COMPARATIVE POLLEN MORPHOLOGY AND ITS RELATIONSHIP TO PHYLOGENY OF POLLEN IN THE HAMAMELIDAE[1]

MICHAEL S. ZAVADA[2,3] AND DAVID L. DILCHER[2]

ABSTRACT

Data on pollen morphological features from 200 species in 20 families commonly included in the Hamamelidae and particular species in the Anacardiaceae and Salicaceae are presented in this paper. The basic descriptive analyses presented are derived from observations by light microscopy, scanning electron microscopy (SEM), and transmission electron microscopy (TEM). Thirty pollen characters showed some variability, and each of the species was scored for these characters. These data were analyzed and similarity cluster analyses were generated. Both an unweighted pair group and a complete linkage strategy dendrogram were produced. Three major clusters of families were defined, based on these analyses. Group I consists of Trochodendraceae, Cercidiphyllaceae, Eupteleaceae, Platanaceae, Hamamelidaceae (including Altingioideae), Eucommiaceae, and Myrothamnaceae. The Liquidambaroideae, Eucommiaceae, and Myrothamnaceae, while closest to Group I, can be viewed as intermediate between Groups I and II in complete linkage strategy and between Groups II and III in unweighted pair group strategy. Group II—consisting of Daphniphyllaceae, Leitneriaceae, Barbeyaceae, and Fagaceae (excluding *Nothofagus*)—has a closer phenetic relationship to Group I than Group III. Group III is the largest of these groups: it consists of Ulmaceae, Cannabaceae, Juglandaceae, Rhoipteleaceae, Betulaceae, Casuarinaceae, and Myricaceae. The Balanopaceae and *Nothofagus* are somewhat isolated and peripheral entities but hold together in both linkage strategies. Thirty pollen characters of 78 taxa were analyzed using PAUP to produce a cladistic tree. The outgroup used was *Tetracentron*. Three phylogenetically related groups sorted out, which are the same as those already recognized in the Groups I, II, and III mentioned above. Group I occurs at the base of the tree (primitive), and Group II occurs as intermediate between Groups I and III (derived). In general, these data support the relationships suggested by Barabe for the Hamamelidae, based upon vegetative and floral features and the classification of Cronquist.

This survey of pollen in the Hamamelidae was initiated with three primary goals in mind: (1) to provide comparative morphological data for assessing the relationships of fossil-dispersed pollen with possible hamamelidaceous affinity, (2) to assess at which taxonomic level pollen characters of extant hamamelidaceous taxa are useful in determining taxonomic position, and (3) to assess the phylogenetic relationships of taxa within the Hamamelidae as elucidated by pollen morphology and ultrastructure.

To achieve these ends we used pollen data [transmission electron microscopy (TEM) and scanning electron microscopy (SEM)] from published literature and added pollen data from 42 previously uninvestigated taxa. We have amassed pollen data from 20 of the 24 families recognized by Cronquist (1981), representing over 200 species (Didymelaceae, Urticaceae, Moraceae, and Cecropiaceae are excluded from the cladistic and phenetic analyses). In addition, pollen data from the Anacardiaceae and Salicaceae are included in the analysis.

In a survey as broad as that presented here, it is often difficult to decide which taxa to include or exclude. Members of the Hamamelidae have been placed in a number of subclasses, and a comprehensive pollen survey of all the families of the different classifications was not attempted here. We decided to use the Cronquist (1981) system as a starting point and introduced into our analysis selected taxa from other subclasses that have been suggested to be phylogenetically related (e.g., Thorne, 1973).

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[2] Department of Biology, Indiana University, Bloomington, Indiana 47405.

[3] Current address: Department of Botany, University of the Witwatersrand, 1 Van Smuts Avenue, Johannesburg, 2001 South Africa.

Methods

All pollen was removed from dry herbarium material. A list of specimens used in this study and the herbarium data are presented in Appendix I. The pollen was first acetolyzed and prepared for TEM by dehydration in an ethanol series and embedded in Spurr's Low Viscosity Resin. Sectioning was done on an MT-2 ultramicrotome; the sections were post-stained in uranyl acetate and lead citrate for 15 minutes, respectively, and viewed on a Phillips EM-300. Acetolyzed pollen was prepared for SEM by mounting the pollen on stubs with the high vacuum wax Apiezon W-100 and coated with gold-palladium. A Cambridge Stereoscan scanning electron microscope was used for viewing.

The terminology used to describe aperture type, tectal and supratectal ornamentation, and pollen wall structure follows Faegri and Iversen (1964). Zavada (1984) discussed the criteria used to identify wall layers. Identification of wall layers relies not only on staining properties but also on some developmental data. However, very few developmental data on hamamelidaceous taxa are available; thus, pollen descriptions in this paper are based on the morphology and staining properties with the electron micrograph stains uranyl acetate and lead citrate.

Descriptive Palynology

TROCHODENDRALES

Trochodendraceae (1 genus, 1 species). This taxon is restricted to Japan and Formosa. Pollen of *Trochodendron aralioides* Sieb. & Zucc. is tricolpate, oblate to slightly prolate. Pollen is about 24 μm in polar diameter and 20 μm in equatorial diameter (Erdtman, 1952). Exine sculpturing is reticulate. Wall structure is tectate-columellate with a relatively thick footlayer. A thin endexine is evident (Praglowski, 1974; Walker, 1976).

Tetracentraceae (1 genus, 1 species). This species is found in China and Burma. Pollen of *Tetracentron sinense* Oliv. ex Hook. is tricolpate, spherical to slightly prolate. Pollen averages about 15 μm in diameter. Exine sculpturing is reticulate (Walker, 1976). Pollen wall structure is tectate-columellate with a footlayer that is underlain by an endexine, which thickens slightly in the apertural region (Praglowski, 1974).

CERCIDIPHYLLALES

Cercidiphyllaceae (1 genus, 1–2 species). Cercidiphyllum japonicum Sieb. & Zucc. is endemic to Japan. Pollen is tricolpate (Walker, 1976; this study) or pericolpate (Walker, 1976; Fig. 1). Pollen averages 36 μm in polar diameter and 31 μm in equatorial diameter (Erdtman, 1952). Pollen shape is spherical to prolate. Exine sculpturing is reticulate (Fig. 1). Pollen wall structure is tectate-columellate with a footlayer of varying thickness (Fig. 2). A thin endexine that does not thicken in the apertural region is evident (Praglowski, 1974; Fig. 2).

EUPTELEALES

Eupteleaceae (1 genus, 2 species). Euptelea pleiosperma Hook. f. & Th. is found in China and India, and *E. polyandra* Sieb. & Zucc. is endemic to Japan. Pollen of *E. polyandra* was studied and is predominately tricolpate (Walker, 1976; this study); however, pericolpate grains have been reported (Praglowski, 1974; Walker, 1976). Shape varies from oblate to prolate (Fig. 3). Pollen ranges between 29 and 39 μm in polar diameter (Erdtman, 1952). The exine sculpturing is reticulate (Fig. 3). Pollen wall structure is tectate-columellate with a thin footlayer (Fig. 4). Endexine underlies the footlayer and is thin in nonapertural regions but thickens somewhat in apertural regions (Praglowski, 1974; this study).

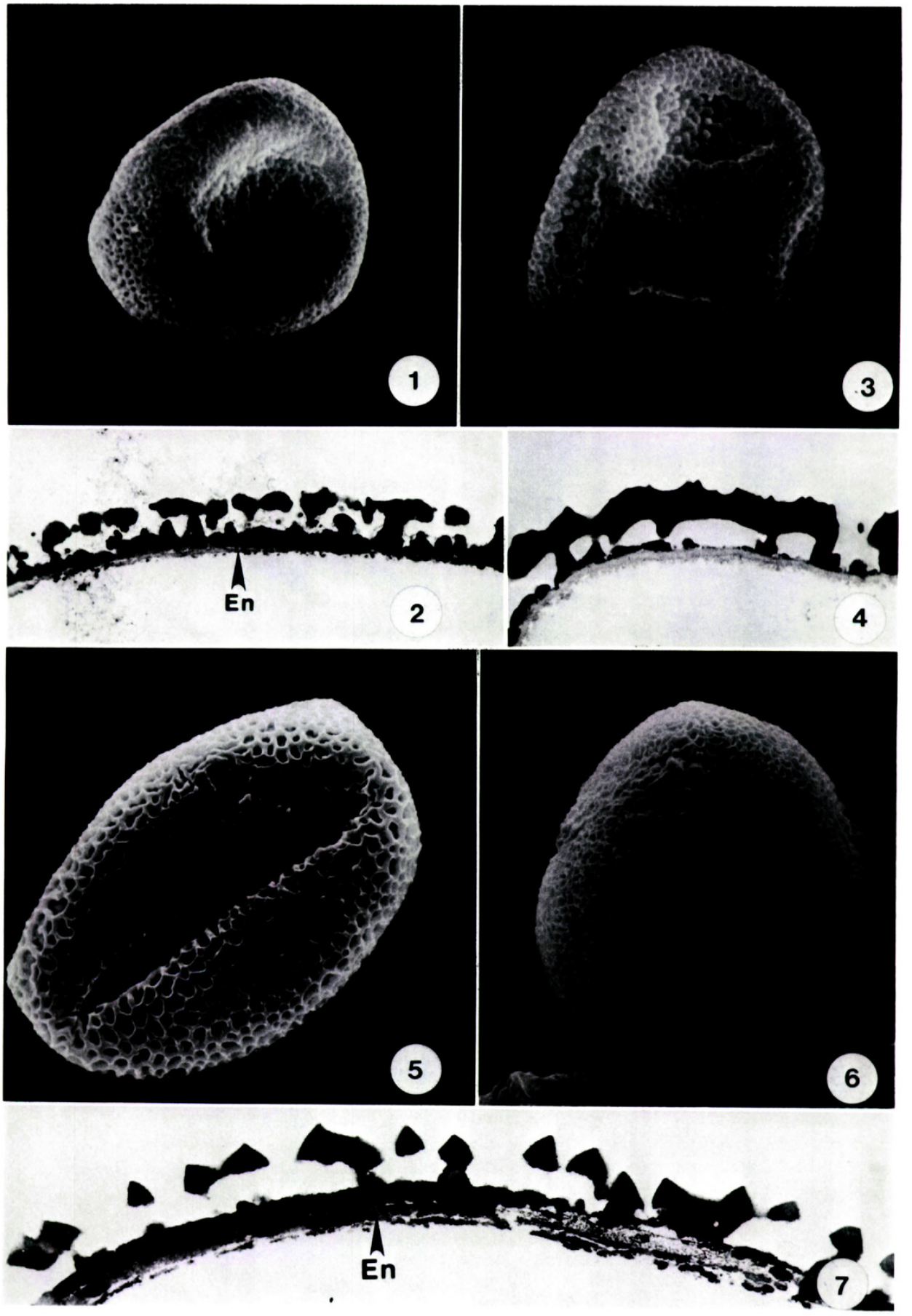
HAMAMELIDALES

Platanaceae (1 genus, 7–12 species). Platanus is widely distributed in temperate and subtropical regions of the Northern Hemisphere. Pollen of seven species was studied with SEM and TEM (Appendix I) and one species was studied by Hesse (1978) using TEM. Pacltova (1982) presented a methodological study of the pollen of some recent and fossil species of *Platanus.*

Platanaceae are a stenopalynous family. All species studied are treated together due to their morphological and ultrastructural similarity.

Pollen is tricolpate (Figs. 5, 6, 8, 11), the colpi are lenticular (Fig. 5) to slightly ovoid (Fig. 11). The grains are spherical to slightly prolate in equatorial view and circular to semi-angular in polar view and 19–24 μm in polar diameter and 17–22 μm in equatorial diameter. The exine sculpturing is reticulate (Figs. 5, 6, 8, 9, 11), the wall structure is tectate-columellate with a footlayer the same thickness as the tectum (Figs. 7, 10, 12–14). A thin endexine may be present (Figs. 7, 10, 13, 14); however, this may be an artifact of staining in some taxa (Fig. 12).

Myrothamnaceae (1 genus, 2 species). This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family of xerophytic shrubs consists of *Myrothamnus moschatus* Baill. in Madagascar and *M. flabellifolia* Welw. in South Africa.

The pollen of *Myrothamnus moschatus* Bail. and *M. flabellifolia* Welw. is usually shed in tetrahedral tetrads (occasionally in tetragonal tetrads) that range between 23 and 25 μm in diameter for *M. moschatus* and 24 and 26 μm for *M. flabellifolia* (Figs. 15, 19, 21). Single pollen grains of *M. moschatus* range between 11 and 14 μm in polar diameter and 12 and 15 μm in equatorial diameter. The pollen of *M. flabellifolia* ranges between 12 and 15 μm in polar diameter and 13 and 16 μm in equatorial diameter. Pollen in both taxa is spherical and triporate (Fig. 21). The three somewhat circular, ill-defined pores are symmetrically positioned and distally offset from the equator. The exine sculpturing consists of clavate processes that are ornamented with minute papillae (Figs. 16, 18, 20, 22). The wall averages 0.7 μm in thickness and is intectate. The pollen wall structure consists of an outer columellate layer. The columellae are the clavate processes easily observed with SEM (Figs. 16–20) and the bases of the clavate columellae are fused to a footlayer (Figs. 18–20) that is at times discontinuous (Fig. 18). Beneath the footlayer is a thin endexine that is not thickened adjacent to the apertural region (Fig. 18). In the region where pollen grains are joined in the tetrad, the columellae are short, stout pegs, and their apices are joined and hold adjacent pollen together (Figs. 17, 19).

The only interspecific differences are that the clavate processes in *Myrothamnus moschatus* are more widely spaced than in *M. flabellifolia* (compare Figs. 16 and 22). In addition, the footlayer in *M. moschatus* is usually thicker than the footlayer of *M. flabellifolia*. However, due to the lack of fertile herbarium material, intraspecific variation is unknown and we do not know how consistent these differences are within wide-ranging populations.

Hamamelidaceae (28 genera, 100 species). This family has a cosmopolitan distribution. Pollen of 12 genera (out of 28) and 16 species (out of 100) was studied ultrastructurally. Bogle and Philbrick (1980) examined 28 genera using SEM. Hesse (1978) described the ultrastructural characteristics of three genera and four species, and Endress (1977) illustrated eight taxa using SEM. The taxa investigated are treated here on the subfamilial level.

Liquidambaroideae. Pollen of *Liquidambar styraciflua* L. and *Altingia obovata* Merr. & Chun were studied with TEM and SEM. Bogle and Philbrick (1980) examined *L. orientalis* Mill. and *A. chinensis* Oliv. ex Hance using SEM. The pollen is spherical, periporate, the pores circular, often with islands of ektexine on the pore membrane (Fig. 31), and 32–58 μm in diameter. Exine sculpturing is finely reticulate with small supratectal rugulae, the wall structure is tectate-columellate, with a footlayer that is the same thickness as the tectum (Figs. 31, 32). The columellae are thin and short in *Liquidambar* (Fig. 31) but somewhat thicker in *Altingia* (Fig. 32). The footlayer is often underlain by a thin, less electron-dense wall layer (presumably endexine) that does not considerably thicken in the apertural region (Figs. 31, 32).

Rhodoleiodeae. Pollen of this monotypic subfamily (*Rhodoleia championii* Hook. f.) was studied with TEM (this study) and SEM (Bogle & Philbrick, 1980). Pollen is tricolpate, shape is subprolate, and 16–26 μm in equatorial diameter and 20–29 μm in polar diameter (Bogle & Philbrick, 1980). Exine sculpturing is finely reticulate (= scrobiculae of Bogle & Philbrick, 1980), and the wall structure is tectate-columellate with a footlayer as thick as the tectum (Fig. 29). The endexine appears as a thickened layer in the apertural region only (Fig. 29).

Exbucklandioideae. Pollen of *Exbucklandia populnea* (R. Br. ex Griff.) R. W. Brown was studied with SEM (Bogle & Philbrick, 1980; this

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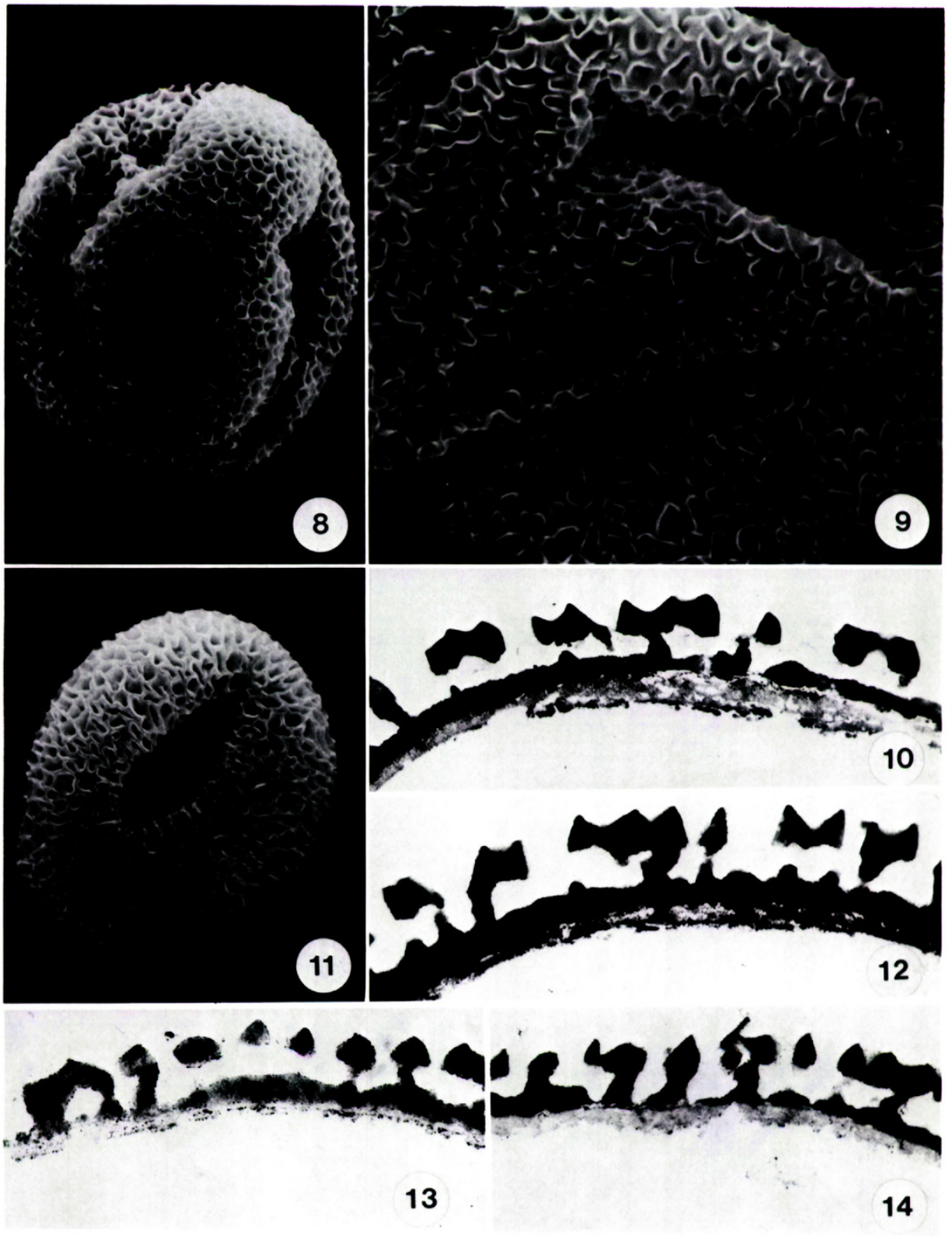
FIGURES 1–7.—1. Scanning electron micrograph of *Cercidiphyllum japonicum* showing reticulate exine sculpturing; × 1,300.—2. Transmission electron micrograph of *C. japonicum* showing tectate-columellate wall structure, footlayer, and thin endexine (En); ×14,660.—3. Scanning electron micrograph of *Euptelea polyandra* showing reticulate exine sculpturing and pericolpate apertures; ×1,300.—4. Transmission electron micrograph of *E. polyandra* showing tectate-columellate wall structure, thin footlayer, and less dense endexine; ×14,600.—5. Scanning electron micrograph of *Platanus acerifolia*; ×3,100.—6. Scanning electron micrograph of *P. mexicana*; ×3,200.—7. Transmission electron micrograph of *P. acerifolia* showing tectate-columellate wall structure, footlayer, and possible endexine (En); ×16,200.



FIGURES 8–14.—8. Scanning electron micrograph of *Platanus occidentalis*; ×3,200.—9. Scanning electron micrograph of *P. occidentalis* showing aberrant apertures, not an uncommon occurrence in this taxon; ×5,800.—10. Transmission electron micrograph of *P. occidentalis* showing tectate-columellate wall structure, footlayer, and possible endexine; ×12,600.—11. Scanning electron micrograph of *P. kerrii*; ×3,100.—12. Transmission electron micrograph of *P. kerrii* showing identical wall structure to the other *Platanus* species; however, differential staining of endexine is not very evident; ×12,540.—13. Transmission electron micrograph of *P. rzedowski*; ×10,260.—14. Transmission electron micrograph of *P. racemosa* showing identical wall structure to other *Platanus* species; ×16,200.

study) and TEM (this study). Pollen of *Mytilaria laosensis* Lecomte and *Chunia bucklandioides* H. T. Chang was studied with SEM by Bogle and Philbrick (1980).

Pollen is tricolpate and spherical to prolate in all three taxa and 26–32 μm in equatorial diameter and 23–37 μm in polar diameter in *E. populnea,* and 26–37 μm in equatorial diameter and 29–38 μm in polar diameter in *C. bucklandioides.* Exine sculpturing is reticulate in *Exbucklandia populnea* and *Mytilaria laosensis* and finely reticulate in *Chunia bucklandioides.* Pollen wall structure of *E. populnea* is tectate columellate with a thin footlayer (Fig. 23). No endexine is evident.

Disanthoideae. Pollen of *Disanthus cercidifolius* Maxim. is tricolpate, spherical to prolate, ranging between 22 and 23 μm in equatorial diameter and 22 and 33 μm in polar diameter, exine sculpturing is reticulate. Wall structure is tectate-columellate with a thin footlayer (Fig. 26). The endexine is thin in nonapertural regions but thickens in the apertural region.

Hamamelidoideae. This is the largest subfamily, with 21 genera. All genera were studied with SEM (Bogle & Philbrick, 1980) and six genera were investigated with TEM [*Hamamelis* (3 spp.), *Lorapetalum* (1 spp.), *Corylopsis* (2 spp.), *Fothergilla* (2 spp.), *Matudaea* (1 spp.), this study; and *Parrotia* (1 sp.), Hesse, 1978].

In most taxa, pollen is tricolpate but varies from tricolpate to pericolpate in *Fothergilla,* and is periporate in *Sycopsis,* tetracolpate to periporate in *Distylium,* and pericolpate in *Matudaea.* Pollen varies from slightly oblate to mostly spherical and prolate and is 16–53 μm in diameter. Exine sculpturing is finely reticulate to coarsely reticulate, often with supratectal verrucae. In all taxa studied with TEM, pollen wall structure is tectate-columellate with well-developed footlayers (Figs. 25, 27, 28, 30). Endexine is evident in *Fothergilla monticola* Ashe (Fig. 28), *Corylopsis pauciflora* Sieb. et Zucc. (Fig. 27), and *Matudaea hirsuta* Lundell (Fig. 30), but absent in *Parrotia persica* (DC.) C. A. Mey. (Hesse, 1978), *Hamamelis japonica* Sieb. et Zucc. (Fig. 24), and *Lorapetalum chinense* Oliv. (Fig. 25).

DAPHNIPHYLLALES

Daphniphyllaceae (1 genus, 35 species). This monotypic order is distributed in eastern Asia and the Malay Archipelago. Five species were investigated with SEM and TEM (Appendix I). Pollen is tricolpate (Figs. 33, 35, 39, 41), spherical to oblate in equatorial view (Figs. 33, 39) and circular in polar view (Figs. 35, 37), 17 μm in polar diameter and 21 μm in equatorial diameter (Erdtman, 1952). Exine sculpturing is somewhat psilate to verrucate (Figs. 34, 36, 38, 40, 42), the wall structure is tectate-columellate with a thin footlayer, and the tectum is occasionally perforated with small channels (Figs. 36, 40, 41). Endexine is present and is thin in nonapertural regions (Figs. 36, 40) but thickens considerably in the apertural region (Figs. 34, 38, 42).

DIDYMELALES

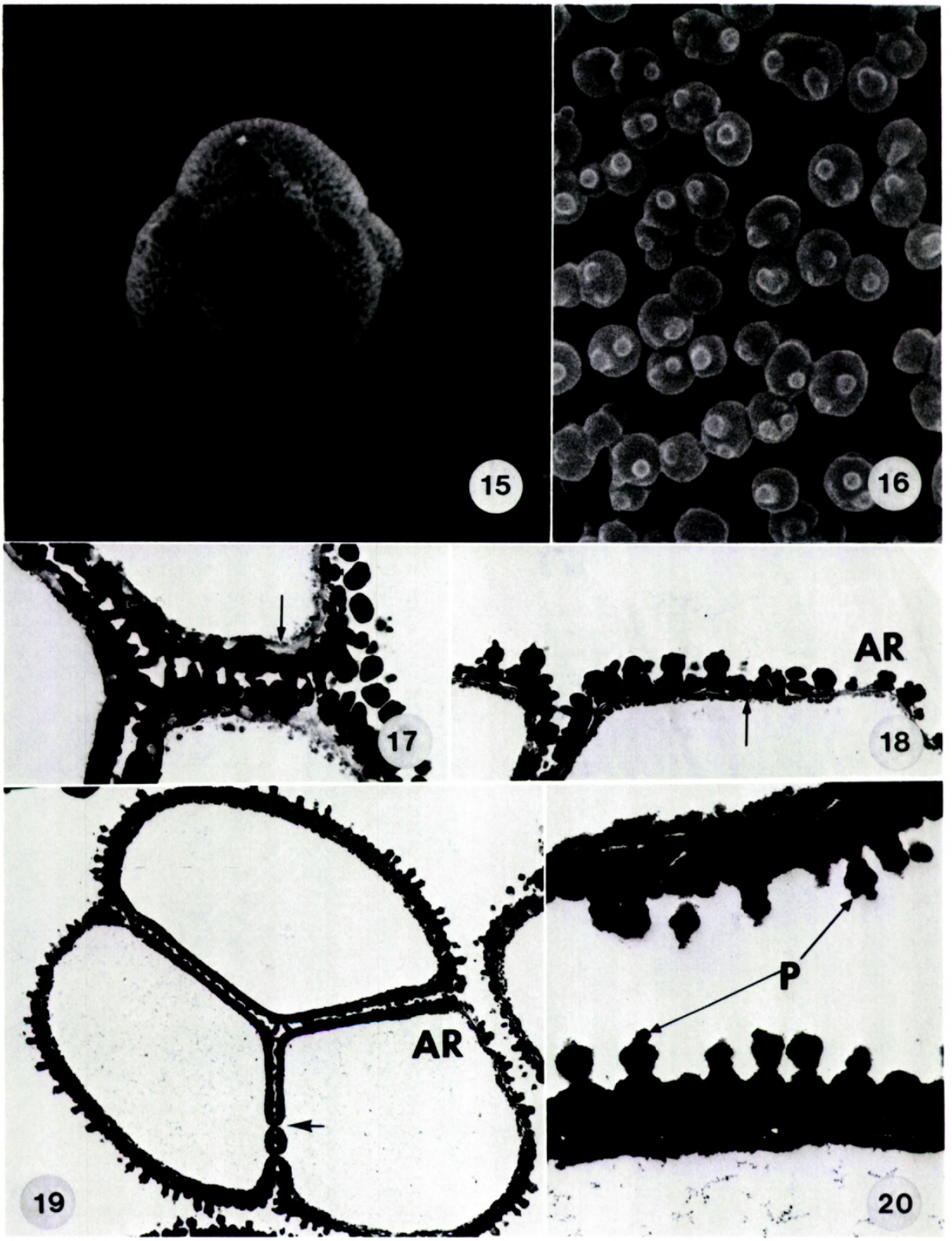
Didymelaceae (1 genus, 2 species). This family is restricted to Madagascar. Pollen is tricolpate with two pores per colpus: one in the distal hemisphere and one in the proximal hemisphere, oblate to spheroidal, about 21 μm in equatorial diameter and 23 μm in polar diameter, exine sculpturing is reticulate (Erdtman, 1952). Little is known of pollen wall structure but it appears to be tectate-columellate with a footlayer. Occurrence of endexine is unknown (Erdtman, 1952).

EUCOMMIALES

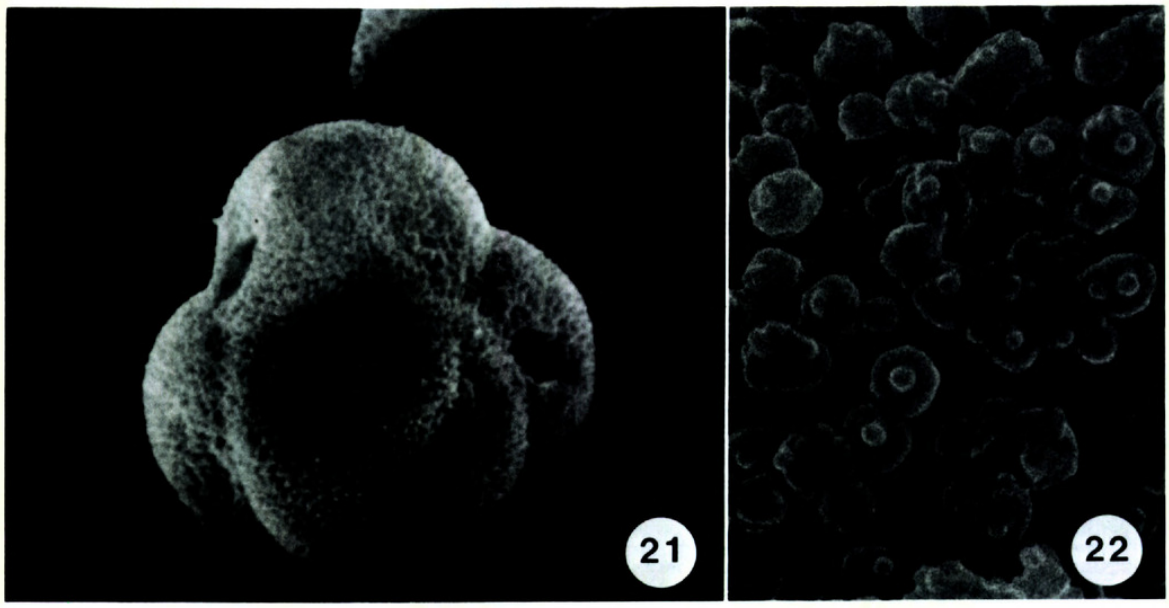
Eucommiaceae (1 genus, 1 species). Eucommia ulmoides Oliv. is found in China. Pollen is prolate and tricolpate: one colpus narrows near the equator but expands in the polar region (Fig. 43), the two other colpi appear straight (Fig. 44). The pollen is about 42 μm in polar diameter and 31 μm in equatorial diameter (Erdtman, 1952). Exine sculpturing is minutely spinulose to verrucate (Figs. 43, 44). Pollen wall structure is atectate, the ektexine homogeneous (Figs. 45–47), a rather thick endexine is present that does not thicken in the apertural regions (Figs. 45–47).

LEITNERIALES

Leitneriaceae (1 genus, 1 species). This monotypic family occurs in the southeastern United States (*Leitneria floridana* Chapm.). Pollen was studied with SEM and TEM. Pollen is tricolporate (occasionally tetracolporate), oblate to spheroidal (Fig. 48), 26–28 μm in size (Erdtman, 1952). Exine sculpturing is minutely verrucate (Fig. 49); the tectum is microperforate (Fig. 50), the wall structure is tectate-columellate with



FIGURES 15–20.—15. Scanning electron micrograph of *Myrothamnus moschatus* showing tetrahedral tetrad with clavate exine sculpturing; ×1,300.—16. Scanning electron micrograph of *M. moschatus* showing clavae with minute papillae; ×15,500.—17. Transmission electron micrograph of *M. flabellifolia* showing attachment of pollen in a tetrad. Note thin endexine (arrow); ×8,094.—18. Transmission electron micrograph of *M. flabellifolia* through the distal face of a pollen grain adjacent to the apertural region (AR). Note thin endexine (arrow), which does not thicken near the aperture and discontinuous footlayer (e.g., above arrow); ×6,840.—19. Transmission electron micrograph of *M. moschatus* showing attachment of pollen in a tetrad. Note inter-



FIGURES 21, 22.—21. Scanning electron micrograph of *M. flabellifolia* showing a tetrahedral pollen tetrad, clavate sculpturing, and porate aperture (A); ×2,000.—22. Scanning electron micrograph showing clavae with minute papillae. Note that the clavae are more crowded than in *M. moschatus* (compare with Fig. 16); ×15,500.

a very thin footlayer (Fig. 50). An endexine is present in nonapertural areas and thickens considerably in apertural regions.

URTICALES

Barbeyaceae (1 genus, 1 species). *Barbeya oleoides* Schweinfurth occurs in northeast Africa. Pollen was studied with SEM and TEM. Pollen is tricolporate (pores are equatorially elongate and wider than the colpi), oblate to spheroidal (Fig. 52), about 26 μm in polar diameter and 22 μm in equatorial diameter (Dickison & Sweitzer, 1970; this study). Exine sculpturing is scabrate (Figs. 52, 53). Pollen wall structure is tectate-columellate with a thick tectum traversed by microperforations (Fig. 51), the tectum is underlain by short, stout columellae (Fig. 51). The columellae rest on what appears to be endexine (Fig. 51). The footlayer is essentially absent. The endexine thickens somewhat in apertural regions.

Ulmaceae (15–17 genera, 150–200 species). The family is distributed throughout temperate and tropical regions of the world and is usually divided into two subfamilies, Ulmoideae and Celtidoideae. Some pollen has been studied with SEM and TEM (Zavada, 1983).

Ulmoideae. The pollen is 4–7-stephanoporate, the pores circular to elliptical, spheroidal to angular in polar view and oblate to spheroidal in equatorial view (Fig. 54), 31 μm in diameter. The exine is generally rugulate, the rugulae correspond to thick areas of the pollen wall (Fig. 54; except in *Planera,* which is psilate). Pollen wall structure consists of a tectum occasionally traversed by minute channels, granular infrastructure, and a thin continuous footlayer (Fig. 55). No endexine is evident (Zavada, 1983).

Celtidoideae. The pollen is 2–5-stephanoporate, the pores circular to slightly elliptical, circular to semi-angular in polar view and oblate to spheroidal in equatorial view, about 20 μm in diameter. Exine sculpturing is scabrate to finely verrucate (Fig. 56), and wall structure consists of an outer tectum that has minute channels. The infrastructure consists of a middle layer of anastomosing rods and an inner layer of irregular-shaped columellae, which rest on a thin basal layer (Fig. 57; Zavada, 1983).

Cannabaceae (2 genera, 2 species). This family occurs in north temperate regions. Pollen of *Cannabis sativa* L. was studied with SEM and TEM. Pollen is triporate with annulate pores; the

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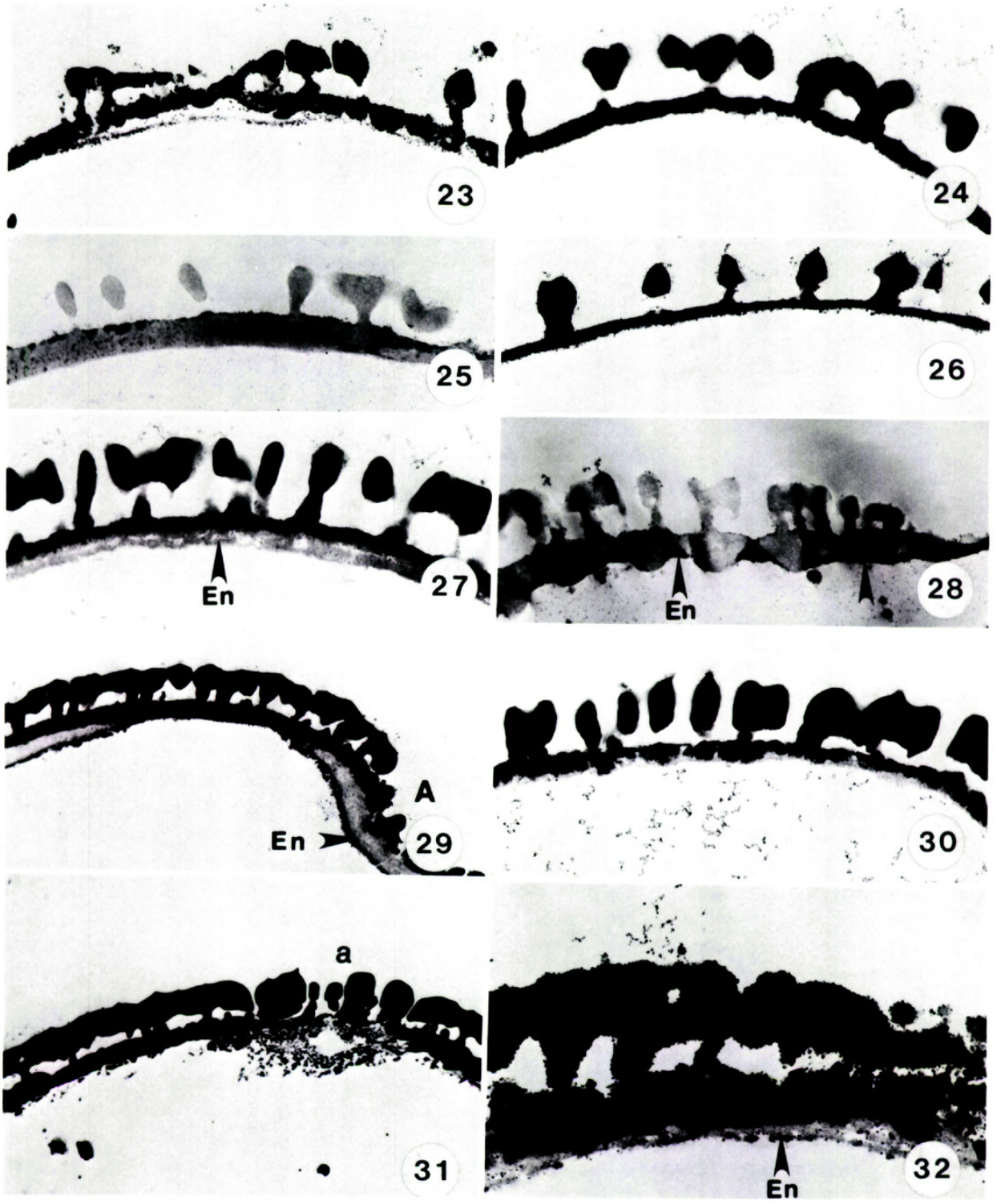
cytoplasmic channels (arrow) and the thin endexinal apertural membrane (AR); ×3,876.—20. Transmission electron micrograph of *M. moschatus* of the distal face of a pollen grain showing clavae with minute papillae (P) and thick basal layer. In this particular section, endexine does not stain differently than ektexine; ×15,960.



FIGURES 23–32. Transmission electron micrographs of pollen of the Hamamelidaceae showing predominance of the tectate-columellate wall structure.—23. *Exbucklandia populnea*; ×8,040.—24. *Hamamelis japonica*; ×12,310.—25. *Loropetalum chinense*; ×16,540.—26. *Disanthus cercidifolius*; ×8,040.—27. *Corylopsis pauciflora*, note the thick endexine (En); ×16,540.—28. *Fothergilla monticola*, note dark-staining discontinuous endexine (En, arrows); ×12,310.—29. *Rhodoleia championii*, note endexine (En) adjacent to apertural region (A); ×16,540.—30. *Matudaea hirsuta*; ×16,540.—31. *Liquidambar styraciflua* (A = apertural area); ×5,600.—32. *Altingia obovata*, note thin endexine (En); ×12,310.

annulus around the pore is formed by an elaboration of the infrastructural layer in this region (Text-Fig. 7F), (Fig. 58), oblate, 30 μm in equatorial diameter. Exine sculpturing is finely spinulose (Hamilton, 1976; this study), and wall structure is tectate-granular (often interspersed among the granules are thin columellae-like structures) with a thin footlayer (Fig. 59) and what appears to be a very thin endexine.

Moraceae (including the Cecropiaceae) (40 genera, 1,000 species). This family is widespread in subtropical and tropical regions of the world. For the size and importance of this family, little is known palynologically. However, a few taxa have been studied ultrastructurally (Niezgoda & Nowaczyk, 1976; Hamilton, 1976; Punt, 1978; Punt & Eetgerink, 1981). Pollen is variable and, in the taxa studied, it is di-stephano- or periporate, spherical to oblate, and averages about 30 μm in diameter. Exine sculpturing can be rugulate to scabrate with small supratectal spinules. Pollen wall structure (only studied in *Dorstenia* sp.; this study) is tectate-granular with a bilayered basal layer (Fig. 73). The tectum is occasionally traversed by minute channels.

Urticaceae (45 genera, 700 species). This family is widely distributed in subtropical and tropical regions of the world. Pollen wall ultrastructure is unknown. Pollen is stephano- or periporate, predominantly oblate, and 10–20 μm in diameter (Erdtman, 1952). Exine sculpturing is scabrate to rugulate with supratectal spinules (Hamilton, 1976).

JUGLANDALES

Rhoipteleaceae (1 genus, 1 species). Rhoiptelea chiliantha Diels et Hand is native to southeast Asia. Pollen has been studied with SEM and TEM by Stone and Broome (1971). The pollen is oblate, tricolporate with very short colpi appearing to approximate the triporate condition, averaging 27 μm in equatorial diameter. Exine sculpturing is scabrate, pollen wall structure is tectate-granular, and the infrastructural area is underlain by a footlayer. The tectum is traversed by minute channels. A thin endexine is evident.

Juglandaceae (8 genera, 60 species). This family is widely distributed in temperate and tropical regions of the Northern Hemisphere. The pollen was studied with SEM and TEM by Stone and Broome (1975). They recognized the four basic pollen types described below.

Engelhardtia-type—Pollen is triporate (varies from 2 to 8), oblate, 14–26 μm in diameter, and lacks pseudocolpi.

Platycarya-type—Pollen is triporate (varies from 2 to 5), oblate, 15–16 μm in equatorial diameter with pseudocolpi.

Carya-type—Pollen is triporate (varies from 1 to 6), oblate, and 33–66 μm in diameter.

Pterocarya-type—Pollen is stephanoporate, oblate to spheroidal, and 28–50 μm in equatorial diameter.

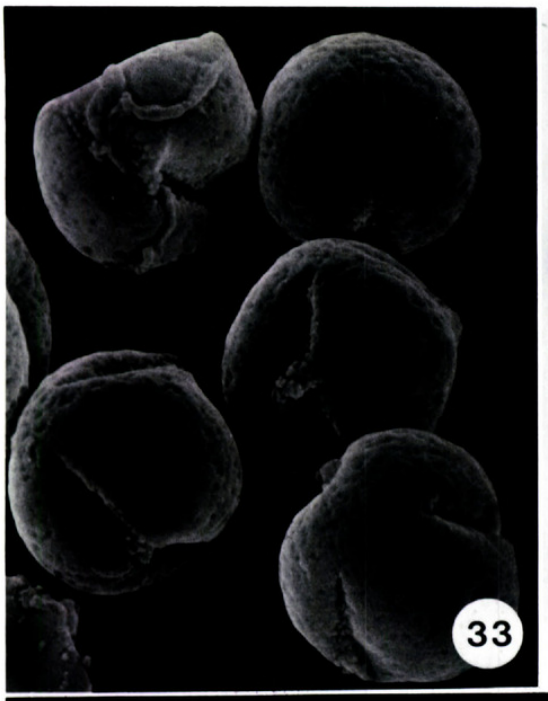
Pollen wall structure in all of the above taxa is tectate-granular with a relatively thick footlayer. The tectum is occasionally traversed by minute channels. A thin endexine is often present that does not thicken in the apertural region (Stone & Broome, 1975).

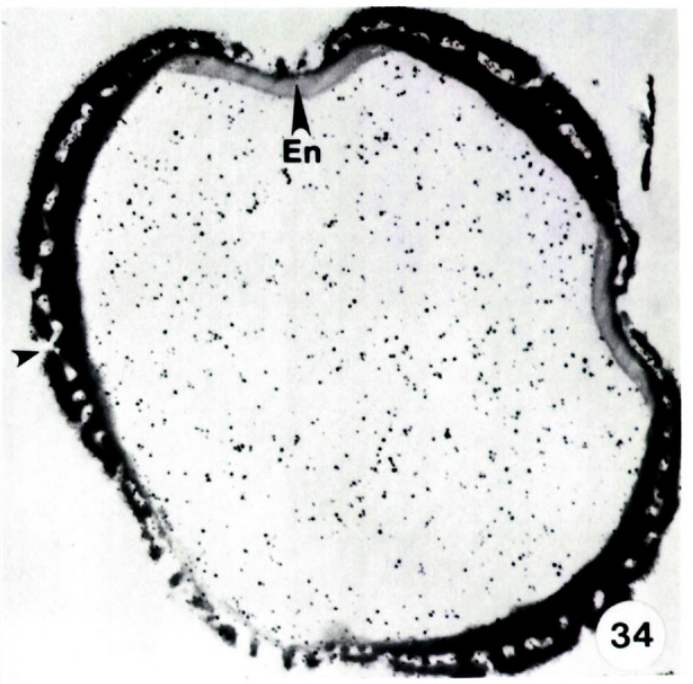
MYRICALES

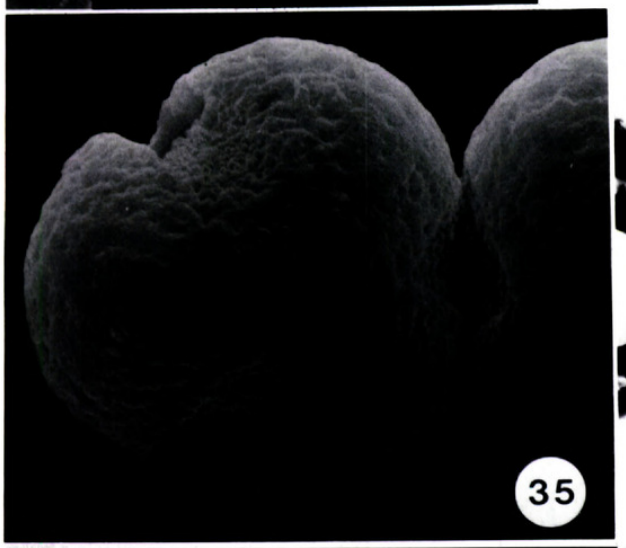
Myricaceae (3 genera, 50 species). This family is distributed in temperate and subtropical regions. Pollen is triporate, oblate, about 26 μm in equatorial diameter. Exine sculpturing consists of small scabrae (Praglowski, 1962; Lieux, 1980). Pollen wall structure of *Myrica asplenifolia* L. was studied with TEM (Fig. 64), and Coetzee and Praglowski (1984) investigated 11 species of *Myrica* with SEM and TEM and found that the pollen in those species is 21–25 μm in polar diameter, 25–35 μm in equatorial diameter. The pollen wall structure is tectate-granular; however, stout columellae are often discernable in the infrastructural layer (Fig. 65). The tectum is traversed by minute channels (Fig. 65). A relatively thin footlayer is present; no endexine is evident.

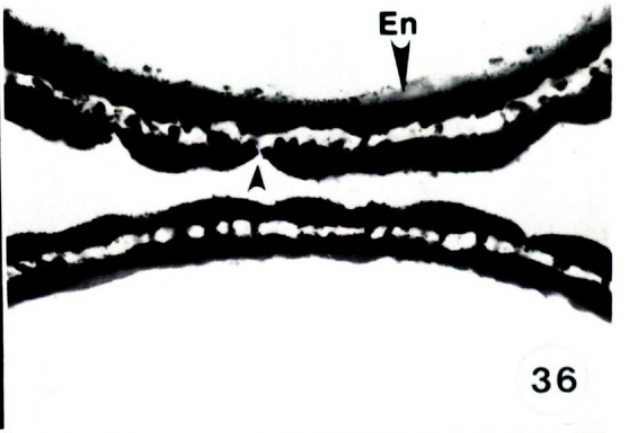
FAGALES

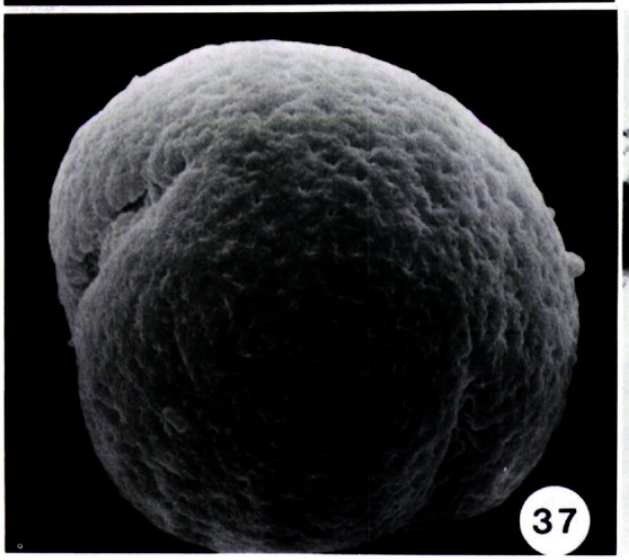
Balanopaceae (1 genus, 9 species). This family is distributed in regions of the southwest Pacific (e.g., New Caledonia). Pollen of *Balanops vitiense* (A. C. Smith) Hjedruqvist is 3–5-colpate, oblate, averaging 35 μm in diameter (Erdtman, 1952). The exine sculpturing consists of small spinules (Fig. 68), the wall structure is tectate-granular to columellate (Fig. 69), and the tectum is traversed by microperforations. The infrastructure consists of both irregular-shaped granules and robust columellae that rest on an uneven and sometimes discontinuous footlayer (Fig. 69). The footlayer is underlain by an endexine that,

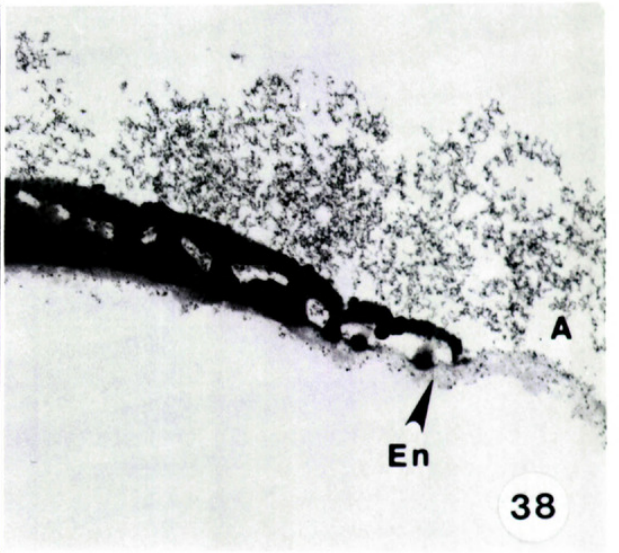




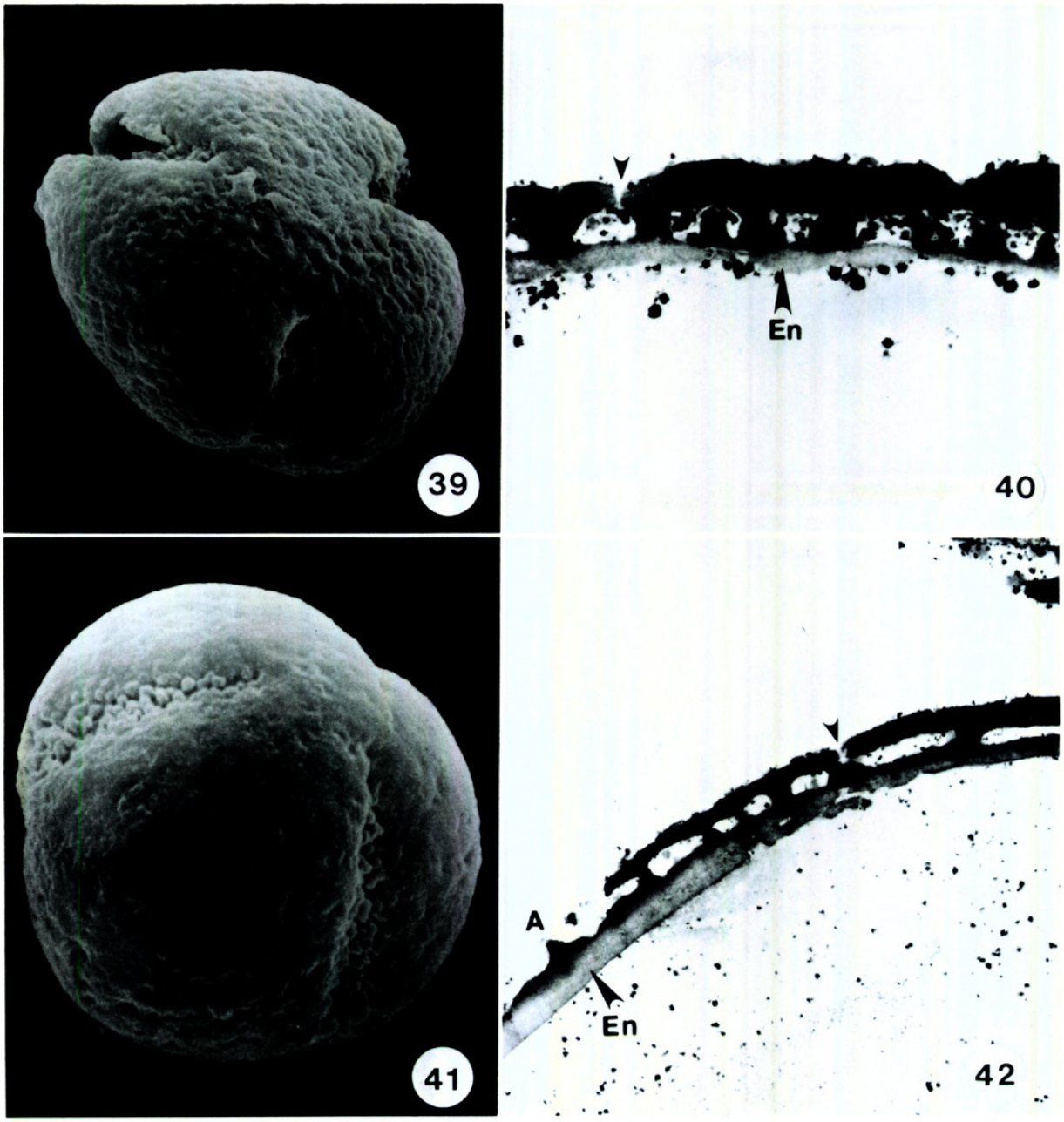








FIGURES 33–38.—33. Scanning electron micrograph of *Daphniphyllum calcinum*; ×2,200.—34. Transmission electron micrograph of *D. calycinum* showing tectate-columellate wall structure, footlayer, and endexine that thickens in apertural region (En); also note tectal perforations (small arrow); ×7,000.—35. Scanning electron



FIGURES 39–42.—39. Scanning electron micrograph of *Daphniphyllum himalayense*; ×3,200.—40. Transmission electron micrograph of *D. himalayense* showing tectate-columellate wall structure, thin footlayer, tectal perforation (small arrow) and endexine (En); ×25,500.—41. Scanning electron micrograph of *D. laurinum*; ×6,000.—42. Transmission electron micrograph of *D. laurinum* showing tectal perforation (small arrow), aperture region (A) with thickened endexine (En); ×15,540.

at times, is discontinuous and thickens somewhat in the apertural region (Fig. 69).

Fagaceae (6–8 genera, 800 species). The family has a cosmopolitan distribution. It is usually separated into three subfamilies.

Castaneoideae. The pollen is tricolporate, prolate, and averages 17 μm in polar diameter and 11 μm in equatorial diameter. Exine sculpturing is striate. The wall structure is tectate-columellate with a well-developed footlayer, the

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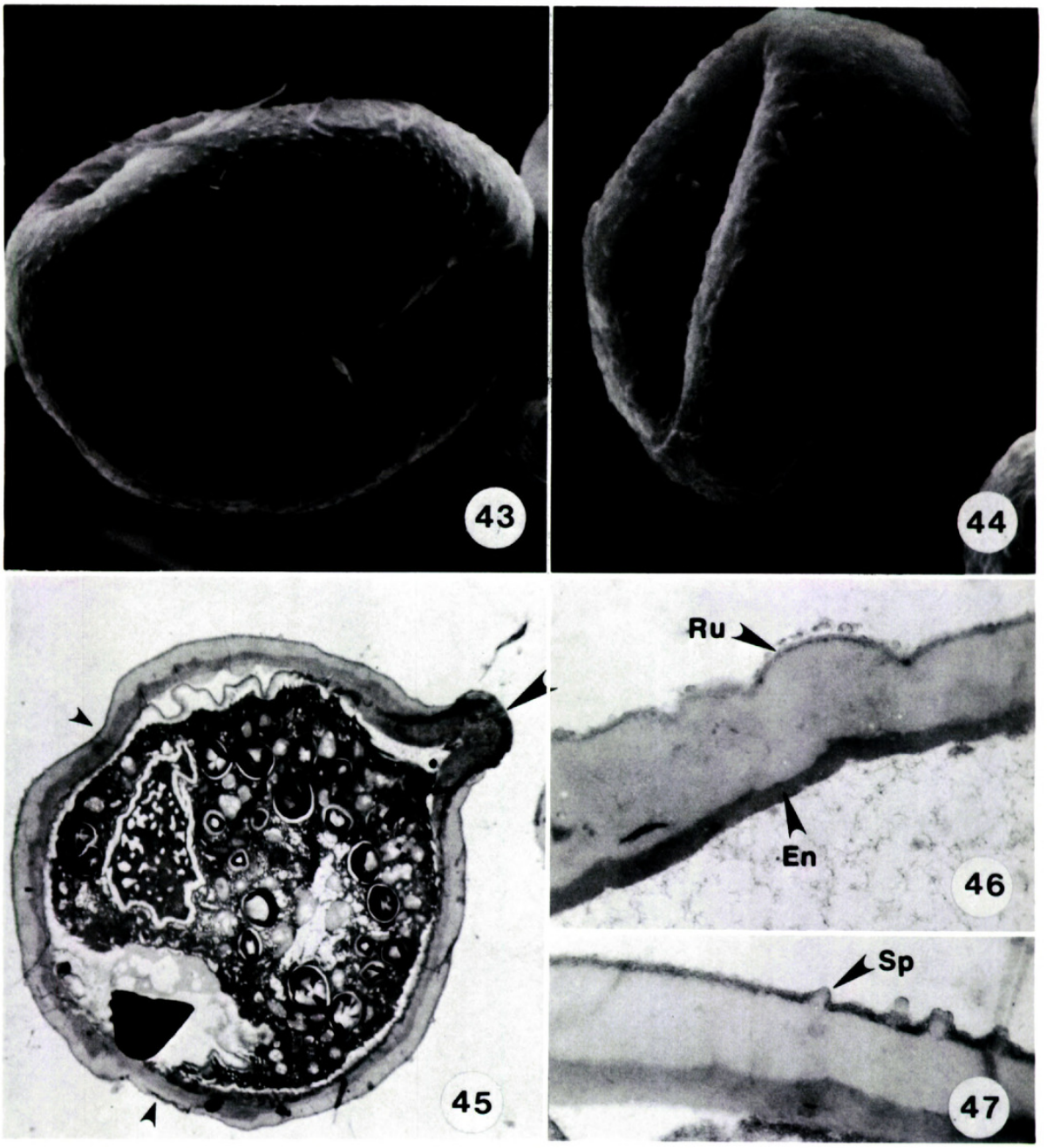
micrograph of *D. gracile*; ×2,900.—36. Transmission electron micrograph of *D. gracile* showing thin endexine in non-apertural region and a tectal perforation (small arrow); ×8,500.—37. Scanning electron micrograph of *D. neilgherrense*; ×3,200.—38. Transmission electron micrograph of *D. neilgherrense* showing aperture region (A) with endexine (En); ×10,000.



FIGURES 43–47.—43. Scanning electron micrograph of *Eucommia ulmoides* showing the colpus that narrows in the equatorial region; ×3,000.—44. Scanning electron micrograph of *E. ulmoides* showing straight, slit-like colpi; ×3,000.—45. Transmission electron micrograph of *E. ulmoides* showing atectate ektexine underlain by endexine, bulging colpus (large arrow), and the thinning of the ektexine in the slit-like apertures (small arrows); ×3,000.—46. Transmission electron micrograph of *E. ulmoides* in the hemisphere with slit-like apertures showing atectate wall, endexine (En), and rugulate (Ru) sculpturing (compare to Fig. 44); ×15,000.—47. Transmission electron micrograph of *E. ulmoides* in the region of the colpus that narrows equatorially showing small spinules (Sp) and wall structure; ×10,000.

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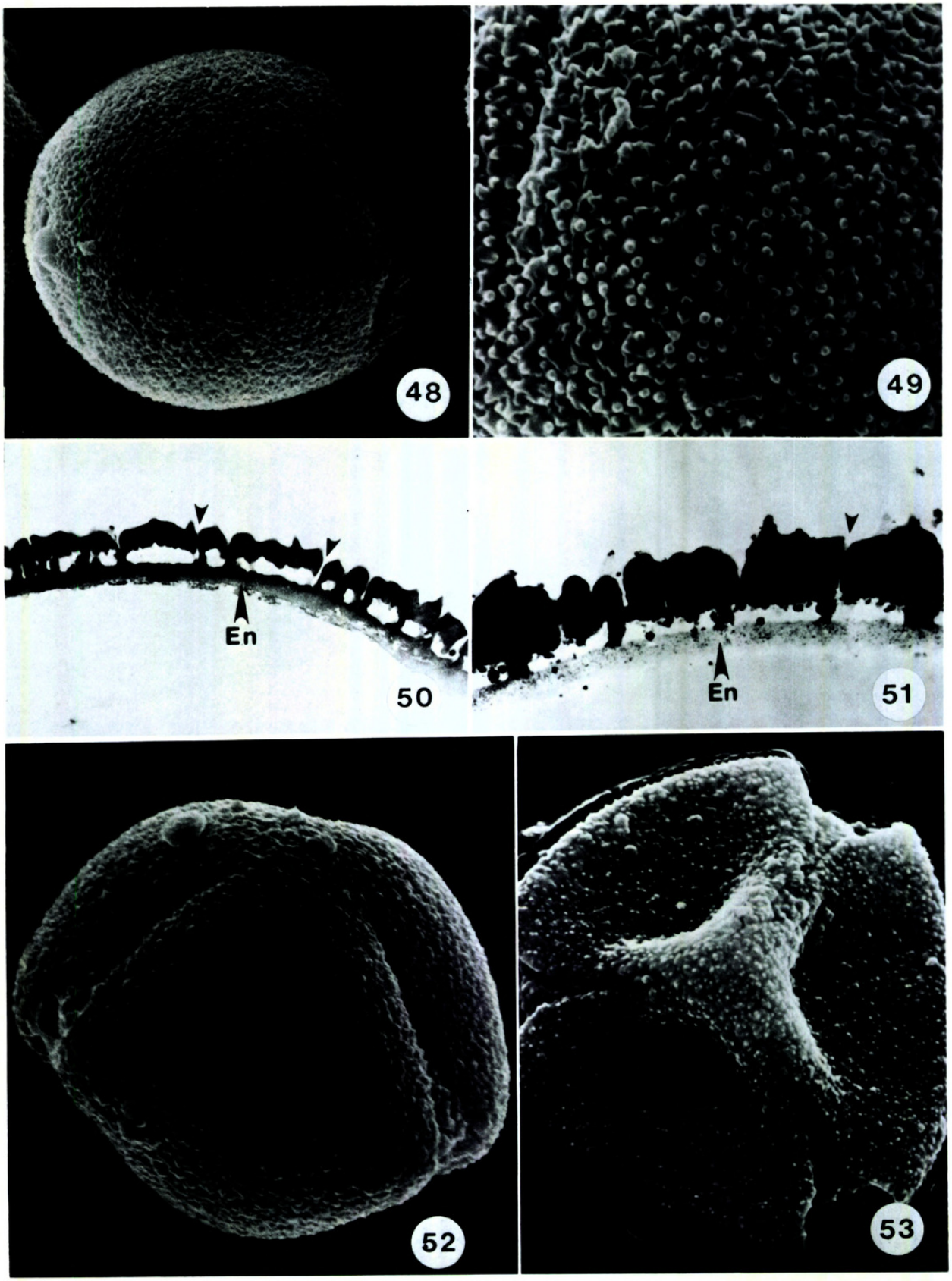
FIGURES 48–53.—48. Scanning electron micrograph of *Leitneria floridana*; ×2,400.—49. Scanning electron micrograph of *L. floridana* showing exine sculpturing; ×6,400.—50. Transmission electron micrograph of *L. floridana* showing tectate-columellate wall structure, thin footlayer, endexine (En), and tectal perforation (small



arrows); ×8,500.—51. Transmission electron micrograph of *Barbeya oleoides* showing thick tectum with small (micro-) perforations (small arrow), lack of footlayer, and thick endexine (En); ×22,520.—52. Scanning electron micrograph of *B. oleoides*; ×3,500.—53. Scanning electron micrograph of a collapsed pollen grain of *B. oleoides* showing trirudiate thick region in the polar region; this characteristic is reminiscent of some fossil normapolles dispersed pollen types; ×3,200.

tectum is traversed by small perforations. A thin endexine underlies the ektexine in nonapertural regions but thickens considerably in apertural regions (Crepet & Daghlian, 1980; Miyoshi, 1983).

Fagoideae. The pollen is tricolporate in *Fagus* and stephanocolpate in *Nothofagus,* and is spherical-oblate (*Fagus*) to oblate (*Nothofagus*). *Fagus* pollen is about 37 μm in polar diameter and 38 μm in equatorial diameter; that of *Nothofagus* is about 20 μm in polar diameter and 32 μm in equatorial diameter. Exine sculpturing in *Fagus* pollen consists of minute striations. Pollen of *Nothofagus* has widely spaced spines. Pollen wall structure of *Fagus* is tectate-columellate with a well-developed footlayer, the tectum is traversed by small perforations. A well-developed endexine, which thickens in the apertural regions, is also evident. Pollen wall structure of *Nothofagus* is tectate-granular with a relatively thick footlayer that is underlain by a well-developed endexine. The endexine becomes thicker in the apertural regions. The tectum is imperforate (Crepet & Daghlian, 1980; Praglowski, 1981, 1982).

Quercoideae. The pollen is tricolporate, prolate to spheroidal, about 28 μm in polar diameter. The exine sculpturing is scabrate to rugulate, the wall structure is tectate-columellate with a thick footlayer that is underlain by an endexine. The endexine thickens in the apertural regions (Smit, 1973; Crepet & Daghlian, 1980; Solomon, 1983a, 1983b).

Betulaceae (6 genera, 120 species). This family is distributed primarily in temperate regions of the Northern Hemisphere. Pollen is triporate (*Betula, Ostrya, Corylus, Ostryopsis, Carpinus*) to stephanoporate (*Alnus*), oblate, 20–30 μm in equatorial diameter. Exine sculpturing is minutely scabrate to slightly rugulate (Fig. 66; Erdtman, 1952; Adams & Morton, 1972; Kedves, 1979; Crane, pers. comm.), the wall structure is tectate-granular (Fig. 67; Erdtman, 1969; Rowley, 1981; Rowley & Prijanto, 1977; this study); however, columellate-like structures are often present in the infrastructural layer. (Dunbar & Rowley, 1984). The tectum is traversed by minute channels (Fig. 67). The footlayer is underlain by a very thin endexine that does not thicken in the apertural regions in *Corylus*; however, in *Betula* it thickens somewhat and is separated from the footlayer to form an atrium.

CASUARINALES

Casuarinaceae (1–2 genera, 50 species). This family is native to some southeast Pacific islands,

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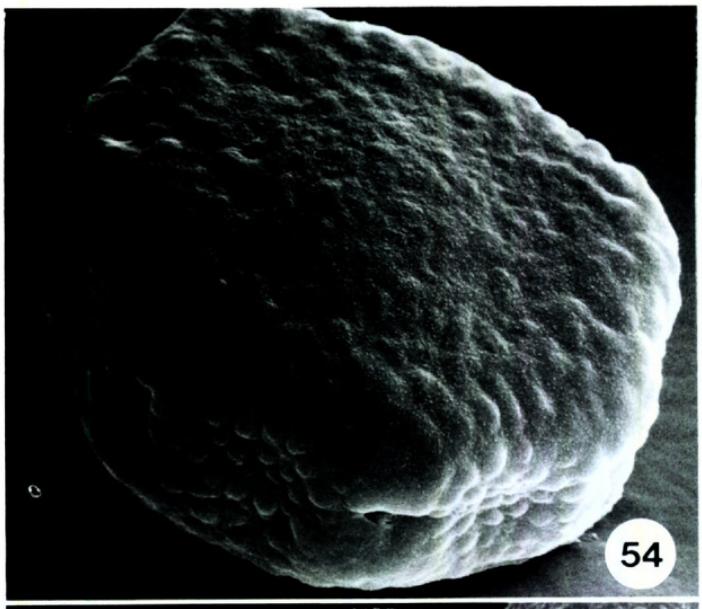
FIGURES 54–59.—54. Scanning electron micrograph of *Ulmus glabra*; ×1,840.—55. Transmission electron micrograph of *U. glabra* showing thin tectum, granular infrastructure, and thin footlayer; ×4,500.—56. Scanning electron micrograph of *Celtis talla*; ×3,310.—57. Transmission electron micrograph of *C. spinosa* showing tectum, infrastructure, and thin footlayer; ×7,100.—58. Scanning electron micrograph of *Cannabis sativa*; ×2,900.—59. Transmission electron micrograph of *C. sativa* showing tectum, granular infrastructure, and thin footlayer. A thin, less dense layer is sometimes evident in this taxon (endexine); ×10,260.

FIGURES 60–67.—60. Scanning electron micrograph of *Casuarina stricta*; ×1,500.—61. Transmission electron micrograph of *C. stricta* showing thick tectum with minute channels (small arrows), granular infrastructure, and thin footlayer; ×10,094.—62. Scanning electron micrograph of *Gymnostoma deplancheanum*; ×2,000.—63. Transmission electron micrograph of *G. deplancheanum* showing tectate-granular wall structure; ×6,840.—64. Scanning electron micrograph of *Myrica asplenifolia*; ×2,900.—65. Transmission electron micrograph of *M. asplenifolia* showing minute tectal channels (small arrows), granular-columellate infrastructure, and footlayer; ×15,540.—66. Scanning electron micrograph of *Betula alba*; ×2,900.—67. Transmission electron micrograph of *B. alba* showing minute tectal channels (small arrow) and granular infrastructure; ×18,960.

FIGURES 68–73.—68. Scanning electron micrograph of *Balanops vitiense* showing spinulose exine sculpturing; ×3,400.—69. Transmission electron micrograph of *B. vitiense* showing minute tectal perforations (small arrows), granular to columellate infrastructure, discontinuous footlayer, and dark-staining endexine (unacetolyzed pollen grain); ×15,540.—70. Scanning electron micrograph of *Pistacia terebinthus* showing porate (ulceroid-like) apertures, finely reticulate tectum with small scabrae; ×2,500.—71. Transmission electron micrograph of *P. terebinthus* showing tectate-columellate wall structure and thick footlayer; ×12,500.—72. Pollen of *Populus deltoides.* (a) Transmission electron micrograph of whole grain showing ektexinal interruptions that may represent small, ulceroid-like pores (arrows); ×4,500. (b) Transmission electron micrograph showing tectate-columellate wall structure and very thin footlayer; ×18,500.—73. Transmission electron micrograph of *Dorstenia* showing tectal perforations (arrows) and granular infrastructure; ×21,000.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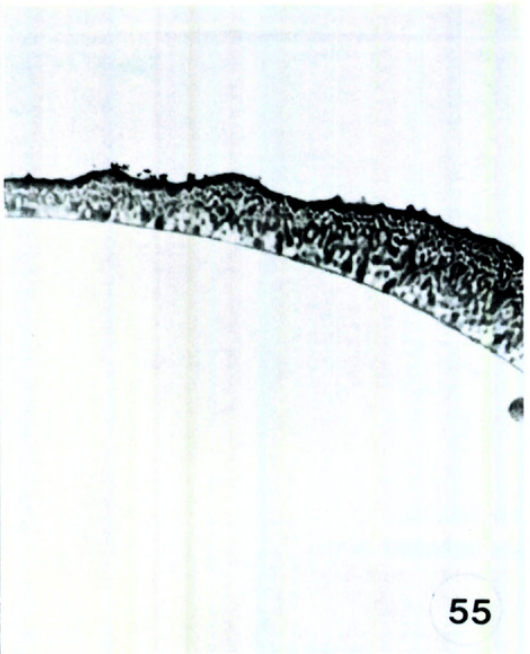
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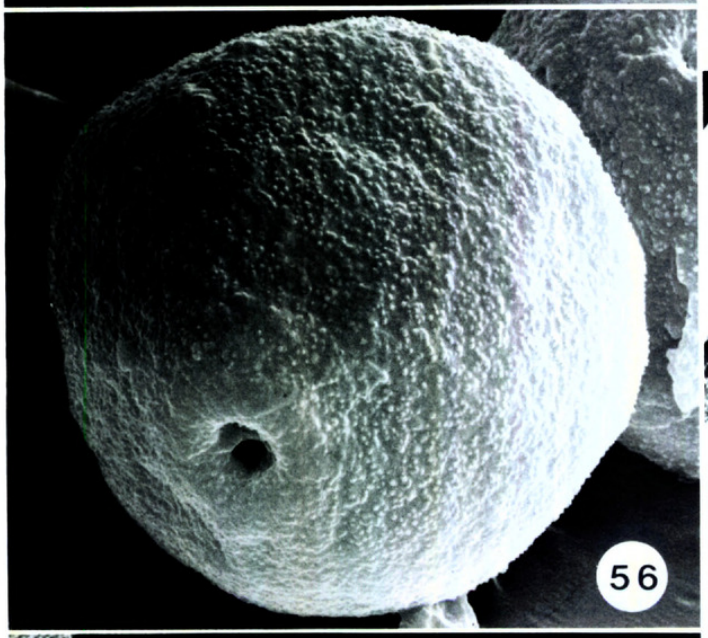
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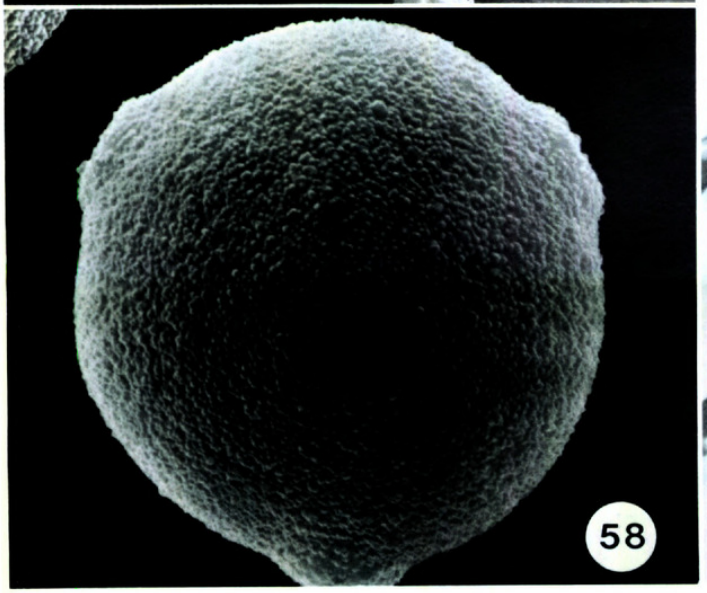
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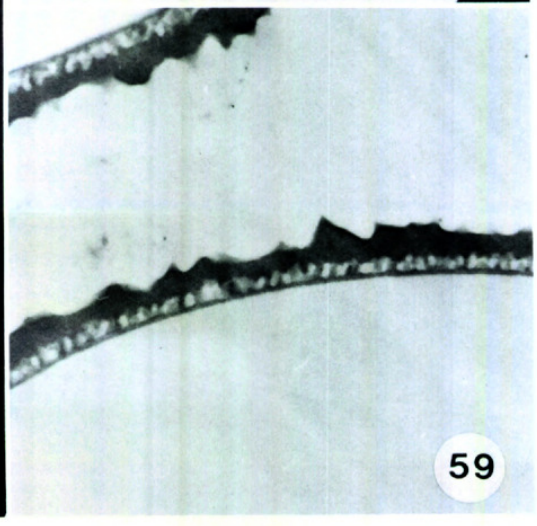
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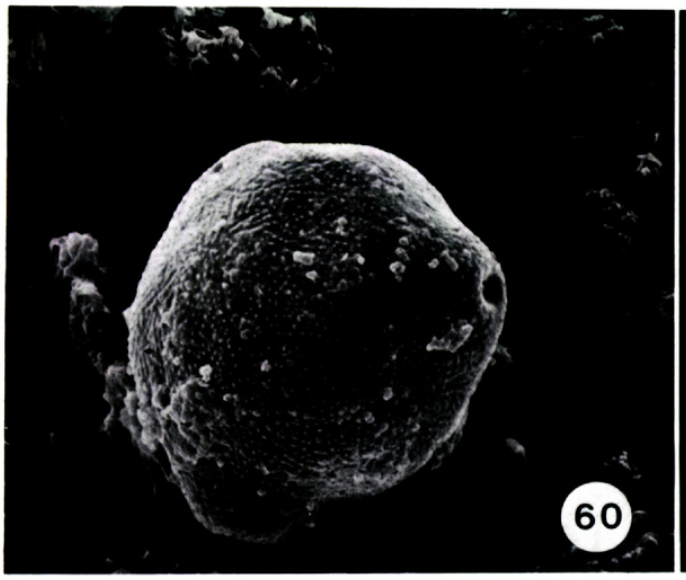
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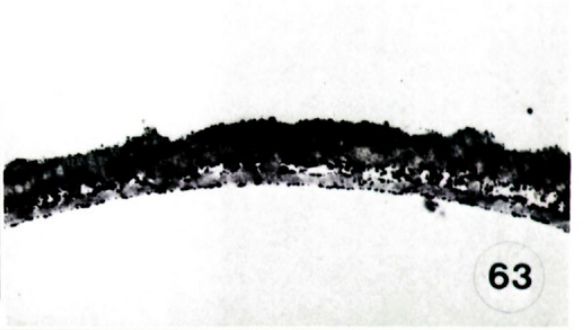
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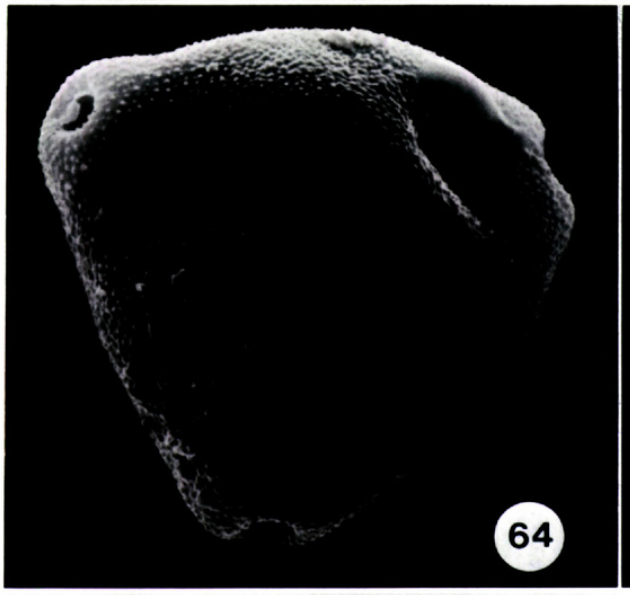
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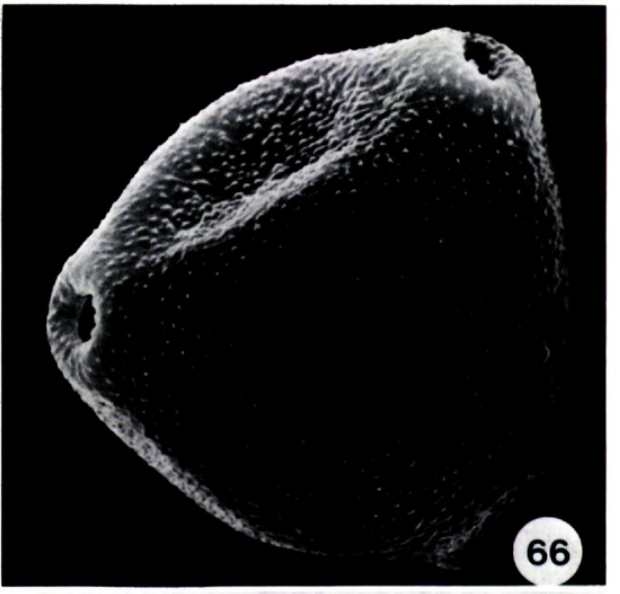
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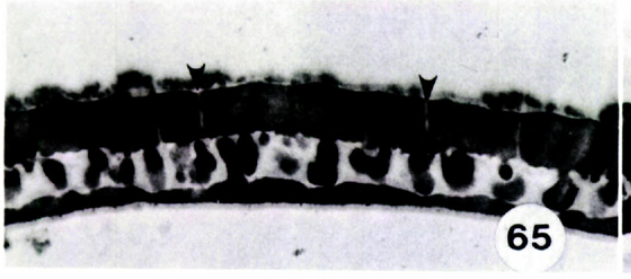
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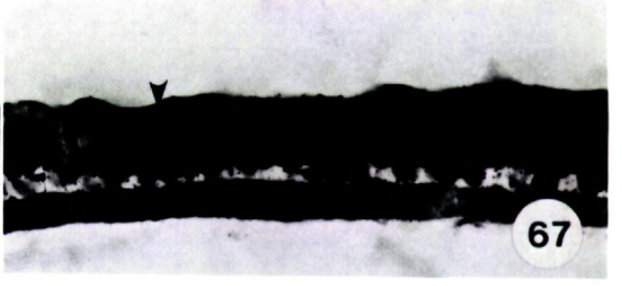
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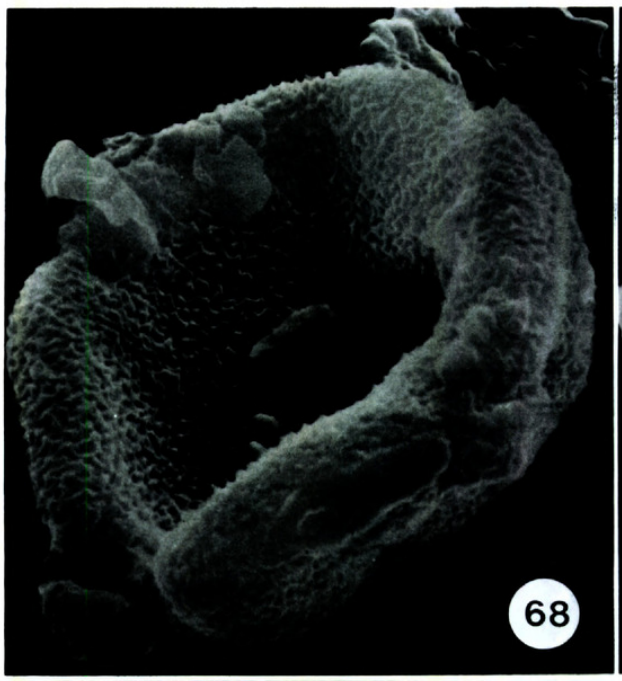
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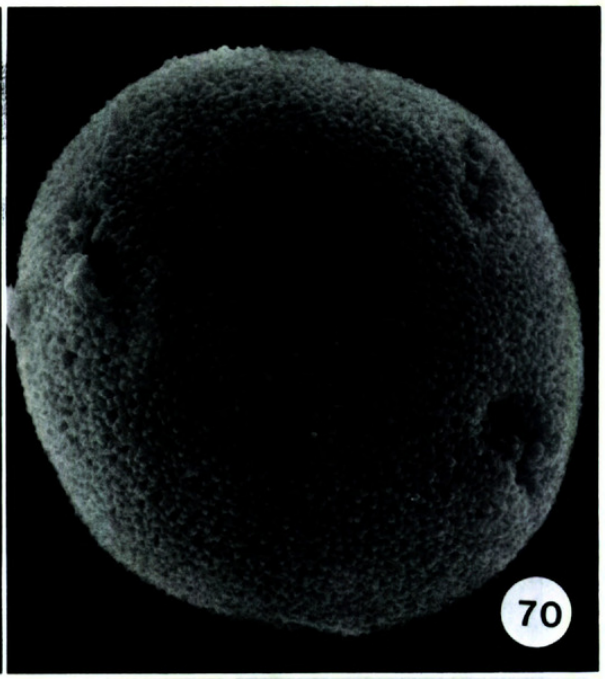
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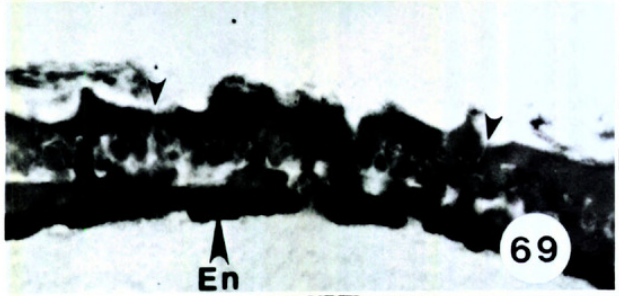
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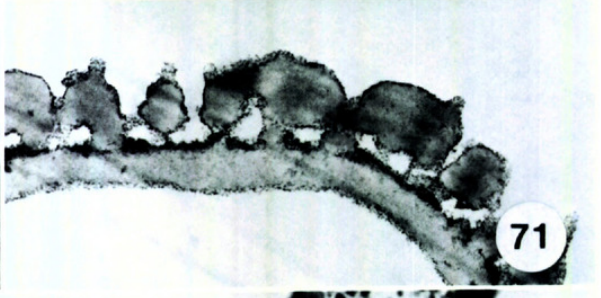
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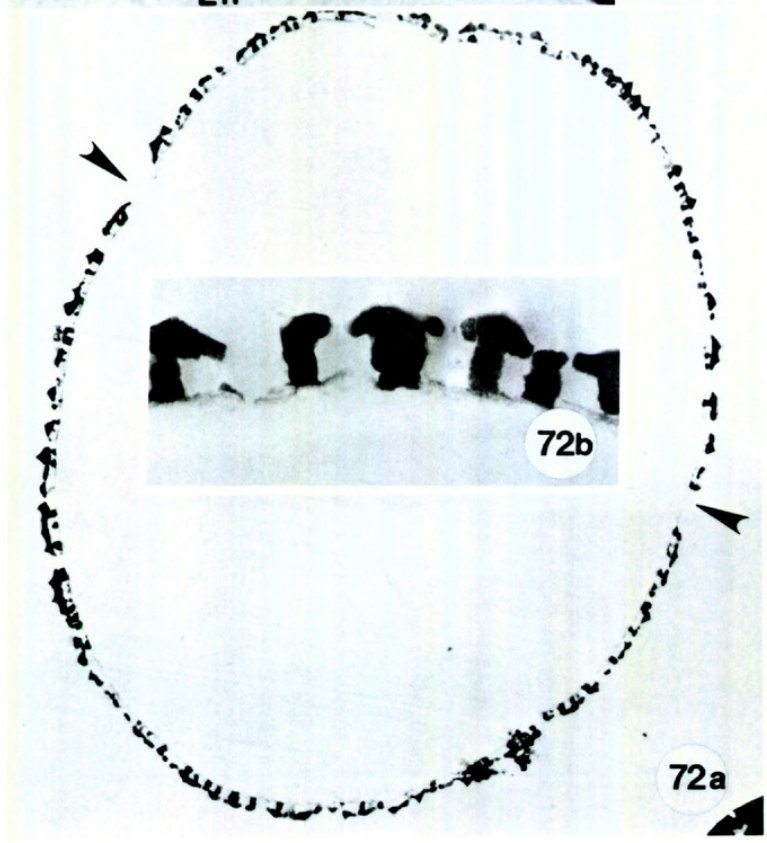
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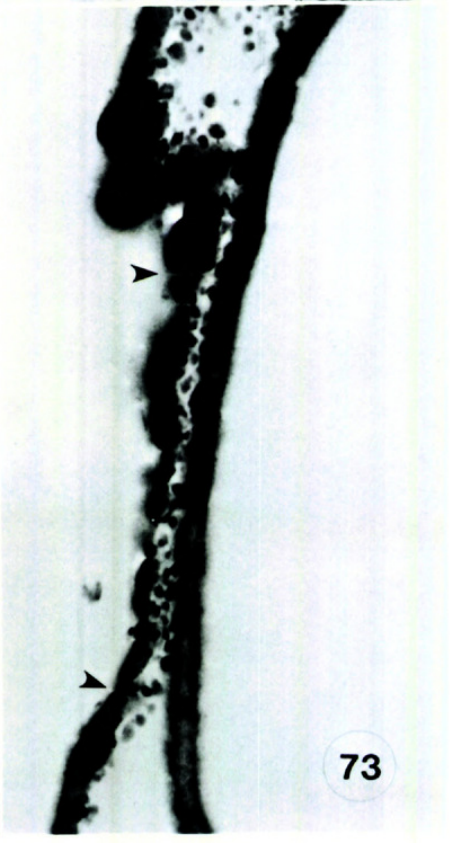
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New Guinea, Sumatra, and Australia. The pollen is triporate, oblate, averaging 29 μm in equatorial diameter (Kershaw, 1970) and 23 μm in polar diameter (Figs. 60, 62). Exine sculpturing consists of small spinules or scabrae and sometimes appear rugulate, the wall structure of *Casuarina* is tectate-granular (Figs. 61, 63), the thick tectum is traversed by minute channels (Fig. 61). A thin footlayer is present that separates from the granular layer in the apertural region to form an atrium. No endexine is evident, but Coetzee and Praglowski (1984) reported a thin endexine in the eight species they investigated. Pollen wall structure in *Gymnostoma* is identical to that in *Casuarina*; however, the footlayer remains in contact with the granular layer in the apertural region (this study).

POLLEN CHARACTERS USED IN THE ANALYSES

The pollen characters chosen for the phylogenetic and similarity cluster analysis of Hamamelidae are those that vary among the taxa investigated. Characters that are present but do not vary are excluded. The characters are of two types: (a) those that are present (1) or absent (0) and no other variation of the character exists, and (b) those that are present (1) or absent (0) and a dependent associated character state also exists that can thus be determined to be present or absent, for example, pollen shed in monads; if pollen is shed in some other unit, the monad character is scored absent (0) and the character state it possesses (e.g., tetrads) is scored present (1). Thirty character states that vary are recognized for pollen of the Hamamelidae (see legend Appendix II). The character states are discussed below, in addition to their association with taxonomic units above the generic level.

POLLEN UNIT (TWO CHARACTER STATES)

All species of Hamamelidae shed their pollen in monads except Myrothamnaceae, which shed pollen in tetrads.

POLLEN SHAPE (THREE CHARACTER STATES)

Pollen shape (prolate, spherical, oblate) varies considerably among species, genera, and families. Taxa with equatorially placed colpi are predominantly prolate to spherical (e.g., Trochodendrales, Hamamelidales). Taxa with equatorially positioned pores are usually oblate (e.g., Juglandales, Casuarinales), and taxa with peri-porate or -colpate pollen are generally spherical (e.g., Liquidambaroideae). If any species varies between two or three of the shape classes, both or all shape characters are scored as present (1).

APERTURE TYPE (NINE CHARACTER STATES)

The predominant aperture type is tricolpate (e.g., Trochodendrales, Hamamelidales). The triporate and stephanoporate (greater than three equatorial-positioned pores) are common in the Juglandales, Myricales, Casuarinales, Ulmaceae, and Betulaceae. The pericolpate and periporate condition occurs in the Liquidambaroideae, Moraceae, and Urticaceae. Stephanocolpate pollen occurs in two taxa: *Balanops vitiensis* (A. C. Smith) Hjedruqvist and *Nothofagus* spp. The tricolporate type is restricted to the Fagales, Leitneriales, and possibly Rhoipteleaceae (Stone & Broome, 1971), and the Barbeyaceae. The diporate type is found in some Moraceae and the Celtidoideae.

SUPRATECTAL SCULPTURING (SIX CHARACTER STATES)

Exine sculpturing is highly variable in many plant groups, including the Hamamelidae. In the semitectate (reticulate) pollen of the Trochodendrales and Hamamelidales, the tectum is often psilate. Another easily recognizable tectal ornament is small spines or spinules. Spinules occur predominantly in the Juglandales, Casuarinales, Myricales, and Betulaceae. Scabrae occur in the Urticales and the rugulate-verrucate sculpturing type in Urticales, Juglandales, and Fagales. Clavate sculpturing occurs only in the Myrothamnaceae, and the striate type only in the Fagaceae (e.g., *Fagus, Castanea*).

WALL STRUCTURE

TECTUM (FOUR CHARACTER STATES)

Pollen of all taxa have a tectum except for *Myrothamnus*, which is intectate. The pollen wall structure of *Eucommia* is unique in having atectate pollen (cf. *Degeneria*). Semitectate (reticulate) pollen is easily recognizable with light microscopy and occurs in the Trochodendrales and Hamamelidales. In Daphniphyllales, Leitneriales, Barbeyaceae, and Fagaceae the tectum is more continuous and is traversed by microperforations discernable only by SEM. In some Ur-

ticales, Juglandales, Myricales, and Casuarinales the tectum appears imperforate with SEM; however, TEM reveals that the tectum is traversed by microchannels.

INFRASTRUCTURE (TWO CHARACTER STATES)

The infrastructural layer of pollen walls in angiosperms is usually columellate or granular. The columellate type, which consists of cylindrical columns supporting the tectum, is found generally associated with the semitectate (reticulate) or microperforate tectal condition (i.e., Trochodendrales, Hamamelidales, Daphniphyllales, Leitneriales, and Fagales). The granular infrastructure (loosely defined here), which can be composed of anastomosing rods, spherical granules, or irregular-shaped columns, is generally associated with taxa that have microchannels (i.e., Urticales, Juglandales, Myricales, and Casuarinales).

FOOTLAYER (ONE CHARACTER STATE)

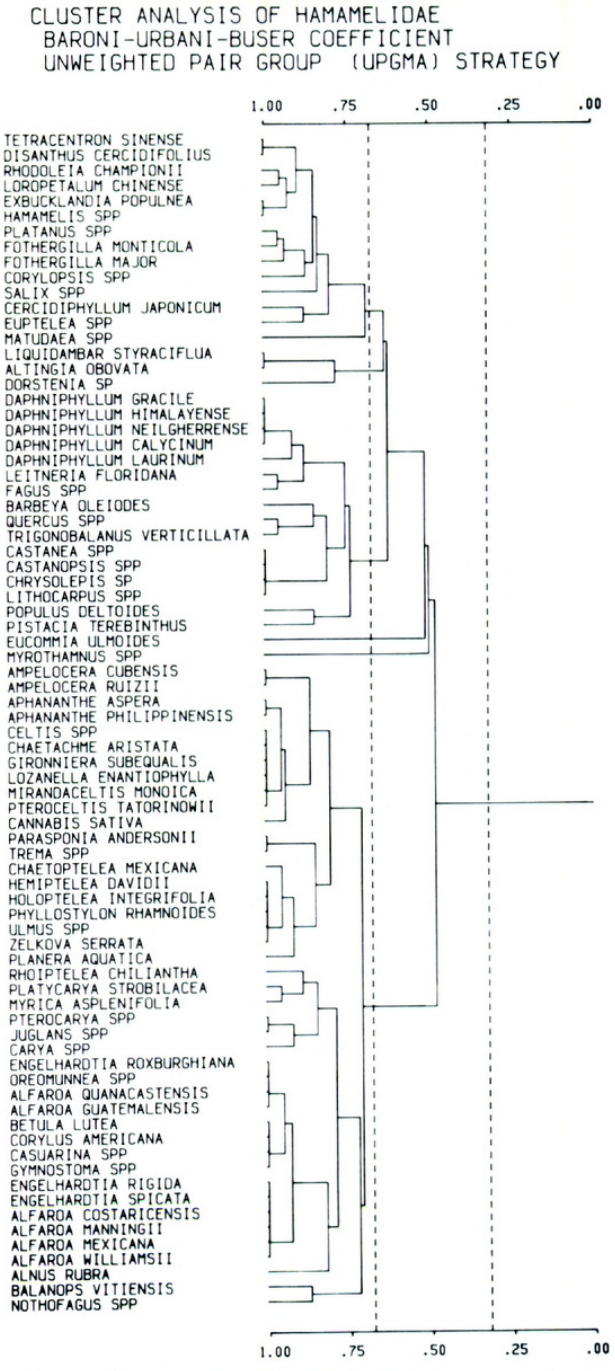
A footlayer is present in all taxa investigated except *Barbeya oleiodes,* in which it is represented by a very thin discontinuous layer, and much of the infrastructural layer rests directly on the endexine.

ENDEXINE (THREE CHARACTER STATES)

The presence, absence, and thickness in apertural and nonapertural regions of endexine varies among taxa. There appears to be no apparent relationship among taxonomic units and the occurrence of endexine. Three character states are recognized for this wall layer: (1) presence or absence, (2) endexine is thicker in the apertural regions than nonapertural regions, and (3) endexine does not thicken in the apertural region relative to nonapertural region. If endexine is absent, all three character states are scored (0). If endexine is present only in apertural region, character states one and three are (0) and two is (1) (this occurs only in *Rhodoleia*). If endexine is present but does not thicken in apertural region, character states one and three are (1) and two is (0).

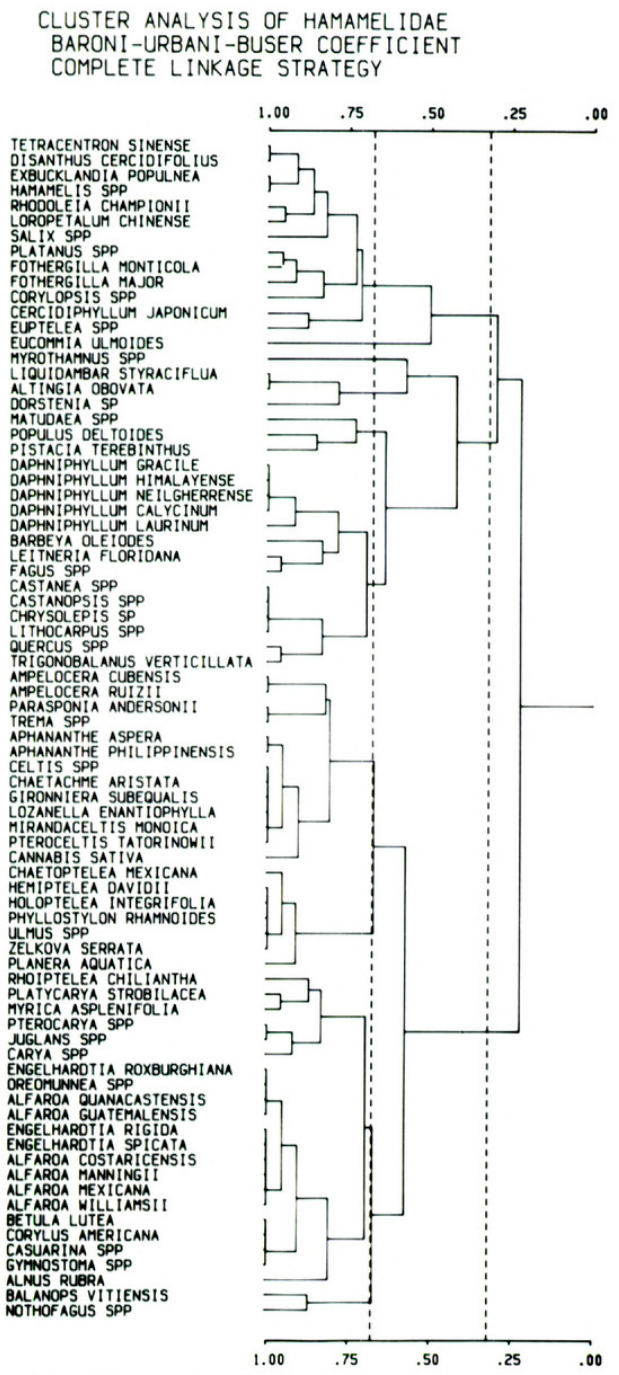
SIMILARITY CLUSTER ANALYSIS

The similarity cluster analysis used the Baroni-Urbani-Buser Coefficient. Using the Cluster Analysis Package of Archer, Hohn, and Horowitz (1984), two dendrograms were generated using the unweighted pair group method (UPGMA; Text-Fig. 1) and complete linkage strategies (CLS; Text-Fig. 2). Both produced similar results.



TEXT-FIGURE 1. Similarity cluster analysis, UPGMA strategy.

Three major groups are discernable, designated Group I, II, and III. Group I in both analyses consists of Trochodendraceae, Cercidiphyllaceae, Eupteleaceae, Platanaceae, Hamamelidaceae (including Liquidambaroideae), Eucommiaceae, and Myrothamnaceae. Group I taxa are prolate to spherical in equatorial view and circular in polar view. The tricolpate aperture pre-



TEXT-FIGURE 2. Similarity cluster analysis, CLS.

dominates; however, the pericolpate (*Euptelea, Matudaea*), periporate (Liquidambaroideae), and triporate (with ulceroid apertures, Myrothamnaceae) apertures are also present. Pollen is usually shed in monads (except in Myrothamnaceae). The tectum is usually reticulate, and the size of the perforations vary (except Eucommiaceae are atectate and Myrothamnaceae have clavate sculpturing). The infrastructure is predominantly columellate and all taxa have a footlayer. Endexine is usually present. Supratectal sculpturing is variable. In both linkage strategies, *Trochodendron* and *Tetracentron* exhibit close phenetic relationships with *Disanthus* of the Hamamelidaceae. The genera *Cercidiphyllum* and *Euptelea* also exhibit a high degree of similarity. Taxa of the Platanaceae and Hamamelidaceae (excluding the Liquidambaroideae) are also phenetically similar.

Some problematic taxa of Group I are the Liquidambaroideae, Eucommiaceae, and Myrothamnaceae. Members of these three groups occupy an intermediate position between Groups I and II, using the complete linkage strategy (Text-Fig. 2). However, using the unweighted pair group method, all three families appear isolated between groups II and III and may be considered groups themselves (Text-Fig. 1).

Group II is small and exhibits closer phenetic relationships with Group I than Group III. It consists of Daphniphyllaceae, Leitneriaceae, Barbeyaceae, and Fagaceae (excluding *Nothofagus*). Pollen is generally spherical but can be prolate or oblate in equatorial view and is tricolpate or tricolporate. Pollen is invariably shed in monads. The tectum is perforate, the perforations are usually not discernable with light microscopy but evident with SEM. The infrastructure of all taxa is columellate. The footlayer is present in all taxa except *Barbeya*. Endexine is occasionally present but best developed in *Barbeya*. Exine sculpturing is variable.

The clustering patterns of the taxa investigated in this group generally reflect familial relationships. The Daphniphyllaceae and Leitneriaceae are closely linked. Taxa of the Fagaceae form a group, except that *Fagus* exhibits a closer relationship with the Leitneriaceae and Daphniphyllaceae in both linkage strategies. The Barbeyaceae, although clearly members of this group, are somewhat isolated from the other taxa in both analyses.

Group III is the largest of the three groups, consisting of the Ulmaceae, Cannabaceae, Juglandaceae, Rhoipteleaceae, Betulaceae, Casuarinaceae, and Myricaceae, and the Balanopaceae and the genus *Nothofagus* as somewhat isolated entities. Pollen of this group is oblate in equatorial view and circular to angular in polar view. Aperture type consists of equatorially placed pores or short colpi, numbering two to many. Pollen is shed in monads. The tectum appears imperforate with SEM; however, TEM reveals that small channels traverse the tectum. Infrastructure varies somewhat but is generally granular to columellate-granular. The infrastructural layer

can consist of irregular-shaped rods, anastomosing rods, or spherical granules. The footlayer is usually thin, but always present. The endexine is relatively rare in this group and when present is usually a very thin layer and exine sculpturing can be rugulate, scabrate, or spinulose.

Branching patterns in this group generally reflect familial relationships. Using the unweighted pair group strategy (Text-Fig. 1), the Ulmaceae appear as three distinct groups: (1) members of the Celtidoideae, (2) *Trema* and *Parasponia,* and (3) Ulmoideae. Using the complete linkage strategy, two groups are evident: Ulmoideae and Celtidoideae (sensu Grudzinskaya, 1967). Cannabaceae link closely with the Celtidoideae in both strategies.

Juglandaceae (sensu Manning, 1978) are separated into four groups based on linkage patterns with the complete linkage strategy (Text-Fig. 2). *Platycarya* (Platycaryeae), isolated from other taxa of the Juglandaceae, exhibits similarities to *Rhoiptelea* and *Myrica. Pterocarya* and *Juglans* (Juglandeae) show close phenetic relationship with *Carya* (Hicoreae). Members of the Engelhardtieae comprise the fourth group closely linked with the Betulaceae and Casuarinaceae. The unweighted pair group strategy produced similar results, however, taxa of the Betulaceae and Casuarinaceae fall within the Engelhardtieae.

The Betulaceae and Casuarinaceae form a closely linked group in both strategies that is near or within the Engelhardtieae (Juglandaceae; Text-Figs. 1, 2).

Balanops and *Nothofagus* of the Fagaceae appear as a close group, isolated, but within Group III in both linkage strategies.

In addition to the taxa already discussed, four other taxa were introduced into the analysis: *Salix, Populus* (Salicaceae, Dillenidae), *Pistacia* (Rosideae), and *Dorstenia* (Moraceae).

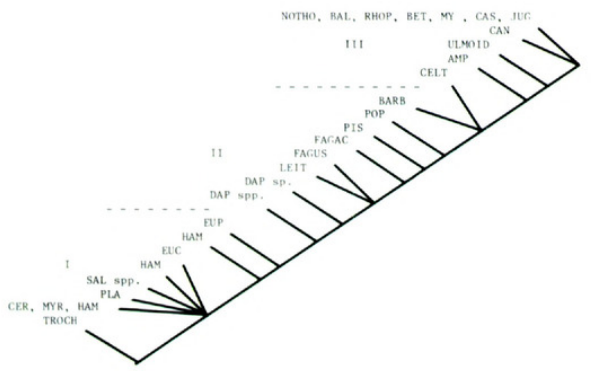
The Salicaceae were placed with amentiferous taxa, which are now members of the Hamamelidae by Engler (1926). *Salix* has tricolpate, spherical to prolate pollen, prolate, reticulate exine sculpturing, and a columellate infrastructure (Erdtman, 1952, 1969). Erdtman (1952) noted the similarity of *Salix* pollen to that of the Platanaceae. In our analysis, *Salix* is most similar to members of the Hamamelidaceae. *Populus* pollen is spherical and usually considered inaperturate; however, our TEM studies reveal a modification of the exine similar to pollen with ulcerate apertures (Fig. 72a). The tectum is perforate and the columellae rest on a very thin footlayer (Fig. 72b). With the complete linkage strategy *Populus* appears as an isolated taxon between Groups I and II (Text-Fig. 2), and between II and III in the unweighted pair group strategy (Text-Fig. 1). In both cases, neither *Salix* or *Populus* exhibits close phenetic relationships with amentiferous taxa of Group III. Pollen of *Pistacia* is 6–7-porate. The pores are distributed irregularly about the equator and are ulceroid in nature (Fig. 70). Pollen is spherical (Fig. 70) and shed in monads, and the tectum is perforate. The infrastructure is columellate; the columellae are fused to a relatively thick footlayer (Fig. 71), and no endexine is evident. Thorne (1973) considered the Juglandaceae and Rhoipteleaceae (Group III taxa, this study) to be closely allied with the Anacardiaceae (Rosideae). However, the pollen of *Pistacia* shows little phenetic relationship with that of the Juglandaceae or Rhoipteleaceae. *Pistacia,* along with the salicaceous taxa, form an isolated group between Groups I and II with the complete linkage strategy (Text-Fig. 2), and between II and III with the UPGMA strategy (Text-Fig. 1).

Pollen of *Dorstenia* (Moraceae), also included in the analysis, is periporate, spherical in shape, and its wall structure is tectate-granular with a well-developed footlayer (Fig. 73). The tectum is occasionally traversed by minute channels (Fig. 73). This taxon shows greatest phenetic similarity with members of the Liquidambaroideae (Hamamelidaceae) (Text-Figs. 1, 2). It is unlikely that the introduction into the analysis of a single taxon from such a large family as the Moraceae with about 1,000 species will accurately reflect familial relationships. Light and SEM studies of a few moraceous taxa (Niezgoda & Nowaczyk, 1976; Hamilton, 1976; Nair & Sharma, 1975; Zamora, 1977) indicate that the pollen is very diverse in the Moraceae, and a much broader survey is necessary before palynology can be used to suggest phenetic relationships with taxa of the Hamamelidae or any other subclass.

The Phylogenetic Analysis

The data set used for the similarity cluster analysis was also analyzed cladistically (Appendix II). The computer program used, Phylogenetic Analysis Uing Parsimony (PAUP), was developed and installed in the Indiana University computer system by David L. Swofford of the Illinois Natural History Survey (Swofford, 1984).

Seventy-eight operational taxonomic units



TEXT-FIGURE 3. Cladistic analysis of the Hamamelidae based on pollen (Adams, 1972, consensus tree). AMP = *Ampelocera,* BAL = Balanopaceae, BARB = Barbeyaceae, BET = Betulaceae, CAN = Cannabaceae, CAS = Casuarinaceae, CELT = Celtidoideae, CER = Cercidiphyllaceae, DAP = Daphniphyllaceae, EUC = Eucommiaceae, EUP = Eupteleaceae, FAGAC = Fagaceae, HAM = Hamamelidaceae, JUG = Juglandaceae, LEIT = Leitneriaceae, MY = Myricaceae, MYR = Myrothamnaceae, NOTHO = *Nothofagus,* PIS = *Pistacia,* PLA = Platanaceae, POP = *Populus,* RHOP = Rhoipteleaceae, SAL = *Salix,* TROCH = Trochodendrales, ULMOID = Ulmoideae.

(OTUs) and 30 pollen characters were analyzed. The character states are unordered; however, an outgroup was chosen. The consensus tree generated rooted the outgroup (Text-Fig. 3).

Tetracentron of the Trochodendrales was chosen as the outgroup for two reasons: (a) the Trochodendrales are considered by Cronquist (1981) and Endress (1986) to be the basal or the plesiomorphic group in the Hamamelidae, and (b) the pollen characters of the taxa in the Trochodendrales are common in many of the alleged primitive families and orders of other subclasses. The commonality of these characters suggests primitiveness (or the plesiomorphic state; see the descriptive palynology section for pollen characters).

From the consensus tree generated, three major phylogenetically related groups are evident. These groups are comparable to the groups recognized in the similarity cluster analysis (Text-Fig. 3; Groups I, II, and III). In addition to the consensus tree, the program generated 250 equally parsimonious trees. The branch swapping in all of the equally parsimonious trees takes place within these three groups, at all times maintaining the phylogenetic relationship of the three groups. Group I taxa always occur at the base of the tree, showing a close phylogenetic relationship with the outgroup. Group II taxa always occur as an intermediate group between I and III (Text-Fig. 3). Group III always occurs as the most derived. All groups exhibit a number of equally parsimonious possibilities within each group. This suggests that it is impossible to resolve the more specific phylogenetic relationships between members of each group based on pollen alone. Not surprisingly, in order to reach a finer resolution of the relationships at the generic or specific levels, characters other than pollen will have to be used.

The taxa from the Salicaceae and Anacardiaceae introduced into the analysis bear no phylogenetic relationship to the amentiferous taxa of Group III, again supporting the results of the similarity cluster analysis. *Salix* exhibits a close cladistic relationship to a member of the Hamamelidaceae, and *Populus* and *Pistacia* appear as paraphylletic groups between Group II and Group III taxa.

It can be concluded from this analysis that Group I taxa are primitive, Group II taxa are intermediate between I and III, and Group III taxa are derived.

DISCUSSION

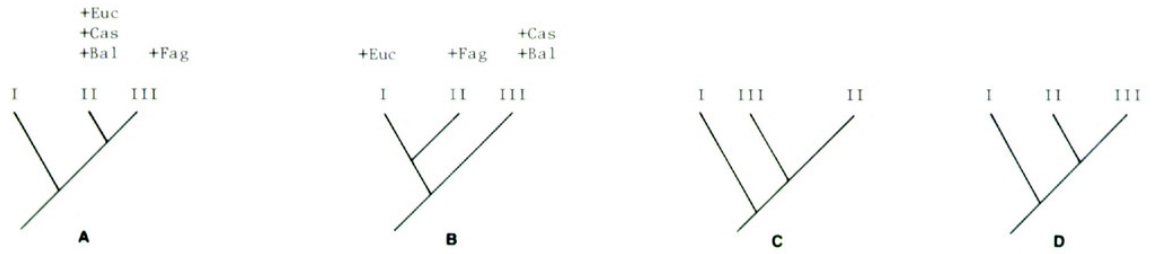
The taxonomic composition (at the family level) of the Hamamelidae has been a subject of controversy for some time. However, there is some agreement on the families that comprise the "core" taxa in this group. Both Thorne (1973) and Cronquist (1981) included the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae, and Platanaceae in the Hamamelidae (Hamamelidiflorae of Thorne, 1973). These families comprise a well-defined phenetic group based on vegetative (Group I of Barabe et al., 1982) and pollen characters (Group I, this study; Text-Figs. 1, 2). In addition, our cladistic analysis also suggests a close phylogenetic relationship among these taxa (Text-Fig. 3). The Eucommiaceae, a family Cronquist (1981) placed in its own order and Tippo (1938, 1940) considered closely related to the Urticales, are most similar to Group I taxa in our analysis. Based on a number of vegetative and floral characteristics, Thorne (1973) considered the Eucommiaceae closely allied with the Hamamelidales, as our analyses also suggest. The Myrothamnaceae are a problematic group. Based on pollen morphology, this family exhibits phenetic similarity to Group I taxa (also see Barabe et al., 1982) but has many unique pollen char-

acters not found in any other taxa in the Hamamelidae (also see Thorne, 1973). Cronquist (1981) placed this taxon in the Hamamelidales without question. Although our phenetic analysis does not show a strong relationship between *Myrothamnus* and other Group I taxa, our cladistic analysis demonstrates a close phylogenetic relationship between *Myrothamnus* and cercidiphyllaceous and hamamelidaceous taxa (Text-Fig. 3; cf. Cronquist, 1981).

Group II consists of a number of small, isolated families (Text-Figs. 1–3), which exhibit many pollen characters that can be considered intermediate between Groups I and III. Of the four families included in this group, Thorne (1973) considered only the Fagaceae as a member of the Hamamelidae. The Barbeyaceae (taxon incertae sedis of Thorne, 1973) are considered by Dickison and Sweitzer (1970) and Cronquist (1981) as closely allied with the Ulmaceae of the Urticales. However, Barabe et al. (1982) placed the family within their Group II (similar in composition to our Group II). On the other hand, our cladistic analysis clearly indicates a close relationship between *Barbeya* and the Celtidoideae of the Ulmaceae. The Daphniphyllaceae have been variously treated. Thorne (1973) considered this family allied with the Buxaceae and Brunelliaceae of the Rosidae. A recent cladistic analysis by Barabe (1984), using vegetative and floral features, lends support to Thorne's treatment. However, pollen data do not support this alliance; pollen of the Buxaceae is predominantly polyporate (Erdtman, 1952), and pollen of the Brunelliaceae, although tricolporate, is prolate with reticulate exine sculpturing (Cuatrecasas, 1970; similar to Group I pollen, this study). *Leitneria* (Leitneriaceae) is interesting because it has many features intermediate between Groups I and III. Its oblate shape and microperforate exine is characteristic of many Group III taxa and its tricolporate apertures are similar to some Group I taxa. In the compressed state (fossil pollen), it has a triradiate polar thickening (Fig. 53) that is reminiscent of some fossil normapollis types (e.g., some *Plicapollis*), a fossil group of dispersed pollen believed to be (in part) related to some Hamamelidae.

Group III taxa form the largest and closest knit phenetic group of the three. Results of the cladistic analysis show that the branching patterns among *Nothofagus, Balanops,* Rhoipteleaceae, Betulaceae, Myricaceae, Casuarinaceae, and Juglandaceae cannot be resolved based on pollen. The remaining taxa, all members of the Urticales, exhibit a high degree of paraphylesis (Text-Fig. 3). The phenetic and cladistic analyses based on pollen support Cronquist's (1981) treatment of these families. Thorne (1973) has argued for the placement of the Rhoipteleaceae, Juglandaceae, and Myricaceae in his Rutiflorae and suggested a close relationship of these families to the Anacardiaceae taxa. Our phenetic and cladistic analyses included the genus *Pistacia,* which Thorne believes to exhibit many characteristics suggestive of this alliance, a relationship our pollen data fails to support (Figs. 70, 71; Text-Figs. 1–3). The pollen characters that define Group III taxa (2–3 to many equatorially placed pores or short colpi, microchanneled tectum, columellate-granular infrastructure, thin footlayer, and thin endexine) represent a unique array of features in the dicots. The Poaceae with wind-pollinated porate pollen are the only family that show some convergence with Group III taxa, but this family has major differences in the placement and structure of the aperture; the annulate, distally located pores of pollen of the Poaceae are constructed by a thickening of the basal layer (Skvarla & Larson, 1966). The protruding pores in Group III taxa (aside from being equatorial apertures) are constructed by an elaboration of the tectum and infrastructure (Text-Fig. 7F–I). Thorne suggested that these taxa, as defined by Cronquist (1981), be separated into two different subclasses. Given the unique combination of characters in Group III, this suggestion finds little support in our analyses. The pollen data presented here lend support to Cronquist's system (1981). The following discussion of phylogenetic relationships of the Hamamelideae relies on the acceptance of these groups as monophyletic (sensu Cronquist, 1981).

The results of the phenetic and cladistic analyses are especially interesting when compared with the recent analysis by Barabe et al. (1982) and what is currently known about the fossil record of the Hamamelidae. The similarity cluster analysis of the Hamamelidae based on vegetative and floral characteristics by Barabe et al. (1982) distinguishes three groups. Group I consists of the same taxa that make up our Group I. Recall that Group I is made up of families that Thorne (1973) and Cronquist (1981) consider "core" taxa. The discrepancy between the analysis of Barabe et al. (1982) and our phenetic analysis concerns the relationship of Group II taxa to Groups I and III and the composition of Groups II and III.



TEXT-FIGURE 4.—A. Phenetic relationships of the major groups recognized by Barabe et al. (1982). Except for the taxa listed above the groups, taxa within that group are the same as in our groups.—B. Phenetic relationships of the major groups determined in our analysis.—C. Phylogenetic relationships of the groups based on the fossil record.—D. Phylogenetic relationships of the major groups based on a cladistic analysis of the pollen characters and first occurrence of the pollen types represented by each group.

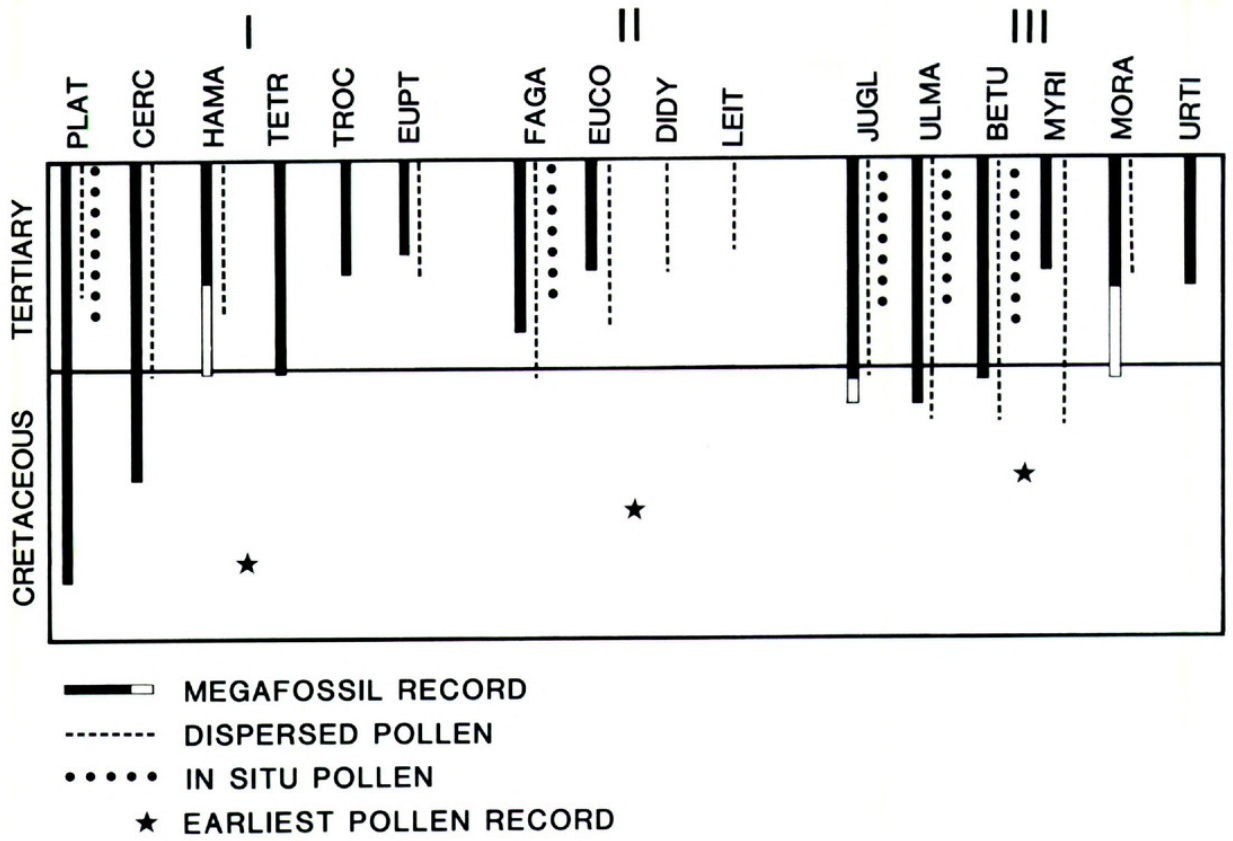
Group II of Barabe et al. (1982) consists of *Leitneria, Barbeya,* members of our Group II, Didymelaceae (not considered in our analysis), *Balanops* (a rather isolated member of our Group III), Casuarinaceae (member of our Group III), and Eucommiaceae (member of our Group I). However, in our study, *Eucommia* occurs as an isolated member between Groups I and II in the complete linkage strategy and between Groups II and III in the unweighted pair group strategy. Group III of Barabe et al. (1982) is very similar to our Group III except for their inclusion of the Fagaceae (Text-Fig. 4). The Fagaceae are members of our Group II. The general picture that emerges from their analysis is that Groups II and III are phenetically closer to each other than to Group I (Text-Fig. 4A). In our phenetic analysis of the pollen groups, I and II are closer to each other than either is to Group III (Text-Fig. 4B).

The relatively close agreement between the phenetic analysis of Barabe et al. (1982) and ours, especially in terms of the members of each group and the phenetic relationship between the three groups using different sets of characters, underscores the gradational nature of pollen, floral, and vegetative features among members of the three groups.

The results of the cladistic analysis compare well with the phenetic analyses of Barabe et al. (1982) and that presented in this study (Text-Fig. 4D). For the most part, the members of each phenetic group are maintained in the same relative position in the cladogram (Text-Fig. 4). The cladistic analyses indicate that Group I taxa are primitive. Group II taxa show features of Group I and III (and are intermediate between them), and Group III taxa are derived. However, the branching patterns within each of these groups are difficult if not impossible to resolve based on pollen data alone and will require an analysis that includes a wider range of characteristics than available in pollen.

The choice of *Tetracentron* (Trochodendrales) as our outgroup (see above), and the use of parsimony to derive the other taxa, orders the pollen characters (Text-Fig. 5). The pollen unit is predominantly a monad in all three groups. The occurrence of tetrads in the Myrothamnaceae is considered a derived condition. Pollen shape is primarily prolate in the primitive groups and oblate in the derived taxa. Likewise, shape in polar view ranges from circular in primitive taxa to angular in the derived groups. The tectum varies from reticulate in Group I to microperforate in Group II to microchanneled in Group III. Pollen wall structure is columellate in Groups

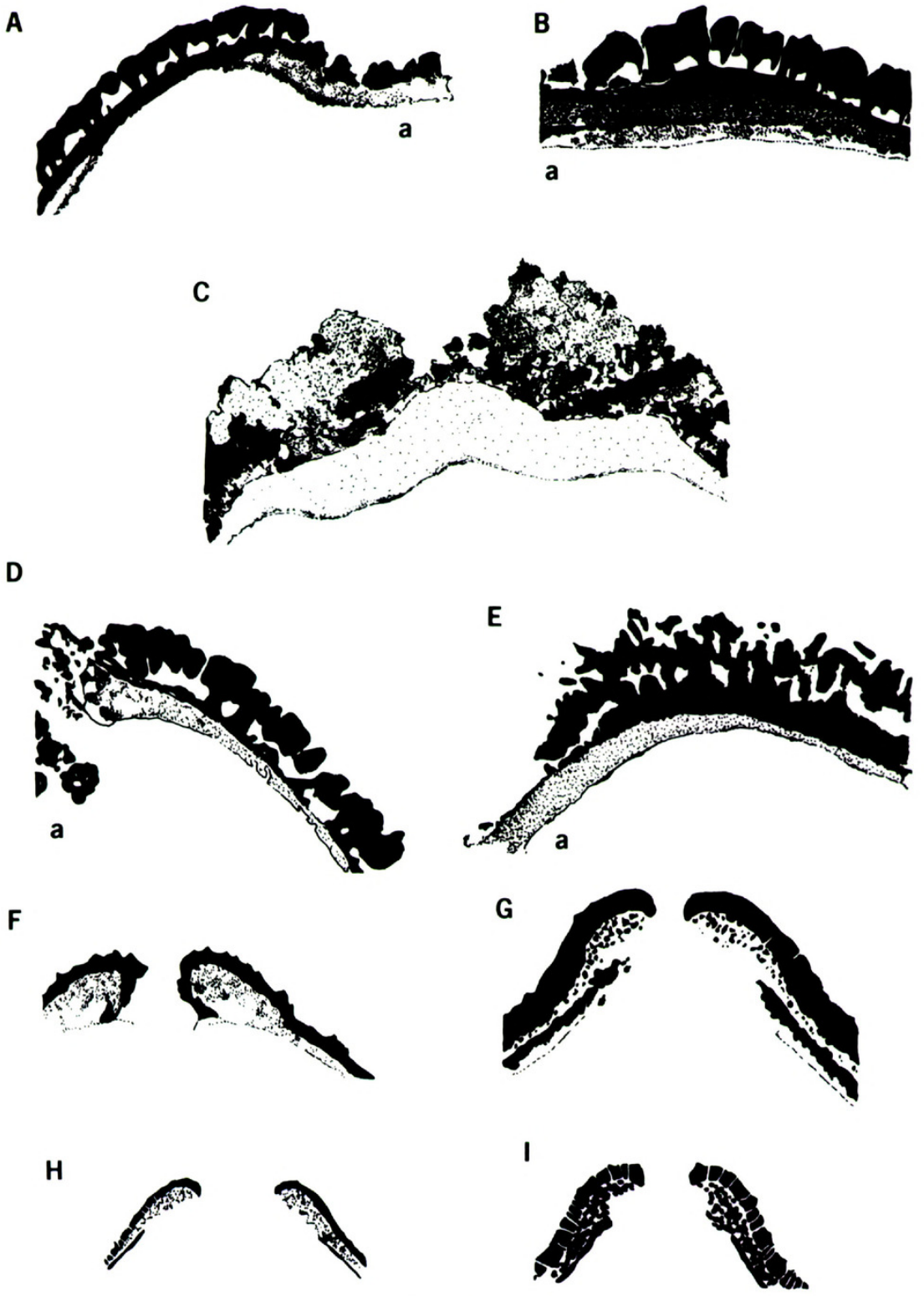
TEXT-FIGURE 5. Evolutionary trends of pollen characters in the Hamamelidae, based on a phenetic and cladistic analysis of extant pollen.



TEXT-FIGURE 6. The known fossil record of hamamelidaceous taxa. The earliest pollen record (*) is the earliest record of pollen similar to that found in the Hamamelidae group (not necessarily of hamamelid affinity). Compiled from Wolfe (1973), Manchester (1981), Jones (1984), Zavada and Crepet (1981), Upchurch (1984), and Crane (pers. comm.).

I and II (the plesiomorphic condition) and columellate to granular in Group III, with some taxa having an infrastructure composed of columellae-like elements and granules (e.g., *Balanops, Betula, Celtis*). The footlayer is present in all taxa except *Barbeya,* and this is considered a derived state. Pollen aperture type is predominantly tricolpate in Group I taxa and is considered the plesiomorphic condition. The periaperturate type may occur in Group I taxa (e.g., *Altingia*) but is considered a derived type in this group. Group II taxa are primarily tricolporate and Group III porate. Although it is convenient to consider Group II as an intermediate aperture type between I and III, it is just as likely that the porate type of Group III is derived directly from the tricolpate type. Thus, the aperture type of Group III can conceivably be derived from the Group II type (tricolporate) or Group I type (tricolpate). However, the most parsimonious transition is from the tricolpate type to porate condition because such a transition does not first require the evolution of the pore and then the reduction of the colpus, but only a reduction of the colpus. The polyporate pollen of the Liquidambaroideae (Group I) is also believed to be derived directly from the colpate condition based on its close phylogenetic relationship to the colpate pollen of some Hamamelidaceae.

The fossil record is also important in interpreting the neontological data. As indicated by the cladistic analysis, we might expect Group I taxa to appear first in the fossil record. The Platanaceae and Cercidiphyllaceae both appear before any of the other hamamelidaceous taxa, corroborating to some extent the neontological data (Text-Fig. 6). Group II taxa, however, appear as megafossils later than Group III taxa (Text-Fig. 6). This situation taken at face value supports our earlier suggestion that Group III taxa are as likely to be derived from Group I as Group II taxa. Thus, the order in which Groups II and III are derived would be reversed (Text-Fig. 3C). If the first occurrence in the fossil record of the pollen type for each of the three groups is considered, we find that Group I pollen appears first,



TEXT-FIGURE 7. A–E. Representative Group I and II taxa with endo-thickenings in the apertural region (redrawn) (a = aperture).—A. *Rhodoleia championii*; ×12,540.—B. *Leitneria floridana*; ×12,540.—C. *Barbeya oleoides*; ×8,094.—D. *Fagus crenata*; ×10,500 (redrawn from Crepet & Daghlian, 1980).—E. *Quercus spinosa*; ×13,250 (redrawn from Crepet & Daghlian, 1980). F–I. Representative Group III taxa with exo-thickenings in the apertural region.—F. *Cannabis sativa*; ×8,094.—G. *Rhoiptelea chiliantha*; ×13,500 (redrawn from Stone & Broome, 1971).—H. *Pterocarya delavayi*; ×3,700 (redrawn from Stone & Broome, 1975).—I. *Juglans mollisa*; ×8,200 (redrawn from Stone & Broome, 1975).

Group II shortly thereafter, and then Group III (Text-Fig. 6). However, unless these pollen types can be taxonomically related to the Hamamelidae, this cannot be construed as strong support for the intermediate position Group II seems to occupy based on the neontological data. However, the elucidation of the taxonomic affinities of many of the dispersed pollen taxa of the Normapollis group may have an influence on our interpretation of Hamamelid phylogeny. Many of these dispersed pollen types are believed to be related to amentiferous taxa (Kedves & Dinitz, 1981). Kedve's (1981, 1983) recent treatment of this fossil-dispersed pollen group is relevant; he recognized three major groups: probrevaxones, normapolles, and postnormapolles. Grains of the probrevaxones group are tricolporate with short colpi, have tectate-columellate wall, and reticulate to psilate to slightly verrucate-scabrate exine sculpturing. The germinal aperture lacks an annulus. Kedves (1981) subdivided the normapolles group into three subgroups: pronormapolles, eunormapolles, and paranormapolles. The pronormapolles are similar in many respects to the probrevaxones types except that they possess endannuli (a thickening in the inner part of the apertural region (e.g., *Complexiopollis, Limaipollenites*; Kedves & Pardutz, 1982). Members of the pronormapolles have, in addition to the tricolpate aperture, a microperforate exine and tectate columellate wall; shape is oblate in equatorial view and angular in polar view. The characters observed in both the probrevaxones and pronormapolles are similar to those in Groups I and II in our analysis. These pollen types are the stratigraphically earlier types and are considered the primitive types by Kedves (1983). The taxa of the subgroups eunormapolles and paranormapolles have many characteristics of our Group III taxa (columellate-granular infrastructure, thin basal layer, oblate equatorial shape, and circular to slightly angular shape in polar view; Stanley & Kedves, 1975; Kedves & Stanley, 1976). The presence of the annulate porate aperture is also common. In these fossil taxa the annulus is constructed of ektexinal material; this is also observed in the extant Group III taxa (Text-Fig. 7; compare Groups I and II taxa A–E with Group III taxa F–I). In addition to sharing many characteristics with Group III taxa, the Eunormapolles and paranormapolles taxa occur stratigraphically higher. Although the taxonomic affinities of the probrevaxones and pronormapolles groups are unknown, their chronistic relationship to the other normapolles—along with a suite of characters suggestive of Group II (or some Group I) taxa—makes it tempting to speculate that the probrevaxones and pronormapolles are hamamelidaceous taxa possibly related to some of the relictual Group II taxa of the extant Hamamelidae. However, elucidation of the taxonomic affinities of these dispersed pollen types will be much better understood when their attachment to megafossils is known. Until this is accomplished, the importance of this fossil material in determining the phylogenetic relationships of the Hamamelidae will remain speculative.

In summary, the phenetic and cladistic analyses based on pollen morphological data suggest the Hamamelidae as defined by Cronquist (1981) are a reasonably circumscribed subclass, and are in general agreement with other phenetic analyses (e.g., Barabe et al., 1982).

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APPENDIX I

Taxon	Collection	Locality	Herbarium
Altingia obovata Mers et Chun	*Liang 64734*	China	US
Balanops vitiensis (A. C. Smith) Hjedruqvist	*Degener 15519*	Fiji	US
Barbeya oleoides Schweinf.	*Burger 1926*	Ethiopia	US
Betula alba L.	*Knowlton*, 5/13/1933	Vermont	IU
Cannabis sativa L.	*Chase*, 8/23/1899	Illinois	IU
Casuarina stricta Ait.	*Christophel 3531*	Australia	–
Cercidiphyllum japonicum Sieb. et Zucc.	*Ya Tokuburchi s.n.*, 1891	Sapporo, Japan	US
Corylopsis pauciflora Sieb. et Zucc.	*Blaney 57613*	Japan (Cult.)	NYBG
Corylopsis willmottiae Rehol. et Wils.	*Rock 8127*	China	US
Daphniphyllum calycinum Benth.	*Chun 6428*	China	US
Daphniphyllum gracile Guff.	*Brass s.n.*	New Guinea	US
Daphniphyllum himalayense var. *chartaceum* (Rozenth.) Uuang	*Datla s.n.*	Siwalik	US
Daphniphyllum laurinum (Benth.) Bail.	*Boeea 7381*	Sumatra	US
Daphniphyllum neilgherrense (Wight) Thw.	*Bernardi 15811*	Ceylon	US
Disanthus cercidifolius Maxim.	*Maelsawa 409*	Japan	US
Dorstenia sp.	Coll. Ig. nom. *s.n.*	Connecticut (Cult.)	CONN
Eucommia ulmoides Oliv.	Coll. Ig. nom., 4/27/1932	Brooklyn Botanical Garden	BKL
Euptelea polyandra Sieb. et Zucc.	*Kobayashi & Oonisi 34579*	Japan	US
Exbucklandia populnea (R. Br. ex Griff.) R. W. Brown	*Rock 7574*	China	US
Fothergillia major Lodd.	*Hurbison 5930*	Georgia	US
Fothergillia monticola Ashe	*Walker 9816*	Pennsylvania	US
Gymnostoma deplancheanum (Miq) L.J.	*Christophel 3488*	New Caledonia	–
Hamamelis japonica Sieb. et Zucc.	*Konta 4923*	Japan	US
Hamamelis vernalis Sarg.	*Sally 1018*	Arkansas	US
Hamamelis virginiana L.	*Fosberg 45888*	Virginia	US
Leitneria floridana Chapm.	*Demaree 31693*	–	IU
Liquidambar styraciflua L.	*Burbank 2012*	Georgia	US
Lorapetalum chinense Oliv.	*Tsung 23400*	China	US
Matudaea hirsuta Lundell	*Bogle 848*	Mexico	US

APPENDIX I. Continued.

Taxon	Collection	Locality	Herbarium
Myrica asplenifolia L.	*Deam 27402*	Indiana	IU
Myrothamnus flabellifolia Welw.	*Bayliss* BS/1762	Swaziland	US
Myrothamnus moschatus Bail.	*Fosberg 52576*	Madagascar	US
Pistacia terebinthus L.	*Young 9105*	Italy	IU
Platanus gentryi Nixon et Poole	*Gentry 5862*	Sinaloa, Mexico	MICH
Platanus kerrii Gagnep.	*Langson 8745*	Vietnam	—
Platanus mexicana Moric.	*Ventura 596*	Veracruz, Mexico	ENCB
Platanus mexicana Moric.	*Vela*, 2/22/1962	Puebla, Mexico	ENCB
Platanus occidentalis L. var. *occidentalis*	*Poole & Watson 2522*	Texas	TEX
Platanus racemosa Nutt.	*Ferris 8505*	Baja, California, Mexico	DS
Platanus racemosa Nutt.	*Elmer 3831*	California	NY
Platanus rzedowski Nixon et Poole	*King 3900*	San Luis Potosí, Mexico	MICH
Platanus wrightii Wats.	*Frye & Frye 2271*	Sonora, Mexico	DS
Platanus wrightii Wats.	*McVaugh 8105*	Hidalgo, Mexico	MICH
Populus deltoides Marsh	*Welch 5436*	Indiana	IU
Rhodoleia championii Hook. F.	*Hu*, 1/14/1972	Hong Kong	US

APPENDIX II

Appendix II lists the presence (1) or absence (0) of the 30 character states for each of the 78 taxa (OTUs). The * indicates the outgroup used in the cladistic analysis.

1	Tricolpate	TET SIN	*Tetracentron sinense*	HEM DAV	*Hemiptelea davidii*
2	Periporate	CER JAP	*Cercidiphyllum japonicum*	HOL INT	*Holoptelea integrifolia*
3	Pericolpate			PHY RHA	*Phyllostylon rhamnoides*
4	Triporate	EUP SPP	*Euptelea* spp.		
5	Atectate	PLA SPP	*Platanus* spp.	PLA AQU	*Planera aquatica*
6	Stephanocolpate	MYR SPP	*Myrothamnus* spp.	ULM SPP	*Ulmus* spp.
7	Tricolporate	LIQ STY	*Liquidambar styraciflua*	ZEL SER	*Zelkova serrata*
8	Stephanoporate	ALT OBO	*Altingia obovata*	CAN SAT	*Cannabis sativa*
9	Diporate	RHO CHA	*Rhodoleia championii*	DOR SP	*Dorstenia* sp.
10	Monads	EXB POP	*Exbucklandia populnea*	LEI FLO	*Leitneria floridana*
11	Tetrads	DIS CER	*Disanthus cercidifolius*	RHO CHI	*Rhoiptelea chiliantha*
12	Prolate	HAM SPP	*Hamamelis* spp.	PLA STR	*Platycarya strobilacea*
13	Spherical	LOR CHI	*Loropetalum chinense*	ENG ROX	*Engelhardtia roxburghiana*
14	Oblate	COR SPP	*Corylopsis* spp.		
15	Intectate	FOT MAJ	*Fothergilla major*	ENG RIG	*Engelhardtia rigida*
16	Semitectate	FOT MON	*Fothergilla monticola*	ENG SPI	*Engelhardtia spicata*
17	Microperforate	MAT SPP	*Matudaea* spp.	ORE SPP	*Oreomunnea* spp.
18	Microchannels	DAP GRA	*Daphniphyllum gracile*	ALF COS	*Alfaroa costaricensis*
19	Columellate	DAP LAU	*Daphniphyllum laurinum*	ALF QUA	*Alfaroa quanacastensis*
20	Granular	DAP HIM	*Daphniphyllum himalayense*	ALF GUA	*Alfaroa guatamalensis*
21	Footlayer			ALF MAN	*Alfaroa mexicana*
22	Endexine	DAP NEI	*Daphniphyllum neilgherrense*	ALF WIL	*Alfaroa manningii*
23	Endexine thickened in apertural region	DAP CAL	*Daphniphyllum calycinum*	ALF WIL	*Alfaroa williamsii*
				PTE SPP	*Pterocarya* spp.
				JUG SPP	*Juglans* spp.
24	Endexine not thickened in apertural region	EUC ULM	*Eucommia ulmoides*	CAR SPP	*Carya* spp.
		BAR OLE	*Barbeya oleiodes*	MYR ASP	*Myrica asplenifolia*
		AMP CUB	*Ampelocera cubensis*	BAL VIT	*Balanops vitiensis*
		AMP RUI	*Ampelocera ruizii*	CSN SPP	*Castanea* spp.
25	Psilate	APH ASP	*Aphananthe aspera*	CAT SPP	*Castanopsis* spp.
26	Scabrate	APH PHI	*Aphananthe philippinensis*	CHR SP	*Chrysolepis* sp.
27	Rugulate-verrucate			LIT SPP	*Lithocarpus* spp.
		CEL SPP	*Celtis* spp.	FAG SPP	*Fagus* spp.
28	Spinulose	CHA ARI	*Chaetachme aristata*	NOT SPP	*Nothofagus* spp.
29	Clavate	GIR SUB	*Gironniera subequalis*	QUE SPP	*Quercus* spp.
30	Striate	LOZ ENA	*Lozanella enantiophylla*	TRI VER	*Trigonobalanus verticillata*
		MIR MON	*Mirandaceltis monoica*		
		PTE TAT	*Pteroceltis tatorinowii*	ALN RUB	*Alnus rubra*
		PAR AND	*Parasponia andersonii*	BET LUT	*Betula lutea*
		TRE SPP	*Trema* spp.	COR AME	*Corylus americana*
		CHA MEX	*Chaetoptelea mexicana*	CAS SPP	*Casuarina* spp.
				GYM SPP	*Gymnostoma* spp.
				POP DEL	*Populus deltoides*
				PIS JER	*Pistacia terebinthus*
				SAL SPP	*Salix* spp.