POLLEN ULTRASTRUCTURE OF THE BIOVULATE EUPHORBIACEAE

MICHAEL G. SIMPSON AND GEOFFREY A. LEVIN[1]

Department of Biology, San Diego State University, San Diego, California 92182-0057; and Botany Department, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112

Pollen ultrastructure of the biovulate Euphorbiaceae, including the subfamilies Phyllanthoideae and Oldfieldioideae, was investigated with light, scanning electron, and transmission electron microscopy. Pollen of Phyllanthoideae, represented by 12 species in nine genera, was prolate to oblate, almost always 3-colporate, rarely 3-porate or pantoporate, and mostly with reticulate, rarely baculate, echinate, or scabrate, sculpturing. The ektexine showed little variation in ultrastructure; almost without exception it was tectate-columellate with a homogeneous foot layer, columellae continuous with both the tectum and the foot layer, and a perforate, homogeneous tectum. The only major exception was *Amanoa guianensis*, which was intectate and baculate as the result of the evolutionary loss of the tectum. Pollen of Oldfieldioideae, in which we studied 28 species from 25 genera, and obtained data from the literature for two of the three remaining genera in the subfamily, was globose to oblate, with four or more, rarely only three, apertures that were either equatorial and brevicolporate to porate or pantoporate, and with echinate, rarely scabrate, sculpturing. The ektexine showed considerable variation in ultrastructure. The most widespread structural type consisted of a foot layer that is either thin and irregular or absent, an interstitium composed of irregular to columellate exine deposits that are discontinuous from the foot layer, if present, and a tectum composed of laterally appressed baculate elements that delimit fine microperforations. A second common structural type differed in having a relatively thick, homogeneous foot layer and thin, granular to tabular, microperforate tectum. Isolated genera have a reduced interstitium and/or a homogeneous tectum or show a reversal to a tectate-columellate architecture. Variation in aperture morphology, sculpturing, and exine ultrastructure is phylogenetically significant in the Oldfieldioideae.

Introduction

Palynological studies of the Euphorbiaceae have been extremely useful in clarifying systematic relationships within the family. Using light microscopy (LM), Erdtman (1952) was the first to point out the great variation in the shape, sculpturing, and apertures of Euphorbiaceae pollen and to suggest that these characteristics were significant systematically. Punt (1962) subsequently conducted a more detailed survey, confirming most of Erdtman's conclusions. Köhler (1965) completed a thorough study of the biovulate genera, i.e., those that produce two ovules per locule, which had long been placed in the subfamily Phyllanthoideae. He concluded that the genera with spinose pollen should be placed in a new subfamily, the Oldfieldioideae.

Subsequent intrafamilial classifications of the Euphorbiaceae have continued to recognize these two subfamilies as well as the Acalyphoideae, Crotonoideae, and Euphorbioideae (Webster 1967, 1975, 1994). The Phyllanthoideae (55 genera, 2,100 species) is probably a basal, paraphyletic taxon, the members of which are united only by sharing a number of ancestral (plesiomorphic) features. The Oldfieldioideae (28 genera, 80 species) appears to be monophyletic, united by the spinose pollen observed by Köhler (1965). The

remaining three subfamilies share the synapomorphy (shared derived character state) of a single ovule per locule. The Acalyphoideae (113 genera, 2,100 species) is probably paraphyletic, differing from the other uniovulate subfamilies mainly in lacking milky or colored latex. The Crotonoideae (64 genera, 1,450 species) share the synapomorphies of stellate, dendritic, or lepidote trichomes, and mostly porate or inaperturate pollen with the distinctive "crotonoid" pattern of exinous processes (Nowicke 1994). The Euphorbioideae (38 genera, 1,800 species) are united by the synapomorphy of a reduced perianth.

Our understanding of relationships within the Phyllanthoideae and Oldfieldioideae has been greatly increased by pollen studies using SEM (Bonnefille and Riollet 1980; Punt 1980, 1987; Poole 1981; Hayden et al. 1984; Webster 1984*a;* Dechamps et al. 1985; El-Ghazaly and Raj 1986; Lobreau-Callen in McPherson and Tirel 1987; Webster et al. 1987; Lobreau-Callen and Suarez-Cervera 1989). However, only three palynological studies of these subfamilies (Poole 1981; Hayden et al. 1984; Lobreau-Callen and Suarez-Cervera 1989) have used TEM to describe the details of exine architecture, and though the authors treated only six genera, they suggested that pollen wall ultrastructure may be systematically valuable.

We investigated pollen ultrastructure in the biovulate Euphorbiaceae with the goal of exploring its contribution to the systematics of these subfamilies. We initially found little variation in exine wall structure within the Phyllanthoideae, whereas pollen of Oldfieldioideae varied consid-

erably. As a consequence we concentrated our efforts on the latter subfamily, examining a small sample of Phyllanthoideae selected to included members of the major groups recognized in Webster's classification (1975, 1994). We also examined *Didymocistus* and *Hymenocardia,* both Phyllanthoideae, because of questions about their relationships.

This article is primarily descriptive. In a separate article (Levin and Simpson 1994*a*), we analyze the pollen characters of the subfamily Oldfieldioideae phylogenetically, both alone and in combination with anatomical and morphological characters. Only the major conclusions of our phylogenetic analysis will be repeated here.

Material and methods

Flowers from dried herbarium specimens were rehydrated either at room temperature or at 60°C in 1% Aerosol OT for 3–5 d, then fixed and stored in FAA. For LM, pollen was cleared in Hoyer's mounting medium (Radford et al. 1974) on a microscope slide preparation. LM observations were made with differential interference contrast optics using a Nikon Microphot-FX photomicroscope. For SEM, whole anthers were dehydrated to 100% ethanol, then gradually infiltrated to 100% Freon 113 or methylal (dimethoxymethane). The anthers were placed in a metal capsule and critical-point dried with a Tousimis critical-point dryer using pressurized carbon dioxide as the transition fluid. Pollen grains were tapped onto a stub covered with double stick tape, sputter-coated with gold/palladium in a Hummer-4 sputtering apparatus, and photographed on a Hitachi S500 scanning electron microscope (20 kV). In addition to our own preparations, we also studied SEM micrographs loaned to us by G. Webster.

For TEM, whole anthers, isolated pollen, or pollen embedded in 2% agar was fixed in cold 4% gluteraldehyde in 0.1 M Sorensen's phosphate buffer for 2 h, followed by several rinses in buffer and further fixation in 2% osmium tetroxide for 2 h. Specimens were quickly rinsed twice in buffer, progressively dehydrated to 100% ethanol, infiltrated in a gradation series of Spurr's resin (Spurr 1969), and finally polymerized at 65°C for 12–18 h. Sections 0.5 μm thick were stained with 1% toluidine blue and mounted on a slide for LM observations. Ultrathin-sections (ca. 95 nm thick) were prepared with a Diatome diamond knife on a Reichert Ultracut-E ultramicrotome, mounted on uncoated hexagonal 200 mesh copper grids, and poststained with a saturated 50% ethanol solution of uranyl acetate for 15 min and 0.2% aqueous lead citrate for 7 min. To inhibit stain precipitation, grids were gently and quickly washed in a running stream of filtered, distilled water between and after poststain changes. Observations and photographs were made on a Phil-

ips EM 410 transmission electron microscope at 80 kV.

Mean pollen grain diameter (polar × equatorial) was determined from LM preparations, mean spine length from either LM observations or TEM micrographs, and mean ektexine foot layer and tectum thicknesses from TEM micrographs. Sample sizes from LM observations included at least 10 pollen grains, whereas those from TEM micrographs were generally very small.

Our terminology generally follows that of Reitsma (1970) and Walker and Doyle (1975). Reitsma (1970) distinguished spines of length >1 μm, which he termed "echinae" (sculpturing "echinate"), from those of length <1 μm, which he termed "scabrae" (sculpturing "scabrate"). To reflect the discontinuities among the taxa in our study, we modified Reitsma's terms and use the terms "echinae" or "echinate" when spines are >0.9 μm in length and "scabrae" or "scabrate" when <0.5 μm in length. With regard to tectal structure, we use the term "microperforate" to describe a tectum penetrated by very narrow pores delimited by closely appressed tectal elements, whereas "homogeneous" refers to the absence of microperforations or any other wall discontinuities. A microperforate tectum may be composed either of laterally appressed baculate elements, a structure that we term "microperforate/baculate," or of laterally appressed granular to tabular elements, a structure that we term "microperforate/granular." "Perforate" refers to a larger hole in the tectum that is not immediately bordered by closely appressed tectal elements; the tectum between perforations may be either microperforate or homogeneous. "Imperforate" simply means that the tectum lacks both perforations and microperforations. With regard to foot layer structure, "homogeneous" refers to a continuous wall whereas "irregular" refers to an interrupted, discontinuous wall. With regard to foot layer thickness, we use the terms "thin" and "thick" to reflect a major discontinuity among investigated taxa as determined by a quantitative analysis (Levin and Simpson 1994*a*); for our purposes, we define "thin" as <0.5 μm and "thick" as >0.5 μm. Because tectum thickness varied almost continuously, we did not recognize any distinct size classes in this feature (Levin and Simpson 1994*a*).

Results and comparisons with previous work

In the results that follow, descriptions of ektexine and endexine correspond to the nonaperural region except where noted. Voucher collection data and herbarium acronym (after Holmgren et al. 1990) are in parentheses following each investigated species name.

SUBFAMILY PHYLLANTHOIDEAE ASCHERSON

In this subfamily the sequence of genera follows Webster (1994).

TRIBE AMANOEAE (PAX AND K. HOFFM.) WEBSTER (2 GENERA, 17 SPECIES).

AMANOA AUBLET (16 SPECIES).

Amanoa guianensis Aublet (Guyana, Tillett et al. 45256, DAV). Pollen oblate (36 × 42 μm), 3-colporate; sculpturing baculate (4.1 μm long), verrucate (fig. 1); ektexine apparently intectate, with a thick (1.0 μm), homogeneous foot layer and elongate distally rounded baculae (fig. 2), these apparently homologous to columellae (Discussion); endexine relatively thin (fig. 2), thickened at apertural border (fig. 3); intine two-to-three-layered, very thick in apertural region (fig. 3).

Descriptions and illustrations of pollen of *A. guianensis* (Punt 1962, 1987; Webster et al. 1987) agree with our observations except that Punt (1962) reported the grains to be 39–46 × 45–52 μm and the baculae to be up to 7 μm long. The specimen with reticulate sculpturing that Erdtman (1952) cited is properly assigned to *Amanoa sinuosa* W. J. Hayden (Hayden 1990).

Amanoa strobilacea Muell. Arg. (Cameroon, Thomas 4125, MO). Pollen oblate (38 × 54 μm), 3-colporate; sculpturing coarsely reticulate, verrucate between muri (fig. 4); ektexine tectate-columellate with a thick (1.4 μm) foot layer, narrow columellae, and a widely perforate, homogeneous tectum (2.7 μm; fig. 5); ektexine extending across aperture as irregular to granular deposits (fig. 6); endexine scanty (fig. 5), thickened at apertural border (fig. 6). Except for larger diameters (50 × 58 μm), Köhler's (1965) description and illustration of this species agree with our observations.

TRIBE PHYLLANTHEAE DUMORT. (19 GENERA, 1,125 SPECIES; 2 OF 6 SUBTRIBES INVESTIGATED).

SUBTRIBE SECURINEGINAE MUELL. ARG. (1 GENUS, 5 SPECIES).

SECURINEGA COMM. EX JUSS. (5 SPECIES).

Securinega durissima J. Gmelin (Mauritius, Lorence 1397, MO). Pollen oblate (22 × 25 μm), 3-colporate, apertures widely elliptic; sculpturing echinate (1.0 μm long); ektexine tectate-columellate, with a thin (0.28 μm), homogeneous foot layer and a perforate homogeneous tectum (0.32 μm; fig. 7); endexine thin and scanty (fig. 7), thickened at apertural border. Pollen of this species was illustrated by Webster (1984*a*). Other species in this genus described or illustrated (Erdtman 1952; Punt 1962; Köhler 1965) are now placed in *Chascotheca, Flueggea,* and *Jablonskia* (Webster 1984*a*, 1984*b*).

SUBTRIBE FLUEGGEINAE MUELL. ARG. (9 GENERA, 1,050 SPECIES).

MARGARITARIA L. F. (14 SPECIES).

Margaritaria discoidea (Baillon) Webster ssp. *nitida* (Pax) Webster (Zimbabwe, Chase 5150, MO). Pollen prolate (27 × 22 μm), 3-colporate (fig. 8), with lalongate endoaperture; sculpturing reticulate; ektexine tectate-columellate with a thin (0.17 μm), homogeneous foot layer and a widely perforate, homogeneous tectum (0.43 μm; figs. 8, 9); endexine thin and irregular (fig. 9), thickened at apertural border (fig. 8); intine of apertural region thickened (fig. 8) Other species of *Margaritaria* have generally similar pollen (Punt 1962; Köhler 1965).

TRIBE DRYPETEAE (GRISEB.) HURUSAWA (4 GENERA, 230 SPECIES).

DRYPETES VAHL (220 SPECIES).

Drypetes lateriflora (Sw.) Krug and Urban. (United States, Chambers and Stern 266, US). Pollen prolate (30 × 20 μm), 3-colporate with a short lalongate endoaperture; sculpturing reticulate; ektexine tectate-columellate, with a thin (0.18 μm), homogeneous foot layer and a perforate, homogeneous tectum (0.37 μm; fig. 10); endexine thin (fig. 10), thickened at apertural border (fig. 11); intine thick, two-layered throughout (figs. 10, 11). Pollen of this species has not been described previously. The few other species of *Drypetes* examined palynologically have generally similar pollen (Punt 1962; Köhler 1965).

TRIBE ANTIDESMEAE (SWEET) HURUSAWA (18 GENERA, 500 SPECIES; 2 OF 5 SUBTRIBES INVESTIGATED).

### SUBTRIBE SCEPINAE (LINDLEY) WEBSTER (8 GENERA, 180 SPECIES).

APORUSA BLUME (80 SPECIES).

Aporusa falcifera Hook. f. (Indonesia, Soepadmo 41, MO). Pollen subprolate (16 × 15 μm), 3-colporate with a lalongate endoaperture; sculpturing reticulate; ektexine tectate-columellate, with a thin (0.17 μm), homogeneous foot layer and a perforate homogeneous tectum (0.29 μm), the latter with distal angular projections that give the tectum a decidedly pitted appearance (fig. 12 [Punt 1987]); endexine moderately thick (fig. 12), greatly thickened at apertural border (fig. 13); intine of apertural region two-layered (fig. 13). Pollen of this species was illustrated by Punt (1987); other species have very similar pollen (Punt 1962; Köhler 1965).

SUBTRIBE ANTIDESMINAE (SWEET) MUELL. ARG. (6 GENERA, 240 SPECIES).

ANTIDESMA L. (200 SPECIES).

Antidesma membranaceum Muell. Arg. (Guinea, Adam 4973, MO). Pollen prolate (23 × 12 μm), 3-colporate with a lalongate endoaperture; sculpturing reticulate; ektexine tectate-columel-
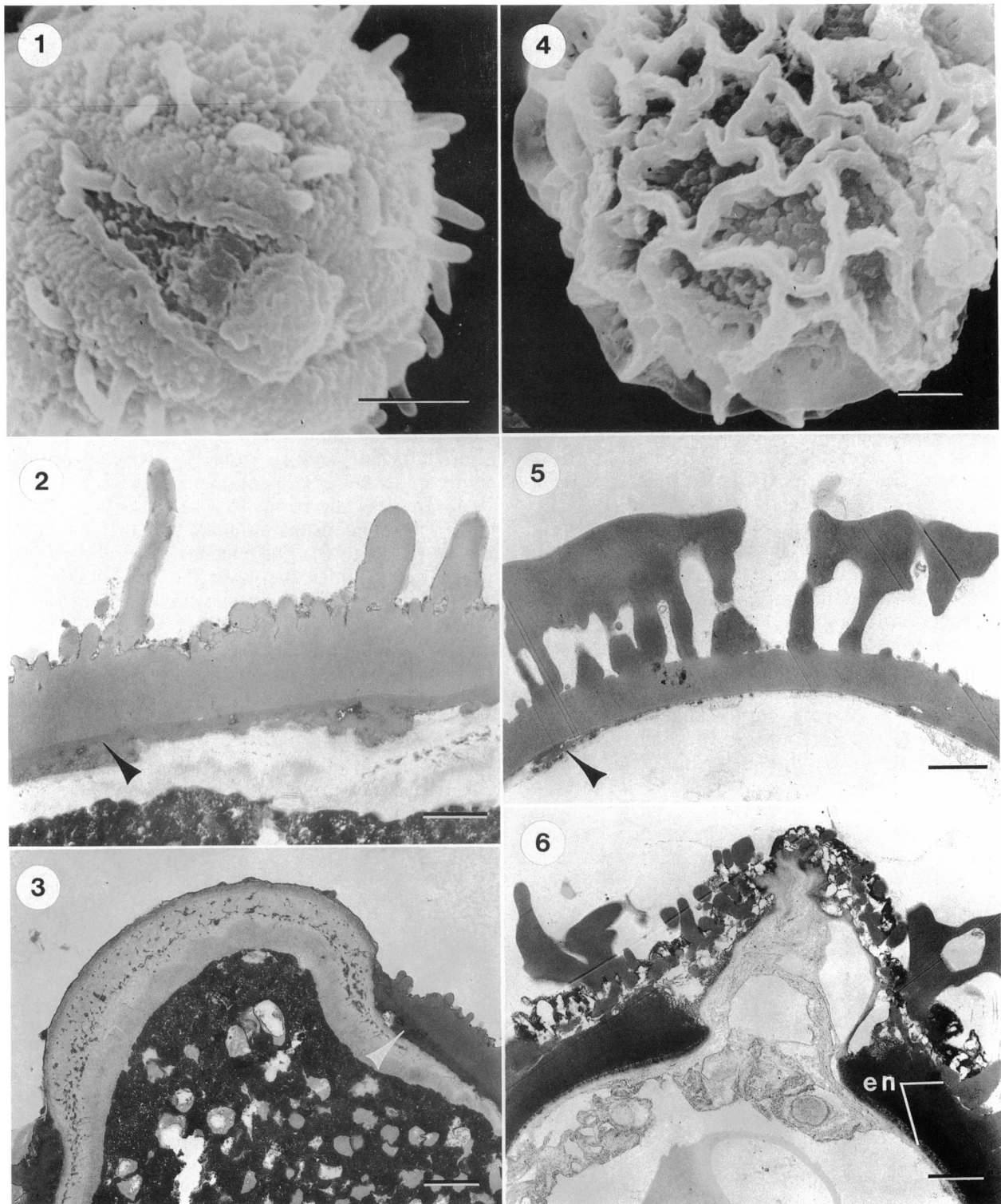
Figs. 1-6 Pollen of Euphorbiaceae subfamily Phyllanthoideae. Figs. 1–3, *Amanoa guianensis.* Fig. 1, Whole pollen grain, SEM, colporate aperture facing; note baculae and verrucae. Fig. 2, Nonapertural wall, TEM; arrow indicates endexine. Fig. 3, Apertural region, TEM; arrow indicates endexine. Figs. 4–6, *Amanoa strobilacea.* Fig. 4, Whole pollen grain, SEM; note reticulate tectum and verrucae. Fig. 5, Nonapertural wall, TEM; arrow indicates endexine. Fig. 6, Apertural region, TEM; note thickened endexine (*en*) at apertural border and outer ektexinous deposits. Scale bars = 1 μm in fig. 2; 2 μm in figs. 3, 5, 6; 5 μm in figs. 1, 4.

late, with a thin (0.11 μm), homogeneous foot layer and a perforate homogeneous tectum (0.30 μm; fig. 14); endexine moderately thick (fig. 14), thickened at aperture border (fig. 15); intine of apertural region very thick, two-layered (fig. 15).

Antidesma venosum Tul. (Swaziland, Kemp 525, MO). Pollen prolate (20 × 12 μm), 3-colporate (fig. 16) with a lalongate endoaperture; sculpturing reticulate; ektexine tectate-columellate, with a thin (0.15 μm), homogeneous foot layer and a perforate homogeneous tectum (0.31 μm; fig. 16); endexine moderately thick, thickened in apertural region (fig. 16).

Punt's (1962) description of these species is entirely consistent with ours. Pollen of other species is very similar (Erdtman 1952; Punt 1962; Köhler 1965).

HYERONIMA ALLEMÃO (15 SPECIES).

Hyeronima alchorneoides Allemão var. *alchorneoides* (Bolivia, Croat 51307, MO). Pollen prolate (33 × 19 μm), 3-colporate with lalongate endoaperture (fig. 17); sculpturing foveolate (fig. 17); ektexine tectate-columellate, with a thin (0.21 μm), homogeneous foot layer and a perforate homogeneous tectum (0.40 μm; fig. 18); endexine moderately thick (fig. 18), thickened at apertural border (fig. 19); intine of apertural region thick, 2-3-layered (fig. 19).

In addition to the cursory references to pollen of this species by Punt (1962, 1987) and Webster (1984a), Franco R. (1990) provided detailed descriptions and illustrations. Our observations are in full agreement with hers, though our small sample size included no grains with horns at the ends of the endoaperture, which she described as sometimes present.

TRIBE HYMENOCARDIEAE (MUELL. ARG.) HUTCH. (2 GENERA, 9 SPECIES).

DIDYMOCISTUS KUHLM. (1 SPECIES).

Didymocistus chrysadenius Kuhlm. (Peru, Dodson and Torres 2961, MO). Pollen globose (12 μm), 3-colporate, apertures narrow and elongate (fig. 20) with a lalongate endoaperture; sculpturing scabrate (0.08 μm long), interspinal sculpturing rugulate (fig. 20); ektexine tectate-columellate, with a thin (0.12 μm), homogeneous foot layer and a perforate homogeneous tectum (0.20 μm; fig. 21); foot layer slightly thickened at aperture border (fig. 22); endexine thin (fig. 21), thickened at apertural border (fig. 22); intine of apertural region thick, two-to-three-layered (fig. 22). Pollen of this monotypic genus has not been described previously.

HYMENOCARDIA WALLICH EX LINDLEY (8 SPECIES).

Hymenocardia acida Tul. (Cameroon, de Wilde 4044, MO). Pollen oblate (25 × 28 μm), 3-porate

(to brevicolporate), apertures slightly elliptic, perpendicular to equator, with a raised rim (fig. 23); sculpturing scabrate (0.07 μm long), interspinal sculpturing rugulate (figs. 23); ektexine tectate-columellate, with a thin (0.18 μm), homogeneous foot layer and a perforate homogeneous tectum (0.26 μm; fig. 24); foot layer thickened at aperture border, this presumably accounting for the raised apertural rim; endexine very thin to absent (fig. 24), slightly thickened at apertural border; intine of apertural region thick, two-layered.

Hymenocardia ulmoides Oliver (Zaire, Lebrun 2119, MO). Pollen oblate (19 × 21 μm), 3-porate; sculpturing scabrate (0.07 μm long), interspinal sculpturing rugulate; ektexine tectate-columellate, with a thin (0.16 μm), homogeneous foot layer and a perforate homogeneous tectum (0.19 μm; fig. 25); ektexine at aperture border with thickened foot layer (fig. 26); endexine very thin (fig. 25); intine of apertural region thick, two-layered (fig. 26).

Pollen of these and other species of *Hymenocardia* have been described and illustrated by Punt (1962), Köhler (1965), and especially Dechamps et al. (1985). Our observations are consistent with these others, though Dechamps et al. (1985) reported that the scabrae may be up to 0.25 μm long.

SUBFAMILY OLDFIELDIOIDEAE KÖHLER AND WEBSTER

In this subfamily we list the genera in order of the cladogram shown in fig. 75, the preferred cladogram of Levin and Simpson (1994a), and follow their classification.

TRIBE CROIZATEAE WEBSTER (1 GENUS, 4 SPECIES).

CROIZATIA STEYERM. (4 SPECIES).

Croizatia naiguatensis Steyerm. (Venezuela, Berry et al. 4124, DAV). Pollen globose (32 μm), 3-brevicolporate; sculpturing echinate (3.3 μm long); ektexine with a thick (0.63 μm), homogeneous foot layer, irregular columellae that generally appear discontinuous with the foot layer, and a microperforate/granular tectum (0.24 μm; figs. 27, 28); apertural region with foot layer considerably thickened and interstitium and tectum reduced (fig. 27); endexine scanty, irregular (fig. 28); intine of apertural region thickened, two-layered (fig. 27). Webster et al. (1987) described and illustrated pollen of this species. Our description is consistent with theirs, except that they reported the diameter of the grains to be 46–56 μm.

TRIBE PODOCALYCEAE WEBSTER (2 GENERA, 3 SPECIES; 2 OF 2 SUBTRIBES INVESTIGATED).

SUBTRIBE PARADRYPETINAE G. LEVIN (1 GENUS, 2 SPECIES).
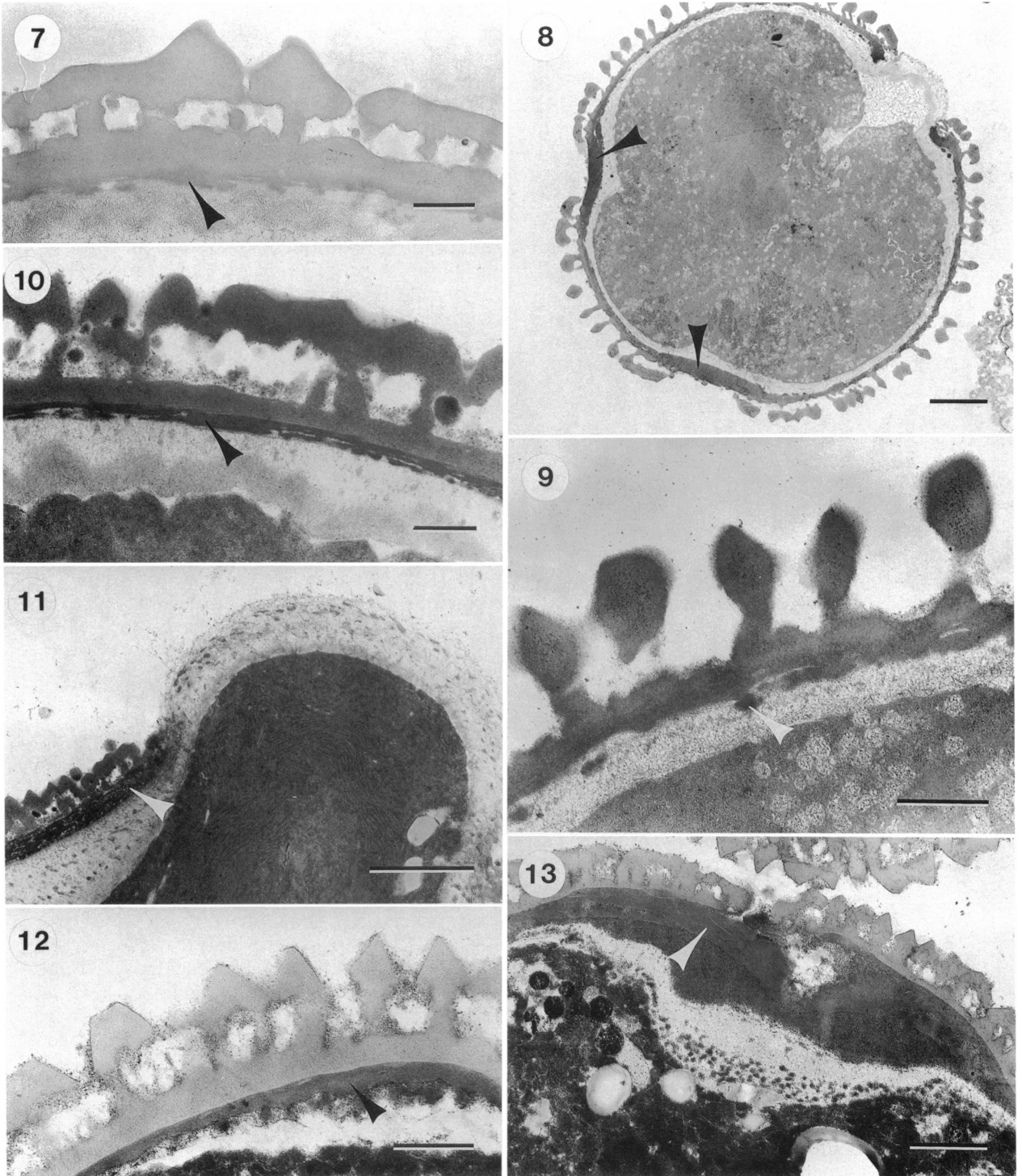
Figs. 7-13 Pollen of Euphorbiaceae subfamily Phyllanthoideae. Fig. 7, *Securinega durissima*. Nonapertural wall, TEM; arrow indicates endexine. Figs. 8, 9, *Margaritaria discoidea*. Fig. 8, Whole grain cross-section, TEM; note three apertures, with thickened endexine (arrows) at two apertural borders. Fig. 9, Nonapertural wall, TEM; arrow indicates endexine. Figs. 10, 11, *Drypetes lateriflora*. Fig. 10, Nonapertural wall, TEM; arrow indicates endexine. Fig. 11, Apertural region, TEM; note thickened endexine layer (arrow). Figs. 12, 13, *Aporusa falcifera*. Fig. 12, Nonapertural wall, TEM; arrow indicates endexine. Fig. 13, Apertural region, TEM; note greatly thickened endexine layer (arrow). Scale bars = 0.5 μm in figs. 7, 9, 10, 12; 1 μm in fig. 13; 2 μm in figs. 8, 11.
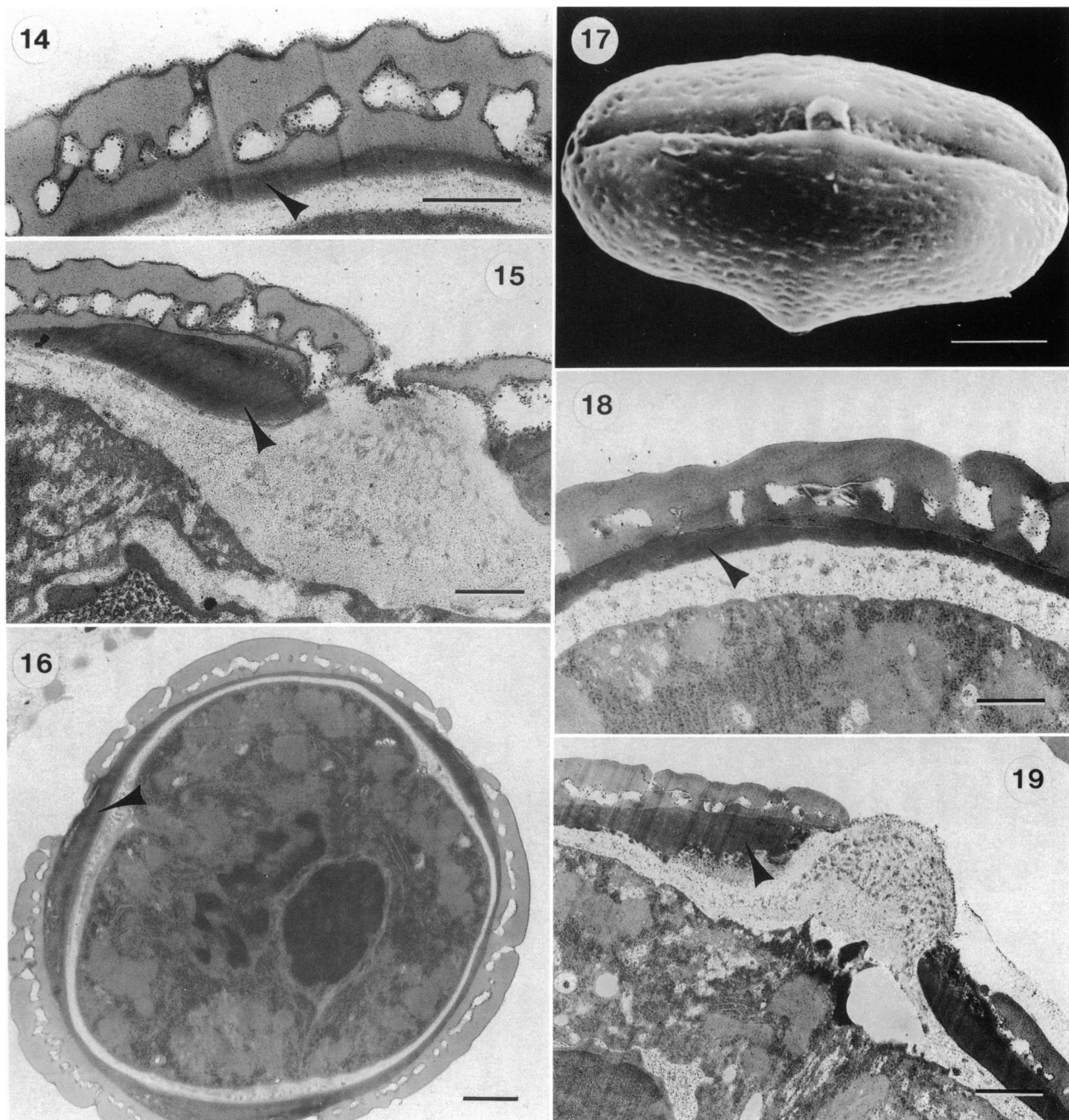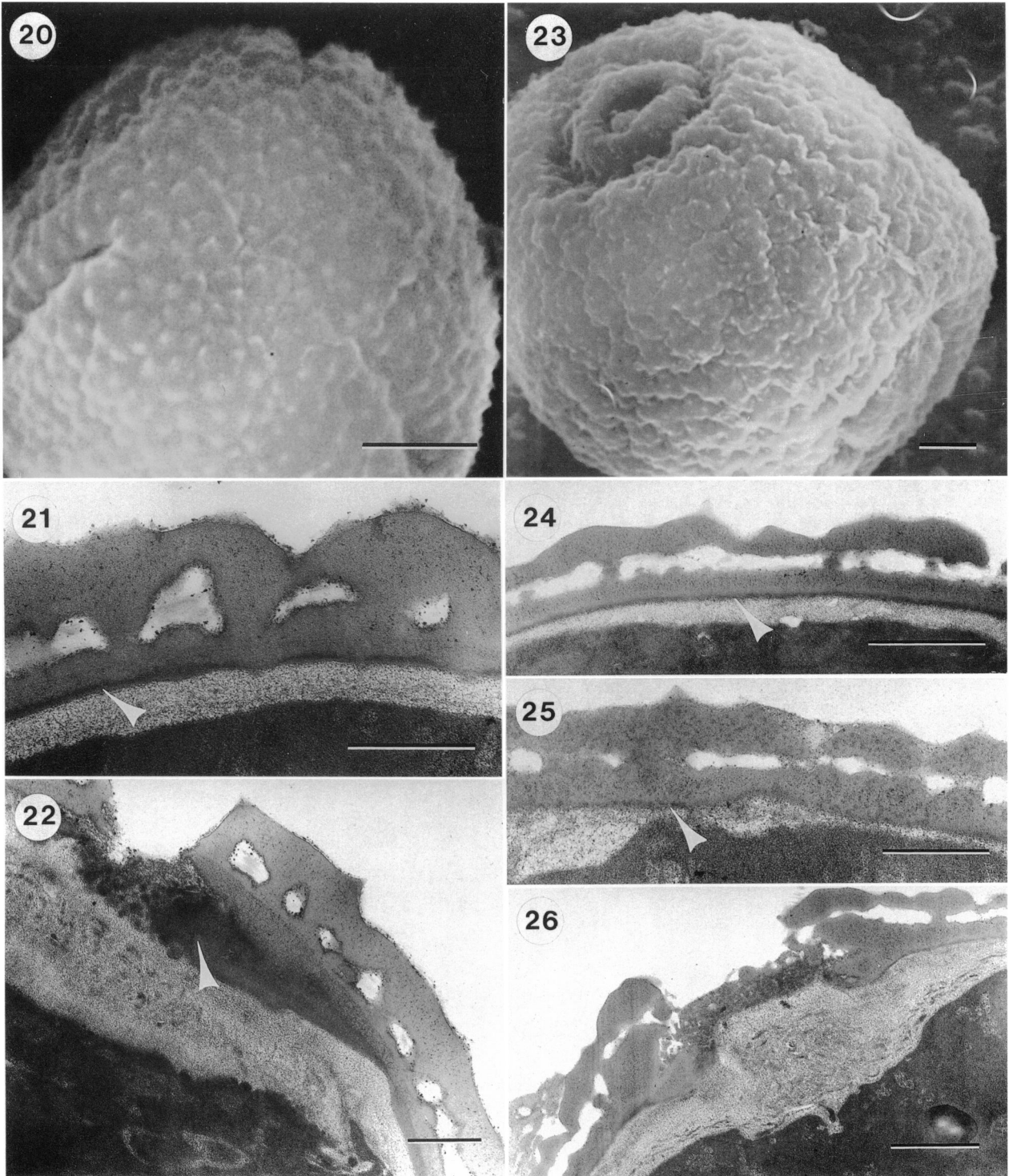
Figs. 14–19 Pollen of Euphorbiaceae subfamily Phyllanthoideae. Figs. 14, 15, *Antidesma membranaceum*. Fig. 14, Nonapertural wall, TEM; arrow indicates endexine. Fig. 15, Apertural region, TEM; note thickened endexine (arrow) at apertural border. Fig. 16, *Antidesma venosum*. Whole grain cross-section, TEM; note three apertures with thickened endexine (arrow). Figs. 17–19, *Hyeronima alchorneoides*. Fig. 17, Whole pollen grain, SEM, colporate aperture facing. Fig. 18, Nonapertural wall, TEM; arrow indicates endexine. Fig. 19, Apertural region, TEM; note thickened endexine (arrow) at apertural border. Scale bars = 0.5 μm in figs. 14, 15, 18; 1 μm.in figs. 16, 19; 5 μm.in fig. 17.

PARADRYPETES KUHLM. (2 SPECIES).

Paradrypetes subintegrifolia G. Levin (Brazil, Krukoff 4999, U [isotype]). Pollen oblate (22 × 27 μm), 4-brevicolporate, zoni-aperturate; colpi linear (length ca. ⅓–½ grain polar diameter), with narrowly elliptic lalongate endoaperture; sculpturing echinate (1.4 μm long), psilate in inter-spinal region (fig. 29); ektexine with commissure delimiting the thin (0.12 μm), irregular foot layer from the imperforate tectum (0.35 μm; fig. 29); interstitium absent (Discussion); endexine thickened at apertural border; intine of apertural region thick, two-layered. More detailed illustrations of this species can be found in Levin (1992).

Figs. 20-26 Pollen of Euphorbiaceae subfamily Phyllanthoideae. Figs. 20–22, *Didymocistus chrysadenius.* Fig. 20, Whole grain, SEM, obliquely polar view; note three apertures. Fig. 21, Nonapertural wall, TEM; arrow indicates thin endexine. Fig. 22, Apertural region, TEM; note thickened endexine (arrow) at apertural border. Figs. 23, 24, *Hymenocardia acida.* Fig. 23, Whole grain, SEM; note two of three porate to brevicolporate apertures. Fig. 24, Nonapertural wall, TEM; arrow indicates very thin endexine. Figs. 25, 26, *Hymenocardia ulmoides.* Fig. 25, Nonapertural wall, TEM; arrow indicates very thin endexine. Fig. 26, Apertural region, TEM; note thickened ektexinous foot layer at apertural border. Scale bars = 0.5 μm in figs. 21, 22, 25; 1 μm in fig. 24, 26; 2 μm in figs. 20, 23.

SUBTRIBE PODOCALYCINAE WEBSTER (1 GENUS, 1 SPECIES).

PODOCALYX KLOTZSCH (1 SPECIES).
Podocalyx loranthoides Klotzsch (Brazil, Vicira et al. 195, MO). Pollen oblate (22 × 25 μm), 4-porate, zoni-aperturate; sculpturing echinate (2.8 μm long; fig. 30); ektexine with a thin (0.11 μm), irregular, somewhat granular foot layer and a microperforate/baculate tectum (0.33 μm; fig. 30), the interstitium apparently lacking (Discussion); endexine thick (fig. 30), thickened further at apertural border (fig. 31).

The description by Köhler ([1965], as *Richeria loranthoides* [Klotzsch] Muell. Arg.) and illustration by Webster et al. (1987) are consistent with our observations. Although we have described the tectum as microperforate/baculate, the tectum is much less segmented than in most Old-fieldioideae with this type of tectum (Discussion).

TRIBE PICRODENDREAE (SMALL) WEBSTER (11 GENERA, 24 SPECIES; 4 OF 4 SUBTRIBES INVESTIGATED).

SUBTRIBE TETRACOCCINAE G. LEVIN (1 GENUS, 4 SPECIES).

TETRACOCCUS ENGELM. EX PARRY (4 SPECIES).
Tetracoccus dioicus Parry (United States, Henry and Dice s.n. [April 8, 1980], SD). Pollen suboblate (46 × 47 μm); 4-porate, zoni-aperturate; sculpturing echinate (4.7 μm long), verrucate in interspinal region (fig. 32); ektexine with a thin (0.35 μm), irregular, granular foot layer, narrow, irregular columellae that are generally discontinuous with the foot layer, and a microperforate/baculate tectum (0.63 μm; fig. 32); endexine thin (fig. 32).

Published descriptions and illustrations of pollen of this species (Köhler 1965; Hayden et al. 1984; Webster et al. 1987) generally agree with our observations. Köhler (1965), however, reported that the grains were smaller (33 × 36 μm) and had (5–)6(–7) apertures. Pollen of other species of *Tetracoccus* is similar, though somewhat smaller and with shorter spines (Punt 1962, 1987; Köhler 1965).

SUBTRIBE PICRODENDRINAE (SMALL) WEBSTER (4 GENERA, 5 SPECIES).

PARODIODENDRON HUNZ. (1 SPECIES).
Parodiodendron marginivillosum (Speg.) Hunz. (Argentina, Verveerst and Cuezzo 7610, US). Pollen oblate (24 × 27 μm), ca. 7-porate, zoni-aperturate; sculpturing echinate (3.1 μm long), verrucate in interspinal region (figs. 33, 34, 39, 40); ektexine with essentially no foot layer, irreg-

ularly spaced columellae, and a highly microperforate/baculate tectum (1.1 μm; fig. 40); endexine composed of a thin basal layer (fig. 40), thickened at apertural border (fig. 39); intine of apertural region conspicuously thickened, two-to-three-layered (fig. 39). Detailed LM observations and illustrations of the pollen of this species published by Villamil (1969) generally agree with ours, though he reported the grains to be larger (33.5 × 36.5 μm) with correspondingly longer spines (4–5[–7] μm).

PIRANHEA BAILLON (2 SPECIES).
Piranhea trifoliata Baillon (Brazil, Berg et al. P19789, MO). Pollen oblate (32 × 35 μm), 6-porate, zoni-aperturate; sculpturing echinate (2.7 μm long; fig. 41); ektexine with no foot layer, irregularly spaced columellae, and a microperforate/baculate tectum (0.39 μm; fig. 41); endexine thin; intine two-layered (fig. 41). Both Punt (1962) and Köhler (1965) described pollen of this species to be somewhat smaller (23–27 × 25–32 μm) with shorter spines; otherwise their descriptions agree with ours. Pollen of *Piranhea longipeduculata* Jabl. appears similar (Hayden et al. 1984).

CELAENODENDRON STANDLEY (1 SPECIES).
Celaenodendron mexicanum Standley (Mexico, Perez and Chang 1776, MO). Pollen suboblate (39 × 40 μm), 7 (8)-porate, zoni-aperturate; sculpturing echinate (2.9 μm long; fig. 42); ektexine with no foot layer, an irregular interstitium, and a microperforate/baculate tectum (0.59 μm; fig. 42); endexine thin (fig. 42), thickened at apertural border (fig. 43); intine moderately thick, two-layered, thickened in apertural region (fig. 43). Pollen of this monotypic genus has not been described previously.

SUBTRIBE PAIVEUSINAE PAX AND K. HOFFM.

OLDFIELDIA BENTH. AND HOOK. F. (4 SPECIES).
Oldfieldia africana Benth. and Hook. f. (Sierra Leone, Fox 157, K). Pollen suboblate (28 × 30 μm), 5–6-porate, zoni-aperturate; sculpturing echinate (3.5 μm long; fig. 44); ektexine with no foot layer, irregularly spaced columellae, and an irregular, microperforate/baculate tectum (0.44 μm; fig. 44); ektexine of apertural region with thickened basal layer; endexine relatively thin, forming a continuous basal layer (fig. 44), slightly thickened at aperture border; intine of apertural region two-layered, thickened. Previous descriptions and illustrations of pollen of this species (Erdtman 1952; Punt 1962; Köhler 1965; Hayden et al. 1984) are consistent with our observations, though reported diameters vary widely (24.5–35.4 × 27.5–43 μm). Köhler (1965) re-
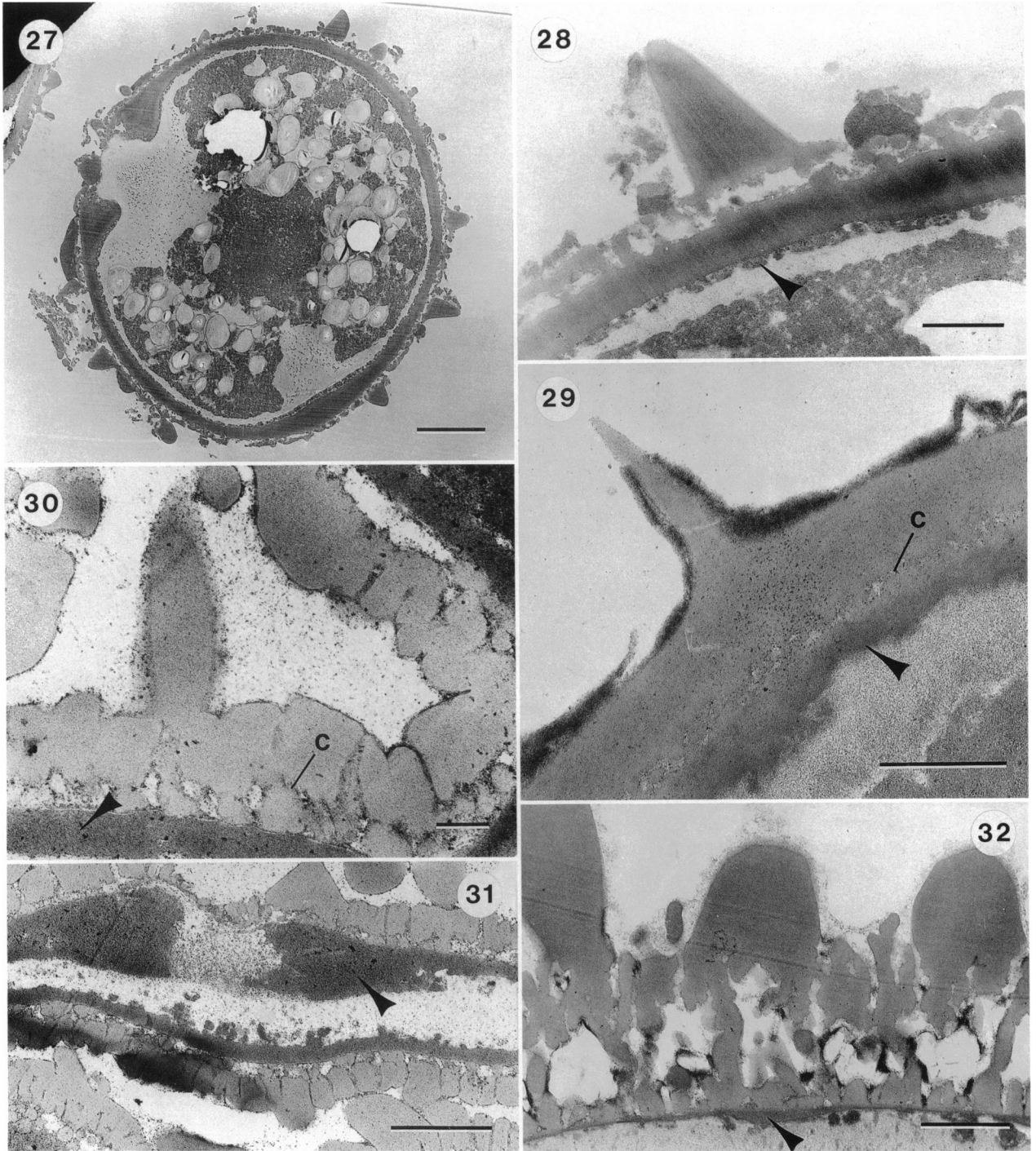
Figs. 27-32 Pollen of Euphorbiaceae subfamily Oldfieldioideae. Figs. 27, 28, *Croizatia naiguatensis*. Fig. 27, Whole grain cross-section, TEM, showing (at upper left) one of three apertures; note thickened ektexinous foot layer at apertural border. Fig. 28, Nonapertural wall, TEM; arrow indicates endexine. Fig. 29, *Paradrypetes subintegrifolia*. Nonapertural wall, TEM, showing commissure (c) delimiting foot layer from tectum; arrow indicates endexine. Figs. 30, 31, *Podocalyx loranthoides*. Fig. 30, Nonapertural wall, TEM, showing commissure (c) delimiting foot layer from tectum; arrow indicates endexine. Fig. 31, Whole grain cross-section, TEM; note thickened endexine (arrow) at apertural border. Fig. 32, *Tetracoccus dioicus*. Nonapertural wall, TEM; arrow indicates thin endexine. Scale bars = 5 μm in fig. 27; 1 μm in figs. 28, 31, 32; 0.5 μm in fig. 29; 0.2 μm in fig. 30.
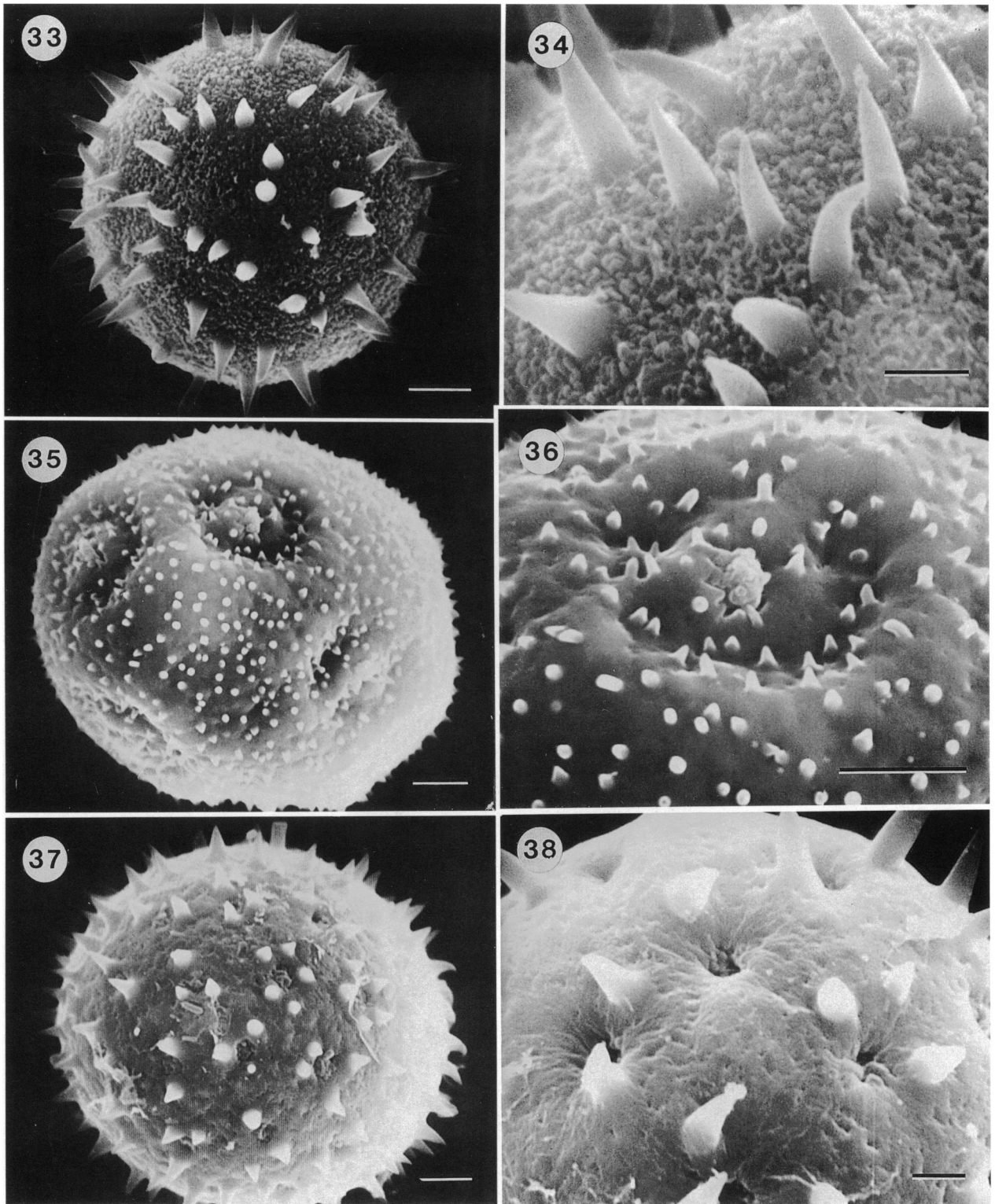
Figs. 33-38   Pollen of Euphorbiaceae subfamily Oldfieldioideae. Figs. 33, 34, *Parodiodendron marginivillosum*. Fig. 33, Whole grain, SEM. Fig. 34, Wall close-up, SEM. Figs. 35, 36, *Androstachys johnsonii*. Fig. 35, Whole grain, SEM. Fig. 36, Close-up of aperture, SEM. Fig. 37, *Micrantheum hexandrum*. Whole grain, SEM; note porate apertures. Fig. 38, *Neoroepera buxifolia*. Close-up of wall, SEM; note porate apertures. Scale bars = 5 μm in figs. 33, 35–37; 2 μm in figs. 34, 38.
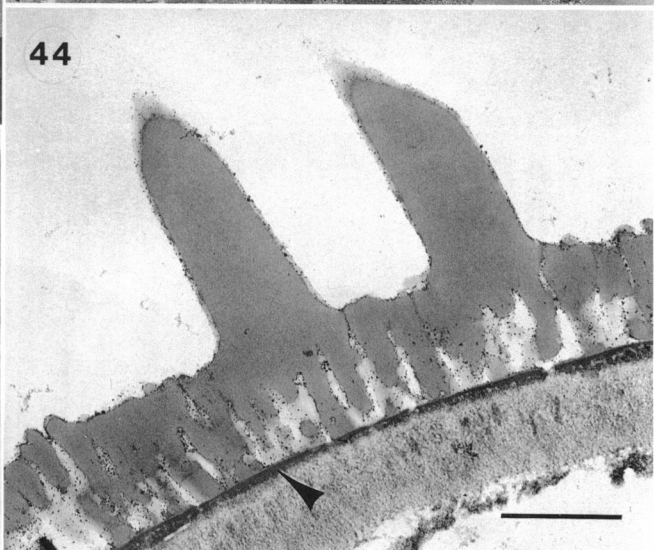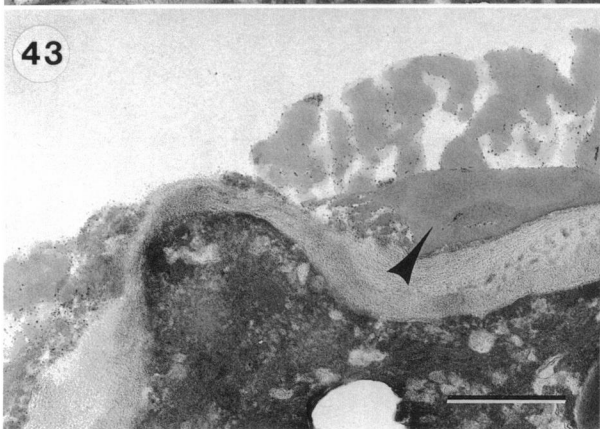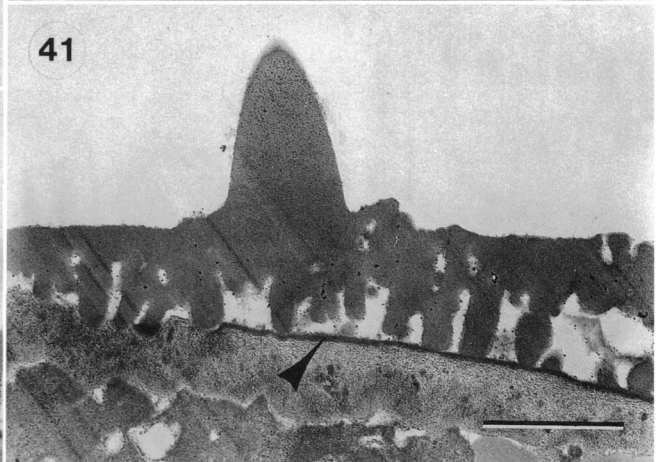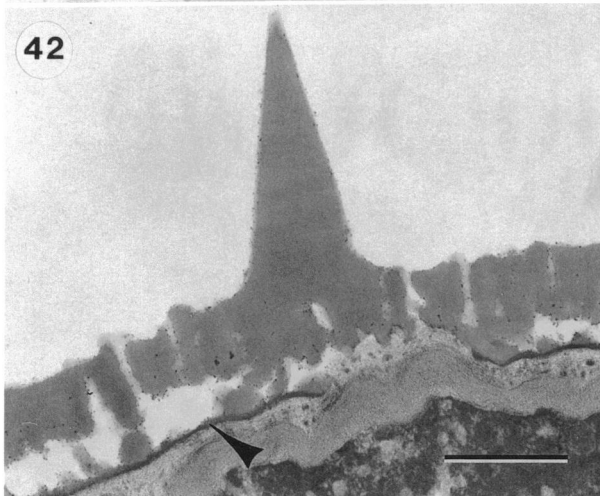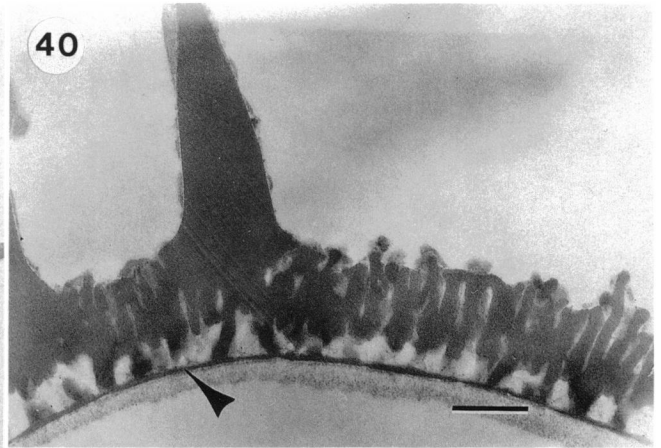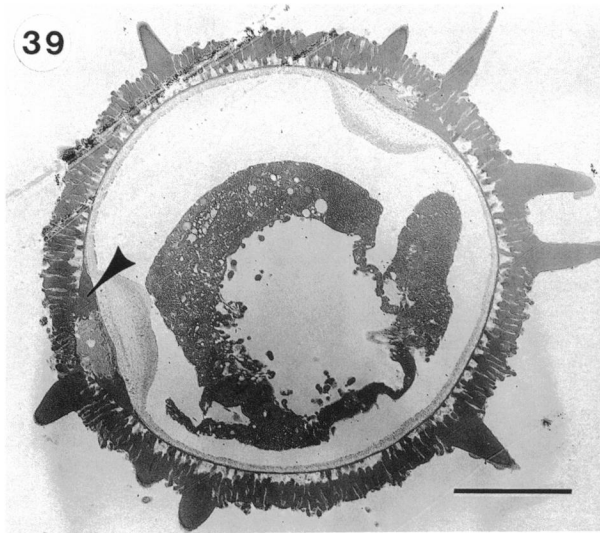
Figs. 39–44 Pollen of Euphorbiaceae subfamily Oldfieldioideae. Figs. 39, 40, *Parodiodendron marginivillosum*. Fig. 39, Whole grain cross-section, TEM; note thickened endexine (arrow) at apertural border. Fig. 40, Nonapertural wall, TEM; arrow indicates thin endexine. Fig. 41, *Piranhea trifoliata*. Nonapertural wall, TEM; arrow indicates thin endexine. Figs. 42, 43, *Celaenodendron mexicanum*. Fig. 42, Nonapertural wall, TEM; arrow indicates thin endexine. Fig. 43, Apertural region, TEM; note thickened endexine (arrow). Fig. 44, *Oldfieldia africans*. Nonapertural wall, TEM; arrow indicates thin endexine. Scale bars = 5 μm in fig. 39; 1 μm in figs. 40–44.

ported the apertures to be up to eight in number. *Oldfieldia dactylophylla* (Oliver) Léonard has similar pollen (Punt 1962; Köhler 1965).

SUBTRIBE MISCHODONTINAE MUELL. ARG. (5 GENERA, 11 SPECIES).

ANDROSTACHYS PRAIN (1 SPECIES).

Androstachys johnsonii Prain (South Africa, Balsinhas 3549, K). Pollen globose (50 μm), 5–7-pantoporate (figs. 35, 36); sculpturing echinate (1.1 μm long), interspinal sculpturing psilate (figs. 35, 36); ektexine tectate-columellate with a thin (varying in thickness; mean 0.07 μm), homogeneous foot layer, sparse narrow columellae that are continuous with the foot layer, and a microperforate tectum (0.36 μm; fig. 45); ektexine of apertural region with foot layer and interstitium reduced (fig. 46); endexine thin and appressed inner to the foot layer; endexine extending as a thin layer across aperture (fig. 46); intine two-layered (figs. 45, 46). The very sparsely microperforate tectum of this species does not show the distinct baculate or granular to tabular structure found in most other microperforate Oldfieldioideae.

Previous reports on the number and distribution of apertures differ considerably. Erdtman (1952) described the pollen as polyforate, i.e., pantoporate with more than 12 apertures (not oligoforate, i.e., with 12 or fewer pores, as misquoted by Dahlgren and van Wyk 1988), with the pores faintly defined and covered with granulate membranes. Köhler (1965), studying the same sample, described the pollen as more or less pantoporate or possibly dizonoporate, with 14–18 inconspicuous, variably shaped apertures covered with granular or smooth membranes. Punt (1962), who studied different material, considered the pollen inaperturate. All these authors used only LM. Dahlgren and van Wyk (1988) used both LM and SEM for another sample and found that most grains were inaperturate but some had a few places where the thin tectum apparently was torn to form a small "pore" with a granular membrane. Our observations are based on both LM and SEM. Though clearly visible with SEM, with LM the apertures often were extremely inconspicuous but could be resolved using Herr's clearing fluid (Herr 1971). The possibility that there are both pantoporate and inaperturate populations should be investigated further. Our observations are otherwise consistent with reports by Erdtman (1952), Punt (1962), Köhler (1965), and Dahlgren and van Wyk (1988).

STACHYANDRA R.-SM. (4 SPECIES).

Stachyandra merana (Airy Shaw) R.-Sm. (Madagascar, Capuron 23335-SF, P [isotype]). Pollen globose (44 μm), 4–6-porate, zoni-aper-

turate; sculpturing echinate (1.4 μm long; fig. 47); ektexine with no foot layer, a somewhat irregular interstitium, and a microperforate/baculate tectum (0.52 μm); endexine forming a thin basal layer, thickened at apertural border; intine two-layered (fig. 47), thickened in apertural region.

Stachyandra rufibarbis (Airy Shaw) R.-Sm. (Madagascar, Capuron 9177-SF, P [holotype]). Pollen globose (46 μm), 5–7-porate, zoni-aperturate; sculpturing echinate (0.9 μm long) (figs. 48, 49); ektexine with no foot layer, an irregular interstitium, and a microperforate/baculate tectum (0.50 μm) (fig. 48); endexine forming a thin basal layer (fig. 48), thickened at apertural border (fig. 49); intine two-layered, thickened in apertural region (fig. 48, 49).

Pollen of this recent segregate from *Androstachys* (Radcliffe-Smith 1990) has not been described previously. Although we describe the tectum as microperforate/baculate in both species of *Stachyandra,* they have fewer microperforations than is characteristic both of other Mischodontinae and of many other Oldfieldioideae.

VOATAMALO CAPURON EX BOSSER (2 SPECIES).

Voatamalo eugenioides Capuron ex Bosser (Madagascar, Capuron 22327-SF, K). Pollen globose (44 μm), 5–6-porate, zoni-aperturate; sculpturing echinate (3.3 μm long); ektexine with a thin (0.14 μm) and irregular to absent foot layer, an irregular interstitium that is generally discontinuous with the foot layer, and a microperforate/baculate tectum (0.38 μm; fig. 50); endexine thin; intine two-layered (fig. 50). Pollen of this genus has not been described previously.

MISCHODON THWAITES (1 SPECIES).

Mischodon zeylanicus Thwaites (Sri Lanka, Waas 336, MO). Pollen globose (38 μm), 5–7-porate, zoni-aperturate; sculpturing echinate (3.8 μm long); ektexine with a thin (0.25 μm), irregular foot layer, an irregular interstitium that is discontinuous with the foot layer, and a microperforate/baculate tectum (0.44 μm; fig. 51); endexine thin; intine two-layered (fig. 51). Our observations are consistent with those of Erdtman (1952), Punt (1962), Köhler (1965), and Hayden et al. (1984).

ARISTOGEITONIA PRAIN (3 SPECIES).

Aristogeitonia monophylla Airy Shaw (Kenya, Faden et al. 45256, K). Pollen oblate (30 × 34 μm), 5–7-brevicolpate (possibly brevicolporate), zoni-aperturate; sculpturing echinate (4.1 μm long); ektexine with no foot layer, an irregular and often very reduced interstitium, and a microperforate/baculate tectum (0.24 μm; fig. 52); endexine consisting of a thin basal layer (fig. 52); intine two-layered, somewhat thickened at apertural border (fig. 53).
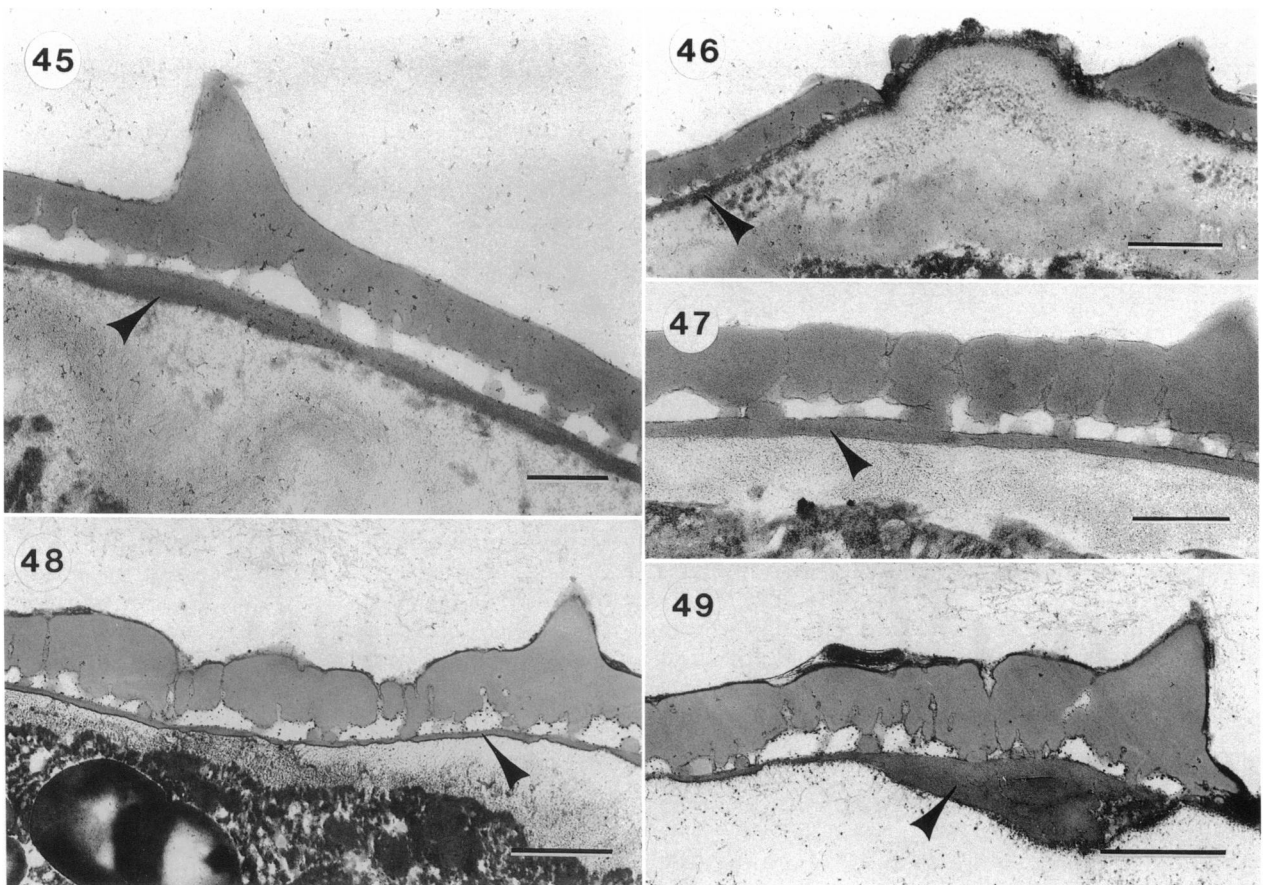
Figs. 45–49   Pollen of Euphorbiaceae subfamily Oldfieldioideae. Figs. 45, 46, *Androstachys johnsonii.* Fig. 45, Nonapertural wall, TEM; arrow indicates scanty endexine beneath foot layer. Fig. 46, Apertural region, TEM; arrow indicates endexine. Fig. 47, *Stachyandra merana.* Nonapertural wall, TEM; arrow indicates endexine. Figs. 48, 49, *Stachyandra rufibarbis.* Fig. 48, Nonapertural wall, TEM; arrow indicates thin endexine. Fig. 49, Wall at apertural region, TEM; note greatly thickened endexine (arrow). Scale bars = 0.5 μm in figs. 45, 47; 1 μm in figs. 46, 48, 49.

Although pollen of this species has not been described, pollen of *Aristogeitonia limoniifolia* Prain and *Aristogeitonia perrieri* (Léandri) R.-Sm. (= *Paragelonium perrieri* Léandri) is similar, apparently differing primarily in having somewhat shorter (2.5–3.5 μm long) spines (Punt 1962; Köhler 1965). These authors were ambivalent about whether the apertures are simple or compound, a problem we, too, have been unable to resolve.

TRIBE CALETIEAE MUELL. ARG. (14 GENERA, 53 SPECIES; 4 OF 4 SUBTRIBES INVESTIGATED).

SUBTRIBE HYAENANCHINAE BAILLON EX MUELL. ARG. (1 GENUS, 1 SPECIES).

HYAENANCHE LAMBERT (1 SPECIES).
Hyaenanche globosa (Gaertner) Lambert (South Africa, Lavranos and Bleck 20843A, MO). Pollen suboblate (40 × 42 μm), 6–7-aperturate, zoni-aperturate; sculpturing echinate (2.1 μm long); ektexine with a thin (0.34 μm), irregular foot lay-

er, an irregular interstitium that is discontinuous with the foot layer, and a microperforate/baculate tectum (0.47 μm; fig. 54); endexine thin (fig. 54), thickened at aperture border (fig. 55); intine two-layered, thickened in apertural region (fig. 55). Descriptions and illustrations of this species (Erdtman 1952; Punt 1962, 1987; Köhler 1965) are generally consistent with our observations. Erdtman and Köhler, however, reported the grains (as *Toxicodendron globosum* [Gaertner] Pax and K. Hoffm.) to be considerably smaller (29–31 × 34 μm), whereas Punt's (1962) measurements (39 × 46 μm) are closer to ours.

SUBTRIBE DISSILIARIINAE PAX AND K. HOFFM. (6 GENERA, 28 SPECIES).

WHYANBEELIA AIRY SHAW AND B. HYLAND (1 SPECIES).
Whyanbeelia terrae-reginae Airy Shaw and B. Hyland (Australia, Hyland 3041, DAV). Pollen oblate (27 × 30 μm), 5–6-porate, zoni-aperturate; sculpturing echinate (4.1 μm long); ektexine with
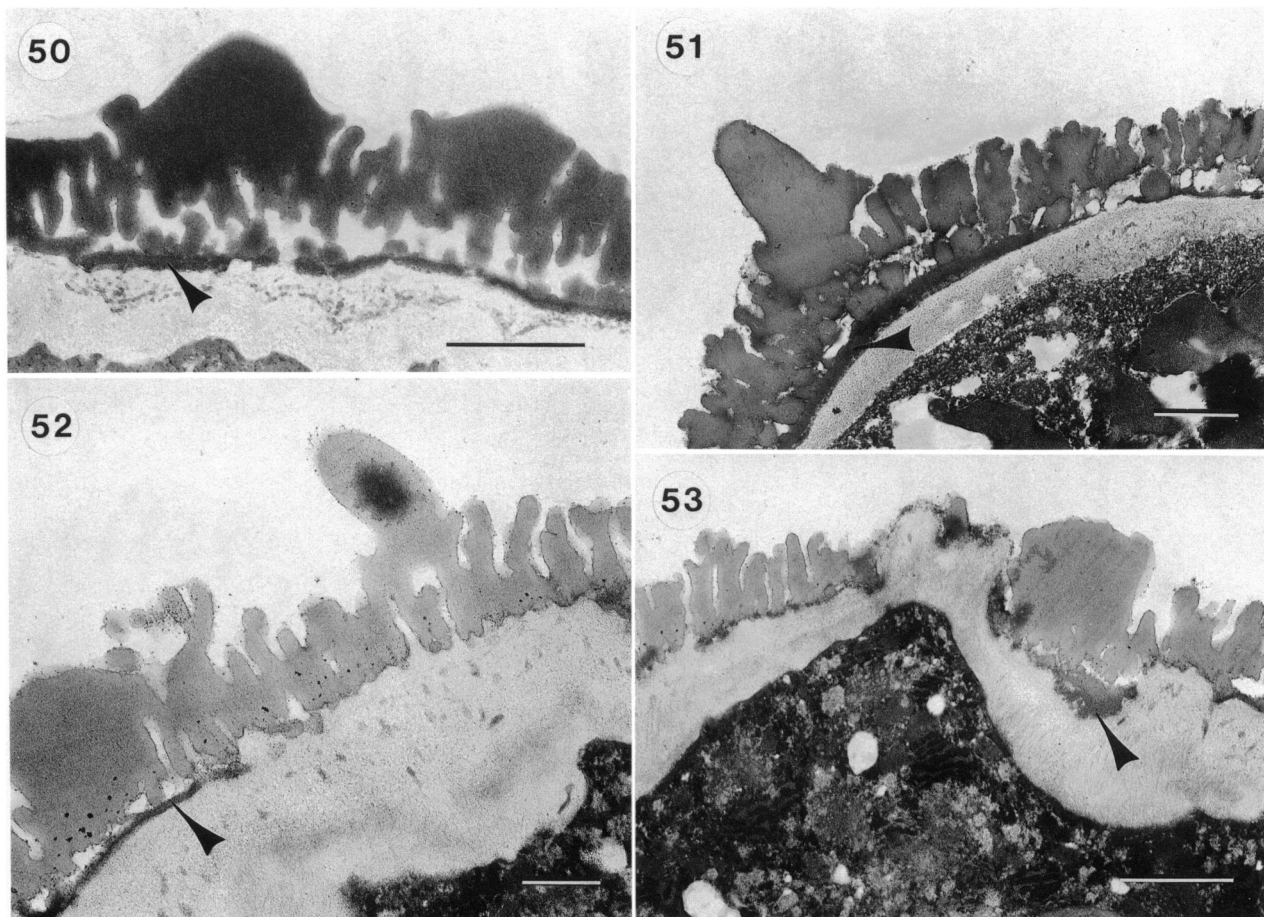
Figs. 50-53 Pollen of Euphorbiaceae subfamily Oldfieldioideae. Fig. 50, *Voatamalo eugenioides*. Nonapertural wall, TEM; arrow indicates endexine. Fig. 51, *Mischodon zeylanicus*. Wall near apertural region, TEM, oblique section; note thickened endexine (arrow). Figs. 52, 53, *Aristogeitonia monophylla*. Fig. 52, Nonapertural wall, TEM; arrow indicates endexine. Fig. 53, Apertural region, TEM; arrow indicates thin endexine. Scale bars = 1 μm in figs. 50, 51, 53; 0.5 μm in fig. 52.

no foot layer, an interstitium of irregularly spaced columnar elements, and a microperforate/baculate tectum (0.48 μm; fig. 56); ektexine at aperture border with thickened basal layer; endexine consisting of a thin basal layer (fig. 56), thickened at aperture border. Pollen of this genus has not been described previously.

LONGETIA BAILLON (1 SPECIES).

Longetia buxoides Baillon (New Caledonia, McPherson 3789, MO). Pollen oblate (27 × 30 μm), 6–7-brevicolporate, zoni-aperturate, with circular endoaperture; sculpturing scabrate (0.4 μm long); ektexine with no foot layer, an interstitium of sparse, irregular to columella-like elements, and a nearly imperforate tectum (0.84 μm) with occasional minute scabrae (fig. 58); ektexine of apertural region with tectum bulging outward, delimiting the outer widely elliptic exoaperture, and with basal thickenings constituting the inner circular endoaperture (fig. 57); endexine moderately thick (fig. 58), thickened slightly at aperture border (fig. 57); intine two-

layered, thick, somewhat more thickened in aperture region (figs. 57, 58).

Prior descriptions and illustrations of this species (Erdtman 1952; Punt 1962, 1987; Köhler 1965; Martin 1974 [as *Austrobuxus buxoides* Baillon]; and Lobreau-Callen in McPherson and Tirel 1987) are generally consistent with our observations, though all authors reported the pollen to be smaller (18–22 × 24–27 μm). Martin's (1974) statement, based on LM, that the sculpturing is finely reticulate is mistaken, as shown by our observations and SEMs published by Lobreau-Callen (in McPherson and Tirel 1987) and Punt (1987). Punt (1962) apparently missed seeing the minute scabrae with LM and incorrectly described the pollen as psilate.

CHORICERAS BAILLON (2 SPECIES).

Choriceras majus Airy Shaw (Australia, Hyland 10633, K). Pollen oblate (26 × 28 μm), 6-porate, zoni-aperturate; sculpturing scabrate (0.2 μm long); ektexine with no foot layer, an irregular interstitium, and a microperforate tec-
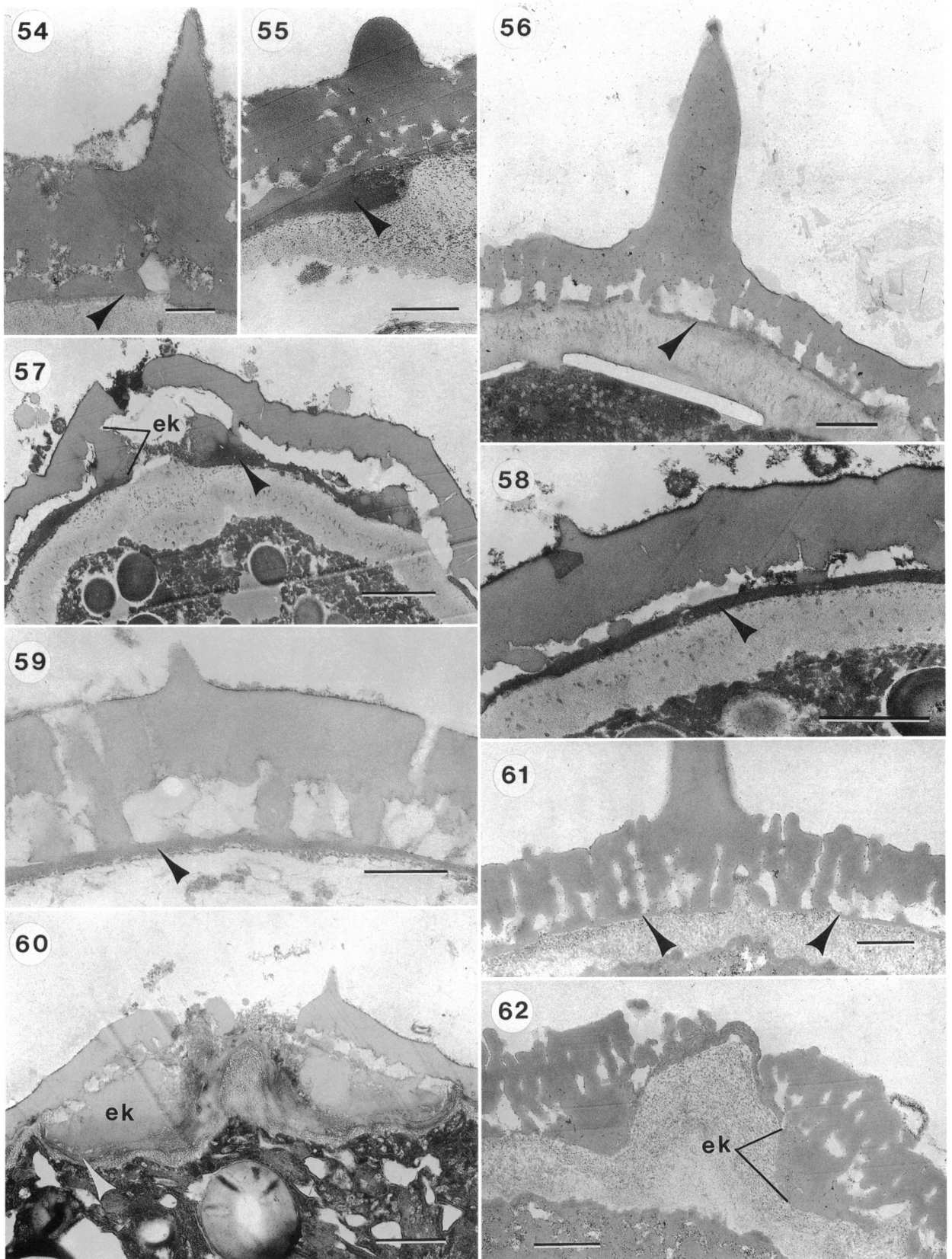
Figs. 54–62 Pollen of Euphorbiaceae subfamily Oldfieldioideae. Figs. 54, 55, *Hyaenache globosa*. Fig. 54, Nonapertural wall, TEM; arrow indicates very thin endexine below foot layer. Fig. 55, Apertural region, TEM, showing thickened endexine (arrow). Fig. 56, *Whyanbeelia terrae-reginae*. Nonapertural wall, TEM; arrow indicates thin endexine. Figs. 57, 58, *Longetia buxoides*.

tum (0.43 μm; fig. 59); ektexine at aperture border with thickened basal layer (fig. 60); endexine forming a thin basal layer (fig. 59), somewhat thickened in apertural region (fig. 60); apertural intine thickened, two-layered (fig. 60).

Although this is the first description of the pollen of this species, pollen of *Choriceras tricorne* (Benth.) Airy Shaw, the only other species in the genus, has been described and illustrated under its synonym *Dissiliaria tricornis* Benth. by several authors (Erdtman 1952; Punt 1962; Köhler 1965; Martin 1974). The two species appear to have very similar pollen, perhaps with that of *C. tricorne* being somewhat smaller (18–22 × 20–25 μm). Martin's (1974) statement, based on LM, that the sculpturing is finely reticulate is contradicted both by our observations and those of the remaining authors cited above. Punt (1962) apparently did not see the scabrae with LM and incorrectly described the pollen as psilate. The tectum of *Choriceras* has fewer microperforations and lacks the baculate structure found in most Oldfieldioideae (Discussion).

DISSILIARIA F. MUELL. EX BAILLON (3 SPECIES).
Dissiliaria baloghioides F. Muell. ex Baillon (Australia, MacPherson s. n. [January 23, 1980], QRS). Pollen suboblate (36 × 38 μm), 5–6-porate, zoni-aperturate; sculpturing echinate (4.1 μm long); ektexine with no foot layer, an irregular interstitium, and a microperforate/baculate tectum (0.75 μm; fig. 61); ektexine at aperture border with thickened basal layer (fig. 62); endexine forming a thin basal layer (fig. 61), apparently extending across aperture (fig. 62); intine of apertural region thick, two-layered (fig. 62). Martin (1974) illustrated pollen of this species and described it as globose with smaller diameter (27–30 μm) and shorter spines (2.5–3 μm).

SUBTRIBE PETALOSTIGMATINAE PAX AND K. HOFFM. (1 GENUS, 6 SPECIES).

PETALOSTIGMA F. MUELL. (6 SPECIES).
Petalostigma pubescens Domin (Australia, Speck 1818, K). Pollen oblate (32 × 34 μm), 5-porate, ± zoni-aperturate; sculpturing echinate (0.9 μm long); ektexine with no foot layer, an irregular interstitium, and a microperforate/baculate tectum (0.38 μm); endexine forming a thin basal layer, thickened at apertural border; intine of apertural region thick, two-layered (not illustrated).

Petalostigma quadriloculare F. Muell. (Australia, Mocanochie 1993, K). Pollen oblate (32 × 34 μm), 5–6-porate, zoni-aperturate; sculpturing echinate (1.0 μm long); ektexine with no foot layer, an irregular interstitium, and a microperforate/baculate tectum (0.51 μm; fig. 63); endexine forming a thin basal layer (fig. 63), thickened at apertural border (fig. 64); intine two-layered (fig. 63), thickened in apertural region (fig. 64).

Erdtman (1952) studied pollen identified as *P. pubescens,* and Punt (1962) and Köhler (1965) studied what they called *P. quadriloculare.* Unfortunately, prior to Airy Shaw's revision of the genus in 1976, many collections were misidentified (Airy Shaw 1976). All our samples came from specimens annotated by Airy Shaw, but he did not cite any of the specimens that were sources for the pollen studied by the others, so we cannot determine if differences in observations reflect variation within species or simply misidentifications. In general our observations are consistent with these earlier descriptions. All authors reported smaller diameters than we measured: 26 × 28 μm for *P. pubescens* (Erdtman 1952) and 25–28.5 × 28–32 μm for *P. quadriloculare* (Punt 1962; Köhler 1965). More significantly, they all reported that the apertures of *Petalostigma* do not lie exactly in the equatorial plane. Our observations are not entirely consistent with theirs. In *P. pubescens* we found that some of the apertures indeed lay outside the equatorial plane, but in *P. quadriloculare* all the apertures were strictly equatorial. Because they are oblique polar views, the LM photographs of this species shown by Martin ([1974], as *Petalostigma haplocladum* Pax and K. Hoffm.) are difficult to interpret. It is possible that aperture distribution in *Petalostigma* may represent a transition between zoni-aperturate and pan-aperturate, particularly if the species themselves are polymorphic.

SUBTRIBE PSEUDANTHINAE MUELL. ARG. (6 GENERA, 18 SPECIES).

NEOROEPERA MUELL. ARG. & F. MUELL. (2 SPECIES).
Neoroepera buxifolia Muell. Arg. & F. Muell. (Australia, White 12095, US). Pollen globose (33 μm), 16–20-pantoporate; sculpturing echinate (5.1 μm long), psilate with evident micropores in interspinal region (fig. 38); ektexine with no foot layer, an interstitium of irregularly spaced columnar elements, and a microperforate/baculate tec-

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Fig. 57, Apertural region, TEM; note thickened basal ektexine (*ek*) and endexine (arrow). Fig. 58, Nonapertural wall, TEM; arrow indicates endexine. Figs. 59, 60, *Choriceras majus.* Fig. 59, Nonapertural wall, TEM; arrow indicates endexine. Fig. 60, Apertural region, TEM. Note thickened, basal ektexine (*ek*) and thin endexine (arrow) at apertural border. Figs. 61, 62, *Dissiliaria baloghioides.* Nonapertural wall, TEM; arrow indicates endexine. Fig. 62, Apertural region, TEM; note thickened ektexinous layer (*ek*) at apertural border. Scale bars = 0.5 μm in figs. 54, 59; 1 μm in figs. 55, 56, 60–62; 2 μm in figs. 57, 58.

tum (0.63 μm; fig. 65); nonapertural endexine forming a thin basal layer (fig. 65). Henderson's (1992) illustration of the pollen of this species is consistent with our observations. Köhler's (1965) description differs from ours in that he reported that the grains were 27 μm in diameter and bore 30–40 pores. Otherwise his description agrees with our observations.

Neoroepera banksii Benth. (Australia, Hyland 6945, K). Pollen globose (36 μm), ca. 25-pantoporate; sculpturing echinate (3.7 μm long); ektexine with a thick (0.98 μm), homogeneous foot layer, an irregular interstitium that is generally discontinuous with the foot layer, and a microperforate, granular tectum (0.26 μm; fig. 66); foot layer at aperture border slightly thickened (fig. 66); endexine not observed; intine two-to-three-layered, the outer one to two layers thickened in apertural region (fig. 66). Punt's (1962) description and Martin's (1974) and Henderson's (1992) illustrations of the pollen of this species are generally consistent with our observations, though Punt reported the pollen to be somewhat larger (40 μm) with shorter spines (2 μm) and up to 30 apertures.

KAIROTHAMNUS AIRY SHAW (1 SPECIES).

Kairothamnus phyllanthoides (Airy Shaw) Airy Shaw (Papua New Guinea, Streimann NFG 24462, K). Pollen globose (26 μm), 10–12-pantoporate; sculpturing echinate (1.8 μm long); ektexine with a thick (0.61 μm), homogeneous foot layer, an interstitium of irregular granular elements that are discontinuous with the foot layer, and a microperforate, granular to tabular tectum (0.21 μm; fig. 67); foot layer at aperture border slightly thickened (fig. 68); endexine obvious only at aperture border (fig. 68); intine two-to-three-layered (figs. 67, 68), the outer one to two layers thickened in apertural region (fig. 68). Pollen of this genus has not been described previously.

SCAGEA MCPHERSON (2 SPECIES).

Scagea oligostemon (Guillaumin) McPherson (New Caledonia, Webster 19181, DAV). Pollen globose (30 μm), 16–20-pantoporate; sculpturing echinate (1.9 μm long); ektexine with a thick (0.70 μm), homogeneous foot layer, an interstitium of irregular, granular elements that are discontinuous with the foot layer, and a microperforate, granular to tabular tectum (0.19 μm; fig. 69); foot layer at aperture border slightly thickened (fig. 70); endexine observed only at aperture border (fig. 70); intine two-layered (fig. 69), the outer layer thickened in apertural region (fig. 70). Descriptions and illustrations of the pollen of this species (Punt [1962], as *Longetia gynotricha* Guillaumin; Lobreau-Callen in McPherson and Tirel [1987]) are consistent with our observations.

MICRANTHEUM DESF. (3 SPECIES).

Micrantheum hexandrum Hook. f. (Australia, Briggs and Johnson 4419, DAV). Pollen globose (34 μm), ca. 30–40-pantoporate (fig. 37); sculpturing echinate (3.0 μm long); ektexine with a thick (1.5 μm), homogeneous foot layer, an irregular interstitium that is discontinuous with the foot layer, and a microperforate, granular tectum (0.33 μm; fig. 71); foot layer at aperture border slightly thickened (fig. 71); endexine absent or very scanty (fig. 71); intine two-to-three-layered, the outer one to two layers thickened in apertural region (fig. 71).

Pollen of this species has been described and/ or illustrated by Erdtman (1952), Punt (1962), Köhler (1965), Martin (1974), and Henderson (1992). These reports differ from ours only in that Punt (1962) stated the pollen diameter to be 45 μm (whereas the others gave diameters very close to our measurement of 34 μm) and that both he and Köhler (1965) reported 40–50 apertures. The pollen of *Micrantheum ericoides* Desf. differs in its smaller size, fewer apertures with spines clustered around them, and thicker exine (Erdtman 1952; Punt 1962; Köhler 1965), indicating that pollen might provide systematically useful information at the infrageneric level in *Micrantheum.*

PSEUDANTHUS SIEBER EX SPRENGEL (7 SPECIES).

Pseudanthus divericatissimus (Muell. Arg.) Benth. (Australia, Coveny 5253, DAV). Pollen globose (23 μm), 10–14-pantoporate; sculpturing echinate (1.2 μm long); ektexine with a thick (0.65 μm) foot layer, an interstitium of irregular columnar elements that are discontinuous with the foot layer, and a microperforate, granular tectum (0.22 μm; figs. 72, 73); foot layer at aperture border thickened (fig. 72); endexine not observed; intine two-to-three-layered, the outer one to two layers thickened in apertural region (fig. 73).

Pollen of this species has not been described previously, but our observations are consistent with descriptions of the pollen of other species (Erdtman 1952; Punt 1962; Köhler 1965). Aperture number varies considerably within the genus, with reports of six to eight apertures in *Pseudanthus nematophorus* F. Muell., *Pseudanthus orientalis* F. Muell. and *Pseudanthus pimeloides* Sieber; 10–14 in *Pseudanthus divericatissimus;* 18–25 in *Pseudanthus virgatus* (Klotzsch) Muell. Arg.; and 20–25 in *Pseudanthus ovalifolius* F. Muell. With further study, aperture number may prove to be of systematic value in this genus.

STACHYSTEMON PLANCHON (3 SPECIES).

Stachystemon polyandrus (F. Muell.) Benth. (Australia, Young Y-325, DAV). Pollen globose (22 μm), ca. 12-pantoporate (apertures obscure); sculpturing echinate (1.8 μm long); ektexine with a thin (0.34 μm), homogeneous foot layer, an
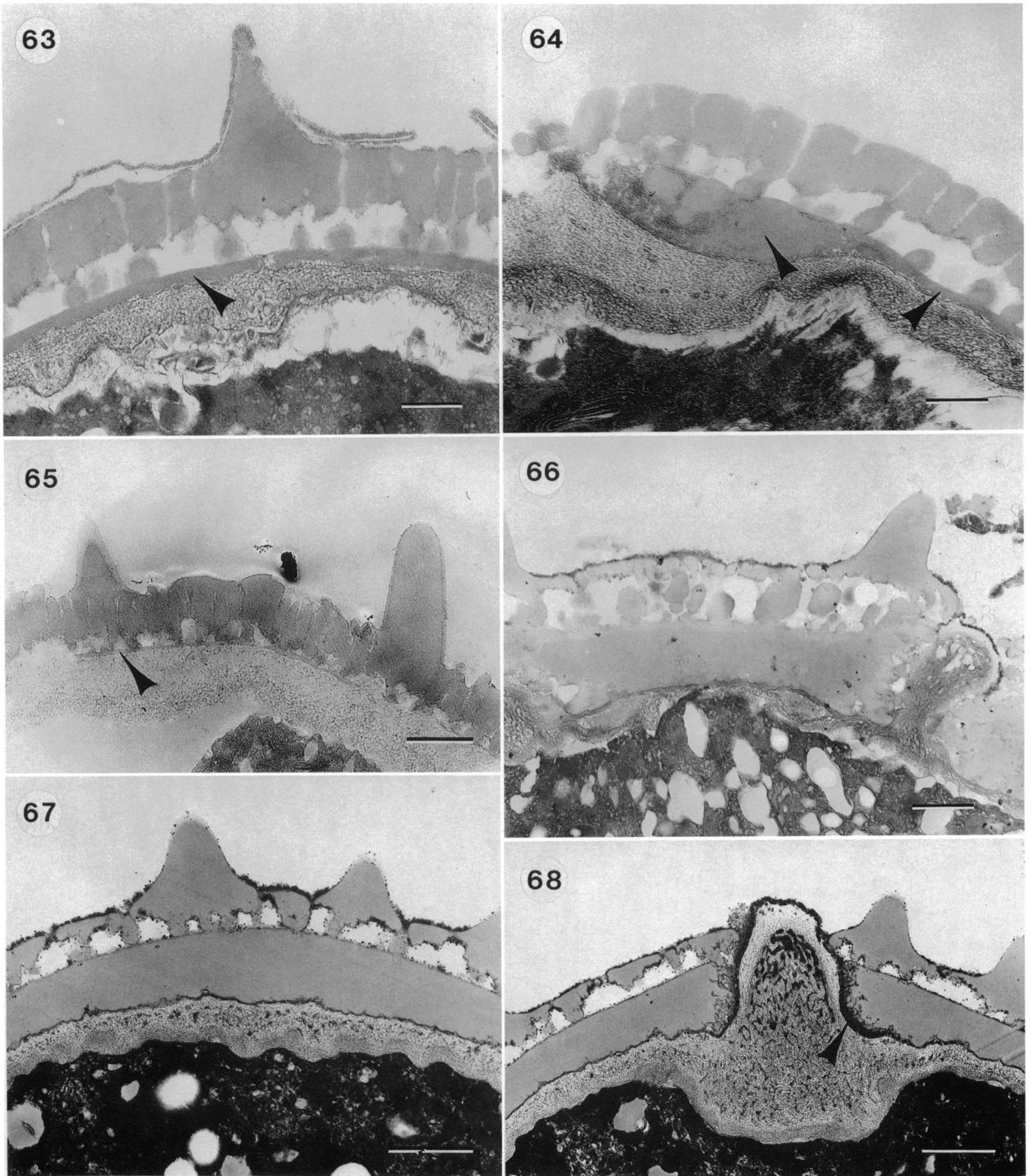
Figs. 63-68 Pollen of Euphorbiaceae subfamily Oldfieldioideae. Figs. 63, 64, *Petalostigma quadriloculare.* Fig. 63, Nonapertural wall, TEM; arrow indicates endexine. Fig. 64, Apertural region, TEM; note endexine (arrow), thickened at apertural border. Fig. 65, *Neoroepera buxifolia.* Nonapertural wall, TEM; arrow indicates thin endexine. Fig. 66, *Neoroepera banksii.* Nonapertural (center) and apertural (far right) walls, TEM; note thick foot layer. Figs. 67, 68, *Kairothamnus phyllanthoides.* Fig. 67, Nonapertural wall, TEM. Fig. 68, Apertural region, TEM; arrow indicates endexine. Scale bars = 0.5 μm in fig. 63, 64; 1 μm in figs. 65–68.

interstitium of irregular columnar elements that are discontinuous with the foot layer, and a microperforate, granular tectum (0.14 μm; fig. 74); foot layer at aperture border thickened (fig. 74); endexine possibly deposited at aperture periphery (fig. 74); intine two-to-three-layered, the outer one to two layers thickened in apertural region (fig. 74). Pollen of this species has not been de-
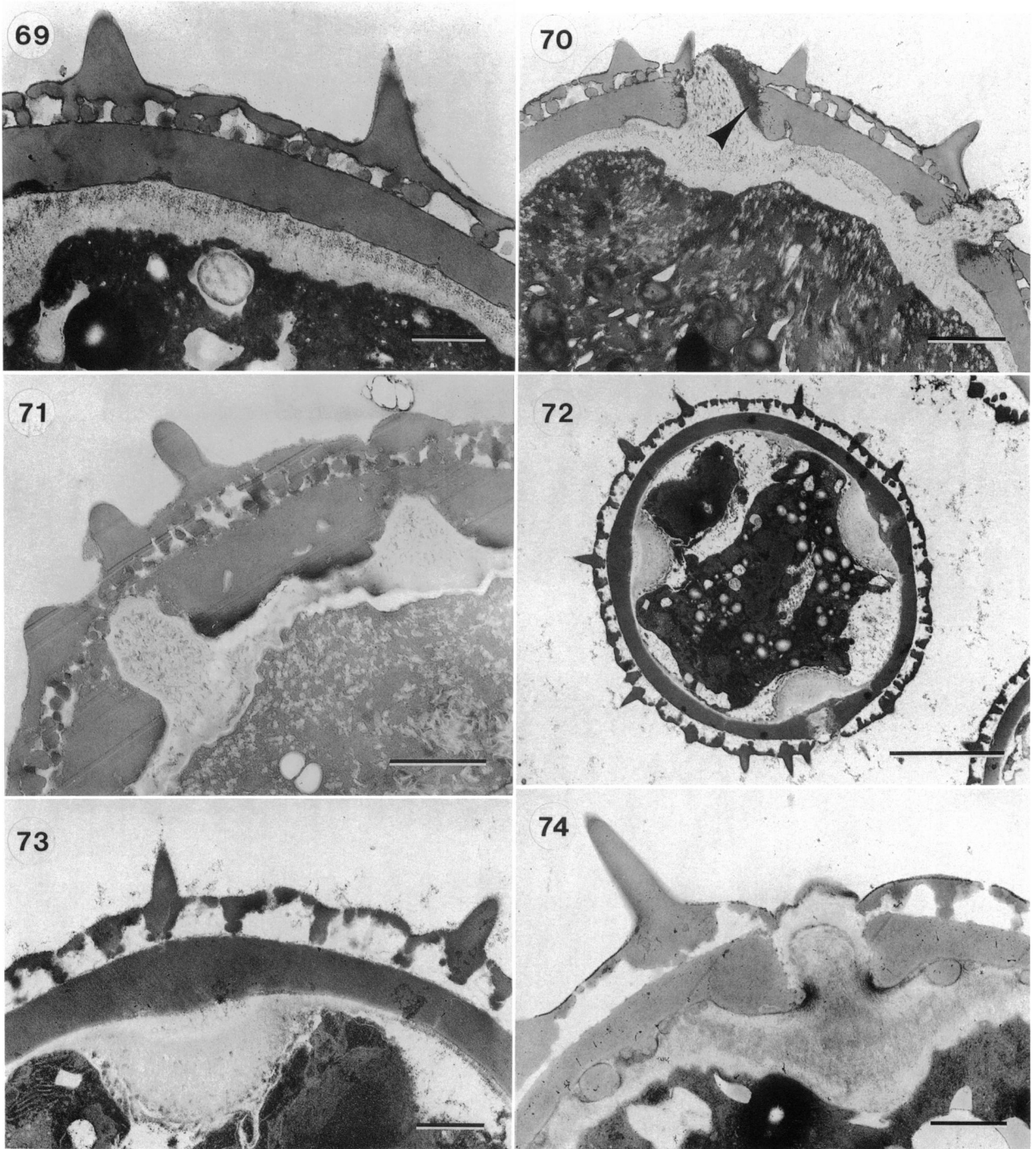
Figs. 69-74   Pollen of Euphorbiaceae subfamily Oldfieldioideae. Figs. 69, 70, *Scagea oligostemon*. Fig. 69, Nonapertural wall, TEM. Fig. 70, Wall, TEM, showing two apertures; arrow indicates endexine. Fig. 71, *Micrantheum hexandrum*. Wall, TEM, showing two apertures. Figs. 72, 73, *Pseudanthus divericatissimus*. Fig. 72, Whole grain cross-section, TEM. Fig. 73, Nonapertural wall, TEM. Fig. 74, *Stachystemon polyandrus*. Wall, TEM, showing one aperture. Scale bars = 1 μm in figs. 69, 73, 74; 2 μm in figs. 70, 71; 5 μm in fig. 72.

scribed previously. Pollen of *Stachystemon vermicularis* Planchon apparently is larger (28–36 μm) but otherwise similar (Erdtman 1952; Punt 1962; Köhler 1965). Aperture number in the latter species is unclear, with Punt (1962) reporting 12 apertures in agreement with our count for *S. polyandrus*, but Köhler (1965) reporting 17–22.

Discussion

These palynological data provide several characters of systematic significance (table 1). We have previously utilized these data, along with morphological and anatomical characters, in a cladistic analysis of the subfamily Oldfieldioideae

(Levin and Simpson 1994a). In that study, relationships in the subfamily Phyllanthoideae were not well resolved. In contrast, phylogenetic relationships within the Oldfieldioideae were well resolved, with the palynological data almost completely compatible with the morphological and anatomical data. We trace four of the pollen characters onto our preferred cladogram (fig. 75) for reference with the following discussion.

POLLEN SHAPE

Most investigated members of the subfamily Phyllanthoideae have prolate grains (table 1; fig. 17). Other studies (Punt 1962; Köhler 1965) have shown that both prolate and globose to oblate pollen grains are widespread in the Phyllanthoideae. All members of the subfamily Oldfieldioideae, as delimited here, have a globose to oblate pollen shape (table 1; figs. 33, 35, 37). It is not clear which pollen shape is evolutionarily derived in these subfamilies (Levin and Simpson 1994a).

POLLEN SIZE

Mode of preparation can greatly influence grain size (reviewed by Moore et al. 1991). In our study, all pollen samples were prepared in the same way and comparisons among them are valid. However, differences in pollen size from other studies are difficult to evaluate because of differing methods of preparation. In addition, we did not evaluate intraspecific variation in pollen size because of our limited samples.

Investigated members of the Phyllanthoideae have pollen grains ranging from ca. 12 to 33 μm maximum diameter, except for *Amanoa* spp., which have distinctly larger grains, ranging from ca. 40–52 μm maximum diameter (table 1). (Pollen of *Phyllanthus* spp., not investigated here, have diameters up to 45 μm [table 1].) In the Oldfieldioideae maximum diameters range from ca. 22 to 50 μm (table 1). Taxa of the tribe Caletieae have on average slightly smaller grains (ca. 22–42 μm maximum diameter) than members of the tribe Picrodendreae (ca. 27–50 μm maximum diameter). The Podocalyceae have relatively small grains (ca. 25–27 μm maximum diameter); *Croizatia* (Croizateae) has intermediate-sized pollen (32 μm maximum diameter). Obviously, there is considerable overlap in pollen size among these taxa, and no clear trends are apparent.

APERTURE SHAPE

All 12 investigated members of the subfamily Phyllanthoideae have colporate apertures with the exception of *Hymenocardia*, which has short, essentially porate apertures (table 1; fig. 23). However, some species of the large genus *Phyllanthus*, not investigated in this study, have porate apertures (table 1). The presence of a lalongate (transversely or latitudinally oriented) endoaperture, also called a "colpus transversalis" (Punt

1962), may constitute a synapomorphy uniting some taxa within the Phyllanthoideae, but our study of this subfamily is too incomplete to verify this. All investigated members of the subfamily Oldfieldioideae have apertures that with SEM appear to be brevicolpate or porate (table 1; figs. 35–38), a synapormorphy for the subfamily (Levin and Simpson 1994a). Structurally, the apertures of most Oldfieldioideae probably are brevicolporate or pororate, i.e., they have a circular, differentially thickened endoaperture in addition to the exoaperture (Punt [1962], Köhler [1965], Hayden et al. [1984], all of whom used LM to study acetolysed pollen grains, the best technique for detecting the endoaperture of colporate or pororate pollen).

APERTURE NUMBER

Croizatia (Oldfieldioideae) and all investigated members of the Phyllanthoideae have 3-aperturate pollen grains (table 1; figs. 8, 16, 20). However, some species of the large genus *Phyllanthus*, not investigated in this study, may have up to 60 apertures (table 1). All members of the Oldfieldioideae (except *Croizatia*) have from four to ca. 40 apertures (table 1). Within the Oldfieldioideae, the occurrence of more than three apertures constitutes a synapomorphy for the tribes Podocalyceae, Picrodendreae, and Caletieae (i.e., for all but *Croizatia*, the most basal taxon of the Oldfieldioideae [Levin and Simpson 1994a]).

A strong correlation exists between aperture shape and aperture number. The 3-aperturate taxa mostly have a colporate (rarely brevicolporate) aperture shape, the exception, mentioned above, being *Hymenocardia*, which has three essentially porate apertures (fig. 23). Taxa with four or more apertures all have porate (to pororate) or brevicolpate (to brevicolporate) aperture shape. Of the Oldfieldioideae with more than three apertures, aperture number varies considerably. No clear discontinuity is apparent between taxa with four and those with up to ca. 40 apertures; a correlation is evident, however, between aperture number and aperture position.

APERTURE POSITION

Pollen of all investigated members of the Phyllanthoideae is zoni-aperturate (table 1; figs. 17, 20, 23). However, some species of the large genus *Phyllanthus*, not investigated in this study, are pan-aperturate (table 1). In the Oldfieldioideae the zoni-aperturate condition is ancestral (fig. 75A). Within this subfamily the pan-aperturate condition (figs. 35–38) is a synapomorphy for the subtribe Pseudanthinae of the tribe Caletieae, and it arose independently in *Androstachys johnsonii* (fig. 75A; Levin and Simpson 1994a).

Aperture position and number are correlated to some degree. Taxa with three apertures are always zoni-aperturate, as are most taxa with four

Table 1

PALYNOLOGICAL CHARACTERS OF INVESTIGATED EUPHORBIACEAE

| | Pollen | | | Exine sculpturing | | | Ektexine structure | | |
Taxon	Shape	Size (P × E, μm)	Aperture type	Spinal	Surface	Foot layer	Interstitium	Tectum	Aperture thickening
Subfamily Phyllanthoideae:									
Amanoa guianensis	Oblate	36 × 42	3-colporate	Baculate (4.1 μm)	Verrucate	Thick (1.0 μm), homogeneous	Columellate (homologous with baculae)	Absent	None
Amanoa strobilacea	Oblate	38 × 54	3-colporate	None	Reticulate (coarse), verrucate	Thick (1.4 μm), homogeneous	Columellate	Widely perforate/homogeneous (2.7 μm)	None
Securinega durissima	Oblate	22 × 25	3-colporate	Echinate (1.0 μm)	Psilate[a]	Thin (.28μm), homogeneous	Columellate	Perforate/homogeneous (.32 μm)	None
Margaritaria discoidea	Prolate	27 × 22	3-colporate, with lalongate endoaperture	None	Reticulate	Thin (.17 μm), homogeneous	Columellate	Widely perforate/homogeneous (.43 μm)	None
Phyllanthus spp.[b,c]	Prolate to globose	45 × 33 to 13 × 13	3-colporate to 60-pantoporate	None	Reticulate	Details unknown	Columellate	Perforate/homogeneous	Unknown
Drypetes lateriflora	Prolate	30 × 20	3-colporate, with lalongate endoaperture	None	Reticulate	Thin (.18 μm), homogeneous	Columellate	Perforate/homogeneous (.37 μm)	None
Aporusa falcifera	Subprolate	16 × 15	3-colporate, with lalongate endoaperture	None	Reticulate/pitted	Thin (.17 μm), homogeneous	Columellate	Perforate/homogeneous (.29 μm)	None
Antidesma membranaceum	Prolate	23 × 12	3-colporate, with lalongate endoaperture	None	Reticulate	Thin (.11 μm), homogeneous	Columellate	Perforate/homogeneous (.30 μm)	None
Antidesma venosum	Prolate	20 × 12	3-colporate, with lalongate endoaperture	None	Reticulate	Thin (.15 μm), homogeneous	Columellate	Perforate/homogeneous (.31 μm)	None
Hyeronima alchorneoides	Prolate	33 × 19	3-colporate, with lalongate endoaperture	None	Foveolate	Thin (.21 μm), homogeneous	Columellate	Perforate/homogeneous (.40 μm)	None
Didymocistus chrysadenius	Globose	12	3-colporate, with lalongate endoaperture	Scabrate (.08 μm)	Rugulate	Thin (.12 μm), homogeneous	Columellate	Perforate/homogeneous (.20 μm)	Present (basal layer slightly thickened)
Hymenocardia acida	Oblate	25 × 28	3-porate (to brevicolporate)	Scabrate (.07 μm)	Rugulate	Thin (.18 μm), homogeneous	Columellate	Perforate/homogeneous (.26 μm)	Present (basal layer thickened)
Hymenocardia ulmoides	Oblate	19 × 21	3-porate (to brevicolporate)	Scabrate (.07 μm)	Rugulate	Thin (.16 μm), homogeneous	Columellate	Perforate, homogeneous (.19 μm)	Present (basal layer thickened)

Subfamily Oldfieldioideae:

Species								
Croizatia naiguatensis	Globose	32	3-brevicolporate	Echinate (3.3 µm)	Foveolate[d]	Thick (.63 µm), homogeneous	Irregular, discontinuous with foot layer	Microperforate/granular (24 µm)	Present (basal layer thickened)
Paradrypetes subintegrifolia	Oblate	22 × 27	4-brevicolporate, zoni-aperturate, with la-longate endoaperture	Echinate (1.4 µm)	Psilate—wrinkled	Thin (.12 µm), irregular	Absent (?)	Imperforate (.35 µm)	None
Podocalyx loranthoides	Oblate	22 × 25	4-porate, zoni-aperturate	Echinate (2.8 µm)	Psilate—wrinkled[d]	Thin (.11 µm), irregular ± granular	Absent	Microperforate/baculate (33 µm)	None
Tetracoccus dioicus	Suboblate	46 × 47	4-porate, zoni-aperturate	Echinate (4.7 µm)	Verrucate[d,e]	Thin (.35 µm), irregular, granular	Irregular, discontinuous with foot layer	Microperforate/baculate (63 µm)	Unknown
Parodiodendron marginivillosum	Oblate	24 × 27	Ca. 7-porate, zoni-aperturate	Echinate (3.1 µm)	Verrucate	Absent	Irregular	Microperforate/baculate (1.1 µm)	None
Picrodendron baccatum[e]	Oblate	26 × 29	5–8-brevicolporate, zoni-aperturate	Echinate (3 µm)	Vermiform[f]	Irregular; thin	Irregular, discontinuous with foot layer	Microperforate/baculate (6–.8 µm)	None
Piranhea trifoliata	Oblate	32 × 35	6-porate, zoni-aperturate	Echinate (2.7 µm)	Verrucate[f]	Absent	Irregular	Microperforate/baculate (39 µm)	Unknown
Celaenodendron mexicanum	Suboblate	39 × 40	7 (8)-porate, zoni-aperturate	Echinate (2.9 µm)	Unknown	Absent	Irregular	Microperforate/baculate (59 µm)	None
Oldfieldia africans	Oblate	28 × 30	5–6-porate, zoni-aperturate	Echinate (3.5 µm)	Verrucate[f]	Absent	Irregular	Microperforate/baculate (44 µm)	Present (basal layer thickened)
Androstachys johnsonii	Globose	50	5–7-pantoporate	Echinate (1.1 µm)	Psilate	Thin, varying in thickness (.07 µm)	Columellate, continuous with foot layer	Microperforate (.36 µm)	None
Stachyandra merana	Globose	44	4–6-porate, zoni-aperturate	Echinate (1.4 µm)	Psilate—wrinkled[f]	Absent	Irregular	Microperforate/baculate (.52 µm)	None
Stachyandra rufibarbis	Globose	46	5–7-porate, zoni-aperturate	Echinate (.9 µm)	Unknown	Absent	Irregular	Microperforate/baculate (.50 µm)	None
Voatamalo eugenioides	Globose	44	5–6-porate, zoni-aperturate	Echinate (3.3 µm)	Unknown	Thin (.14 µm), irregular to absent	Irregular, discontinuous with foot layer	Microperforate/baculate (.38 µm)	Unknown

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Table 1 (*Continued*)

| Taxon | Pollen | | Aperture type | Exine sculpturing | | Ektexine structure | | | |
	Shape	Size (P × E, μm)		Spinal	Surface	Foot layer	Interstitium	Tectum	Aperture thickening
Mischodon zeylanicus	Globose	38	5–7-porate, zoni-aperturate	Echinate (3.8 μm)	Unknown	Thin (.25 μm), irregular	Irregular, discontinuous with foot layer	Microperforate/baculate (.44 μm)	Unknown
Aristogeitonia monophylla	Oblate	30 × 34	5–7-brevicolpate, zoni-aperturate	Echinate (4.1 μm)	Unknown	Absent	Irregular to reduced	Microperforate/baculate (.24 μm)	None
Hyaenanche globosa	Suboblate	40 × 42	6–7-aperturate, zoni-aperturate	Echinate (2.1 μm)	Verrucate[c,f]	Thin (.34 μm), irregular	Irregular, discontinuous with foot layer	Microperforate/baculate (.47 μm)	Unknown
Austrobuxus spp.[c,e,f,g,h]	Oblate	25 × 28, 29 × 33	5–7-porate, zoni-aperturate	Echinate (3–5.5 μm)	Foveolate	Irregular	Irregular, discontinuous with foot layer	Microperforate/baculate (.9–1.4 μm)	Unknown
Whyanbeelia terrae-reginae	Oblate	27 × 30	5–6-porate, zoni-aperturate	Echinate (4.1 μm)	Foveolate[f]	Absent	Irregular	Microperforate/baculate (.48 μm)	Present (basal layer thickened)
Longetia buxoides	Oblate	27 × 30	6–7-brevicolporate, zoni-aperturate	Scabrate (.4 μm)	Psilate[c,h]	Absent	Irregular	Nearly imperforate (.84 μm)	Present (basal layer thickened)
Choriceras majus	Oblate	26 × 28	6-porate, zoni-aperturate	Scabrate (.2 μm)	Unknown	Absent	Irregular	Microperforate (.43 μm)	Present (basal layer thickened)
Dissiliaria baloghioides	Suboblate	36 × 38	5–6-porate, zoni-aperturate	Echinate (4.1 μm)	Unknown	Absent	Irregular	Microperforate/baculate (.75 μm)	Present (basal layer thickened)
Petalostigma pubescens	Oblate	32 × 34	5-porate, ± zoni-aperturate	Echinate (.9 μm)	Unknown	Absent	Irregular	Microperforate/baculate (.38 μm)	None
Petalostigma quadriloculare	Oblate	32 × 34	5–6-porate, zoni-aperturate	Echinate (1.0 μm)	Unknown	Absent	Irregular	Microperforate/baculate (.51 μm)	None
Neoroepera buxifolia	Globose	33	16–20-pantoporate	Echinate (5.1 μm)	Foveolate	Absent	Irregular	Microperforate/baculate (.63 μm)	Unknown
Kairothamnus phyllanthoides	Globose	26	10–12-pantoporate	Echinate (1.8 μm)	Foveolate[f]	Thick (.61 μm), homogeneous	Irregular, discontinuous with foot layer	Microperforate/granular (.21 μm)	None to slight basal thickenings

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Scagea oligostemon	Globose	30	16–20-pantoporate	Echinate (1.9 μm)	Foveolate[h]	Thick (.70 μm), homogeneous	Irregular, discontinuous with foot layer	Microperforate/granular (.19 μm)	None to slight basal thickenings
Neoroepera banksii	Globose	36	Ca. 25-pantoporate	Echinate (3.7 μm)	Unknown	Thick (.98 μm), homogeneous	Irregular, discontinuous with foot layer	Microperforate/granular (.26 μm)	None to slight basal thickenings
Micrantheum hexandrum	Globose	34	Ca. 30–40-pantoporate	Echinate (3.0 μm)	Foveolate[f]	Thick (1.5 μm), homogeneous	Irregular, discontinuous with foot layer	Microperforate/granular (.33 μm)	None
Pseudanthus divericatissimus	Globose	23	10–14-pantoporate	Echinate (1.2 μm)	Unknown	Thick (.65 μm), homogeneous	Irregular, discontinuous with foot layer	Microperforate/granular (.22 μm)	Present (basal layer thickened)
Stachystemon polyandrus	Globose	22	12-pantoporate	Echinate (1.8 μm)	Unknown	Thin (.34 μm), homogeneous	Irregular, discontinuous with foot layer	Microperforate/granular (.14 μm)	Present (basal layer thickened)

Note. Data are from present study except where noted. Pollen size is listed as polar × equatorial (P × E, μm). Measurements (in μm) listed under "Exine sculpturing—Spinal" refer to mean spine length; for echinate or scabrate pollen, "surface" sculpturing refers to that between the spines. Ektexine measurements (in μm) refer to mean foot layer or tectum thickness.

[a] Webster 1984.
[b] Punt 1962, 1980.
[c] Punt 1987.
[d] Webster et al. 1987.
[e] Hayden et al. 1984.
[f] G. Webster, unpublished data.
[g] Köhler 1965; Martin 1974.
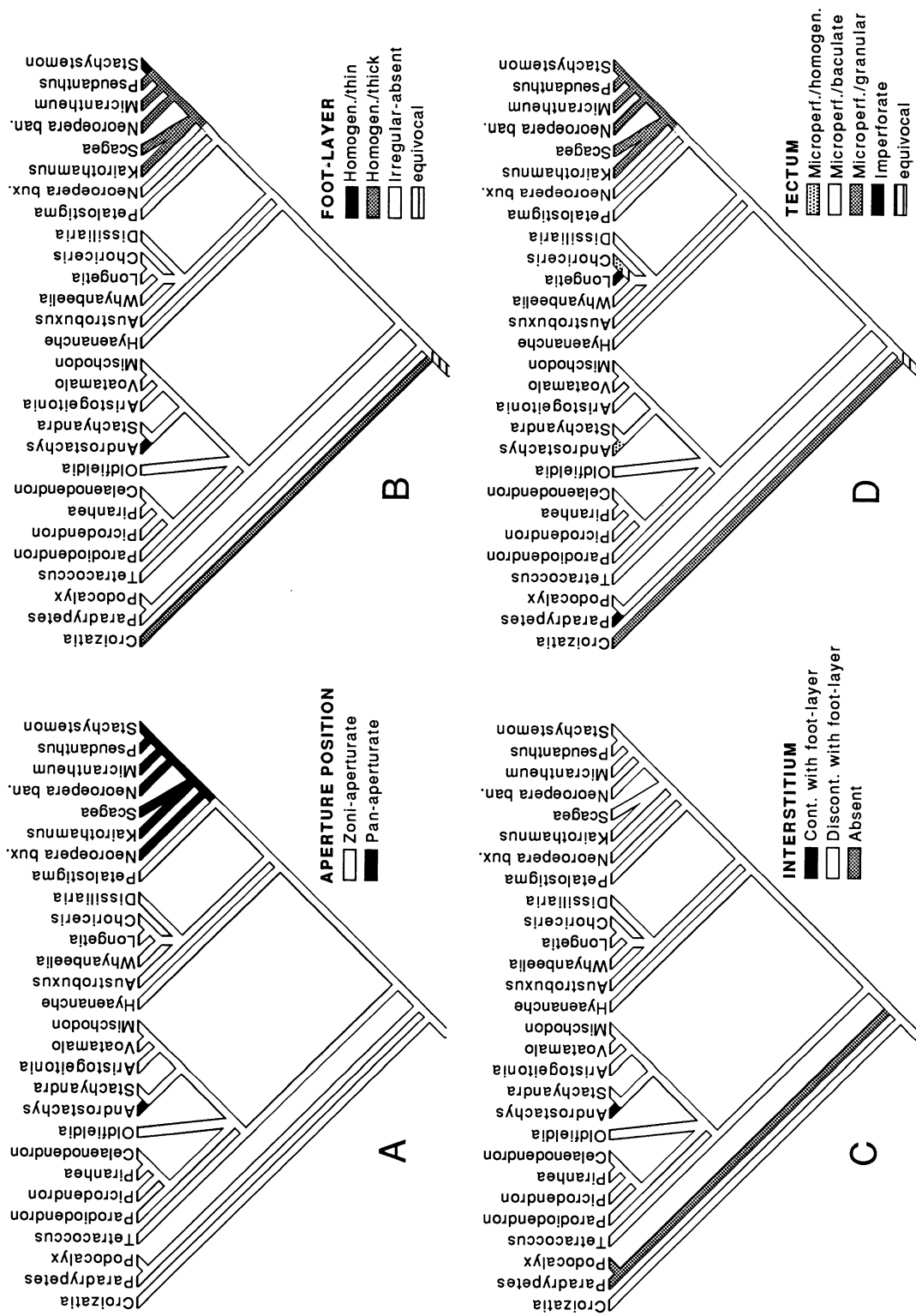[h] Lobreau-Callen 1987.

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Fig. 75 Cladograms of Euphorbiaceae subfamily Oldfieldioideae (after Levin and Simpson 1994a) showing character state distributions of selected pollen characters. *A*, Aperture position. *B*, Foot layer structure. *C*, Interstitium structure. *D*, Tectum structure.

to eight apertures (table 1). The exception is *A. johnsonii,* which has five to seven apertures (fig. 35), and some species of *Pseudanthus* that we did not investigate, which have six to eight apertures (Punt 1962, Köhler 1965). Taxa with 10 or more apertures are always pan-aperturate.

POLLEN SCULPTURING

Almost all investigated members of the Phyllanthoideae have pollen with nonspinose, reticulate to foveolate exine sculpturing (fig. 17). Isolated exceptions are *Amanoa guianensis* (fig. 1), which has baculate sculpturing apparently derived from an ancestrally reticulate condition, and *Securinega* (fig. 7), which is echinate with psilate interspinal sculpturing. *Didymocistus* (figs. 20) and *Hymenocardia* (figs. 23, 25) both have minute scabrae with rugulate interspinal sculpturing, partial evidence for a close relationship between them (Levin and Simpson 1994*b*).

All investigated Oldfieldioideae have pollen with radially elongate, sharply tapering spines that are continuous with the tectum (figs. 40–42), which constitutes a synapomorphy for the subfamily Oldfieldioideae as a whole (Levin and Simpson 1994*a*). The spines of most Oldfieldioideae are prominent echinae, ranging from 0.9 μm to as long as 5.5 μm in length (table 1). Within the Oldfieldioideae, *Choriceras* (figs. 59, 60) and *Longetia* (figs. 57, 58) have very short scabrae less than 0.4 μm long, a synapomorphy for these two genera (Levin and Simpson 1994*a*). The baculate pollen of *A. guianensis* and the echinate pollen of *Securinega* (both Phyllanthoideae) appear to have evolved independently from similar pollen in the Oldfieldioideae (Levin and Simpson 1994*a*).

The surface sculpturing pattern between the spines in Oldfieldioideae is often ambiguous. The appearance may depend on pollen preparation and the presence of pollenkitt, which may obscure the underlying exine (figs. 29, 49, 63). Interspinal sculpturing of several taxa is verrucate (fig. 34) and for others foveolate (fig. 38); remaining taxa have either smooth or "wrinkled" interspinal sculpturing (fig. 36). We detected no clear phylogenetic patterns (Levin and Simpson 1994*a*).

EXINE ULTRASTRUCTURE

All investigated members of the Phyllanthoideae except *A. guianensis* have a typical three-layered tectate-columellate ektexine architecture consisting of a perforate/homogeneous tectum, a homogeneous foot layer, and intervening columellae that are continuous with the foot layer (fig. 14). *Amanoa guianensis,* in contrast, has a two-layered ektexine consisting of a thick, ektexinous basal layer and baculae (fig. 2). All other species of *Amanoa* resemble *Amanoa strobilacea* in hav-

ing tectate pollen in which the tectum and columellae form a coarse reticulum (figs. 4, 5; Erdtman 1952; Köhler 1965; Punt 1962). The structure in *A. guianensis* may have evolved either by loss of the foot layer and interstitium, and addition of the baculae, or by loss of the tectum with the columellae appearing as baculae. We accept the latter hypothesis mainly because of the similarity in ektexine structure between *A. guianensis* and *A. strobilacea.* The basal layer of *A. guianensis* is homogeneous and unstratified, resembling in both structure and thickness the foot layer of *A. strobilacea.* The baculae of *A. guianensis* are similar in size to the columellae of *A. strobilacea.* In addition, some grains of *A. guianensis* show occasional distal connections between adjacent baculae, resembling partial muri of a reticulate exine (e.g., Punt 1987, fig. 9). We therefore interpret the pollen of *A. guianensis* as being intectate *sensu* Walker and Doyle (1975), the baculae being homologous with the columellae of other *Amanoa* species. The similarity between the distally rounded baculae of *A. guianensis* and the distally pointed echinae of the Oldfieldioideae is, therefore, only superficial and not the result of homology (Levin and Simpson 1994*a*).

Hymenocardia has sometimes been removed from the Euphorbiaceae and placed near the Urticales, in part on the basis of palynology (Airy Shaw 1965; Dechamps et al. 1985). Our observations show that *Hymenocardia* (figs. 24, 25) has the tectate-columellate exine structure typical of the Phyllanthoideae, which is very unlike that found in the Urticales (Zavada and Dilcher 1986), thus supporting the retention of this genus in the Euphorbiaceae (Levin and Simpson 1994*b*).

In the subfamily Oldfieldioideae there are several basic ektexinous structures, all different from those we observed in the Phyllanthoideae. The predominant structural pattern in the Oldfieldioideae (figs. 32, 40) consists of (1) a foot layer that is either thin and irregular or absent, a synapomorphy for the Oldfieldioideae except *Croizatia* (fig. 75*B*); (2) an interstitium consisting of irregular columellate to granular elements that are discontinuous from the foot layer, a synapomorphy for the Oldfieldioideae as a whole (fig. 75*C*); and (3) a microperforate/baculate tectum, composed of laterally appressed baculate elements that delimit fine perforations, a synapomorphy for the Oldfieldioideae except *Croizatia* (fig. 75*D*). Köhler (1965), using LM, described this assemblage of structural features as the *Tetracoccus* type.

Within the Oldfieldioideae, all members of the subtribe Pseudanthinae except *Neoroepera buxifolia* (fig. 65)—thus including *Kairothamnus* (figs. 67, 68), *Scagea* (figs. 69, 70), *Neoroepera banksii* (fig. 66), *Micrantheum* (fig. 71), *Pseudanthus* (figs.

72, 73), and *Stachystemon* (fig. 74)—have an exine architecture quite different from that typical of the subfamily (Levin and Simpson 1994*a*). Although similar in having an irregular interstitium, the exine of these taxa has a homogeneous (not irregular), relatively thick foot layer and a relatively thin, microperforate tectum in which the tectal elements are granular to tabular rather than baculate. Köhler (1965), using LM, described this assemblage of structural features as the *Micrantheum* type. Both the foot layer and tectum conditions are synapomorphies for the Pseudanthinae, minus *N. buxifolia* (fig. 75*B, D*) Note that the "relatively thick" foot layer of these Pseudanthinae is not always absolutely thicker than all other Oldfieldioideae; however, the foot layer to tectum ratio for all Pseudanthinae (except *N. buxifolia*) is greater than 2.5, whereas that for all other Oldfieldioideae (including *N. buxifolia* but with the exception of *Croizatia*) is less than 1. Although McPherson and Tirel (1987) referred *Scagea* to the Crotonoideae because of its uniovulate locules, our study shows that it has pollen ultrastructure identical to other Pseudanthinae (Levin and Simpson 1994*a*) and very different from that of the Crotonoideae (Nowicke 1994). The structurally similar exine of *Croizatia* (figs. 27, 28) evolved independently of that in the Pseudanthineae (fig. 75*B, D*).

Paradrypetes (fig. 29) and *Podocalyx* (figs. 30, 31) are unusual in having a two-layered exine consisting of an irregular inner layer that is discontinuous from an imperforate or microperforate/baculate outer layer. We interpret the outer layer to be homologous to the tectum in other Oldfieldioideae because it is continuous with the echinae and, in *Podocalyx,* it exhibits the microperforate/baculate structure found in most Oldfieldioideae. Because the interstitial elements of all other Oldfieldioideae are continuous with the tectum, we interpret the inner exine layer of *Paradrypetes* and *Podocalyx* as homologous with the foot layer, not the interstitium; thus, the interstitium is absent, a synapomorphy for these two genera (fig. 75*C*). A close relationship between these two genera is also supported by anatomical characters (Levin and Simpson 1994*a*). The tectum of *Podocalyx,* though microperforate/baculate, is less segmented than that in most Oldfieldioideae and may be evolutionarily intermediate between the typical microperforate/baculate structure of many Oldfieldioideae and the homogeneous tectum found in *Paradrypetes.*

Androstachys (fig. 45) is exceptional in the Oldfieldioideae in having a tectate-columellate exine architecture, as in all investigated Phyllanthoideae. Our cladistic analysis of palynological and other data (Levin and Simpson 1994*a*) showed that *Androstachys,* rather than being a member of the Phyllanthoideae, is nested within the Old-

fieldioideae and most closely related to *Stachyandra* (fig. 75). Thus, the exine structure of *Androstachys* is independently derived from that of the Phyllanthoideae (fig. 75 *B–D*). In fact, the exine structure of *Androstachys* and the Phyllanthoideae differ in that *Androstachys* has a much thinner foot layer (0.07 μm vs. 0.11 μm for the thinnest investigated Phyllanthoideae), very sparse, delicate columellae, and a microperforate/homogeneous tectum. The two investigated species of *Stachyandra* have a tectum that, though microperforate/baculate, may be transitional to that found in *Androstachys* in having fewer microperforations and a less baculate structure than most other Oldfieldioideae. A similar but evolutionarily independent loss of microperforations and baculate structure is apparently shown by *Choriceras* and *Longetia* (fig. 75*D*).

In most taxa of the Oldfieldioideae, the foot layer and/or endexine are thickened at the border of the aperture, which may function to provide structural support for the aperture. This basal thickening presumably is equivalent to the margin of an endoaperture or "os." In most of the observed taxa, this is the result of an abrupt thickening of the endexine and an associated thinning of the ektexinous foot layer. However, in the genera *Whyanbeelia, Longetia, Choriceras,* and *Dissiliaria* the apertural border thickening occurs not in the endexine but in the ektexinous foot layer (figs. 60, 62). Based on the cladistic study of Levin and Simpson (1994*a*), this thickening of the ektexinous foot layer represents a synapomorphy of these four genera. Similar ektexinous thickenings are found in *Croizatia,* some Pseudanthinae, and questionably *Oldfieldia,* but are usually less well developed and are all independently derived (Levin and Simpson 1994*a*).

In conclusion there is considerable palynological diversity in the subfamilies Phyllanthoideae and Oldfieldioideae of the Euphorbiaceae. Our observations, particularly those using TEM, not only reinforce results from prior studies but also provide significant new data. This is especially true with regard to exine wall structure. Cladistic analysis (Levin and Simpson 1994*a*) of our palynological data along with data from morphology and anatomy has demonstrated their phylogenetic significance, particularly for delimiting the Oldfieldioideae and inferring its phylogeny. These results, like those of Nowicke's (1994) study of the Crotonoideae, emphasize the importance of TEM in palynological studies and underscore the need for more extensive use of this technique in studies of the Euphorbiaceae.

Acknowledgments

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