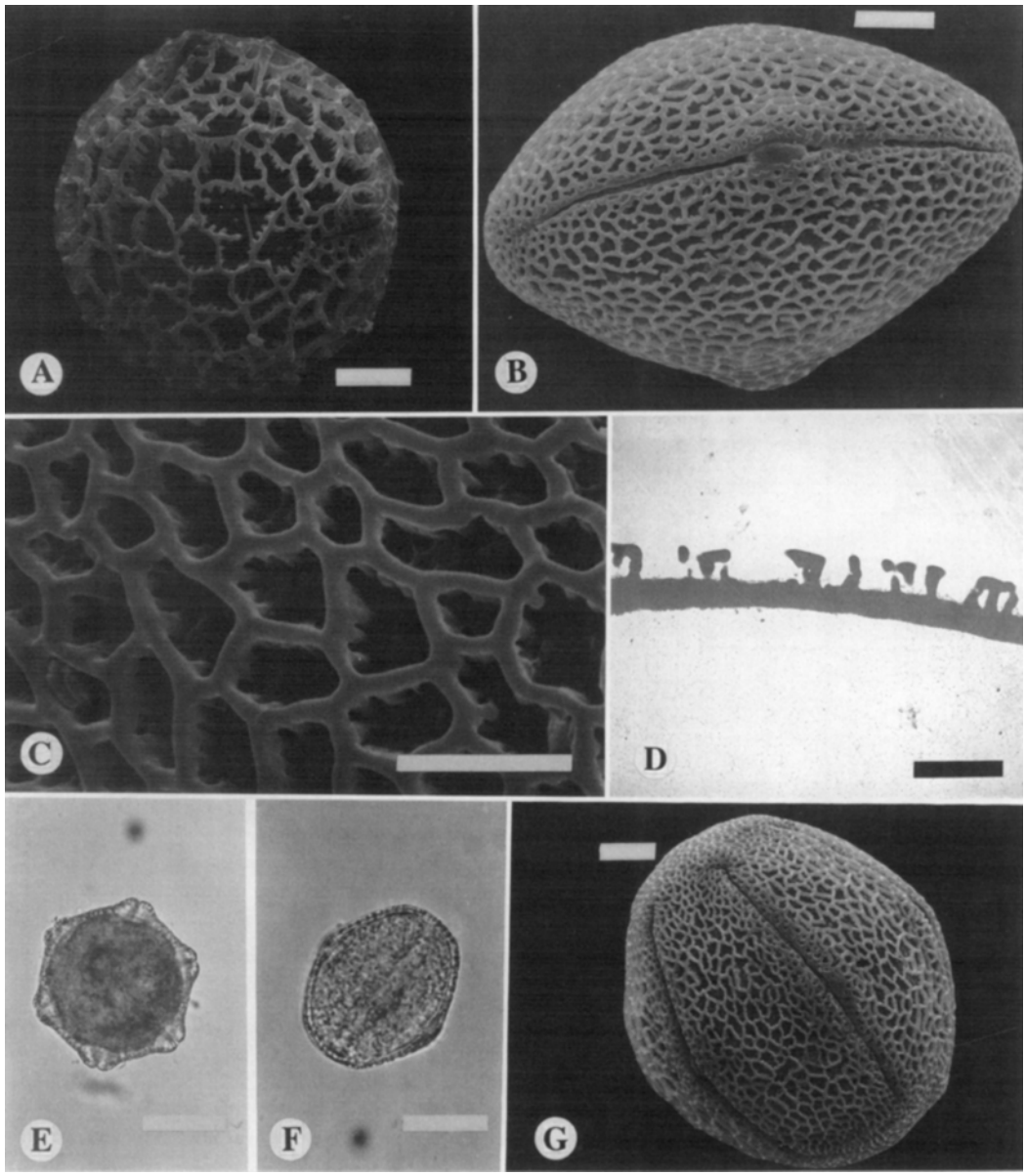

FIG. 9. Pollen of Cuspariinae. **A.** *Ravenia leonis* (*Bro. Clemente 6240*). Polar view showing reticulate sculpturing. **B-D.** *Raveniopsis ruellioides* (B, *Huber et al. 8078*; C, D, *Maguire et al. 42447*). **B.** Equatorial view showing reticulate sculpturing and long ectoaperture. **C.** Surface view showing lumina without infratectal rod-like structures. **D.** Radial section through mesocolpium showing semitectate exine. **E.** *Raveniopsis stelligera* (*Maguire & Maguire 35262*). Polar view showing 6 apertures. **F, G.** *Raveniopsis pedunculariis* (F, *Maguire 32815*; G, *Huber 10401*). **F.** Equatorial view of prolate-spheroidal grain. **G.** Equatorial view showing reticulate sculpturing and lumina with occasional infratectal rod-like structures. (Scale bars: A, G = 10 μm; B = 12 μm; C = 20 μm; D = 4 μm; E, F = 30 μm.)

no small granules covering the surface. Endoapertures circular. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with dense, long to short infratectal rod-like structures. Exine structure columellate, semitectate, with a nonapertural exine ca. 4.6 μm thick, stratified into a distinguishable ektexine and a reduced or

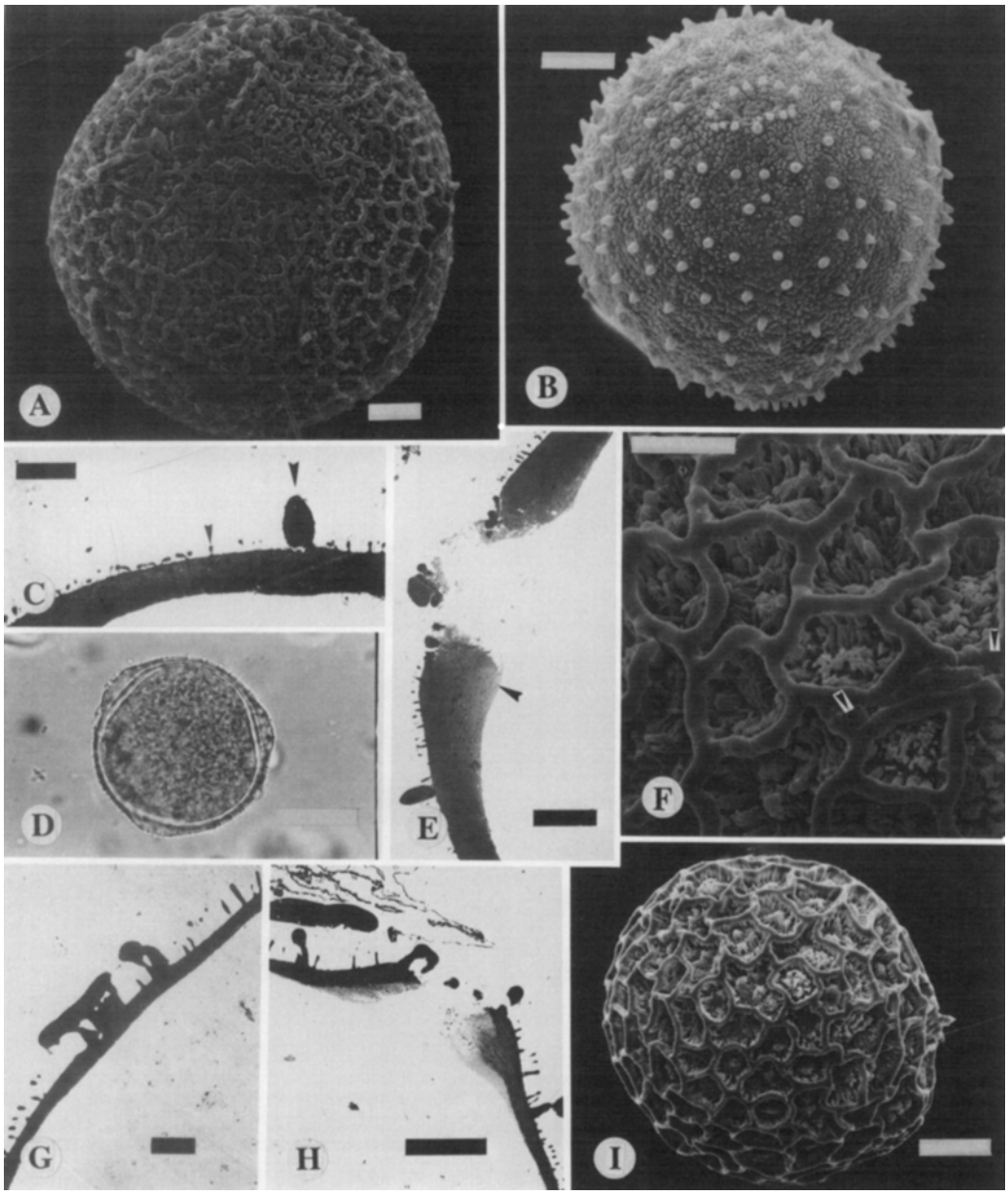

FIG. 10. Pollen of Cuspariinae. **A.** *Sigmatanthus trifoliatus* (*Rosa et al. 4048*). Equatorial view showing colporate apertures and reticulate sculpturing with dense infratectal rod-like structures. **B-E.** *Spiranthera odoratissima* (B, E, *Harley et al. 18650*; C, *Irwin et al. 23085*; D, *Heringer 15954*). **B.** Equatorial view showing porate aperture and echinate sculpturing. **C.** Radial section through mesocolpium showing spine (large arrow) and reduced rod-like structures (small arrow). **D.** Polar view showing 3 apertures. **E.** Radial section showing endexine (arrow) near the aperture. **F-I.** *Ticorea* cf. *longiflora* (*Cid Ferreira et al. 6858*). **F.** Surface view showing lumina with dense rod-like structures. Note short-colporate aperture (arrows at ends of aperture). **G.** Radial section through mesocolpium showing semitectate exine. **H.** Radial section showing endexine near aperture. **I.** Polar view showing reticulate sculpturing. (Scale bars: A = 8 μm; B, F, H = 10 μm; C = 2 μm; D = 30 μm; E, G = 4 μm; I = 20 μm.)

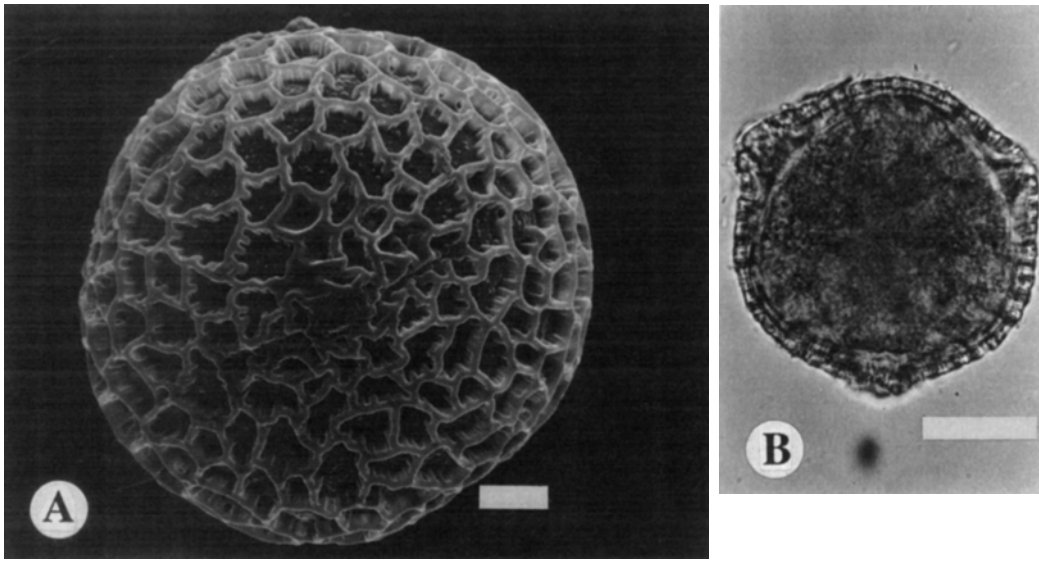

FIG. 11. Pollen of Cuspariinae. **A.** *Toxosiphon trifoliatus* (*Klug 2729*). Equatorial view showing reticulate sculpturing with occasional infratectal rod-like structures. **B.** *Toxosiphon lindenii* (*Lent 2588*). Polar view showing 3 apertures. (Scale bars: A = 10 μm; B = 30 μm.)

absent endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well-developed, ca. 32% of the total exine thickness, the columellae distinct, ca. 37% of the total exine thickness, the foot-layer prominent, ca. 31% of the total exine thickness. Endexine absent in the mesocolpium and thin under and along the margins of the colpi.

Toxosiphon Baill. (Fig. 11)

Pollen grains 3-colporate, oblate-spheroidal, large. Ectoapertures of medium length (ave. CL/PL 0.5), narrow, with sparse small granules covering the surface. Endoapertures lalongate. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with occasional infratectal rod-like structures. Exine structure columellate, semitectate.

POLLEN OF POSSIBLE RELATIVES

Hortia Vand. (Fig. 12)

Pollen grains solitary, radially symmetrical, isopolar, 3-colporate, subprolate, or euprolate, medium. Ectoapertures meridionally aligned, of medium length (ave. CL/PL 0.58), narrow, with either sparse or no polymorphic granules covering the surface. Endoapertures lalongate. Exine sculpturing psilate-perforate, the lumina infrequent, when present circular, small. Exine structure columellate, tectate-imperforate to infrequently perforate, with a nonapertural exine ca. 3.6 μm thick, stratified into a distinguishable ektexine and thin endexine. Ektexine composed of tectum, columellae and foot-layer, the tectum well-developed, ca. 25% of the total exine thickness, the columellae reduced, ca. 7% of the total exine thickness, the foot-layer very prominent, ca. 68% of the total exine thickness. Endexine thin in mesocolpium (at least in the few instances in which it was stained sufficiently to be observed) and thick under and along the margins of the colpi.

Rutaneblina Steyerm. & Luteyn

Pollen grains solitary, radially symmetrical, isopolar, 3-colporate, subprolate, medium. Ectoapertures meridionally aligned, long (ave. CL/PL 0.72), narrow, with sparse to dense small granules covering the surface. Endoapertures inconspicuous. Exine sculp-

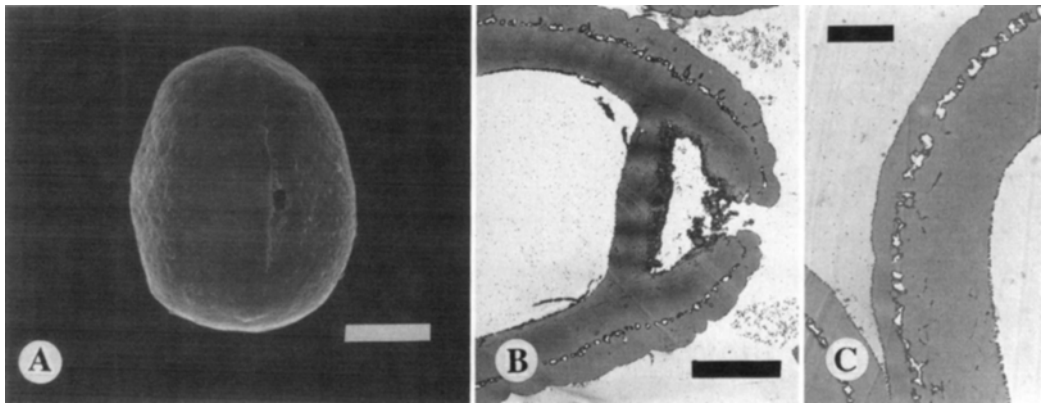

FIG. 12. Pollen of *Hortia*. A-C. *H. brasiliana* (*Fonseca 843*). A. Equatorial view showing psilate-perforate sculpturing with perforations infrequent and small. B. Radial section showing endexine under and along the margin of the aperture. C. Radial section through mesocolpium showing thick foot-layer, reduced columellae, and solid tectum. (Scale bars: A = 10 μm; B = 4 μm; C = 2 μm.)

turing reticulate, the lumina irregular in outline, small to medium, with infratectal rod-like structures. Exine structure columellate, semitectate.

Discussion

POLLEN CHARACTERS IN THE RUTACEAE

No survey of the pollen of the family has been published. The published observations that do exist usually appear as a sampling of taxa found in geographically oriented pollen surveys (Barth, 1982, 1983, 1985; Erdtman, 1971; Heusser, 1971; Selling, 1947; Ybert, 1979). Data are available for some representatives of all subfamilies but one (i.e., for Rutoideae, Toddalioideae, Citroideae, Dictyolomatoideae, and Flindersioideae but not for Spathelioideae). These data (Barth, 1982, 1983, 1985; Erdtman, 1971; Heusser, 1971; Selling, 1947; Ybert, 1979) indicate that pollen of the Rutaceae is (2) 3 (4–6)-colporate (rarely 3-pororate), usually reticulate, rarely echinate, striate, foveolate, or psilate, prolate to suboblate (rarely perprolate), and 15–100 μm through the longest axis. That of the Rutoideae reflects this entire range of variation with the exception of the 2-colporate state.

The only previously published observations of pollen of the Cuspariinae are those of Erdtman (1971) and Barth (1982). Erdtman (1971) examined one species in each of six genera of the Cuspariinae. Except for minor differences in the reported measurements of the axes, our observations of the same genera correlate with his. Barth (1982) reported observations of 12 genera and approximately 20 species. No voucher specimens are cited, specific epithets for some of the genera examined are lacking, photographs are present for only eight species, and full, comparable descriptions of the pollen of each genus are not given. Thus, an accurate comparison of our results is not possible, but, for the most part, our observations agree with hers.

POLLEN CHARACTERS AND GENERIC DELIMITATION IN THE CUSPARIINAE

Each of seven genera is uniquely characterized (Table III) by a single pollen type—*Almeidea* (type 2), *Leptothyrsa* (type 7), *Apocaulon* (type 8), *Spiranthera* (type 9), *Erythrochiton* (type 10), *Nycticalanthus* (type 11), and *Angostura* (type 12).

The two largest genera, *Raveniopsis* and "Angostura-1," exhibit more than a single pollen type. The grains of *Raveniopsis* are reticulate, but are either 3-colporate (Fig. 9B) and type 5 or 5- or 6-colporate (Fig. 9E, G) and type 6. These two types correlate almost perfectly with two groups of species in *Raveniopsis*; the species with type 5 (Ta-

ble III) have simple trichomes, and, with one exception, the species with type 6 (Table III) have branched trichomes. The exception is *R. sericea,* which has type 6 and simple trichomes. *Raveniopsis fraterna,* which has type 5, and *R. sericea* are quite similar in macromorphological features—so much so that they have been considered to be one species (Steyermark, 1984). That these two apparently closely related species have different pollen types argues against the usefulness of aperture number as a distinguishing character of the two groups within the genus.

Like the macromorphological characters, the pollen characters of "Angostura-1" are highly variable. Five pollen types occur in the genus. The sculpture pattern ranges from perforate (Fig. 3E, F) to foveolate (Fig. 3C) to foveolate-reticulate (Fig. 3A) to reticulate (Fig. 3D), i.e., all patterns present in the subtribe except the intectate pattern (types 9–12). Aperture class ranges from 3–6-colporate, i.e., all except pantocolporate (type 2) and porate (type 9). Because pollen of only 10 of the ca. 35 species has been examined, it is likely that additional variation in pollen characters will be found in other species. Sculpture pattern and aperture number are not useful in solving the generic problem in "Angostura-1."

Each of the fifteen other genera examined exhibits only one of three pollen types (1, 5, or 6), but these types are distributed among several genera (Table III) and, therefore, are not unique identifiers of genera. The pollen characters are taxonomically useful, however, in supporting the separation of the apocarpous species described in *Galipea* (e.g., *G. longiflora,* here assigned to *Angostura*) from the syncarpous species of true *Galipea.* The former species have baculate, 5- or 6-colporate pollen (type 12; Fig. 2A, B, D), and the latter have reticulate, 3- or 4-colporate pollen (type 5; Fig. 5F, G). The presence in *Angostura trifoliata* of pollen type 12 (Table III; Fig. 2A, B) correlates with other macromorphological characters (discussed in the introduction to this paper) and supports its separation from all other species described in *Angostura* and its alliance with the apocarpous species of *Galipea* (Fig. 2D).

Furthermore, as discussed by Kallunki (1992), the semitectate pollen of *Toxosiphon* (Fig. 11), in combination with several macromorphological characters, supports its segregation from *Desmotes* and *Erythrochiton,* which have intectate pollen (Figs. 4H, 5B, D).

Because *Lubaria* (Fig. 7A, B), *Raputia* (Fig. 8A), and *Ravenia* (Fig. 9A) all have type 6 pollen, pollen data offer no additional support for, but do not negate, the alignment of *Lubaria szczerbanii* and *Ravenia amazonica* with *Raputia.*

Although morphological characters support the separation of *Neoraputia, Raputiarana,* and *Sigmatanthus* from *Raputia,* pollen data are equivocal with respect to the separation or union of these genera; *Raputia* and *Sigmatanthus* have pollen of type 6 and *Neoraputia* and *Raputiarana* of type 5.

A COMPARISON OF POLLEN AND OTHER CHARACTERS IN THE CUSPARIINAE

The taxa with perforate to foveolate (types 1–4) pollen grains, i.e., *Almeidea, Rauia, Euxylophora,* and some species of "Angostura-1," have free petals, stamens, and carpels and five rather than only two fertile anthers and may be more closely related to each other than to other genera in the subtribe. *Almeidea* is similar to many species of "Angostura-1" in its choripetalous flowers, five fertile stamens, and free carpels, but its anthers appear to be dorsifixed rather than basifixed as in most "Angostura-1," and its pollen is pantocolporate (Fig. 1E), unique in the subtribe.

Rauia was distinguished from "Angostura-1" (as *Cusparia*) by Engler (1931) only by characters of dubious value: in *Rauia* the carpels initially united ventrally and ultimately becoming free in fruit and the petals valvate, and in "Angostura-1" the carpels free from the beginning and the petals imbricate. The species described in *Rauia* have linear petals, usually narrower than those in "Angostura-1," and some species have unequal cotyledons, a character not found so far in "Angostura-1." *Rauia* is, however,

similar to most species of "Angostura-1" in the free or only slightly coherent petals that are narrowly imbricate not valvate, free stamens, and two fertile stamens with unappendaged anthers. Given the variation in most characters in "Angostura-1," the addition to "Angostura-1" of *Rauia* with its characters of slightly connate carpels, narrower petals, and unequal cotyledons would not be discordant (cf. Gereau, 1990). Pollen characters do not negate this possibility.

Euxylophora resembles *Rauia* and some species of "Angostura-1" in its narrow, free petals and its free stamens bearing five fertile, unappendaged anthers, but differs from them by being a large tree rather than a shrub or treelet and by having connate carpels and no cupular disc. That the pollen characters—aperture number, aperture type, and sculpture pattern—of "Angostura-1," *Rauia*, and *Euxylophora* are similar (Table III; Figs. 3E, 5E, 8E) may indicate that they are related.

The taxa with reticulate pollen form a variable group. Splitting these further into two groups (types 5 and 6) based on number of colpi results in variable groups as well. An examination of the genera in these groups will illustrate this point. "Angostura-1," as mentioned in the previous section, has a wide range of pollen types, of which types 5 and 6 are only two. *Adiscanthus* is quite unlike the other genera with type 5. It has actinomorphic 5-merous flowers with free petals, stamens, and carpels, and with dorsifixed, unappendaged anthers, and no cupular disc, while others have zygomorphic flowers with coherent or connate petals, basifixed, basally appendaged anthers, and a cupular disc. Its relationships are not known. *Decagonocarpus* and the species of *Raveniopsis* with pollen of type 5 and *Ertela, Lubaria, Raputia, Ravenia,* and the species of *Raveniopsis* with pollen of type 6 form an apparently related group of genera characterized by opposite leaves, free, imbricate sepals, connate petals, and free carpels and usually by connate, appendaged anthers with a gland-dotted dorsum and by conduplicate, bilobed cotyledons. *Galipea, Neoraputia, Toxosiphon* (with type 5) and *Ticorea* (with type 6) form a group characterized by, among other features, connate carpels, and *Raputiarana* (with type 5) and *Sigmatanthus* (with type 6) form another characterized by free carpels. That the otherwise similar taxa within each of these two groups have different pollen types argues against the usefulness of aperture number as a generic character.

Striate-reticulate grains (types 7 and 8) occur in both *Leptothyrsa* and *Apocaulon*. In *Leptothyrsa*, the ektexine of the mesocolpium is longitudinally deeply ridged (Fig. 6A, C–E), while in *Apocaulon* the ektexine is not ridged (Fig. 4A). This difference in pollen structure correlates with differences in a multitude of macromorphological characters that distinguish these two genera, and despite their striate-reticulate pollen these two genera are probably not closely related. *Leptothyrsa* is a treelet with actinomorphic flowers ca. 2 cm long in which all anthers are fertile and unappendaged and the embryo is straight with planate cotyledons oriented sagittally to the floral axis. *Apocaulon* is a low, rhizomatous herb with zygomorphic flowers ca. 7 mm long in which only two anthers are fertile and basally appendaged and the embryo is curved with conduplicate cotyledons oriented proximally to the floral axis. *Apocaulon* despite its alternate leaves, shares many macromorphological characters with members of a group of genera with opposite leaves—including *Decagonocarpus, Ertela, Lubaria, Raputia* (sensu Kallunki, 1990), *Ravenia*, and *Raveniopsis*. Unlike *Apocaulon*, however, these latter six genera have reticulate pollen of type 5 or 6. In this case, *Apocaulon* may be closely related to this group of genera despite the difference in pollen characters.

Apart from this group of genera, opposite leaves occur only in *Desmotes*, which differs, however, in its echinate pollen, large, connate, valvate, rose-colored sepals, coherent petals, and free anthers without a gland-dotted dorsum. Although originally described, because of the large, colored calyx, as a species of *Erythrochiton, D. incomparabilis*, the only species of the genus, differs in several features from *Erythrochiton*

(Kallunki, 1992). Its relationships are obscure, in part because it is known only by the flowering type collection and its fruit and seeds are unknown, but it pollen is echinate like that of some *Erythrochiton.*

The four genera with intectate (echinate, clavate, or baculate) pollen (types 9–12) [*Spiranthera* (Fig. 10B, D), *Nycticalanthus* (Fig. 7F, G), *Erythrochiton* (Figs. 4H, 5D), and *Angostura* (Fig. 2A, D)] fall into two groups based on macromorphological characters. These two groups may not be related to each other, but within each, however, the taxa may indeed be closely related. *Nycticalanthus* (an endemic of the Brazilian Amazon) and *Spiranthera* (a genus of three or four species ranging from northern South America to Bolivia and southern Brazil) share rather large, choripetalous flowers, five fertile stamens bearing unappendaged anthers, and a gynophore. *Erythrochiton* and *Angostura* share connate petals, tuberculate seeds, free anthers with free appendages, and free carpels.

In Kallunki's (1992) revision, she mentioned that exceptional individuals of *Erythrochiton* from Iquitos, Peru resembled *E. brasiliensis* in their actinomorphic flowers with red calyx and five fertile stamens, but differed from typical representatives of that species in, for example, their shorter and rather equally 3-dentate calyces and smaller anthers. Only one (*Thomas 6782*) of the specimens of *E. brasiliensis* examined for the present study has been collected in the Iquitos area. Its pollen grains were smaller than those of a typical representative (*Mori et al. 9361*) of the species (compare samples 2 and 5 in Table II).

The pollen of *Hortia,* characterized by a psilate exine with rare perforations, a very thick foot-layer, and reduced columellae (Fig. 12), is unlike that of any member of the Cuspariinae. Our observations differ from Barth's (1983) in that she reported the grains to be "punctate," i.e., possessing a perforate tectum, and somewhat larger, e.g., with a mean polar axis length of 50.5–51.0 μm vs. ours of 33.4–34.4 μm. In any case, data from pollen characters offer no support for the transfer of this genus from the Todalioideae to the Cuspariinae, as was suggested based on chemical characters (Fernandes da Silva et al., 1988).

Rutaneblina was described by Steyermark and Luteyn (Steyermark, 1984) without reference to tribal affinity or possible relationships. Its 3-colporate, reticulate, subprolate, medium-sized pollen is similar to the type 5 Cuspariinae pollen but also to that of the Pilocarpinae (Morton, unpubl.). Pollen characters offer equivocal evidence as to its placement within either subtribe.

Preliminary observations of the pollen of three genera (*Pilocarpus, Metrodorea,* and *Esenbeckia*) of the Pilocarpinae (Morton, unpubl.) show that the range of pollen characters in this subtribe fall within that of the Cuspariinae and support a close relationship between the two.

Conclusions

As discussed earlier in this paper, aperture number is not a useful generic character in *Raveniopsis* or in "Angostura-1." On this basis, types 5 and 6 may be better considered as a single type—reticulate and 3–6-colporate, thus uniting the species of *Raveniopsis.* The pollen characters that may be most useful at the generic level may be more broadly defined sculpture patterns and aperture classes defined without reference to aperture number, i.e., pantocolporate, colporate, and porate.

This survey of the pollen of the Cuspariinae has demonstrated the variety of pollen characters in the subtribe and has confirmed the taxonomic usefulness of such characters in delimiting some genera. The use of these characters in phylogenetic analyses will show whether or not such characters are also useful indicators of relationships among these genera. Our study suggests that systematic examination of the pollen of other groups throughout the Rutaceae may provide information useful in assessing relationships within this diverse family.

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Appendix I

Specimens from which pollen samples were obtained for this study. All are dried herbarium specimens deposited at NY unless indicated otherwise. The sample number (used in Table II) is boldfaced. If a species is recognized in this study as belonging to a described genus to which it has not been transferred or to an undescribed genus, the name of that genus is indicated in parentheses, and in quotes if undescribed, after the species' name. Such indications are not nomenclatural transfers.

Adiscanthus fusciflorus Ducke
1) *Daly et al. 5722,* **2)** *Klug 723* (US), both Loreto, Peru; **3)** *Ducke 234,* Amazonas, Brazil

Almeidea limae I. M. Silva
Martinelli 9904, Rio de Janeiro, Brazil

Almeidea rubra A. St.-Hil.
1) *G. L. Farias 118,* Espírito Santo, Brazil; **2)** *Octávio RB-96444,* Rio de Janeiro, Brazil

Angostura larensis (Tamayo & Croizat) Albuq. (="Angostura-1")
Dorr et al. 5641, Barinas, Venezuela

Angostura macrophylla (J. C. Mikan) Albuq. (="Angostura-1")
1) *Mori et al. 13072,* **2)** *Thomas et al. 6817,* both Bahia, Brazil

Angostura pentagyna (A. St.-Hil.) Albuq. (="Angostura-1")
1) *Mori et al. 10692,* **2)** *F. Sousa Santos 453,* both Bahia, Brazil

Angostura ramiflora (Engl.) Albuq. (="Angostura-1")
1) *Cid Ferreira 9327,* Amazonas, Brazil; **2)** *Maguire et al. 36790,* Amazonas, Venezuela

Angostura silvestris (Nees & Mart.) Albuq. (="Angostura-1")
1) *Maas & Tawjoeran LBB-10888,* Surinam; **2)** *Schatz et al. 944,* Maranhão, Brazil

Angostura sp. nov.
Silva & Bahia 2883, Pará, Brazil

Angostura cf. *transitionalis* Rizzini (="Angostura-1")
Pinard 860, Acre, Brazil

Angostura trifoliata (Willd.) T. S. Elias
1) *Colella et al. 1393,* **2)** *Stergios et al. 5909* (MO), both Bolívar, Venezuela

Angostura ucayalina (Huber) Albuq. (="Angostura-1")
1) *Daly et al. 1835,* Pará, Brazil; **2)** *Schunke 5635,* San Martín, Peru

"Angostura-1" sp. 1
Mori et al. 9579, Bahia, Brazil

"Angostura-1" sp. 2
Schunke 4495, San Martín, Peru
"Angostura-1" sp. 3
Mattos Silva et al. 1822, Bahia, Brazil
"Angostura-1" sp. 4
Mattos Silva et al. 1488, Bahia, Brazil
Apocaulon carnosum R. S. Cowan
Maguire & Maguire 29188, Amazonas, Brazil
Decagonocarpus cornutus R. S. Cowan
Holst & Liesner 3352, Amazonas, Venezuela
Decagonocarpus oppositifolius Engl.
Maguire et al. **1)** *30457*, **2)** *37493*, **3)** *42618*, all Amazonas, Venezuela
Desmotes incomparabilis (L. Riley) Kallunki
Collenette in Riley 470 (MO), Panama
Ertela trifolia (L.) Kuntze
Beck et al. 321, Pará, Brazil
Erythrochiton brasiliensis Nees & Mart.
1) *Harris 58* (herbarium ?), cult. in Jamaica; **2)** *Mori et al. 9361*, **3)** *Pinheiro & dos Santos 2340* (CEPEC), both Bahia, Brazil; **4)** *Prance 9312*, Roraima, Brazil; **5)** *Thomas 6782* (pickled), Loreto, Peru; **6)** *Oldeman 2047* (US), French Guiana
Erythrochiton fallax Kallunki
1) *Daly et al. 6445*, Beni, Bolivia; **2)** *Idrobo & Schultes 830* (US), Colombia; **3)** *M. Saldías 78*, Santa Cruz, Bolivia
Erythrochiton gymnanthus Kallunki
1) *Hammel et al. 13958* (MO), **2)** *Kallunki 294* (pickled), **3)** *Kallunki 309* (pickled), all Costa Rica
Euxylophora paraensis Huber
1) *Ducke 27-9-23*, **2)** *Rosa & Santos 2227*, both Pará, Brazil
Galipea davisii Sandwith
Ducke RB-35598 (US), Amazonas, Brazil
Galipea jasminiflora (A. St.-Hil.) Engl.
1) *W. R. Anderson 6358*, Goiás, Brazil; **2)** *W. R. Anderson 12331* (US), Rondônia, Brazil; **3)** *W. Hoehne 15252*, **4)** *E. Kuhn*, 9 Mar 1967, both São Paulo, Brazil
Galipea longiflora K. Krause (=*Angostura*)
Daly 6382, La Paz, Bolivia
Galipea sp. nov. 1
Daly et al. **1)** *1630*, **2)** *1891*, both Pará, Brazil
Hortia arborea Engl.
Mori et al. 12692, Bahia, Brazil
Hortia brasiliana Vand.
1) *S. G. Fonseca 843*, Distrito Federal, Brazil; **2)** *Hatschbach 43860* (US), Minas Gerais, Brazil
Hortia excelsa Ducke
Rabelo & Cardoso 2900, Amapá, Brazil
Leptothyrsa sprucei Hook. f.
1) *Killip & Smith 29844*, **2)** *McDaniel & Rimachi Y. 29660*, both Loreto, Peru
Lubaria aroensis Pittier
1) *A. L. Bernardi 5824*, Miranda, Venezuela; **2)** *Ruiz & Rondon 3775*, Falcón, Venezuela
Lubaria szczerbanii Steyerm. (=*Raputia*)
Boom 9491, Bolívar, Venezuela
Neoraputia alba (Nees & Mart.) Emmerich
Pirani et al. 2489, Espírito Santo, Brazil
Neoraputia paraensis (Ducke) Emmerich
Foster & Baldeón 12600, Madre de Dios, Peru
Neoraputia trifoliata (Engl.) Emmerich
D. A. Folli 764, Bahia, Brazil
Nycticalanthus speciosus, Ducke
Ducke 99, Amazonas, Brazil
Raputia heptaphylla Pittier (=*Raputiarana*)
Steyermark 91443, Distrito Federal, Venezuela
Raputia maroana (R. S. Cowan) Kallunki
Guánchez & Melgueiro 3460 (MO), Amazonas, Venezuela
Raputia sp. nov. 1
Klug 544, Loreto, Peru
Raputia sp. nov. 2
Prance et al. 17015, Amazonas, Brazil
Raputia ulei (K. Krause) Kallunki
Maas & Maas 490, Amazonas, Brazil
Raputiarana subsigmoidea (Ducke) Emmerich
1) *Davidson 5209*, **2)** *Rimachi Y. 2728*, both Loreto, Peru
Rauia resinosa Nees & Mart.
1) *Duarte 6291* (US), Guanabara, Brazil; **2)** *Mori et al. 9379*, **3)** *Mori et al. 11540*, both Bahia, Brazil
Rauia sp. nov. 1
Thomas et al. 7674, Bahia, Brazil
Rauia spicata Haye
Steyermark 87821 (US), Bolívar, Venezuela
Rauia subtruncata Steyerm.
FDBG F1729, British Guiana
Ravenia biramosa Ducke
Schunke 5711, San Martín, Peru
Ravenia leonis Vict.
Bro. Clemente 6240 (US), Cuba
Ravenia rosea Standl.
Kallunki 297 (pickled), Costa Rica
Ravenia urbanii Engl.
J. A. Duke 7515 (US), Puerto Rico
Raveniopsis breweri Steyerm.
Huber et al. 8092, Bolívar, Venezuela
Raveniopsis fraterna R. S. Cowan
1) *Huber et al. 10215*, **2)** *Pruski & Huber 3597*, both Bolívar, Venezuela
Raveniopsis linearis (Gleason) R. S. Cowan
M. Fariñas et al. 418, Amazonas, Venezuela
Raveniopsis peduncularis Pittier & Lasser
1) *Huber 10401*, **2)** *Maguire 32815*, both Bolívar, Venezuela
Raveniopsis ruellioides (Oliv.) R. S. Cowan
1) *Huber et al. 8078*, **2)** *Wurdack 34166*, both Bolívar, Venezuela; **3)** *Maguire et al. 42447*, Amazonas, Venezuela
Raveniopsis sericea R. S. Cowan
Steyermark et al. 128764, Bolívar, Venezuela
Raveniopsis stelligera (R. S. Cowan) R. S. Cowan
Maguire & Maguire 35262, Amazonas, Venezuela
Raveniopsis steyermarkii R. S. Cowan
Luteyn & Steyermark 9575, Bolívar, Venezuela
Rutaneblina pusilla Steyerm. & Luteyn
1) *Boom & Weitzman 5770*, **2)** *Liesner 16030*, both Amazonas, Venezuela
Sigmatanthus trifoliatus Emmerich
1) *Fróes 11796*, Maranhão, Brazil; **2)** *N. A. Rosa et al. 4048*, Pará, Brazil
Spiranthera odoratissima A. St.-Hil.
1) *Harley et al. 18650*, Bahia, Brazil; **2)** *Heringer*

15954, Distrito Federal, Brazil; **3)** *Irwin et al. 23085* (US), Minas Gerais, Brazil

Spiranthera parviflora Sandwith
N. A. Rosa 2417A, Pará, Brazil

Ticorea foetida Aubl.
Granville 2795, French Guiana

Ticorea longiflora DC.
Cid Ferreira et al. 6858, Amazonas, Brazil

Ticorea cf. *longiflora* DC.
Prance et al. 24022, Amazonas, Brazil

Toxosiphon carinatus (Little) Kallunki
Dodson & Gentry 9859, Ecuador (MO or SEL)

Toxosiphon lindenii Baill.
Lent 2588, Costa Rica

Toxosiphon trifoliatus (K. Krause) Kallunki
1) *Camp 999,* Ecuador; **2)** *Klug 2729,* San Martín, Peru

ANNOUNCEMENT

The Award Committee of the Lawrence Memorial Fund invites nominations for the 1994 Lawrence Memorial Award. Honoring the memory of Dr. George H. M. Lawrence, founding Director of the Hunt Institute for Botanical Documentation, the Award ($1,000) is given biennially to support travel for doctoral dissertation research in systematic botany or horticulture, or the history of the plant sciences, including literature and exploration.

Major professors are urged to nominate outstanding doctoral students who have achieved official candidacy for their degrees and will be conducting pertinent dissertation research that would benefit significantly from travel enabled by the Award. The Committee will not entertain direct applications. A student who wishes to be considered should arrange for nomination by his/her major professor; this may take the form of a letter which covers supporting materials prepared by the nominee.

Supporting materials should describe briefly but clearly the candidate's program of research and how it would be significantly enhanced by travel that the Award would support. Letters of nomination and supporting materials, including seconding letters, should be received by the Committee no later than 1 May 1994 and should be directed to: Dr. R. W. Kiger, Hunt Institute, Carnegie Mellon University, Pittsburgh, PA 15213-3890 U.S.A. Tel. (412) 268-2434.