

FINE STRUCTURE OF MISTLETOE POLLEN VI. SMALL-FLOWERED NEOTROPICAL LORANTHACEAE¹

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ABSTRACT

Pollen of small-flowered neotropical Loranthaceae (8 genera; ca. 135 species) was examined in the light, scanning, and transmission electron microscopes. Pollen is typically medium-sized and oblate. Pollen *amb* is more variable than equatorial shape, ranging from trilobate deeply concave to circular. Both isopolar and heteropolar pollen grains occur within the complex, the latter restricted to species of *Phthirusa* and *Struthanthus* in which the apertures differ at each of the polar faces. Simple apertures arranged in a diploaperturate configuration predominate. Such apertures range from diploporate to diplobrevidemicolpate to diplosyn- and diploparasyndemicolpate types. Compound apertures are rare, restricted to *Oryctanthus* and particular species of *Cladocolea* and *Struthanthus*. The (3-)4-5 colpate apertures of *Ixocactus* are unique in the family. Sculpturing is basically uniform with sculpturing elements ranging from perforations to shallow ridges and/or striato-rugulae. Ultrastructurally, the basic ectexine structure is composed of a thin, perforate tectum, granular/columellate interstitium, and a thick continuous foot layer usually twice as thick as the tectum plus interstitium. Pollen data suggest two basic groupings of small-flowered genera: Group I, composed of *Dendropemon*, *Phthirusa* pro parte, and *Oryctanthus*; and Group II, containing *Phthirusa* pro parte, *Cladocolea*, *Struthanthus*, *Maracanthus*, and *Oryctina*. Among Group I genera, *Dendropemon* is closely linked to *Phthirusa* through the species *P. pyrifolia* and *P. platyclada*. *Oryctanthus* is a highly derived genus with only remote ties to other Group I taxa. Among Group II genera, pollen data indicate a close relationship between *Cladocolea* and the Mexican species of *Struthanthus*. Pollen characters of *Ixocactus* indicate no relationship with any small-flowered neotropical genus. Rather its pollen features are closer to those of the Eremolepidaceae and the African species of *Viscum*.

In a previous paper we detailed the pollen of the large-flowered neotropical Loranthaceae (Feuer & Kuijt, 1980). The present paper focuses on pollen characters of the small-flowered genera. Data from these two complexes will be used to analyze pollen evolution among neotropical Loranthaceae.

The small-flowered neotropical complex comprises eight genera: *Struthanthus* (ca. 50 spp.), *Cladocolea* (ca. 25 spp.), *Phthirusa* (ca. 30 spp.), *Dendropemon* (ca. 12 spp.), *Cladocolea* (ca. 25 spp.), *Phthirusa* (ca. 30 spp.) *Dendropemon* (ca. 12 spp.), *Oryctanthus* (10 spp.), *Maracanthus* (2 spp.), *Oryctina* (2 spp.), and *Ixocactus* (1 sp.). The small flower size and generally inconspicuous flower color (often pale green, buff) suggest an insect pollination mechanism, sharply contrasting with the large, showy bird-pollinated flowers of most Old and other New World mistletoes (Kuijt, 1969, 1981a).

In addition to having small flowers, the group

also shows a marked tendency towards unisexual flowers and dioecism. Only three of the eight genera exhibit strictly bisexual flowers (*Oryctanthus*, *Dendropemon*, *Ixocactus*); two genera (*Phthirusa*, *Cladocolea*) include some species with strictly bisexual flowers and others with exclusively unisexual flowers; three genera (*Struthanthus* excluding *S. panamensis*, *Maracanthus*, *Oryctina*) demonstrate only unisexual flowers. Small flower size, the tendency towards unisexual flowers and dioecism, and an $x = 8$ chromosome number (Barlow & Wiens, 1971) together suggest an independent evolution of this group unlike Old World and other New World Loranthaceae.

MATERIALS AND METHODS

Dried flowers were collected from sheets in the following herbaria: A, CAS, F, GH, K, LEA, MO, NY, RB, S, SMU, U, UBC, UC, US, and UT. Pollen was processed according to methods out-

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TABLE 1. Summary of pollen data for small-flowered neotropical Loranthaceae.

Taxon	Size (μm)		Polarity	Shape	
	Polar	Equatorial		<i>Amb</i>	P/E
<i>Cladocolea</i> Tieghem (ca. 25 spp.)	13–31	23–45	isopolar	triangular to rounded convex, rarely slightly concave	0.64–0.70 oblate
<i>Dendropemon</i> Blume (12 spp.)	23–46	38–56	isopolar	triangular slightly to deeply concave	0.52–0.98 oblate, suboblate, rarely oblate spheroidal
<i>Ixocactus</i> Rizz. (1 sp.)					
<i>I. hutchisonii</i> Kuijt					
<i>Cuatrecasas</i> 23970 (F), Colombia	29.7 \pm 0.13 (27.8–32) ^a	36.4 \pm 0.14 (34.2–38.5)	isopolar	circular	0.82 (0.74–0.87) suboblate
<i>Hutchison & Idrobo</i> 3008 (F), Colombia	28.4 \pm 0.09 (27.3–29.8)	32.8 \pm 0.10 (31.1–34)	isopolar	circular	0.86 (0.80–0.93) suboblate
<i>Steyermark et al.</i> 111592 (F), Venezuela	28.1 \pm 0.17 (26.9–30.1)	37.9 \pm 0.11 (36.6–38.6)	isopolar	circular	0.74 (0.69–0.81) oblate
<i>Tamayo</i> 2526 (ILL), Venezuela	—	—	isopolar	circular	—
<i>Maracanthus</i> Kuijt (2 spp.)					
<i>M. chlamydatum</i> (Rizz.) Kuijt					
<i>Steyermark</i> 99522 (UC), Venezuela	17.5 \pm 0.28 (14.4–19.9)	28.9 \pm 0.29 (25.8–29.5)	isopolar	triangular to slightly convex	0.60 (0.46–0.71) oblate
<i>Oryctanthus</i> Eichler (10 spp.)	27–35	45–56	isopolar	triangular rounded convex to circular	0.56–0.70 oblate
<i>Oryctina</i> Tieghem (2 spp.)					
<i>O. subaphylla</i> Rizz.					
<i>Anderson et al.</i> 36949 (RB), Brazil	15.8 \pm 0.11 (14.3–17.8)	24.9 \pm 0.09 (23.2–26.1)	isopolar	triangular rounded convex	0.63 (0.55–0.65) oblate
<i>Phthirusa</i> Martius (ca. 30 spp.)	17–39	27–51	isopolar; heteropolar; isopolar-heteropolar ^b	triangular to slightly concave; trilobate (2 spp.)	0.60–0.77 oblate, suboblate, oblate spheroidal
<i>Struthanthus</i> Martius (ca. 50 spp.)	14–38	28–50	isopolar; heteropolar; isopolar-heteropolar	triangular to rounded convex, rarely concave	0.53–0.91 oblate to suboblate, rarely oblate spheroidal

TABLE 1. Continued.

Apertures	Sculpturing	Exine Structure
simple, compound; diplo- and synaperturate (diploparasyntheticolpate, diploparasyntheticolporate, diplosyntheticolpate, parasyntheticolpate)	psilate-foveolate, low profile striato-rugulate	granular/columellate, granular ^c
simple; diploaperturate (diploporate to diplobrevicolpate)	psilate-imperforate polar exine; psilate-perforate equatorial exine	columellate/baculate
4(-5)-colpate	irregular bifurcating processes and spines	—
4-colpate	irregular bifurcating processes and spines	—
(3-4), 5-colpate	irregular bifurcating processes and spines	granular
4-colpate	irregular bifurcating processes and spines	—
syncolpate	short ridges, low profile striato-rugulate, perforate	columellate/granular
compound(?); diploaperturate (three sagittate slits at each face form the endoapertures)	psilate-imperforate	ektexinous strands traversing narrow osmiophilic zone
diplosyntheticolpate	psilate, foveolate(?), perforate(?)	—
simple; diplo-, rarely synaperturate (1 sp.) (diplosyntheticolpate, diplobrevicolpate, diploporate, diplo-2-demicolpate, syncolpate)	psilate-perforate; short furrows, ridges; low profile striato-rugulate	columellate/granular, columellate/baculate, columellate
simple, compound; diplo- and synaperturate (syncolpate, 3-demicolpate, diplosyntheticolpate, diploparasyntheticolpate, syncolporate, parasyncolporate, diplosyntheticolporate, diplosyntheticolporate, diploparasyntheticolporate)	pronounced striato-rugulate, tectate-perforate with low profile rugulae; psilate-perforate to imperforate	granular, rarely with sporadic columellae

^a Populational mean followed by standard deviation; range in parentheses.^b Occurring within same population.^c Listed in order of dominant interstitial element.

lined in Feuer and Kuijt (1978) with the following addition. For light microscopy, acetolyzed pollen was mounted in glycerine jelly and photographed with a Nikon-UFX system at either 200× or 500× using Agfapan (ASA 25) black and white 35 mm film developed for five minutes at 68°F in Rodinal diluted 1 : 25. Specimens examined with the transmission electron microscope (TEM) are marked with an asterisk.

Aperture terms used in the present paper are briefly defined followed by a listing of all aperture types occurring among the small-flowered genera. The term: 1) demi- is used to describe a pair of apertures running perpendicularly to the equator but not confluent, thus appearing as if each set of apertures were derived by equatorial constriction and subsequent splitting; 2) diplo- is used to denote two sets of apertures (in these cases usually three to a set), each set restricted to a polar face and not continuous across the equator; 3) syn- is used to denote apertures fusing at the pole; and 4) parasyn- refers to apertures bifurcating at the pole, the bifurcations isolating a portion of exine at the center of the polar face. The following aperture combinations occur within the small-flowered complex: syncolpate (e.g., Figs. 83, 84), parasyncolpate (e.g., Figs. 68–71), diplosyndemicolpate (e.g., Fig. 74), diploparasyndemicolpate (e.g., Figs. 74–77), 2- and 3-demicolpate (e.g., Fig. 78), and compound variations (-colporoidate and colporate) of these same types, as well as diploporate (e.g., Figs. 25–29), diplobrevidemicolpate (e.g., Figs. 1, 52) and 3–4–5 colpate (e.g., Figs. 99, 100).

Pollen characters of the small-flowered genera are summarized in Table 1.

GENERIC POLLEN DESCRIPTIONS

Cladocolea Tieghem (Figs. 5–11, 68, 69, 72, 73, 87–89).

TYPE I

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular concave; oblate. Apertures: diplosyndemicolpi; colpi broad, of uniform width, with granular membranes. Sculpturing: short ridges to low profile striato-rugulae. Exine equatorially thickened near apertures.

Species and specimens examined: *Cladocolea inconspicua* (Benth.) Kuijt, *Gentry 7056* (F), Mexico (Sinaloa).

TYPE II

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular to rounded convex; oblate. Apertures: diploparasyndemicolpori; ectoapertures shallow colpi delimiting a prominent round or triangular apocolpium; endoapertures ranging from U-shaped to elliptical slits to large circular subsurface thinnings lying perpendicular to and in midregion of colpi on polar faces. Sculpturing: psilate-foveolate to shallow striato-rugulate. Equatorial exine thickened near apertures.

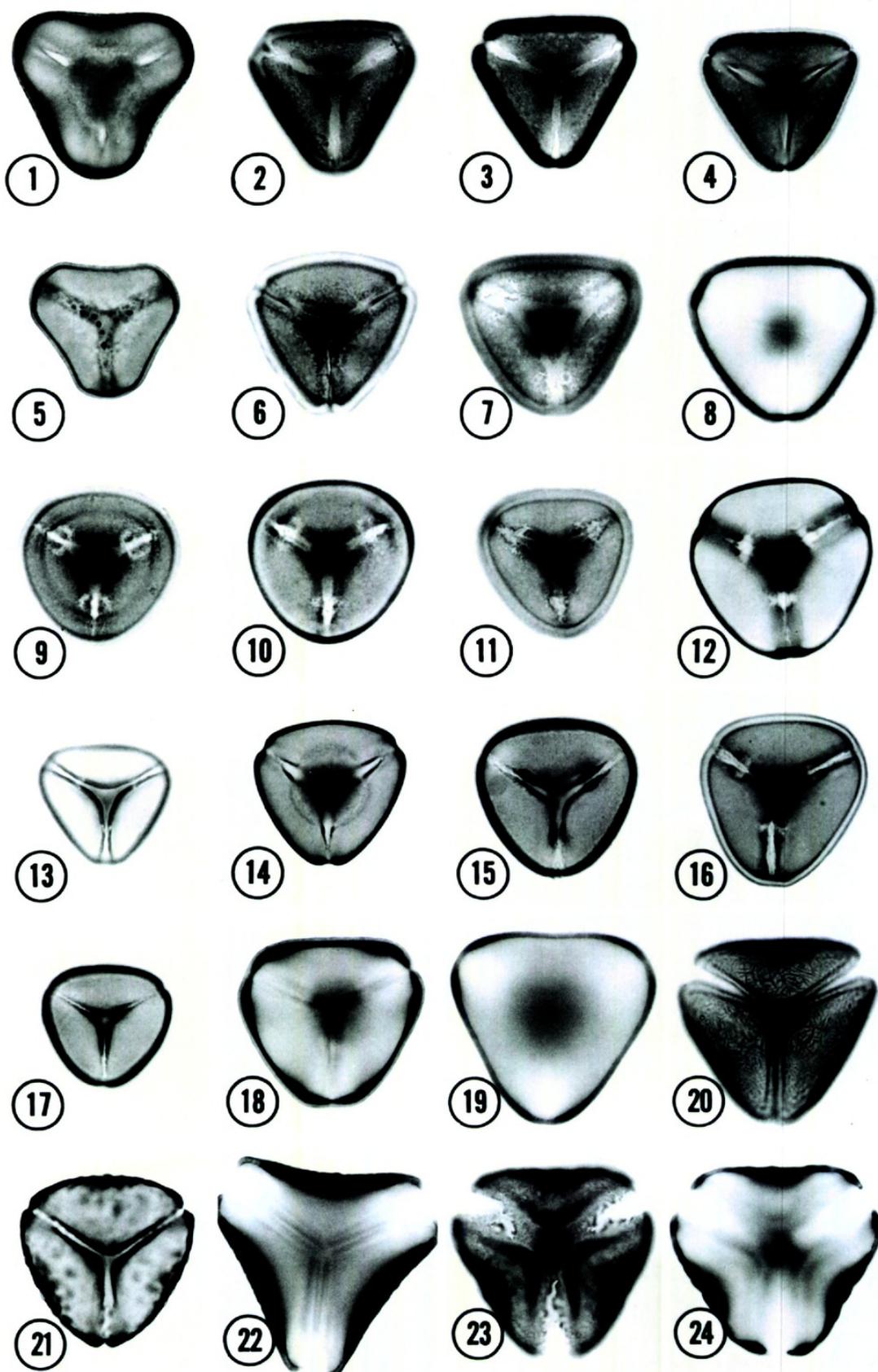
Species and specimens examined: *Cladocolea andrieuxii* Tieghem, *Pringle 10244* (SMU), Mexico (Oaxaca); *C. loniceroides* (Tieghem) Kuijt, *Hinton 3796* (UC), Mexico (Mexico), *Hinton 10500* (GH), Mexico (Guerrero); *C. microphylla* (H.B.K.) Kuijt, **Pringle 4369* (UC), Mexico (Jalisco).

TYPE III

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular to slightly rounded convex; oblate. Apertures: parasyncolpi; colpi delimiting a small apocolpium. Sculpturing: psilate-foveolate to shallow striato-rugulate. Exine evenly thickened at equator.

Species and specimens examined: *Cladocolea*

FIGURES 1–24. Polar views of *Phthirusa* spp. (1–3), *Maracanthus chlamydatus* Rizz. (4), *Cladocolea* spp. (5–11), *Oryctina subaphylla* Rizz. (17), and *Struthanthus* spp. (12–16, 18–24). All light micrographs, ×700.—1. *P. lepidobotrys* Eichler, Jamaica.—2. *P. retroflexa* (Ruíz & Pavón) Kuijt, *Nee & Hansen 14038* (F), Panama. Polar face with protruding colpal margins.—3. *P. retroflexa* (Ruíz & Pavón) Kuijt, *Nee & Hansen 14038* (F), Panama. Opposite polar face of same grain.—4. Focal plane slightly below apocolpial exine.—5. *C. inconspicua* (Benth.) Kuijt.—6. *C. pringlei* Kuijt, *Pringle 4697* (UC), Mexico.—7. *C. andrieuxii* Tieghem. Focal plane at the level of the endoapertures.—8. *C. andrieuxii* Tieghem. Focal plane at the equator. Note prominently thickened exine at the apertures.—9. *C. microphylla* (H.B.K.) Kuijt. Grain with U-shaped endoapertures.—10. *C. microphylla* (H.B.K.) Kuijt. Grain with elliptical endoapertures.—11. *C. loniceroides* (Tieghem) Kuijt, *Hinton 10500* (GH), Mexico.—12. *S. densiflorus* Standley.—13. *S. leptostachyus* (H.B.K.) G. Don, *Skutch 2618* (A), Costa Rica. Grain with barely discernible endoapertures.—14. *S. costaricensis* Standley.—15. *S. palmeri* Kuijt.—16. *S. belizensis* Lundell.—17. Focal plane at apocolpium.—18. *S. oerstedii* Standley, *Barlow 1443* (UC), Costa Rica.—



19. *S. panamensis* (Rizz.) Barlow & Wiens, *Davidson 431* (MO), Panama.—20. *S. concinnus* Martius.—21. *S. uraguensis* (Hook. f. & Arnell) G. Don, *Hatschbach 17641* (UC), Brazil.—22. *S. uraguensis* var. *brevipedunculata* Chodat & Hassler.—23. *S. vulgaris* Martius. Focal plane at the apocolpium.—24. *S. vulgaris* Martius. Focal plane at the equator.

glauca Kuijt, *Borys et al.* 6 (LEA), Mexico (Puebla); *C. grahamii* (Benth.) Tieghem, *Hinton 10149* (GH), Mexico (Oaxaca), *Pringle 6987* (F), Mexico (Mexico); *C. harlingii* Kuijt, **Harling 6094* (S), Ecuador, *Wiens 3781* (LEA, UT), Ecuador, *Wiens 3800* (UT), Ecuador; *C. pringlei* Kuijt, *Breckon & Breckon 803* (GH), Mexico (Oaxaca), *Conzatti 1899* (F), Mexico (Oaxaca), *Pringle 4697* (UC), Mexico (Oaxaca).

TYPE IV

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular; oblate. Apertures: diplo-syndemicolpi. Sculpturing: short ridges to low profile rugulae. Polar faces exhibiting central circular thickening; equatorial exine evenly thickened.

Species and specimens examined: *Cladocolea oligantha* (Standley & Steyererm.) Kuijt, *Rzedowski 22674* (CAS), Mexico (Guerrero).

Endomorphology: ektexine and endexine present. Ektexine organized into tectum, interstitium, and foot layer. Tectum evenly thickened, occasionally foveolate, rarely perforate. Interstitium narrow, typically sparse and finely granulate with short, irregularly shaped columellae sometimes present; in *C. harlingii* interstitium characterized by short projections pendent from tectum or projecting upwards from foot layer, these intercalated between horizontally coalescing ektexinous strands. Foot layer with typically smooth upper surface and shallowly scalloped lower edge. Endexine absent in interapertural equatorial regions, present in central regions of polar faces and regions adjacent to colpi; polar endexine bistratified with upper zone adjacent to foot layer characterized by numerous osmiophilic channels, basal zone slightly thicker, homogeneous; endexine near apertures irregularly thickened, disrupted by numerous small gaps; apertural endexine thin, disrupted, loosely organized into small lamellae or more granular strands.

Tectum/Equatorial interstitium//Foot layer: 1:2.

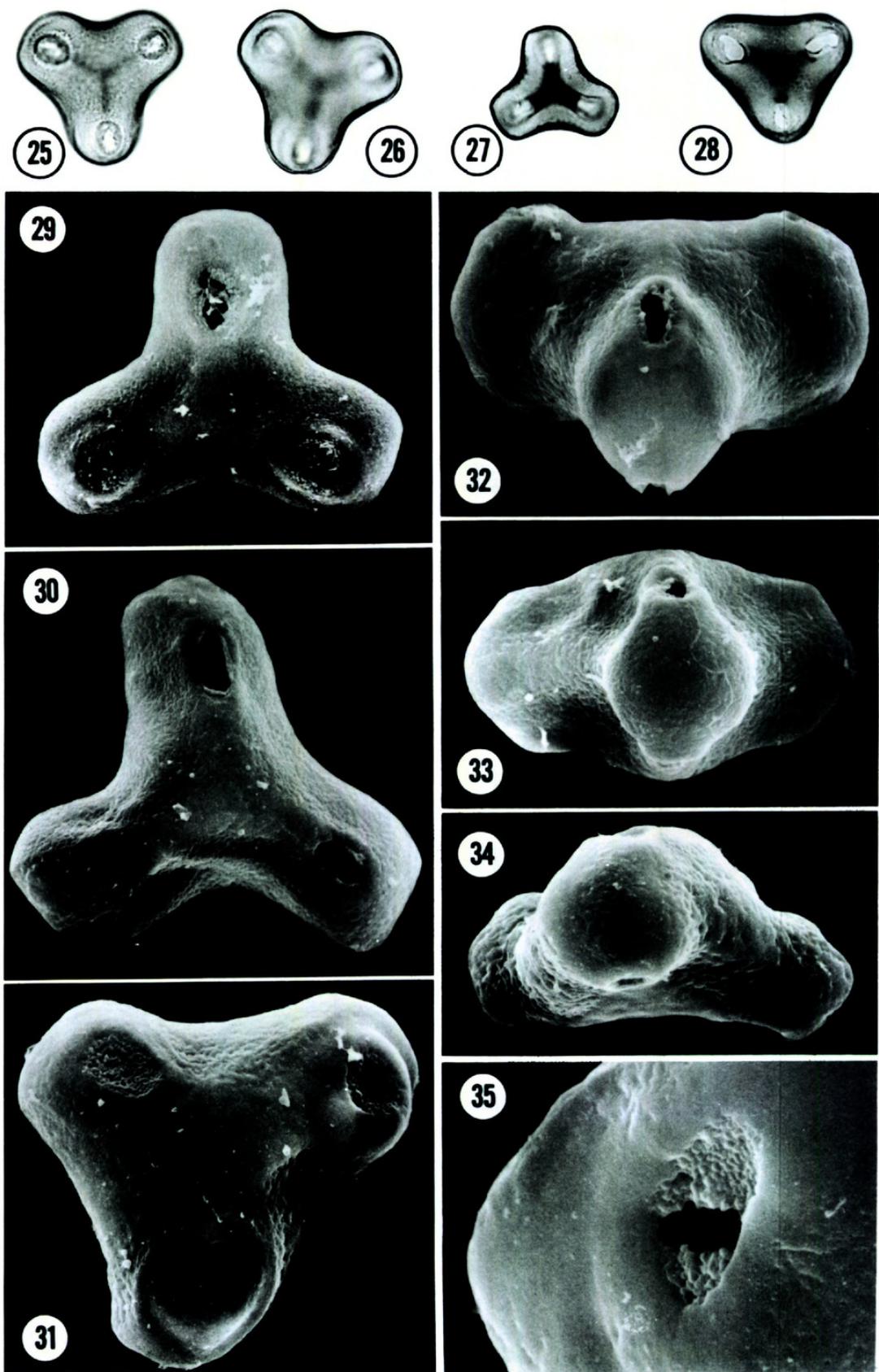
Species and specimens examined: all species listed under exomorphology that are marked by an asterisk.

Dendropemon Blume (Figs. 25, 26, 29, 32, 36–40).

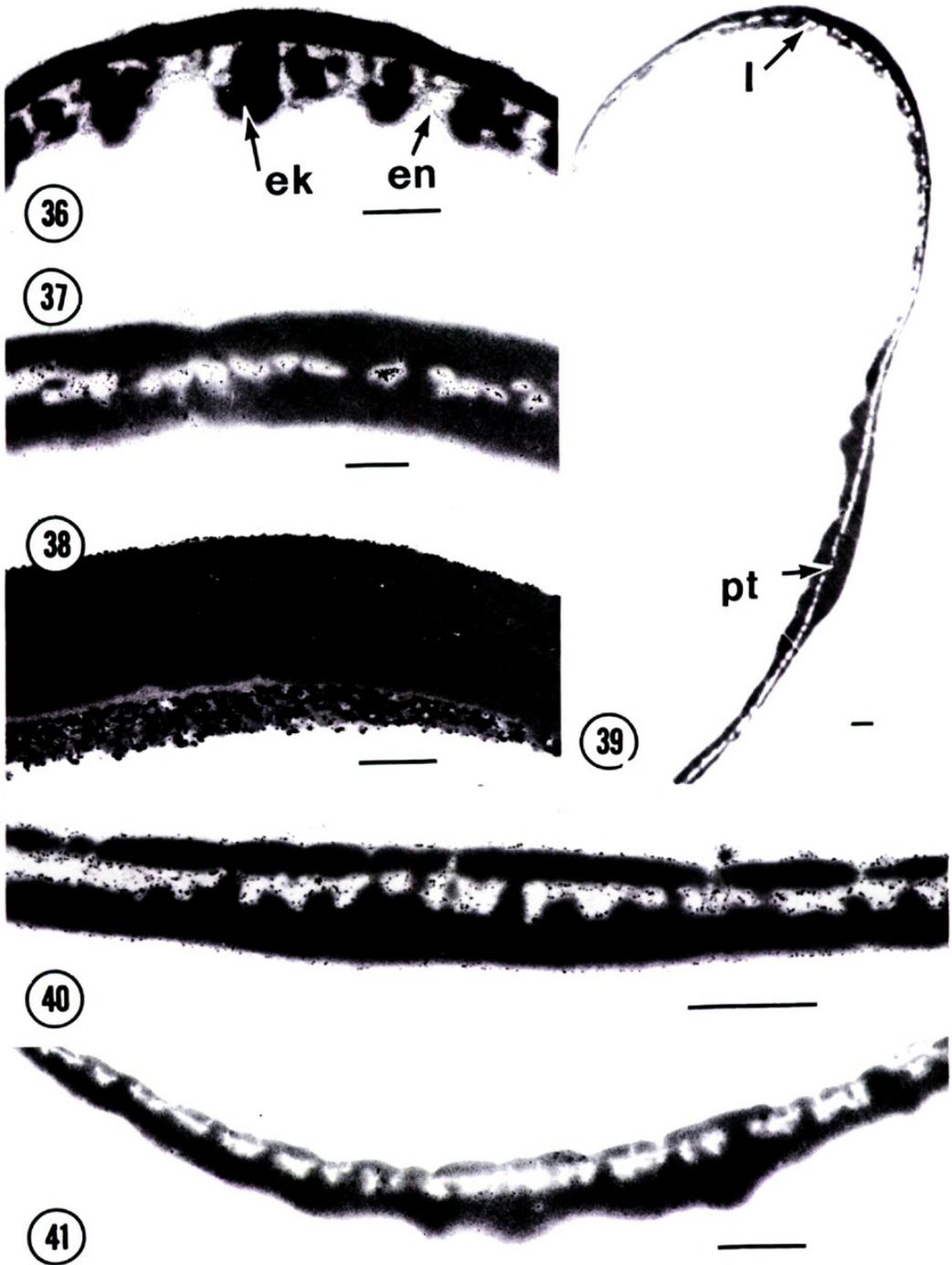
Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular slightly concave to trilobate deeply concave; oblate to suboblate or oblate spheroidal. Grains diploaperturate. Apertures: ranging from elliptical pores to broad brevicolpi, typically restricted to tips of pollen lobes and encircled by subsurface thickened exine continuous with subsurface triradiate polar thickening, membranes disrupted. Sculpturing: psilate imperforate at the polar faces and tips of pollen lobes, exine minutely perforate in interapertural equatorial areas. Exine with triradiate thickening at polar faces and equatorially thickened lobes.

Endomorphology: ektexine and endexine present. Differences in interapertural equatorial, lobar equatorial, and polar ektexine organizations. Interapertural equatorial ektexine organized into tectum, columellate/baculate interstitium, and foot layer. Tectum with narrow perforations. Interstitium exhibiting short, basally thickened columellae interspersed among rounded baculae pendent from tectum or extending up from foot layer. Foot layer thick with smooth upper and lower surfaces. Lobar equatorial ektexine organized into large irregularly shaped ektexinous masses pendent from thick imperforate tectum. Polar ektexine thicker than equatorial ektexine, bistratified; upper stratum imperforate with smooth upper surface; lower stratum significantly thicker, upper surface slightly granular; strata separated by a narrow, poorly defined zone often filled with granules and occasionally bridged by extremely narrow short columellae. Endexine ranging from thick, continuous and coarsely granular to thin and locally absent beneath the

FIGURES 25–35. Comparisons between *Dendropemon* Blume and *Phthirusa* Martius (LM, SEM). 25, 26, 29, 32. *Dendropemon* spp. 27, 28, 30, 31, 33–35. *Phthirusa* spp.—25. *D. uniflorus* Steud., *Leonard et al.* 15026 (UC), Haiti. Focal plane just below the apocolpial exine, $\times 500$.—26. *D. uniflorus* Steud., *Leonard et al.* 15026 (UC), Haiti. Light micrograph with focal plane at equator, $\times 500$.—27. *P. platyclada* Ule. Light micrograph with focal plane just below the apocolpial exine, $\times 500$.—28. *P. pyrifolia* (H.B.K.) Eichler, *Greenhouse-collected* Kuijt, Costa Rica. Light micrograph with focal plane just below the apocolpial exine, $\times 500$.—29. *D. purpureus* Krug & Urban, *Liogier 15253* (F), Hispaniola. Polar view, $\times 1,330$.—30. *P. platyclada* Ule. Polar view, $\times 2,000$.—31. *P. pyrifolia* (H.B.K.) Eichler, *Greenhouse-collected* Kuijt, Costa Rica. Polar view, $\times 2,080$.—32. *D. constantiae*



Krug & Urban. Equatorial view, $\times 1,400$.—33. *P. platyclada* Ule. Equatorial view, $\times 2,000$.—34. *P. pyrifolia* (H.B.K.) Eichler, *Greenhouse-collected Kuijt*, Costa Rica. Equatorial view, $\times 2,100$.—35. *P. pyrifolia* (H.B.K.) Eichler, *Greenhouse-collected Kuijt*, Costa Rica. Detail of aperture. Note the symmetrical break in the aperture membrane, $\times 6,000$.



FIGURES 36–41. Ultrastructural comparisons between *Dendropemon* Blume (36–40) and *Phthirusa* Martius (41) (TEM).—36. *D. bahamensis* Britton. Detail of lobar exine. The ektexine (ek) is organized into irregularly shaped pendent structures connected by thin strands of endexine (en), $\times 9,000$.—37. *D. bahamensis* Britton. Detail of polar exine, $\times 7,500$.—38. *D. pycnophyllus* Krug & Urban. Detail of polar exine exhibiting well-developed endexine, $\times 9,750$.—39. *D. bahamensis* Britton. Section through polar thickening (pt) and adjacent lobe (l), $\times 2,400$.—40. *D. bahamensis* Britton. Detail of equatorial exine revealing columellate/baculate interstitium and narrow stratum of endexine, $\times 16,100$.—41. *P. platyclada* Ule. Ektexine composed of sporadic, irregularly shaped columellae and irregularly thickened foot layer, $\times 11,000$. All lines in micrographs equal 1 μm .

polar faces, thinning in lobar regions present here as thin strands connecting lower surfaces of irregularly shaped ektexinous segments, typically absent in interapertural equatorial areas, but in some species (e.g., *D. bahamensis*) present as a thin continuous stratum.

Tectum/Equatorial interstitium//Foot layer: 1:3 to 2:1.

Species and specimens examined: *Dendropepon bahamensis* Britton, **Popenoe* 5 (A), Bahama Is.; *D. caribaeus* Krug & Urban, Britton et al. 45 (MO), West Indies (St. Thomas), Duss 2419 (GH), West Indies (Guadeloupe); *D. constantiae* Krug & Urban, Cicero et al. 6040 (MO), Hispaniola; *D. emarginatus* Steud., Correll 44095 (MO), Bahama Is., Correll & Correll 47922 (F), Bahama Is. (Great Exuma), Smith et al. 3345 (F), Cuba; *D. pauciflora* Tieghem, Maxon 8761 (GH), Jamaica; *D. picardiae* Krug & Urban, Ekman H12947 (GH), Hispaniola; *D. purpureus* Krug & Urban, Liogier 15253 (F), Hispaniola, Wilson 7647 (F), Bahama Is. (Caicos Is.); *D. pycnophyllus* Krug & Urban, *Liogier 17966 (F), Hispaniola; *D. rostratus* Urban, Ekman H10199 (GH), Hispaniola; *D. uniflorus* Steud., Leonard & Leonard 12470 (MO), Haiti (Tortue Is.), Leonard et al. 15026 (UC), Haiti.

***Ixocactus* Rizz. (Figs. 98–104).**

Exomorphology: radial symmetry, isopolar. Shape: *amb* circular; oblate, suboblate rarely oblate spheroidal. Apertures: colpi, varying in number within and among populations from (3 to) 4 to 5 colpate. Sculpturing: densely clustered blunt-tipped spines and more irregularly shaped often bifurcating segments. Exine thickest in interapertural equatorial regions thinning slightly near apertures.

Endomorphology: ektexine and endexine present. Non-apertural ektexine exhibiting two types of organization on same grain: Type I with bi-stratified ektexine; upper stratum composed of variably thick, solid, broad, frequently irregularly branching segments, the branches sometimes elaborated into blunt-tipped spines; basal stratum solid, variably thick with granular upper and slightly scalloped lower surfaces; both strata separated by extremely narrow, sparsely granular interstitium; and Type II, composed of a basically single stratum of ektexine similar in structure to Type I resting on small, highly channeled, loosely aggregated ektexinous segments randomly attached to lower surface of upper ektexine.

Endexine, beneath Type I ektexine, solid, continuous irregularly thickened but, beneath Type II, organized into loosely arranged, small isolated segments attached to ektexine.

Tectum/Equatorial interstitium//Foot layer: 4:1 (Type I ektexine).

Species and specimens examined: *Ixocactus hutchisonii* Kuijt, Cuatrecasas 23970 (F), Colombia, *Hutchison & Idrobo 3008 (F), Colombia, Steyermark et al. 111592 (F), Venezuela, Tamayo 2526 (ILL), Venezuela.

***Maracanthus* Kuijt (Figs. 4, 50, 53, 67).**

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular to slightly convex; oblate. Apertures: syncolpi; colpi narrow, shallow, slightly broader on the polar faces, narrowing at the equator. Sculpturing: short ridges, low profile striato-rugulae, exine foveolate and perforate, these most common in interapertural equatorial areas; polar faces psilate, imperforate. Exine thickened in a circular configuration directly at the center of the polar faces.

Endomorphology: ektexine and endexine present. Slight structural differences between equatorial and polar ektexine. Equatorial ektexine organized into tectum, columellate/granular interstitium, and foot layer. Tectum evenly thickened, foveolate, perforate, and channeled, the latter thin and not continuous through tectum. Interstitium clearly defined, composed of irregularly thickened columellae interspersed among baculae and baculae-like structures, the latter pendent from the tectum and surrounded by a finely granular matrix. Foot layer discontinuous in small localized areas, extremely thick, with a smooth upper surface and sporadically scalloped lower edge. Polar ektexine thinner than equatorial ektexine, organized into a thick, rarely perforate or foveolate tectum and poorly delimited, predominantly granular interstitium exhibiting a few short, irregularly thickened columellae. Foot layer thinner than that in equatorial areas, irregularly thickened, highly scalloped lower edge. Endexine present at the polar faces and beneath apertures but typically absent in equatorial areas though sometimes filling the small gaps in lower edge of foot layer.

Tectum/Equatorial interstitium//Foot layer: 1:2.

Species and specimens examined: *Maracanthus chlamydatus* (Rizz.) Kuijt, *Steyermark 99522 (UC), Venezuela.

Oryctanthus Eichler (Figs. 42–49).

Exomorphology: radial symmetry, isopolar. Shape: *amb* circular; polar face characterized by three circular depressions each bounded by a narrow, raised rounded ridge, the ridges confluent at the center of the polar face forming a triradiate configuration; equatorial ridge also present; oblate. Grains compound diploaperturate. Apertures: ectoaperture a short, elliptical colpus; endoaperture a sagittate opening; apertures placed 120° apart at the tips of the triradiate central ridge and between the ridges which encircle each of the polar depressions. Sculpturing: psilate, imperforate with loosely granular exine occasionally present in depressed circular polar areas. Exine thickened in equatorial areas aligned with apertures and in the center of each of the three circular polar depressions.

Endomorphology: ektexine and endexine present. Ektexine typically bistratified, organized into upper and lower solid strata separated by a narrow, highly undulate, osmiophilic layer; strata connected by numerous, sporadic, extremely short strands of ektexine; equatorial ridges formed by the outward looping and subsequent appression or fusion of the bistratified ektexine; ektexinous strata at the base of the polar depressions separated by a broad, coarsely granular zone, the upper stratum giving rise to a thin network of fine, randomly anastomosing granules. Endexine not continuous around grain, absent beneath polar depressions but prominent and irregularly thickened directly beneath equatorial ridges, thin and locally discontinuous in nondepressed polar areas; apertural endexine thin, loosely granular.

Tectum/Equatorial interstitium//Foot layer: 1:1.

Species and specimens examined: *Oryctanthus alveolatus* (H.B.K.) Kuijt, *Steyermark 87665* (GH), Venezuela; *O. asplundii* Kuijt, *Prance et al. 7284* (UT), Brazil; *O. cordifolius* (Presl) Urban, *Fryxell 683a* (UT), Mexico, **Kuijt 2571* (UBC), Costa Rica; *O. florulentus* (Rich.) Urban, *Broadway 681* (GH), French Guiana, *Wiens 3741* (UT), Ecuador; *O. occidentalis* (L.) Eichler, *Kuijt*

2440 (UBC), Costa Rica; *O. phanerolomus* (Standley) Kuijt, *Gentle 1405* (GH), British Honduras; *O. spicatus* (Jacq.) Eichler, **Killip & Smith 16807* (GH), Colombia.

Oryctina Tieghem (Fig. 17).

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular slightly convex; oblate. Apertures: diplosyndemicolpi; colpal membranes slightly disrupted on polar faces approaching equator, demicolpi separated by extremely narrow bridge of exine at equator. Sculpturing: psilate, foveolate and perforate(?). Exine evenly thickened at equator, slightly thicker along colpal margins at centers of polar faces.

Endomorphology: not examined.

Species and specimens examined: *Oryctina subaphylla* Rizz., *Anderson, Stieber & Kirkbride 36949* (RB), Brazil.

Phthirusa Martius (Figs. 1–3, 27, 28, 30, 31, 33–35, 41, 51, 52, 54–56).

TYPE I

Exomorphology: similar to *Dendropemon* spp. with *Phthirusa* species differing by smaller grain size.

Endomorphology: similar to that of *Dendropemon* spp., particularly *D. bahamensis*.

Tectum/Equatorial interstitium//Foot layer: 1:1.66.

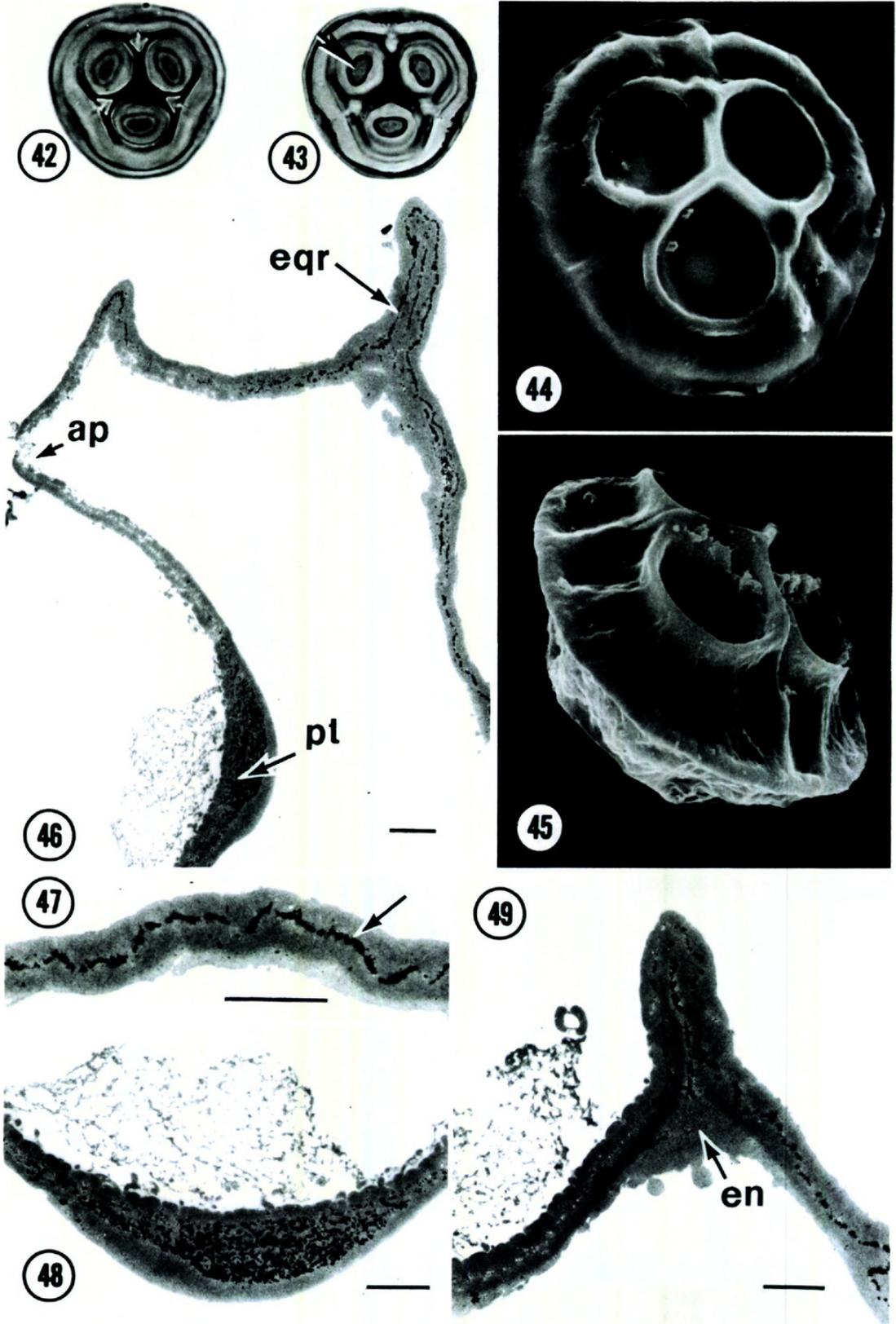
Species and specimens examined: *Phthirusa pyrifolia* (H.B.K.) Eichler, *Croat 18038* (LEA), Peru, *Revilla 2173* (MO), Peru, **Greenhouse* (collected Kuijt), Costa Rica; *P. platyclada* Ule, **Asplund 12376* (S), Peru.

TYPE II

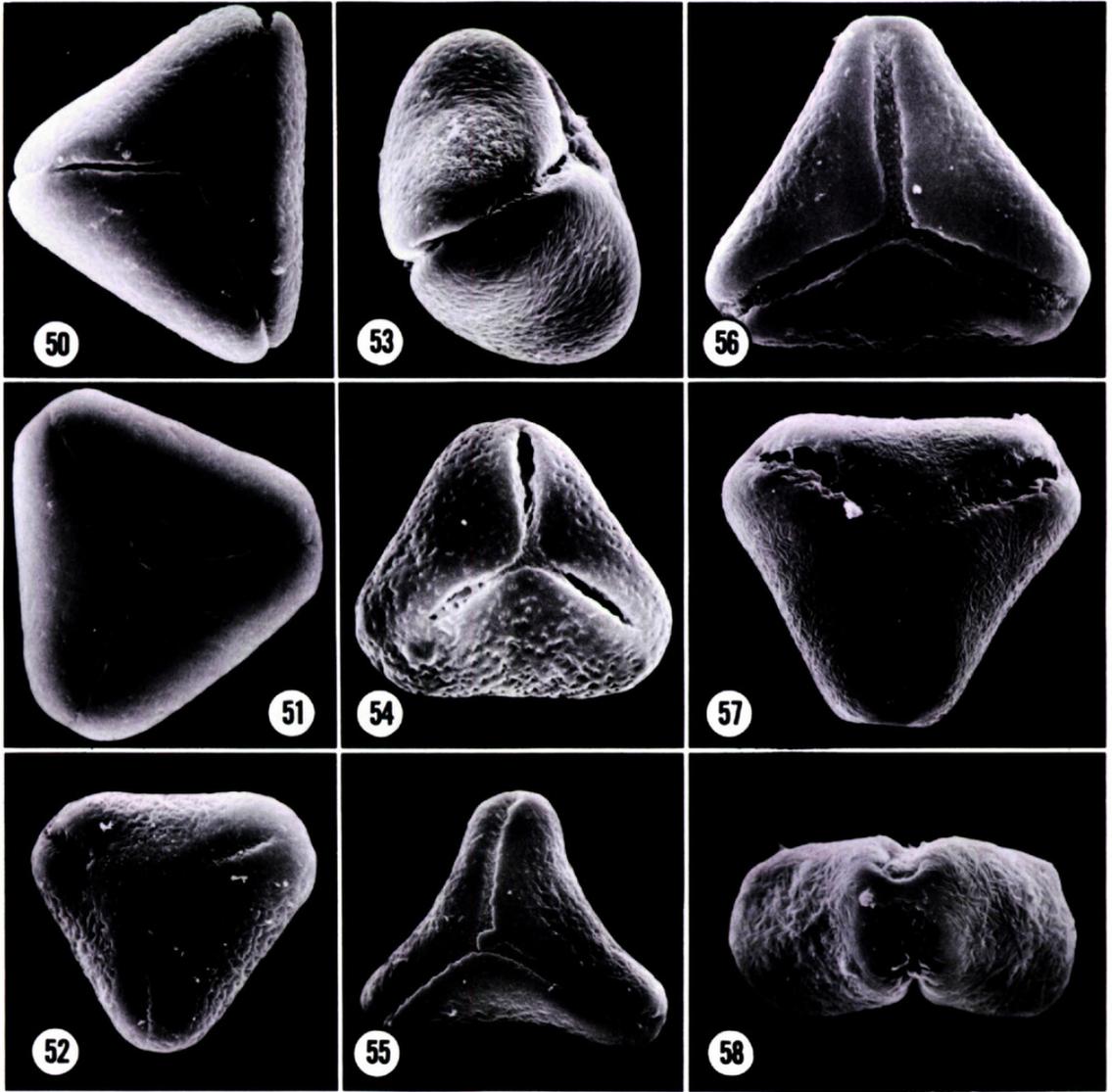
Exomorphology: radial symmetry, iso- and/or heteropolar. Shape: *amb* triangular to slightly concave; oblate to suboblate. Differences in polarity, aperture types and sculpturing distinguish the following subtypes:

Subtype A. Grains isopolar. Apertures: dip-

FIGURES 42–49. *Oryctanthus* Eichler. 42, 43. *O. spicatus* (Jacq.) Eichler. 44–49. *O. cordifolius* (Presl) Urban, *Kuijt 2571* (UBC), Costa Rica.—42. Light micrograph (LM) with focal plane at the level of the triradiate polar thickening revealing three sagittate apertures, $\times 500$.—43. LM with focal plane at the equator clearly revealing central polar thickenings in each of the polar depressions (arrowhead), $\times 500$.—44. Polar view. The sagittate apertures, though prominent in the LM, are barely discernible in the SEM, $\times 1,340$.—45. Oblique equatorial view revealing equatorial ridge and raised polar thickening, $\times 1,535$.—46. Thin section perpendicular to polar



face through a polar depression including its central thickening (pt), an adjacent aperture (ap), and equatorial ridge (eqr), $\times 6,000$.—47. Detail of polar exine. Narrow bands of ektexine (arrow) connect the ektexinous strata, $\times 14,000$.—48. Detail of polar thickening which lies at the center of each of the polar depressions. In some species a finely granular matrix is attached to the tectum, $\times 8,700$.—49. Detail of equatorial ridge adjacent to polar depression revealing looped appressed ektexine and thickened endexine (en), $\times 8,700$. All lines in micrographs equal $1 \mu\text{m}$.



FIGURES 50–58. Comparisons between *Maracanthus* Kuijt and *Phthirusa* Martius (SEM). 50, 53. *Maracanthus chlamydatus* (Rizz.) Kuijt. 51, 52, 54–58 *Phthirusa* spp.—50. Polar view of syncolpate grain, $\times 1,250$.—51. *P. coarctata* A. C. Smith. Polar view of diplosyndemicolpate grain (Type II-A), $\times 1,330$.—52. *P. lepidobotrys* Eichler. Polar view of 3-diplodemibrevicolpate grain (Type II-B3), $\times 1,250$.—53. Oblique equatorial view, $\times 1,250$.—54. *P. micrantha* Eichler. Polar view of diplosyndemicolpate grain (Type II-A), $\times 1,500$.—55. *P. magdalenae* (Cham. & Schldl.) Eichler. Polar view showing protruding colpal margin of diplosyndemicolpate grain (Type II-C1), $\times 1,250$.—56. *P. ovata* (Pohl) Eichler. Polar view of diplosyndemicolpate grain (Type II-B2), $\times 1,250$.—57. *P. theloneura* Eichler. Diplosyndemicolpate grain (Type II-C2). Polar view, $\times 1,200$.—58. *P. theloneura* Eichler. Equatorial view, $\times 1,200$.

losyndemicolpi; colpi terminating subequatorially, broadening near equator with membranes frequently disrupted. Sculpturing: psilate, exine perforate and foveolate, these occurring randomly, tending to be more numerous in equatorial than polar areas.

Species and specimens examined: *Phthirusa coarctata* A. C. Smith, *Smith 2204* (U), British Guiana; *P. micrantha* Eichler, *Carreira 31* (RB), Brazil, *Spruce 1782* (K), Brazil; *P. monetaria*

Sandw., *Forest Dept. #2942* (K), British Guiana; *P. sandwithii* Maguire, *Sandwith 1404* (K), British Guiana.

Subtype B. Grains isopolar. Sculpturing: numerous randomly arranged short furrows and perforations frequently surrounded by low coarse ridges. Exine bordering apertures and apocolpium (when present), psilate, imperforate. Differences in apertures distinguish the following species:

B1. Apertures: syncolpi.

Species and specimens examined: *Phthirusa squamulosa* Klotzsch ex Eichler, *Maguire & Stahl 24972 (F), Surinam.

B2. Apertures: diplosyndemicolpi; colpi narrow becoming slightly broader near equator.

Species and specimens examined: *Phthirusa ovata* (Pohl) Eichler, *Irwin et al. 7974 (UC), Brazil; *P. rufa* var. *tentaculifera* Rizz., Ducke 26 (RB), Brazil, *Ducke 1919 (K), Brazil.

B3. Apertures: 3-diplobrevidemicolpi; colpi displaced entirely onto polar faces, forming large psilate, imperforate apocolpia.

Species and specimens examined: *Phthirusa lepidobotrys* Eichler, *Nichols s.n. (K), Jamaica.

Subtype C. Grains iso- and/or heteropolar with respect to apertures. Isopolar grains diplosyndemicolpate. Heteropolar grains with one polar face syndemicolpate, opposite face 3-demicolpate, rarely 2-demicolpate, the latter through extrusion of a colpal margin and subsequent fusion with opposite colpal border. Sculpturing: ranging from ridges to striato-rugulae on same grain; ridges short, undulating, largely confined to midequatorial regions; striato-rugulae in low relief, largely confined to areas bordering psilate margins of colpi. Differences in polarity distinguish the following species:

C1. Grains isopolar and heteropolar within populations.

Species and specimens examined: *Phthirusa lobatae* Ferrari, Steyermark et al. 120118 (MO), Venezuela; *P. magdalenae* (Cham. & Schldl.) Eichler, *Langenheim 3101 (UC), Colombia; *P. retroflexa* (Ruíz & Pavón) Kuijt, Gentry & Berry 14667 (MO), Venezuela, *Nee & Hansen 14038 (F), Panama.

C2. Grains isopolar.

Species and specimens examined: *Phthirusa krukovii* A. C. Smith, Krukoff 5938 (A), Brazil; *P. retroflexa* (Ruíz & Pavón) Kuijt, *Allen 80 (MO), Colombia; *P. theloneura* Eichler, *Spruce s.n. (K), Brazil.

C3. Grains heteropolar.

Species and specimens examined: *Phthirusa angulata* Krause, Maguire & Fanshawe s.n. (K), British Guiana; *P. jamaicensis* Krug & Urban, Purdie (K), Jamaica; *P. stenophylla* Eichler, Spruce 3307 (GH), Brazil.

Endomorphology: exine organization similar to that of *Maracanthus*. *Phthirusa* species differ in the following characters: 1) tectum ranges from highly to rarely perforate; 2) a strictly columellate

interstitium exists in several species where the columellae, though small and sporadic, are not associated with granular elements; and 3) continuous foot layer.

Tectum/Equatorial interstitium//Foot layer: 1:1.33.

Species and specimens examined: all species listed under exomorphology that are marked by an asterisk.

Struthanthus Martius (Figs. 12–16, 18–24, 70, 71, 74–86, 90–97).

TYPE I

Exomorphology: radial symmetry, grains isopolar or heteropolar. Shape: *amb* triangular to triangular convex; oblate, suboblate, rarely oblate spheroidal. Apertures: compound. Ectoaperture a smooth-margined colpus. Endoaperture ranging from a small well-developed rectangular to elliptical slit to an obscurely margined area lying perpendicular to and in midregion of ectocolpus on the polar faces. Sculpturing: psilate-imperforate to perforate or rarely low profile striato-rugulae. Differences in apertures and polarity distinguish the following subtypes:

Subtype A. Endoapertures well developed.

A1. Grains isopolar; diplosyndemicolporate.

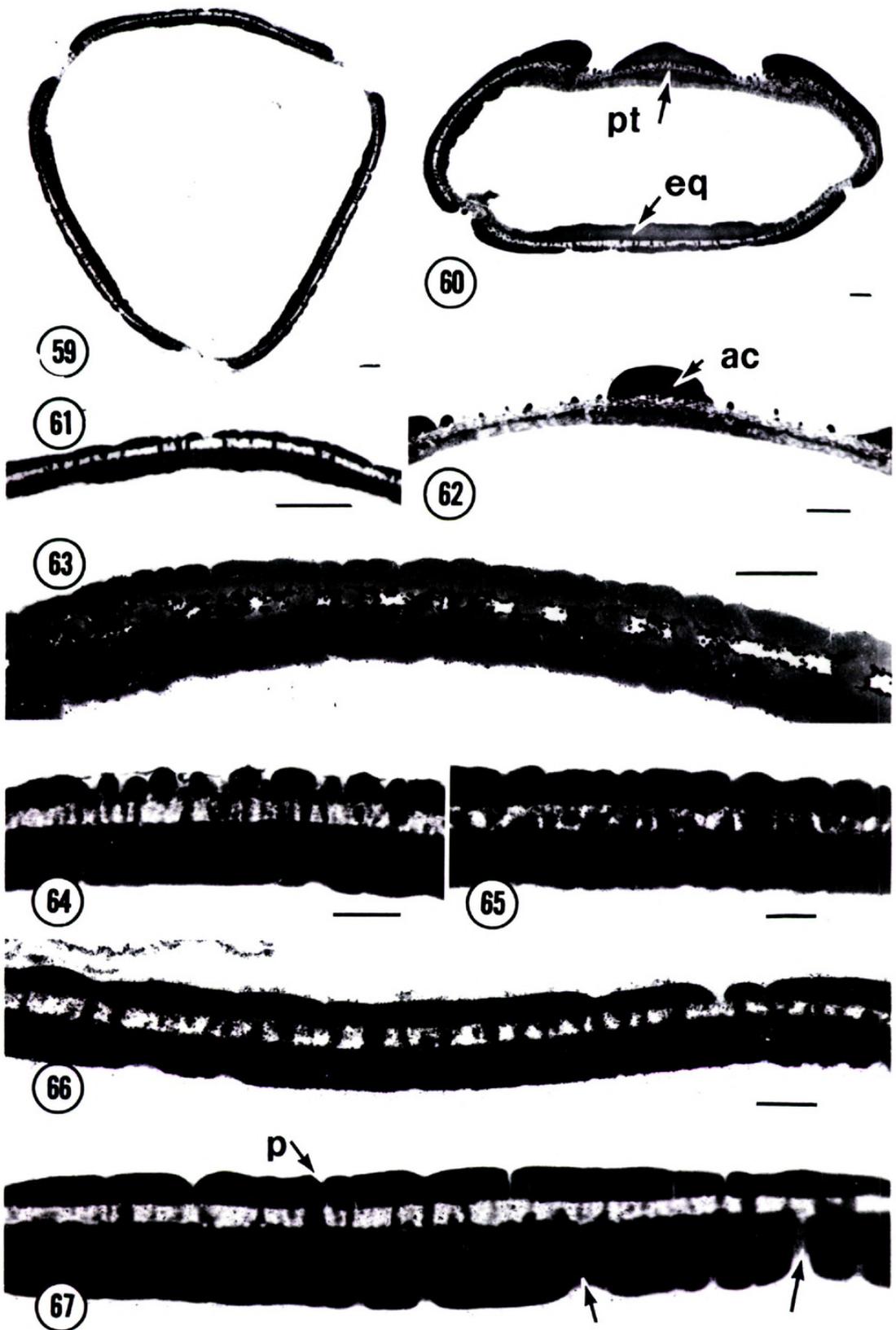
Species and specimens examined: *Struthanthus belizensis* Lundell, *Lundell 6273 (SMU), British Honduras; *S. densiflorus* Standley, *Moore & Wood 3666 (UC), Mexico (Hidalgo); *S. leptostachyus* (H.B.K.) G. Don, Mori & Kallunki 5308 (LEA), Panama; *S. quercicola* (Cham. & Schldl.) Blume, *Barlow 1429 (UT), Costa Rica, Chrysler 5031 (F), Costa Rica, Smith A519, 11479 (F), Costa Rica; *S. rotundatus* Rizz., Lewis et al. 600 (MO), Panama, Nee 10651, 14137 (MO), Panama.

A2. Grains heteropolar with respect to apertures; diploaperturate: one polar face parasyndemicolporate, opposite face either syndemicolporate or 3-demicolporate.

Species and specimens examined: *Struthanthus dichotrianthus* Eichler, *Smith 1279 (MO), Colombia, Woytkowski 8269 (UC), Peru.

A3. Grains isopolar; syncolporate.

Species and specimens examined: *Struthanthus orbicularis* (H.B.K.) Blume, Barlow 1507 (UT), Costa Rica, *Burger & Baker 10095 (F), Costa Rica; Williams 16049 (F), Costa Rica; Ortiz 798 (UC), Guatemala.



FIGURES 59–67. Ultrastructural comparisons between *Phthirusa* Martius and *Maracanthus* Kuijt (TEM). 59–62. *Phthirusa ovata* (Pohl) Eichler. 63–66. *Phthirusa* spp. 67. *Maracanthus chlamydatus* (Rizz.) Kuijt.—59. Section through equator, $\times 4,500$.—60. Section through polar thickening (pt) at the apocolpium and opposite equatorial exine (eq), $\times 3,200$.—61. Detail of equatorial exine revealing short, sparsely distributed columellae, $\times 11,250$.—62. Detail of apocolpial exine (ac), $\times 6,000$.—63. *P. theloneura* Eichler. Detail of equatorial exine,

Subtype B. Endoapertures poorly developed with often obscure margins.

B1. Grains isopolar; diplosyndemicolporoidate.

Species and specimens examined: *Struthanthus escuintlensis* Lundell, *Matuda 4185* (A), Mexico (Chiapas); *S. leptostachyus* (H.B.K.) G. Don, *Skutch 2618* (A, US), Costa Rica; *S. macrostachyus* Lundell, *Breedlove 25943* (MO), Mexico (Chiapas), *Janzen s.n. acc. #303522* (UC), Mexico (Oaxaca).

B2. Grains heteropolar; diploaperturate; one polar face parasyndemicolporoidate, opposite face either syndemicolporoidate or demicolporoidate.

Species and specimens examined: *Struthanthus marginatus* (Desr.) Blume, **Barlow 1420* (UC), Costa Rica, *Thorne & Lathrop 40173* (UT), Mexico (Chiapas).

B3. Grains heteropolar; synaperturate, one polar face parasyncolporoidate, opposite face syncolporoidate.

Species and specimens examined: *Struthanthus deppeanus* (Cham. & Schldl.) Blume, **Balls 4340* (A), Mexico (Veracruz).

TYPE II

Exomorphology: radial symmetry, grains isopolar or heteropolar, rarely subisopolar. Shape: oblate, suboblate, rarely oblate spheroidal. Apertures simple, diplo- or synaperturate, the colpi sometimes broader in midregions of polar faces narrowing at the equator. Sculpturing: psilate-perforate and/or foveolate, rarely low profile striato-rugulae. Differences in *amb*, aperture characters, and patterns of exine thickening distinguish the following species:

Subtype A. Grains isopolar; triangular to rounded convex; syncolpate; exine evenly thickened around grain.

Species and specimens examined: *Struthanthus costaricensis* Standley, **Barlow 1402* (UC, UT), Costa Rica; *S. interruptus* (H.B.K.) Blume, *Nagel 8026* (GH), Mexico (Morelos).

Subtype B. Grains isopolar rarely subisopolar (*S. cassythoides*) the latter with one polar face

less rounded convex than opposite face; triangular rounded convex; diploparasyndemicolpate; exine evenly thickened around equator but thinning beneath colpi at periphery of polar faces.

Species and specimens examined: *Struthanthus cassythoides* Millsp. ex Standley, *Gentle 1660* (UC), British Honduras; *S. palmeri* Kuijt, **LeSueur 1071* (F, GH), Mexico (Chihuahua).

Subtype C. Grains isopolar; triangular to concave; diplosyndemicolpate; exine thinning in midequatorial regions and beneath colpi in peripheral regions of polar faces, thickening near apertures in equatorial areas and at centers of polar faces.

Species and specimens examined: *Struthanthus oerstedii* Standley, *Barlow 1443* (UC, UT), Costa Rica, *Howell 10243* (F), Costa Rica, *Utley et al. 2701* (F), Costa Rica; *S. panamensis* (Rizz.) Barlow & Wiens, **Davidson 431* (MO, US), Panama, *Luteyn 3786* (F), Panama.

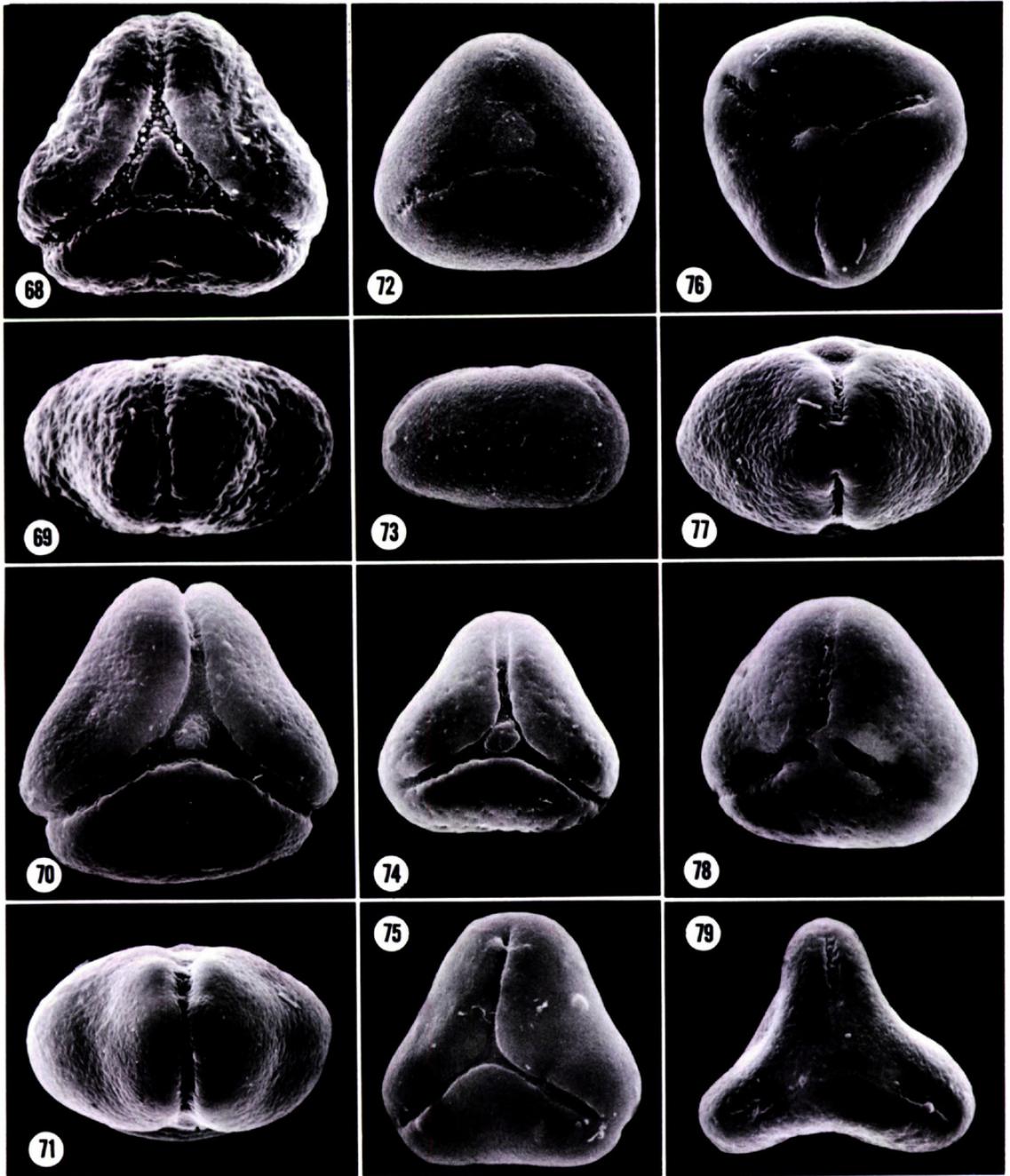
Endomorphology: ektexine and endexine present. Ektexine organized into tectum, interstitium, and foot layer. Tectum regularly thickened, rarely perforate. Interstitium narrow, poorly defined, coarsely granular occasionally exhibiting irregularly shaped columellae and columellae-like structures. Foot layer continuous, with an uneven upper surface and typically smooth lower surface showing an occasional small gap. Endexine present at polar faces and beneath apertures, rarely present in interapertural areas and then only filling gaps in lower edge of foot layer; polar endexine slightly thicker than apertural endexine, homogeneous.

Tectum/Equatorial interstitium//Foot layer: 1:1.

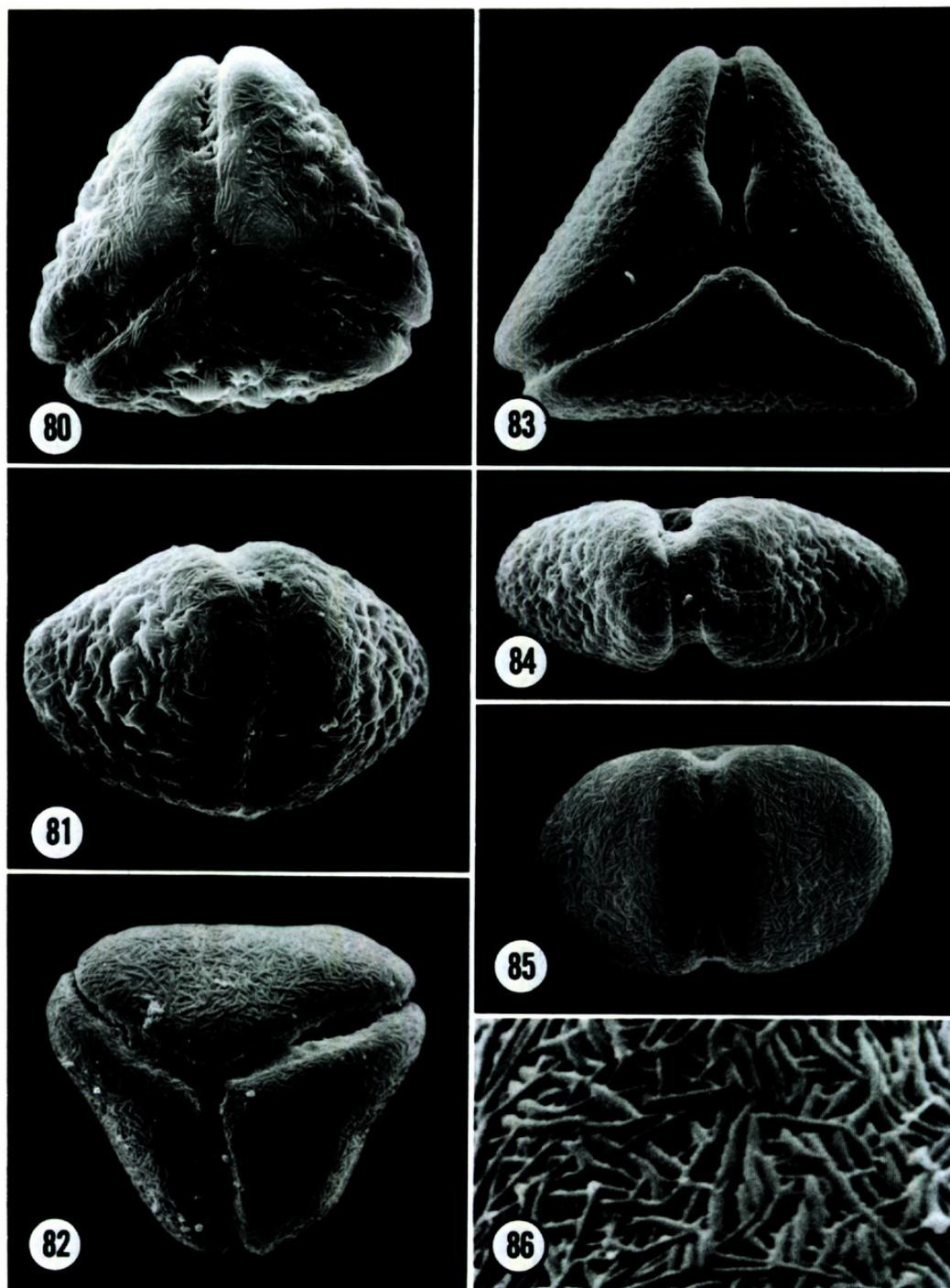
Species and specimens examined: all species marked by an asterisk and exhibiting Types I and II exomorphologies, excluding *S. panamensis*.

Endomorphology: ektexine and endexine present. Ektexine organized into tectum, interstitium, and foot layer. Tectum irregularly thick-

←
 ×11,000.—64. *P. rufa* var. *tentaculifera* Rizz., *Ducke 1919* (K), Brazil. Detail of equatorial exine, ×8,700.—65. *P. magdalenae* (Cham. & Schldl.) Eichler. Detail of equatorial exine, ×6,900.—66. *P. retroflexa* (Ruíz & Pavón) Kuijt, *Nee & Hanson 14038* (F), Panama. Detail of equatorial exine, ×7,200.—67. Detail of equatorial exine. Note interrupted foot layer filled with endexine (long arrow) and localized endexine along lower surface of foot layer (short arrow). Perforation (p), ×8,000. All lines in micrographs equal 1 μm.



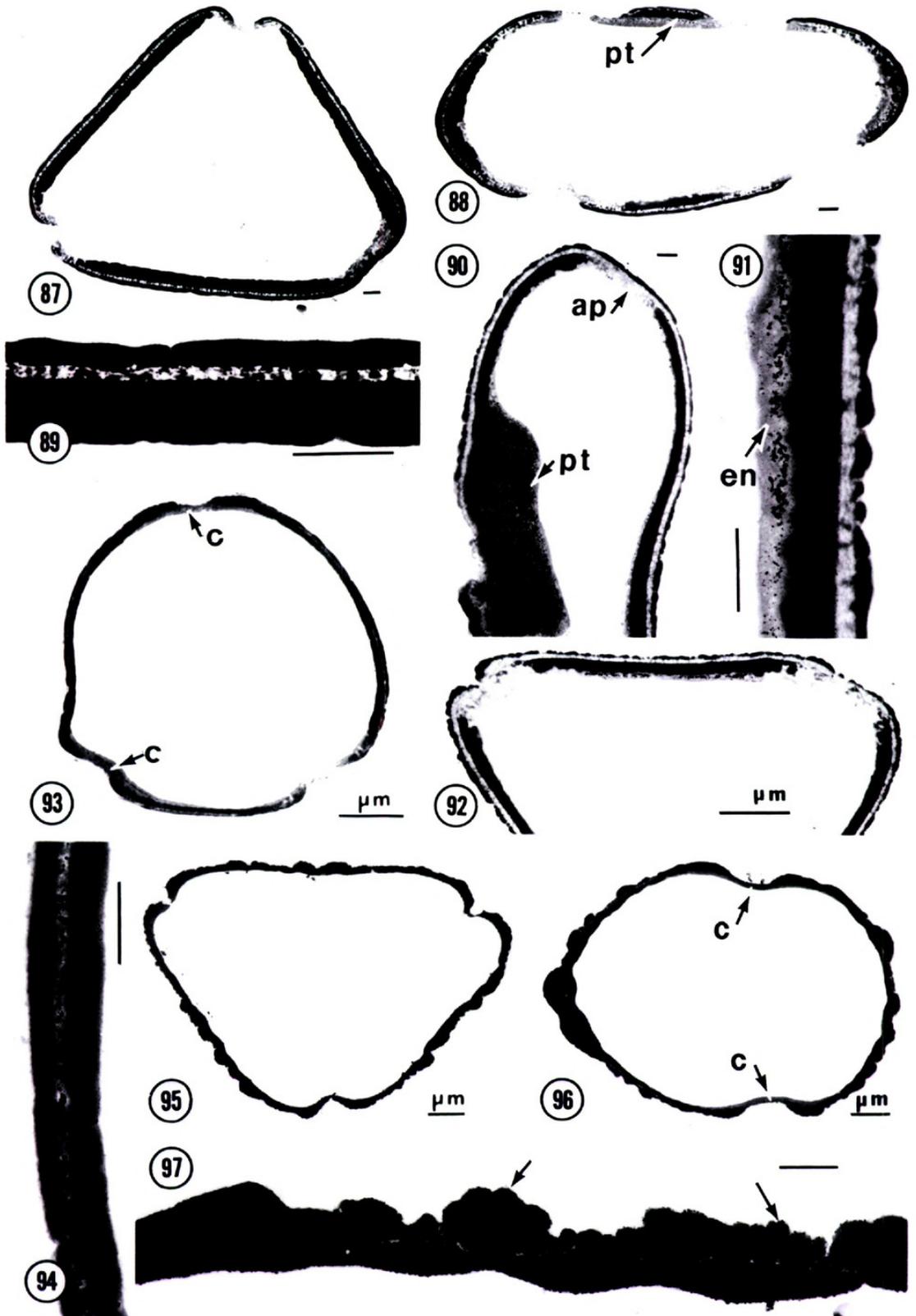
FIGURES 68–79. Comparisons between *Cladocolea* Tieghem (68, 69, 72, 73) and *Struthanthus* Martius (70, 71, 74–79) (SEM).—68. *C. glauca* Kuijt (Type III). Polar view of parasyncolpate grain with low profile striato-rugulae, $\times 1,120$.—69. *C. glauca* Kuijt. Equatorial view, $\times 1,120$.—70. *S. deppeanus* (Cham. & Schldl.) Blume (Type I-B2). Polar face of parasyncolporoidate heteropolar grain, $\times 1,400$.—71. *S. deppeanus* (Cham. & Schldl.) Blume (Type I-B2). Equatorial view, $\times 1,400$.—72. *C. microphylla* (H.B.K.) Kuijt (Type II). Polar view of diploparasyndemicolporate grain. The prominent endoapertures are not visible in the SEM, $\times 1,120$.—73. *C. microphylla* (H.B.K.) Kuijt (Type II). Interapertural equatorial view, $\times 1,120$.—74. *S. dichotrianthus* Eichler, *Woytkowski 8269* (UC), Peru (Type I-A2). Polar view of diploparasyndemicolporate heteropolar grain. Opposite face of this grain is diplosyncolporate, $\times 1,120$.—75. *S. belizensis* Lundell (Type I-AI). Polar face with barely discernible endoapertures, $\times 1,400$.—76. *S. marginatus* (Desr.) Blume, *Barlow 1420* (UC), Costa Rica (Type I-B2). Polar face of diploparasyndemicolporoidate heteropolar grain. Opposite face 3- or rarely 2-demicolporoidate, $\times 1,120$.—77. *S. marginatus* (Desr.) Blume, *Barlow 1420* (UC), Costa Rica (Type I-B2). Equatorial view showing apertures discontinuous at the equator, $\times 1,120$.—78. *S. dichotrianthus* Eichler, *Woytkowski 8269* (UC), Peru (Type I-A2). Polar face of 3-demicolporate heteropolar grain. Opposite face syndemicolporate, $\times 1,120$.—79. *S. panamensis* (Rizz.) Barlow & Wiens, *Davidson 431* (MO), Panama (Type II-C). Note the concave shape and poorly defined colpi near the center of the polar face, $\times 1,120$.



FIGURES 80-86. Brazilian *Struthanthus* spp. (Type III).—80. *S. uraguensis* (Hook. f. & Arnell) G. Don, *Hatschbach 17641* (UC), Brazil. Polar view, $\times 1,500$.—81. *S. uraguensis* (Hook. f. & Arnell) G. Don, *Hatschbach 17641* (UC), Brazil. Equatorial view, $\times 1,500$.—82. *S. concinnus* Martius. Polar view, $\times 1,500$.—83. *S. vulgaris* Martius. Polar view, $\times 1,500$.—84. *S. vulgaris* Martius. Equatorial view, $\times 1,500$.—85. *S. concinnus* Martius. Equatorial view, $\times 1,500$.—86. *S. concinnus* Martius. Detail of equatorial sculpturing revealing striato-rugulae, $\times 6,000$.

ened, highly perforate. Interstitium well defined, granular rarely exhibiting columellae or columellae-like structures. Foot layer continuous, with smooth upper and scalloped lower edge. Endex-

ine continuous around grain. Polar endexine extremely thick, up to eight times thicker than equatorial ectexine, dense, filled with osmiophilic granules; equatorial endexine irregularly



FIGURES 87-97. Ultrastructural comparisons between *Cladocolea* Tieghem and *Struthanthus* Martius (TEM). 87-89. *C. harlingii* Kuijt, *Harling 6094* (S), Ecuador. 90-92. *S. panamensis* (Rizz.) Barlow & Wiens, *Davidson 431* (MO), Panama. 93, 94. *S. costaricensis* Standley. 95-97. *S. uraguensis* (Hook. f. & Arnell) G. Don, *Hatschbach 17641* (UC), Brazil.—87. Thin section through equator, $\times 1,200$.—88. Section perpendicular to polar face through polar thickening (pt) at apocolpium and adjacent colpi, $\times 2,800$.—89. Detail of equatorial exine revealing rarely perforate tectum, granular interstitium, and thick foot layer, $\times 14,000$.—90. Section perpendicular to pole

thickened with small internal gaps often filled with osmiophilic granules thickest in midequatorial regions, thinning near ektexine bordering apertures; apertural endexine loosely granular.

Tectum/Equatorial interstitium//Foot layer: 1:2.

Species and specimens examined: *Struthanthus panamensis* (Rizz.) Barlow & Wiens.

TYPE III

Exomorphology: radial symmetry, isopolar. Shape: *amb* variable ranging from triangular to triangular slightly concave and convex; oblate rarely suboblate. Apertures: syncolpi, rarely parasyncolpi, colpi typically broadening and disrupted near the equator; colpal margins often thickened at the center of the polar face. Sculpturing: ranging from uniformly to nonuniformly prominent striato-rugulate sculpturing elements sometimes randomly coalescing in equatorial areas to form mounds or more elongate ridges; colpal margins psilate or more rarely exhibiting striato-rugulae. Exine usually evenly thickened at equator, but several species (e.g., *S. flexicaulis*, *S. vulgaris*) exhibiting thickened midequatorial exine.

Endomorphology: ektexine and endexine present. Ektexine organized into tectum, granular interstitium, and foot layer. Tectum irregularly thickened, outer surface elaborated into small excrescences representing striae in cross-section, rarely perforate. Interstitium narrow, granular, surrounded by a finely granular matrix. Foot layer thick, continuous, upper surface ranging from smooth to granular, lower edge randomly scalloped. Endexine homogeneous, absent in interapertural equatorial areas, present beneath apertures and polar faces.

Tectum/Equatorial interstitium//Foot layer: 1:2 to 2:1.

Species and specimens examined: *Struthanthus concinnus* Martius, *Irwin 2250* (UC), Brazil;

S. flexicaulis Martius, *Irwin et al. 10771* (MO), Brazil, *Lima 7366* (UC), Brazil; *S. polyrhizus* Martius, *Bradi 16933* (GH, MO), Brazil; *S. pterygopus* Martius, *Glaziou 2599, 4821* (NY), Brazil; *S. salicifolius* Martius, *Pereira 897* (MO), Brazil; *S. syringifolius* Martius, *Krukoff 562AA* (NY), Brazil; *S. uraguensis* (Hook. f. & Arnell) G. Don, **Hatschbach 17641* (UC), Brazil, *Smith & Reitz 12449* (MO), Brazil; *S. uraguensis* var. *brevipedunculata* Chodat & Hassler, *Hassler 7531* (A), Paraguay; *S. vulgaris* Martius, **Hatschbach 16483* (UC), Brazil.

DISCUSSION

The following sections discuss pollen characters among small-flowered neotropical Loranthaceae and their bearing on the interpretation of intra- and intergeneric relationships within the complex.

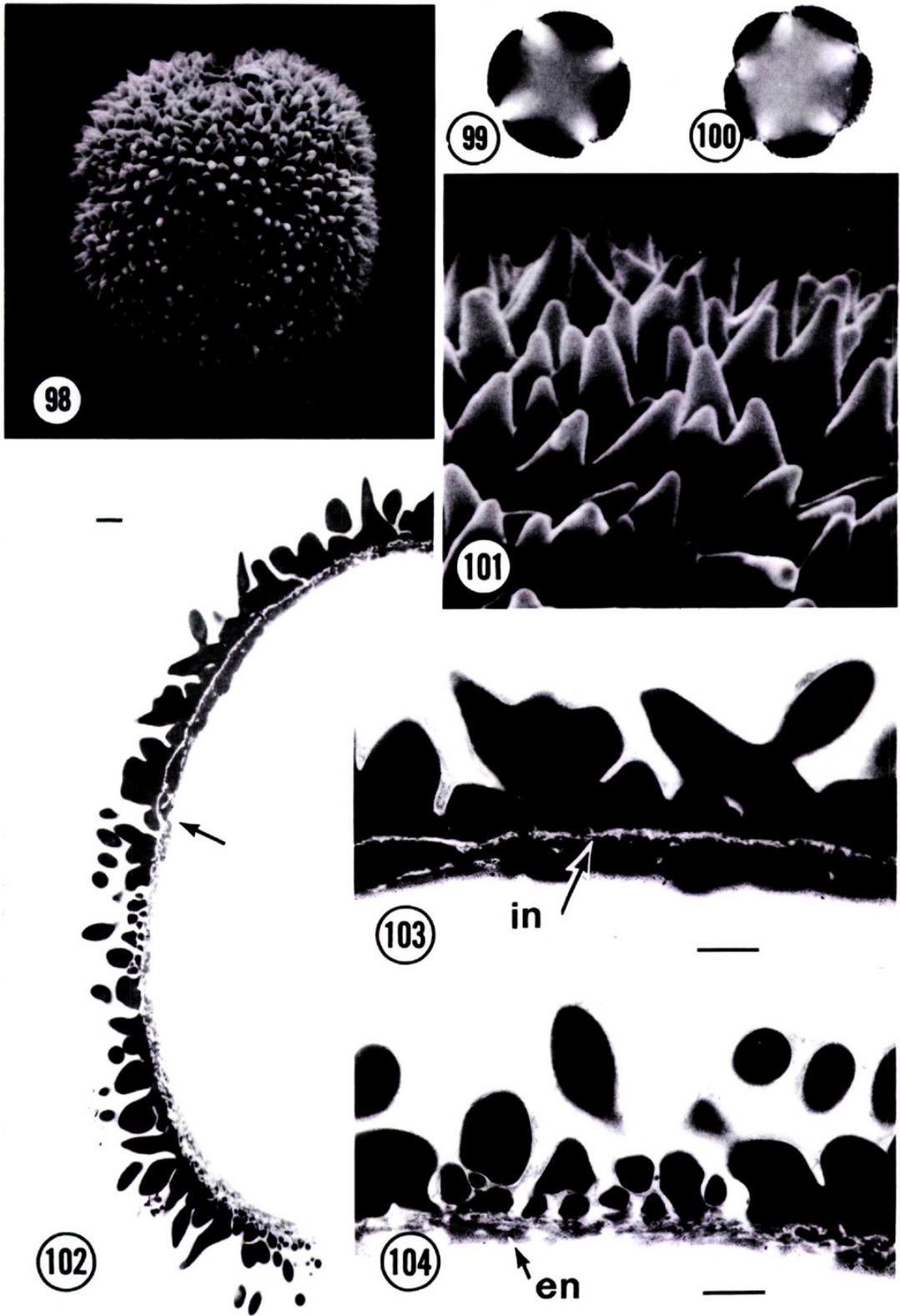
SIZE

Most small-flowered genera possess medium-sized grains which, because of their predominantly oblate shape, exhibit a significantly longer equatorial than polar axis.

The majority of largest size pollen (P: 25–30 μm ; E: 32–50 μm) characterizes *Dendropemon*, *Oryctanthus*, and *Ixocactus*. At the opposite end of the range, the smallest size pollen occurs in *Maracanthus* and *Oryctina* (P: 14–20 μm ; E: 23–30 μm).

Pollen size is variable among species of *Phthirusa*, *Cladocolea*, and *Struthanthus*. Both *Cladocolea* and *Struthanthus* exhibit clusters of species whose pollen sizes significantly differ. In *Cladocolea*, pollen of *C. harlingii* (15 μm by 25 μm), for example, is significantly smaller than that of *C. grahamii* (28 μm by 41 μm). Similarly, pollen of *Struthanthus leptostachyus* (15 μm by 30 μm) is strikingly smaller than pollen of most Brazilian *Struthanthus*, particularly that of *S. syringifolius* (33 μm by 47 μm) (cf. Figs. 13, 22).

← revealing prominent polar thickening (pt), granular-filled aperture (ap), and equatorial exine, $\times 2,500$.—91. Detail of equatorial exine revealing perforate tectum, well-defined interstitium, thick foot layer, and well-developed endexine (en), $\times 11,500$.—92. Thin section of portion of grain through equator showing granular filled apertures and interapertural equatorial endexine, $\times 2,000$.—93. Section through equator including colpal membranes (c), $\times 1,500$.—94. Detail of equatorial exine organized into rarely perforate tectum, poorly defined, granular interstitium, and foot layer, $\times 11,500$.—95. Section through equator, $\times 1,250$.—96. Section perpendicular to equator along polar axis encompassing equatorial sculpturing and colpal membranes (c), $\times 1,250$.—97. Detail of equatorial exine organized into irregularly thickened tectum representing striae in cross-section (arrows), narrow, poorly defined interstitium and irregularly thickened undulate foot layer, $\times 8,500$. All lines in micrographs, unless otherwise indicated, equal 1 μm . Micrographs with μm marking on photograph equal 5 μm .



FIGURES. 98–104. *Ixocactus hutchisonii* Kuijt.—98. Polar view (SEM), *Tamayo 2526* (ILL), Venezuela, $\times 1,950$.—99. Polar view of 4-aperturate grain (LM), *Steyermark et al. 111592* (F), Venezuela, $\times 500$.—100. Polar view of 5-aperturate grain (LM), *Steyermark et al. 111592* (F), Venezuela, $\times 500$.—101. Detail of surface sculpturing (SEM), *Tamayo 2526* (ILL), Venezuela, $\times 10,500$.—102. Section through exine including portion of aperture (lower right) (TEM). The point of demarcation between Types I and II exine organization is marked by the arrow, $\times 3,200$.—103. Detail of Type I exine organization showing solid sculptural-structural elements and a solid, variably thickened foot layer separated by a narrow, granular interstitium (in) (TEM), $\times 8,000$.—104. Detail of Type II exine organization. The ektexinous elements rest on a thin, loosely organized, discontinuous endexine (en) (TEM), $\times 8,000$. All lines in micrographs equal $1 \mu\text{m}$.

POLARITY

Though all small-flowered genera are typified by isopolar pollen, several species of *Phthirusa* and *Struthanthus* exhibit heteropolar pollen which may be uniformly present within a population or mixed with isopolar grains.

Heteropolar pollen features are restricted primarily to differences in aperture types between the two polar faces. The most common heteropolar aperture combination is associated with species of *Struthanthus* in which, among diploaperturate grains, one polar face is parasyntheticolpate while the opposite face is either syndemicolpate or, less frequently, 3-demicolpate (cf. Figs. 74, 78). Rarely, one set of apertures is longer than those of the opposite face (e.g., *Phthirusa angulata*, *Struthanthus cassythoides*).

SHAPE

Oblate pollen characterizes the small-flowered complex. Though all genera, excluding the suboblate *Ixocactus*, exhibit a mean oblate pollen shape, species of *Cladocolea*, *Oryctina*, and *Oryctanthus* are strictly oblate in contrast to those of *Dendropemon*, *Phthirusa*, and *Struthanthus* which also possess suboblate, and more rarely, oblate spheroidal grains.

Pollen *amb* is more variable than equatorial shape ranging from trilobate extremely concave among *Dendropemon* and *Phthirusa* pro parte to circular in *Oryctanthus* and *Ixocactus*. Despite this wide variation, the *amb* of most small-flowered genera is triangular to triangular slightly convex or, less frequently, concave.

APERTURES

Small-flowered genera are predominantly simple aperturate though particular species of *Cladocolea* and *Struthanthus* do, however, exhibit small, rectangular to elliptical to U-shaped slits lying perpendicular to the colpus at the periphery of the polar thickening (Figs. 7–11).

The simple apertures of small-flowered genera are predominantly diploaperturate, i.e., a set of apertures each restricted to a polar face and discontinuous at the equator usually separated by a narrow bridge of exine. Three diploaperturate types prevail: 1) diploporate-diplobrevidemicolpate; 2) diplosyndemicolpate; and 3) diploparasyndemicolpate.

The first type characterizes all *Dendropemon* and three *Phthirusa* species. Apertures in these taxa are connected by a subsurface triradiate po-

lar thickening at each face (Figs. 25, 27, 28). The second type characterizes all remaining *Phthirusa* (excluding *P. squamulosa*) and particular species of *Cladocolea* and *Struthanthus*. The third type is restricted to a few species of *Cladocolea* and *Struthanthus*.

Though a diploaperturate condition predominates among the small-flowered genera, *Phthirusa squamulosa*, *Maracanthus*, and several species of *Struthanthus* and *Cladocolea* possess synaperturate grains.

The compound apertures among species of *Cladocolea* and *Struthanthus* range from poorly defined colporoidate to well-defined prominent colporate and sagittate types largely associated with diploaperturate arrangements.

The compound apertures of *Oryctanthus* are unique within the family. When viewed in the scanning electron microscope they appear as narrow, short, slightly opened slits to broad, short, open, elliptical colpi located at the tips of the raised triradiate polar thickening. Optical sections just below the pollen surface reveal, however, a sagittate endoaperture (Figs. 42–45).

The (3–)4–5 colpate apertures of *Ixocactus*, which vary within and among populations (see Table 1), are unique within the family (Figs. 99, 100).

SCULPTURING

Small-flowered genera are basically uniformly sculptured though some species do show slight sculptural differences between polar and/or colpal margins and equatorial areas.

Most taxa exhibit only slightly sculptured surfaces ranging from psilate-perforate and/or foveolate to shallowly ridged and/or striato-rugulate. All three sculpturing types occur among *Cladocolea*, *Phthirusa*, and *Struthanthus*. Among Brazilian species of *Phthirusa* and *Struthanthus*, the exine is elaborated into pronounced striato-rugulae and ridges. In *Struthanthus uraguensis*, *S. flexicaulis*, *S. vulgaris*, and *S. polyrhizus* these striato-rugulae coalesce to form small rounded mounds with striate bases and psilate apices (Figs. 80, 81, 83, 84).

The sculpturing of *Ixocactus*, composed of blunt-tipped spines and rectangular to more irregularly shaped ramifying elements, is unique in the complex.

EXINE STRUCTURE

The following section details exine characters within the complex. The unique exine features

of *Ixocactus* are reviewed separately at the end of this section.

The exine of all small-flowered genera (including *Ixocactus*) is divisible into ektexine and endexine.

Ektexine. The ektexine is basically of uniform organization throughout the grain. Only *Oryctanthus* and to a lesser degree *Dendropemon* exhibit disparate polar and equatorial ektexine structures. The equatorial ektexine is composed of tectum, interstitium, and foot layer.

The tectum is typically perforate ranging from rarely to highly perforate. Only *Oryctanthus* and a few species of *Struthanthus* exhibit an imperforate tectum throughout the grain. Usually evenly thickened, the tectum is variably thickened in *Struthanthus panamensis* (Fig. 91) and those species of *Phthirusa* and *Struthanthus* with pronounced striato-rugulate sculpturing (Figs. 95–97).

A granular or granular-columellate interstitium characterizes most genera. These columellae, ranging from narrow to broad, are typically irregularly shaped, often sporadic and clustered, and usually associated with a granular matrix (Figs. 63–65, 67, 89, 94). Strictly collumellate or columellate/baculate interstitia are rare, restricted to a few species each of *Dendropemon* (Fig. 40) and *Phthirusa* (Fig. 61). These columellae and/or baculae, though the dominant structural elements, remain generally small, thin, and/or irregularly shaped. In *Oryctanthus*, the interstitial organization is difficult to interpret. Thin sections reveal a narrow undulating osmiophilic zone traversed by extremely thin ektexinous strands (modified columellae?) (Fig. 47).

All genera, excluding *Maracanthus*, exhibit a continuous foot layer. Varying at the species level, the foot layer ranges from evenly thickened to undulate and variably thickened, the latter most pronounced in *Phthirusa platyclada* and the Brazilian species of *Struthanthus* (Figs. 41, 97). The upper surface is either smooth and clearly defined or granular and poorly defined. The lower surface can be smooth, coarsely granular, and/or broken by small gaps (Figs. 67, 89, 92).

In most genera, the foot layer ranges from as thick as or up to twice as thick as the tectum plus equatorial interstitium (1:1 to 1:2) with the reverse ratio (2:1) occurring among Brazilian *Struthanthus* where the tectum is prominently sculptured.

In most genera the polar ektexine reflects an

organization similar to that in equatorial areas. The former differs in the usually thicker imperforate tectum and narrower less well-defined interstitium. *Oryctanthus*, with its strikingly different polar and equatorial ektexine organizations, is unique within the complex. Here the thick polar interstitium, filled with irregularly shaped ektexinous segments and numerous osmiophilic granules, is in sharp contrast to the equatorial interstitium represented by a narrow osmiophilic stratum traversed by thin ektexinous strands (cf. Figs. 47, 49).

Ektexine organization in lobar and peripheral equatorial areas near apertures is represented by isolated, irregularly shaped segments pendent from a solid, imperforate tectum (Figs. 36, 39, 88).

In *Ixocactus*, the organization of the upper ektexine into large, solid, irregularly shaped segments and bifurcating spines as well as the absence of an interstitium and basal ektexine in large non-apertural regions of the grain, isolate this genus from other members of the small-flowered complex.

Endexine. Endexine is typically present in apertural, lobar, and polar regions but absent in interapertural equatorial areas. In most *Struthanthus*, *Cladocolea*, *Phthirusa* species and *Maracanthus*, polar endexine is thickest at the center of the polar faces, this reaching its greatest development in *Struthanthus panamensis* (Fig. 90).

Endexine patterns in *Oryctanthus*, *Dendropemon*, and *Phthirusa* species with trilobate pollen differ from the majority of small-flowered genera. Polar endexine is typically absent but equatorial endexine is present though thin, irregularly thickened, and locally discontinuous. In *Oryctanthus*, endexine is also present and prominently thickened beneath the equatorial ridge (Fig. 49). The absence of polar endexine in these taxa suggests that the triradiate polar thickening visible in the light microscope is largely due then to development of ektexine rather than endexine, in contrast to those polar thickenings among *Cladocolea* and *Struthanthus* species.

The highly discontinuous granular endexine restricted to certain portions of the pollen wall in *Ixocactus* is unique within the complex.

POLLEN TRENDS

The following sections analyze pollen trends among the small-flowered genera. Pollen char-

acters of the more primitive large-flowered neotropical genera are used for out-group comparisons. Pollen features of *Ixocactus* are discussed separately at the end of these sections.

Polarity. Isopolarity is basic for the complex while heteropolarity represents the derived state. Heteropolarity, characterizing several species in the morphologically more advanced genera *Struthanthus* and *Phthirusa*, has developed independently among small-flowered loranth. The recent evolutionary occurrence of heteropolarity is suggested by its frequent occurrence alongside isopolar grains within the same population, its characterization of species rather than genera, and a consistent association with aperture anomalies.

Shape. A trilobate *amb* is primitive for the complex. Restricted to *Dendropemon* and two species of *Phthirusa*, this shape most closely approaches that typical of the large-flowered genera and Loranthaceae as a whole. The rounded convex *amb* in *Oryctina* and particular species of *Cladocolea* and *Struthanthus* is derived. The truly circular *amb*, found among a few species of *Oryctanthus*, is also a highly derived condition having arisen through modification of a rounded convex shape typical of most *Oryctanthus* species.

Oblate pollen shape is basic for the complex. The presence of suboblate and, more rarely, oblate spheroidal shapes among several advanced genera as well as the absence of such shapes among large-flowered loranth suggest their derived nature.

Apertures. A diploaperturate arrangement of simple apertures is basic for the complex. The basic type consists of colpi typically fused at the poles (syn-) but narrowly discontinuous at the equator (diplodemi-) with smooth, narrow membranes sometimes disrupted and/or broader near the equator. Both the parasy- colp form and the synaperturate arrangement, largely peculiar to species of *Cladocolea* and *Struthanthus*, represent derived conditions.

The status of the diploporate-diplobrevidemicolpate apertures is obscure. Their occurrence in *Dendropemon* and three *Phthirusa* species and their closer similarity to apertures of the large-flowered *Psittacanthus* [see for example *P. dilatatus*, *P. peronopetalus* (Feuer & Kuijt, 1979)] than to any small-flowered taxa suggest primitive, probably vestigial, character states. Though primitive, the pori-brevicolpi of the small-flowered taxa do show unique modifications: encir-

lement of each aperture by thickened, often slightly raised exine and interconnection of all apertures by a narrow, clearly defined triradiate subsurface polar thickening.

The compound apertures of *Oryctanthus*, *Cladocolea*, and *Struthanthus* are judged to be "incipient" and recently derived both because of their often ill-defined shape and the absence of a compound aperture type among Loranthaceae to date (Feuer & Kuijt, 1978, 1979, 1980, work in progress). The close palynological similarities between *Cladocolea* and *Struthanthus* suggest that their elliptical to U-shaped endoapertures may have developed independently from those of *Oryctanthus*.

Sculpturing. Though the psilate-perforate sculpturing of *Dendropemon-Phthirusa* pro parte is primitive for the complex, the basic sculpturing elements adopted by most small-flowered taxa are low profile ridges and/or rugulae and/or striato-rugulae.

Two sculpturing trends are evident within the complex. The first is the development of imperforate psilate exine. This has occurred once in the morphologically remote *Oryctanthus* and again among particular Mexican and Central American *Struthanthus* and *Cladocolea* species. A second and opposite trend, restricted to Brazilian populations of *Struthanthus*, involves the elaboration of the exine into pronounced striatorugulae which sometimes coalesce into short mounds in equatorial areas.

Exine structure. Similar ektexine organizations in polar and equatorial areas is a derived, though widely adopted, condition among the small-flowered genera. The disparate polar/equatorial ektexine organization in *Oryctanthus* may be an independently derived character within the small-flowered complex but is common among large-flowered neotropical genera.

The basic ektexine of most small-flowered taxa is organized into a thin, perforate tectum, granular/columellate or columellate/granular interstitium and a thick, continuous foot layer typically twice as thick as the tectum plus interstitium. The imperforate tectum in *Oryctanthus* and particular species of *Struthanthus* and *Cladocolea* is a derived feature. The absence of well-developed columellae in the complex combined with the increase of purely granular interstitia among species of the morphologically advanced genera such as *Struthanthus* and *Cladocolea* suggest an overall loss of columellae. The extremely narrow

interstitial strands in *Oryctanthus* would then represent highly modified, though vestigial columellae.

Endexine patterns of most small-flowered genera are strikingly similar to those of large-flowered genera. Both groups exhibit triradiately configured, thickened, often stratified polar endexine but no interapertural equatorial endexine. The thickened polar endexine arranged in a circular configuration in particular species of *Cladocolea* and *Struthanthus* is unique to the flowered complex and represents a derived condition.

INTRAGENERIC RELATIONSHIPS

Only *Phthirusa*, *Cladocolea*, and *Struthanthus* exhibit significant specific pollen variation to permit a discussion of intrageneric relationships; of these, only *Cladocolea* has been monographed (Kuijt, 1975).

Phthirusa. Pollen characters divide the genus into two major groups: Group I composed of *P. platyclada* and *P. pyrifolia* and Group II containing all remaining species. Group I species are characterized by trilobate pollen with diploporate apertures, midequatorial and triradiately thickened polar exine, and a columellate/baculate exine structure. In contrast, pollen of Group II taxa, excluding *P. squamulosa*, are diplosyndemicolpate with evenly thickened midequatorial and columellate/granular exine. *Phthirusa lepidobotrys*, with its unique diplobrevidemicolpate pollen, midequatorial and triradiately thickened polar exine but consistent triangular shape and columellate granular exine, occupies an intermediate position between the two groups.

Cladocolea. Pollen characters indicate a particularly close relationship among *C. andrieuxii*, *C. loniceroides*, and *C. microphylla*, the latter two closer to each other than either is to *C. andrieuxii*. These species exhibit the only endoapertures in the genus; the latter two additionally share a rounded convex *amb* and a triangular polar thickening along colpal margins. The naturalness of this group, as suggested by the pollen data, is corroborated by similarities in floral and inflorescence structure (Kuijt, 1975, 1981a). Other species relationships are more obscure. The unique triangular concave pollen shape and uniformly wide colpal membranes in *C. inconspicua* suggest an isolated position within the genus. However, pollen of the closely related *C. inornata* and *C. clandestina* was unavailable for study. *Cladocolea oligantha* also occupies an isolated

position with its triangular pollen shape, thick exine, and sharply defined circular central polar thickening. Morphologically, this species is distinguished by dimorphic inflorescences—a feature present in only one other *Cladocolea* species.

Struthanthus. Two major groups are delimited by pollen characters: Group I containing Brazilian species populations and Group II composed of remaining non-Brazilian species populations which range from Mexico to South America. This geographic distinction refers largely to populations of species since the *Struthanthus* taxa which occur in several regions (e.g., *S. marginatus*, *S. orbicularis*, *S. rotundatus*) were not examined throughout their total range.

Pollen data suggest that the Brazilian species populations are particularly closely interrelated. Pollen is uniformly isopolar, syncolpate with pronounced striato-rugulate sculpturing. In contrast, Group II species are palynologically diverse. Both iso- and heteropolar grains occur, which can exhibit either simple or compound apertures arranged in either syn- or diploporate arrangements. Sculpturing ranges from typically tectate-perforate to low profile striato-rugulate to rarely psilate-imperforate. The unique occurrence of highly sculptured exines among Group I species and the restriction of heteropolar pollen, compound apertures, and psilate-imperforate features to Group II species suggest two independently evolving complexes.

Among Group II species, *S. panamensis* is distinguished by its trilobate, slightly concave pollen, thinning midequatorial exine and the presence of a well-defined interstitium and midequatorial endexine, features closer to those of *Cladocolea harlingii* than other *Struthanthus* species. The isolated position of this species, as suggested by the pollen data, is confirmed by floral and inflorescence structure. This species is distinguished from all other *Struthanthus* species by its bisexual flowers arranged in monads as opposed to unisexual triads in all other species. Such characters have led to the proposal that *S. panamensis* may represent an independent branch leading into the *Struthanthus* pool (Kuijt, 1981a).

INTERGENERIC RELATIONSHIPS

Excluding the disparate pollen characters of *Ixocactus*, the pollen data suggest two basic groupings of small-flowered genera: a first group composed of *Dendropemon*, *Phthirusa* pro parte, and *Oryctanthus* and a second generic cluster

containing *Phthirusa* pro parte, *Cladocolea*, *Struthanthus*, *Maracanthus*, and *Oryctina*. Such an arrangement does not, however, preclude weaker intergroup relationships.

Within Group I, *Dendropemon* is closely linked to *Phthirusa* through the species *P. pyrifolia* and *P. platyclada*. All exhibit trilobate, extremely concave pollen *amb*, diploporate apertures, and a midequatorially thickened columellate/baculate exine structure. *Phthirusa lepidobotrys*, with its diplobrevicolpate midequatorially thickened but triangular pollen links the *Dendropemon*-like *Phthirusa* species to the remaining 28 *Phthirusa* species, the pollen of which is strikingly similar to particular *Struthanthus* species.

Pollen characters support a relationship between *Oryctanthus* and *Dendropemon-Phthirusa* pro parte as suggested by floral and inflorescence structures (Kuijt, 1976a) but offer no evidence for an affinity with *Maracanthus* (Kuijt, 1976b). *Oryctanthus* pollen, though quite distinct, does possess several features common to *Dendropemon-Phthirusa* pro parte pollen: a narrow, well-defined triradiate polar thickening, small diploapertures restricted to the tips of this triradiate thickening, and an equatorial ectexine structure similar to the polar ectexine organization of *Dendropemon*. *Oryctanthus*, however, exhibits several uniquely derived pollen features: circular *amb*, raised polar ridges encircling polar depressions, compound apertures composed of sagittate endoapertures, and an equatorial interstitium traversed by numerous thin strands. Such unique characters suggest that *Oryctanthus* is a highly derived genus with only remote ties to the *Dendropemon-Phthirusa* pro parte complex.

Among the second generic cluster, pollen characters indicate a relationship between *Struthanthus* and *Phthirusa* on the one hand and *Struthanthus* and *Cladocolea* on the other.

Struthanthus is linked to *Phthirusa* through pollen characters of heteropolarity, oblate-spheroidal shape, apertures with protruding colpal margins, and pronounced striato-rugulate sculpturing. *Phthirusa* species remain palynologically distinct from *Struthanthus* through consistent triangular *amb* and a well-defined columellate-granular interstitium—the latter closely resembling a *Dendropemon* feature.

Pollen suggests an even closer relationship between the Mexican–Central American *Struthanthus* species and *Cladocolea*, particularly species with Types II and III pollen. The *Struthanthus-Cladocolea* species constellation similarly ex-

hibits a triangular rounded convex *amb*, simple and compound apertures, syn- and parasyncolpi arranged in either diplo- or synaperturate arrangements, and a granular poorly defined interstitium. The parasyncolpi, the elliptical to U-shaped endoapertures, and granular interstitium are features unique to this group. The strong ties suggested by the pollen data are corroborated by gross morphology. The unique occurrence of geniculate styles among particular *Cladocolea* and Mexican *Struthanthus* evinces close interspecific relationships. Striking morphological similarities between certain intergeneric species pairs (*C. harlingii*, *S. orbicularis*; *C. lenticellata*, *S. polystachyus*; *C. pedicellata*, *S. deppeanus*) have been used to purport a polyphyletic origin for *Struthanthus* (Kuijt, 1981a). Since pollen of several key *Cladocolea* species was not examined and as *Struthanthus* pollen in each of the species pairs is not strikingly different from other *Struthanthus* nor closer to particular *Cladocolea* species, the data do little to support or deny polyphyletism in the genus.

The proposed affinity of *Maracanthus* and *Oryctanthus* (Kuijt, 1976a) is unsupported by the pollen data. Rather, the following pollen characters indicate an intermediate position between *Struthanthus* and *Phthirusa*: triangular to rounded convex *amb*, syncolpate apertures, perforate tectum with low profile striato-rugulae, circular polar thickening, and a well-developed columellate/granular interstitium.

Little pollen evidence exists for the suggested relationship between *Oryctina* and *Maracanthus* (Kuijt, 1981b) though these two genera are closer to each other than either is to *Oryctanthus*. In *Oryctina*, the rounded convex diploaperturate, psilate pollen with thickened apocolpial colpal margins resembles pollen of *Struthanthus* species, particularly *S. leptostachyus* and *S. palmeri*.

The pollen characters of *Ixocactus* indicate no relationship with any small-flowered genus. The intra- and interpopulational aperture variation, the irregularly spinulose sculpturing, and ectexine structure characteristic of *Ixocactus* are closer to those of the New World Eremolepidaceae and Old World genus *Viscum*, particularly the African species, than to any Loranthaceae sensu stricto.

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