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A PALYNOLOGICAL STUDY OF CROTONOIDEAE (EUPHORBIACEAE)¹

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ABSTRACT

Pollen of 69 species representing 34 genera from 12 of the 13 tribes of Crotonoideae sensu Webster was examined in light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). The pollen of the vast majority of the subfamily is inaperturate, and all Crotonoideae exines have a similar architecture: triangular suprategal elements attached to a network of muri having short or irregular columellae. These three components, triangular suprategal elements, muri, and modified columellae constitute the Croton structure. The triangular elements, designated subunits, can be psilate, striate, furrowed and ridged, or pitted, and with echinate, rounded, or long-attenuate apices; the subunits can be closely spaced or arrayed in more open configurations. A Croton sculpture refers to the presence of triangular sculpture elements, which may or may not have muri and modified columellae. Inaperturate grains have thin footlayers and thin endexines, whereas colpate pollen has both footlayer and endexine well developed; in porate grains, the footlayer and endexine appear intermediate between inaperturate and colpate. Tribes Micrandreae (*Hevea*, *Micrandra*, *Micrandropsis* examined) and Adenoclineae (*Adenocline*, *Ditta*, *Glycydendron*, *Endospermum*, *Klaineanthus*, *Tetrorchidium*) are 3-colpate and probably primitive, having retained not only apertures but (prominent) footlayers and endexines as well; Manihoteae (*Manihot*, *Cnidocolus* examined) and Gelonieae (*Suregada*) are porate. The thicker aperturate exines, especially in the colpate grains, may be linked with retention of apertures. The remaining 22 genera examined, including the two largest, *Croton* and *Jatropha*, have inaperturate pollen. A thin footlayer/endexine also occurs in Oldfieldioideae, and a tectum with triangular elements is found in some Acalyphoideae. In both morphology and exine structure, the pollen of Crotonoideae closely resembles the (porate) pollen of Thymelaeaceae.

In a family as large and diverse as Euphorbiaceae (300 genera, 7500 species), variation in pollen morphology/structure would be expected. In fact, there is a striking array of pollen diversity as demonstrated by Punt's (1962) classic study of Euphorbiaceae in which numerous pollen types are illustrated with line drawings. Even genera, e.g., *Phyllanthus* (Punt, 1987) and *Zimmermannia* (Poole, 1981), can be highly variable in pollen morphology, thus casting some doubt on the taxonomic value of pollen data in this family.

In his 1962 study, Punt followed the treatment of Euphorbiaceae in Pax & Hoffmann (1931), recognizing only two subfamilies, Crotonoideae and Phyllanthoideae. Later, he (1987) considered Webster's (1975) system that elevated three Crotonoideae tribes to subfamily status, Oldfieldioideae, Acalyphoideae, and Euphorbioideae, in addition to Phyllanthoideae and the remaining Crotonoideae, to represent the best concept of the

family to date. In part, pollen data support Webster's classification (see Discussion).

By segregating the above three tribes from Crotonoideae, the remaining members of this subfamily form a much more natural alliance that may or may not be monophyletic.

The Crotonoideae, sensu Webster, comprise 13 tribes and approximately 73 genera, of which three, *Croton*, *Jatropha*, and *Manihot*, account for half of the 2000 species. Crotonoideae now appear to be the exception to pollen diversity and have surprisingly uniform pollen morphology, united by the croton-pattern. This term apparently originated with Erdtman (1952, 1966: 173) for pollen with a sexine that "consists of well defined, regularly arranged excrescences (triangular or more or less circular in cross section), supported (always?) by a baculate, baculoidate, or spongy layer." He noted that most of the croton-pattern pollen was nonaperturate and spheroidal. Punt (1962) examined at

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least 50 species that are referable to the reduced Crotonoideae, all of which have a pollen type that he designated as the Croton Configuration. This configuration was delimited by (1962: 47): "Croton-pattern present. Structure elements on the tectum are usually clavae but can also be echinae, baculae etc. Sometimes the structure elements are located on ridges (e.g., *Croton matourensis*, *Manihot saxicola*). Tectate." Punt reserved "Croton type" for the inaperturate grains, "Manihot type" for the periporate, "Klaineanthus type" for tricolpate, "Hevea type" for tricolpate with opercula, etc. In view of the results presented here, both Erdtman's and Punt's concept of a Croton pattern in Euphorbiaceae pollen have to be amended.

Inaperturate pollen is an unusual condition in the angiosperms, and Crotonoideae have at least 1500 species whose pollen lacks preformed thin areas. In an effort to expand the limited information from light microscopy, which was all that was available to Erdtman (1952) and Punt (1962), a study emphasizing electron microscopy was initiated. The presence of 3-colpate and pantoporate pollen in Crotonoideae provides a rare opportunity to compare exine structure modifications between inaperturate and aperturate grains of related taxa. Sixty-nine species were examined in light microscopy (LM) and scanning electron microscopy (SEM), and 33 of the 69 were embedded and examined in transmission electron microscopy (TEM). In addition, representative species from Acalyphoideae, Euphorbioideae, Phyllanthoideae, and Oldfieldioideae were examined and are briefly discussed. A potentially close relationship between Crotonoideae and Thymelaeaceae (Nowicke, Skvarla & Patel, unpublished data) based on pollen similarities is also discussed. For ease of reference, examples of some subfamilies and Thymelaeaceae are illustrated.

The thrust of this effort is to expand the pollen data set for Crotonoideae and not to provide an exhaustive search of the literature (see Punt, 1987, for references to that date).

All species examined, with voucher data and figure number(s), are given in Table 1.

MATERIALS AND METHODS

Anthers were removed from herbarium specimens, and pollen for all preparations was first acetolyzed as outlined by Erdtman (1966), but heating time was reduced from two minutes to one in an attempt to alleviate collapse and fragmentation. This reduction had varying degrees of success.

Glass slides for LM were made with glycerin jelly and sealed with paraffin.

For SEM, acetolyzed pollen was pipetted onto specimen stubs in 50% alcohol and allowed to dry. After coating with carbon and then gold-palladium, the samples were examined and photographed in a Hitachi 911b scanning electron microscope.

For TEM, acetolyzed pollen was incorporated into 2% agar, fixed with osmium tetroxide, stained with uranyl acetate, and embedded in Spurr's or in L. R. White Acrylic Resin. After sectioning with diamond knives the sections were stained with lead citrate, and then examined and photographed with a JEOL 1200EX transmission electron microscope.

Electron micrographs and glass slides are deposited at the Palynological Laboratory, National Museum of Natural History, Smithsonian Institution.

RESULTS

The Results are organized as follows: a Crotonoideae pollen description; characterization of exine structure for inaperturate, porate, and colpate pollen; the range of variation in tecta, subunits, muri, columellae, footlayers, and endexines; and a brief discussion of pollen in each of the 12 tribes examined.

CROTONOIDEAE, FIGURES 1-88

Pollen mostly spheroidal, occasionally subprolate; inaperturate, sometimes pantoporate, more rarely 3-colpate, or very rarely 3-colporate; the tectum incomplete and consisting of the distal muri, the lumina usually with shallow free columellae/globules of ektexine, the muri with triangular or rounded-triangular supracteal elements designated as subunits, the subunits frequently forming continuous (triangular) arrays, their surface psilate, pitted, striate, or furrowed and ridged, their apices echinate, rounded, flat, or attenuate, the subunits densely spaced or arrayed in more open configurations, absent in one species. In TEM, the endexine mostly very thin, irregular and discontinuous, consisting of granules or sometimes lamellae, or (in porate grains) the endexine thin but more consistent, or more rarely (in colpate grains) the endexine forming a discrete layer and sometimes detached (after acetolysis); the footlayer mostly very thin, irregular and discontinuous, occasionally seeming to consist of granules, or sometimes (in porate grains) uneven but consistently present, or more rarely (in colpate grains) the footlayer prominent and continuous; the supporting columellae (in in-

aperturate grains) short but well defined, sometimes appearing to be in two rows, or (in porate grains) the columellae more elongate but irregular, or more rarely (in colpate grains) the columellae granular; the tectum consisting of the distal muri, the muri thin to thick, the subunits (as demonstrated in tangential section) triangular to rounded-triangular, with or without grooves.

Although variation in the suprategal elements makes some pollen distinctive, all Crotonoideae examined here (Table 1), inaperturate and aperturate, are fundamentally similar: triangular suprategal elements are attached to muri having short or irregular/granular columellae. The presence of triangular suprategal elements, referred to as subunits, their attachment to a network of muri, and the modified columellae, constitute the Croton structure. This definition incorporates information from transmission electron microscopy not available to either Erdtman (1952) or Punt (1962). Radial thin sections show that the subunits are always attached to muri, e.g., Figures 11, 14, 17, 23, 26, 31, 36, 39, 41 inset, 47 inset, 63, 69, 72, 75, 82, and 88; and tangential sections show that the basic shape of the subunits in cross section is triangular or rounded-triangular, e.g., Figures 6, 8, 13, 18, 21, 27, 33, 37, 47, 65, 79, and 85.

A Croton sculpture refers only to the presence of triangular suprategal elements.

INAPERTURATE POLLEN, FIGURES 34-88

The inaperturate exines can be further characterized by: a footlayer/endexine that, even taken together, usually comprise a very thin layer (e.g., Figs. 36, 44, 54, 63, 78, 82, 83); and a thick, uniformly distributed intine. This exine structure can be demonstrated in tangential section, e.g., *Jatropha hastata* (Fig. 37) and *Ostodes zeylanica* (Fig. 47). In both, the outermost solid discrete objects are the subunits cut at various levels and angles, (proceeding inward) the distinctly smaller circular objects (wavy arrows) are free columellae and/or globular masses of ectexine in the lumina, next are the more or less solid bars (arrows) of the restricted muri (restricted because in these two species the muri are thin and occupy only a small proportion of the area), and in the center of the sections are the paired supporting columellae (arrowheads) organized into lines, as well as more free columellae cut closer to the base. Radial sections of *J. hastata* (Fig. 36) and *O. zeylanica* (Fig. 47 inset) confirm the thinness of the muri, as well as

demonstrate the thin footlayer/endexine characteristic of most inaperturate Crotonoideae.

PORATE POLLEN, FIGURES 25-33

One of the porate tribes, Manihoteae (Figs. 25-30), has irregular, sometimes elongate, columellae, an uneven yet recognizable footlayer, and a thin endexine. However, only one species of *Manihot* (Figs. 26, 27) and one of *Cnidocolus* (Fig. 29 inset) were examined in thin section and any structural characterization is a preliminary one.

The exine of the second porate tribe, Gelonieae (Figs. 31-33), has a threadlike footlayer/endexine and is similar to the inaperturate grains (see discussion of tribe).

COLPATE POLLEN, FIGURES 1-24

The exines of the colpate tribes, Micrandreae (Figs. 1-9) and Adenoclineae (Figs. 10-24), are distinguished by well-developed footlayers (e.g., Figs. 3, 6, 11, 13, 14, 17, 18, 23), a recognizable endexine (e.g., Figs. 3, 11, 14, 20, 23), at least under the colpi (e.g., Fig. 17), and mostly granular columellae (e.g., Figs. 6, 18, 23; unpublished data).

POLLEN MORPHOLOGY/EXINE STRUCTURE

At most, the Crotonoideae have an incomplete tectum, which consists only of the outer muri, i.e., the fused distal margins of the columellae. The attached subunits are considered sculpture.

Subunit refers to the triangular suprategal elements attached to the muri. Their fundamental shape in cross section is triangular, and these elements form or can form a continuous triangular array, e.g., Figures 25, 28, 62, and 67. Although the subunits in some grains do not appear triangular in SEM, tangential sections that cut across numerous subunits demonstrate a triangular or at least rounded-triangular shape, e.g., Figures 6, 8, 13, 18, 21, 33, 37, 47, 65, 85. The subunits can be modified by striations, e.g., Figures 24, 64, 66, and 81, or furrows and ridges, e.g., Figures 43, 48, and 70. Their apices can be echinate, e.g., Figures 14, 15, 20, 23, and 55, long attenuate, e.g., Figures 43, 53, 54, and 70, or simply rounded, e.g., Figures 31, 35, 36, 68, and 69, or even flat, e.g., Figures 25 and 26. Occasionally two or three subunits fuse.

In some Crotonoideae the muri are well developed, e.g., Figures 8, 18, 38, and 39; in others they are thin, e.g., Figures 41, 78, 79, and 82.

TABLE 1. Species examined, voucher data, and figure number if illustrated. All collections US unless indicated otherwise.

Euphorbiaceae			
Subfamily Crotonoideae			
Tribe 1. Micrandreae			
<i>Micrandra elata</i> Müll. Arg.	Haught 1289	Colombia	
<i>M. kubeorum</i> R. E. Schult.	Schultes & Cabrera 13922	Colombia	4
<i>M. lopezii</i> R. E. Schult.	Tillet et al. 45050	British Guiana	5, 6
<i>M. minor</i> Benth.	Schultes & Cabrera 13820	Colombia	
<i>M. siphonioides</i> Benth.	Schultes & Lopez 8700	Brazil	1-3
<i>Micrandropsis scleroxylon</i> W. A. Rodrigues	Rodrigues et al. 6961, NY	Brazil	7
	Rodrigues & Loureiro 9520, MO	Brazil	
<i>Hevea guianensis</i> Aubl.	Asplund 13299	Peru	8, 9
Tribe 2. Adenoclineae			
<i>Adenoline bupleuroides</i> (Meisn.) Prain	Rogers 24550	Natal	10-12
<i>Ditta myricoides</i> Griseb.	Ekman 12802	Hispaniola	13-15
<i>Glycydendron amazonicum</i> Ducke	Black 148	Brazil	18
<i>Klaineanthus gaboniae</i> Pierre ex Prain	Zenker 583	Cameroon	16, 17
<i>Tetrorchidium rubrivenium</i> Poepp.	Patino 556	Colombia	19-21
<i>Endospermum diadenum</i> (Miq.) Airy Shaw	Krukoff 4109, MO	Sumatra	
<i>E. formicarium</i> Becc.	Floyd 3452	New Britain	24
<i>E. moluccanum</i> Becc.	Havel 15409, MO	New Guinea	
<i>E. ovatum</i> Merr.	Rojo 299, MO	Philippines	
<i>E. peltatum</i> Merr.	Sulit PNH 22900	Philippines	22, 23
	Feniz 479	Philippines	
	Merritt 6891, MO	Philippines	
Tribe 3. Manihoteae			
<i>Cnidoscolus angustidens</i> Torr.	Gentry 21176	Mexico	
<i>C. maculatus</i> (Brandege) Pax & K. Hoffm.	Carter & Reese 4569	Mexico	
<i>C. rotundifolius</i> (Müll. Arg.) McVaugh	J. & M. Breckon 1295	Mexico	29
<i>C. sinaloensis</i> Breckon	Breckon & Webster 947	Mexico	inset 29, 30
<i>Manihot aesculifolia</i> (Kunth) Pohl	McVaugh 15355	Mexico	25-27
<i>M. brachyloba</i> Müll. Arg.	Haught 1664	Colombia	
<i>M. esculenta</i> Crantz	Fosberg 32263	Carolina Islands	
<i>M. grahami</i> Hook.	Renvoize et al. 3177	Argentina	
<i>M. irwinii</i> D. J. Rogers & Appan	Irwin et al. 34338	Brazil	
<i>M. marajoara</i> Huber	Huber s.n., Apr. 1908	Brazil	
<i>M. pilosa</i> Pohl	Maxwell & Wasshausen 19774	Brazil	28
<i>M. pentaphylla</i> Pohl	Irwin et al. 34019	Brazil	
<i>M. pringlei</i> S. Watson	Pringle 3826	Mexico	
<i>M. tweediana</i> Müll. Arg.	Rojax s.n., Nov. 1933	Brazil	
<i>M. tripartita</i> (Spreng.) Müll. Arg. emend. D. J. Rogers & Appan	Irwin et al. 18650	Brazil	
<i>M. violacea</i> Pohl	Heringer 18246	Brazil	
Tribe 4. Gelonieae			
<i>Suregada glomerulata</i> (Blume) Baill.	Ahern s.n., 1901	Philippines	31-33

TABLE 1. Continued.

Tribe 5. Jatropeae			
<i>Deutzianthus tonkinensis</i> Gagnep.	<i>Petelot 6388</i>	Vietnam	34
<i>Jatropha cinerea</i> (Ortega) Müll. Arg.	<i>Wiggins 16117</i>	Mexico	
<i>J. glandulifera</i> Roxb.	<i>Nowicke & Jayasuriya</i> 386	Sri Lanka	
<i>J. hastata</i> Jacq.	<i>Lundell 1577</i>	Yucatan	35-37
<i>J. podagrica</i> Hook.	<i>Blackbern E10</i>	Caroline Island	
Tribe 6. Elateriospermeae			
<i>Elateriospermum tapos</i> Blume	<i>Suvarnakoses 1872</i>	Thailand	38, 39
Tribe 7. Codiaeeae			
<i>Baliospermum axillare</i> Blume	<i>Nicolson 2870</i>	Nepal	
<i>Codiaeum variegatum</i> (L.) Blume	<i>Calderon 1339</i>	El Salvador	40, 41
<i>Dimorphocalyx luzoniensis</i> Elmer	<i>Andaya s.n.</i> , 18 Mar. 1949	Philippines	45
<i>Ostodes zeylanica</i> Müll. Arg.	<i>Jayasuriya & Bandara-</i> <i>nayake 1761</i>	Sri Lanka	46, 47
<i>Pantadenia adenanthera</i> Gagnep.	<i>Poilane 15385, A</i>	Cambodia	42
<i>Pausandra densiflora</i> Lanj.	<i>Ducke 1860</i>	Brazil	48
<i>Sagotia racemosa</i> Baill.	<i>Prance et al. 22670</i> <i>Mexia 6051, A</i>	Brazil	43, 44
Tribe 8. Trigonostemoneae			
Tribe 9. Ricinocarpeae			
<i>Alphandia furfuracea</i> Baill.	<i>Kajewski 809</i>	New Hebrides	49
<i>Beyeria leschenaultii</i> (DC.) Baill.	<i>Muir 1130</i>	Australia	52-54
<i>Ricinocarpos bowmannii</i> F. Muell.	<i>Boorman 17155</i>	Australia	
	<i>Boorman s.n.</i>	Australia	51
<i>R. glaucus</i> Endl.	<i>Helms s.n.</i>	Australia	50
<i>R. stylosus</i> Diels	<i>Webster 18714, DAV</i>	Australia	55
<i>Bertya gummifera</i> Planch.	<i>Johnson & Constable</i> 16024	Australia	56, 57
Tribe 10. Crotonaeae			
<i>Croton argyratus</i> Blume	<i>Toroës 5241</i>	Sumatra	
<i>C. balsamifer</i> L.	<i>Smith 10452</i>	West Indies	60
<i>C. californicus</i> Müll. Arg.	<i>Wheeler s.n.</i> , 16 Nov. 1929	California	
<i>C. draco</i> Schltr.	<i>Salazar s.n.</i> , 11 Mar. 1913	Mexico	62, 63
<i>C. floribundus</i> Spreng.	<i>Mexia 5292</i>	Brazil	61
<i>C. lachnocarpus</i> Benth.	<i>Chun 6261</i>	China	
<i>C. matourensis</i> Aubl.	<i>Arch 8209</i>	Brazil	58, 59
<i>C. mutisianus</i> HBK	<i>Uribe 1322</i>	Colombia	
<i>C. pyramidalis</i> Donn. Sm.	<i>Dwyer 11073</i>	Belize	64
<i>C. texensis</i> Müll. Arg.	<i>White s.n.</i> , 26 Aug. 1946	Nebraska	65, 66
Tribe 11. Joannesieae			
<i>Annesijoa novoguineensis</i> Pax & K. Hoffm.	<i>Brass 32333</i>	New Guinea	70-72
<i>Joannesia princeps</i> Vell.	<i>Macedo 5335</i>	Brazil	67-69
Tribe 12. Aleuritideae			
<i>Ricinodendron rautanenii</i> Schinz	<i>Gibson 19</i>	Angola	76-79
<i>Aleurites fordii</i> Hemsl.	<i>Peterson 2805</i>	Argentina	73-75

TABLE 1. Continued.

Tribe 13. Neoboutonieae			
<i>Anomalocalyx uleanus</i> (Pax & K. Hoffm.) Ducke	Ducke 64	Brazil	80-82
<i>Grossera major</i> Pax	Zenker 469	Cameroon	83, 84
<i>Crotonogyne argentea</i> Pax	Zenker 3078	Cameroon	85-88
Subfamily Phyllanthoideae			
<i>Drypetes lateriflora</i> (Sw.) Krug & Urb.	Contreras 1788	Guatemala	
<i>Phyllanthus acuminatus</i> Vahl	Standley 23316	El Salvador	96
<i>P. saffordii</i> Merr.	Fosberg 46286	Guam	
<i>P. simplex</i> Retz.	Toroës 4319	Sumatra	
<i>Flueggea flexuosa</i> Müll. Arg.	Wenzel 67	Philippines	
Subfamily Oldfieldioideae			
<i>Hyaenanche globosa</i> (Gaertn.) Lamb. & Vahl	Godfrey SH-1257	South Africa	
<i>Longetia buxoides</i> Baill.	Baumann 14418	New Caledonia	92, 93
Subfamily Acalyphoideae			
<i>Dalechampia humilis</i> Müll. Arg.	Hernger & Rizzini 17544	Brazil?	89-91
<i>D. dioscoreifolia</i> Poepp. & Endl.	Allen 5342	Costa Rica	
<i>Galearia celebica</i> Koord.	Brass 29233	New Guinea	
<i>G. filiformis</i> (Blume) Pax	Rahmat Si Boëea 7927	Sumatra	
<i>G. fulva</i> (Tul.) Miq.	J. & M. Clemens 3528	Vietnam	
<i>G. phlebocarpa</i> (R. Br.) Miq.	Rahmat Si Toroës 4429	Sumatra	
	Rahmat Si Toroës 4892	Sumatra	
<i>Macaranga denticulata</i> Müll. Arg.	Collins 1119	Thailand	
<i>M. griffithiana</i> Müll. Arg.	Sinclair 4990	Malaya	
<i>M. tanarius</i> (L.) Müll. Arg.	Rabil 338	Thailand	
<i>Microdesmis casearifolia</i> Planch.	Lei 514	China	
<i>M. pierlotiana</i> J. Léonard	Troupin 3549	Congo	
<i>M. puberula</i> Planch.	Baldwin 9058	Liberia	
<i>Omphalea diandra</i> L.	Irwin et al. 48498	Guiana	
<i>Panda oleosa</i> Pierre	Hladik s.n., 12 Nov. 1971	Gabon	
	Hall & Amponsah 46547	Ghana	
Subfamily Euphorbioideae			
<i>Euphorbia pulcherrima</i> Willd.	Wheeler 12310	Sri Lanka	94, 95
<i>Hippomane mancinella</i> L.	Killip 41829	Florida	
<i>Mabea montana</i> Müll. Arg.	Standley 25156	Panama	
Thymelaeaceae			
<i>Gnidia glauca</i> (Fresen.) Gilg	Hoogland 11563	Ceylon	101
<i>Gyrinopsis cumingiana</i> Decne.	Ramos s.n., Jul.-Aug. 1915	Philippines	97, 98
<i>Pimelea ligustrina</i> Labill.	Constable 45248	New South Wales	102
<i>P. prostrata</i> (J. R. Forst. & G. Forst.) Willd.	Anderson 186	New Zealand	100
<i>Schoenobiblus grandifolia</i> Urb.	Cowan 1548	Tobago	99

In the Ricinocarpeae (Figs. 49-57), the muri appear to be reduced (see discussion of tribe).

The supporting columellae are variable, but in most inaperturate Crotonoideae they are short and many appear to be in two rows, e.g., Figures 37, 41 inset, 47, 54, 57, 78, and 83. All Adenoclineae and most Micrandreae have granular columellae (Figs. 6, 17, 23; unpublished data).

In the exines of inaperturate Crotonoideae, the

footlayer and endexine are frequently so thin they cannot be distinguished from each other—at the proximal boundary of the columellae there are small granules above and below a “thread of exine,” e.g., Figures 44, 59, 78, 82, and 83. Sometimes all the granules have the same electron density (Fig. 44). In a few taxa, a very thin lamellate endexine is present (Figs. 54, 57).

The footlayer of Adenoclineae (Figs. 10-24),

Elateriospermeae (Fig. 39), and some Micrandreae (Figs. 3, 6), is uniformly well-developed, whereas in the single species of the porate *Manihot* examined in thin section (Fig. 26), it is irregular.

Adenoclineae and Micrandreae have an endexine layer, at least beneath the apertures, although in Adenoclineae it frequently separates from the ectexine (Figs. 11, 14, 20, and 23). In Manihoteae, the endexine forms a thin consistent layer in *Cnidoscolus sinaloensis* and a thicker, but sometimes discontinuous, one in *Manihot aesculifolia* (Fig. 26).

Because of the reduced heating time in the acetolysis procedure (see Materials and Methods), some inaperturate pollen retained part, if not all, of the cytoplasmic contents and intine (Figs. 47 inset, 72, and 88).

The inaperturate Crotonoideae are known to have a very thick intine layer throughout the grain, a condition that Thanikaimoni et al. (1984) referred to as omniaperturate (in aperturate grains, a thick intine is usually present only under the apertures). In some inaperturate Crotonoideae, the acetolyzed exines have extensive surface areas where the wall consists of only a thin granular endexine/footlayer, e.g., Figures 36, 44, 59, 63, 75, 78, 82, and 83. The thick intine (Thanikaimoni et al., 1984: figs. 14, 15) may provide some mechanical/structural support, partially compensating for the extreme reduction of footlayer and endexine.

TRIBAL DESCRIPTIONS

Micrandreae, Figures 1–9

The seven species (Table 1) examined in the Micrandreae are 3-colpate. *Micrandra lopezii* (Figs. 5, 6), *M. siphonioides* (Figs. 1–3), and *Hevea guianensis* (Figs. 8, 9) were examined in thin section. *Micrandra* has a recognizable, mostly continuous, granular/lamellate endexine and a prominent footlayer. In radial sections of *M. lopezii*, the subunits are elongate, the muri very thin, and the columellae consist of a very thin granular layer—the proportion of the tangential section (Fig. 6) that each component occupies reinforces this characterization. In *M. siphonioides*, the muri appear obvious in SEM (Fig. 1) but not in TEM, and the columellae, while prominent, are irregular. This species is one of the very few in Crotonoideae that lack a Croton sculpture. In *M. kubeorum* (Fig. 4) the subunits are very irregular, and while muri are not demonstrated in Figure 4, they are in other SEMs of this sample (G. Webster, unpublished data). A fourth species, *M. elata*, examined only

in SEM, has a tectum with triangular subunits, much like those illustrated in Figures 25, 28, and 62. A more extensive examination of *Micrandra* is warranted.

Micrandropsis (Fig. 7) also has a modified sculpture—the subunits are finely divided or very reduced, and the network of muri is irregular.

Hevea guianensis (Figs. 8, 9) has very small suprategal subunits, a finer network of muri with smaller lumina (compare Fig. 6 with Fig. 8; the latter is illustrated at a magnification five times greater than the former). In radial section, this species has a continuous endexine, an irregular but recognizable footlayer, and granular columellae.

Adenoclineae, Figures 10–24

Ten species representing six genera were examined. The 3-colpate grains of Adenoclineae have a distinctive yet remarkably uniform exine: a well-developed endexine (Fig. 17), frequently detached after acetolysis (Figs. 11, 14, 20, 23), a prominent footlayer (Figs. 11, 13, 14, 17, 18, 23), granular columellae (Figs. 17, 18, 23), and mostly thick muri (Figs. 14, 18, 21, 23). In addition, *Ditta*, *Endospermum*, *Glycydendron*, *Klaineanthus*, and *Tetrorchidium* have striate subunits with echinate apices. *Tetrorchidium rubrivenium* has been reported as 3-colporate (Punt, 1962), but only 3-colpate grains were found in the collection examined here (Table 1). *Klaineanthus*, however, is 3-colporate as demonstrated in Figure 16 and confirmed in LM. A few tetrads occurred in *Endospermum peltatum*. In thin section, *E. formacarium* is very similar to the exine portrayed in Figure 23 of *E. peltatum*.

In LM, the Adenoclineae can be easily distinguished from all other Crotonoideae by their colpi and thick exines—a prominent footlayer and thick, elongate or deep subunits. The deep subunits are especially noticeable in *Ditta* and *Tetrorchidium*.

These thick exines may be correlated with the development or retention of apertures since such walls could prove difficult to rupture in the germination process, and the increased pressure might be lethal to the sperm nuclei.

Manihoteae, Figures 25–30

Cnidoscolus and *Manihot* are characterized by large pantoporate (*M. tweediana* may be excepted) pollen. Only two species, one in *Manihot* and one in *Cnidoscolus*, were examined in TEM and any structural characterization is premature. *Manihot* has substantial muri, columellae that are irregular/granular yet collectively form a significant com-

ponent, an irregular but recognizable footlayer, and a discontinuous endexine (Figs. 26, 27). The wall structure of *Cnidoscolus* (Fig. 29 inset) is similar to *Manihot*, but on a smaller scale—it has a thin continuous footlayer and thin discontinuous endexine, and irregular/granular columellae. Like *Micrandreae* and *Adenoclineae*, the presence/retention of apertures appears correlated with thicker exines.

In *Manihot*, the subunits are conspicuously triangular, i.e., their flat or slightly rounded distal wall does not mask or detract from the triangular shape as do echinate or attenuate apices (as well as furrows and ridges). *Manihot tweediana* is unusual in that some grains appeared 15-pantocolpate (5-5-5) and/or 15-pantoporate.

Gelonieae, Figures 31–33

Suregada, the only genus in this tribe, comprises perhaps 40 species found in the warmer regions of the Old World. The pollen is of interest because it is porate, yet has an exine structure more characteristic of inaperturate pollen. The pores of *Suregada glomerulata* are small and even after acetolysis they retain a poorly defined aperture cover of smaller subunits (the term operculum is not appropriate because the margins are not defined). As a result, the pores are not conspicuous in SEM (arrows, Fig. 32). In thin section, columellae are difficult to identify—frequently there is an empty space between the muri and the thread-like footlayer/endexine (Fig. 31), or the muri are very thick and in direct contact with the footlayer/endexine. In tangential section, the free columellae or ektexine globules appear as black dots organized in circular groups (Fig. 33). The footlayer and endexine are extremely thin (Fig. 31), and even near the apertures the endexine remains thin. In the SEM preparation, there were threadlike, acetolysis-resistant filaments aggregating some of the sample into small groups of grains, usually no more than half dozen.

All remaining tribes have inaperturate pollen.

Jatrophaeae, Figures 34–37

In this tribe, only one species, *Jatropha hastata* (Figs. 35–37), was examined in thin section, but the structure is typical of other inaperturate *Crotonoideae*. The subunits are rounded-triangular in front view, the muri very thin, and the columellae short and irregular. Both footlayer and endexine together constitute only a thread with occasional small granules.

Dehgan & Webster (1979), in an infrageneric study of *Jatropha*, illustrated the pollen of 12

species in SEM (plates XXVII–XXIX), documenting the thin muri as well as supracteal subunits with striations; smooth subunits are present only in *Jatropha* subg. *Jatropha* sect. *Peltatae*.

Elateriospermeae, Figures 38–39

The exine of *Elateriospermum* can be distinguished from other inaperturate *Crotonoideae* by a well-developed, continuous footlayer and thick muri, both easily recognizable in LM. In some sections, columellae appear to hang from the muri. In SEM, there are some grains with one or two very small openings, probably a lumen without a footlayer. The radial section in Figure 39 illustrates a possible aperture—the gradual thinning of the footlayer and the size reduction of the subunits indicate a preformed opening, not a mechanical break in the exine; and, although not visible in the print in Figure 39, there is a very thin, less electron-dense endexine under the narrow footlayer. Given the thick footlayer, which could make germination difficult, the presence of apertures is not unexpected.

Codiaeae, Figures 40–48

This tribe reflects its large size, some 20 genera, in the subunit variation (Figs. 40, 42, 43, 46, 48). With the exception of *Pantadenia adenanthera* (Fig. 42), all remaining taxa examined (Table 1) have striate, furrowed, or ridged subunits. *Codiaeum variegatum* (Figs. 40, 41) has large lumina with free columellae/ektexine globules. *Pantadenia adenanthera* (Fig. 42) also has large lumina, but the actual muri are obscure. *Sagotia racemosa* (Figs. 43, 44) has subunits with long-attenuate tips (Fig. 43) and a footlayer/endexine (Fig. 44) that appears to consist of small granules above and below a thread of exine. Another collection of this species (Table 1) has large lumina similar to *Croton matourensis* (Fig. 58). The identification of both collections was verified. *Ostodes zeylanica* (Figs. 46, 47) has rounded, faintly grooved subunits with the widest part above the middle; some grains in this sample retained the cytological contents (Fig. 47 inset) including intine. *Pausandra densiflora* (Fig. 48) has more slender subunits with deep striations.

Ricinocarpeae, Figures 49–57

In this small tribe of five genera, *Alphandia*, *Bertya*, *Beyeria*, *Cocconerion*, and *Ricinocarpos*, the pollen of some species could be interpreted as derived—both muri and subunits are modified and/or difficult to delimit. *Beyeria leschenaultii* (Fig.

54) appears to have lost definable muri—the subunits rest on a trace of footlayer over a thin lamellate endexine; however, no Crotonoideae pollen examined in TEM has hollow suprategal subunits, and if the areas marked by small arrowheads (Fig. 54) are closed up, muri of a sort, supported by thick paired columellae, would be present. *Bertya gummifera* (Fig. 57) has shallow muri with paired columellae. In *Alphandia furfuracea* (Fig. 49) and *B. gummifera* (Fig. 56), some adjacent subunits have fused together. In *Ricinocarpos bowmannii* (Fig. 51), the subunits are small striate spines limited to the junctions of the widely spaced muri, and most of the surface area of the exine consists of lumina with free columellae; however, two other species, *R. glaucus* (Fig. 50) and *R. stylosus* (Fig. 55), have a more conventional Croton structure.

The two species examined in thin section, *Beyeria leschenaultii* (Fig. 54) and *Bertya gummifera* (Fig. 57), show a very thin, sparsely granular footlayer and a thin lamellate endexine.

In LM and in TEM, the exine of *Bertya* has breaks in the footlayer/endexine where the upper ectexine appears to “unravel” outward (Fig. 57, top right), forming a pouchlike protrusion, giving the appearance of pores.

Crotoneae, Figures 58–66

Of the 13 species of *Croton* examined, *C. matourensis* (Figs. 58, 59) is the most distinctive: clavaelike suprategal elements occur only at the junctions of the widely spaced but thick muri (see legends of Figs. 58, 59). In this species, almost all of the acetolyzed pollen wall is lumina consisting of small granules above and below a thread of exine. The mostly radial section of *C. draco* (Fig. 63) reflects the morphology depicted in SEM (Fig. 62)—large subunits and lumina with fine granules. Most of the *Croton* species examined here (Table 1) have subunits that are striate or ridged to some extent, and one of the more distinctive is *C. floribundus* (Fig. 61) with umbrellalike subunits; even tangential sections, e.g., *C. texensis* (Fig. 65), show furrows. Clearly, the diversity of suprategal size, distribution, and striation reflects the large number of species in *Croton*.

Joannesieae, Figures 67–72

The two species examined in this small tribe, *Joannesia princeps* (Figs. 67–69) and *Annesijoa novoguineensis* (Figs. 70–72), have well-defined muri and, for Crotonoideae, thick columellae. In the latter species, the subunits (Fig. 70) have attenuate tips and prominent furrows/ridges; the footlayer (barely visible in Fig. 72) appears to con-

sist of a thin layer of tiny granules, and is subtended by a thin but recognizable endexine in both tangential (Fig. 71) and radial sections (Fig. 72). The grain in Figure 72 is only partially acetolyzed and the clear layer (delimited by open arrowheads) is the remains of intine. The footlayer/endexine in Figure 69 of *Joannesia* appears nonexistent, but in other thin sections is present as a sparsely and loosely granular zone.

Aleuritideae, Figures 73–79

In another small tribe comprising scarcely a dozen species, two species were examined in SEM and TEM. *Aleurites fordii* (Figs. 73–75) has subunits with rounded apices, thin muri, and an irregular, discontinuous footlayer/endexine. *Ricinodendron rautanenii* (Figs. 76–79) also has thin muri with a threadlike continuous footlayer/endexine. Figures 76 and 77 illustrate the variation in subunit spacing found within a collection (Table 1), but the open configuration (Fig. 77) is much more common than the denser one (Fig. 76). From the spacing of the subunits in Figure 78, this section is probably from a grain more like that in Figure 77 than in Figure 76.

Neoboutonieae, Figures 80–88

In this large tribe of 13 genera, the three species examined, *Anomalocalyx uleanus* (Figs. 80–82), *Grossera major* (Figs. 83, 84), and *Crotonogyne argentea* (Figs. 85–88), have striate subunits, well-defined muri, lumina with at least some free columellae, and a thin granular footlayer/endexine. Although the thin section of *G. major* (Fig. 83) does not include muri, they are visible in SEM (Fig. 84) and in other sections. The deep subunit striations in *C. argentea* are prominent even in TEM (Figs. 85, 88).

The pollen morphology/exine structure of the remaining four subfamilies is briefly described.

Phyllanthoideae, *Oldfieldioideae*, *Acalyphoideae*, and *Euphorbioideae*

Webster (1987) considered Phyllanthoideae as comprising 50 genera and 2000 species. According to Punt (1962, 1987), this subfamily has two distinct, yet related, pollen lines: one is 3-colporate, prolate, and mostly reticulate without much ornamentation; the other line is distinctly, often coarsely, reticulate, and more or less oblate. Certainly the vast majority of Phyllanthoideae pollen illustrated in LM by Köhler (1965) appear to be 3-colporate. Poole (1981), using LM, SEM, and TEM, documented the wide diversity in seven species of *Zimmermannia*. The pollen of *Flueggea*

flexuosa, examined but not illustrated here (Nowicke, unpublished data), is very similar in TEM to *Euphorbia pulcherrima* (Fig. 95), which in turn could be representative of dicotyledons in general.

Phyllanthus, however, has diverse aperture types as well as a wide array of tecta. Punt (1987: 137) described the pollen of *Phyllanthus acuminatus* as being "inaperturate and pilate, but there are more endoapertures [than in *P. orbiculatus*] and they are usually arranged at random." However, the collection examined here (Table 1) has pilate pollen (Fig. 96) but with three (ecto-) apertures, each consisting of an elongate, prominently bordered "colpus" that is joined midway between the rounded ends. These "bowtielike" apertures are placed equidistant from each other and, if my interpretation is correct, they are vertically oriented (the long axis is perpendicular to the equator of the grain). To the best of my knowledge, this aperture is unique. The collection sampled is within the range of variation of those remaining identified as *P. acuminatus*.

Most Oldfieldioideae appear to be multiaperturate, brevicolporate or porate, and zonoaperturate or pantoporate (Köhler, 1965; Punt, 1962, 1987). The pollen of *Longetia buxoides* (Figs. 92, 93) is spinulose and 6–8-zonocolporate with the colpi extremely short, not much longer than the endoaperture. Thin section (Fig. 93) reveals an exine consisting mostly of a thick tectum with short columellae. The very thin footlayer and thin nonapertural endexine are similar to many Crotonoideae, but both layers are noticeably and irregularly thickened near the colporus.

In terms of genera (110), if not species (1500) (Webster, 1987), Acalyphoideae are the largest subfamily and may well have the greatest diversity of pollen (Punt, 1962). In Galearieae, all three genera, *Galearia*, *Microdesmis*, and *Panda*, were examined in SEM and TEM by Nowicke (1984) as Pandaceae. The pollen morphology and exine structure are unremarkable and thus have limited taxonomic value. The same conclusion and interpretation would apply to three species of *Macaranga* (Table 1). One of the more unusual grains in this subfamily is that of *Dalechampia humilis* (Figs. 89–91), in which a colpus transversalis (Punt, 1962) is bordered by two very prominent costae.

Certain members of Acalyphoideae, e.g., *Acidoton nicaraguensis* (Gillespie, 1994, this issue), and certain taxa in tribe Adelleae, *Adelia triloba*, *A. vaseyi*, *A. vicinella*, and *Leucocroton cordifolius* (G. Webster, unpublished data), appear to have a crotonoid tectum—triangular suprategal elements, but the elements are small and not always

distinct from each other. The tectum in *A. triloba* does form a continuous triangular array. However, none of the above species have been examined in TEM.

Euphorbioideae have never been the subject of a detailed study in SEM and TEM, but Punt (1962, 1987) did examine representative species and characterized the pollen as being consistent in shape, ornamentation, and size. Based on the above conclusions by Punt (1962, 1987), Weber-El Ghobary (1985), and El-Ghazaly (1989), the pollen of *Euphorbia pulcherrima* (Figs. 94, 95) is representative of the subfamily and could be representative of the dicots in general: 3-colporate with a perforate tectum, an endexine that is thin in the mesocolpus but thickened beneath the apertures, well developed, even elongate, columellae, and a thin footlayer.

In a largely unpublished study of Thymelaeaceae pollen (Nowicke, Patel & Skvarla), 70 species from 39 genera were examined. These pantoporate grains, illustrated here (Figs. 97–102) in SEM and in Nowicke et al. (1985) in SEM and TEM, are remarkably similar in exine structure to Crotonoideae: triangular suprategal elements are attached to prominent thick muri with short or narrow columellae, and both footlayer and endexine are thin and/or irregular.

DISCUSSION

Pollen data from electron microscopy support and reinforce the present concept of the Crotonoideae. As demonstrated in thin section, virtually every species examined, aperturate or inaperturate, has pollen with the Croton structure—triangular suprategal elements, called subunits, attached to a network of muri having short or irregular columellae. Inaperturate exines can be further characterized by a very thin or even threadlike footlayer/endexine.

Crotonoideae are the only large assemblage in the dicotyledons to have a preponderance of inaperturate pollen. Of the 2000 species that Webster (1987) estimated for this subfamily, at most only 300 have apertures.

Colpate apertures and a particular exine structure—granular columellae, a prominent footlayer, and well-developed endexine—reinforce the segregation of *Adenocline*, *Ditta*, *Endospermum*, *Glycydendron*, *Klaineanthus*, and *Tetrorchidium* as the tribe Adenoclineae and emphasize their close relationship to each other.

It is difficult to characterize the exine structure of the 3-colpate Micrandreae until more taxa are

investigated, especially in *Micrandra*. Of all species examined here (Table 1), only *M. siphonioides* (Figs. 1–3) clearly lacks the suprategal subunits, although they appear modified in *M. kubeorum* (Fig. 4).

Within the subfamily, the pollen data suggest that Micrandreae and Adenoclineae may be primitive, having retained not only apertures but exines with well-developed footlayers and endexines.

The Manihoteae, in which two large genera (*Manihot* (170 species) and *Cnidoscolus* (75)) account for most of the 300 aperturate Crotonoideae, have porate apertures, irregular yet elongated columellae, and a thinner (than Adenoclineae) footlayer and endexine. This characterization is based on TEM data from only two species, however, and thus should be considered as preliminary.

The pollen of *Suregada*, the only genus in Gelonieae, is pantoporate but has the threadlike footlayer/endexine characteristic of the inaperturate exines. Punt (1962) classified the two species he examined as belonging to the Manihot type (periporate, tectate, Croton-pattern), but he believed the pollen similarity between *Suregada* and *Manihot* to be accidental and the result of a parallel development. I would agree that the two genera are not closely related but my opinion is based on the distinction of their pollen as revealed in thin sections, Figure 26 versus 31 and Figure 27 versus 33. The seemingly absent supporting columellae in *Suregada* further obscure its relationships with other Crotonoideae.

Although Micrandreae, Adenoclineae, Manihoteae, and Gelonieae have apertures, they have the Croton structure and are clearly allied to inaperturate Crotonoideae.

The remaining Crotonoideae have inaperturate pollen, and all species examined in thin section have the Croton structure. Although TEMs of inaperturate pollen portray a structurally weak exine—much of the surface area is covered by lumina with a wall consisting of a threadlike footlayer/endexine (e.g., Figs. 36, 44, 59, 75, 78)—acetolysis has removed the very thick intine. As demonstrated by Thanikaimoni et al. (1984: figs. 14, 15, 25, 26, 33), the intine layer is very thick and present throughout the grain. They reported intines 2–3 μm thick in *Croton matourensis*, 1.5 μm in *Domohinea perrieri*, and 1.0 μm in *Sagotia racemosa*. In contrast to other inaperturate pollen with thick intines, e.g., *Heliconia* (Kress & Stone, 1982), *Canna* (Rowley & Skvarla, 1986), *Sassafras* (Stone, 1987), the Crotonoideae exine is considerably thicker. Clearly, the pollen wall of

inaperturate Crotonoideae is more substantial than the TEMs illustrated here would suggest.

Inaperturate pollen is a restricted condition in the dicotyledons, and its predominance in this large subfamily and rarity in the remaining Euphorbiaceae, would support the monophyly of inaperturate tribes.

It would be difficult to characterize any one, two, or even three inaperturate tribe(s) as having either advanced or generalized pollen morphology relative to those remaining. The diversity of modifications to the subunits might suggest Crotonae, but that diversity reflects, in part, the large number of species assigned to *Croton* (750 species, Willis, 1966). Some Ricinocarpeae show the most modification, a size reduction and loss of distinction of subunits.

The exine structure of Crotonoideae is more similar to Thymelaeaceae than to any remaining subfamily of Euphorbiaceae. In fact, the very uniformity of the pollen in Thymelaeaceae and in Crotonoideae is perplexing. Thirty-three of the 39 genera examined in Thymelaeaceae have grains like those in Figures 97–102 (Nowicke, Patel & Skvarla, unpublished data).

Cronquist (1981, 1989), while acknowledging a proposed relationship between Euphorbiaceae and Thymelaeaceae based on pollen and uniovulate locules, assigned Thymelaeaceae to the Myrtales and Euphorbiaceae to the Euphorbiales. But however well Thymelaeaceae may fit in Myrtales on other bases, pantoporate pollen is virtually unknown in the order, as is the Croton structure.

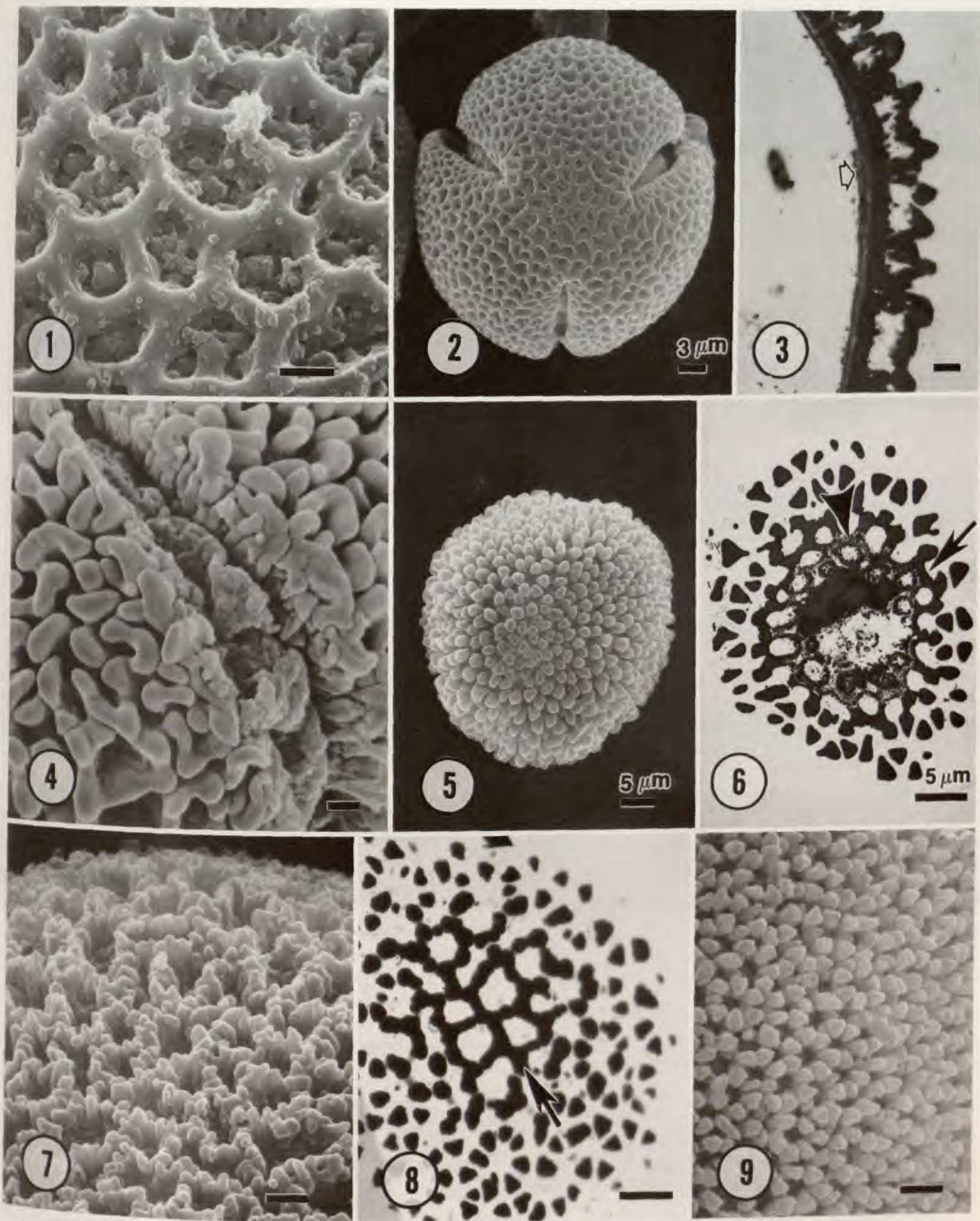
Punt (1987: 134) stated that each of the five subfamilies recognized by Webster (1989) was “more or less characterized by a basic pollen type; the subfamily Acalyphoideae is an exception to this generalization.” But it seems, at least to me, that Phyllanthoideae are also an exception.

When considering all Euphorbiaceae, the pollen data are perplexing: Oldfieldioideae, Crotonoideae, and Euphorbioideae each have a basic pollen type, but it is specialized in the first two and generalized in the third; Phyllanthoideae and Acalyphoideae have diverse pollen types. In Oldfieldioideae, the pollen is brevicolporate, spinulose with a thick tectum, slender columellae, a thin footlayer, and well-developed apertural endexine. The pollen of Crotonoideae has the Croton structure and is mostly inaperturate. The pollen of Euphorbioideae, 3-colp(or)ate and tectate perforate, appears unspecialized, at least in comparison with the other subfamilies. But unspecialized or not, pollen morphology certainly does not argue against the present concept of Euphorbioideae. Pollen morphology

suggests that these three subfamilies are natural assemblages. How then, to judge the taxonomic value of pollen diversity in Phyllanthoideae and Acalyphoideae? Probably on a generic and/or tribal level. The remarkable pollen variation within *Phyllanthus* (Punt, 1987) is difficult to explain or interpret, but there are other genera with almost as much pollen diversity, e.g., *Polygonum* (Nowicke & Skvarla, 1977).

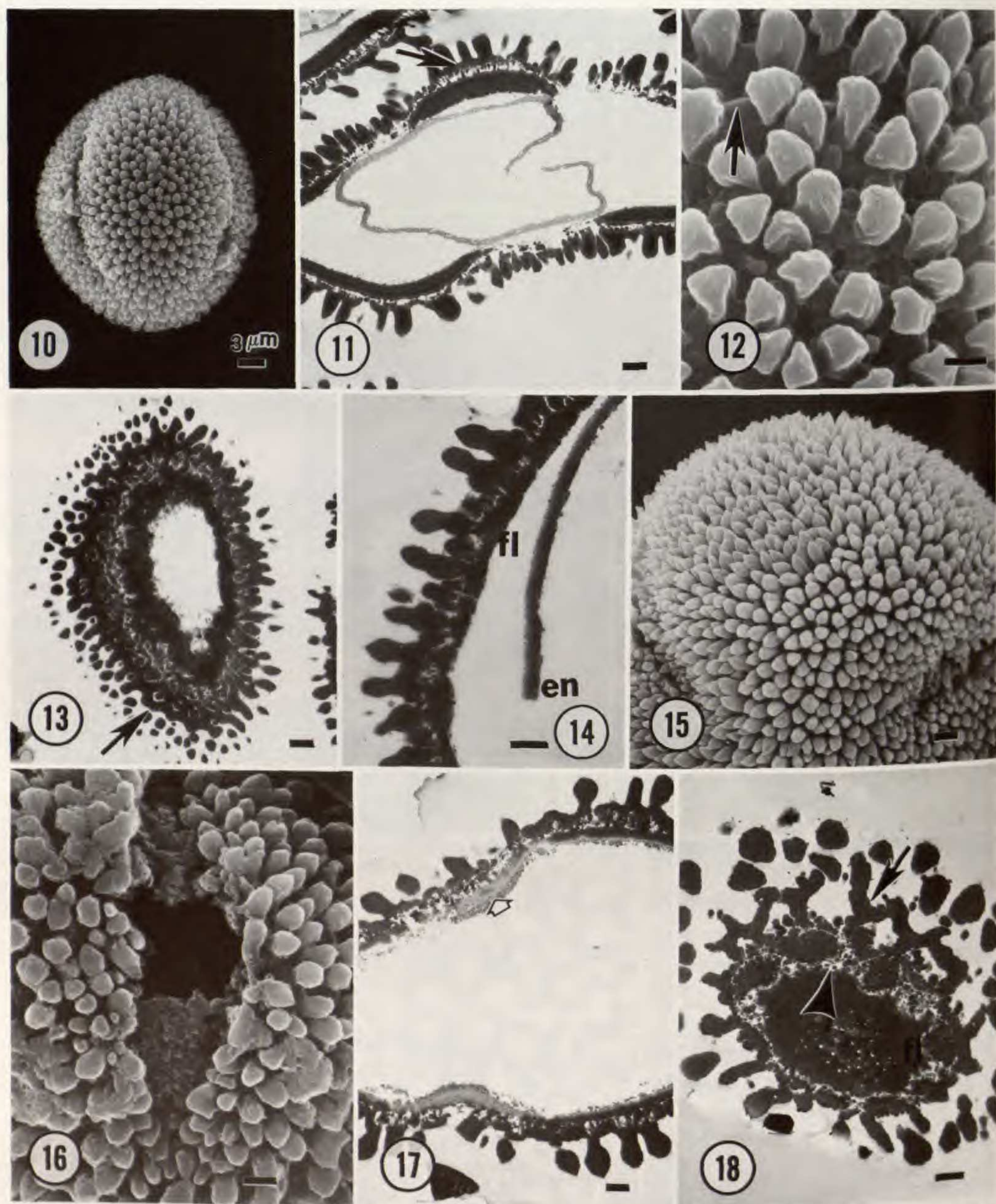
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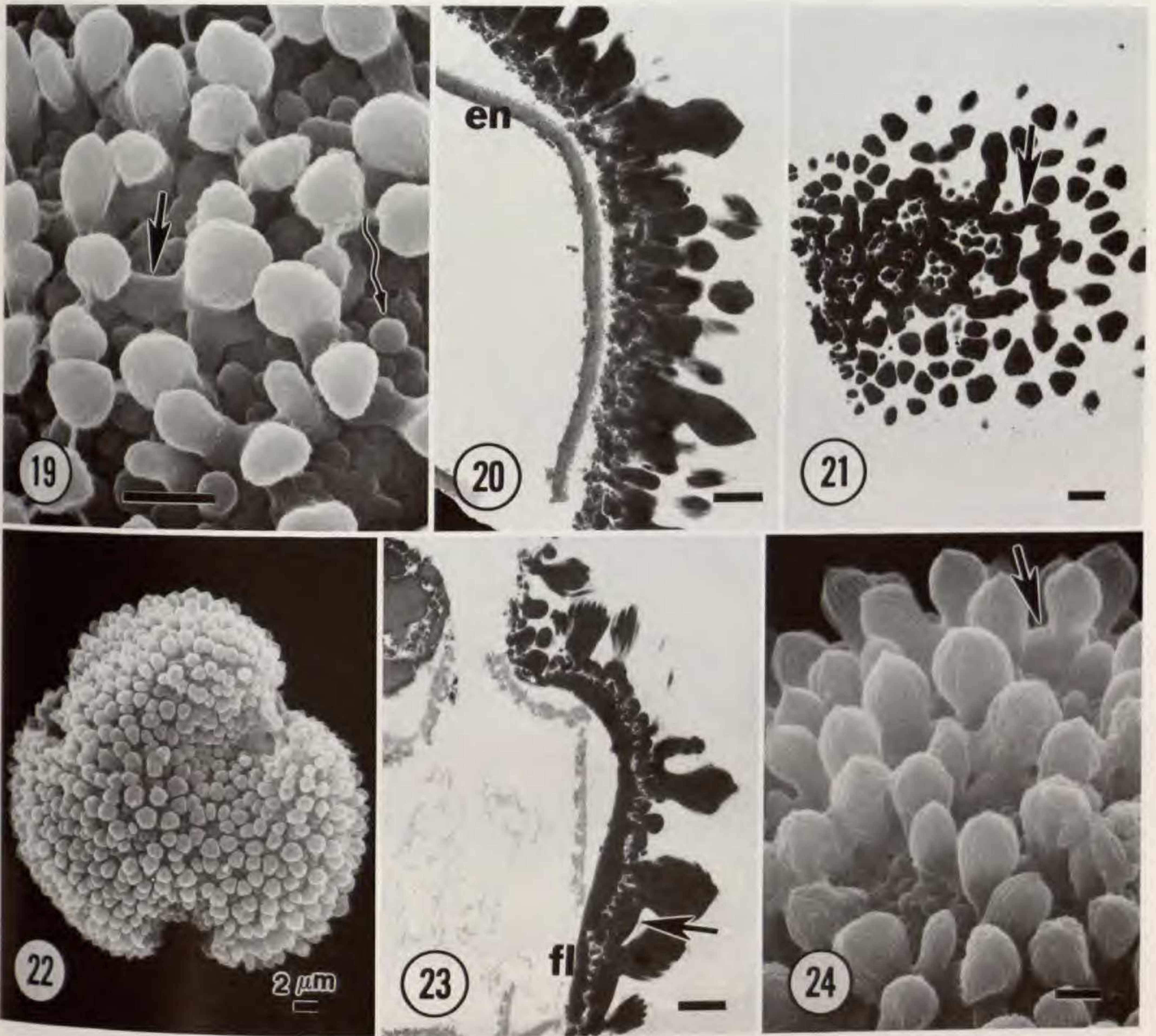


FIGURES 1-9.³ SEM and TEM of pollen in tribe Micrandreae. 1-3. *Micrandra siphonioides*. —1. Tectum. This is a very rare example of a Crotonoideae species in which the muri lack triangular subunits; this condition could represent a loss of the subunits or a stage prior to their development, but the absence of any clear vestiges of the subunits would support the latter interpretation. —2. Polar view. —3. Radial section. Note prominent footlayer and well-developed, consistent endexine (arrow). —4. *M. kuberum*. Note irregular subunits. 5, 6. *M. lopezii*. —5. Whole grain. Although not apparent on this grain, this species is 3-colpate. —6. Tangential section. Note: triangular shape of subunits in cross section; muri (arrow); granular columellae (arrowhead); and footlayer cut obliquely (half moon-shaped central solid area). —7. *Micrandropsis scleroxylon*. The subunits are finely divided; a second collection (see Table 1) has a tectum more similar to that in Figure 9. 8, 9. *Hevea guianensis*. —8. Tangential section. The muri are prominent and the very small lumina appear devoid of ektexine globules. —9. Tectum with very small triangular subunits.

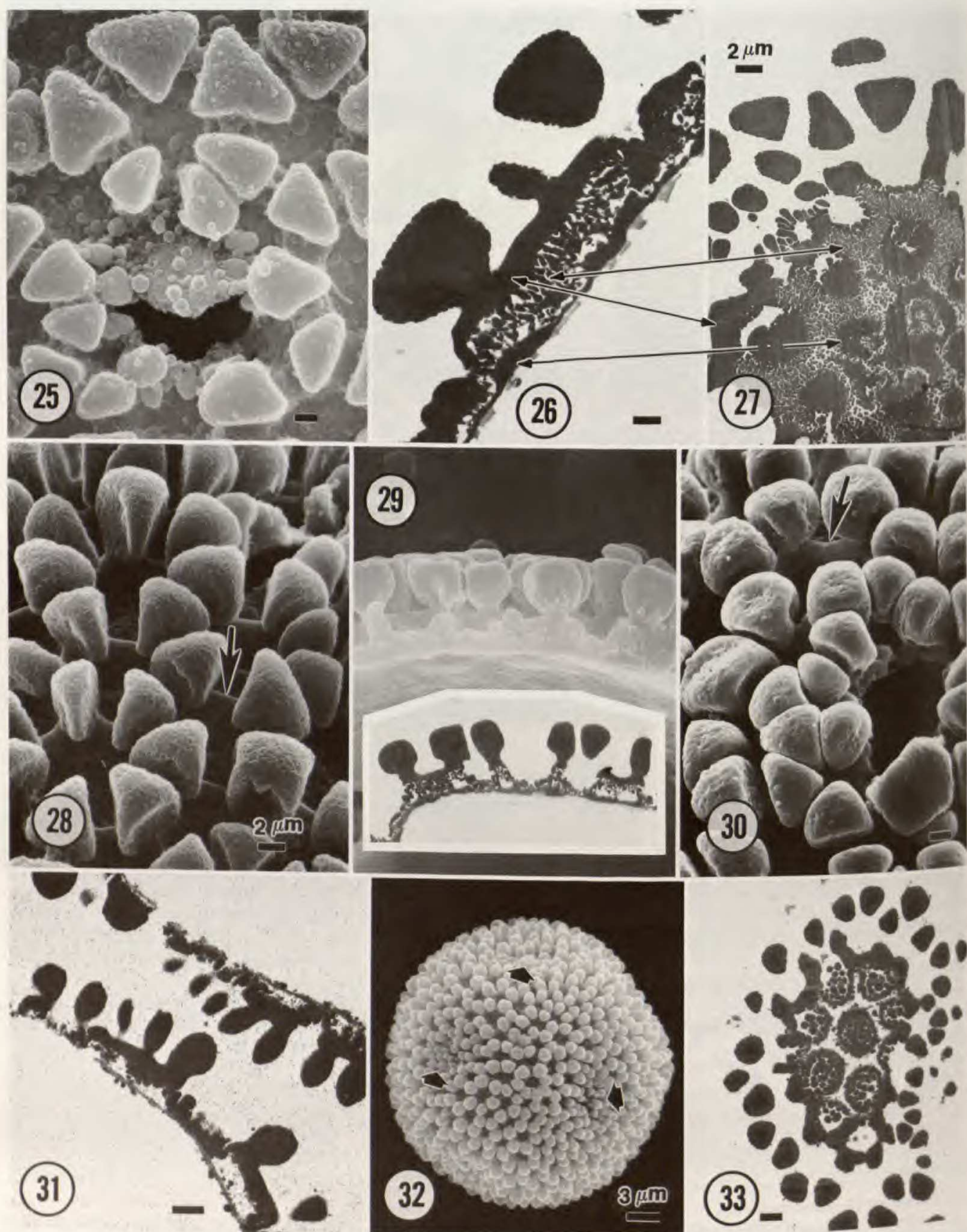
³ Muri are indicated by a straight arrow; supporting columellae by an arrowhead; free columellae/globules of ektexine by a wavy arrow. All scale bars equal 1 micron unless otherwise indicated.



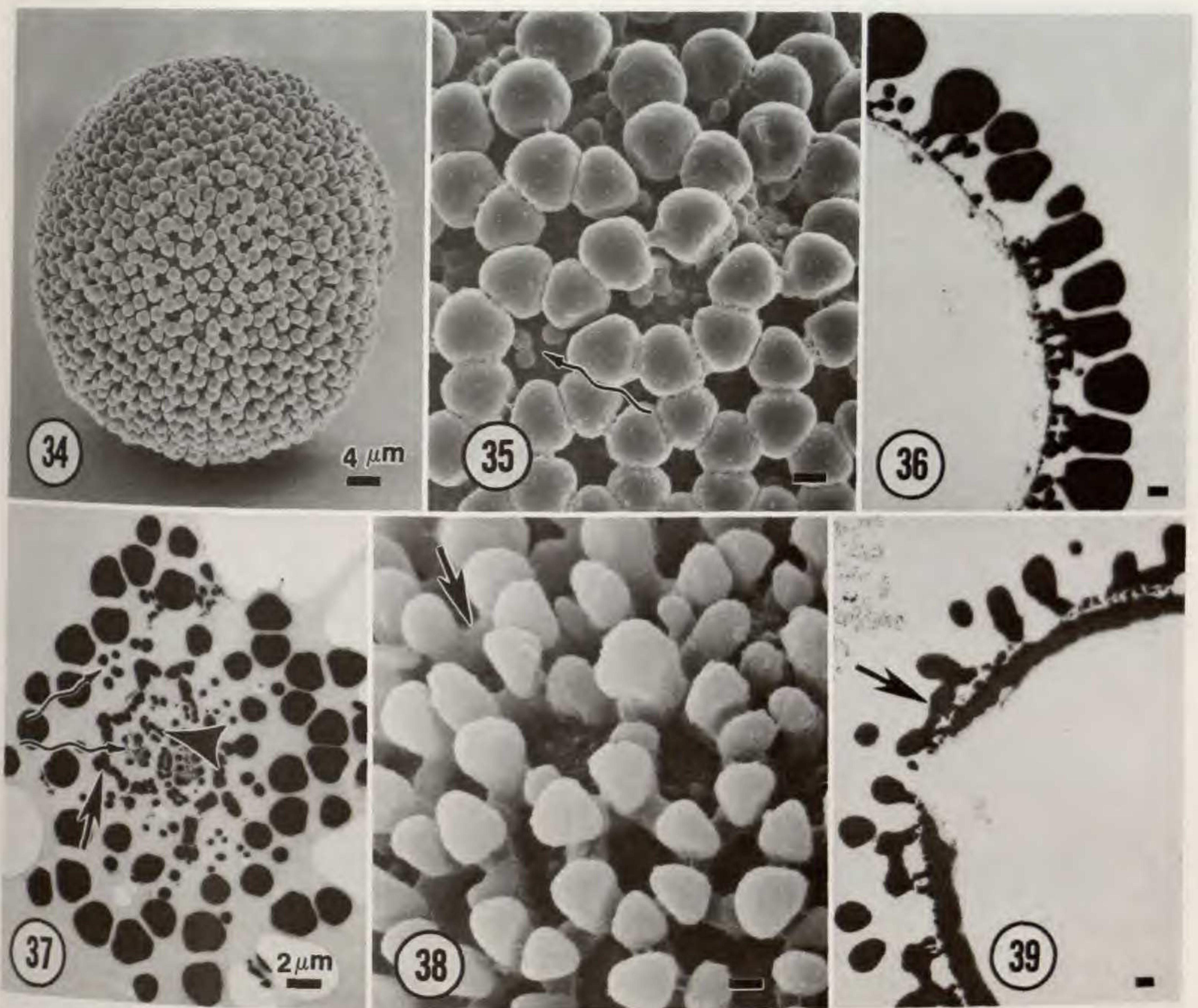
FIGURES 10-18.³ SEM and TEM of pollen in tribe Adenoclineae. 10-12. *Adenocline bupleuroides*.—10. Whole grain.—11. Oblique radial section. Note well-developed footlayer, granular columellae, and an endexine layer separating from ectexine (see also Figs. 14, 20, 23).—12. Tectum. 13-15. *Ditta myricoides*.—13. Tangential section. The structures, in order from the outside, are triangular subunits, then solid bars of muri, granular columellae, and solid footlayer; the seemingly absent endexine layer is assumed to be detached.—14. Radial section. Both this species and *Tetrorchidium rubrivenium* (Fig. 20) have elongate echinate subunits that are recognizable even in LM; fl = footlayer, en = endexine.—15. Tectum. 16, 17. *Klaineanthus gaboniae*.—16. This was the only species examined with colporate apertures.—17. Radial section including two apertures (arrow); although not illustrated in this grain, others had a fragmented irregular endexine similar to that in Figure 23.—18. *Glycydendron amazonicum*. Tangential section. Structural components are same as in Figure 13. en = endexine; fl = footlayer.



FIGURES 19-24.³ SEM and TEM of pollen in tribe Adenoclineae. 19-21. *Tetrorchidium rubrivenium*.—19. Tectum at high magnification. The muri are prominent, subunits are deep/long, and most lumina are covered with ektexine globules.—20. Radial section. Although muri are poorly defined, they are clearly present in Figure 19 and in the tangential section in Figure 21.—21. Tangential section. Section is too shallow to include granular columellae or footlayer. 22, 23. *Endospermum peltatum*.—22. Whole grain, polar view. A very minor portion of this sample (see Table 1) appears to have been shed as tetrads, but the tetrad-members have varying degrees of cohesion.—23. Radial section near aperture. Note: endexine layer separating from ektexine; thick irregular footlayer; granular columellae; detached endexine.—24. *E. formicarium*. Tectum with variously sized, striate subunits. en = endexine; fl = footlayer.

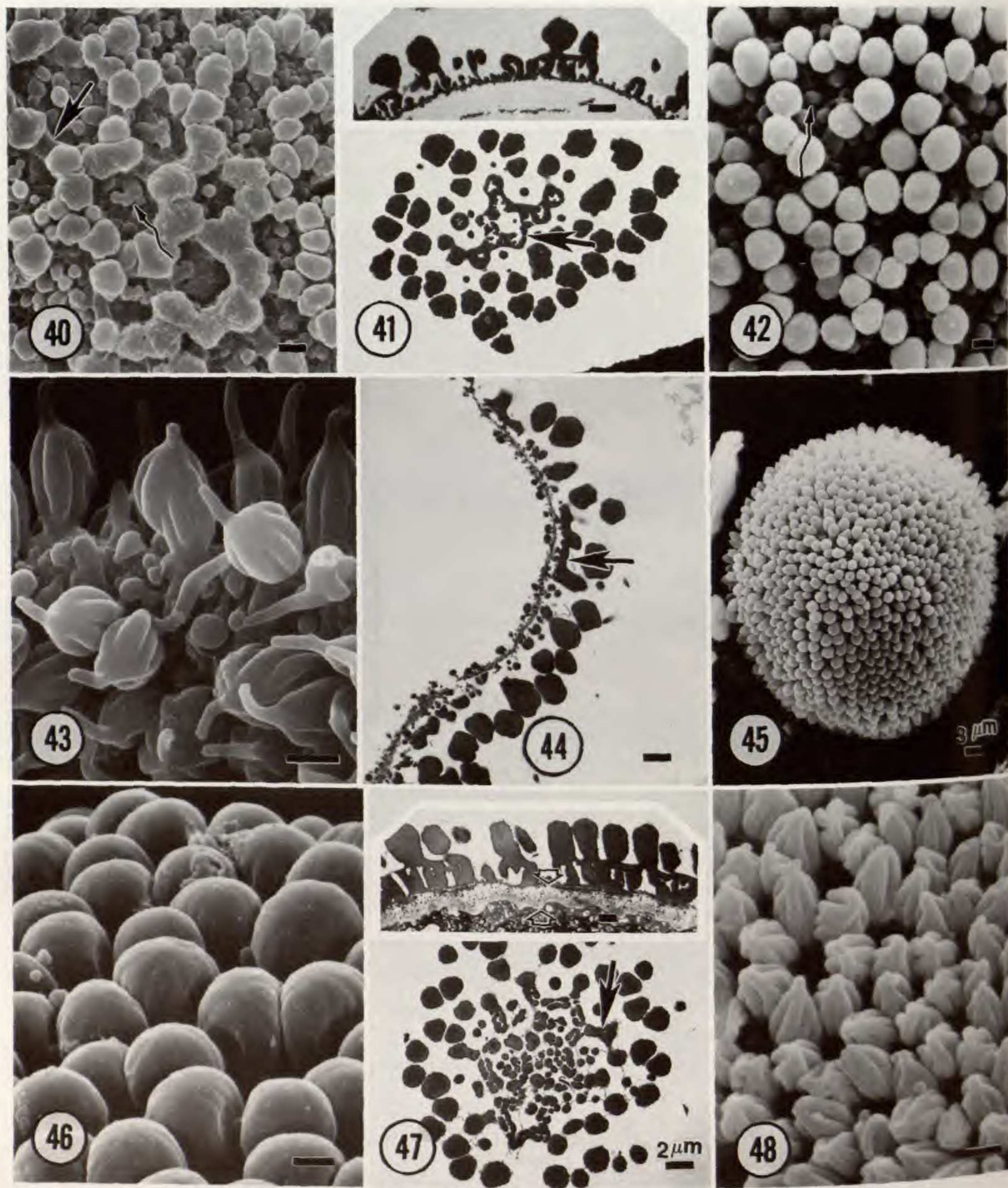


FIGURES 25-33.³ SEM and TEM of pollen in tribes Manihoteae (25-30) and Gelonieae (31-33). 25-27. *Manihot aesculifolia*. — 25. Tectum including partially covered porate aperture; muri are inconspicuous and lumina have only sparse shallow globules of ectexine. Of all genera examined here, *Manihot* has the most consistently triangular subunits. — 26. Radial section. Arrows connect (from top downward) supporting columellae, muri, and footlayer in this radial section with their counterparts in the tangential section in Figure 27; the supporting columellae are very irregular, even granular; note discontinuous but recognizable, less electron-dense endexine. — 27. Tangential section. See legend of Figure 26. — 28. *Manihot pilosa*. Note pitted surface of subunits, a characteristic found in many *Manihot* species examined here. — 29. *Cnidoscolus rotundifolius*. Fracture illustrating relatively thick footlayer/endexine. Inset, *C. sinaloensis*. Note irregular columellae and irregular footlayer; in other sections the supporting columellae appear similar to those in Figure 26. — 30. *C. sinaloensis*. Tectum with pore. — 31-33. *Suregada glomerulata*. — 31. Radial sections of two grains. There is a paucity of columellae below the well-developed muri; in

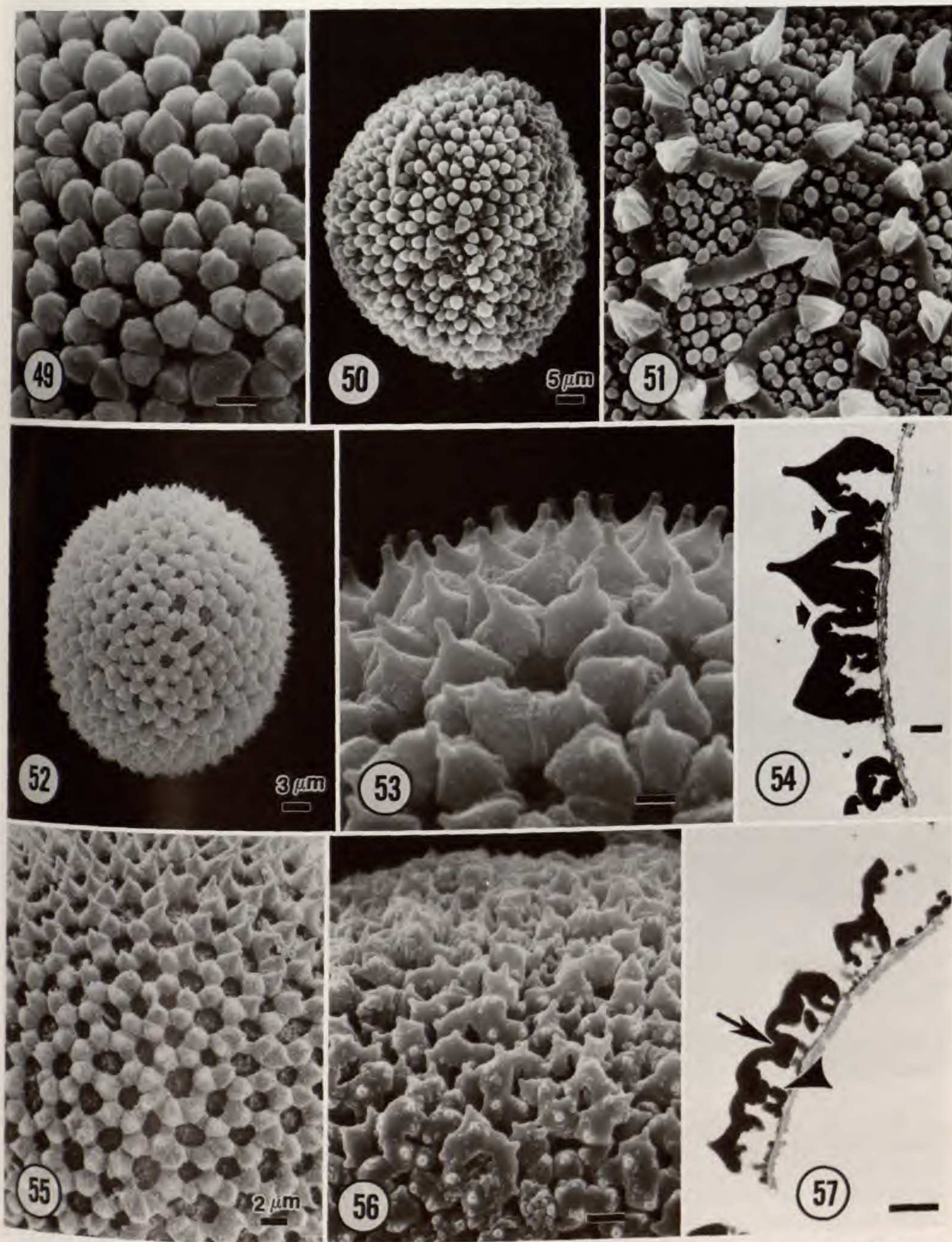


FIGURES 34-39.³ SEM and TEM of pollen in tribes Jatropeae (34-37) and Elateriospermeae (38, 39).—34. *Deutzianthus tonkinensis*. 35-37. *Jatropha hastata*. —35. Tectum. The large size and dense spacing of the subunits obscures the muri; some subunits appear to be connected by thin strands of exinous material.—36. Radial section. Muri are very thin; there is an almost clear (very weakly electron-dense) endexine layer with a few granules delimiting the inner boundary.—37. Tangential section. Small circular objects between subunits, and between subunits and muri, are free columellae (see Fig. 35); note paired support columellae. 38, 39. *Elateriospermum tapos*. —38. Tectum with conspicuous muri and large lumina.—39. Radial section. The gradual thinning (left) of the well-developed footlayer suggests a preformed aperture (as opposed to a break). However, apertures could not be verified in LM.

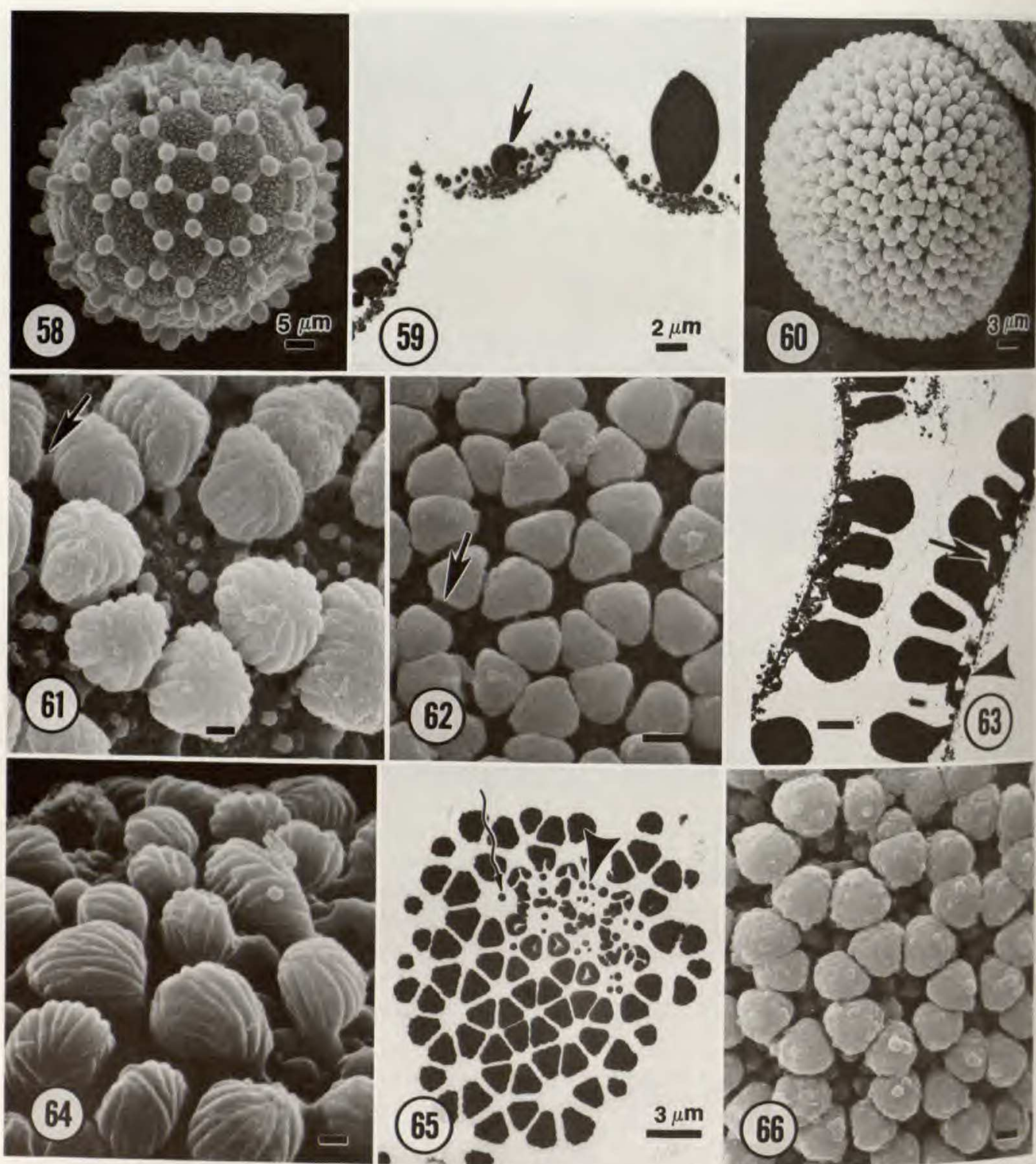
both grains the footlayer/endexine consists of small, occasional granules above and below a thread of exine; in upper grain, the size reduction of subunits indicates proximity to an aperture, but even here the endexine is threadlike.—32. Whole grain with at least three depressions (small arrowheads) indicating apertures; in high-magnification SEMs, the lumina are covered with shallow, free columellae/globules of ectexine.—33. Tangential section.



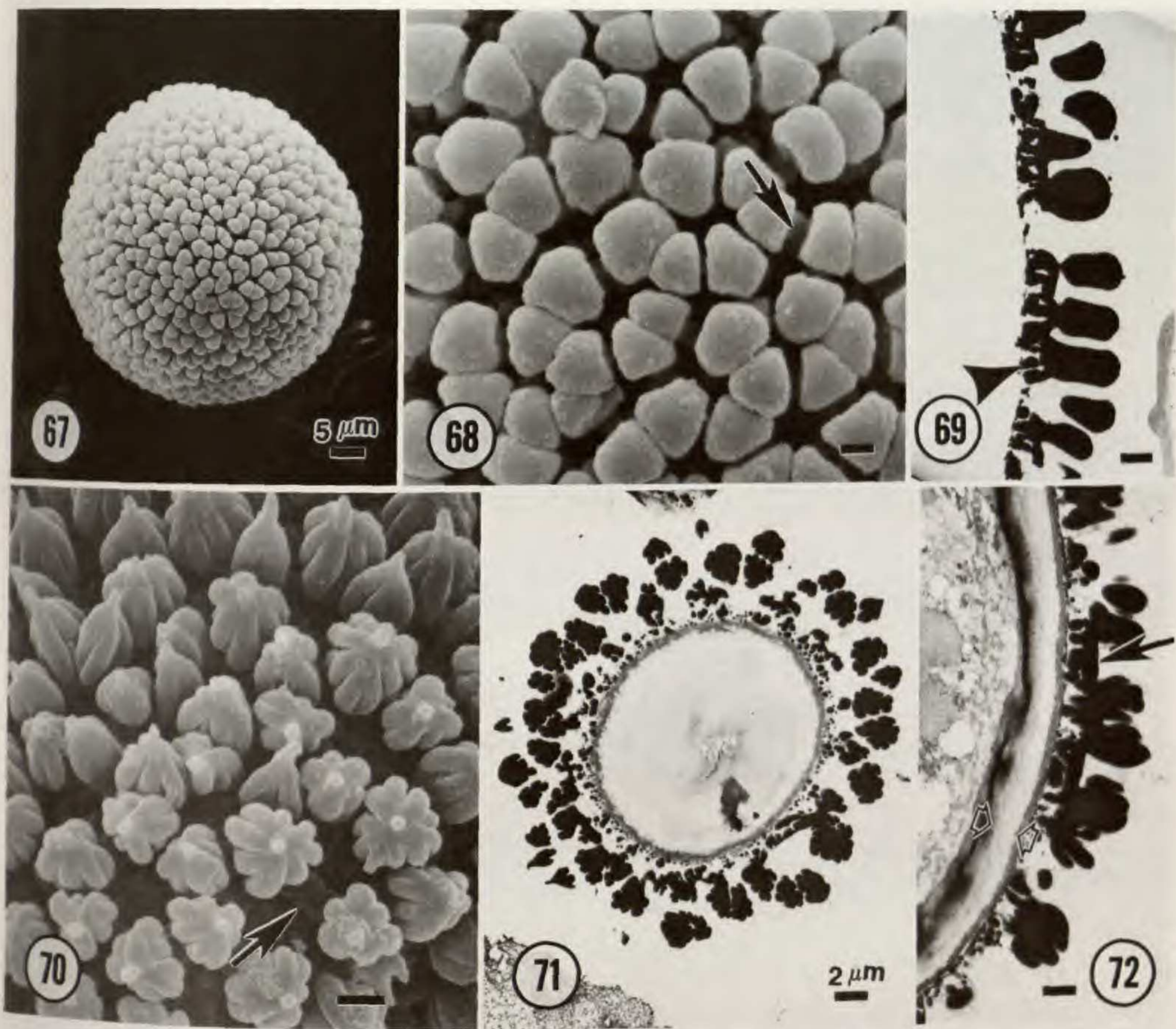
FIGURES 40-48.³ SEM and TEM of pollen in tribe Codieae. 40, 41. *Codiaeum variegatum*. —40. Tectum with open configuration, irregularly shaped subunits, and lumina with free columellae or ektexine globules. —41. Tangential section. Inset, radial section. —42. *Pantadenia adenanthera*. Tectum with irregular muri and large lumina. 43, 44. *Sagotia racemosa*. —43. Tectum. This is one of the more distinct tecta in the subfamily; in some grains there are areas where the subunits fuse together. A similar tectum is present in *Annesijoa novoguineensis* (Fig. 70). —44. Oblique section. This section emphasizes the unusual footlayer/endexine—granules above and below a thread of exine. —45. *Dimorphocalyx luzoniensis*. 46, 47. *Ostodes zeylanica*. —46. Tectum. Although subunits are densely spaced here, other grains had a more open configuration; note faint furrows in subunits. —47. Tangential section. Inset: radial section of portion of incompletely acetolyzed grain; area between open arrowheads is intine. —48. *Pausandra densiflora*. Supratectal subunits are deeply striate.



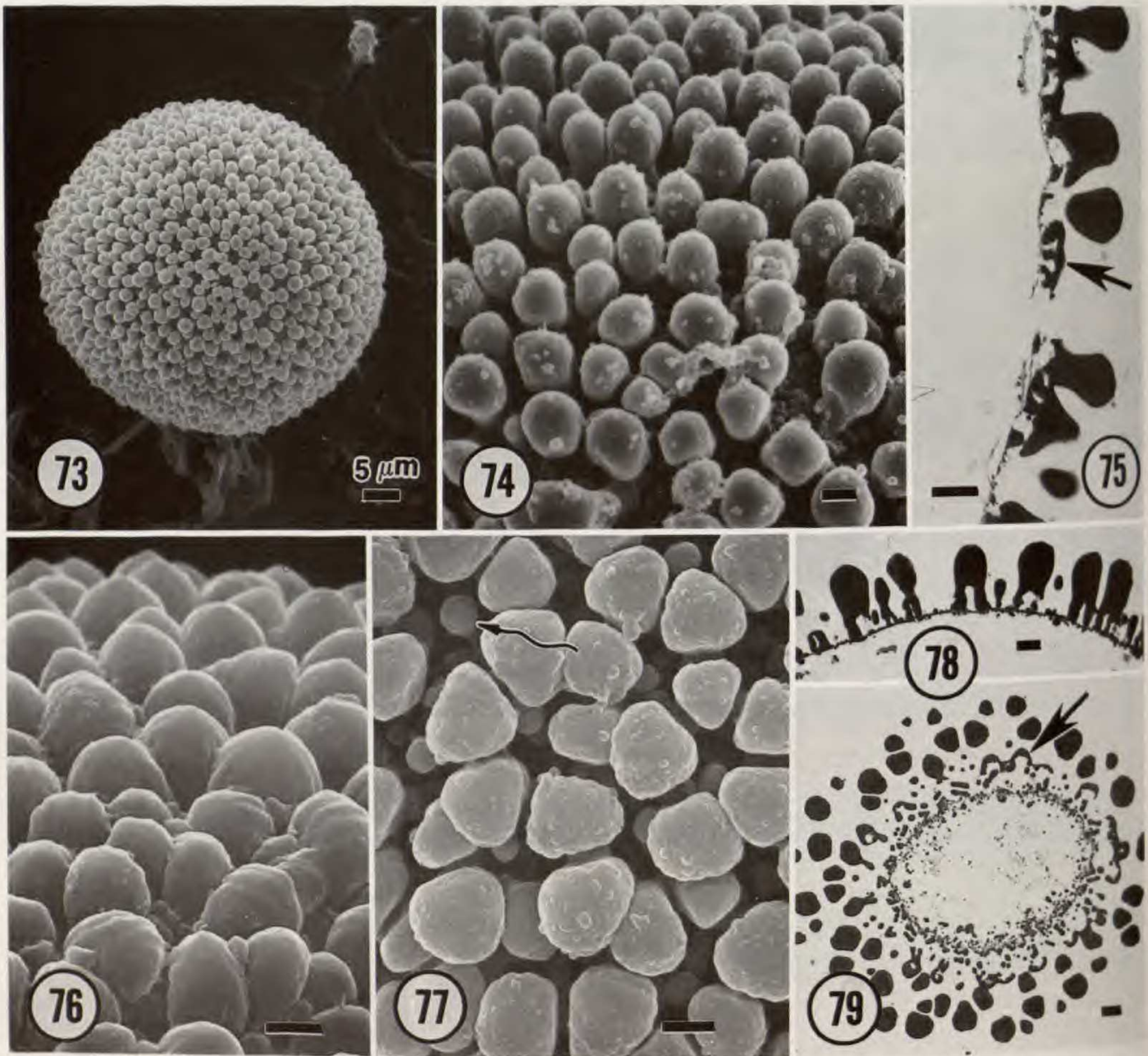
FIGURES 49-57.³ SEM and TEM of pollen in tribe Ricinocarpeae. —49. *Alphandia furfuracea*. —50. *Ricinocarpos glaucus*. Whole grain, partially collapsed. —51. *R. bowmannii*. Tectum. This species and *Croton matourensis* (Figs. 58, 59) have the most open tectal configuration of all Crotonoideae examined here. 52-54. *Beyeria leschenaultii*. —52. Whole grain. —53. Tectum. See discussion of Figure 54. —54. Radial section. Although subunits appear to rest on a trace of footlayer and thin lamellate endexine, no subunit examined in TEM is hollow; thus only the solid upper portion is the subunit. If the gaps (small arrowheads) were closed up, the muri would be recognizable. —55. *Ricinocarpos stylosus*. This species has a typical tectum. 56, 57. *Bertya gummifera*. —56. Tectum. This grain shows one of the more modified Croton structures—many subunits have fused together (another collection of this species is similar to the common structure). —57. Radial section. Note: paired columellae that support muri; granular footlayer; and thin, but well-delimited endexine.



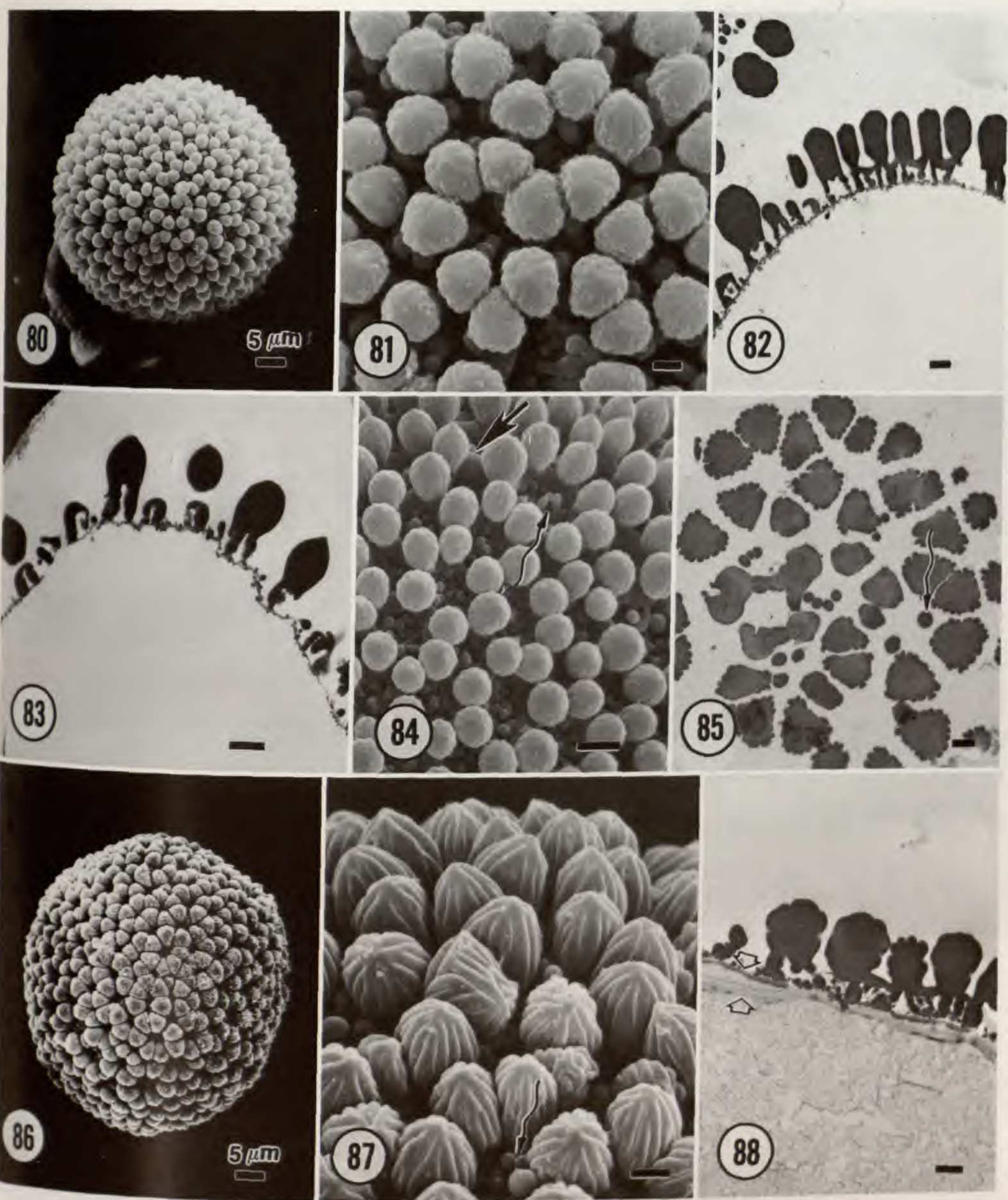
FIGURES 58-66.³ SEM and TEM of pollen in tribe Crotoneae, *Croton*. 58, 59. *C. matourensis*.—58. Whole grain. One of the most distinctive pollen morphologies in Crotonoideae, but a similar one occurs in *Ricinocarpus bowmannii* (Fig. 51).—59. Radial section. The vast majority of the surface area consists of lumina that have numerous fine granules above and below a very thin, irregular footlayer/endexine; two solid components at middle and left are muri cut at right angles to their long axes; at right is a large subunit cut in longitudinal section; although not readily apparent at this magnification, the thick muri rest on granules or granular columellae.—60. *C. balsamifer*.—61. *C. floribundus*. The lumina have scattered free columellae. 62, 63. *C. draco*.—62. Tectum.—63. Radial sections of two grains. Both have an irregular footlayer/endexine.—64. *C. pyramidalis*. The rounded apices and striate surface of the subunits are similar to Figure 61. 65, 66. *C. texensis*.—65. Tangential section. The thin muri show some evidence of paired columellae.—66. Tectum.



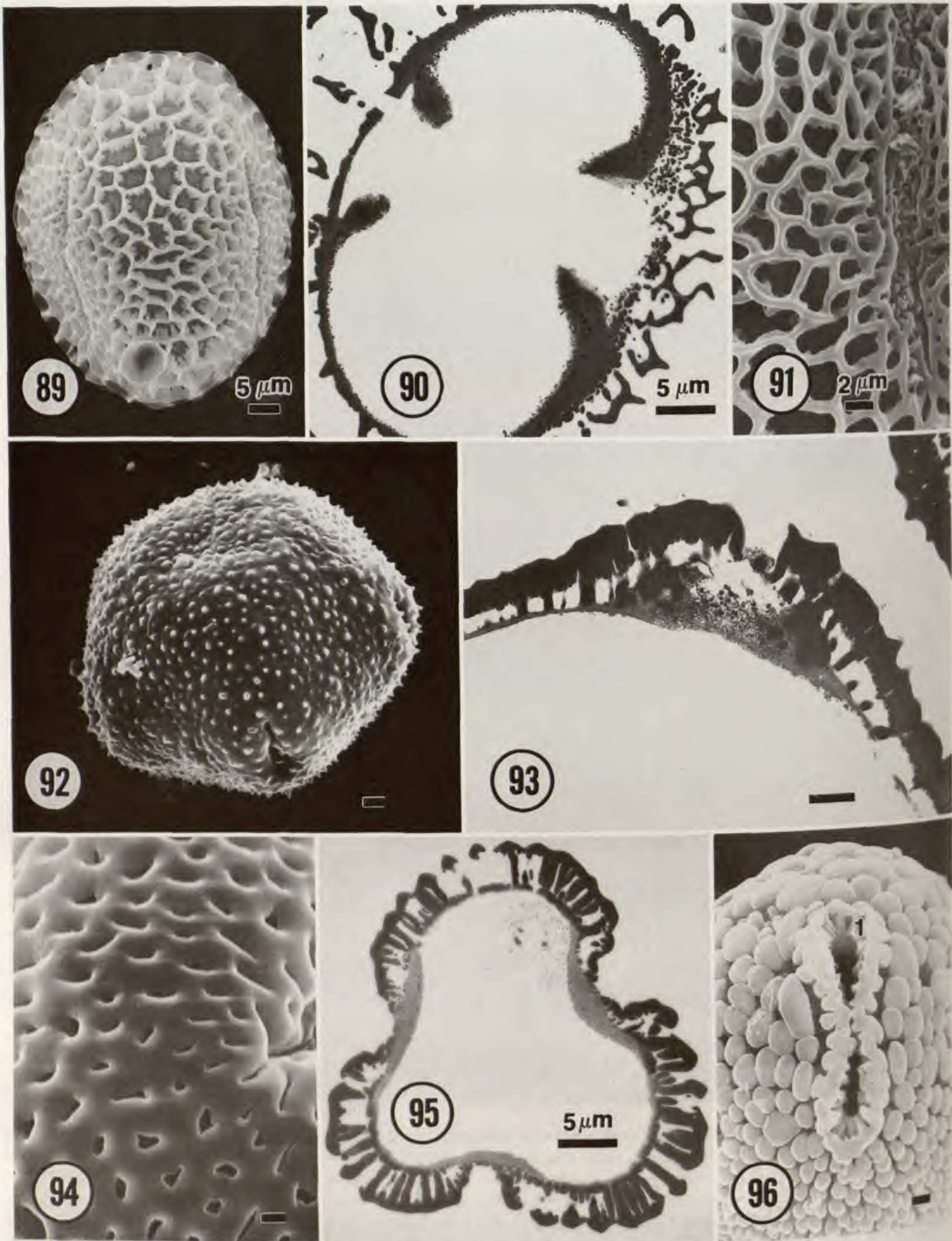
FIGURES 67-72.³ SEM and TEM of pollen in tribe Joannesieae. 67-69. *Joannesia princeps*.—67. Whole grain.—68. Tectum.—69. Radial section. Columellae here are well delimited; other sections show numerous granules above and below a trace of footlayer. 70-72. *Annesijoa novoguineensis*.—70. Tectum. Even though obscured by the deeply striate surface and elongate apices, at least some subunits (those in frontal view) show the basic triangular shape.—71. Tangential section. Even in tangential section, which enhances the thickness of layers, the footlayer is almost nonexistent, but the endexine is identifiable as the thin, innermost, less electron-dense layer.—72. Radial section of portion of incompletely acetolyzed grain; area between open arrowheads is assumed to be intine; note thin, but consistent, lamellate endexine; muri are much better demonstrated here than in Figure 71.



FIGURES 73-79.³ SEM and TEM of pollen in tribe Aleuritideae. 73-75. *Aleurites fordii*.—73. Whole grain.—74. Tectum.—75. Radial section. The footlayer/endexine are unusually thin, but other sections show numerous granules and a trace of footlayer. 76-79. *Ricinodendron rautanenii*.—76, 77. Tectal variation within pollen sample.—78. Radial section. The spacing of the subunits suggests that this grain is more like Figure 77 than Figure 76; note paired supporting columellae under center muri cut at a right angle to its long axis.—79. Tangential section. Muri are very thin; footlayer/endexine are highly irregular.



FIGURES 80-88.³ SEM and TEM of pollen in tribe Neoboutonieae. 80-82. *Anomalocalyx uleanus*. —80. Whole grain. —81. Tectum. —82. Radial section. Note thin muri and short columellae. 83, 84. *Grossera major*. —83. Radial section. The spacing of the subunits reflects the pattern in Figure 84; the muri have paired supporting columellae, the lumina have much smaller globules of ectexine. 85-88. *Crotonogyne argentea*. —85. Tangential section. Subunits reflect the deep striae illustrated in Figure 87. Small circles near center are free columellae cut in cross section; the section is not deep enough to include supporting columellae. —86. Whole grain. —87. Tectum. —88. Radial section. Like Figures 47 and 72, this grain is only partially acetolyzed, and the layer between the open arrowheads includes both endexine and intine.



FIGURES 89–96.³ SEM and TEM of pollen of Euphorbiaceae. 89–91. Acalyphoideae. *Dalechampia humilis*.—89. Equatorial view.—90. Slightly oblique longitudinal section. Grain is 3-colporate and the zonorate endoaperture is delimited by very prominent costae. At right, section has passed along center of colpus and endoaperture; note prominent costae of equatorial band.—91. Tectum along colpus. 92, 93. Oldfieldioideae. *Longetia buxoides*.—92. Oblique view of an oblate, 5-brevicolporate grain.—93. Radial section through aperture. Note thick tectum, slender columellae, and at left and right, the thin footlayer/endexine; apertural thickening is partially footlayer (same electron density as the columellae and tectum) and partially endexine. 94, 95. Euphorbioideae. *Euphorbia pulcherrima*.—94. Tectum near pole.—95. Radial section of whole grain. Note elongate columellae, thin but consistent footlayer in mesocolpus, endexine accumulation under apertures, and perforate tectum.—96. Phyllanthoideae. *Phyllanthus acuminatus*. This unusual grain has three of these bordered “colpi” that are united midlength and a pilate tectum in which the pila at one pole are noticeably larger than at the other.