

Pollen ultrastructure of the Haemodoraceae and its taxonomic significance

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The classification of the genera and tribes of the monocot family Haemodoraceae has been variable and uncertain. In order to provide additional taxonomic characters, SEM and TEM were used in describing the pollen ultrastructure of seventeen genera and nineteen species of the family. The Haemodoraceae as a whole, with the exception of *Lanaria* and *Lophiola*, is palynologically united by the absence of a typical tectate-columellate exine architecture. Within the family, all eight genera of the tribe Haemodoreae have boat-shaped, monosulcate, heteropolar pollen grains with a verrucate (foveolate in one genus) exine wall sculpturing. In contrast, all six genera of the tribe Conostylideae (as defined here) possess variously shaped 2-, 3-, or 7–8-porate, isopolar or apolar grains with a characteristic rugulate sculpturing. A distinctive 2-layered exine, lacking a foot-layer, occurs in all members of the Conostylideae and in four genera of the Haemodoreae. The four other genera of the Haemodoreae are linked to the 2-layered members by a hypothesized gradation in wall architecture. Additional ultrastructural evidence supports the delimitation of the tribes Haemodoreae and Conostylideae, the placement of *Phlebocarya* within the tribe Conostylideae, and the recognition of subgroups of genera within each tribe. In contrast to the Haemodoraceae, members of the Tecophilaeaceae possess a tectate-columellate exine, arguing against the classification of that family as a third tribe (Conanthereae) of the Haemodoraceae. *Lanaria* and *Lophiola* are aberrant within the Haemodoraceae in having tectate-columellate exine walls with monosulcate, exine-less apertures. The classification of *Lanaria* or *Lophiola* within the tribes Haemodoreae or Conostylideae or within the Tecophilaeaceae is refuted based on palynological evidence. The pollen of *Pauridia*, which also has a tectate-columellate architecture, is otherwise distinct from that of *Lanaria* and *Lophiola* in having disulcate apertures and in lacking an ektexinous foot-layer. The inclusion of *Pauridia* in the Haemodoraceae versus the Hypoxi-
daceae is unresolved based on the present study.

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INTRODUCTION

The Haemodoraceae is a monocot family of 13–17 genera and approximately 80 species with distributions in southern Africa, northern South America, Central America, Mexico, eastern North America, Australia, and New Guinea. Members of the family are characterized as perennial, rhizomatous herbs with equitant, unifacial leaves and trimerous flowers in a terminal, cymose inflorescence (Geerinck 1968,

1969, Hutchinson 1973, Robertson 1976). The intrafamilial classification of the Haemodoraceae has varied considerably in past treatments (see Geerinck 1968 for a detailed synopsis). The four family tribes originally proposed by Bentham & Hooker (1883), Euhaemodoreae (= Haemodoreae), Conostyleae (= Conostylideae), Conanthereae, and Ophiopogoneae, have been shifted in various combinations to other families. For example, Pax

(1888, 1930) and Pax & Hoffmann (1930) considered the family Haemodoraceae to be equivalent to Bentham & Hooker's tribe Euhaemodorea; the Conostylideae and Conanthereae were placed in the Amaryllidaceae (subfamily Hypoxidoideae) and the Ophiopogoneae in the Liliaceae. Baillon (1894) viewed the Haemodoraceae as an unnatural assemblage. Melchior (1964) treated the family as consisting of three tribes: Haemodorea, Conostylideae, and Conanthereae. However, the most recent treatments (Hutchinson 1934, 1959, 1973, Geerinck 1969) have recognized two family tribes: Haemodorea (10–11 genera) and Conostylideae (3–6 genera). Hutchinson, furthermore, grouped the Haemodoraceae with five other families in the order Haemodiales, but treated the tribe Conanthereae as a distinct family, the Tecophilaeaceae, in the Liliales. In addition to these conflicts of family definition, the circumscription of tribes has varied. Three genera, *Lanaria*, *Lophiola*, and *Phlebocarya*, have been variably transferred between the tribes Haemodorea and Conostylideae, even by recent authors (see Geerinck 1968, Robertson 1976). *Lanaria*, moreover, is sometimes classified in the Liliaceae or Tecophilaeaceae (De Vos 1961, 1963, Willis 1973). The genus *Pauridia*, placed in the tribe Haemodorea by Pax (1888, 1930), is included in the family Hypoxidaceae in most recent treatments (Geerinck 1969, Hutchinson 1973; see Thompson 1979).

Because of past uncertainties in the classification of the Haemodoraceae and presumed closely related taxa, evidence has been used increasingly from the fields of anatomy (Schulze 1893, Stenar 1927, 1938, Green 1959, Cheadle 1968, 1969, Simpson & Dickison 1981), biochemistry (Hegnauer 1963, Edwards, Churchill, & Weiss 1970, Cooke & Edwards 1981), cytogenetics (Green 1960, Hilliard & Burt 1971, Ornduff 1979), and embryology (Stenar 1927, 1938, Dellert 1933, De Vos 1956, 1961, 1963, Simpson 1981a). However, pollen studies (Erdtman 1966, Radulescu 1973), using light microscopy and acetolyzed preparations, have probably proven most useful in assessing taxonomic relationships in the family.

Erdtman (1966) recognized three pollen types within the family. Six genera of the tribe Haemodorea (sensu Pax 1930), *Haemodorum*, *Pauridia*, *Dilatris*, *Lachnanthes*, *Wachendorfia*, and *Xiphidium*, are characterized by monosulcate pollen (20–90 μm long) with a “usually not very distinct” exine

stratification and sexine pattern (Erdtman 1966: 198–199). In contrast, five genera of the tribe Conostylideae (sensu Pax & Hoffmann, 1930), *Angiozanthos*, *Blancoa*, *Conostylis*, *Phlebocarya*, and *Tribonanthes*, have isopolar, subisopolar, or apolar grains with either 2, 3 or 8 porate apertures (24–53 μm) and with a consistent and characteristic LO pattern: “at low adjustment, dark islands (with fainter darker dots = bacula) separated by brighter channels” (Erdtman 1966: 46). Erdtman emphasized that this common LO-pattern unites these genera despite their shifting aperture number. Finally, two other genera of the family, *Lanaria* and *Lophiola*, comprise a third pollen type of monosulcate grains (29–35 μm) with a thin exine and finely reticulate sculpturing.

Radulescu (1973), using light microscopy of acetolyzed preparations, described twelve species of *Conostylis* (tribe Conostylideae), 1 species each of *Dilatris* and *Schiekia* (tribe Haemodorea), and 1 species of *Cyanella* (tribe Conanthereae of the Haemodoraceae, sensu Melchior 1964). The pollen of the tribe Conostylideae (i.e., the 12 spp. of *Conostylis*) was characterized as porate with 0, 2, or 3 apertures, having reticulate exine sculpturing (verrucate in 2-porate grains of *C. setosa*) which is pilate or pilate-tegillate in optical cross-section. Radulescu described pollen of the Haemodorea as monosulcate and heteropolar with a reticulate-foveolate sculpturing and a tegillate-baculate exine. *Cyanella* of the Conanthereae only differs from the Haemodorea in having a pilate-tegillate exine.

Despite numerous studies in many different fields of the taxa of the Haemodoraceae and related families, “the substantial and continuing disagreements concerning the limits of the Haemodoraceae and the relationships of the genera assigned to it indicate that the family merits additional detailed study” (Ornduff 1979). The purpose of the present study is to provide additional characters from pollen ultrastructure in assessing taxonomic and phylogenetic relationships. Specific questions asked in this study are: (1) What, if any, pollen ultrastructural features characterize the Haemodoraceae as a whole? (2) Does pollen wall architecture support the classification of the Tecophilaeaceae (= tribe Conanthereae) within the Haemodoraceae? (3) What similarities and differences, based on wall structure, are evident between the tribes Haemodorea and Conostylideae? (4) Does pollen ultrastructure clarify the tribal classification of *Phlebo-*

carya, *Lanaria*, or *Lophiola*? (5) Is the classification of *Pauridia* within the Haemodoraceae supported palynologically? (6) What is the pollen ultrastructural basis for the three pollen groups of Erdtman?

MATERIALS AND METHODS

Pollen samples were obtained either from herbarium sheets or from liquid preserved field collections. Anthers from dried herbarium specimens ("DRIED") were re-expanded in Aerosol OT for 1–4 days, followed by several H₂O rinses. Flowers from field collections were fixed in either formalin/acetic acid/alcohol ("FAA") or a solution of 4% glutaraldehyde and 4% formalin in 0.1 M Sorensen's phosphate buffer ("GLUT").

The following 19 species, in 17 genera, were examined: *Anigozanthos flavidus* DC. "FAA"—M. G. Simpson 231X81J (DUKE); *Barberetta aurea* Harv. "FAA"—R. Ornduff 7661 (UC); *Blancoa canescens* Lindl. "GLUT"—M. G. Simpson 181X81AA (DUKE); *Conostylis bealiana* F. Muell. "FAA"—Arboretum, U. C. Santa Cruz, 3 Nov. 1980 (UCSC); *Dilatris corymbosa* Berg. "FAA"—P. Goldblatt 3242 (MO); *D. pilansii* Barker "DRIED"—E. Werdermann & H.-D. Oberdieck 754 (US); *Haemodorum spicatum* R. Br. "FAA"—M. G. Simpson 161X81C (DUKE); *H. simplex* Lindl. "GLUT"—M. G. Simpson 201X81A (DUKE); *Lachnanthes caroliniana* (Lam.) Dandy "FAA"—M. G. Simpson 14VI80A (DUKE); *Lanaria lanata* (L.) Dur. & Schinz (= *L. plumosa* Ait.) "DRIED"—R. D. A. Bayliss 4369 (US); *Lophiola aurea* Ker-Gawler "FAA"—M. G. Simpson 14VI80B (DUKE); *Macropidia fuliginosa* (Hook.) Druce "FAA"—M. G. Simpson 181X81DD (DUKE); *Pauridia minuta* (L.f.) Dur. & Schinz (= *P. hypoxidoides* Harv.) "DRIED"—P. MacOwan & H. Bolus 291 (US); *Phlebocarya ciliata* R. Br. "GLUT"—M. G. Simpson 161X81A (DUKE); *Pyrrorrhiza neblinae* Maguire & Wurdack "DRIED"—B. Maguire, J. J. Wurdack & G. S. Bunting 37222 (US); *Schiekia orinocensis* (Kunth) Meisn. "FAA"—B. Maguire 41569 (NY); *Tribonanthes australis* Endl. "DRIED"—A. J. Eames & A. T. Hotchkiss, 23 Aug. 1953 (US); *Wachendorfia thyrsiflora* L. "FAA"—R. Ornduff 7691 (UC); *Xiphidium coeruleum* Aubl. "FAA"—J. M. MacDougal 1043 (DUKE).

For SEM studies, whole dehiscent anthers containing mature pollen were placed in a modified capsule between two 2 µm Millipore filters or two 0.1 or 5 µm Nucleopore filters. If the pollen of a species was later observed to be covered with debris or pollen-kit, the technique of Lynch & Webster (1975) was followed and the isolated pollen placed in the capsules. Anthers or free pollen were dehydrated to 100% ethanol, then infiltrated with 100% Freon 113 (intermediate fluid). The material was critical-point dried in a BOMAR SPC 900/EX drier with CO₂ (transition fluid). Pollen grains were tapped onto a stub covered by double-stick Scotch tape, sputter coated (ca. 200 Å thickness) with gold/palladium (60/40), and viewed with a Joel JSM-S1 SEM. Optionally, cross sections of pollen grains were prepared using a freezing microtome.

The pollen sections were dehydrated, critical-point dried, mounted on a stub, and coated as before for SEM viewing (see Fig. 7E, 8E).

For TEM analysis of wall architecture, pollen samples were fixed in 4.2% glutaraldehyde for 1–2 hours, rinsed several times in 0.1 M Sorensen's phosphate buffer, and post-fixed in 2% OsO₄ for 1 hour. After two rapid H₂O rinses and dehydration to 100% ethanol, the material was infiltrated in a series of increasing concentrations of Spurr's resin (Spurr 1969). Fully infiltrated grains were placed in an obconical BEAM capsule and polymerized 8–12 hours in a 65°C oven. Sections ca. 500–800 Å thick were prepared using a Dupont diamond-knife on a Cambridge-Huxley ultramicrotome, and mounted on uncoated 200 mesh copper grids. Preparations were post-stained with uranyl acetate (15 min) and lead citrate (7 min) and viewed with a Siemens Elmiskop 101 TEM.

Hagenbachia brasiliensis C. Nees & Mart. (Haemodoraceae, sensu Hutchinson 1973), which recently has been recognized as a species of *Chlorophytum* of the Liliaceae (Ravenna 1977), is not included in the present study. Pollen terminology generally follows that of Walker & Doyle (1975).

RESULTS

Tribe Haemodoreae

Dilatris (2 of 5 species examined)

D. pilansii Barker.—Pollen grains monosulcate and heteropolar (Fig. 1A) with verrucate to baculate non-apertural sculpturing (Fig. 1B) and gemmate to pilate apertural sculpturing (Fig. 1C). Non-apertural exine 2-layered, a commissural line occurring at the junction of the two layers (Fig. 1E). Outer exine layer composed of irregularly baculate, laterally fused elements (Fig. 1D), the distal ends forming the verrucate sculpturing; inner exine layer composed of smaller, distinct, generally papillate elements (Fig. 1E). Apertural wall with an exine of scattered, 2-layered, gemmate elements atop a relatively thick, 2-layered intine (Fig. 1F), the thickened outer intine with radially oriented, channel-like structures (Fig. 1F).

D. corymbosa Berg.—Grains monosulcate, heteropolar (Fig. 1G). Sculpturing of non-apertural wall verrucate (Fig. 1H) and of apertural wall finely gemmate (Fig. 1I); larger wart-like elements scattered among the minute gemmate elements near the aperture border (Fig. 1I). Non-apertural exine bordering the aperture and at the ends of the grain smooth and perforated (Fig. 1H, I). Non-apertural exine 2-layered by presence of a commissural line (Fig. 1J); inner exine layer composed of discontinuous to fused baculate elements (Fig. 1J). Exine

and intine of apertural wall (Fig. 1 K) similar to those in *D. pilansii*. Outer exine layer thin at interface between apertural and non-apertural walls, corresponding to the perforated border (Fig. 1 L).

Xiphidium (monotypic)

X. coeruleum Aubl.—Pollen monosulcate and heteropolar (Fig. 2 A). Sculpturing of the non-apertural wall verrucate with granular material between the major verrucae (Fig. 2 B), a relatively smooth border encircling the aperture (Fig. 2 A). Apertural wall sculpturing verrucate (Fig. 2 C). Non-apertural exine composed of closely spaced, baculate elements, 2-layered as defined by a median commissure (Fig. 2 E); exine between the major baculate elements granular, particularly in the lower exine layer. Intine of non-apertural wall 2-layered (Fig. 2 E). Aperture wall composed of distinct, closely spaced, verrucate to baculate exine elements atop a relatively thick, 2-layered intine (Fig. 2 D, G). Outer layer of aperture intine thickened at the interface with the non-apertural wall (Fig. 2 F).

Wachendorfia (1 of 5 species examined)

W. thyrsiflora L.—Pollen monosulcate and heteropolar (Fig. 3 A). Aperture wall convex in shape (Fig. 3 A), consisting of widely separated, 2-layered baculate exine elements (Fig. 3 C) over a relatively thick fibrillar intine (Fig. 3 D, F). Non-apertural wall proximally verrucate (Fig. 3 A, D), a granular material present between adjacent verrucae (Fig. 3 B). Exine of the proximal region 2-layered, a commissural line present between the large, verrucate elements of the outer layer and smaller, irregular granular elements of the inner layer (Fig. 3 G). Aperture wall encircled by a smooth non-apertural border, pitted with micropores (Fig. 3 A, C, D). Exine of the border continuous with that of proximal wall exine and 2-layered, a prominent commissure present between the homogeneous, micropore-filled outer layer and the irregular, somewhat granular inner layer (Fig. 3 H). Intine of non-apertural wall generally 2-layered (Fig. 3 G). Outer intine layer at the aperture interface thickened (Fig. 3 E), comprising the bulk of the apertural intine wall (Fig. 3 F).

Barberetta (monotypic)

B. aurea Harv.—Pollen monosulcate, heteropolar with verrucate to baculate apertural sculpturing

(Fig. 4 A). Non-apertural wall with a verrucate proximal surface (Fig. 4 B), and a smooth, micropore dense border surrounding the aperture (Fig. 4 A, B). Non-apertural exine 2-layered, with a commissure between the layers (Fig. 4 C, D). Outer layer composed either of distinct, closely appressed verrucate elements in the proximal region (Fig. 4 C) or relatively homogeneous in the smooth border region (Fig. 4 D). Inner exine layer throughout of appressed, radially elongate elements comprising 1/2–2/3 of the exine thickness (Fig. 4 C, D). Aperture with a relatively thick intine and an exine of closely spaced, 2-layered, baculate elements, the inner exine layer reduced (Fig. 4 E).

Pyrrothiza (monotypic)

P. neblinae Maguire & Wurdack.—Grains monosulcate and heteropolar (Fig. 4 F) with verrucate non-apertural and gemmate to verrucate apertural wall sculpturing (Fig. 4 G). Non-apertural wall composed of a thin intine and an exine with 2-layers: a continuous outer layer with a verrucate outer surface and an inner layer of amorphous, discontinuous, somewhat granular exine material (Fig. 4 I); inner exine layer along the border of the aperture reduced (Fig. 4 H). Apertural wall composed of scattered verrucate exinous elements atop a thick, 2-layered intine (Fig. 4 J). Outer intine layer expanded at the aperture periphery (Fig. 4 H) and containing radially oriented, channel-like structures (Fig. 4 J).

Schiekia (monotypic)

S. orinocensis (Kunth) Meisn.—Grains monosulcate and heteropolar (Fig. 5 A), with foveolate-fossulate non-apertural exine (Fig. 5 B) and verrucate to gemmate apertural sculpturing (Fig. 5 C). Apertural wall of scattered gemmate exine elements and a thick, homogeneous intine (Fig. 5 D, E). Non-apertural exine composed of 3 layers: an outer, perforated homogeneous layer; a middle layer of discontinuous, amorphous exine deposits; and a continuous, somewhat granular inner layer (Fig. 5 F). Middle and inner exine layers reduced at the aperture periphery (Fig. 5 E) and absent along two apparent regions of constriction of the proximal wall (Fig. 5 D, G).

Haemodorum (2 of 20 species examined)

H. spicatum R. Br.—Grains monosulcate, heteropolar (Fig. 6 A) with verrucate non-apertural and

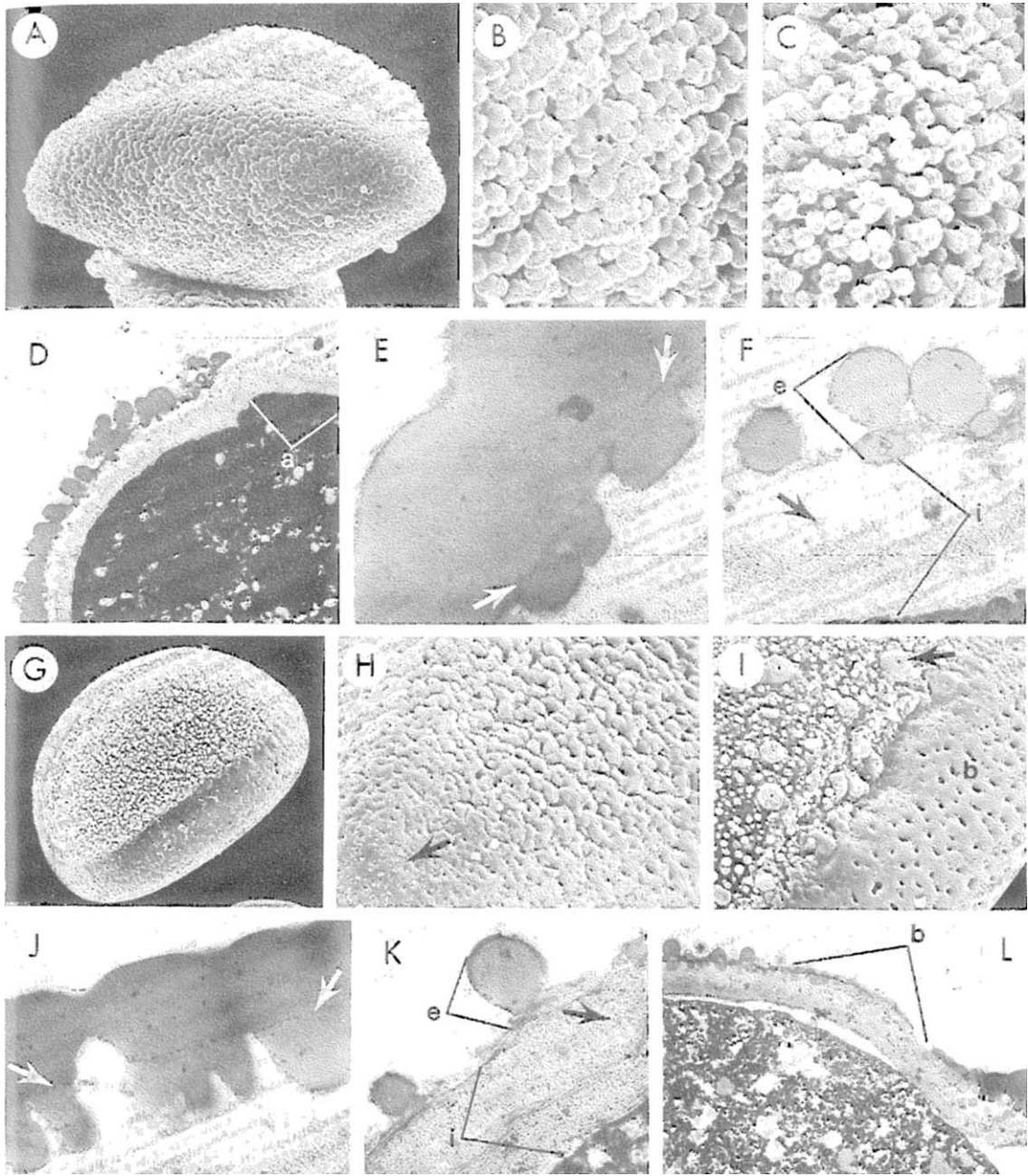


Fig. 1. *Dilatris* (Haemodoraceae). A–F: *D. pilansii* Bark (A) Pollen grain, with monosulcate aperture above. SEM $\times 1500$. (B) Close-up of verrucate non-apertural wall. SEM $\times 5600$. (C) Close-up of aperture, showing pilate-gemmate exine elements. SEM $\times 5500$. (D) Interface between non-apertural wall (left) and apertural wall (a); note the 2-layered intine. TEM $\times 3900$. (E) Non-apertural wall, showing commissural line (arrows) between inner (papillate) and outer exine layers. TEM $\times 54800$. (F) Apertural wall, composed of a 2-layered intine (i) and 2-layered exine elements (e); note channel-like structures (arrow) of outer intine layer. TEM $\times 19500$.

G–L: *D. corymbosa* Berg. (G) Pollen grain, aperture

facing. SEM $\times 1000$. Verrucate proximal wall; note smooth, perforated exine at the end of grain (arrow). SEM $\times 2700$. (I) Close-up of aperture edge, showing foveolate border (b) and numerous gemmate exine elements of aperture wall; larger, warty exine elements (arrow) occur sparingly at aperture border. SEM $\times 2700$. (J) Non-apertural wall; note commissural line between two exine layers (arrows). TEM $\times 28400$. (K) Apertural wall, showing 2-layered intine (i) and gemmate exine elements (e); note channel-like structures of outer intine layer (arrow). TEM $\times 24700$. (L) Interface between apertural (left) and non-apertural (right) walls; note aperture border (b). TEM $\times 8100$.

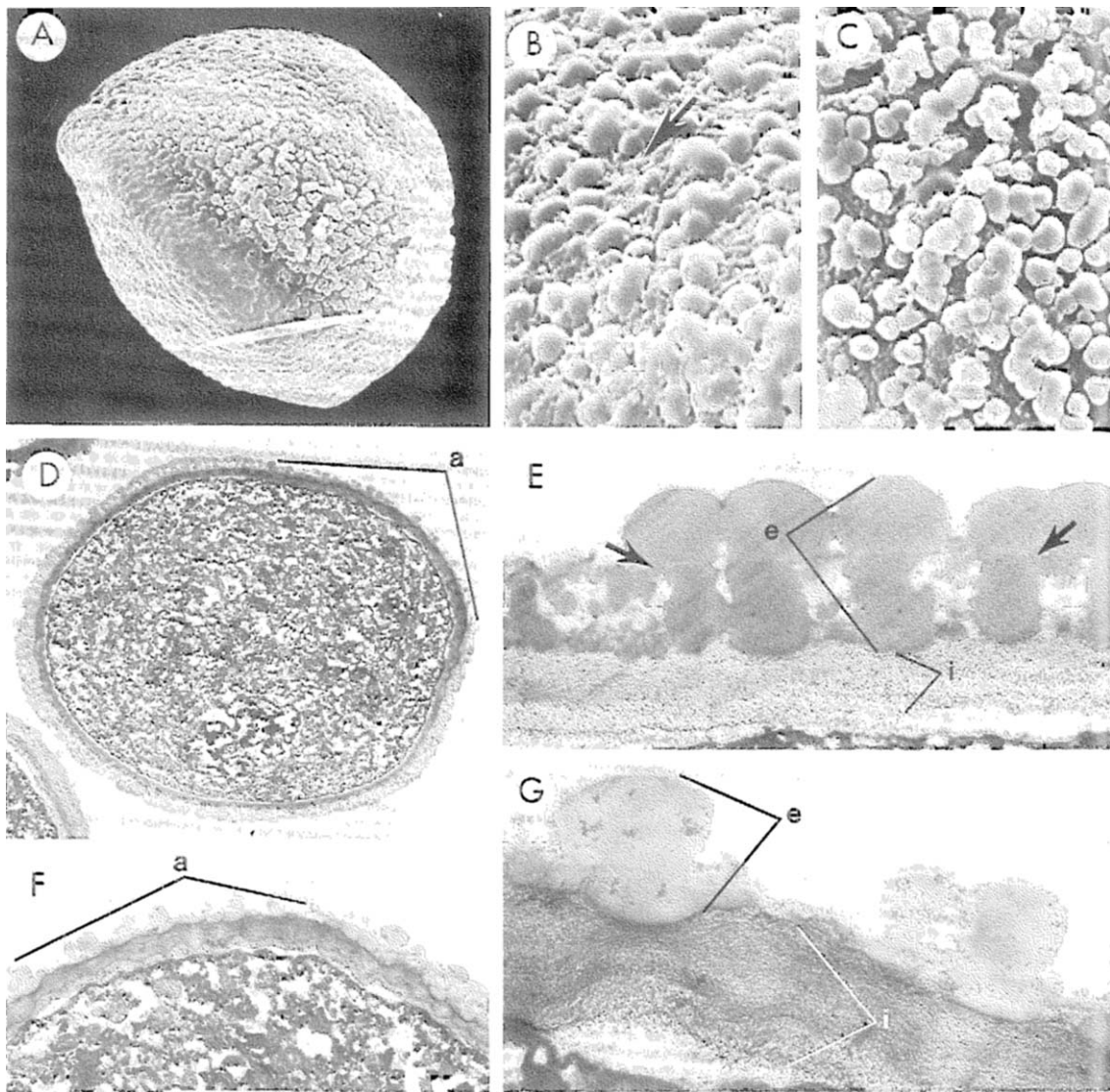


Fig. 2. *Xiphidium coeruleum* Aubl. (Haemodorea). (A) Whole grain, aperture at right; note raphide crystal. SEM $\times 2100$. (B) Non-apertural wall; note granular exine (arrow) between major verrucae. SEM $\times 9000$ (C) Verrucate apertural wall. SEM $\times 7700$. (D) Cross-section of whole grain, showing aperture (a). TEM $\times 2400$. (E) Non-apertural wall, showing 2-layered intine (i) and 2-layered exine

(e), with commissural line between the exine layers (arrows); note granular exine between major elements. TEM $\times 22400$ (F) Interface between aperture (a) and non-apertural wall (right); note thickening of outer intine layer in the apertural wall. TEM $\times 6000$. (G) Apertural wall, showing 2-layered intine (i) and scattered exine elements (e). TEM $\times 30900$.

gemmate apertural sculpturing (Fig. 6B). Non-apertural exine composed of laterally appressed, baculate structural elements basally interconnected by thin exinous material (Fig. 6C, E); commissure not present. Apertural wall of scattered baculate to gemmate elements atop a thick, 2-layered intine (Fig. 6C, F). Outer intine layer containing radially

oriented, electron transparent channel-like structures (Fig. 6F) and thickened at interface between non-apertural and apertural walls (Fig. 6D).

H. simplex Lindl.—Grains monosulcate, heteropolar with verrucate non-apertural and apertural wall sculpturing (Fig. 6G). Aperture region indistinct, defined only by the slightly more separated

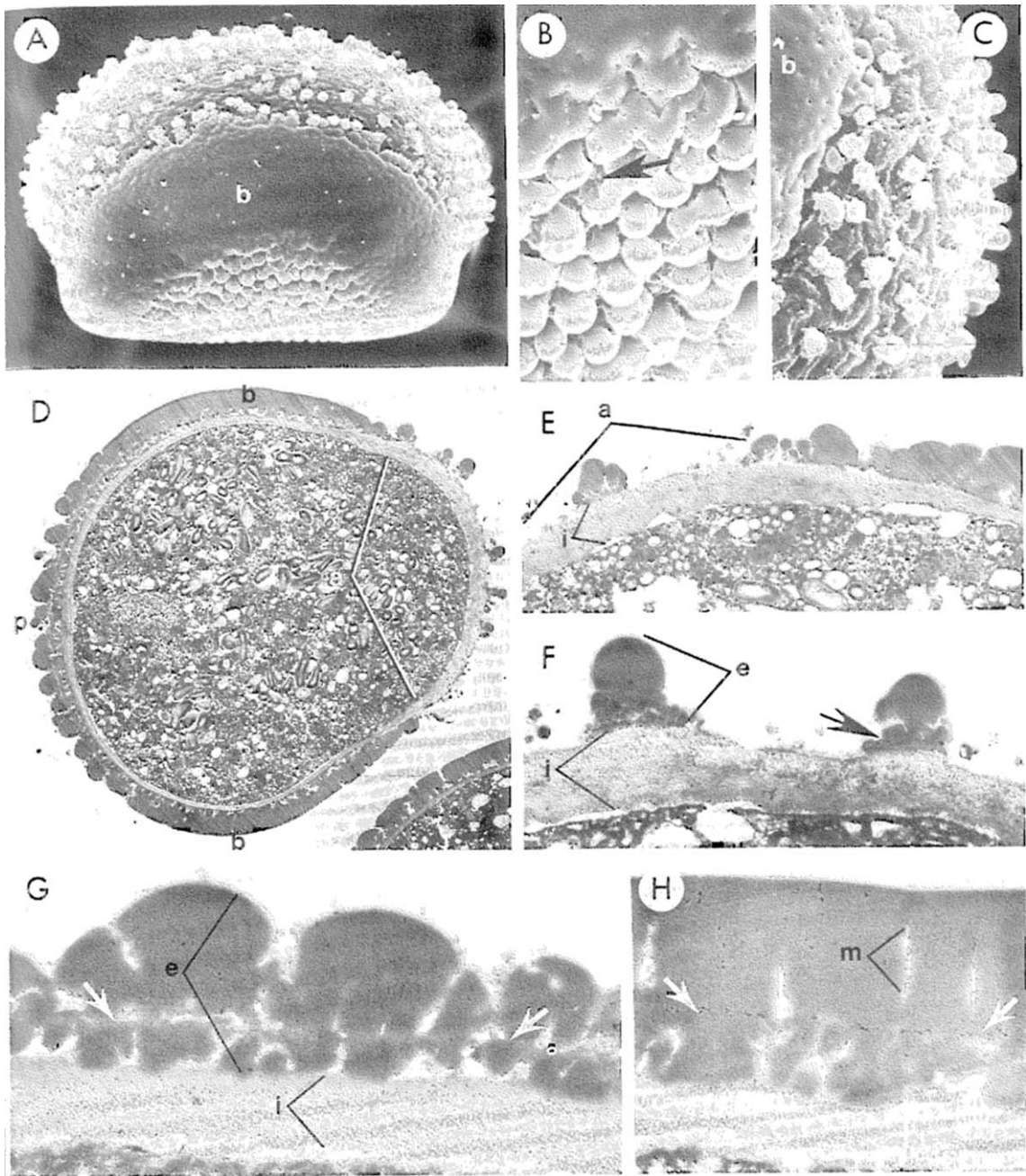


Fig. 3. *Wachendorfia thyrsiflora* L. (Haemodoreaee). (A) Whole grain, showing convex aperture (above) and flattened proximal surface (below); note smooth aperture border (b). SEM $\times 1\ 600$. (B) Close-up, proximal surface, showing granular exine (arrow) between major verrucae. SEM $\times 5\ 500$. (C) Close-up, aperture; note smooth micropore-filled border (b). SEM $\times 3\ 600$. (D) Cross-section of whole grain, showing proximal wall (p), aperture (a), and border (b). TEM $\times 2\ 600$. (E) Interface between apertural (a) and non-apertural (right) walls; note thickening of

outer layer of the 2-layered intine (i). TEM $\times 6\ 500$. (F) Aperture wall, showing 2-layered intine (i) and 2-layered exine (e); note junction between exine layers (arrow). TEM $\times 11\ 200$. (G) Non-apertural, proximal wall, showing 2-layered intine (i) and 2-layered exine (e), with commissural line between the two exine layers (arrows). TEM $\times 21\ 300$. (H) Non-apertural wall of smooth border region; note commissural line between two exine layers (arrows) and micropores (m). TEM $\times 20\ 300$.

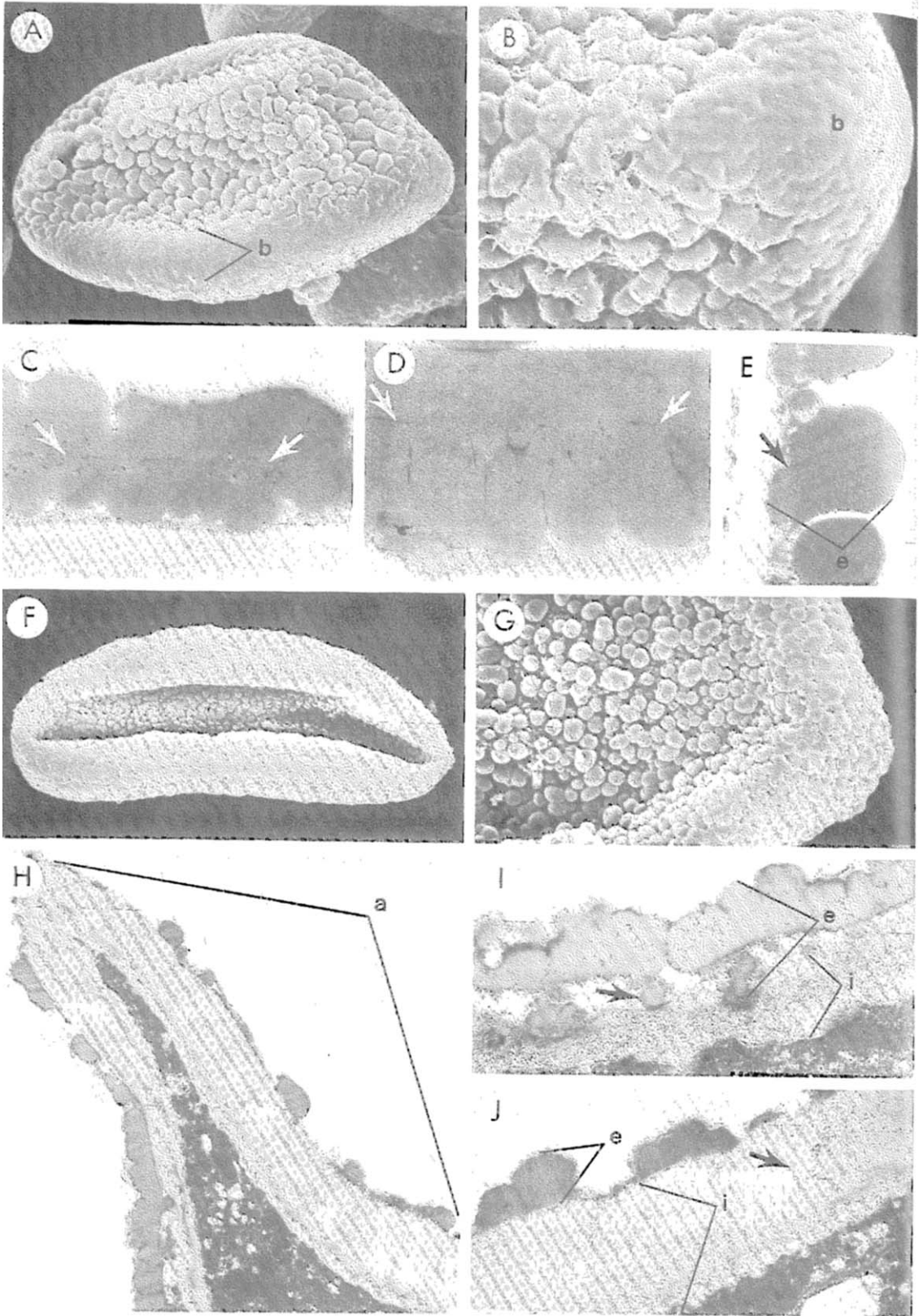


Fig. 4.

exine elements. Exine composed of laterally appressed to separated baculate elements (Fig. 6H); some exine elements occasionally 2-layered, the inner layer very thin (Fig. 6I). Intine of apertural and non-apertural walls indistinguishable, 2-layered, with radially oriented, electron transparent channel-like structures in the outer layer throughout (Fig. 6H).

Lachnanthes (monotypic)

L. caroliniana (Lam.) Dandy.—Grains monosulcate, heteropolar (Fig. 7A). Sculpturing of the non-apertural wall verrucate; that of the apertural wall gemmate (Fig. 7B). Tetrads of pollen from immature anthers decussate, with apertures positioned at the distal pole (Fig. 7C); thus, grains absolutely heteropolar. Exine of the non-apertural wall composed of laterally appressed, apparently fused baculate structural elements, the distal ends forming the verrucate sculpturing (Fig. 7D, E); exine elements homogeneous with commissure absent (Fig. 7D). Apertural wall of distinct psilate to gemmate exine elements atop a thick, 2-layered intine; a fibrillar material often (but not always) present between the exine elements (Fig. 7F). Outer intine layer thickened at interface of non-apertural and apertural walls (Fig. 7G), containing channel-like structures (Fig. 7F).

Fig. 4. A–E: *Barberetta aurea* Harv. (Haemodoraceae). (A) Whole pollen grain, aperture facing. Note smooth, micropore-pitted border (*b*) surrounding aperture. SEM $\times 2700$. (B) Close-up of proximal wall, showing large verrucae and smooth, micropore-pitted region at end of grain (*b*). SEM $\times 5600$. (C) Non-apertural, proximal wall; note 2-layered exine, with commissural line (arrows). TEM $\times 22800$. (D) Non-apertural wall of border region, showing 2-layered exine with commissural line (arrows). TEM $\times 21200$. (E) Apertural wall. Note junction (arrow) between two layers of exine elements (*e*). TEM $\times 13800$.

F–J: *Pyrrothiza neblinae* Maguire & Wurdack (Haemodoraceae) (F) Pollen grain, collapsed aperture facing. SEM $\times 2500$. (G) Close-up of wall, showing apertural (left) and non-apertural (right) walls. SEM $\times 6800$. (H) Interface between aperture (*a*) and non-apertural wall (lower right); note thickening of outer intine layer and reduction of inner exine layer. TEM $\times 8100$. (I) Non-apertural wall showing 2-layered intine (*i*) and 2-layered exine (*e*); scattered amorphous elements (arrow) make up the lower exine layer. TEM $\times 21400$. (J) Apertural wall; note scattered exine elements (*e*) and 2-layered intine (*i*) with channel-like structures in the outer layer (arrow). TEM $\times 20100$.

Tribe Conostylideae

Angiozanthos (1 of 10 species examined)

A. flavidus DC.—Pollen grains isopolar, usually diporate (Fig. 8A), rarely (in the same anther) triporate (Fig. 8C). Apertural wall protrusions hemispheric in shape (Fig. 8A, B). Non-apertural wall with a rugulate sculpturing; apertural wall psilate to slightly scabrate (Fig. 8B). Non-apertural exine composed of irregular, tangentially elongate structural elements (Fig. 8D, E); major tangential exine elements interconnected by thin, presumably exinous basal strands, demonstrated in acetolyzed grains (Fig. 8D). Inner exine layer composed of distinctive papillate protuberances (Fig. 8E, F), a line of breakage or a commissure often visible between papillate protuberances and the major structural elements (Fig. 8F). Apertural wall essentially free of exine, consisting of a thick, 3-layered fibrillar intine (Fig. 8G). Middle intine layer thickened in the interface region of the aperture and containing numerous, radially extended channel-like structures (Fig. 8G).

Macropidia (monotypic)

M. fuliginosa (Hook.) Druce.—Grains isopolar and diporate with hemispheric to obconical shaped apertural walls (Fig. 8H). Non-apertural walls rugulate; apertural walls psilate (Fig. 8I). Aperture wall lacking exine (Fig. 8J), consisting of a thick, 3-layered intine with prominent channel-like structures in the middle layer (Fig. 8K). Non-apertural exine composed of sinuous, tangentially elongate elements with papillate protuberances on the inner surface (Fig. 8L); commissure present between the outer exine and the inner protuberances, indicating a 2-layered nature to the wall (Fig. 8M).

Conostylis (1 of 24 species examined)

C. bealiana F. Muell.—Pollen grains isopolar, usually triangular and triporate; aperture walls hemispheric in shape (Fig. 9A). Aberrant 3-, 2-, or 4-aperturate grains occasionally present (Fig. 9C, D, E). Non-apertural walls rugulate; apertural walls psilate to scabrate (Fig. 9B). Non-apertural wall comprised of an exine of continuous, tangentially elongate elements with minute papillate protuberances on the inner face (Fig. 9G). Apertural wall without exine (Fig. 9I), composed of a relatively thick, obscurely layered intine, with radially oriented, channel-like structures (Fig. 9H).

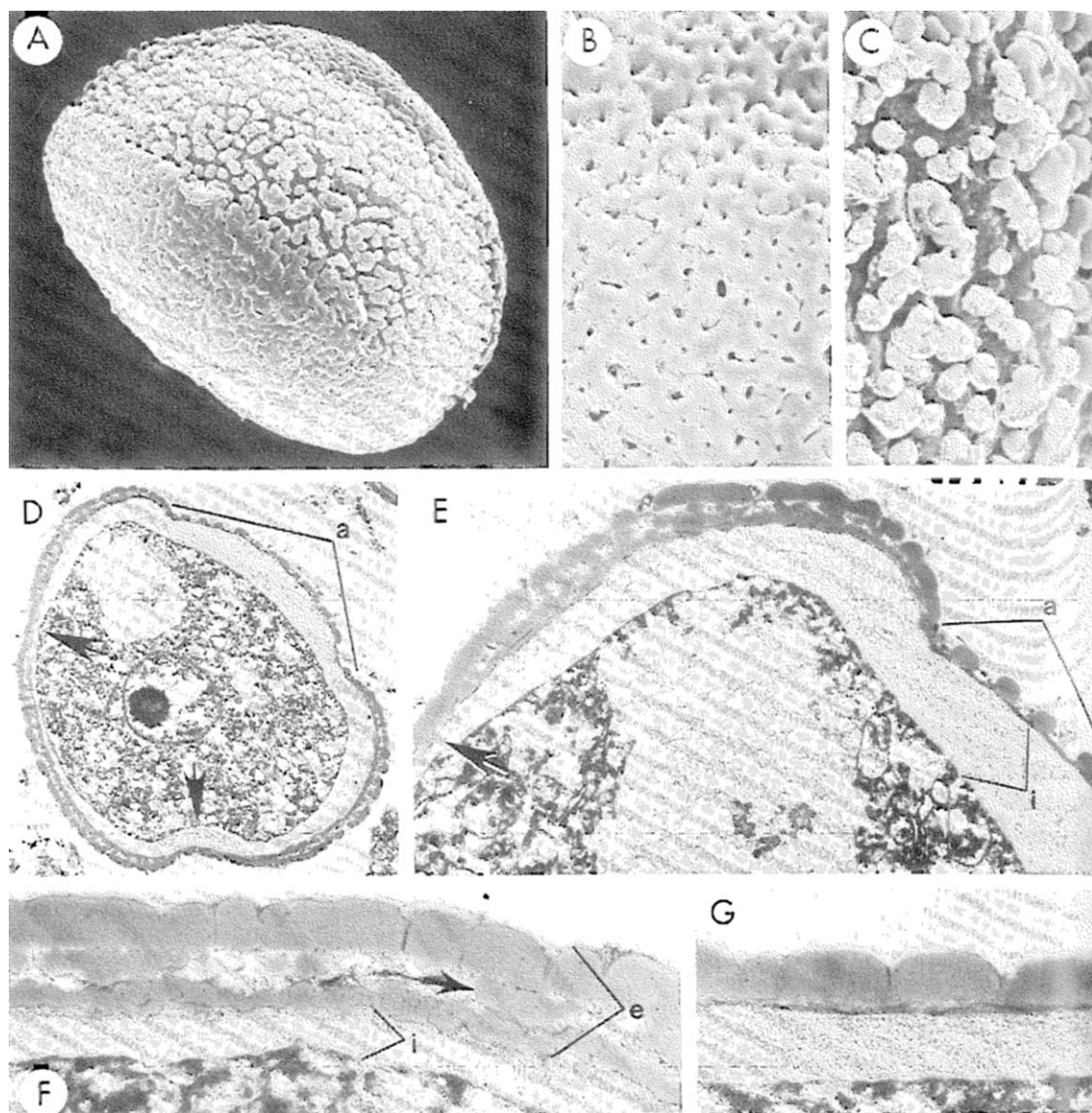


Fig. 5. *Schiekia orinocensis* (Kunth) Meisn. (Haemodorea). (A) Pollen grain, aperture at upper right. SEM $\times 3000$. (B) Non-apertural wall. SEM $\times 8700$. (C) Apertural wall, showing scattered exine elements. SEM $\times 8700$. (D) Cross-section of whole pollen grain, showing aperture (*a*); note two points of constriction (arrows) of the non-apertural wall. TEM $\times 2700$. (E) Interface between non-apertural wall (left) and aperture (*a*); note thick, relatively

homogeneous intine (*i*) of aperture and reduction of middle and lower exine layers of non-apertural wall at constriction region (arrow). TEM $\times 9500$. (F) Non-apertural wall, showing intine (*i*) and exine (*e*); note 3 layers of exine, with scattered, amorphous elements comprising the middle layer (arrow). TEM $\times 23000$. (G) Wall at region of constriction, composed of upper exine layer only. TEM $\times 23500$.

Blancoa (monotypic)

B. canescens Lindl.—Pollen grains diporate and isopolar with elongate, hemispheric to obconical shaped aperture walls (Fig. 9J); triporate grains rarely present in the same anther (Fig. 9L). Sculp-

turing of the non-apertural wall rugulate, that of the apertural wall somewhat scabrate (Fig. 9K). Apertural wall essentially devoid of exine, consisting of a thick, 3-layered intine, the middle layer expanded at the aperture interface (Fig. 9M). Non-apertural

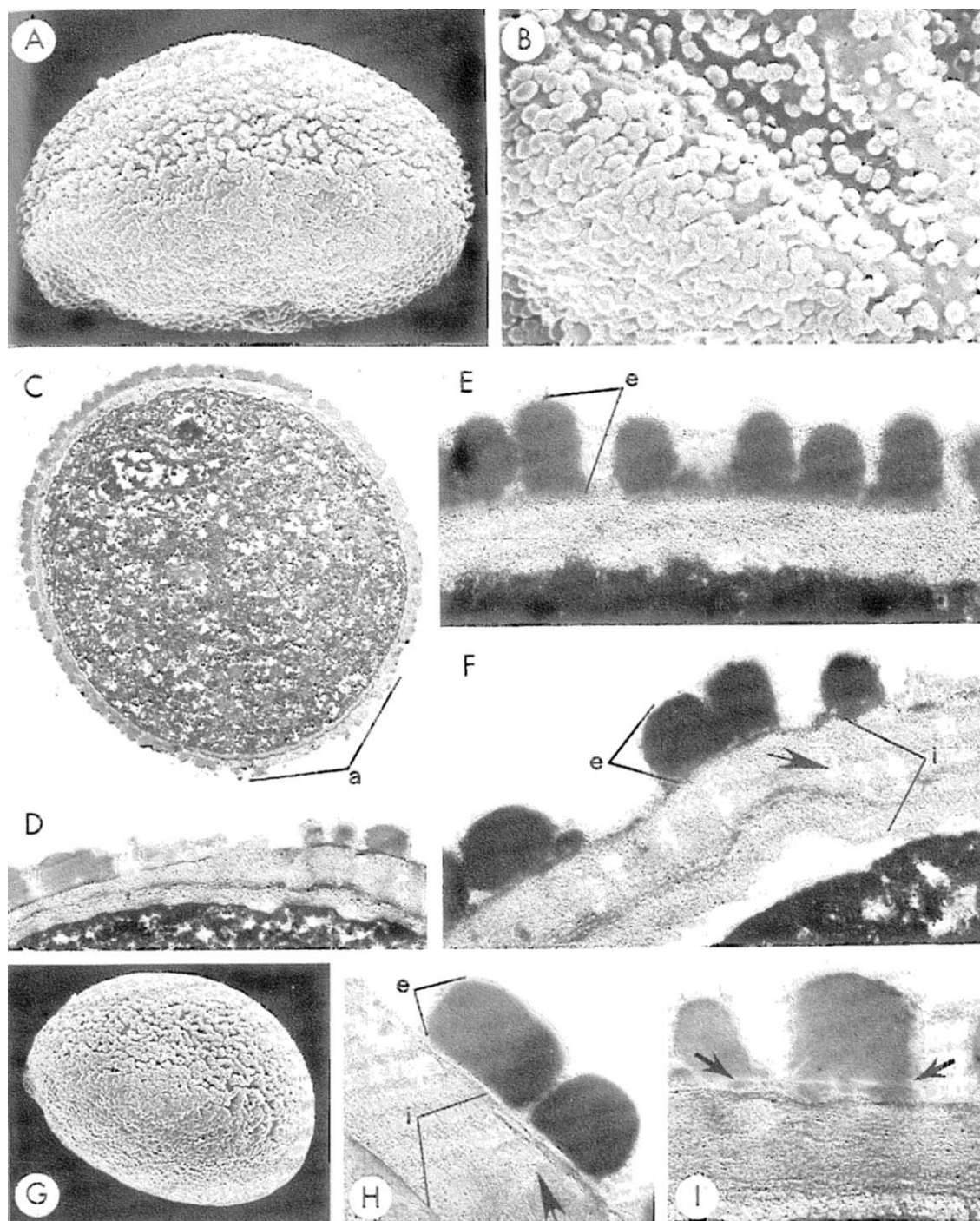


Fig. 6. *Haemodorum* (Haemodorea). **A–F:** *H. spicatum* R. Br. (A) Pollen grain, aperture above. SEM $\times 3600$. (B) Close-up of grain, showing non-apertural (lower left) and apertural (upper right) walls. SEM $\times 7900$. (C) Cross-section of whole grain; note apertural region (a). TEM $\times 4200$. (D) Interface between non-apertural (left) and apertural wall (right), showing thickening of outer intine wall at the aperture. TEM $\times 18400$. (E) Non-apertural wall, showing 1-layered exine (e). TEM $\times 38100$. (F) Apertural wall: note exine elements (e) and 2-layered

intine (i) with channel-like structures in outer layer (arrow). TEM $\times 37100$.

G–I: *H. simplex* Lindl. (G) Whole pollen grain; note indistinct aperture region (above). SEM $\times 1600$. (H) Pollen grain wall, showing exine elements (e) and 2-layered intine (i); channel-like structures (arrow) occur in the outer intine layer. TEM $\times 32400$. (I) Pollen grain wall, showing occasional 2-layered exine, with commissural line (arrows). TEM $\times 41400$.

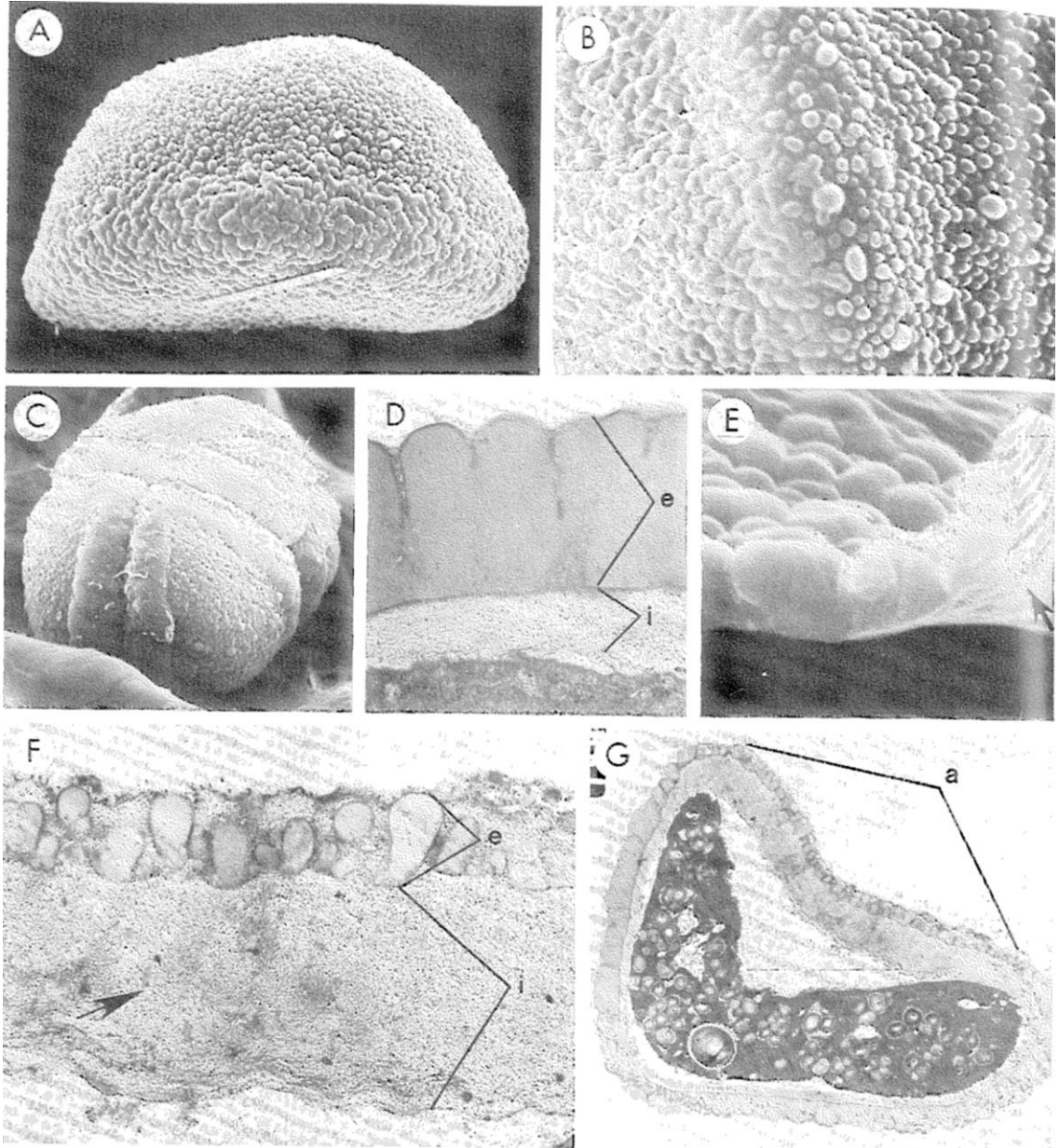


Fig. 7. *Lachnanthes caroliniana* (Lam.) Dandy (Haemodorea). (A) Pollen grain, aperture above; note raphide crystal. SEM $\times 2500$. (B) Close-up of wall, with verrucate non-apertural wall (left) and gemmate apertural wall (right). SEM $\times 5200$. (C) Pollen tetrad, showing decussate arrangement of microspores and distal orientation of apertures. SEM $\times 1300$. (D) Non-apertural wall; note intine (*i*) and 1-layered exine (*e*). TEM $\times 31600$. (E) Acetolyzed non-apertural exine; note laterally appressed

baculate elements and apparent micropore channel openings at inner surface (arrow). SEM $\times 22300$. (F) Aperture wall; note 2-layered intine (*i*), exine elements (*e*), and fibrillar deposit between exine elements; outer intine layer contains apparent channel-like structures (arrow). TEM $\times 23000$. (G) Cross-section of whole grain. Note aperture (*a*), with greatly thickened outer intine layer. TEM $\times 4400$.

wall composed of a thin intine and a continuous, 2-layered exine, a commissural line evident between the outer homogeneous and inner papillate exine layers (Fig. 9 N).

Tribonanthes (1 of 3 species examined)

T. australis Endl.—Pollen apolar, globose with 7–8 porate apertures (Fig. 10 A). Non-apertural wall sculpturing rugulate, that of the apertural wall irregular (Fig. 10 B). Exine of the non-apertural wall 2-layered, a commissure occurring between the continuous outer layer and the inner layer of discontinuous, generally papillate elements (Fig. 10 D). Intine of the non-apertural wall 2-layered, the inner layer thicker (Fig. 10 C, D). Apertural wall composed of closely spaced verrucate exinous elements atop a thick 2-layered intine (Fig. 10 E). Outer apertural intine layer contiguous with that of the non-apertural wall (Fig. 10 C) and greatly thickened in the aperture region (Fig. 10 C, E), containing prominent, radially-oriented, channel-like structures (Fig. 10 E).

Phlebocarya (1 of 3 species examined)

P. ciliata R. Br.—Pollen grains cylindrical, diporate, and isopolar; sculpturing of non-apertural and apertural walls rugulate (Fig. 10 F). Exine of non-apertural wall composed of two equally thick layers, a prominent commissural face occurring at the junction of the layers (Fig. 10 H). Toward the aperture, lower exine layer gradually reduced to thinner, distinct, papillate structures (Fig. 10 I). Apertural wall composed of a thick, 3-layered intine, with channel-like structures apparent in the middle layer (Fig. 10 G); scattered exine elements present outside apertural intine wall (Fig. 10 G).

Additional taxa

Lanaria (monotypic)

L. lanata (L.) Dur. & Schinz.—Grains monosulcate and heteropolar (Fig. 11 A) with a foveolate non-apertural wall and a psilate apertural wall (Fig. 1 B). Non-apertural wall exine tectate-columellate tectate-perforate with a thick foot-layer, a commissural junction present at the center of the columellae (Fig. 11 C). Non-apertural intine thin, 2-layered (Fig. 11 C). Apertural wall composed of a thick, 3-layered intine (Fig. 11 E). Middle intine layer thickened at junction of aperture and non-

apertural walls (Fig. 11 D), containing irregular, sinuous, channel-like structures (Fig. 11 E).

Lophiola (monotypic)

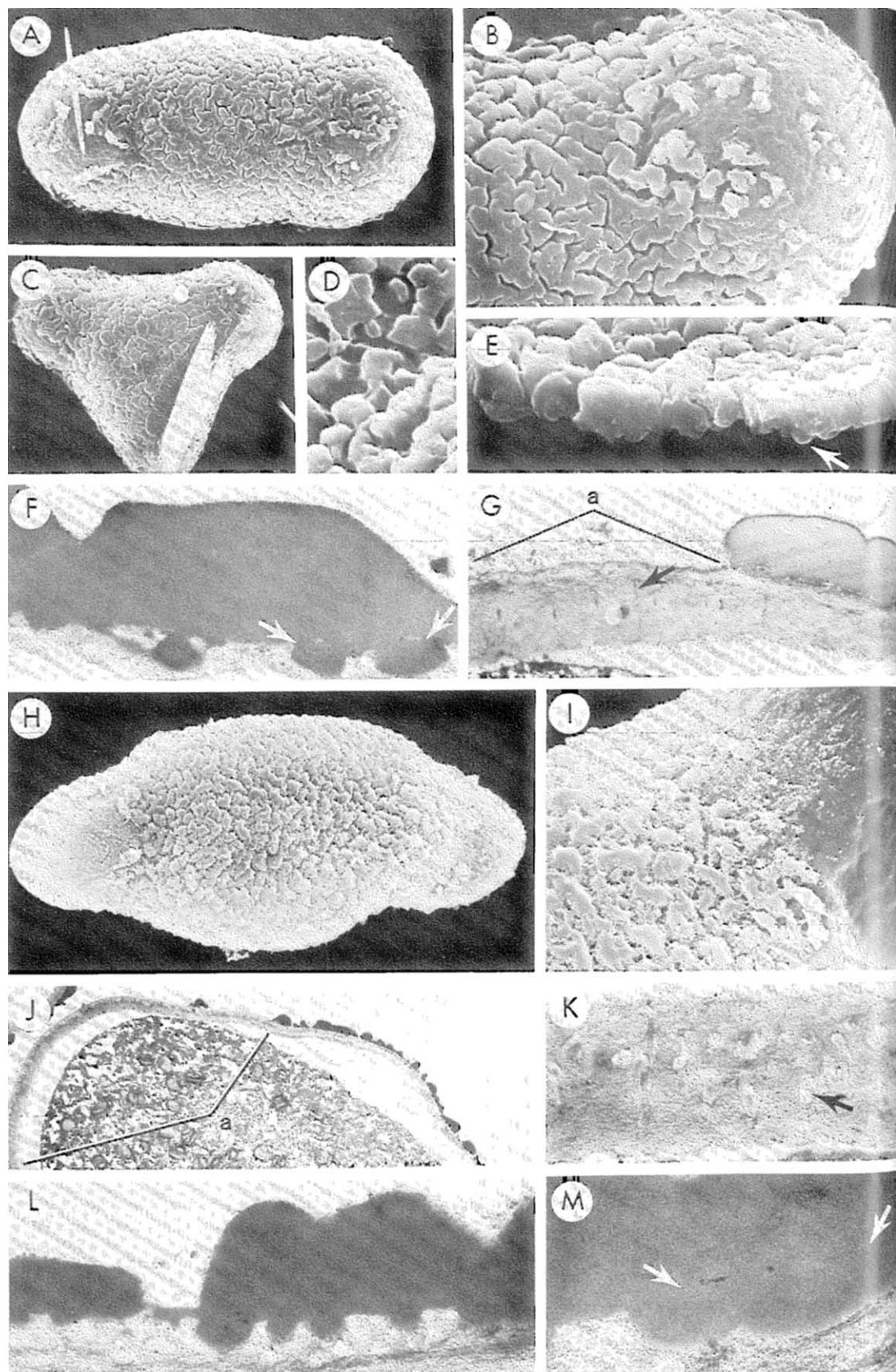
L. aurea Ker-Gawler.—Grains monosulcate and heteropolar (Fig. 12 A). Non-apertural wall re-

Fig. 8. A–G: *Anigozanthos flavidus* D.C. (Conostylidae). (A) Pollen grain, showing two hemispheric apertural walls and attached raphide crystal. SEM $\times 1200$. (B) Close-up of wall; note rugulate sculpturing of non-apertural wall (left) and paucity of exine on aperture (right). SEM $\times 2600$. (C) Rare, 3-porate grain; note raphides. SEM $\times 900$. (D) Acetolyzed non-apertural wall, showing basal exine material interconnecting major exine elements. SEM $\times 5000$. (E) Cross-section of acetolyzed non-apertural wall, showing three-dimensional structure; note papillate protuberances (arrow) on inner surface of wall. SEM $\times 8000$. (F) Non-apertural wall, showing exine with inner papillate elements and commissural line (arrows). TEM $\times 22700$. (G) Interface between aperture (a) and non-apertural wall (right); note exine-less, 3-layered apertural intine, with a thickened middle layer containing channel-like structures (arrow). TEM $\times 13000$.

H–M: *Macropidia fuliginosa* (Hook.) Druce (Conostylidae). (H) Pollen grain; note two pores. SEM $\times 1200$. (I) Close-up of wall; note rugulate sculpturing of non-apertural wall (lower left) and exine-less apertural wall (upper right). SEM $\times 3200$. (J) Longitudinal-section of grain, showing aperture wall (a), devoid of exine. TEM $\times 1300$. (K) Apertural wall, 3-layered; note extensive channel-like structures of middle layer (arrow). TEM $\times 21100$. (L) Non-apertural wall; note characteristic papillate elements of inner exine layer. TEM $\times 28600$. (M) Close-up of non-apertural wall, showing 2-layered exine with a commissure (arrows) between the layers. TEM $\times 58700$.

Fig. 9. A–I: *Conostylis bealiana* F. Muell. (Conostylidae). (A) Pollen grain, showing 3 hemispheric pores, devoid of exine; note raphide crystals. SEM $\times 1600$. (B) Close-up of wall; note rugulate sculpturing of non-apertural wall (upper left). SEM $\times 3100$. (C) Rare 4-porate grain. SEM $\times 900$. (D) Rare 2-porate grain. SEM $\times 1000$. (E) Aberrant 3-porate grain. SEM $\times 900$. (F) Slightly oblique section of whole grain, showing 3-apertures (a), which are devoid of exine. TEM $\times 1600$. (G) Non-apertural wall; note papillate protuberances on inner surface of exine (arrows). TEM $\times 16200$. (H) Fibrillar apertural wall, showing channel-like structures (arrow). TEM $\times 19500$. (I) Interface between aperture (a) and non-apertural wall (right). TEM $\times 10400$.

J–N: *Blancoa canescens* Lindl. (Conostylidae). (J) Pollen grain; note two hemispheric apertures. SEM $\times 1700$. (K) Close-up of wall, showing rugulate non-apertural wall (right) and exine-less aperture (left). SEM $\times 2900$. (L) Rare 3-porate grain. SEM $\times 1200$. (M) Interface between aperture (a) and non-apertural wall (right). TEM $\times 9300$. (N) Non-apertural wall; note papillate protuberances of inner exine; commissural line (arrows) is faintly visible. TEM $\times 62100$.



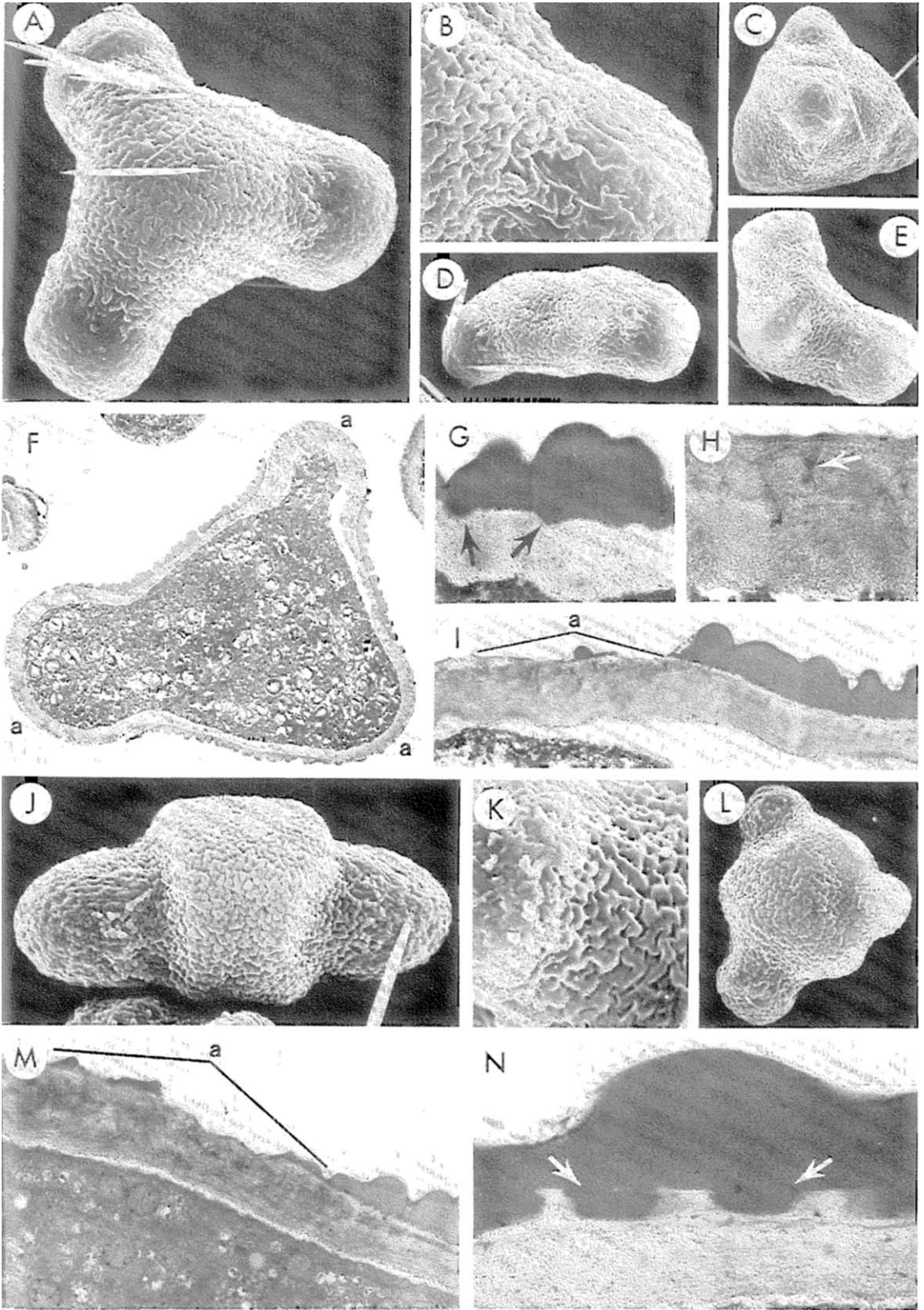


fig. 9

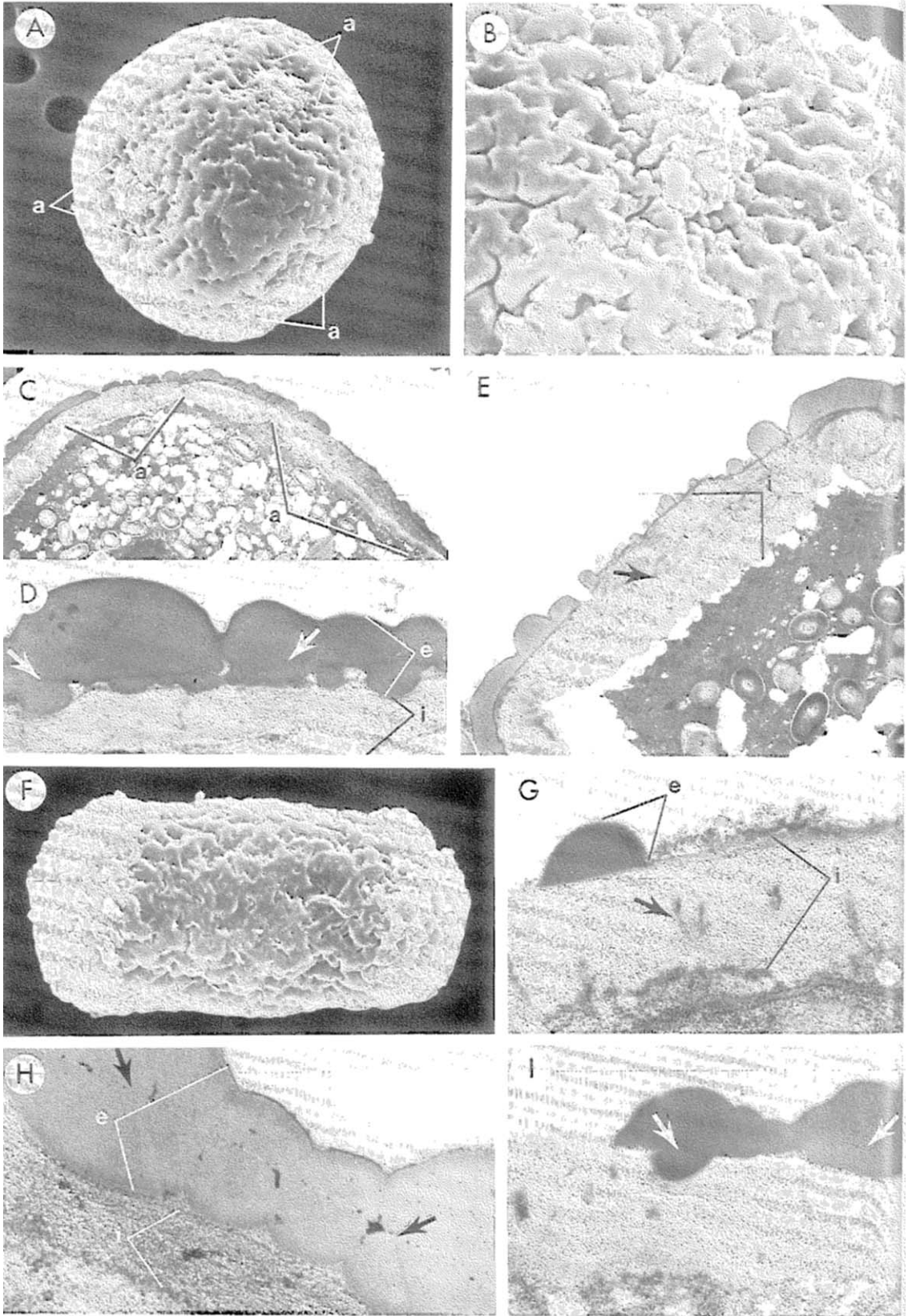


Fig. 10

ticulate; apertural wall scabrate to shallowly ridged (Fig. 12B). Non-apertural wall composed of a tectate-columellate (semitectate) exine with a thick foot-layer and a relatively thin, 2-layered intine (Fig. 12C). Apertural wall exineless, consisting of a thick, 3-layered intine (Fig. 12C). Distinctive radially oriented, electron dense regions present in the middle intine layer, these regions usually corresponding to a papilla or ridge of the aperture (Fig. 12D).

Pauridia (1 of 2 species examined)

P. minuta (L.f.) Dur. & Schinz.—Pollen grains discolpate and heteropolar (Fig. 12E, G, H). Sculpturing of the non-apertural wall foveolate, with minute supracteal papillae (Fig. 12F). Apertural sculpturing verrucate (Fig. 12E, F, H). Non-apertural exine tectate-columellate (tectate-perforate) with a thin, electron-dense, apparently endexinous basal layer; ektexinous foot-layer absent (Fig. 12I). Apertural wall with scattered exinous verrucae atop a thick, 2-layered intine (Fig. 12J).

DISCUSSION

Palynological characteristics

Ultrastructural features of the pollen wall provide excellent characters for noting similarities and discontinuities between genera and tribes of the Haemodoraceae. The Haemodoraceae (sensu

Hutchinson 1973) as a whole, with the exception of *Lanaria* and *Lophiola*, is palynologically united by the absence of a typical tectate-columellate architecture. Even *Schiekia*, which has a 3-layered exine, does not have columellae, possessing instead a discontinuous, amorphous, granular middle layer. Furthermore, in all six genera of the tribe Conostylideae and in four genera of the tribe Haemodoreae, the non-apertural exine lacks a foot-layer and is 2-layered, the difference between genera being primarily in the thickness and continuity of the lower exine layer. The remaining four genera of the Haemodoreae are linked to the 2-layered members of that tribe by a gradation in exine wall structure (Fig. 13). Thus, the occurrence of a common pollen wall architecture in the tribes Conostylideae and Haemodoreae (excluding *Lanaria* and *Lophiola*) argues strongly for their close relationship and the monophyly of the family, sensu Hutchinson (1973). In contrast to the Haemodoraceae, all 7 genera of the Tecophilaeaceae (sensu Hutchinson 1973) possess a characteristic tectate-columellate wall stratification with a continuous, ektexinous foot-layer (Simpson 1981*b*, work in progress). The taxonomic treatment by Melchior (1964), which classified the Tecophilaeaceae as the tribe Conanthereae of the Haemodoraceae, is not supported based on evidence from the present study.

A distinctive commissural plane delimits the exine layers in the ten genera of the Haemodoraceae with 2-layered exine walls. Although the commissure almost always appears to be a real boundary between layers, it may in some cases represent a region of structural weakness (and therefore breakage during sectioning). In either case, a structural distinction can be made between outer and inner exine layers in these taxa. However, no difference in staining properties and no endexine/ektexine differentiation can be observed between the two exine layers. Preliminary studies by the author using brightfield and fluorescence microscopy staining techniques indicate that both exine layers in these genera have an ektexinous chemical reaction. Further studies by the author are planned to determine the exact chemical nature and ontogeny of the exine in "2-layered" taxa of the Haemodoraceae.

Members of the Haemodoraceae also possess a common intine wall structure. Non-apertural intines characteristically have 2-layers, which are distinguished based on differences in staining pro-

Fig. 10. A–E: *Tribonanthes australis* Endl. (Conostylideae). (A) Whole grain, showing three visible apertures (*a*). SEM $\times 1900$. (B) Close-up, showing rugulate non-apertural wall and aperture with irregular exine elements. SEM $\times 5200$. (C) Section of pollen grain, showing two apertures (*a*). TEM $\times 2400$. (D) Non-apertural wall, showing 2-layered intine (*i*) and 2-layered exine (*e*); a commissural line (arrows) occurs between the 2 exine layers; note papillate protuberances of inner exine layer. TEM $\times 19600$. (E) Apertural wall, showing thick intine (*i*) and outer, scattered exine elements; note thickening of outer intine layer, which contains numerous channel-like structures (arrow). TEM $\times 5500$.

F–I: *Phlebocarya ciliata* R. Br. (Conostylideae). (F) Whole pollen grain; note 2-porate apertures at ends of grain. SEM $\times 2300$. (G) Aperture wall, with thick intine (*i*) and occasional exine elements (*e*); note channel-like structures (arrow) of intine. TEM $\times 22000$. (H) Non-apertural wall, showing intine (*i*) and 2-layered exine (*e*); a commissural line (arrows) occurs between the two exine layers. TEM $\times 45800$. (I) Region of aperture border; note papillate protuberances of inner exine layer and commissure (arrows). TEM $\times 21400$.

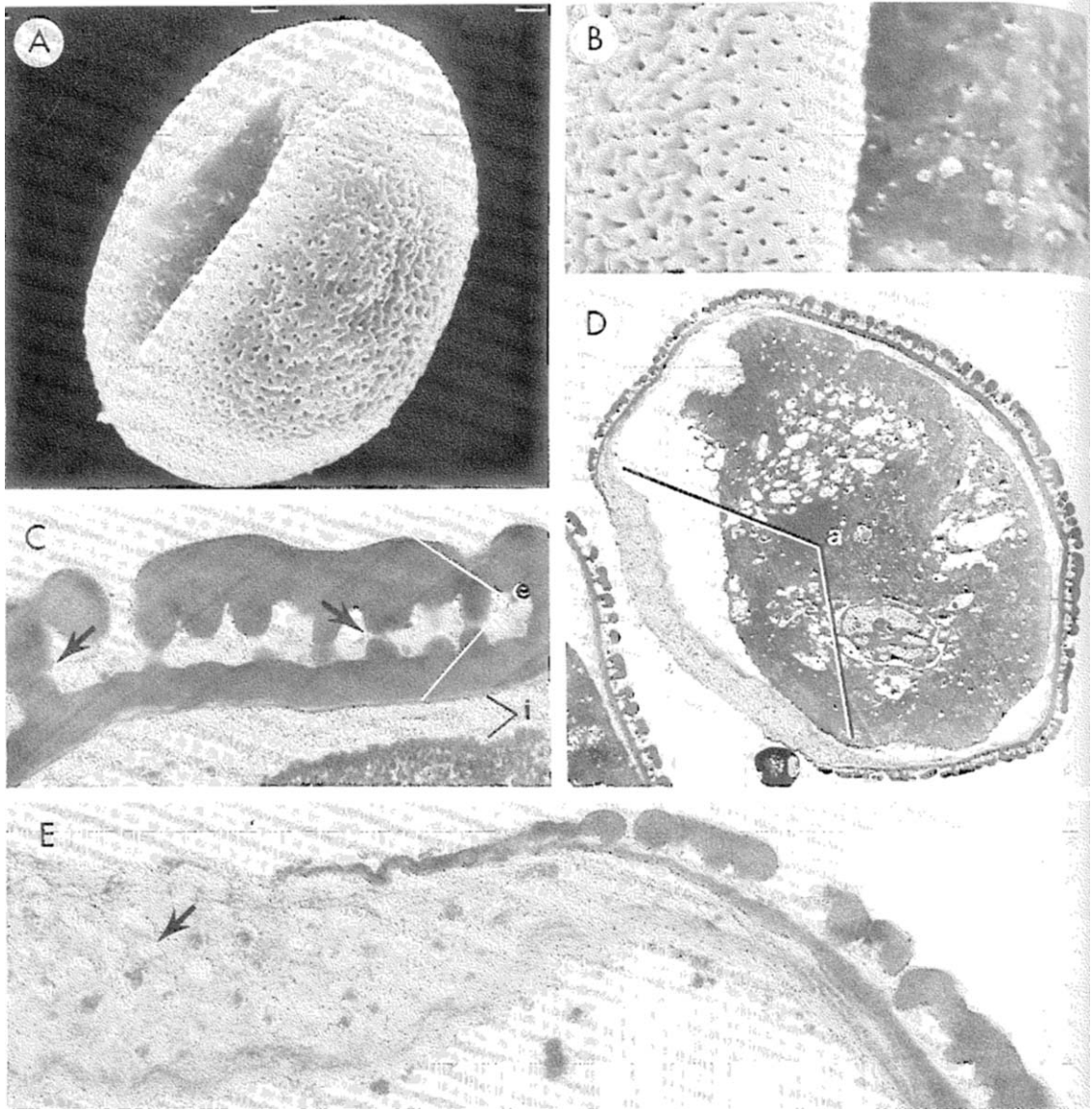


Fig. 11. *Lanaria lanata* (L.) Dur. & Schinz. (A) Whole pollen grain, aperture at left. SEM $\times 4000$. (B) Close-up of wall, showing foveolate non-apertural wall (left) and psilate aperture wall (right). SEM $\times 8100$. (C) Non-apertural wall, showing 2-layered intine (*i*) and tectate-columellate exine (*e*); note commissural line at middle of colu-

mellae (arrows). TEM $\times 24100$. (D) Longitudinal-section of pollen grain; note aperture (*a*), devoid of exine. TEM $\times 3500$. (E) Interface between apertural (left) and non-apertural wall (right); note 3-layered intine of aperture with numerous, sinuous, channel-like structures (arrow). TEM $\times 21500$.

properties or fibrillar structure. Initial chemical investigations of some members of the Haemodoraceae indicate that the inner layer is primarily cellulosic and the outer composed of pectic compounds, as has been found for numerous angiosperms, both monocots and dicots (Kress & Stone

1982). Progressing from the non-apertural to the apertural wall, the outer intine layer becomes substantially thickened and is traversed with narrow, radially oriented channel-like structures. *Lophiola* lacks these channel-like structures, possessing instead curious undulating, electron dense regions

in the apertural intine. In some taxa, mainly of the tribe Conostylideae, there is an additional thin, rather ill-defined layer of the apertural intine external to the other two intine layers.

The tribes Haemodoreae and Conostylideae can be differentiated based on pollen characters. As originally noted by Erdtman (1966), members of the Haemodoreae have monosulcate, heteropolar grains while those of the Conostylideae have 2 or more porate, isopolar, subisopolar, or apolar grains. This trend, supported by Radulescu (1973) for *Schiekia*, is here confirmed for *Barberetta*, *Macropidia* and *Pyrrothiza* (Table 1). (It should be noted that only in *Lachnanthes* is pollen polarity absolutely determined, based on observations of tetrads in the present study.) The only ultrastructural character which diagnostically separates the two tribes is sculpturing. In the Haemodoreae non-apertural walls are verrucate, except for *Schiekia* which is somewhat foveolate-fossulate. In contrast, all members of the Conostylideae have a characteristic rugulate non-apertural wall sculpturing (Table 1). Additionally, all members of the Haemodoreae have exine as a component of the apertural wall, whereas in most members of the Conostylideae, apertural exine is lacking.

Within the tribe Haemodoreae four basic types of wall structures can be distinguished (Table 1). Four genera of the tribe, *Barberetta*, *Dilatris*, *Wachendorfia*, and *Xiphidium*, possess a distinctive 2-layered exine, evident by the presence of a commissural "line" in electron micrographs. Further similarities can be noted between *Wachendorfia* and *Xiphidium*, which both have a partially granular lower exine layer, and between *Barberetta* and *Wachendorfia*, which have a similar proximal wall sculpturing and identical psilate, micropore-pitted apertural borders (differing from the smooth, perforated border of *Dilatris corymbosa*). A second wall structure type of the tribe occurs in *Haemodorum* and *Lachnanthes*. These two genera possess an exine composed of laterally appressed, basally fused, baculate structural elements. These elements are not 2-layered, except very rarely in isolated portions of the pollen wall of *H. simplex*; the occasional presence of this thin, inner exine layer in *H. simplex* may be evidence of a structural homology with 2-layered members of the family. Thus, the wall structure of *Haemodorum* and *Lachnanthes* may be homologous with the upper exine layer of the 2-layered members of the tribe (Fig. 13). *Pyr-*

rorhiza has a third type of wall architecture, possessing a 2-layered exine, the inner layer being discontinuous, amorphous, and somewhat granular. Finally, a fourth type is present in *Schiekia*, which has a 3-layered exine, the middle layer of which resembles the inner exine layer in *Pyrrothiza*.

Unlike that of other members of the tribe, the exine sculpturing of *Schiekia* is foveolate-fossulate, resembling that of tectate-columellate taxa, such as *Lanaria* of the Haemodoraceae (present study) or *Cyanella* and *Odontostomum* of the Tecophilaeaceae (Simpson 1981b). In fact, the three exine layers of *Schiekia* show resemblances to a typical foot-layer, columellae, and tectum and may represent an evolutionary modification from the typical tectate-columellate architecture. The wall of *Schiekia* differs, however, in that the middle exine layer is structurally discontinuous with the inner and outer layers and is amorphous, not columnar, in shape. *Pyrrothiza*, which has a verrucate sculpturing and lacks a third, inner exine layer, is somewhat intermediate between *Schiekia* and 2-layered members of the Haemodoreae. Thus, a structural gradation can be hypothesized between *Schiekia*, *Pyrrothiza*, and the 2-layered members of the tribe Haemodoreae (Fig. 13). It should be pointed out, however, that suggestions of an evolutionary gradation in pollen wall structure presupposes the monophyly of the Haemodoraceae. Such a gradation can only be substantiated based on comparative analyses with other taxa using a wide range of characters.

Subgroups of pollen morphologies can be noted in the tribe Conostylideae. Four genera of the tribe, *Angiozanthos*, *Blancoa*, *Conostylis*, and *Macropidia*, are very similar in having relatively smooth, hemispheric to obconical aperture wall protrusions. *Conostylis* has 3-porate, triangular grains, while the other three genera have 2-porate, fusiform pollen grains. However, the fact that occasional 2- or 4-porate grains are found in *Conostylis* and 3-porate grains in *Anigozanthos* is indicative of an intergradation of pollen morphology between these genera. (SEM observations of pollen from several other species of both *Anigozanthos* and *Conostylis* indicate morphologies very similar to the species described here; palynological studies may prove useful in resolving relationships of species complexes within the two genera). *Phlebocarya* differs in the tribe in having cylindrical pollen grains with two circular, flattened aperture walls. *Tribonanthes*

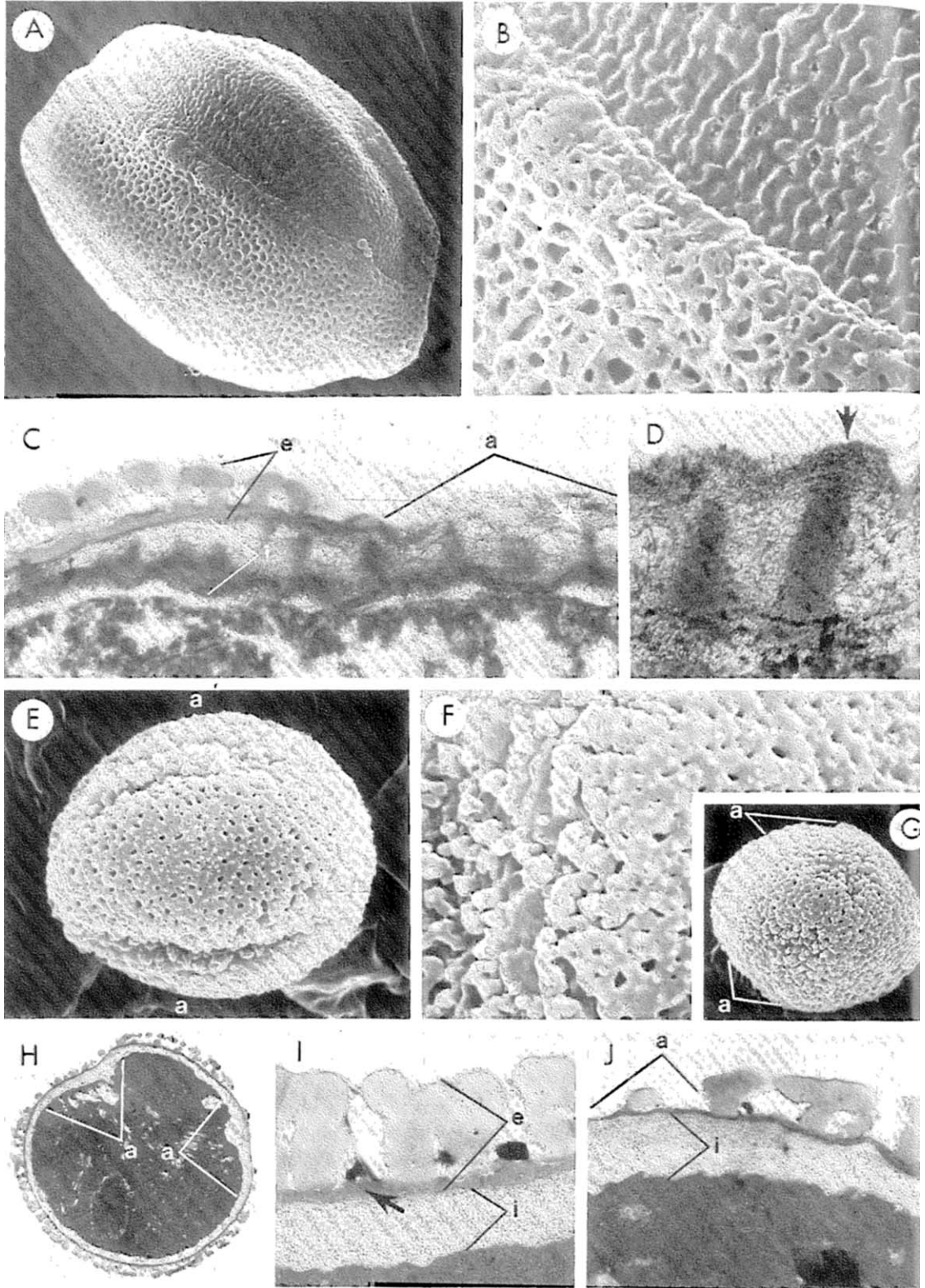


Fig. 12

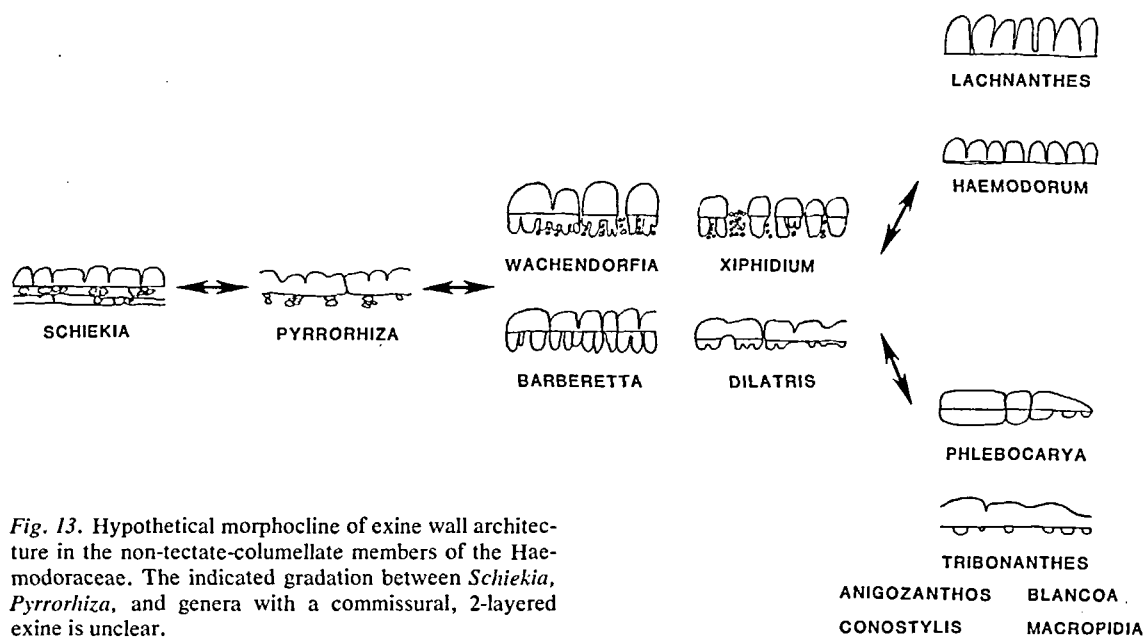


Fig. 13. Hypothetical morphocline of exine wall architecture in the non-TECTATE-COLUMELLATE members of the Haemodoraceae. The indicated gradation between *Schiekia*, *Pyrrorhiza*, and genera with a commissural, 2-layered exine is unclear.

is unique in the whole family in possessing spherical pollen with 7–8 pores.

All genera of the Conostylideae have a 2-layered exine, the lower layer being composed of discontinuous papillate elements (a 2-layered exine was not observed in *Conostylis*; however, perhaps be-

cause of the small size of the inner exine papillae). A gradation is evident between the exine structure in the Conostylideae and the 2-layered wall structure of four genera of the Haemodoreae. *Phlebocarya* especially corroborates this gradation in having a thick, continuous inner exine (resembling that of 2-layered members of the Haemodoreae), which, in the aperture region, becomes thin, discontinuous and papillate (resembling the exine of the rest of the Conostylideae) (Fig. 13).

Taxonomic implications

The taxonomic position of *Phlebocarya* is clarified with reference to pollen wall ultrastructure. *Phlebocarya* has been classified in either the tribe Conostylideae (Pax 1888, Pax & Hoffmann 1930) or Haemodoreae (Bentham & Hooker 1883, Hutchinson 1973, Geerinck 1969). However, the pollen of *Phlebocarya* has at least three structural features shared only with genera of the tribe Conostylideae: (1) grains with 2 or more porate apertures (2) rugulate sculpturing (3) a papillate inner exine layer (found only near the aperture in *Phlebocarya*). It is proposed that these are shared derived characters and that the classification of *Phlebocarya* in the tribe Conostylideae, as done only by Pax (1888) and Pax & Hoffmann (1930), is supported. The placement of the genus in the tribe Haemodoreae has been based primarily on the common occurrence of an im-

Fig. 12. A–D: *Lophiola aurea* Ker.-Gawler. (A) Monosulcate pollen grain, aperture at upper right. SEM $\times 4000$. (B) Close-up of wall, showing reticulate non-apertural wall (lower left) and ridged aperture wall (upper right); note apparent “fusion” of exine elements at aperture border. SEM $\times 15200$. (C) Interface between apertural (*a*) and non-apertural (left) wall; note tectate-columellate non-apertural exine (*e*) and 3-layered intine (*i*); middle intine layer is expanded at aperture border and contains radially-oriented, electron dense regions (arrow). TEM $\times 32800$. (D) Aperture wall, showing general correspondence of electron dense regions with the ridged apertural wall sculpturing (arrow). TEM $\times 55700$.

E–J: *Pauridia minuta* (L.f.) Dur. & Schinz. (E) Pollen grain, apparent polar view, showing two sulcate apertures (*a*). SEM $\times 4000$. (F) Close-up of aperture (left) and non-apertural wall (right). SEM $\times 9400$. (G) Apparent equatorial view of pollen grain showing two apertures (*a*). SEM $\times 2700$. (H) Cross-section of grain; note two apertures (*a*) with outer exine elements, thickened intine, and plasmolyzed regions beneath. TEM $\times 2700$. (I) Non-apertural wall showing intine (*i*) and tectate-columellate exine (*e*); note thin, electron dense foot-layer (arrow). TEM $\times 33500$. (J) Interface between aperture (*a*) and non-apertural wall (right); note thick 2-layered intine (*i*). TEM $\times 20400$.

Table I. Pollen characters of the Haemodoraceae

Apo. = apolar; Circ. = circular; Fov. = foveolate; Foss. = fossulate; Hemisph. = hemispheric; Het. = heteropolar; Iso. = isopolar; Pap. = papillate; Por. = porate; Psil. = psilate; Retic. = reticulate; Rugul. = rugulate; Sulc. = sulcate; Verr. = verrucate. * *Lachnanthes* is known to be absolutely heteropolar; polarity in all other genera is assumed

	Aperture					Non-apertural wall	
	No.	Type	Shape	Polarity	Exine	Sculpturing	Exine stratification
Tribe Haemodoreae							
<i>Barberetta</i>	1	Sulc.	Furrow	Het.	+	Verr./Psil.	2-layered, inner baculate
<i>Dilatris</i>	1	Sulc.	Furrow	Het.	+	Verr.	2-layered, inner baculate-papillate
<i>Haemodorum</i>	1	Sulc.	Furrow	Het.	+	Verr.	1-layered
<i>Lachnanthes</i>	1	Sulc.	Furrow	Het.*	+	Verr.	1-layered
<i>Pyrrorhiza</i>	1	Sulc.	Furrow	Het.	+	Verr.	2-layered, middle amorphous
<i>Schiekia</i>	1	Sulc.	Furrow	Het.	+	Fov.-Foss.	3-layered, middle amorphous
<i>Xiphidium</i>	1	Sulc.	Furrow	Het.	+	Verr.	2-layered, inner baculate-granular
<i>Wachendorfia</i>	1	Sulc.	Hemisph.	Het.	+	Verr./Psil.	2-layered, inner granular
Tribe Conostylideae							
<i>Anigozanthos</i>	2 (3)	Por.	Hemisph.	Iso.	-	Rugul.	2-layered, inner papillate
<i>Blanca</i>	2	Por.	Hemisph.	Iso.	-	Rugul.	2-layered, inner papillate
<i>Conostylis</i>	3 (2, 4)	Por.	Hemisph.	Iso.	-	Rugul.	2-layered?, inner papillate
<i>Macropodia</i>	2	Por.	Hemisph.	Iso.	-	Rugul.	2-layered, inner papillate
<i>Phlebocarya</i>	2	Por.	Circ.	Iso.	+	Rugul.	2-layered, inner baculate-papillate
<i>Tribonanthes</i>	7-8	Por.	Circ.	Apo.	+	Rugul.	2-layered, inner papillate
<i>Lanaria</i>	1	Sulc.	Furrow	Het.	-	Fov.	Tectate-columellate, foot-layer thick
<i>Lophiola</i>	1	Sulc.	Furrow	Het.	-	Retic.	Tectate-columellate, foot-layer thick
<i>Pauridia</i>	2	Sulc.	Furrow	Het.	+	Fov./Pap.	Tectate-columellate, basal layer thin, endexinous

bricate perianth (Benthám & Hooker 1883, Hutchinson 1934, Geerinck 1969), which is almost certainly a primitive character for the group and should not be used in delimiting hypothesized monophyletic taxa (sensu Hennig 1966).

In contrast to all other members of the Haemodoraceae, *Lanaria* and *Lophiola* possess a tectate-columellate wall architecture, with a thick, continuous foot-layer (interestingly, however, the columellae of *Lanaria* often appear to be 2-layered). Apertural exine is absent in the two genera, whereas all genera of the similarly monosulcate Haemodoreae have a prominent cover of apertural exine elements. *Lanaria* and *Lophiola* are also aberrant within the family with respect to anatomy (Schulze 1893, Simpson & Dickison 1981), chemistry (Edwards et al. 1970), and embryology (De Vos 1963, Simpson 1981a). These data, applied to a cladistic analysis of the complex (Simpson, unpublished), argue strongly against the classification of the two genera in either the tribe Haemodoreae or Conostylideae. Erdtman (1966) proposed that *Lanaria* and *Lophiola* are palynologically more similar, in size and sculpturing, to the tribe Conanthereae (=

Tecophilaeaceae, sensu Hutchinson 1973), whose members have monosulcate grains with operculate sulci. The wall ultrastructure of the seven genera of the Tecophilaeaceae is, like *Lanaria* and *Lophiola*, tectate-columellate (Simpson 1981b, work in progress), thus seemingly supporting Erdtman's contention. However, other families presumed to be closely related to the Haemodoraceae (sensu Cronquist 1981, Dahlgren 1980, Hutchinson 1973, Takhtajan 1980, Thorne 1981) also possess a tectate-columellate pollen wall architecture similar to that of *Lanaria*, *Lophiola*, and the genera of the Tecophilaeaceae. The taxa investigated to date include *Barbacenia* of the Velloziaceae (Ayensu & Skvarla 1974), *Curculigo* & *Hypoxis* of the Hypoxidaceae; *Helmholtzia* & *Philydrella* of the Philydraceae; *Tacca* of the Taccaceae; and *Liriope* of the Liliaceae, tribe Ophiopogoneae (Simpson, work in progress). Although additional studies are needed, it is hypothesized here that the tectate-columellate wall structure is ancestral, based on outgroup comparison (Simpson, unpublished), for the complex as a whole, as it probably is for the angiosperms as a whole (Van Campo 1971). If this interpretation

is correct, the exine of members of the Haemodoraceae may conceivably represent the loss of a foot-layer from an ancestral tectate-columellate condition. Additionally, the common occurrence of a tectate-columellate wall in *Lanaria*, *Lophiola*, and members of the Tecophilaeaceae cannot provide evidence for their classification in one taxon. In fact, the operculate aperture of members of the Tecophilaeaceae is almost certainly, for that family, a shared derived character based on outgroup comparison (Simpson, unpublished). The absence of an operculum in *Lanaria* and *Lophiola* argues against their classification in the Tecophilaeaceae. However, whether *Lanaria* and *Lophiola* should be included within their own tribe of the Haemodoraceae or transferred (perhaps not together) to some other taxon will remain unclear until additional characters are found and comparative analyses with other families are made. Anatomical evidence has recently been presented which supports the classification of *Lophiola* in the Liliaceae, tribe Melanthioideae (Ambrose 1980).

The genus *Pauridia* is palynologically distinct from members of the Haemodoraceae. Although the pollen of *Pauridia* resembles that of *Lanaria* and *Lophiola* in having an apparent tectate-columellate exine stratification, it differs in having: (1) two apertures with a cover of apertural exine elements, (2) a supracteal papillate sculpturing, and (3) a very thin, apparently endexinous basal layer with ektexinous foot-layer absent. The observation in the present study of disulcate pollen in *Pauridia* confirms a similar report by Thompson (1979) but conflicts with Erdtman's (1966) description of the genus as monosulcate. Although Erdtman treated *Pauridia* within the tribe Haemodoreae, he did report resemblances in size and sculpturing between *Pauridia* and members of the Hypoxidaceae (sensu Hutchinson). Preliminary studies by the author indicate that two genera of the Hypoxidaceae, *Curculigo* and *Hypoxis*, are similar to *Pauridia* in having a tectate-columellate architecture. However, pollen grains of the former two genera differ from *Pauridia* in having a monosulcate aperture and in possessing a thicker, continuous, ektexinous foot-layer, similar to that of *Lanaria*, *Lophiola*, or members of the Tecophilaeaceae. In fact, the absence of a continuous ektexinous foot-layer in *Pauridia* indicates similarity to the 2-layered members of the tribe Haemodoreae. Although the placement of *Pauridia* in the Hypoxidaceae is supported based on embry-

ological (De Vos 1961) and anatomical (Schulze 1893) characters, no clear taxonomic conclusions can be drawn based on pollen wall architecture. Further palynological studies are needed to verify the taxonomic placement of *Pauridia* within the Hypoxidaceae.

Comparisons with past studies

Clarifications regarding the three pollen groups in the Haemodoraceae recognized by Erdtman (1966) can be made with reference to the present ultrastructural study. Erdtman's description of wall structure in six genera of the tribe Haemodoreae as "not very distinct" is probably a reflection of the atectate architecture found in all members of that tribe. The characteristic LO-pattern he observed for five genera of the Conostylideae can be explained ultrastructurally. The "dark islands... separated by brighter channels" probably correspond to the rugulae separated by fissures in the wall. Also, the "fainter darker dots = bacula" almost certainly correspond to the papillate protuberances of the inner exine layer characteristic of the tribe. Finally, the reticulate exine wall of *Lanaria* and *Lophiola* corresponds with a tectate-columellate architecture as seen with the electron microscope.

Erdtman's (1966: 199) description of a "coarsely granular, distinctly convex operculum" in *Wachendorfia* is incorrect. This is not an operculum, but simply an aperture wall with an outer layer of closely spaced exine structural elements. Radulescu's (1973) description of granules or verrucae on the apertures of *Dilatris* and *Schiekia* corresponds to these exine elements. Similar aperture walls are found in all other genera of the tribe Haemodoreae; the apertures often disintegrate during acetolysis, probably because of the lack of continuous exine material between the elements. The use of the term reticulate by Radulescu (1973) for the sculpturing of *Conostylis* and *Dilatris* is in disagreement with Erdtman (1966) and the present study. Radulescu's report of a pilate-tegillate wall structure in *Conostylis* and a tegillate-baculate exine for *Dilatris* and *Schiekia* inadequately describe the major structural elements observed here.

CONCLUSIONS

Observations of pollen ultrastructure are useful in characterizing and delimiting the Haemodoraceae,

family tribes, and groups of genera within tribes. Suggestions regarding the classification of family taxa and the intergradation of wall types have been made based on these pollen characters. Of especial interest in this study is the general occurrence in the family of a 2-layered exine wall lacking a foot-layer. Based on comparisons with taxa of several other, presumably closely related families, it is proposed that the exine structure of the Haemodoraceae is derived and the tectate-columellate architecture is probably primitive for the complex. However, comparative analyses, such as cladistic techniques, using all known characters should be made to test hypotheses regarding homology and character polarity. The pollen of many more monocotyledonous taxa need to be studied before broad taxonomic comparisons can be noted. The additional families of the Haemodiales, sensu Hutchinson (1973) and Dahlgren (1980), are under current investigation by the author.

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