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Pollen morphology of endemic species of the Horton Plains National Park, Sri Lanka

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Premathilake, R. & Nilsson, S. 2001: Pollen morphology of endemic species of the Horton Plains National Park, Sri Lanka. – Grana 40: 256–280. ISSN 0017-3134.

The pollen morphology of 27 endemic and palaeoecologically-important species belonging to 16 families and 20 genera from the mountain rain forests of Sri Lanka was studied using both light (LM) and scanning electron microscopy (SEM). The pollen grains exhibit a wide range of morphological characters. Their sizes (P and E) are in the range $10\text{--}53 \times 9\text{--}60\ \mu\text{m}$, and they are distributed among seven shape classes. All the taxa have radially-symmetrical pollen grains except for *Impatiens* (bilateral). The amb varies from rounded to triangular, with intermediate shapes possible. The pollen grains of all the Lauraceae species studied are inaperturate and microspinose, with a thin, fragile, perforated exine. *Sarcococca zeylanica* (Buxaceae) has pantoporate pollen grains and a *Croton*-pattern consisting of faintly striate pegs of various shapes attached or enveloping the smooth rings. Colp(orate), syncolpate to parasyncolp(orate) pollen grains with rugulate to perforate exine patterns occur in *Eugenia mabaeoides* ssp. *mabaeoides* and *Syzygium* ssp. (Myrtaceae). *Osbeckia walkeri* (Melastomataceae) has heterocolpate pollen with fossulate, foveolate to perforate exine pattern. 3-colporate, microreticulate pollen grains are met with in *Euonymus revolutus* (Celastraceae), and scabrate-microreticulate ones in *Calophyllum walkeri* (Clusiaceae). *Hedyotis lawsoniae* (Rubiaceae) pollen is microreticulate to perforate, while pollen of the *Elaeocarpus* (Elaeocarpaceae) species is 3-colporate, smooth to scabrate-perforate. *Casearia thwaitesii* (Flacourtiaceae) has 3-colporoidate pollen grains with a smooth, imperforate to occasionally sparsely perforate exine. *Mastixia* spp (Cornaceae) have a granular–perforate exine pattern, while *Adinandra lasiopetala* (Theaceae) has a smooth-perforate exine pattern.

Triangular 3 (4)-colporate, and indistinctly faintly microreticulate-perforate pollen was found in *Rhamnus arnottianus* (Rhamnaceae), rugulate-perforate in *Isonandra montana* (Sapotaceae) and verrucate-perforate in *Symplocos elegans* (Symplocaceae). *Glochidion coriaceum* (Euphorbiaceae) has a 5-colporate grain with a coarsely reticulate exine pattern. Pollen grains of *Impatiens walkeri* and *I. thwaitesii* (Balsaminaceae) are bilateral, 4-colpate, reticulate and granular. A pollen key based on light microscope is constructed for all the taxa studied.

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The Horton Plains National Park ($6^{\circ}46'\text{--}6^{\circ}51'\text{N}$ and $80^{\circ}45'\text{--}80^{\circ}50'\text{E}$) is part of the third and highest peneplain of Sri Lanka (Fig. 1), located between 2100 m and 2300 m above sea level. The second and third highest mountain peaks in Sri Lanka, Kirigalpotta (2398 m a.s.l.) and Totupola (2359 m a.s.l.), rise up from these plains. It covers an area of 3160 ha in the central, mountainous part of the country and is demarcated as a National Park for the preservation of the montane ecosystem and its habitats. The vegetation of the Horton Plains consists of upper montane rain forests and grasslands. Totally, 57 woody species belonging to 31 families have been encountered whereof 50% are endemic to Sri Lanka (Balasubramaniam et al. 1993).

Evidence relevant to the late Quaternary vegetation and climate history of the Horton Plains National Park has been obtained by the analysis of pollen from sedimentary sequences (Premathilake 1997, 2000). The area was occasionally inhabited by a prehistoric human population between 14,000 and 3000 ^{14}C years BP. Although this evidence indicates that changes in climate and vegetation have occurred, a solid pollen-analytical background for the

Horton Plains is not yet fully available, because of a lack of comprehensive pollen morphological studies. Premathilake et al. (1999) presented an introductory paper on the pollen morphology of four selected species from the National Park. The present study was undertaken to provide reference material for pollen analysis of late Quaternary deposits in the Horton Plains. This work involves the examination of 27 endemic species belonging to 20 genera and 16 families. It is also the first of its kind related to a pollen flora of Horton Plains, Sri Lanka, apart from the previously published paper by Premathilake et al. (1999). In selecting the material, special attention was given to the following factors: (1) Endemicity of the species. (2) Status as ecological indicator species e.g., with respect to climate and human impact (Fig. 2). (3) Presence in the late Quaternary sequences from the Horton Plains. (4) Representation in the present vegetation of the Horton Plains (Dassanayake et al. 1980–2000).

MATERIAL AND METHODS

Polliniferous material of all the species studied was collected from the National Herbarium, Peradeniya, Sri Lanka (PDA).

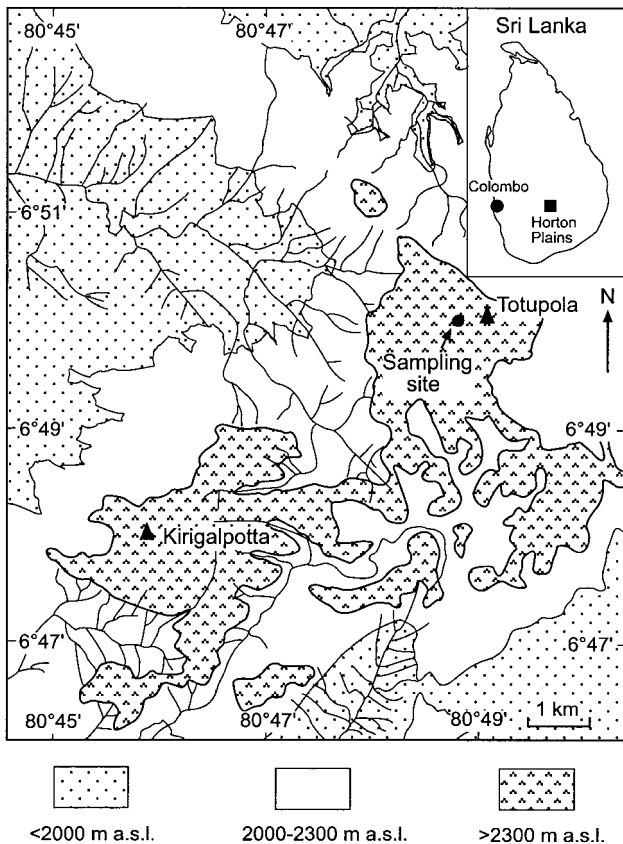


Fig. 1. Map showing the main topographical features of the Horton Plains and surrounding area. Dendritic patterns indicate major streams (modified and re-drawn from Deraniyagala 1992). Inset map of Sri Lanka.

Abbreviations are in accordance with the Index Herbarium (Holmgren et al. 1990).

The acetolysis method (Erdtman 1960) was used to process pollen material, which was then mounted in glycerine jelly on a glass slide with a cover slip sealed with paraffin. Permanent slides for Lauraceae species were made from non-acetolyzed, fuchsin-stained pollen grains.

All the species were studied under an Axiophot microscope (LM) with photo equipment at the Department of Quaternary Research (DQR), nowadays the Department of Physical Geography and Quaternary Geology, Stockholm University, Sweden, and Post-graduate Institute of Archaeology (PGIAR), University of Kelaniya, Sri Lanka. More than ten pollen grains of each species were measured in the polar axis and equatorial diameter then mean values were calculated. Exine thickness was measured at the centre of the mesocolpia of pollen grains in polar view, including microspines in all the species of Lauraceae. Leitz, Laborlux-S and Zeiss, Axioplane 2 microscopes were used for LM micrography. A Sanyo video camera, Image Access programme together with bright fields was used for LM photography in Axioplane 2 microscope.

For scanning electron microscopy (SEM), acetolysed pollen grains were mounted on aluminium stubs and coated with gold. The SEM studies were carried out at the Palynological Laboratory, Swedish Museum of Natural History, and the DQR. The terminology used follows Punt et al. (1994). E_1 and E_2 correspond to length of the longest and shortest axes in horizontal plane of the bilateral pollen grains, respectively.

The nomenclature of the taxa follows Dassanayake et al. (1980–2000). A pollen key has been constructed and limited to the endemic species studied.

RESULTS

Balsaminaceae

Impatiens walkeri (Fig. 3 A–C)

LM. – Pollen grains 4-colpate, $(38-)40(-43)$ (E_1) $\times$ $(28-)31(-35)$ (E_2) μm , bilateral. Colpi very short, located near the corners of the elliptic amb. Exine, c. $1 \mu\text{m}$ thick, sexine as thick as nexine, coarsely reticulate, heterobrochate, muri c. $1 \mu\text{m}$ wide, simpli- to duplicolumellate. Lumina of different sizes and shapes, $\pm$ rounded, $2-5 \times 2-3 \mu\text{m}$ in diameter; with relatively few granules.

SEM. – Muri usually simplicolumellate, lumina $\pm$ rounded; cf. *I. thwaitesii*

Impatiens thwaitesii (Fig. 3 D, E)

LM. – Pollen grains 4-colpate, $(35-)36.5(-38)$ (E_1) $\times$ $(20-)23(-26)$ (E_2) μm , bilateral. Amb elliptic and colpi very short, located near the corners of the amb. Exine $1-2 \mu\text{m}$ thick, sexine as thick as nexine, reticulate, heterobrochate, muri c. $1 \mu\text{m}$ wide, duplicolumellate. Lumina $2-5 \times 2-3 \mu\text{m}$, angular, decreasing in size towards the colpi and filled with numerous granules.

SEM. – Lumina angular; cf. *I. walkeri*.

Buxaceae

Sarcococca zeylanica (Fig. 4 A–D)

LM. – Pollen grains pantoporate; $15-18$ pores, $(35-)38.5(-42)$ μm in size, spheroidal. Pores circular, $3-4 \mu\text{m}$ in diameter. Exine $5-6 \mu\text{m}$, sexine much thicker than nexine, with *Croton*-pattern, consisting of $5-18$ peg-like elements on top of attached to or enveloping a ring, triangular to rectangular in shape, bacula-like in optical cross-section.

SEM. – The peg-like elements on top of or enveloping the smooth ring that delimits the foveoloid areas are of different shapes, with a faintly striate surface pattern. The pores are not always distinctly delimited (Fig. 4 D, arrowhead) and appear to be covered with granular elements.

Celastraceae

Euonymus revolutus (Fig. 5 A–F)

LM. – Pollen grains 3-colporate, $(20-)23.5(-27) \times (24-)27(-30)$ μm , suboblate to oblate spheroidal ($P/E = 0.83-0.96$). Amb rounded to sub-angular. Apocolpia c. $6 \mu\text{m}$ in diameter. Colpi long, $18-23 \times 1-2 \mu\text{m}$, with acute ends and thickened margins. Ora $5-7 \times 2-3 \mu\text{m}$, lolongate. Exine $3-4 \mu\text{m}$ thick. Sexine as thick as nexine, gradually thinning towards the colpus margin, coarsely reticulate, simplicolumellate. The lumina decrease markedly in size towards the colpus margin and in the polar areas.

SEM. – Lumina $0.5-2 \mu\text{m}$, rounded to angular, elongated to slit-like, decreasing in size towards the colpus margin.

Clusiaceae

Calophyllum walkeri (Fig. 5 G–K)

LM. – Pollen grains 3-colporate, $(35-)38.5(-41) \times (33-)37.5(-42)$ μm , spheroidal to subprolate ($P/E = 0.97-1.14$). Amb more or less sub-angular. Apocolpia c. $9 \mu\text{m}$ in

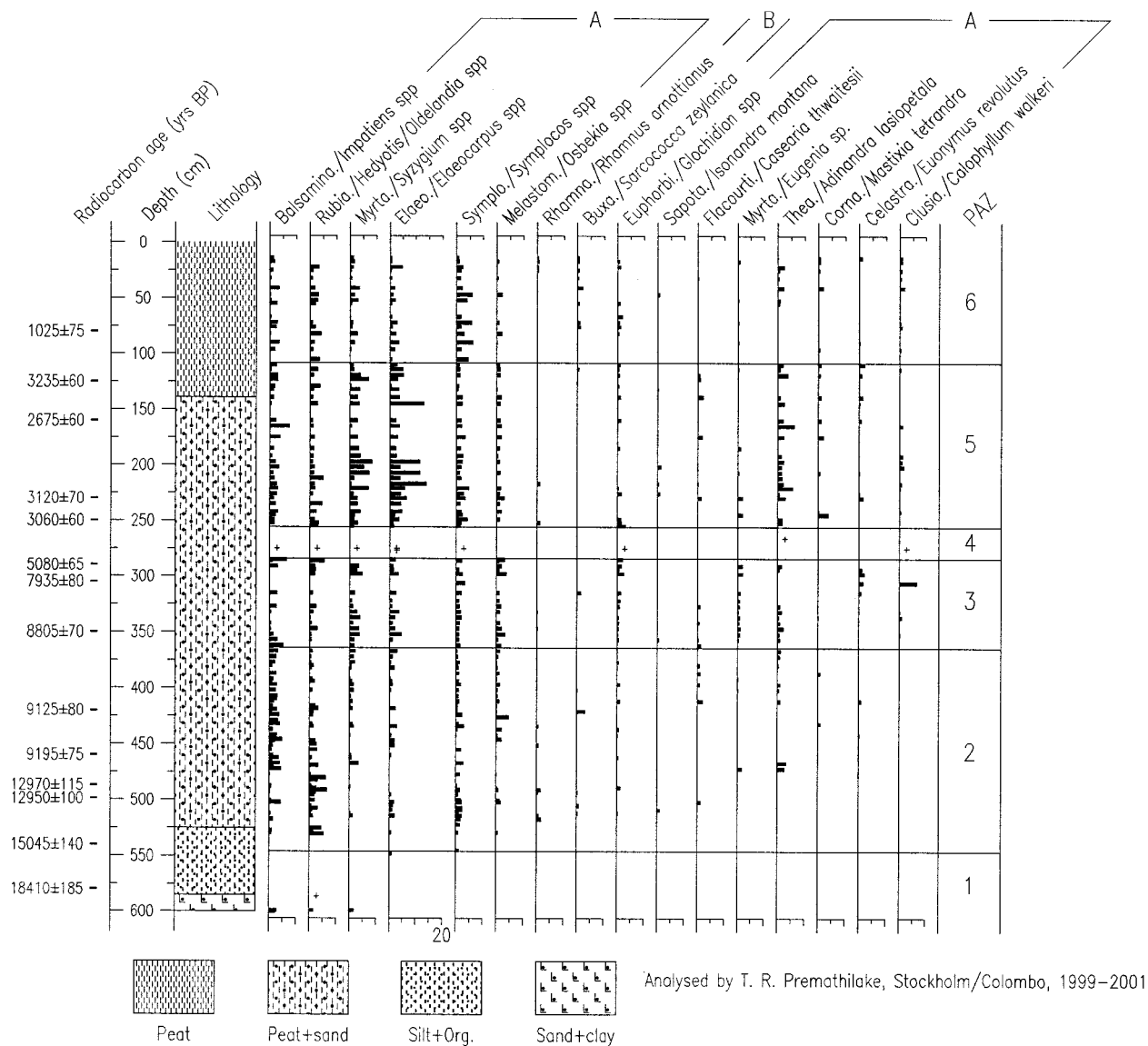


Fig. 2. Pollen diagram from the late Quaternary sedimentary sequence at the Horton Plains showing the succession of 16 taxa studied in this paper. *Syzygium* spp., *Elaeocarpus* spp and *Symplocos* spp are the most common tree taxa found in the sequence indicating change in climate from semi-arid to humid condition (Group A). *Rhamnus arnottianus* and *Sarcococca zeylanica* are shrubs associated with human activities (Group B). Location of the sampling site are indicated. PAZ = Pollen assemblage zone. + = occurrence.

diameter. Colpi $30\text{--}34 \times 2\text{--}3 \mu\text{m}$ long, rather wide, not rarely constricted at equator with indistinctly delimited ends and thickened margin. Ora $5\text{--}8 \times 9\text{--}15 \mu\text{m}$ long, $\pm$ rectangular. Exine $3\text{--}4 \mu\text{m}$ thick, sexine as thick as nexine, perforate.

SEM. – Sexine scabrate-perforate. Perforations of different sizes, more abundant in the polar areas; some of them are occasionally fused with adjacent ones. Scabrate elements smooth, of variable thickness and width, rounded to angular, partly keeled.

Cornaceae

Mastixia montana (Fig. 6 A–C)

LM. – Pollen grains 3-colporate, $(50\text{--})54\text{--}(58) \times (40\text{--})45\text{--}(50) \mu\text{m}$, oblate spheroidal to subprolate (P/E =

1.07–1.30). Amb more or less sub-angular. Apocolpia c. $12 \mu\text{m}$ in diameter. Colpi long $40\text{--}45 \times 2\text{--}4 \mu\text{m}$ with acute ends, margin thickened. Ora $12 \times 5\text{--}8 \mu\text{m}$ long. Exine $4\text{--}5 \mu\text{m}$ thick, sexine as thick as nexine, granular-perforate.

M. tetrandra var. *thwaitesii* (Fig. 6 D, E)

LM. – Pollen grains 3-colporate, $(43\text{--})48\text{--}(53) \times (40\text{--})44.5\text{--}(49) \mu\text{m}$, spheroidal to subprolate (P/E = 1.07–1.21), Amb, more or less sub-angular. Apocolpia c. $12 \mu\text{m}$ in diameter. Colpi long $37\text{--}47 \times 3\text{--}5 \mu\text{m}$ with acute ends, margin thickened. Ora c. $8\text{--}10 \times 12\text{--}15 \mu\text{m}$, long. Exine $4\text{--}5 \mu\text{m}$ thick, sexine as thick as nexine, granular-perforate.

SEM. – Sexine granular to microverrucate, densely perforated; perforations of different sizes and usually rounded; some perforations are fused together to form a slit.

Elaeocarpaceae*Elaeocarpus glandulifer*

LM. – Pollen grains 3-colporate, (11-)11.5(-12) × (9-)9.5(-10) μm , prolate spheroidal to subprolate (P/E = 1.10–1.20). Amb rounded, trilobate to subangular. Apocolpia 2–3 μm . Colpi 7–8 × 1–1.5 μm long with indistinct ends. Ora alongate to circular, c. 1 μm in diameter. Exine c. 1 μm thick, sexine as thick as nexine, smooth.

E. montanus (Fig. 7 A–D)

LM. – Pollen grains 3-colporate, (10-)12(-14) × (8-)9.5(-11) μm , subprolate (P/E = 1.25–1.27). Amb circular to sub-angular, trilobate. Apocolpia c. 3–4 μm . Colpi 10–11 × 1–1.5 μm long, with indistinct ends. Ora lolongate, 4 × 2 μm . Exine < 1 μm thick, sexine slightly thicker than nexine, smooth.

SEM. – Sexine smooth to scabrate-perforate; at poles with relatively large perforations separating elongated (rugulate) sexine elements.

E. obovatus (Fig. 7 E, F)

LM. – Pollen grains 3-colporate, (13-)14(-15) × (11-)11.5(-12) μm , subprolate (P/E = 1.18–1.25). Amb circular to sub-angular, trilobate. Apocolpia c. 3 μm . Colpi long, 11–12 × 0.5–1 μm , with indistinct ends, margin thickened. Ora lolongate, 2 × 1.5 μm . Exine < 1 μm thick, sexine slightly thicker than nexine, smooth.

SEM. – Sexine smooth to scabrate-perforate. Colpi constricted at the equator due to overlapping sexine (Fig. 7 E).

Euphorbiaceae*Glochidion coriaceum* (Fig. 8 A–E)

LM. – Pollen grains 5-colporate, (41-)42(-43) μm , spheroidal to prolate spheroidal (P/E 1.02). Amb rounded, slightly indented. Apocolpia 10–12 μm . Ora lolongate c. 2 × 5 μm . Colpi 30–32 × 1–2 μm with distinct, thickened margin. Exine 3–4 μm thick, sexine thicker than nexine, coarsely reticulate.

SEM. – Lumina, 2–3 μm in diameter, elongated to rounded; muri 0.5–1 μm wide. Colpus margin well delimited, smooth and narrow (Fig. 7 E, *arrow*).

Flacourtiaceae*Casearia thwaitesii* (Fig. 8 F–I)

LM. – Pollen grains 3-colporoidate, (21-)21.5(-22) × (15-)17.5(-20) μm , prolate spheroidal to prolate (P/E = 1.10–1.40). Amb, rounded. Apocolpia c. 5 μm . Colpi 15–16 × 1–1.5 μm with acute ends, colpus margin irregular and obscure. Ora indistinct. Exine 3–4 μm thick, sexine slightly thicker than nexine, very smooth.

SEM. – Sexine exceedingly smooth, only occasionally perforate.

Lauraceae*Actinodaphne ambigua* (Figs. 9 A, B & 10 A, B)

LM. – Pollen grains inaperturate, rounded (diam. 28–30 μm). Exine 1–1.5 μm thick, microspinose. Intine thicker than exine.

SEM. – Microspines < 1 μm high, cone-shaped and smooth, with a thickened, well delimited cushion at their base, c. 1 μm wide and located on a granular exine.

A. speciosa (Figs. 9 C, D & 10 C)

LM. – Pollen grains inaperturate, rounded (diam. 34–35 μm). Exine c. 1 μm thick, microspinose. Intine thicker than exine.

SEM. – Microspines 1–1.5 μm high, cone-shaped, weakly striate in appearance, with a smooth basal cushion c. 2.5 μm wide located on a granular exine. Sexine indistinctly depressed in places, with few microspines.

A. stenophylla

LM. – Pollen grains inaperturate, rounded (diam. 30–31 μm). Exine 1 μm thick, microspinose. Intine thicker than exine.

SEM. – Microspines < 1 μm high, cone-shaped, with a smooth to granular, well delimited basal cushion c. 1.5 μm in diameter on top of a granular exine. Sexine with slightly depressed and perforate areas, more or less devoid of microspines.

Cinnamomum ovalifolium (Figs. 9 E, F & 10 D)

LM. – Pollen grains inaperturate, rounded (diam. 32–34 μm). Exine < 1 μm thick, microspinose. Intine thicker than exine.

SEM. – Microspines 0.5–1 μm high, cone-shaped, on a smooth cushions < 1.5 μm wide on a granular exine. Sexine with a single delimited rounded, perforated depression beset with relatively few microspines (Fig. 10 D, *arrowhead*).

Litsea ovalifolia (Figs. 9 G, H & 10 E, F)

LM. – Pollen grains inaperturate, rounded (diam. 26–31 μm). Exine < 1 μm thick, microspinose. Intine thicker than exine.

SEM. – Sexine granular, beset with cone-like microspines, 1–2 μm high, faintly striate and often bent, on smooth cushions c. 0.5 μm wide at their base.

Neolitsea fuscata (Figs. 9 I, J & 10 G, H)

LM. – Pollen grains inaperturate, rounded (diam. 33–35 μm). Exine 1–2 μm thick, microspinose. Intine thicker than exine.

SEM. – Sexine granular, occasionally perforate, beset with cone-like microspines on cushion-like thickenings c. 2 μm wide at the base. Sexine with a well-delimited, oval-shaped area with few or no microspines (Fig. 10 G, *arrowhead*).

Melastomataceae*Osbeckia walkeri* (Fig. 11 A–E)

LM. – Pollen grains heterocolpate with alternating colpi, (30-)32(-33) × (22-)24(-26) μm , subprolate to prolate (P/E = 1.19–1.40). Amb 6-lobed. Apocolpia c. 7 μm . Colpi, 18–22 × 1–2 μm with acute ends and thickened margins. Colpori of the same length as colpi, with acute ends; the colpori often have two, alongate ora, 4–11 × 3–6 μm , separated by an exinous bridge or not rarely fused into one lolongate os. Exine 1–2 μm thick, sexine as thick as nexine, smooth to scabrate.

SEM. – Sexine undulated, folded to rugulate, fossulate to foveolate, with small perforations; sexine pattern distinctly smooth at the colpus margin and at the apocolpia.

Myrtaceae

Eugenia mabaeoides ssp. *mabaeoides* (Fig. 12 A–D)

LM. – Pollen grain 3-colp(or)ate (15-)16(-17) × (20-)25(-34) µm, oblate to suboblate (P/E = 0.75–0.50). Amb triangular, sub-angular, with straight to slightly convex sides. Colpi 11–15 µm long, sometimes the grains are syncolp(or)ate at one pole and parasyncolp(or)ate at the other. Exine 1–2 µm thick, sexine thinner than nexine, usually smooth.

SEM. – Sexine microverrucate-perforate

Syzygium rotundifolium (Fig. 12 E, F)

LM. – Pollen grains 3–syncolp(or)ate to 3–parasyncolp(or)ate, (11-)12(-13) × (16-)17(-18) µm, oblate (P/E = 0.61–0.72). Amb triangular to lobate with slightly convex-straight to concave sides. The apocolpial fields are triangular, c. 4 µm in diameter. Colpi indistinct, 7–8 × 0.5–1.0 µm, gradually tapering to acuminate. Exine c. 1 µm thick, sexine as thick as nexine, smooth to finely scabrate.

Syzygium sclerophyllum (Fig. 12 G, H)

LM. – Pollen grain 3–syncolp(or)ate to 3–parasyncolp(or)ate, (9-)9.5(-10) × (14-)14.5(-15) µm, oblate (P/E = 0.64–0.66). Amb triangular, with slightly convex sides. Apocolpial fields c. 4 µm. Colpi 7–8 × 1–2 µm, gradually tapering to acuminate. Exine 1–2 µm thick, sexine as thick as nexine, smooth.

SEM. – Sexine smooth, unevenly rugulate-perforate. Colpus margin markedly smooth.

Rhamnaceae

Rhamnus arnottianus (Fig. 13 A–G)

LM. – Pollen grains, 3–(4)-colporate (15-)21(-26) × (15-)19(-23) µm, suboblate to prolate-spheroidal (P/E = 0.80–1.1). Amb triangular. Apocolpia c. 9 µm. Colpi 12–17 × 1–2 µm, narrow, with acuminate ends and smooth irregularly wide and thick margins, which are elevated at the equator (pollen grains aspidote). Ora narrow, c. 1 × 3 µm, lalongate with a distinctly thickened margin. Exine 2–3 µm thick, sexine as thick as nexine, perforate to microreticulate.

SEM. – Sexine uneven, shallow lumina with numerous perforations at the mesocolpia; colpus margin exceedingly smooth, non-perforate and laterally protruding. Perforations and microgranular elements within the shallow lumina.

Rubiaceae

Hedyotis lawsoniae (Fig. 14 A–E)

LM. – Pollen grains 3-colporate, (20-)28(-36) × (21-)25(-29) µm, prolate spheroidal to prolate (P/E =

1.11–1.50). Amb rounded, trilobate. Apocolpia c. 8 µm. Colpi 18–24 × 1–2 µm with acute ends, margin thickened. Upper ora c. 2 µm, rounded; lower ora c. 2 × 6 µm, lalongate, with triangular-shaped extensions usually laterally fused to an equatorial band. Exine 2–3 µm thick, sexine much thicker than nexine, microreticulate.

SEM. – Sexine microreticulate to perforate. Muri smooth, curved to straight. Lumina with granules.

Sapotaceae

Isonandra montana (Fig. 14 F, G)

LM. – Pollen grains 3-(4)-colporate, (38-)39(-40) × (30-)31(-32) µm, subprolate (P/E = 1.18–1.30). Apocolpia c. 3 µm. Colpi narrow, 25–29 × 1–2 µm, slightly constricted at the equator, due to sexine protrusions with acute ends. Ora 6–10 µm lalongate and lens-shaped, margin thickened polewards. Exine 2–3 µm thick, sexine as thick as nexine, rugulate-perforate (low profile).

SEM. – Sexine rugulate, with perforations occasionally fused with adjacent ones; the sexine forms a bridge at the centre of the colpus.

Symplocaceae

Symplocos elegans (Fig. 15 A–D)

LM. – Pollen grains 3–(4) colporate, (25-)33(-53) × (36-)40(-60) µm, suboblate to oblate, spheroidal (P/E = 0.83–0.95). Amb triangular to square-shaped. Apocolpia very large, 20–32 µm in diameter. Colpi very short, 7–9 × 1–3 µm, ± oval-shaped with rounded ends and conspicuously thickened margin protruding over the os. Ora lalongate, 3–8 × 2–3 µm. Exine 1–3 µm, sexine slightly thicker than nexine, granular to finely verrucate.

SEM. – Sexine finely verrucate-perforate; verrucae larger and partly fused at the polar areas. Colpus margin markedly thickened at the apertures.

Theaceae

Adinandra lasiopetala (Fig. 15 E–G)

LM. – Pollen grains 3-colporate, (22-)24 (-27) × (19-)20(-22) µm, subprolate to prolate (P/E = 1.20–1.42). Amb rounded. Apocolpia 5–7 µm. Colpi relatively long, very narrow, 18–19 × 1–1.5 µm, with thickened margin and acute ends. Ora lalongate to rounded, c. 2 µm in diameter. Exine 1–3 µm thick, sexine slightly thicker than nexine, smooth-perforate.

SEM. – Sexine smooth and uneven, perforate at the mesocolpia. Colpus margin imperforate and exceedingly smooth.

POLLEN KEY TO SPECIES INVESTIGATED

Based on Light Microscopy.

1. Pollen grains bilateral
 2. Muri sinuous *Impatiens walkeri*
 2. Muri straight *I. thwaitesii*
1. Pollen grains radially symmetrical
 3. Inaperturate
 4. Diameter $<30\text{ }\mu\text{m}$ *Actinodaphne ambigua*, *Litsea ovalifolia*
 4. Diameter $>30\text{ }\mu\text{m}$ *A. speciosa*, *A. stenophylla*, *Cinnamomum ovalifolium*, *Neolitsea fuscata*
 3. Aperturate
 5. Porate *Sarcococca zeylanica*
 5. Not porate
 6. Colpate
 7. Syncolp(or)ate
 8. Polar axis $>15\text{ }\mu\text{m}$ *Eugenia mabaeoides* ssp. *mabaeoides*
 8. Polar axis $<15\text{ }\mu\text{m}$
 9. Amb triangular, mostly convex sides *Syzygium sclerophyllum*
 9. Amb triangular, mostly concave sides *S. rotundifolium*
 7. Not syncolp(or)ate (heterocolpate) *Osbeckia walkeri*
 6. Colporate
 10. 5-colporate *Glochidion coreaceum*
 10. 3–4-colporate
 11. Sexine psilate
 12. Ora distinct
 13. Ora lalongate
 14. Polar axis $>22\text{ }\mu\text{m}$ *Adinandra lasiopetala*
 14. Polar axis $<22\text{ }\mu\text{m}$ *Elaeocarpus glandulifer*
 13. Ora lolongate *E. obovatus*, *E. montanus*
 12. Ora indistinct *Casearia thwaitesii*
 11. Sexine not psilate
 15. Exine scabrate
 16. Ora lalongate, rectangular *Calophyllum walkeri*
 16. Ora lalongate, lens-shaped *Isonandra montana*
 15. Exine not scabrate
 17. Exine verrucate *Symplocos elegans*
 17. Exine not verrucate
 18. Exine granular
 19. Ora lolongate *Mastixia montana*
 19. Ora lalongate *M. tetrandra* var. *thwaitesii*
 18. Exine not granular
 19. Exine distinctly reticulate
 20. Coarsely reticulate *Euonymus revolutus*
 20. Microreticulate *Hedyotis lawsoniae*
 19. Exine indistinctly reticulate *Rhamnus arnottianus*

DISCUSSION

The pollen morphology of the 27 endemic species studied here is of considerable value as a taxonomic tool. The species are discussed here with reference to the families and the LM and SEM observations compared with earlier published data. The following general characters are particularly considered: symmetry, size, shape, apertures and exine patterns. The pollen grains of the investigated taxa of the following families are easily distinguished from each other on generic level: Balsaminaceae (*Impatiens*), Buxaceae (*Sarcococca*), Elaeocarpaceae (*Elaeocarpus*), Euphorbiaceae (*Glochidion*), Flacourtiaceae (*Casearia*), Lauraceae (*Actinodaphne*, *Cinnamomum*, *Litsea*, *Neolitsea*), Melastomataceae (*Osbeckia*), Myrtaceae (*Eugenia*, *Syzygium*), Rhamnaceae (*Rhamnus*), Rubiaceae (*Hedyotis*) and Symplocaceae (*Symplocos*). With special reference to the sexine pattern (SEM) the remaining taxa of the Celastraceae (*Euonymus*), Clusiaceae (*Calophyllum*), Cornaceae (*Mastixia*), Sapotaceae (*Isonandra*) and Theaceae (*Adinandra*) are well separated from each other. This present study was very useful in order to recognize the fossil pollen types in the sediment sequences analyzed, enabling a number of pollen types to be identified to even species level. Pollen of Lauraceae, one of the most common families in the present vegetation of the Horton Plains, was not recorded in the fossil pollen flora seemingly due to the fragile exine. The delimited areas observed with few or no microspines on the exine are not found to be reported earlier.

Balsaminaceae

Impatiens walkeri and *I. thwaitesii* – The two species are different as to shape of lumina and the number of granules in the lumina and their density. In *I. thwaitesii*, the floor of the lumen is filled with numerous granules, but in *I. walkeri* there are relatively fewer. In addition, the lumina of *I. thwaitesii* are more angular than those of *I. walkeri*. The muri in *I. walkeri* are sinuous compared to *I. thwaitesii*. The two species are 4-colpate, $38\text{--}43 \times 28\text{--}35\ \mu\text{m}$ and $35\text{--}38 \times 20\text{--}26\ \mu\text{m}$ with usually duplicolumellate muri. In the 14 established sections of *Impatiens*, based on morphological characters, Huynh (1968) placed *I. walkeri* in Sect. 13, distinguishing a number of pollen types, which were distributed on four pollen groups, e.g. 4-aperturate-rectangular to square grains, 3-aperturate, and 5, or less often 6-aperturate. According to his LM observations, *I. walkeri* has duplicolumellate pollen grains with a granular lumen floor (cf. above). Vasanthy (1976) described 3- to 6-colporate, reticulate pollen grains of 15 *Impatiens* species, but her observations on apertures (4-colpate pollen grains) do not agree with our results. Gupta & Sharma (1986) describe 4-colpate (very short colpi), reticulate pollen in *I. balsamina* and *I. racemosa*, and Nayar (1990) reports the same aperture conditions in *I. balsamina*.

Buxaceae

Sarcococca zeylanica – *S. zeylanica* pollen (c. $42\ \mu\text{m}$ in diameter) has a *Croton*-pattern with rectangular to triangular,

weakly-striate sexine elements on rings, which generally encompass pores. The pores (max. 18 in number) are not always distinctly delimited; the lumen floor is usually granular, with or without pore. The pollen morphology of the genus *Sarcococca* is highly variable. In describing the species *S. hookeriana* and *S. zeylanica*, Nowicke & Skvarla (1984) stated that “there is a wide range of morphological characters” in the genus. Gupta & Sharma (1986), Khan (1968), Nowicke & Skvarla (1984) found the general size of *Sarcococca* pollen to range from 35 to $42\ \mu\text{m}$ in diameter. Gray & Sohma (1964) established two major groups with reference to size differences within the genus: pollen grains with an average size exceeding $42\ \mu\text{m}$ and grains with a general size $42\ \mu\text{m}$ or below, of which *S. zeylanica* in the present study conform to the second group. Most *Sarcococca* species studied by Gray & Sohma (1964) show a wide range in pore number (18–56), and these authors established three pore-number classes (I–III), with pores being arranged in apparent isometric, pentagonal and hexagonal configurations. Pore number class III (20–29 pores) and the hexagonal configuration more or less agree with the pore number and arrangements of *S. zeylanica*, although its pores do not exceed 18 in number. Nowicke & Skvarla (1984) reported a crotonoid pattern in *S. hookeriana* and *S. zeylanica*.

Celastraceae

Euonymus revolutus – The 3-colporate pollen grains of *E. revolutus*, $20\text{--}27 \times 24\text{--}30\ \mu\text{m}$, have a rounded to subangular amb with clearly thicker exine at the centre of the mesocolpia. Lieux (1983) found a similarly thick exine, gradually thinning towards the colpus margin in *E. americanus*. Huang (1972) and Lieux (1983) reported angular to lobate amb. Pollen of the genus *Euonymus* was studied by Nair (1965), Gupta & Sharma (1986), and Tissot et al. (1994), who like Huang (1972) described pollen grains in the size range of $21\text{--}35 \times 23\text{--}29\ \mu\text{m}$, which places them in the same size class as *E. revolutus*. Gupta & Sharma (1986) found circular ora in *E. echinatus*, and indistinct ora in *E. fimbriatus*, while Huang (1972) observed lalongate ora in *E. acuto-rhombifolia*, *E. cochinchinensis*, *E. laxiflorus*, and lolongate ora in *E. revolutus*.

Clusiaceae

Calophyllum walkeri – *C. walkeri* has 3-colporate pollen grains, $35\text{--}41 \times 33\text{--}42\ \mu\text{m}$, with a scabrate-perforate exine. Seetharam (1985) reported granular colpus membranes. *C. walkeri* pollen falls within the size range of $21\text{--}50 \times 19\text{--}40\ \mu\text{m}$ reported by Seetharam for 40 species of *Calophyllum*. Seetharam (1985) concluded that the genus has reticulate pollen grains (SEM), while Xi (1979) found a rugulate to rugulo-reticulate exine in the species he studied. According to Seetharam (1985), *C. inophyllum* pollen has a densely perforated exine with perforations of similar size in the non-apertural region. These results partly agree with those for *C. walkeri*, with scabrate-perforate sexine.

Cornaceae

Mastixia montana and *M. tetrandra* var. *thwaitesii*. – Both species investigated have 3-colporate, 50–58 × 40–50 and 43–53 × 40–49 µm, spheroidal to subprolate pollen grains with lolongate (*M. montana*) and lalongate (*M. tetrandra* var. *thwaitesii*) ora. The exine is relatively thick in both species (4–5 µm thick) and granular to densely perforated. Ferguson (1977) reported oblate pollen grains, 28–49 × 29–57 µm in size, in his *Mastixia*-type. Our results agree with these as to the size variations, but not as to the shape. Ferguson (1977) reported a complex H-shaped aperture, which was not observed in our two species studied.

Elaeocarpaceae

Elaeocarpus glandulifer, *E. montanus* and *E. obovatus*. – No clear differences in pollen size were found between the *Elaeocarpus* species examined, which range from 10–15 × 8–10 µm. There are some differences in the shape of the amb, being circular, or triangular to trilobate in *E. montana* and *E. obovatus* whereas no triangular amb was found in *E. glandulifer*. The exine pattern is smooth (LM) in the *Elaeocarpus* species studied (cf. *E. serratus* in Tissot et al. 1994), but there is a scabrate-perforate sexine pattern in *E. montanus* and *E. obovatus* (SEM). Huang (1972) examined five species of *Elaeocarpus* in Taiwan with smooth, granular to indistinct sexine patterns, while Ikuse (1956) reported finely reticulate pollen of *E. sylvestris* var. *ellipticus* and *E. photiniaefolius*.

Euphorbiaceae

Glochidion coriaceum. – The pollen grains of *G. coriaceum* are ± rounded, 42 µm in average size, 5-colporate and coarsely reticulate; the colpus margin is smooth and well delimited in appearance (SEM). Gupta & Sharma (1986) and Khan (1968) reported the pollen to be less than 30 µm in diameter, 3–4-colporate and finely reticulate. According to the Khan (1968) species, *G. neilgherrense* has psilate exine pattern. *G. coriaceum* clearly differs in several respects e.g. size, number of apertures (5) from the other *Glochidion* species studied. Vasanthy (1976) reported 4-colporate, reticulate pollen grains of *G. pauciflorum*.

Flacourtiaceae

Casearia thwaitesii. – The 3-colporoidate pollen grains with completely smooth, occasionally perforated tectum (SEM) measure 21–22 × 15–20 µm. Keating (1973) listed a wide range of morphological features when describing 29 species of the genus *Casearia*, reported that the size of the 3–(4)-colporate pollen grains with lalongate ora ranges from 18–58 × 18–45 µm, amb subtriangular, and exine semi-tectate to tectate, psilate to mostly reticulate or per-reticulate. A microperforate exine was found in *C. nitida* (Keating 1975).

Lauraceae

Actinodaphne ambigua, *A. speciosa*, *A. stenophylla*, *Cinnamomum ovalifolium*, *Litsea ovalifolia*, *Neolitsea fuscata*.

– The pollen grains of all the species of Lauraceae investigated are rounded and inaperturate, and they range from 26 to 35 µm in diameter. The exine is extremely thin (less than 1.5 µm), and its granular surface is beset with microspines. The exine is in general granular-perforate, has fewer or no microspines in certain marked areas, which is regarded so far as new observations. All species have cone-shaped microspines, with an average height of 1 µm. The surface of the microspines is generally smooth, but in *A. speciosa* and *L. ovalifolia* they have a weak, striate pattern. The microspines are usually bent in *L. ovalifolia*. All the species have more or less smooth basal cushions, which are delimited by granular rings. The diameter of the basal cushions is less than 1.5 µm, except in *A. ambigua* and *N. fuscata*, which have a relatively wide basal cushion (c. 2.5 µm) with few granules on top of it. The intine is mostly thicker than the exine in all the species observed. Similar features of the exine and intine were described by Raj & Werff (1988) in most of the Lauraceae species, which they studied.

Melastomataceae

Osbeckia walkeri. – The pollen grains of *O. walkeri* are heterocolpate, 30–33 × 22–26 µm with alternating colpi and a smooth to scabrate exine (LM). In SEM the exine is rugulate, fossulate to foveolate. The amb is hexalobate. According to Vasanthy (1976) and Erdtman (1952), pollen grains of the genus are 3-colporate with three pseudocolpi. The exine pattern of *O. leschenaultiana* is reported rugulate to areolate (Vasanthy 1976). A smooth to obscure exine pattern was found in *O. stellata* (Gupta & Sharma 1986), while the exine in *O. polycephala* (Patel et al. 1984) is reported to be verrucate to rugulate. Guers (1974) recognized a striate exine pattern in *O. decandra* and *O. tubulosa* (LM) and scabrate pattern in *O. praviantha* (SEM).

Myrtaceae

Eugenia mabaeoides ssp. *mabaeoides*, *Syzygium rotundifolium*, and *S. sclerophyllum*. – The pollen grains of the two genera are 3-colp(or)ate, 3-syncolpate to 3-parasyncolp(or)ate, usually with a smooth exine (LM), verrucate (SEM) in *Eugenia*, or finely scabrate, rugulate, perforate in LM and faintly rugulate-perforate in *Syzygium* (SEM). The pollen of *Eugenia* is in the size range 15–17 × 20–34 µm and that of *Syzygium* 9–13 × 14–18 µm. The amb is triangular to subtriangular in *Eugenia* and *S. sclerophyllum*, but lobate (concave mesocolpia) to subtriangular in *S. rotundifolium*. Wyk & Dedekind (1985), in their detailed study of the pollen morphology of male and hermaphrodite flowers of *Eugenia* in southern Africa, distinguished two major pollen types. Type A, includes syncolpate to indistinctly parasyncolpate grains, more or less similar to *E. mabaeoides*, and type B, which consists of inaperturate or colpate grains. They also described microscabrate, microrugulate and rugulate exine patterns in the genus. Our observation, that the colpus membrane of *E. mabaeoides* ssp. *mabaeoides* lies over the poles and is usually covered by verrucae or gemmae, is in agreement with that of Wyk & van der Dedekind (1985). Similarly, 3-syncolpate, rugulate pollen was found in *E. capuli* (Patel et al. 1984).

and 3-colporate, scabrate pollen in *E. thwaitesii* (Tissot et al. 1994). 3-colporate grains have been reported in *E. mabaeoides* ssp. *mabaeoides*. It was possible to separate the two species of *Syzygium* by reference to the shape of the amb, which had mostly concave sides in *S. rotundifolium* and straight or slightly convex sides in *S. sclerophyllum*. Vasanthy (1976) found parasyncolpate, syncolpate and psilate to scabrate pollen grains in *S. arnottianum* and *S. montanum*, while Tissot et al. (1994) described 3-syncolporate and smooth pollen for *S. gardneri*, *S. laetum*, *S. mundagam*, and *S. occidentale*. Gupta & Sharma (1986) and Chauhan & Bera (1990) described 3-colporate, parasyncolpate pollen grains with an obscure exine pattern (*S. cuminii*), and Nayar (1990) reported both parasyncolporate and tetrazonocolporate pollen grains with psilate patterns in *S. cuminii*. The latter author also recognized three subtypes of *S. heyneanum*. His subtype I being similar in its morphological features to the pollen of *S. rotundifolium* and *S. sclerophyllum* but with differences as to aperture conditions. Sowunmi (1973) and Bonnefille (1971) reported 3–4-colporate pollen grains in *S. guineense*. Pollen grains of five *Syzygium* species in the flora of Taiwan (Huang 1972) were described as 3 (4)-colporate or syncolporate.

Rhamnaceae

Rhamnus arnottianus. – The pollen grains of *R. arnottianus* are 3-(4)-colporate, $15\text{--}26 \times 15\text{--}23\ \mu\text{m}$, suboblate to prolate-spheroidal, amb triangular, perforate to faintly microreticulate. There are perforations and granular elements in the shallow, rounded suprastectal (?) lumina (SEM). The colpus margin is relatively broad and smooth, with only a few perforations; the colpus widens at the equator and the lateral, sexinous aperture margin protrudes over the os. The polar areas are thickened and smooth. The *Rhamnus*-type of pollen is reported to be oblate-spheroidal to spheroidal in *Krugiodendron ferreum* and *Karwinskia oblongifolia* (Schirarend & Köhler 1993), and the same authors report straight to convex mesocolpia, protruding apertures and elliptic to circular shapes in equatorial view. Our results for *R. arnottianus* are in good agreement with these observations. Similarly, Miyoshi (1987) studied two species of *Rhamnus* (*R. crenata* and *R. japonica*), which are similar to *R. arnottianus*. Lobreau-Callen (1976) described suprareticulate and rugulate exine patterns in *R. utilis*.

Rubiaceae

Hedyotis lawsoniae. – Pollen grains of *H. lawsoniae* are 3-colporate (with compound ora), $20\text{--}36 \times 21\text{--}29\ \mu\text{m}$ and microreticulate to perforate with straight muri. There are distinct granules within the lumina. The 31 species of *Hedyotis* were divided into 5 palynological groups by Lewis (1965) on the basis of aperture structure; groups 2–4 being characterized by compound ora. In general, the pollen of *H. lawsoniae* resembles the description by Lewis (1965). Bahadur & Swamy (1993) observed thrum and pin pollen in *H. caerulea* and *H. procumbens*, that of the former species being 3-colporate and reticulate while that of the latter was 3-colpate and reticulate. Gupta & Sharma (1986) reported

4-colpate, reticulate pollen in *H. stipulata*. These observations differ from those of *H. lawsoniae*, however. Huang (1972) described 1 to 9-colporate, finely reticulate to reticulate pollen for the genus *Hedyotis*, and according to Nair (1965), *H. hirsuta* has 3-colporate, reticulate pollen. *H. lawsoniae* clearly differs from *H. hirsuta* with respect to apertures and exine pattern.

Sapotaceae

Isonandra montana. – The pollen grains of *I. montana* are 3–4-colporate, $38\text{--}40 \times 30\text{--}32\ \mu\text{m}$ with lalongate, lens-shaped ora. The scabrate sexine (LM) that forms a bridge above the ora is rugulate-perforate (SEM). Tissot et al. (1994) reported 4-colporate pollen grains with a scabrate exine pattern for *I. lanceolata*, and our observations on *I. montana* are in agreement with this.

Symplocaceae

Symplocos elegans. – Premathilake et al. (1999) show that *S. elegans* has the same general pollen features as *S. bractealis*, but ranges in shape between suboblate and oblate spheroidal, with relatively larger apocolpia $25\text{--}53 \times 36\text{--}60\ \mu\text{m}$ in size. Van der Meijden (1970) recognized two major pollen types with the Symplocaceae: the *Symplocos*-type and the *Hopea*-type, with 11 subtypes altogether. The pollen morphology of *S. elegans* resembles that of the *Fasciculata*-subtype (*Hopea*-type). Detailed morphological studies of 25 species of Brazilian *Symplocos* by Barth (1979) enabled four pollen types to be recognized (Types I–IV). All the species studied were 2 or 3-colporate with the reference to their apertures and exine pattern, while *S. elegans* (3- or 4-colporate) in the present study appeared to be most similar to her types II and IV. Nagamasu (1989) described 23 Japanese *Symplocos* species and distinguished two major pollen types and five subtypes, in which case the pollen morphology of *S. elegans* resembles his type II, subtype II b (verrucate tectum).

Theaceae

Adinandra lasiopetala. – The pollen grains of *Adinandra lasiopetala* are 3-colporate, subprolate to prolate, $22\text{--}27 \times 19\text{--}22\ \mu\text{m}$ in size with a smooth pattern and numerous perforations concentrated at the mesocolpia, while the colpus margin is smooth and non-perforate. A similar type of pollen was observed in *A. hainanensis* (LM; Wang et al. 1995).

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SPECIMENS INVESTIGATED

All the specimens were collected from the National Herbarium, Peradeniya (PDA), Sri Lanka.

Balsaminaceae

Impatiens walkeri Hook. f. Central Province: Nuwara Eliya. 08.1980; Alston 1211; Slide nr.25348 (PL).

I. thwaitesii Hook. f. ex Grey-Wilson. Central Province: Adam's Peak. 25. 07.1970; Meijer 496; Slide nr.25351 (PL).

Buxaceae

Sarcococca zeylanica Baill. Central Province: Horton Plains. 01.11.1971; NBK 1030; Slide nr. 25329 (PL).

Celastraceae

Euonymus revolutus Wight. Uva Province: Namunukula kanda. 06.05.1976; Wass 1617; Slide nr.25330 (PL).

Clusiaceae

Calophyllum walkeri Wight. Central Province: Horton Plains. 10.12.1975; Bernardi 15880; Slide nr.25331 (PL).

Cornaceae

Mastixia montana (Wight ex Thw.) Clarke. Central Province: Cobert's gap. 11.10.1975; Wass 203; Slide 25410 (PL).

M. tetrandra var. *thwaitesii* Clarke. Central Province: Horton Plains. 10.10.1975; Wass 3232; Slide nr.5332 (PL).

Elaeocarpaceae

Elaeocarpus glandulifer (Hook. ex Wight) Mast. Central Province: Horton Plains. 1975; Sumithraarachchi 951; Slide nr. 25333 (PL).

E. montanus Thw. Central Province: Hevaheta. 23.08.1984; Jayasuriya 2861; Slide nr. 25352 (PL).

E. obovatus Arn. Central Province: Horton Plains. 29. 01. 1974; Jayasuriya 1467; Slide nr.25353 (PL).

Euphorbiaceae

Glochidion coriaceum Thw. Central Province: Pattiyagama Estate. 22.10.1978; Fosberg 57913; Slide nr.25336 (PL).

Flacourtiaceae

Casearia thwaitesii Briq. Central Province: Pidurutalagala. 25.10.1974; Dell & Sumithraarachchi 8073; Slide nr. 25337 (PL).

Lauraceae

Actinodaphne ambigua (Meisn.) Hook. f. Central Province: Kandy. 25. 0.1984; Jayasuriya 3443; Slide nr.25360 (PL).

A. speciosa Nees Central Province: Kandy. 25. 10. 1984; Jayasuriya 841025; Slide nr. 25361 (PL).

A. stenophylla Thw. Central Province: Matale. Jayasuriya 268; Slide nr. 25362 (PL).

Cinnamomum ovalifolium Wight. Central Province: Horton Plains. Stone 11257 (PDA); Slide nr. 25363 (PL).

Litsea ovalifolia (Wight) Hook. f. Central Province: Horton Plains. Hladik 868; Slide nr. 25377 (PL).

Neolitsea fuscata (Thw.) Alston. Central Province: Horton Plains. Hladik 730; Slide nr. 25376 (PL).

Melastomataceae

Osbeckia walkeri Arn. Central Province: Horton Plains. 19.09.1969; C. F. & Beusekom 1498 (PDA). Slide nr. 25451 (PL).

Myrtaceae

Eugenia mabaeoides ssp. *mabaeoides* Wight. Central Province: Adam's Peak. 19.11.1977; Huber 673; Slide nr. 25354 (PL).

Syzygium rotundifolium Arn. Central Province: Horton Plains. 29.03.1968; Fosberg 50115; Slide nr.25359 (PL).

S. sclerophyllum Thw. Central Province: Pidurutalagala. Ashton 2300; Slide nr. 25357 (PL).

Rhamnaceae

Rhamnus arnottianus Gardn. ex Thw. Central Province: Pidurutalagala. 21.11.1974; Gerrit Davides 8641; Slide nr. 25358 (PL).

Rubiaceae

Hedyotis lawsoniae (DC) Wight & Arn. Central Province: Knuckles. 22.08.1993; Weerasooriya 1925; Slide nr. 25355 (PL).

Sapotaceae

Isonandra montana (Thw.) Gamble. Central Province: Rangala. 29.03.1968; Nooteboom 643; Slide nr. 25356 (PL).

Symplocaceae

Symplocos elegans Thw. Central Province: Horton Plains. 06.09.1973; Wass 137; Slide nr. 25349 (PL).

Theaceae

Adinandra lasiopetala (Wight) Choisy. Central Province: Horton Plains. 03.11.1971; NBK 1043; Slide nr. 25350 (PL)

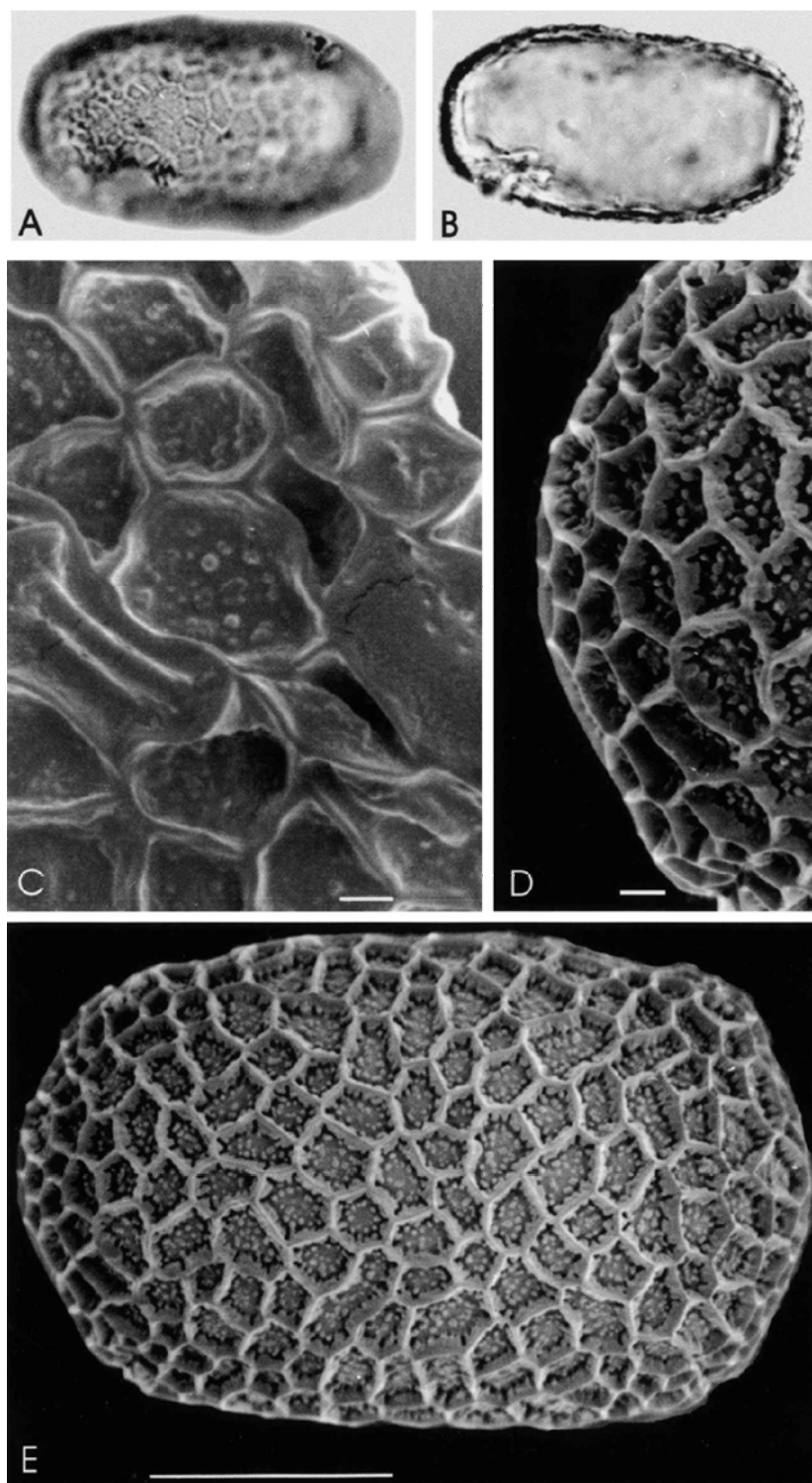


Fig. 3. A–C. *Impatiens walkeri* (Balsaminaceae). (A) Coarsely reticulate pollen grain in polar view, high focus; (B) The same pollen grain; optical cross-section; (C) Detail of reticulate exine, muri sinuous, lumina $\pm$ smooth with few granules. D, E. *I. thwaitesii*. (D) Detail of reticulate exine, muri straight, numerous granules in the lumina; (E) Pollen grain in polar view with duplicolumellate muri. A, B. LM, $\times 1000$. C–E. SEM. Scale bars: C, D – 1 μm , E – 10 μm .

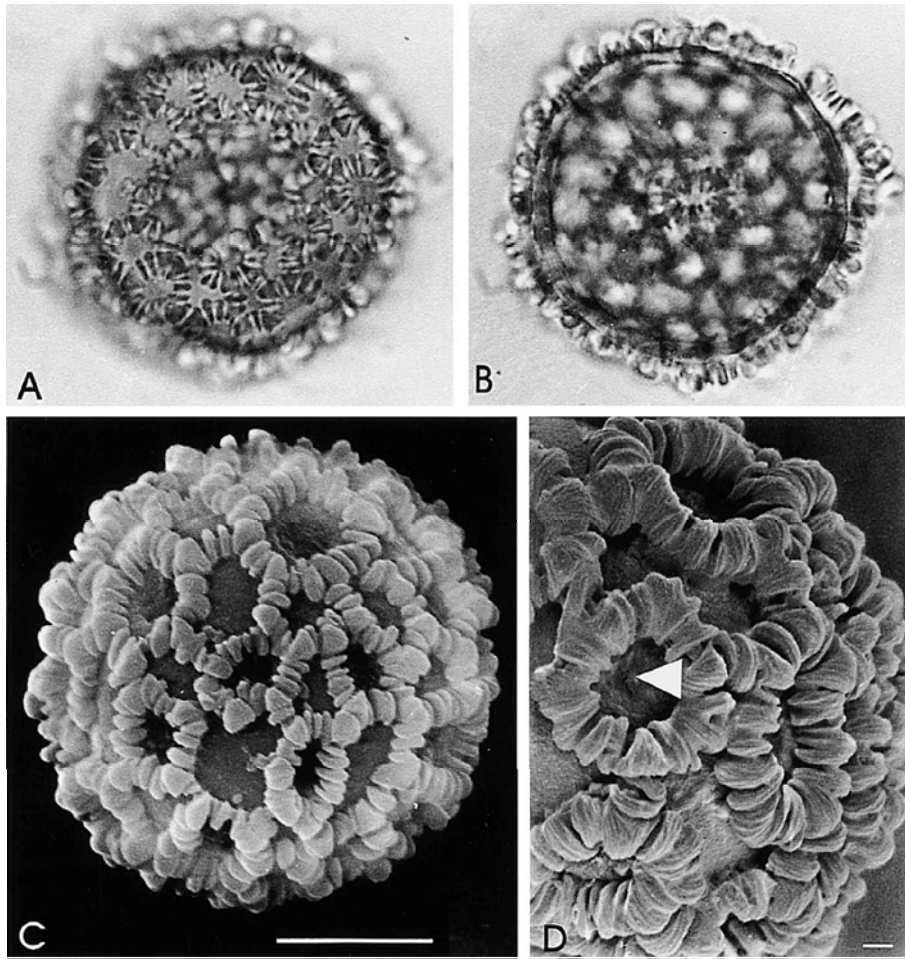


Fig. 4. A–D. *Sarcococca zeylanica* (Buxaceae). (A) Pantoporate pollen grain in medium focus; (B) The same pollen grain, optical cross-section; (C) Pollen grain showing *Croton* pattern; (D) Detail of *Croton*-pattern consisting of vertical disc-like elements attached to or enveloping rings encircling a faintly delimited pore (arrowhead). A, B. LM, $\times 1000$. C, D. SEM. Scale bars: C – $5\ \mu\text{m}$, D – $1\ \mu\text{m}$.

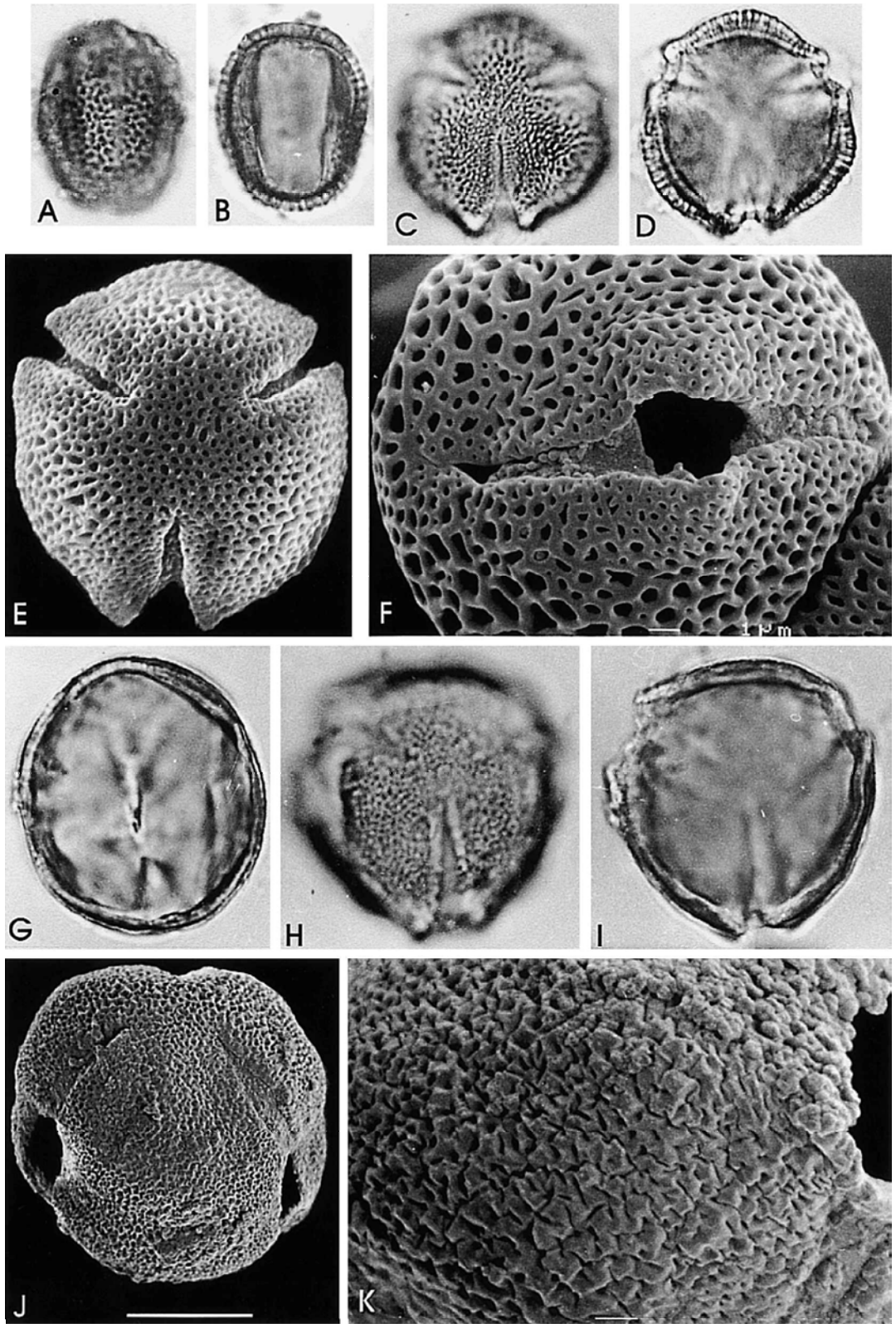


Fig. 5. (For legend see page 269).

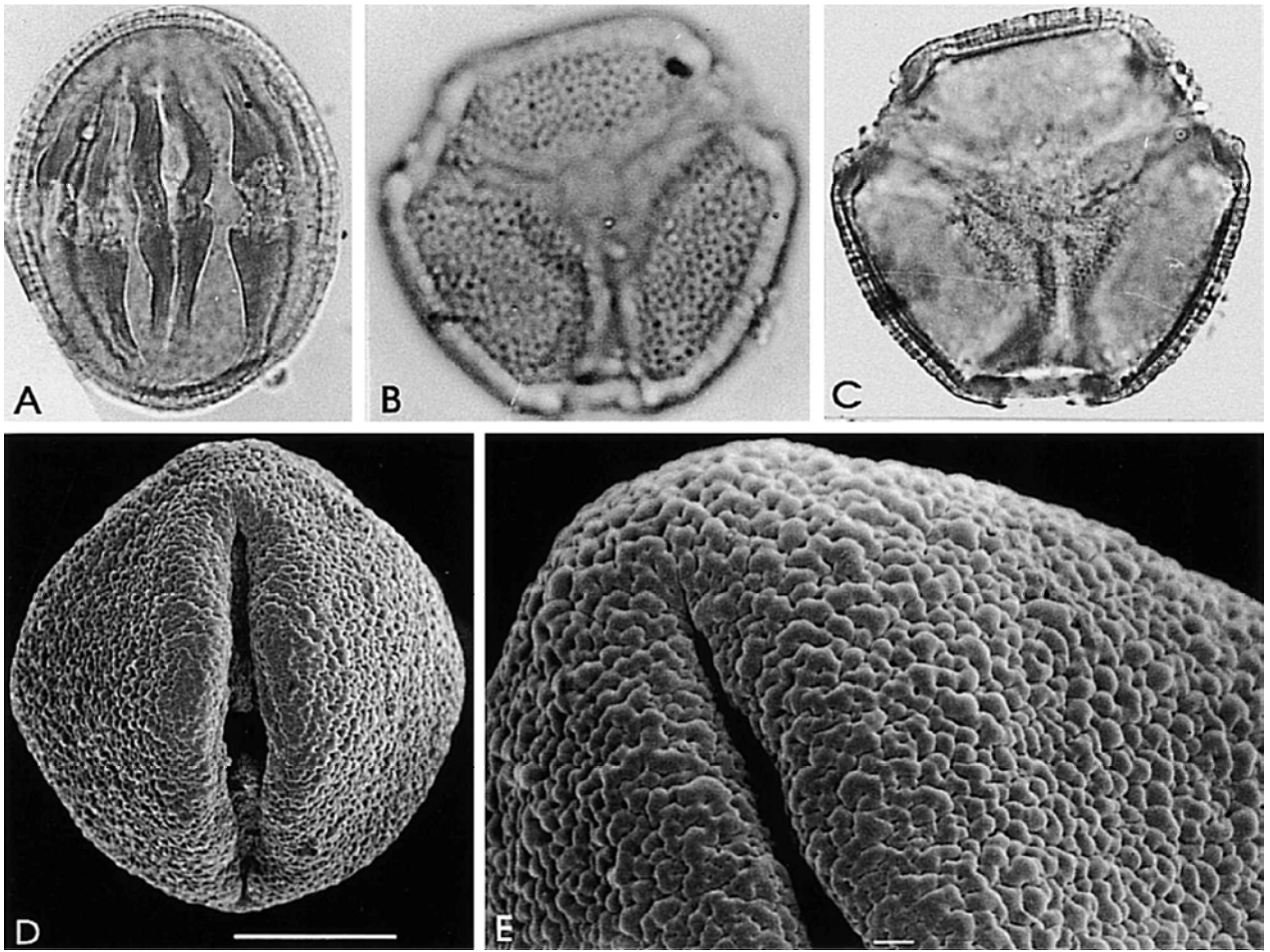


Fig. 6. A–C. *Mastixia montana* (Cornaceae). (A) 3-colporate pollen grain in equatorial view, nearly optical cross-section; (B) Granular to microverrucate-perforate pollen grain, high focus; (C) The same pollen grain, optical cross-section. D, E. *M. tetrandra* var. *thwaitesii* (Cornaceae). (D) 3-colporate, granular to microverrucate-perforate pollen grain in slightly oblique equatorial view; (E) Detail of granular to microverrucate-perforate exine. A–C. LM, $\times 1000$. D, E. SEM. Scale bars: D – 10 μm , E – 1 μm .

Fig. 5. A–F. *Euonymus revolutus* (Celastraceae). (A) Coarsely reticulate pollen grain in equatorial view, high focus; (B) The same pollen grain, optical cross-section; (C) Pollen grain in polar view relatively high focus; (D) The same pollen grain, optical cross-section; (E) Reticulate pollen grain in polar view; (F) Detail of 3-colporate, reticulate pollen grain near the aperture; lumina diminishing in size towards the colpus margin. G–K. *Calophyllum walkeri* (Clusiaceae). (G) 3-colporate pollen grain in equatorial view, optical cross-section; (H) Scabrate pollen grain in polar view; (I) The same pollen grain, optical cross-section; (J) 3-colporate pollen grain in oblique, equatorial view; (K) Detail of scabrate-perforate exine. A–D, G–I. LM, $\times 1000$; E–F, J–K. SEM. Scale bars: E, J – 10 μm , F, K – 1 μm .

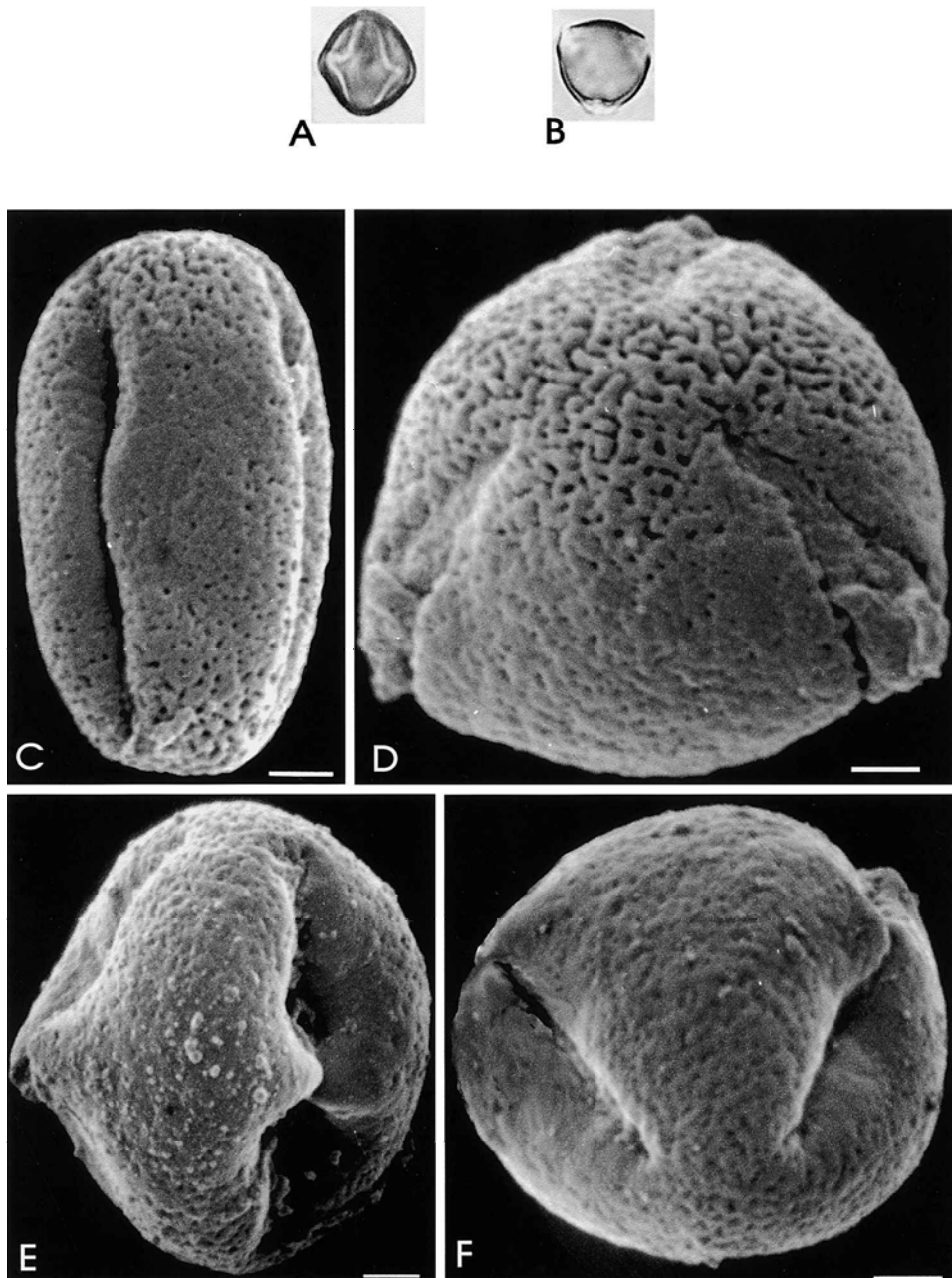


Fig. 7. A–D. *Elaeocarpus montanus* (Elaeocarpaceae). (A) 3-colporate pollen grain in equatorial view, optical cross-section; (B) Pollen grain in polar view, optical cross-section; (C) Smooth-perforate pollen grain in equatorial view; (D) Pollen grain in slightly oblique polar view, perforations denser and larger towards the polar areas. E, F. *E. obovatus* (Elaeocarpaceae). (E) 3-colporate smooth-scabrate pollen grain in oblique equatorial view; sexine protruding over the ora at the equator (arrow); (F) Smooth to scabrate rugulate-perforate pollen grain in oblique polar view. A–B. LM, $\times 1000$. C–F. SEM. Scale bars – $1\mu\text{m}$.

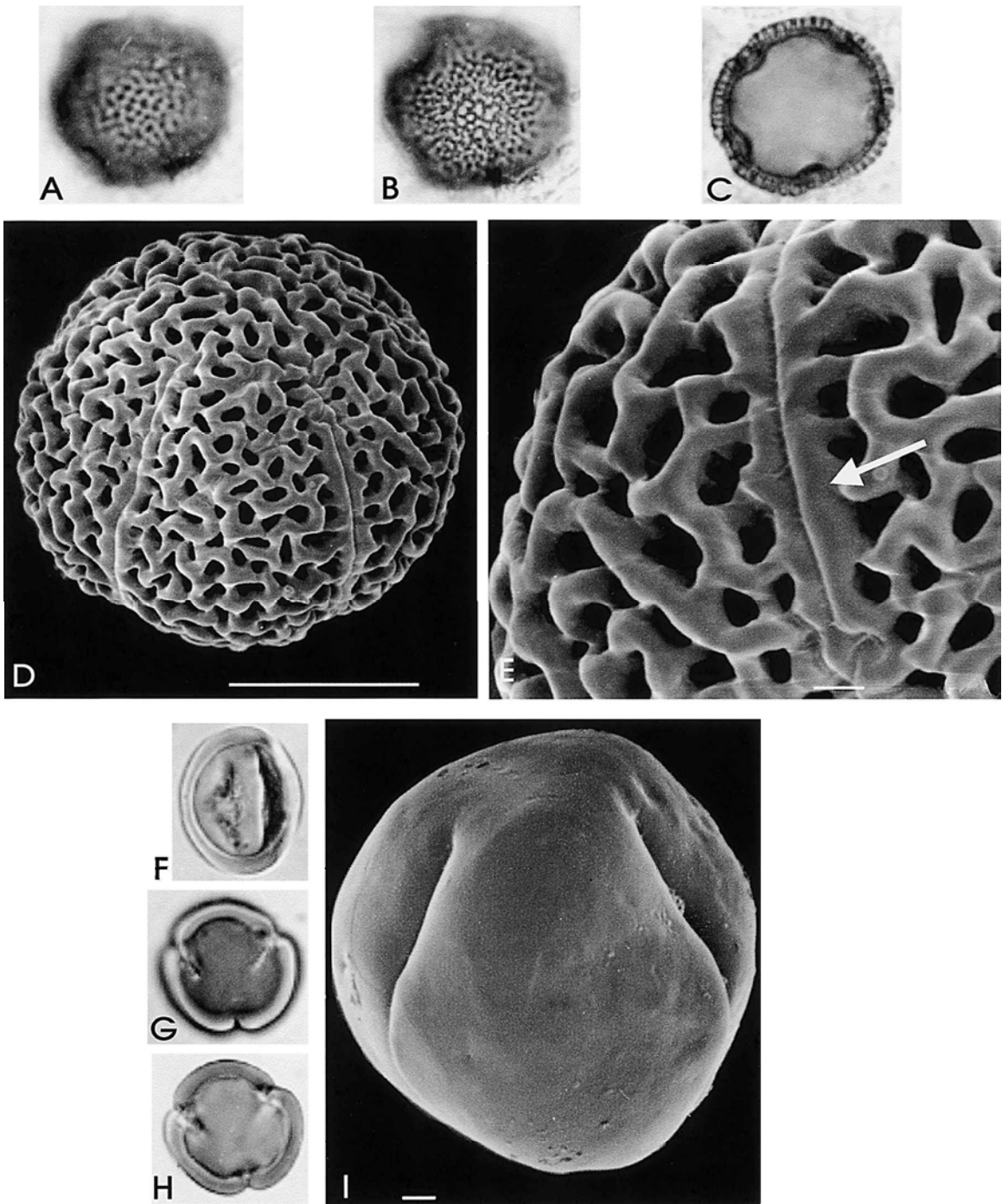


Fig. 8. A–E. *Glochidion coriaceum* (Euphorbiaceae). (A) 5-colporate, coarsely reticulate pollen grain in polar view, high focus; (B) The same pollen grain, low focus; (C) The same pollen grain, optical cross-section; (D) 5-colporate coarsely reticulate pollen grain in oblique equatorial view; (E) Detail of reticulate exine, colpus with a smooth, elongated narrow and straight margin (arrow). F–I. *Casearia thwaitesii* (Flacourtiaceae). (F) 3-colporoidate pollen grain in equatorial view, optical cross-section; (G) Smooth pollen grain in oblique polar view; (H) The same pollen grain; optical cross-section; (I) Smooth pollen grain in slightly oblique equatorial view. A–C, F–H. LM, $\times 1000$. D, E, I. SEM. Scale bars: D – 10 μm , E, I – 1 μm .

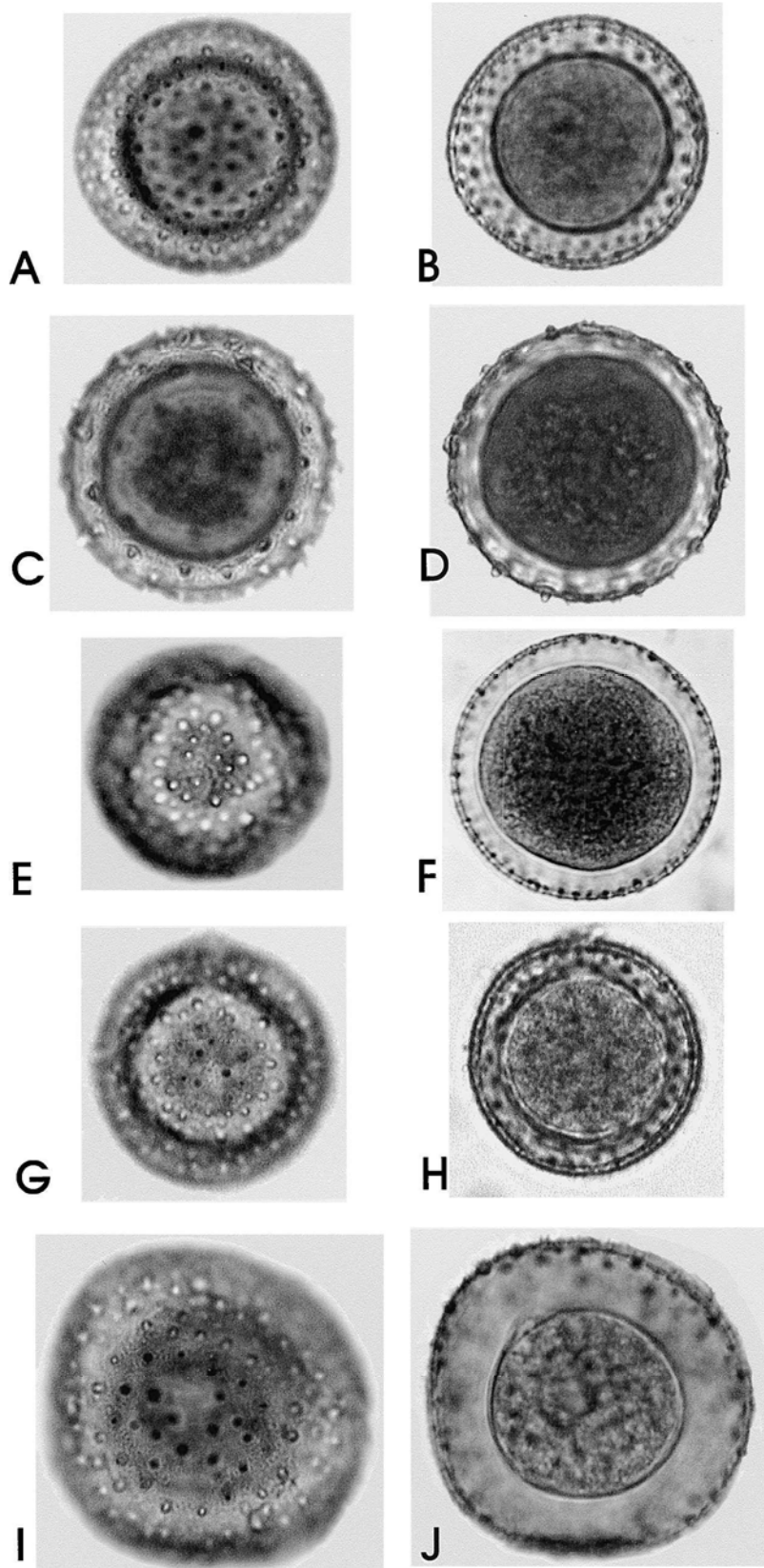


Fig. 9. (For legend see page 274).

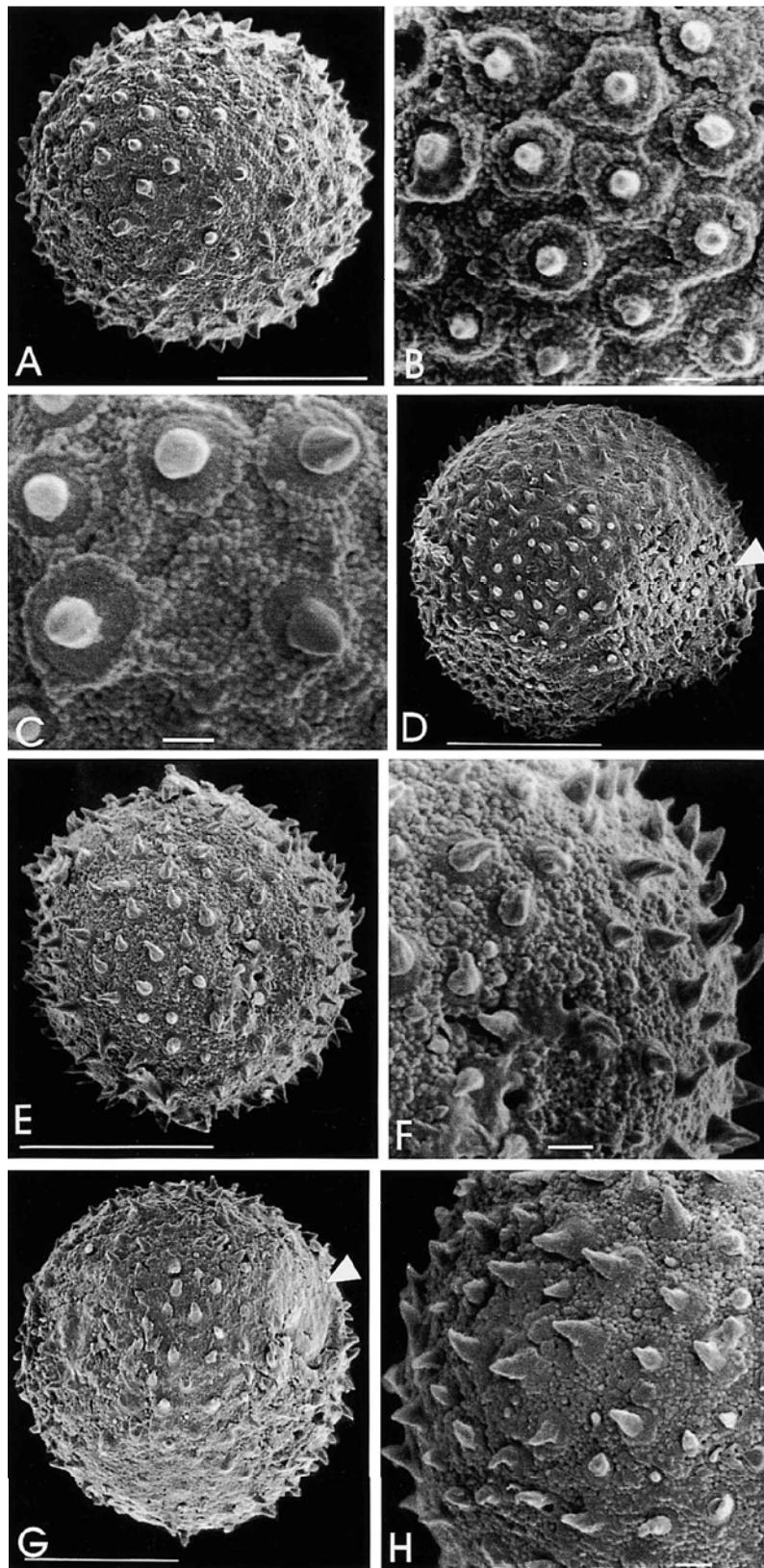


Fig. 10. (For legend see page 274).

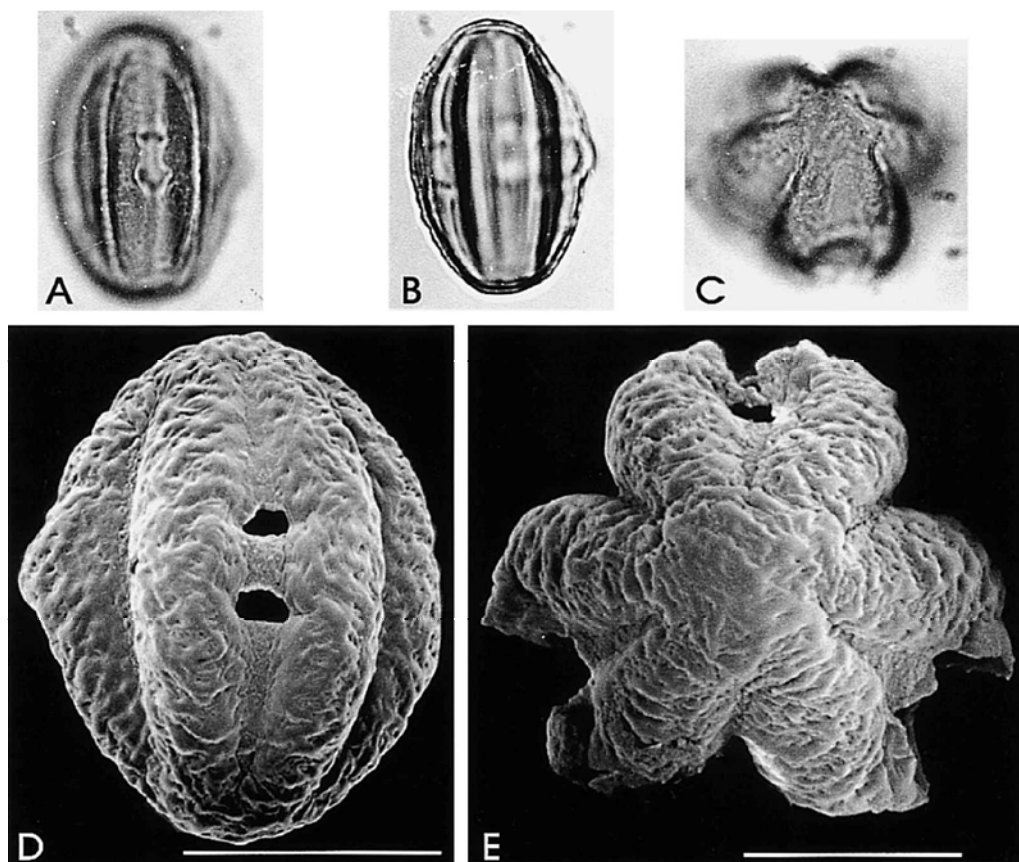


Fig. 11. A–E. *Osbeckia walkeri* (Melastomaceae). (A) Heterocolpate pollen grain in equatorial view with alternating colpi, the colpi have two lalongate ora (diploporate, diorate); (B) The same pollen grain in equatorial view, optical cross-section; (C) Scabrate pollen grain in oblique polar view, low focus; (D) Heterocolpate-colporate pollen grain in equatorial view, two ora visible, exine variably folded to rugulate; (E) 6-lobate pollen grain in polar view. A–C. LM, $\times 1000$. D, E. SEM. Scale bars – 10 μm .

Fig. 9. A–J. LM micrographs of the Lauraceae species. A, B. *Actinodaphne ambigua*. (A) Inaperturate, microspinose pollen grain, low focus; (B) The same pollen grain; optical cross-section. C, D. *A. speciosa*. (C) Inaperturate, microspinose pollen grain, low focus; (D) The same pollen grain, optical cross-section. E, F *Cinnamomum ovalifolium*. (E) Inaperturate, microspinose pollen grain, high focus, (F) The same pollen grain, optical cross-section. G, H. *Litsea ovalifolia*. (G) Inaperturate, microspinose pollen grain, high focus, (H) The same pollen grain, optical cross-section. I, J. *Neolitsea fuscata*. (I) Inaperturate, microspinose pollen grain, high to low focus, (J) The same pollen grain, optical cross-section. A–J. $\times 1000$.

Fig. 10. A–H. SEM micrographs of the Lauraceae species. A, B. *Actinodaphne ambigua* (A) Inaperturate, microspinose pollen grain; (B) Detail of exine; cone-shaped microspines on thickened basal cushions beset with and delimited by small granules. C. *A. speciosa*. Detail of granular exine with cone-shaped, faintly striate microspines. D. *Cinnamomum ovalifolium*. Inaperturate, microspinose pollen grain with a rounded faintly delimited perforated depression with few microspines (arrowhead). E–F. *Litsea ovalifolia*. (E) Inaperturate, microspinose pollen grain; (F) Detail of granular exine with cone-shaped and bent microspines. G, H. *Neolitsea fuscata*. (G) Inaperturate, microspinose pollen grain with a rounded smooth area devoid of microspines (arrowhead); (H) Detail of granular-perforate exine with cone-like microspines. A–H. Scale bars: A, D, E & G – 10 μm ; B, C, F & H – 1 μm .

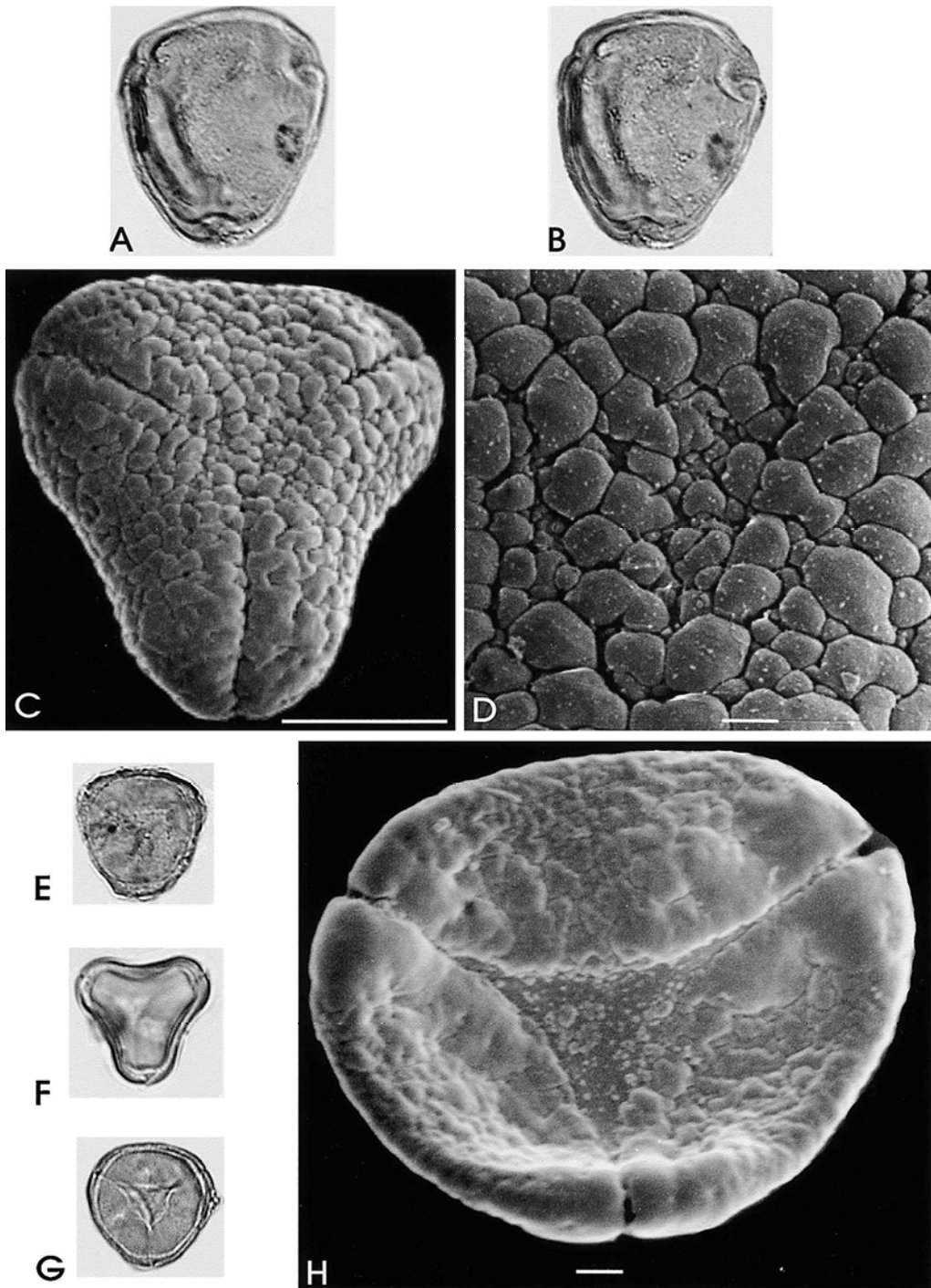


Fig. 12. A–D. *Eugenia mabaeoides* ssp. *mabaeoides*. (Myrtaceae). (A) 3-colporate pollen grain in polar view, (B) The same pollen grain, optical cross-section; (C) 3-colporate verrucate-perforate pollen grain in polar view; (D) Detail of verrucate exine. E, F. *Syzygium rotundifolium* (Myrtaceae). (E) 3-parasyncolp(or)ate pollen grain with slightly convex to straight sides in polar view, optical cross-section; (F) Pollen grain in polar view with concave mesocolpia, optical cross-section. G, H. *S. sclerophyllum*. (G) 3-parasyncolp(or)ate pollen grain in polar view, optical cross-section; (H) smooth, rugulate-perforate pollen grain with convex mesocolpia, polar view. A, B & E–F. LM, $\times 1000$. C, D & H. SEM. Scale bars: C – $10\ \mu\text{m}$; D, H – $1\ \mu\text{m}$.

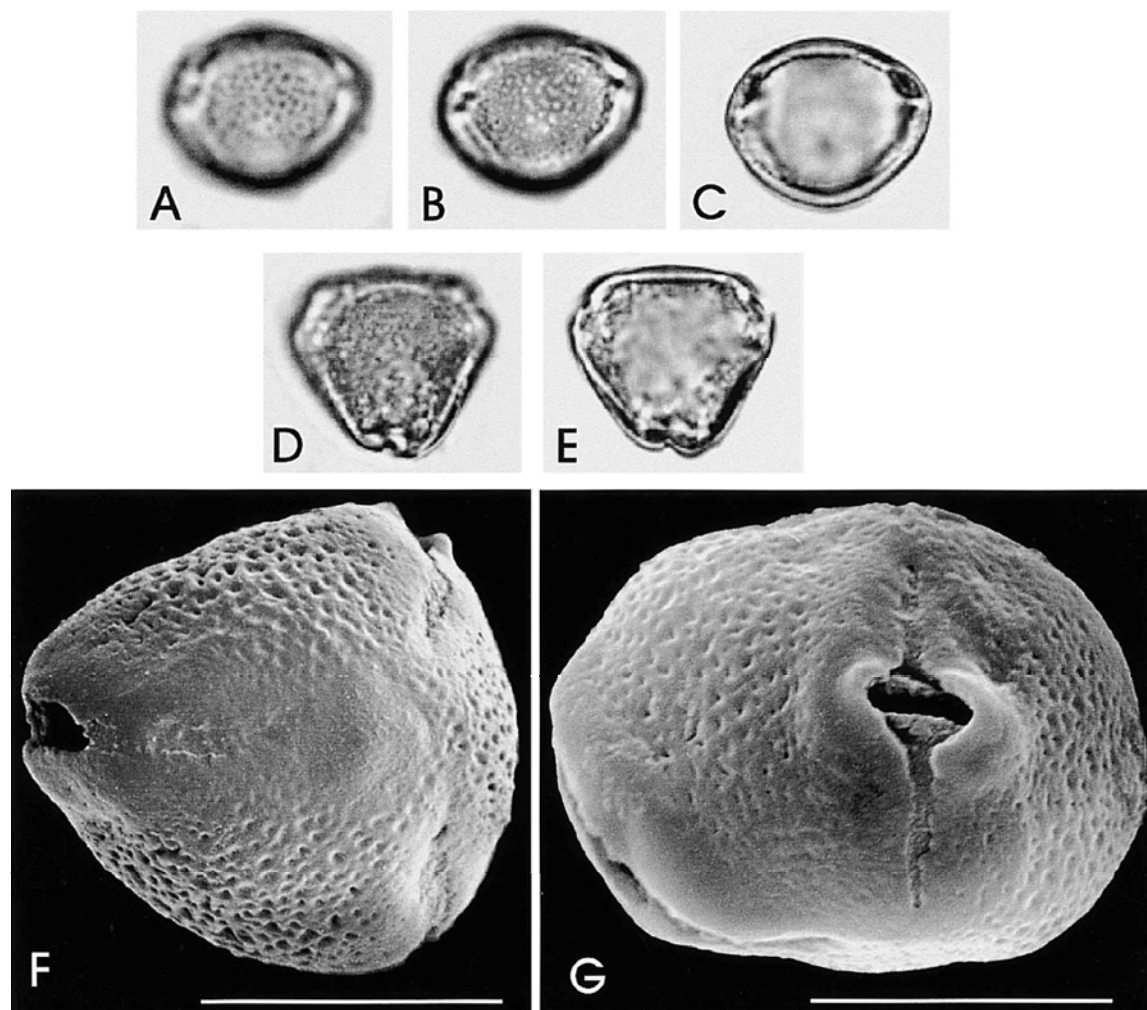


Fig. 13. A–G. *Rhamnus arnottianus* (Rhamnaceae). (A) 3-colporate pollen grain in equatorial view, high focus; (B) The same pollen grain, low focus; (C) The same pollen grain, optical cross-section; (D) Pollen grain in polar view, low focus; (E) The same pollen grain, optical cross-section; straight mesocolpia; (F) Perforate pollen grain in oblique polar view; colpus margin relatively wide and smooth; (G) Pollen grain in equatorial view; sexine protruding above the elongate os. A–E. LM, $\times 1000$. F, G. SEM. Scale bars – 10 μm .

Fig. 14. A–E. *Hedyotis lawsoniae* (Rubiaceae). (A) 3-colporate, microreticulate pollen grain in equatorial view, relatively high focus; ora laterally fused to a band; (B) The same pollen grain, low focus; (C) Pollen grain in oblique polar view, optical cross-section; (D) Microreticulate pollen grain in equatorial view; (E) Detail of microreticulate exine near the aperture. F, G. *Isonandra montana* (Sapotaceae). (F) Pollen grain in equatorial view, optical cross-section; (G) Rugulate-perforate low profile pollen grain in equatorial view; sexine protruding to form a bridge over the ora at the equator. A–C, F. LM, $\times 1000$. D, E & G. SEM. Scale bars: D, G – 10 μm ; E – 1 μm .

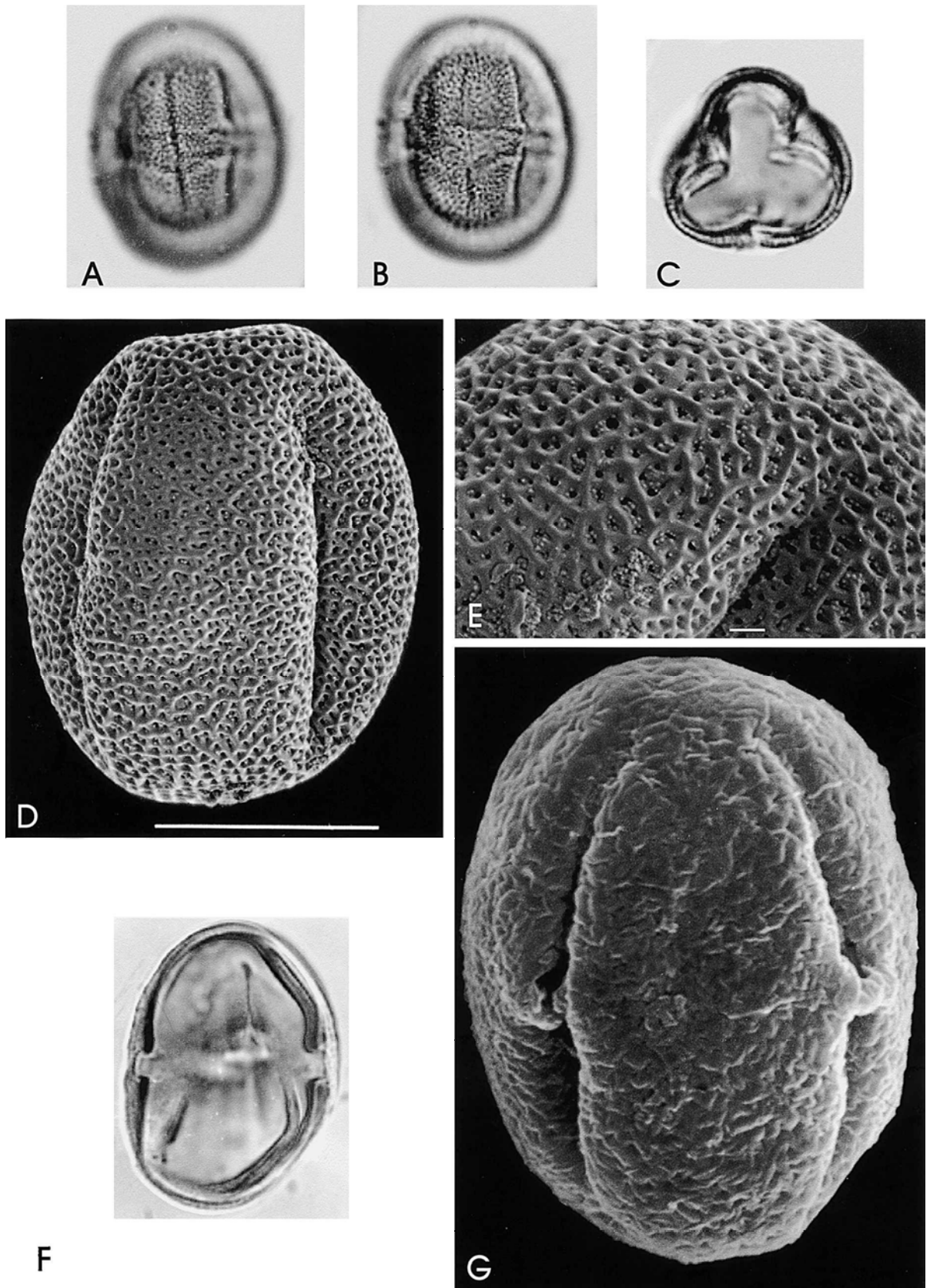


Fig. 14. (For legend see page 276).

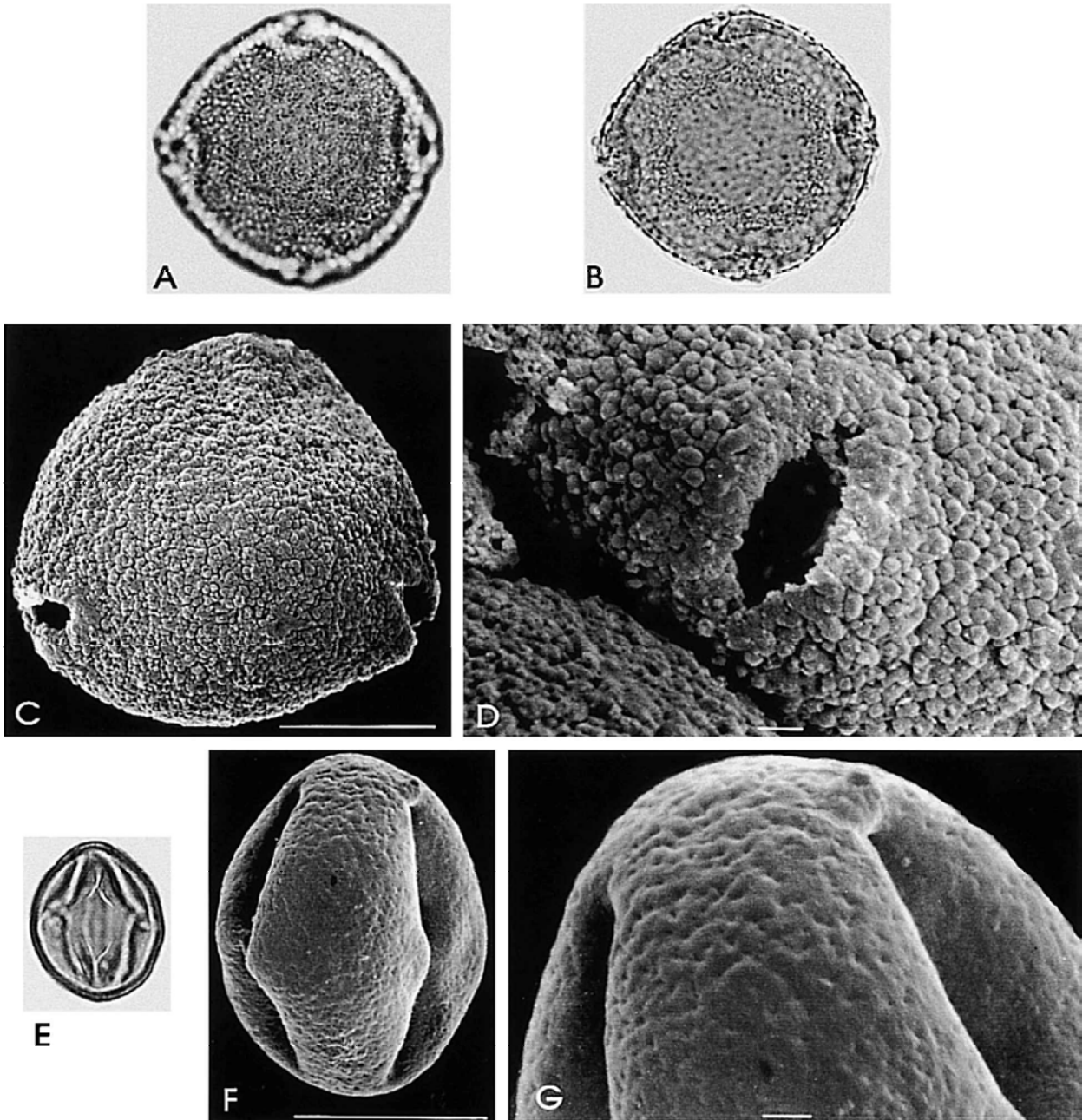


Fig. 15. A–D *Symplocos elegans* (Symplocaceae) (A) 4-colporate pollen grain in polar view, medium focus; (B) The same pollen grain, nearly optical cross-section; (C) 3-colporate, scabrate-verrucate pollen grain in oblique polar view; (D) Detail of verrucate exine near the aperture; colpus oval-shaped and delimited by a protruding margin over the os. E–G. *Adinandra lasiopetala* (Theaceae). (E) 3-colporate pollen grain in equatorial view; optical cross-section; (F) Smooth pollen grain in equatorial view; (G) Smooth undulate-perforate exine. A, B, E. LM, $\times 1000$. C, D & F, G. SEM. Scale bars: C, F – $10\mu\text{m}$; D, G – $1\mu\text{m}$.

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