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World Pollen and Spore Flora 23. Malvaceae Adams. P.p.

Subfamilies: Grewioideae, Tilioideae, Brownlowioideae

ANJUM PERVEEN, ELISABETH GRAFSTRÖM and GAMAL EL-GHAZALY†

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The pollen morphology of 85 species (89 collections) from 32 genera, i.e. *Ancistrocarpus, Apeiba, Berrya, Brownlowia, Carpodiptera, Christiana, Clappertonia, Colona, Corchorus, Desplatsia, Diplodiscus, Duboscia, Eleutherostylis, Entelea, Erinocarpus, Glyphaea, Goethalsia, Grewia, Hainania, Heliocarpus, Luehea, Lueheopsis, Microcos, Mollia, Mortoniodendron, Pentace, Sparmannia, Tetralix, Tilia, Trichospermum, Triumfetta*, and *Vasivaea* of family Malvaceae was examined by light microscope (LM), scanning electron microscope (SEM) and transmission electron microscope (TEM). Three types are recognized on the basis of aperture types, exine pattern and pollen shape classes 1) *Berrya*-type, 2) *Corchorus*-type and 3) *Mortoniodendron*-type. The *Berrya*-type has two subtypes: *Berrya*-subtype A and *Berrya*-subtype B. *Corchorus*-type has two subtypes: *Corchorus*-subtype A and *Corchorus*-subtype B. In the *Berrya*-type, *Corchorus*-type and *Mortoniodendron*-type pollen grains are colporate, in one case (*Tilia*) colp(or)ate. The pollen morphological trends are discussed with special reference to pollen size, shape and exine sculpturing.

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Molecular phylogenetic studies have shown that the traditional families Bombacaceae, Malvaceae, Sterculiaceae and Tiliaceae form a strongly supported group (Chase et al. 1993, Soltis et al. 1997, 2000; Alverson et al. 1998, 1999; Bayer et al. 1999, Whitlock et al. 2001). As a result, the four traditional families have been submerged into a single family, Malvaceae s.l. (Bayer et al. 1999, Bayer & Kubitzki 2002). Within this expanded Malvaceae s.l., nine subfamily-level clades are recognized (Bayer et al. 1999, Bayer & Kubitzki 2002). Byttnerioideae and Grewioideae form a clade that is sister to a clade consisting of the remainder of Malvaceae (Whitlock et al. 2001). While within the remainder of Malvaceae, Malvoideae and Bombacoideae constitute a well-supported clade (Alverson et al. 1999, Bayer et al. 1999, Baum et al.: in press), the relationships among the other subfamilies remain uncertain (Nyffeler et al.: submitted).

The present study, initiated prior to the recent systematic changes to Malvales, investigates the pollen morphology of the former Tiliaceae, but now reports pollen morphology within the three subfamilies Grewioideae, Tilioideae and Brownlowioideae of Malvaceae. The morphology of pollen in genera of the former Tiliaceae has been widely reported by light and scanning electron microscopy (see Appendix). However, to date there has been no synthesis across these groups. The present study describes the pollen of the majority of genera belonging to Grewioideae (*Ancistrocarpus, Apeiba, Clappertonia, Colona, Corchorus, Desplatsia, Duboscia, Eleutherostylis, Entelea, Erinocarpus, Glyphaea, Goethalsia, Grewia, Heliocarpus, Hydrogaster, Luehea, Lueheopsis, Microcos, Mollia, Pseudocorchorus, Sparrmannia, Tetralix, Trichospermum, Triumfetta, Vasivaea*), Brownlowioideae (*Berrya*, *Brownlowia, Carpodiptera, Christiana, Diplodiscus, Jarandersonia, Pentace, Pithyranthe* and *Hainania*) and Tilioideae (*Tilia*) and the problematic genus *Mortoniodendron*.

† [d. 2001]

MATERIAL AND METHODS

This study is based on herbarium material from Bogor (BO), Meise (BR), Edinburgh (E), Chicago (F), Hamburg (HBG), Leiden (L), Saint Louis (MO), Belém (IAN), Manaus (INPA), Paris (P), and Stockholm (S) (Holmgren et al. 1990). 85 taxa were investigated by LM and 80 samples by SEM. The polleniferous material intended for light microscopy (LM) and scanning electron microscopy (SEM) was subjected to acetolysis (Erdtman 1969). For LM pollen grains were inbedded in glycerin jelly and sealed with paraffin wax. A Leitz Laborlux light microscope was used for observation, magnification × 1000. At least ten pollen grains of each sample were observed and polar axis, equatorial diameter, exine and nexine were measured. For SEM the acetolyzed polleniferous material was dehydrated in alcohol, mounted on aluminum stubs and gold sputtered with an EMITECH K 550 before examined in a Jeol 6300.

Three taxa were selected for transmission electron microscopy (TEM). The pollen material from herbarium sheets was rehydrated and embedded in TAAB 812 resin. Sections were cut with a LKB Ultrotome V, using a diamond knife. Sections were post-stained in uranyl acetate and lead citrate prior to examination in a LEO 906E transmission electron microscope.

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Terminology

Terminology generally follows that of Erdtman (1952), Fægri & Iversen (1975), Praglowski & Punt (1973), and Punt et al. (1994).

GENERIC POLLEN DESCRIPTIONS

The detailed pollen morphology data of Brownlowioideae, Grewioideae and Tilioideae studied are clustered in Table I.

Ancistrocarpus Oliver

LM (Fig. 6 A, B; Ancistrocarpus bequaertii)

Pollen grains single, isopolar, prolate to subprolate. P=(38−) 43 (−48) μm. E=(27−) 31.5 (−36) μm. P/E ratio: 1.30–1.39. Amb rounded-triangular with slightly convex mesocolpia, equatorial view elliptical.

Pollen grains 3-colporate. Colpi long, narrow with distinct costae. Ora distinct lalongate, rectangular, 5 × 10 μm. Exine 2–3 μm thick. Sexine thicker or thinner than nexine, sometimes slightly thicker at the poles, reticulate, nexine ca. 1 μm.

SEM (Fig. 6 C–E; Ancistrocarpus bequaertii)

In *Ancistrocarpus bequaertii* the exine sculpturing is coarsely reticulate and pattern of muri irregular. Lumina variable in shape and size, 0.6–2.1 μm in diameter, lumina size gradually reduced towards the colpi, lumina perforated between the muri; perforations 0.09–0.5 μm in diameter; perforations more distinct towards the margin. Colpi long, narrow with tapering ends, colpal membrane granulated. In A. *densispinosus* colpi margins are rough.

TEM (Fig. 6 F, G; Ancistrocarpus bequaertii)

The exine consists of a supratectal reticulum with perforated lumina, supported by stout columellae on an equally solid foot-layer. Endexine appears absent.

Apeiba Aublet

LM

Pollen grains single, isopolar, suboblate, rarely oblate-spheroidal. P= (29−)31(−33) μm. E= (29−)32(−35) μm. P/E ratio: 0.92–1.00. Amb rounded-triangular with slightly convex mesocolpia, equatorial view transverse elliptical.

3-colporate. Colpi short, narrow with costae. Ora distinctly lalongate, more or less circular, 4 × 2 μm. Exine 1.5–2 μm. Sexine thinner than nexine, nexine 1–2 μm.

SEM (Fig. 5 A–C; Apeiba albiflora)

In *Apeiba albiflora* exine sculpturing is a medium reticulate, more or less irregular pattern of muri with spinules. Lumina variable in shape and size, 0.18–1.3 μm in diameter. Lumina perforated between the muri; perforations 0.02–0.17 μm in diameter. Colpi short, narrow with acute ends. In *A. burchelli*, exine sculpturing is medium rugulate-reticulate with 'Crotonoid' muri, lumina perforated, colpi short, narrow (slit like) with acute ends.

Berrya Roxb.

LM (Fig. 1 A–C; Berrya cordifolia)

Pollen grains single, isopolar, suboblate, P= (22−)23.5 (−25) μm. E= (23−)30.5(−38) μm. P/E ratio: 0.70–1.00. Amb rounded-triangular with slightly convex mesocolpia, equatorial view transverse elliptical.

3-colporate. Colpi short, narrow with costae. Ora slightly lalongate, more or less circular, small, not distinct in light microscope. Exine 1.5–2 μm thick. Sexine thinner than nexine, nexine ca. 1 μm thick.

SEM (Fig. 1 D, E; Berrya cordifolia)

In *Berrya cordifolia* exine sculpturing is medium rugulate-reticulate with spinulose muri (more or less scabrate), lumina 0.1–0.5 μm in diameter. Colpi short, narrow with acute ends. In *B. mollis* exine sculpturing is medium rugulate-reticulate with irregular pattern of muri.

Brownlowia Roxb.

LM (Fig. 1 F, G; Brownlowia tabularis)

Pollen grains single, isopolar, suboblate to oblate-spheroidal. P= (23−)27(−31) μm. E= (28−)31(−34) μm. P/E ratio: 0.80–0.85. Amb rounded-triangular with slightly convex mesocolpia, equatorial view transverse elliptical.

3-colporate. Colpi short, narrow with costae. Ora slightly lalongate, more or less circular, not distinct in light microscope. Exine 2–3.5 μm thick. Sexine thinner than nexine, nexine 0.5–1.5 μm thick.

SEM (Fig. 1 H, I; Brownlowia tabularis)

In *Brownlowia argentatai* exine sculpturing is finely reticulate, lumina more or less circular. Muri thick, 0.05–0.4 μm in diameter. Colpal membrane granulated.

In *B. tabularis* the exine sculpturing is rough, finely reticulate or more or less foveolate.

Carpodiptera Griseb.

LM (Fig. 5 E–G; Carpodiptera africana)

Pollen grains single, isopolar, suboblate, rarely oblate-spheroidal. P= (19−)22(−25) μm. E= (23−)31(−40) μm. P/E ratio: 0.68–1.00. Amb rounded-triangular with slightly convex mesocolpia, equatorial view transverse elliptical.

Pollen grains 3-colporate. Colpi short, narrow with costae, 4–5.5 μm long. Ora lalongate, not distinct in light microscope. Exine 2–3 μm thick. Sexine thicker than nexine, nexine 0.5–1 μm.

Table I. *Pollen morphological data for Malvaceae subfamilies Brownlowioideae, Grewioideae and Tilioideae.*

*– Number of established species; P – polar axis, mean value; E – equatorial diameter, mean value; P/E – pollen shape (ratio). Abbreviations for exine patterns: C – coarsely, D – densely, M – medium, F – fine, Fovt foveolate, Rt – reticulate, Ru – rugulate.

Taxa	Exine sculpturing	Aperture(s)	P (μm)	E (μm)	P/E
Ancistrocarpus Oliver (5*)					
A. bequaertii Troupin 4636 (BR)	CRt	3-colporate	45.0 (42–48)	32.5 (30–35)	1.39
A. comperei Nsimundle 1122 (BR)	CRt	3-colporate	41.5 (38–45)	31.5 (27–36)	1.33
A. densispinosus Mildbraed 5218 (HBG)	CRt	3-colporate	41.0 (38–44)	31.5 (29–34)	1.30
Apeiba Aublet					
A. albiflora Da Silva et al. 299 (HBG)	MRt	3-colporate	31.0 (29–33)	33.5 (32–35)	0.92
A. burchelli Cordeiro et al. l 1413 (HBG)	MRt-Ru	3-colporate	29.0	29.0	1.00
Berrya Roxb. (6*)					
B. cordifolia Malabar s.n. (HBG); Kostermans 25114 (BO)	MRu-Rt	3-colporate	23.5 (22–25)	33.5 (29–38)	0.70
B. mollis Kostermans 720 (BO)	MRu-Rt	3-colporate	24.0 (23–25)	24.0 (23–25)	1.00
Brownlowia Roxb. (25*)					
B. argentatai Kajewski 2460 (BO)	FRt	3-colporate	25.0 (23–27)	31.0 (28–34)	0.80
B. tabularis Bejaud 450 (BO)	Fovt	3-colporate	29.0 (27–31)	34.0	0.85
Carpodiptera Griseb. (8*)					
C. africana Holst 2216 (HBG)	CRu-Rt	3-colporate	24.5 (24–25)	31.0 (28–34)	0.80
C. cubensis Gentle 169 (S)	CRu-Rt	3-colporate	24.0 (23–25)	24.0 (23–25)	1.00
C. floribunda Hahn 944 (P)	FRu-Rt	3-colporate	22.0 (19–25)	33.0 (26–40)	0.68
Christaana DC. (2*)					
C. africana Mildbraed 4456 (HBG)	MRu-Rt	3-colporate	24.5 (22–27)	32.0 (26–38)	0.78
C. eburnea Spruce 6260 (K)	MRu	3-colporate	33.5 (29–38)	30.0	1.16
Clappertonia Meissner (3*)					
C. ficifolia Van Harten 73 (HBG)	CRt-Ru	3-colporate	70.5 (64–77)	48.5 (42–55)	1.50
C. polyandra Bos et al. 10543 (P)	CRt	3-colporate	61.5 (53–70)	28.0 (23–33)	2.21
Colona Cav. (30*)					
C. auriculata Winkler B230 (HBG)	CRt	3-colporate	28.5 (24–33)	21.0 (19–23)	1.35
C. javanica Koorders 33058B (WAG)	CRt	3-colporate	26.5 (25–28)	19.0 (16–22)	1.45
C. scabra BSIP 10525(WAG)	CRt	3-colporate	23.5 (22–25)	18.0 (16–20)	1.35
C. serratifolia Elmer 19930 (HBG)	CRt	3-colporate	29.0 (25–33)	19.0 (16–22)	1.55
C. velutina Kajewski 2437 (L)	CRt	3-colporate	27.0 (26–28)	20.5 (19–22)	1.35
Corchorus L.					
C. aestuans Polhill & Paulo 1314 (BR)	CRt	3-colporate	39.5 (37–42)	19.0 (17–21)	2.08
C. asplenifolius Dinter 4396 (HBG)	CRt	3-colporate	55.0 (50–60)	30.0 (28–32)	1.85
C. hirsutus Eiggers 142 (HBG)	CRt	3-colporate	31.0 (27.5–35)	20.5 (18–23)	1.55
C. pongolensis Schlieben 7419 (HBG)	CRt	3-colporate	30.5 (23–38)	21.5 (20–23)	1.45
Desplatsia Bocquillon. (7*)					
D. chrysochlamys Leeuwenberg 1970 (HBG)	CRt	3-colporate	47.0 (42–52)	28.5 (26–31)	1.65
D. dewevrei Dinklage 718 (HBG)	CRt	3-colporate	39.0 (35–43)	27.5 (28–27)	1.43
D. subericarpa Bos 4162 (WAG)	CRt	3-colporate	40.5 (38–43)	28.0 (25–31)	1.45
Diplodiscus Turcz. (7*)					
D. hookerianus King 315 (L.)	FRt-Ru	3-colporate	–	19.0 (18–20)	–
D. longifolius Nootebom 4095 (L.)	Rt-Ru	3-colporate	–	39.0 (37–41)	–
D. paniculatus Elmer 16659 (HBG)	FRt-Ru	3-colporate	20.0 (19–21)	28.5 (26–31)	0.70
D. parviflorus San 38123 (L.)	FRt-Ru	3-colporate	20.0 (19–21)	28.5 (26–31)	0.70
Duboscia Bocquillon (3*)					
D. macrocarpa Mildbraed 4320 (HBG)	CRu-Rt	3-colporate	22.0 (20–24)	16.5 (15–18)	1.30
D. viridiflora Zenker 260 (Wag.)	CRt	3-colporate	25.0 (22–28)	18.5 (16–21)	1.35
Eleutherostylis Burret. (1*)					
E. renistipulata Hoogland 5044 (L); Kostermans & Soegeng 554 (L)	CRt	3-colporate	38.5 (32–45)	23.0 (21–25)	1.66
Entelea R.Br. (1*)					
E. arborescens Chapman 258569 (L)	CRt	3-colporate	31.5 (29–34)	22.5 (21–24)	1.40
Erinocarpus Nimo ex Graham (1*)					
E. nimmonii Stock & Low s.n. (P)	CRt	3-colporate	56.0 (52–60.5)	34.5 (29–40)	1.62

Table 1. (*Continued*)

Taxa	Exine sculpturing	Aperture(s)	P (μm)	E (μm)	P/E
Glyphaea Hook.f. (3*)					
G. brevis Mildraed 5078 (HBG)	CRt	3-colporate	34.5 (33 – 36)	23.0 (21 – 25)	1.50
G. tomentosa Barbosa 2604 (BR)	CRt	3-colporate	37.0 (34 – 40)	24.0 (22 – 26)	1.54
G. lateriflora Andrews 1352 (BR.)	CRt-Ru	3-colporate	33.5 (31 – 36)	24.5 (21 – 28)	1.37
Goethalsia Pittier (1*)					
G. meiantha Wilbur 27398 (F); Lent 2318 (P)	CRt	3-colporate	28.5 (21 – 36)	18.5 (15 – 22)	1.54
Grewia L. (150*)					
G. carpinifolia Brynaert 143 (BR)	Rt-Ru	3-colporate	54.5 (52 – 57)	26.5 (27 – 26)	2.05
G. flavescens Germain 1187 (BR)	CRt	3-colporate	59.0 (54 – 64)	31.5 (27 – 36)	1.89
G. forbesii Semsei 4251 (BR)	CRt	3-colporate	55.0 (48 – 62)	30.5 (27 – 34)	1.80
G. louisii Lebrun 6772 (BR)	CRt	3-colporate	27.5 (26 – 29)	18.0 (16 – 20)	1.54
G. orientalis Robyns 6933 (BR)	CRt	3-colporate	67.0 (63 – 71)	53 (48 – 58)	1.27
G. villosa Bamps & Martins (BR)	CRt	3-colporate	43.0 (37 – 49)	31.5 (26 – 37)	1.37
Hainania Merr. (1*)					
H. trichosperma Lau 476 (P)	Ru-Rt	3-colporate	22.5 (22 – 23)	33.0 (30 – 36)	0.68
Heliocarpus L.					
H. americanus Bourgeau 1574 (L)	CRt	3-colporate	38.5 (33 – 44)	24.5 (23 – 26)	1.56
H. americanus var. ***popayaensis*** Pires 10005 (IAN)	CRt	3-colporate	38.5 (33 – 44)	24.5 (23 – 26)	1.56
H. terebinthinaceus Purpus 3062 (L)	CRt	3-colporate	36.0 (34 – 38)	23.0 (22 – 24)	1.56
Luehea Willd. (20*)					
L. conwentzii Kummrov 2959 (HBG)	CRu-Rt	3-colporate	31.5 (25 – 38)	25.5 (18 – 33)	1.27
L. divaricata Ule 1002 (HBG)	CRt	3-colporate	40.5 (37 – 44)	26.0 (23 – 29)	1.56
L. paniculata Ule 2764 (HBG)	CRt	3-colporate	45.5 (42 – 49)	29.5 (26 – 33)	1.54
L. speciosa Siva & Rosario s.n. (IAN)	CRt	3-colporate	48.5 (44 – 53)	39 (37 – 41)	1.24
Lueheopsis Burret. (9*)					
L. althaeiflora Stergois et al. 13093(HBG)	CRt	3-colporate	39.0 (36 – 42)	31.5 (29 – 34)	1.24
L. rosea Coelho 26 (INPA)	CRt	3-colporate	32.0 (29 – 35)	27.5 (25 – 30)	1.16
Microcos L. (53*)					
M. barombiensis Wellens 198 (BR)	CRt	3-colporate	33.0 (29 – 37)	26.5 (23 – 30)	1.25
M. conocarpoides De Witte 3213 (BR)	CRt	3-colporate	27.0 (26 – 28)	21.0 (20 – 22)	1.29
M. coriacea Thomas & Nemba 5930 (BR)	CRt	3-colporate	32.5 (30 – 35)	19.0 (18 – 20)	1.71
M. floribunda Donis 1339 (BR); Raimundo et al. (BR)	Rt-CRu	3-colporate	22.0 (19 – 25)	16.5 (13 – 20)	1.36
Mollia C. Martius (15*)					
M. grandiflora Maguier 41684 (IAN)	DRu	3-colporate	41.0 (36 – 46)	25.0 (20 – 30)	1.67
M. speciosa Kubitzki (HBG)	DRu-Rt	3-colporate	31.5 (25 – 38)	25.5 (18 – 33)	1.27
Mortoniodendron Standley & Steyerm. (5*)					
M. anisophyllum Haber & Bello 8383 (MO)	CRt	3-colporate	19.5 (18 – 21)	29.5 (28 – 31)	0.66
M. costaricense Haber et al. 4937 (MO)	CRt	3-colporate	18.0 (17 – 19)	26.0 (25 – 27)	0.69
M. guatemalense Berhoulli 405 (BR)	CRt	3-colporate	18.5 (16 – 21)	27.0 (26 – 28)	0.68
Pentace Hassk. (25*)					
P. borneensis Elmer 21317 (HBG)	Ru-Rt	3 – colporate	18.5 (18 – 19)	27.0 (24 – 30)	0.69
P. chartacea San 4036 (L)	Rt-Ru	3 – colporate	15.0	22.5 (21 – 24)	0.67
P. cordata Lundell 17271 (LL)	CRt	3-colporate	19.5 (21 – 18)	13 (11 – 15)	1.55
P. curtisii Kostermans 28475 (L)	Rt-Ru	3-colporate	18.5 (18 – 19)	31.0 (29 – 33)	0.60
P. laxiflora Wign San 38980 (L)	MRt-Ru	3-colporate	22.5 (19 – 26)	28.0 (26 – 30)	0.80
P. rigida Brunig 17521 (HGB)	CRt	3-colporate	26.0	41.0	0.63
Sparmannia L.f. (7*)					
S. abyssinica Volkens 414 (HBG)	CRt	3-colporate	40.5 (36 – 45)	33.0 (30 – 36)	1.23
Tetralix Griseb. (2*)					
T. brachypetalus Wright 1993 (P)	CRt	3-colporate	42.5 (40 – 45)	32.0 (29 – 35)	1.33
T. jaucoensis Bisse 20129 (JE)	CRt	3-colporate	42.5 (38 – 47)	28.0 (26 – 30)	1.51
Tilia L. (50*)					
T. platyphyllos Gautier 1794	FRt	3-colp(or)ate	27.0 (25 – 29)	47.5 (43 – 52)	0.57
Trichospermum Blume (20*)					
T. arachnoideum Burn-Murdochs Coll. BSIP 7153 (L)	CRt	3-colporate	42.5 (40 – 45)	32.0 (29 – 35)	1.33

Table 1. (*Continued*)

Taxa	Exine sculpturing	Aperture(s)	P (μm)	E (μm)	P/E
T. calyculatum Smith 9081 (L)	CRt	3-colporate	40.0 (37–43)	28.5 (26–31)	1.40
T. discolor Sulit Phil 9950 (L)	CRt	3-colporate	32.5 (30–35)	22.0 (20–24)	1.48
T. eriopodum Rames B.SC 17695 (L)	CRt	3-colporate	39.5 (37–42)	29.5 (28–31)	1.34
T. fletcheri Koorders 855 (L)	CRt	3-colporate	38.0 (36–41)	22.5 (21–24)	1.71
T. incaniopsis Nilsm 967 (P)	CRt	3-colporate	36.0 (35–37)	22.5 (20–25)	1.62
T. tripyxis Koster BW 1135 (L)	CRt	3-colporate	40.0 (37–43)	25.5 (26–25)	1.57
Triumfetta L. (150*)					
T. cana Mousseh s.n. (HBG)	CRt	3-colporate	48.5 (45–52)	26.5 (22–31)	1.86
T. semitrilobata Turckheim 2623 (BR)	CRt	3-colporate	39.0 (37–41)	25.0 (22–28)	1.57
Vasivaea Baillon					
V. alchorneoides Piers 3535 (IAN); (2*)	CRt	3-colporate	44.0 (42–46)	33.5 (26–41)	1.31

SEM (Figs 2 A–B; 5 D, H & I; Carpodiptera floribunda and C. africana)

Exine sculptring in *Carpodiptera africana* is coarsely rugulate-reticulate and in *C. floribunda* finely rugulate-reticulate. Colpi short, narrow, with rounded ends, colpal membrane granulated.

Christiana DC.

LM (Fig. 2 C–E; Christiana eburnea)

Pollen grains single, isopolar, suboblate, rarely oblate-spheroidal. P= (22−)30(−38) μm. E= (26−)32(−38) μm. P/E ratio: 0.94. Amb rounded-triangular or trilobed triangular with convex mesocolpia, equatorial view elliptical.

Pollen grains 3-colporate. Colpi short, narrow with costae, 4–5 μm long. Ora lalongate. Exine 1–2 μm thick. Sexine thicker than nexine, nexine 0.5–2 μm.

SEM (Fig. 2 F, G; Christiana eburnea)

In *C. africana* exine sculpturing is medium rugulate-reticulate and in *C. eburnea* medium rugulate-striate. Colpus membrane granulated.

Clappertonia Meissner

LM (Fig. 7 A, B; Clappertonia polyandra)

Pollen grains single, isopolar, prolate, rarely per-prolate. P= (53−)65(−77) μm. E =(23−)39(−55) μm. P/E ratio: 1.67. Shape in polar view trilobed with slightly convex mesocolpia, equatorial view elliptical. 3–4-colporate. Colpi long, narrow, 23–34 μm. Ora lalongate, 8.5–10 μm. Exine 1–3 μm thick. Sexine thicker than nexine, nexine 0.5–1 μm.

SEM (Figs 6 H, I & 7 C–E; Clappertonia ficifolia and C. polyandra)

In *Clappertonia ficifolia* exine sculpturing is coarsely reticulate-rugulate with finely perforated lumina, more or less irregular pattern of muri. Lumina variable in shape and size, 0.33–1 μm in diameter. Lumina perforated, perforations 0.01 μm in diameter. In *C. polyandra* exine sculpturing is coarsely reticulate, lumina 0.7–1 μm in diameter. Apocolpial region more or less punctate-subpsilate.

Colona Cav.

LM (Fig. 7 F–H; Colona auriculata)

Pollen grains single, isopolar, mainly prolate. P= (22−)27.5 (−33) μm. E= (16−)19.5(−23) μm. P/E ratio: 1.41. Amb trilobed with slightly convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 18–29 μm, vestibuli. Ora lalongate, ca. 4 μm. Exine 0.5–2 μm thick. Sexine thicker than nexine, nexine 0.5–1 μm.

SEM (Fig. 7 I, J; Colona auriculata)

Exine sculpturing coarsely reticulate, more or less irregular pattern of muri. Lumina variable in shape and size, 0.2–1 μm in diameter, lumina perforated, perforations 0.01–0.4 μm in diameter; perforations more distinct towards the margins. Colpal membrane granulated.

Corchorus L.

LM (Fig. 8 A; Corchorus aestuans)

Pollen grains single, isopolar, usually prolate, rarely prolate-spheroidal. P=(23−) 41.5 (−60) μm. E=(17−) 24.5 (−32) μm. P/E ratio: 1.7. Amb triangular or triangular-trilobed with convex mesocolpia, equatorial view elliptical.

Pollen grains 3-colporate. Colpi long, narrow with costae, 32–52 μm. Ora lalongate, rarely lolongate, 3−8 × 5−9 μm. Exine 1.5–3.5 μm thick. Sexine thicker than nexine, nexine 0.2–1 μm.

SEM (Fig. 8 B–D; Corchorus aestuans)

Exine sculpturing coarsely reticulate, more or less irregular pattern of muri. Lumina variable in shape and size, 0.2–1.5 μm in diameter, lumina perforated, perforations 0.01–0.2 μm in diameter; perforations evenly distributed. Colpal membrane granulated.

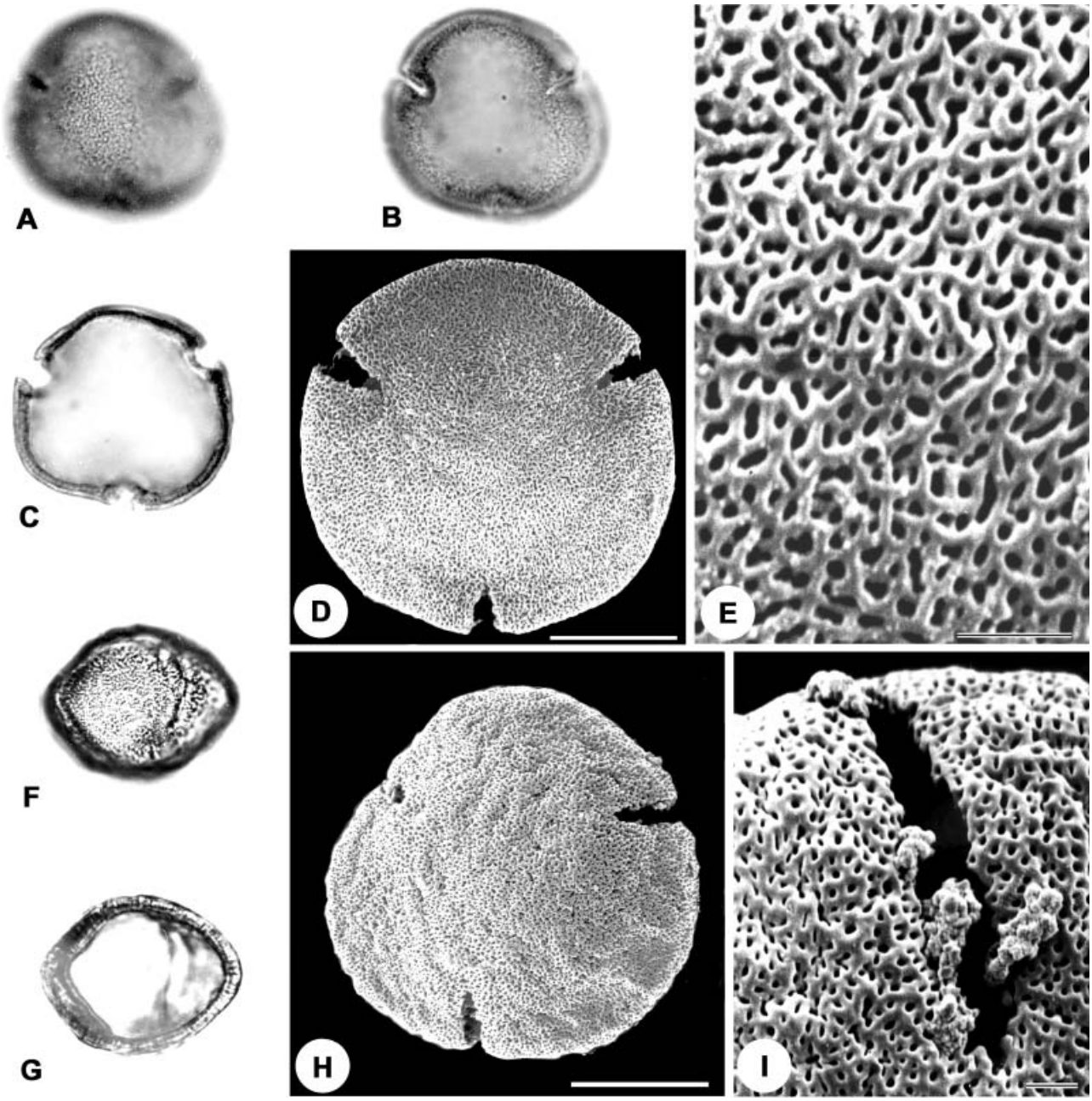

Fig. 1. A–E. *Berrya cordifolia* (Hb. Gay, HBG). (A) Pollen grain, polar view, high focus, LM. (B) Polar view, mid focus, LM. (C) Polar view, low focus, LM. (D) Pollen grain, polar view, SEM. (E) Detail of exine pattern, showing microreticulate tectum, SEM. F-I. *Brownlowia tabularis* (Bejaud 450, BO). (F) Pollen grain, equatorial view, high focus, LM. (G). Equatorial view, low focus, LM. (H) Polar view, SEM. (I) Detail of colpus and tectum surface, SEM. All LM — × 1000. Scale bar — 1 μm (*E, I*); 10 μm (*D, H*).

Desplatsia **Bocquillon**

LM (Fig. 8 E–G; Desplatsia subericarpa)

Pollen grains single, isopolar, prolate, rarely prolate-spheroidal. P= (35−)43.5(−52) μm. E= (25−)28(−31) μm. P/E ratio: 1.55. Shape in polar view trilobed with slightly convex mesocolpia, equatorial view elliptical. Pollen 3-colporate. Colpi long, narrow with costae. Ora lalongate, 3−6 × 4−6.9 μm. Exine 2–3 μm thick. Sexine thicker than nexine, nexine 0.5–1 μm thick.

SEM (Fig. 8 H, I; Desplatsia subericarpa)

Exine sculpturing coarsely reticulate in all species, more or less irregular pattern of muri. Lumina variable in shape and size, 0.4–2 μm in diameter, lumina perforated, perforations

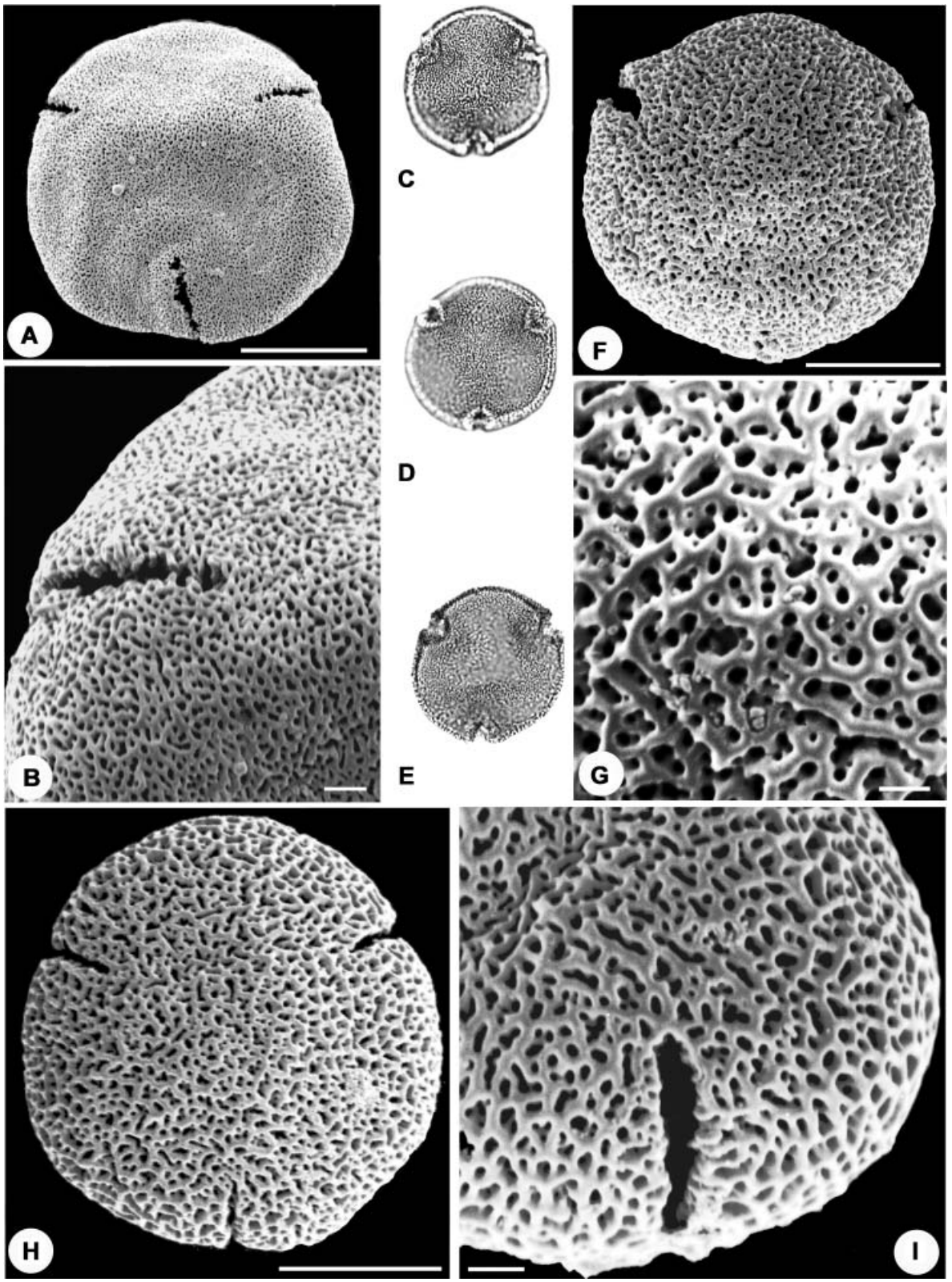

Fig. 2. A, B. *Carpodiptera floribunda* (Hahn 944, P). (A) Pollen grain, polar view, showing rounded mesocolpia, SEM. (B) Detail of tectum suface, showing colpus and microreticulate tectum, SEM. C–G. *Christiana eburnea* (Spruce 6260, K). (C) Pollen grain, polar view, high focus, LM. (D) Polar view, mid focus, LM. (E) Polar view, low focus, LM. (F) Polar view, SEM. (G) Detail of tectum suface, showing microreticulate tectum, SEM. H–I. *Diplodiscus hookerianus* (King 315, L.) (H) Polar view, SEM. (I) Detail of tectum surface, showing colpus, SEM. All LM — × 1000. Scale bar — 1 μm (*B, G, I*); 10 μm (*A, F, H*).

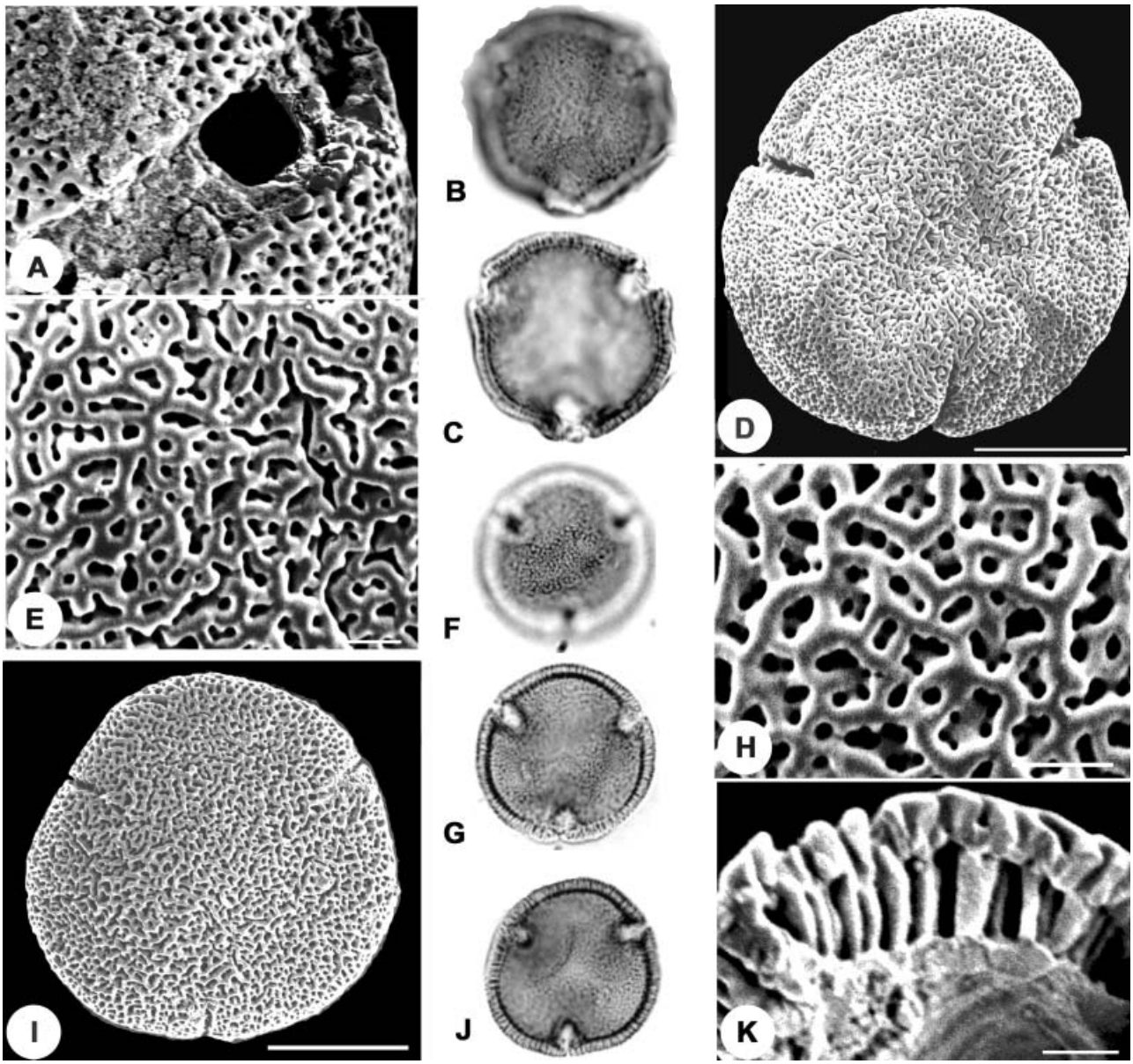

Fig. 3. A. *Diplodiscus longifolius* (Nootebon 4095, L). Detail of tectum surface, showing colpus with granulated colpus margine and distinct ora, SEM. B – E. *Hainania trichosperma* (Lau 476, P). (B) Pollen grain, polar view, high focus, LM. (C) Polar view, low focus, LM. (D) Pollen grain, polar view, SEM. (E) Detail of tectum surface, SEM. F – K. *Pentace borneensis* (Elmer 21317, HBG). (F) Pollen grain, polar view, high focus, LM. (G) Polar view, mid focus, LM. (H) Polar view, low focus, LM. (I) Pollen grain, polar view, SEM. (J) Detail of tectum surface, SEM. (K) Section of the pollen wall, note the branched columellae, SEM. All LM — × 1000. Scale bar — 1 μm (*A, E, H, K*); 10 μm (*D, I*).

0.01 – 0.2 μm in diameter; perforations more distinct towards the margins.

Colpi short, narrow, 5 – 11 μm long. Ora lalongate. Exine 2 – 2.5 μm thick. Sexine thicker than nexine, nexine 0.2 – 0.9 μm.

Diplodiscus Turcz.

LM

Pollen grains single, isopolar, oblate. P = (19 −)20(−21) μm, E = (18 −)29.5(−41) μm. P/E ratio: 0.68. Amb rounded-triangular or trilobed triangular with convex mesocolpia, equatorial view transverse elliptical. Pollen grains 3-colporate.

SEM (Figs 2 H, I & 3 A; Diplodiscus hookerianus and D. longifolius)

Exine sculpturing is reticulate-rugulate in all species. In *D. longifolius* exine sculpturing is roughly reticulate. Colpal membrane granular.

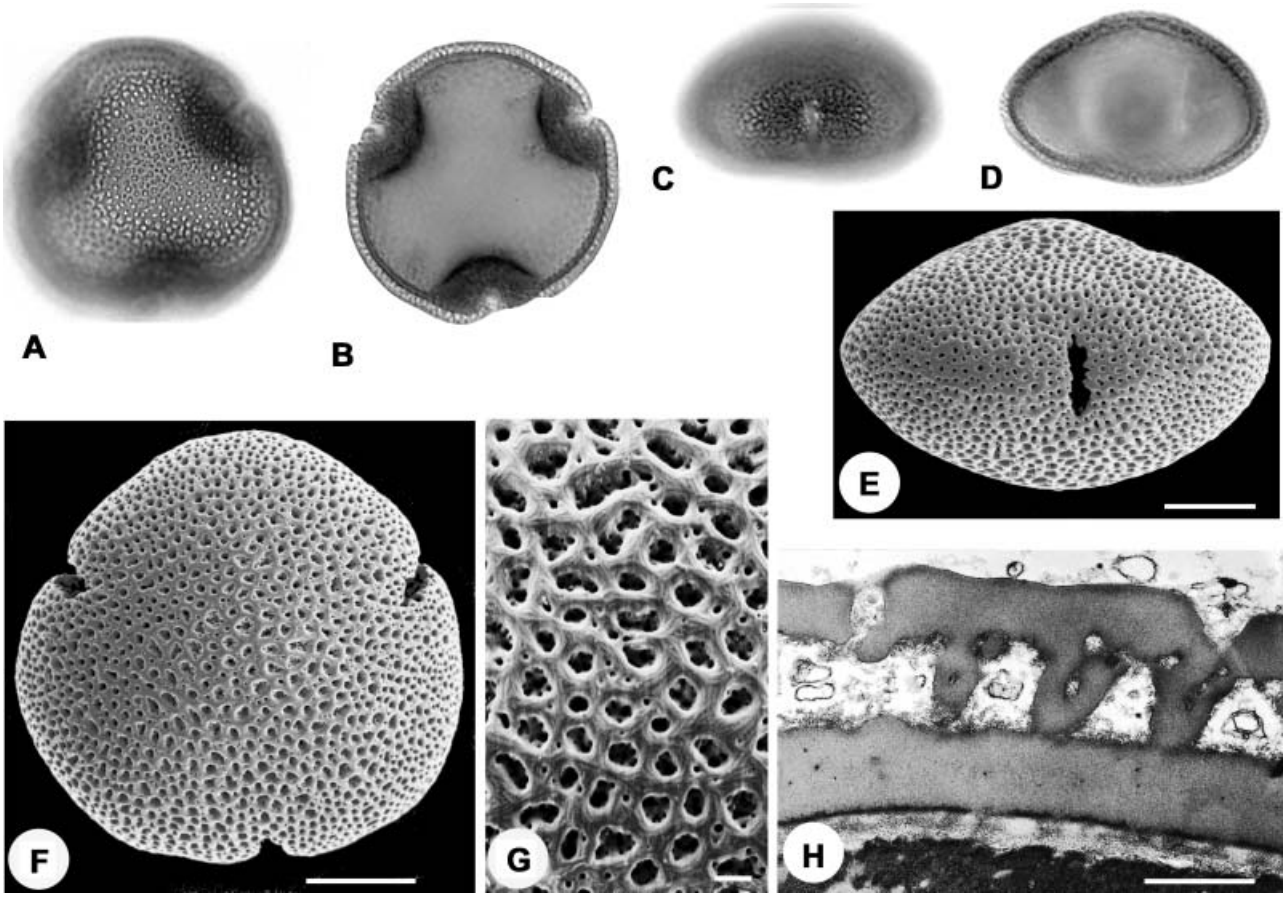

Fig. 4. A – H. *Tilia platyphyllos* (Gautier 1794, S) (A) Polar view, high focus, LM. (B) Pollen grain, polar view, mid focus, LM. (C) Equatorial view, high focus, LM. (D) Equatorial view, low focus, LM. (E) Pollen grain, equatorial view, SEM. (F) Pollen grain, polar view, SEM. (G) Detail of exine, SEM. (H) Section of exine stratified into a compact perforated tectum, columellate infratectal stratum, and foot-layer subtended by a thin endexine, and intine, TEM. All LM — × 1000. Scale bar — 1 μm (*G, H*); 10 μm (*E, F*).

Duboscia Bocquillon

LM (Figs 9 A – C& 16 A – C; Duboscia viridiflora and D. macrocarpa)

Pollen grains single, isopolar, prolate. P = (20−)24 (−28) μm. E = (15−)18(−21) μm. P/E ratio: 1.35. Amb rounded-trilobed with slightly convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 14 – 20 μm. Ora lalongate, 1.1 – 3 μm. Exine 1.8 – 2.5 μm thick. Sexine thicker than nexine, nexine 0.2 – 0.9 μm.

SEM (Figs 9 D, E & 16 D – F; Duboscia viridiflora and D. macrocarpa)

In *Duboscia macrocarpa* exine sculpturing is coarsely reticulate-rugulate, colpal margin psilate. In *D. viridiflora*, exine sculpturing is coarsely reticulate, more or less irregular pattern of muri. Lumina variable in shape and size, 0.6 – 1.4 μm diameter, lumina perforated, perforations 0.1 – 0.5 μm in diameter; perforations more distinct towards the margins.

Eleutherostylis Burret.

LM (Fig. 9 F, G; Eleutherostylis renistipulata)

Pollen grains single, prolate, isopolar. P = (32−)38 (−45) μm, E = (21−)23(−25) μm.

P/E ratio: 1.41. Amb trilobed with convex mesocolpia, equatorial view elliptical.

3-colporate. Colpi long, narrow, 27 – 35 μm long. Ora lalongate, ca. 3 μm in diameter. Exine 2 – 3 μm thick. Sexine thicker than nexine, nexine 1 μm.

SEM (Fig. 9 H – J; Eleutherostylis renistipulata)

Exine sculpturing coarsely reticulate, more or less irregular pattern of muri. Lumina variable in shape and size, 0.4 – 2.85 μm in diameter, lumina gradually reduced towards the colpus forming distinct colpal margin, lumina perforated, perforations 0.01 – 0.3 μm in diameter. Colpi long, narrow with tapering ends. Colpal membrane granulated.

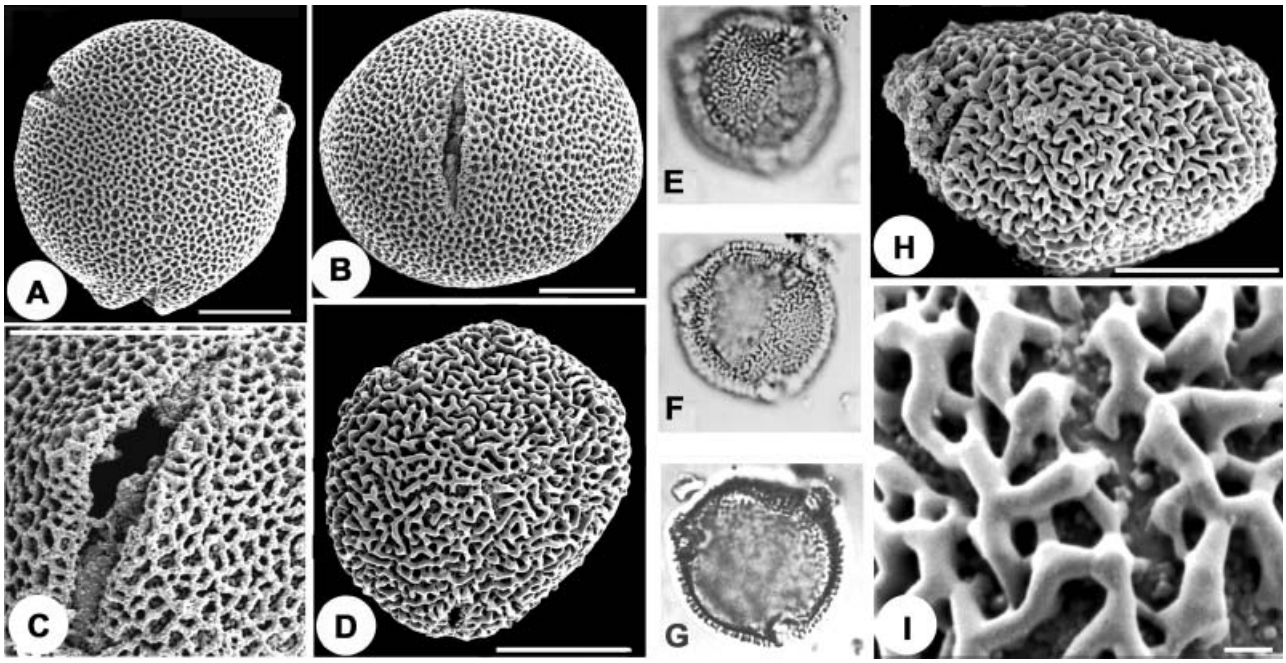

Fig. 5. A–C. *Apeiba albiflora* (Da Silva et.al 299, HBG). (A) Pollen grain, polar view; SEM. (B) Equatorial view; SEM. (C) Detail surface, showing microreticulate tectum; SEM. D–I. *Carpodiptera africana* (Holst 2216, HBG). (D) Pollen grain, polar view; SEM. (E) Pollen grain, polar view, high focus; LM. (F) Polar view, mid focus; LM. (G) Polar view, low focus; LM. (H) Equatorial view; SEM. (I) Detail of tectum surface showing coarsely reticulate rugulate — reticulate pattern, SEM. All LM — × 1000. Scale bar — 1 μm (*C, I*); 10 μm (*A, B, D, H*).

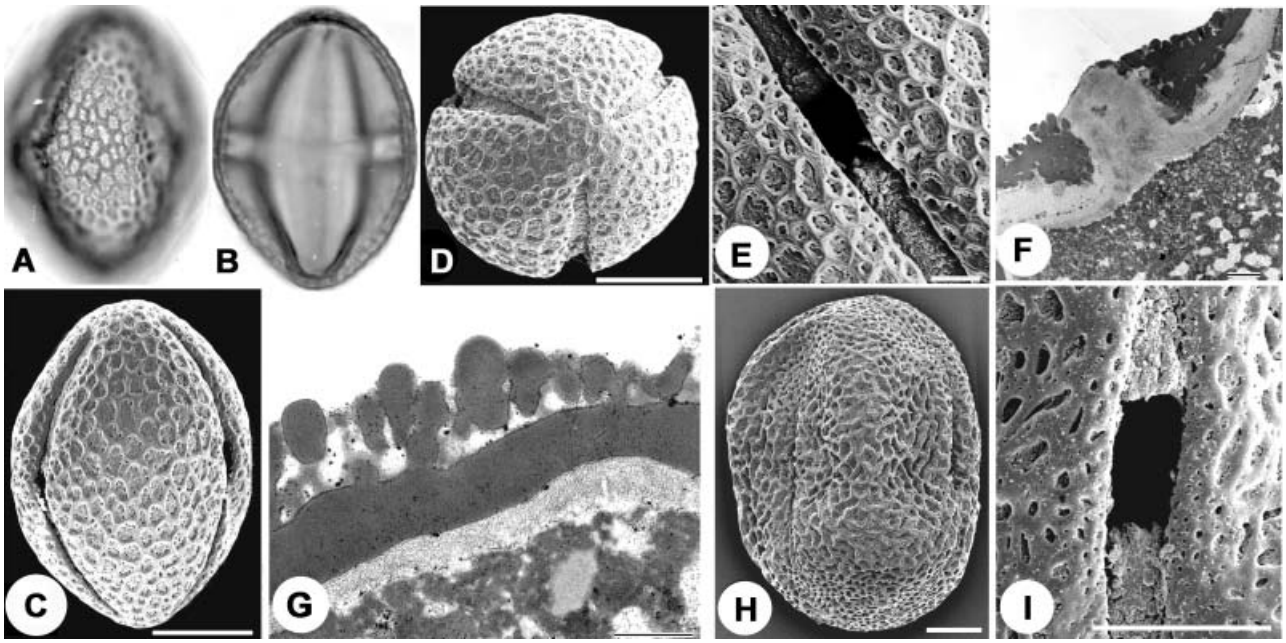

Fig. 6. A–G. *Ancistrocarpus bequaertii* (Troupin, 4636 BR). (A) Pollen grain, equatorial view, high focus, LM. (B) Equatorial view, low focus, LM. (C) Equatorial view of mesocolpium, SEM. (D) Pollen grain, polar view, showing convex mesocolpia, SEM. (E) Detail of exine pattern, showing coarsely reticulate tectum with perforated lumina, lumina size gradually reduced towards colpus forming colpal membrane, SEM. (F) Section through an aperture, exine thickened towards margin, TEM (G) Exine showing muri in cross-section (supratectal reticulum and perforated lumina) subtended by a solid foot-layer on itine. Endexine appears absent, TEM. H–I. *Clappertonia ficifolia* (Van Harten 73, HBG). (H) Pollen grain, equatorial view, SEM. (I) Detail of exine on colpus region, showing densely granulated colpus membrane, SEM. All LM — × 1000. Scale bar — 1 μm (*E, F, G, I*); 10 μm (*C, D, H*).

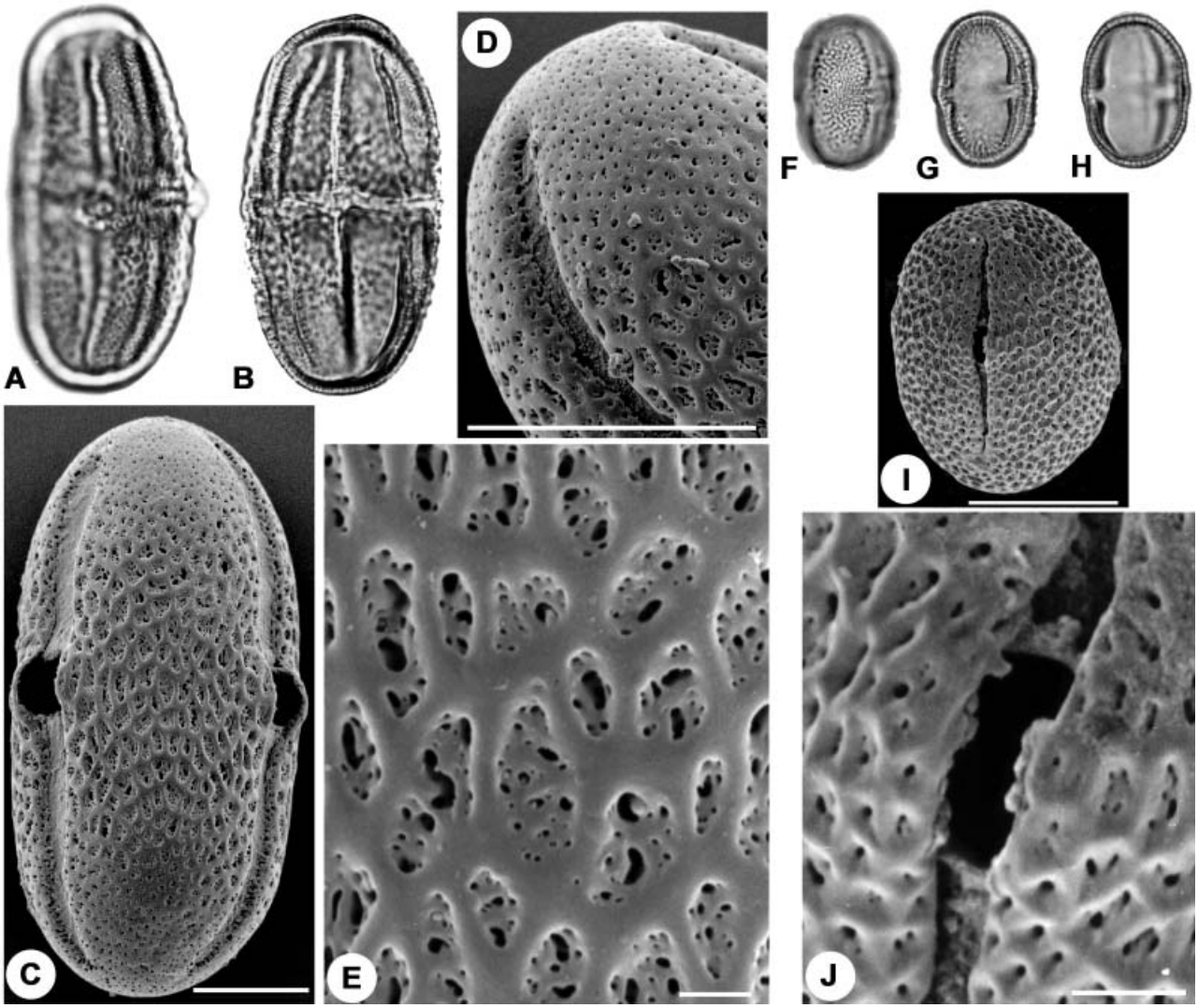

Fig. 7. A – E. *Clappertonia polyandra* (Bos et al., 10453, HBG). (A) Pollen grain, equatorial view, high focus, LM. (B) Equatorial view, low focus, LM. (C) Pollen grain, equatorial view showing distinct ora, LM. (D) Detail of tectum surface, showing at apocolpial region, SEM. (E) Detail of the surface, SEM. F – J *Colona auriculata* (Winkler B230, HBG) (F) Pollen grain, equatorial view, high focus, LM. (G) Equatorial view, mid focus, LM. (H) Equatorial view, low focus, LM. (I) Pollen grain, equatorial view, SEM. (J) Detail of tectum surface, showing granulated colpal membrane, SEM. All LM — × 1000. Scale bar — 1 μm (*E, J*); 10 μm (*C, D, I*).

***Entelea* R. Br.**

LM

Pollen grains prolate, isopolar. P = (29−)31.5(−34) μm, E = (21−)22.5(−24) μm.

P/E ratio: 1.40. Amb trilobed with convex mesocolpia, equatorial view elliptical.

3-colporate. Colpi long, narrow, 22 – 26 μm. Ora lalongate, 2.1−4.1 × 7−10 μm. Exine 1.5 – 2 μm thick. Sexine thicker than nexine, nexine 0.5 – 0.8 μm.

SEM (Fig. 10 A, B; Entelea arborescens)

Exine sculpturing coarsely reticulate with scabrae, irregular pattern of muri, lumina 0.4 – 0.8 μm in diameter, lumina perforated, perforations 0.01 – 0.1 μm in diameter. Colpi long, narrow with tapering ends. Colpal membrane granulated.

***Erinocarpus* Nimmo**

LM (Fig. 10 C, D; Erinocarpus nimmonii)

Pollen grains prolate, isopolar. P = (52−)56(−60.5) μm, E = (29−)34.5(−40) μm.

P/E ratio: 1.62. Shape in polar view trilobed with convex mesocolpia, equatorial view elliptical. 4-colporate. Colpi long, narrow, 42 – 58 μm. Ora not distinct. Exine 1.4 – 1.6 μm thick. Sexine thicker than nexine, nexine 0.4 – 0.6 μm.

SEM (Fig. 10 E, F; Erinocarpus nimmonii)

Exine sculpturing coarsely reticulate, more or less irregular pattern of muri. Lumina variable in shape and size, 0.41 – 2.95 μm in diameter. Lumina gradually reduced towards the colpus forming distinct colpal margin, lumina perforated, perforations 0.01 – 0.3 μm in diameter. Colpi

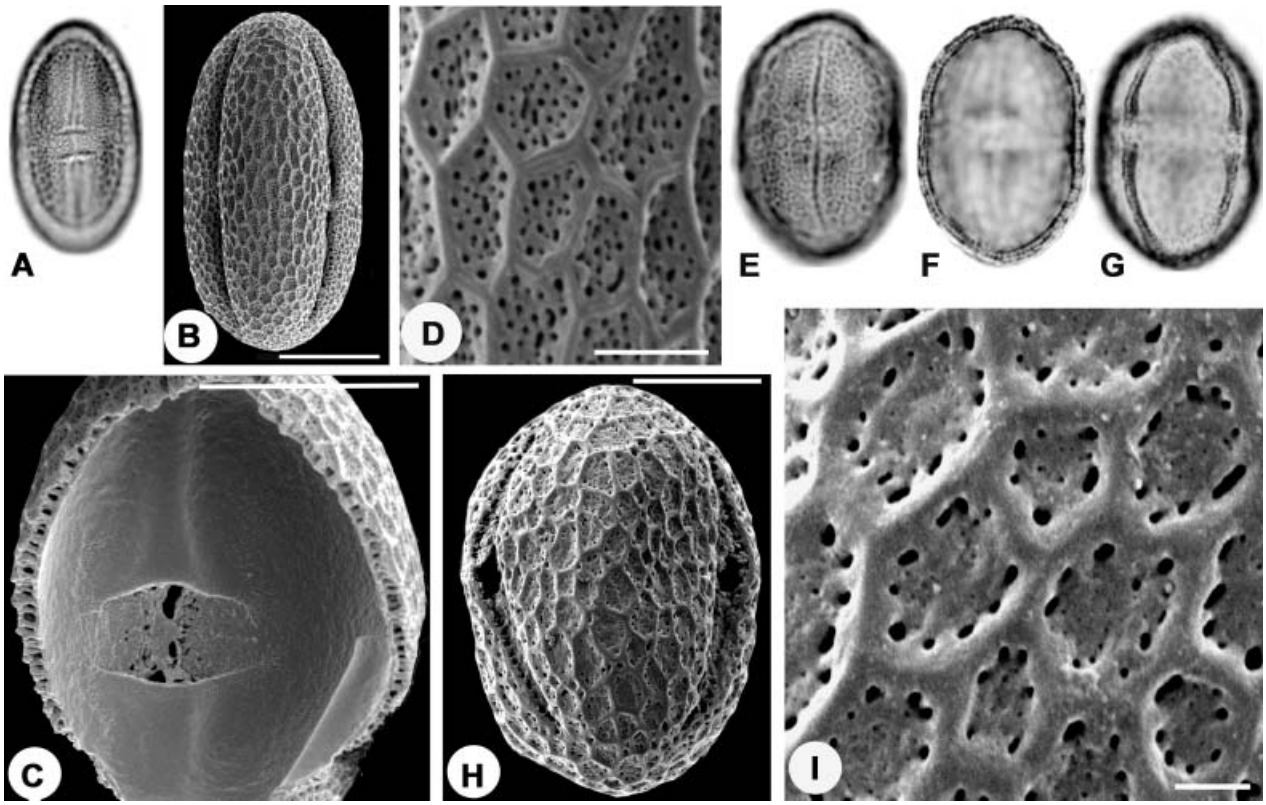

Fig. 8. A–D. *Corchorus aestuans* (Polhill & Paulo 1314, BR). (A) Pollen grain, equatorial view, LM. (B) Pollen grain, equatorial view, showing mesocolpium, SEM. (C) Fragment of pollen showing internal view of the pollen grain and particularly the lolongate endoaperture, SEM. (D) Detail of tectum surface, showing coarsely reticulate tectum with perforated lumina, perforations evenly distributed, SEM. E–I. *Desplatsia subericarpa* (Bos 4162, WAG). (E) Pollen grain, equatorial view, high focus, LM. (F) Equatorial view, mid focus, LM. (G) Equatorial view, low focus, LM. (H) Pollen grain, equatorial view, SEM. (I) Detail of exine pattern, showing coarsely reticulate tectum, perforations restricted at the margin, SEM. All LM — × 1000. Scale bar — 1 μm (*D, I*); 10 μm (*B, C, H*).

long, narrow with tapering ends. Colpal membrane granulated.

Glyphaea Hook.f.

LM

Pollen grains single, isopolar, prolate. P= (31−)35.5 (−40) μm. E= (21−)24.5(−28) μm. P/E ratio: 1.37–1.54. Shape in polar view trilobed with slightly convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 27–35 μm. Ora lalongate, ca. 2 μm. Exine 2.1–3 μm thick. Sexine thicker than nexine, nexine 0.9–1.1 μm.

SEM

Exine sculpturing coarsely reticulate, more or less irregular pattern of muri. Lumina variable in shape and size, 0.2–2.1 μm in diameter, lumina perforated, perforations 0.01–0.2 μm in diameter; perforations more distinct towards the margins. Colpi long, narrow, with tapering ends.

Goethalsia Pittier

LM (Fig. 11 A, B; Goethalsia meiantha)

Pollen grains prolate, isopolar. P= (21−)28.5(−36) μm, E= (15−)18.5(−22) μm.

P/E ratio: 1.54. Amb trilobed with convex mesocolpia, equatorial view elliptical.

3-colporate. Colpi long, narrow, 19–25 μm. Ora lalongate, 2 × 5 μm. Exine 1–2 μm thick. Sexine thicker than nexine, nexine 0.5–1 μm.

SEM (Fig. 11 C, D; Goethalsia meiantha)

Exine sculpturing coarsely reticulate, more or less irregular pattern of muri, lumina variable in shape and size, 0.4–1.55 μm in diameter, lumina perforated, perforations 0.05–0.1 μm in diameter. Colpi long, narrow with tapering ends, colpal membrane granulated.

Grewia L.

LM

Pollen grains single, isopolar, prolate. P= (26−)48.5 (−71) μm. E= (16−)37(−58) μm. P/E ratio: 1.27–2.05.

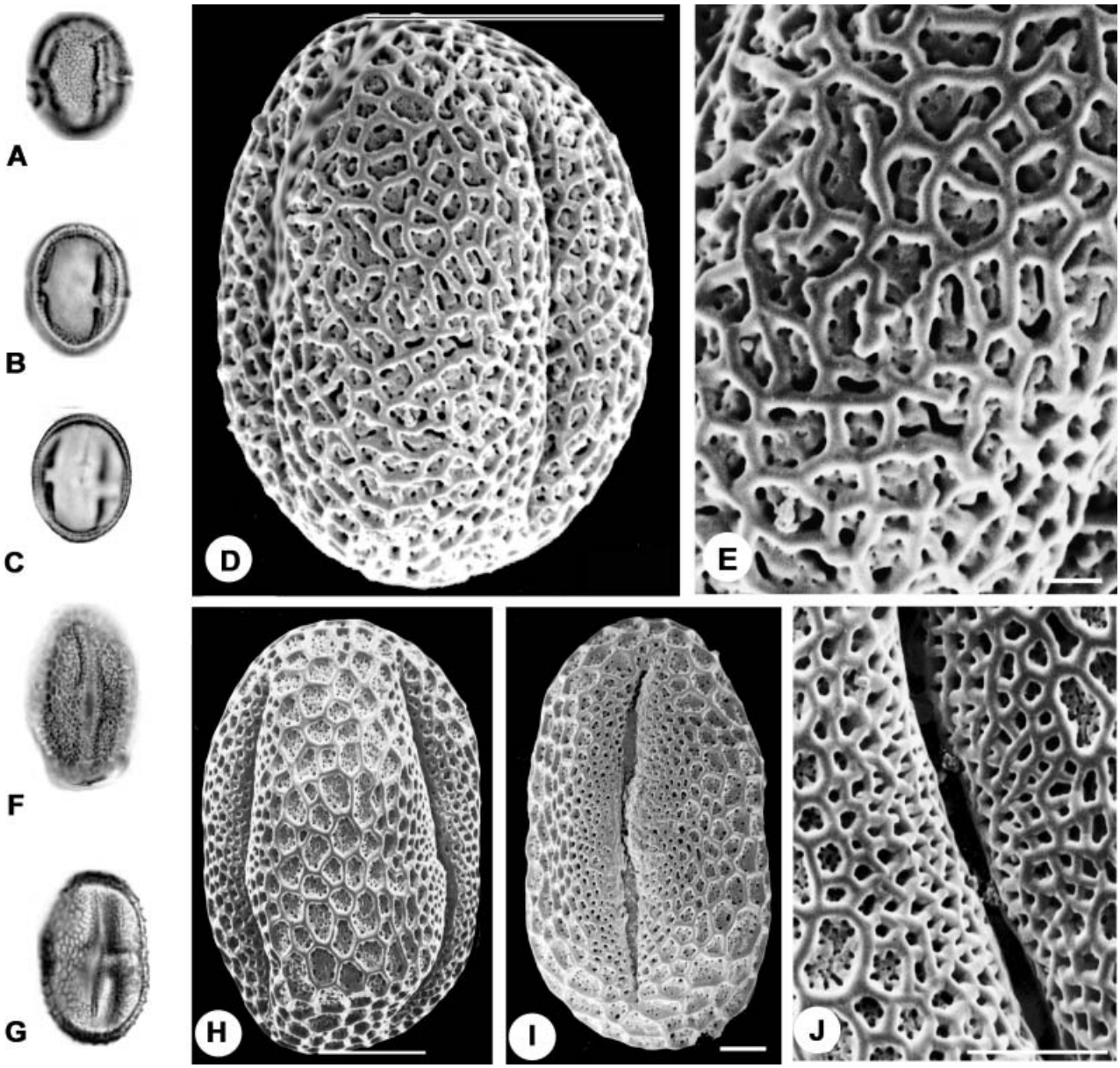

Fig. 9. A–E. *Duboscia viridiflora* (Zenker 260, WAG.). (A) Pollen grain, equatorial view, high focus, LM. (B) Equatorial view, mid focus, LM. (C) Equatorial view, low focus, LM. (D) Pollen grain, equatorial view, SEM. (E) Detail of tectum surface, showing reticulate tectum with irregular pattern of muri, SEM. F–J. *Eleutherostylis renistipulata* (Hoogland 5044, L). (F) Pollen grain, equatorial view, high focus, LM. (G) Equatorial view, mid focus, LM. (H) Pollen grain, equatorial view, SEM. (I) Pollen grain, equatorial view, showing reducing lumina towards colpus forming distinct colpal margin, SEM. (J) Detail of exine pattern at colpus region, SEM. All LM — × 1000. Scale bar — 1 μm (*E, J*); 10 μm (*D, H, I*).

Amb trilobed with slightly convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 33–57 μm. Ora lalongate, 1.9−4 × 6−8 μm. Exine 0.2–0.9 μm thick. Sexine thicker than nexine, nexine 2–3.5 μm.

SEM (Fig. 11 E–H; 12 A, B. Grewia forbesii and G. villosa)

Exine sculpturing coarsely reticulate, more or less irregular pattern of muri. Lumina variable in shape and size, 0.4–3.6 μm in diameter, lumina perforated, perforations 0.01–0.8 μm in diameter; perforations more distinct towards the margins and evenly distributed within the lumina. Colpi long, narrow, with tapering ends.

***Hainania* Merr.**

LM (Fig. 3 B, C; Hainania trichosperma)

Pollen grains single, isopolar, oblate. P= (22−)22.5 (−23) μm. E= (30−)33(−36) μm. P/E ratio: 0.68. Amb

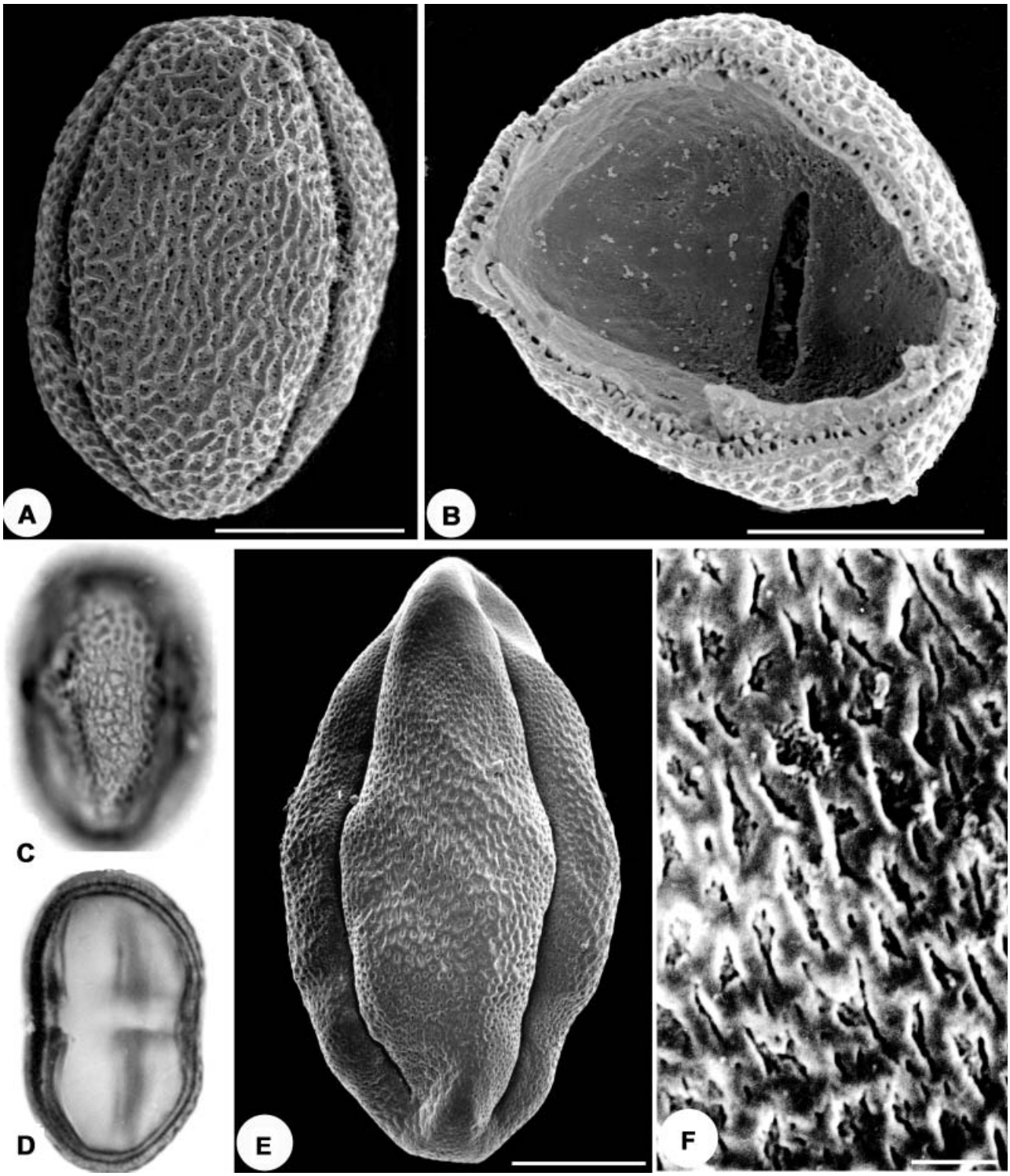

Fig. 10. A – B. *Entelea arborescens* (Chapman 258569, L). (A) Pollen grain, equatorial view, SEM. (B) Fragment showing part of internal view of the pollen grain and the endoaperture, SEM. C – F. *Erinocarpus nimmonii* (Stock & Low s.n., P). (C) Pollen grain, equatorial view, high focus, LM. (D) Equatorial view, low focus, LM. (E) Pollen grain, equatorial view, SEM. (F) Detail of exine pattern, note coarsely reticulate tectum, SEM. All LM — × 1000. Scale bar — 1 μm (*F*); 10 μm (*A, B, E*).

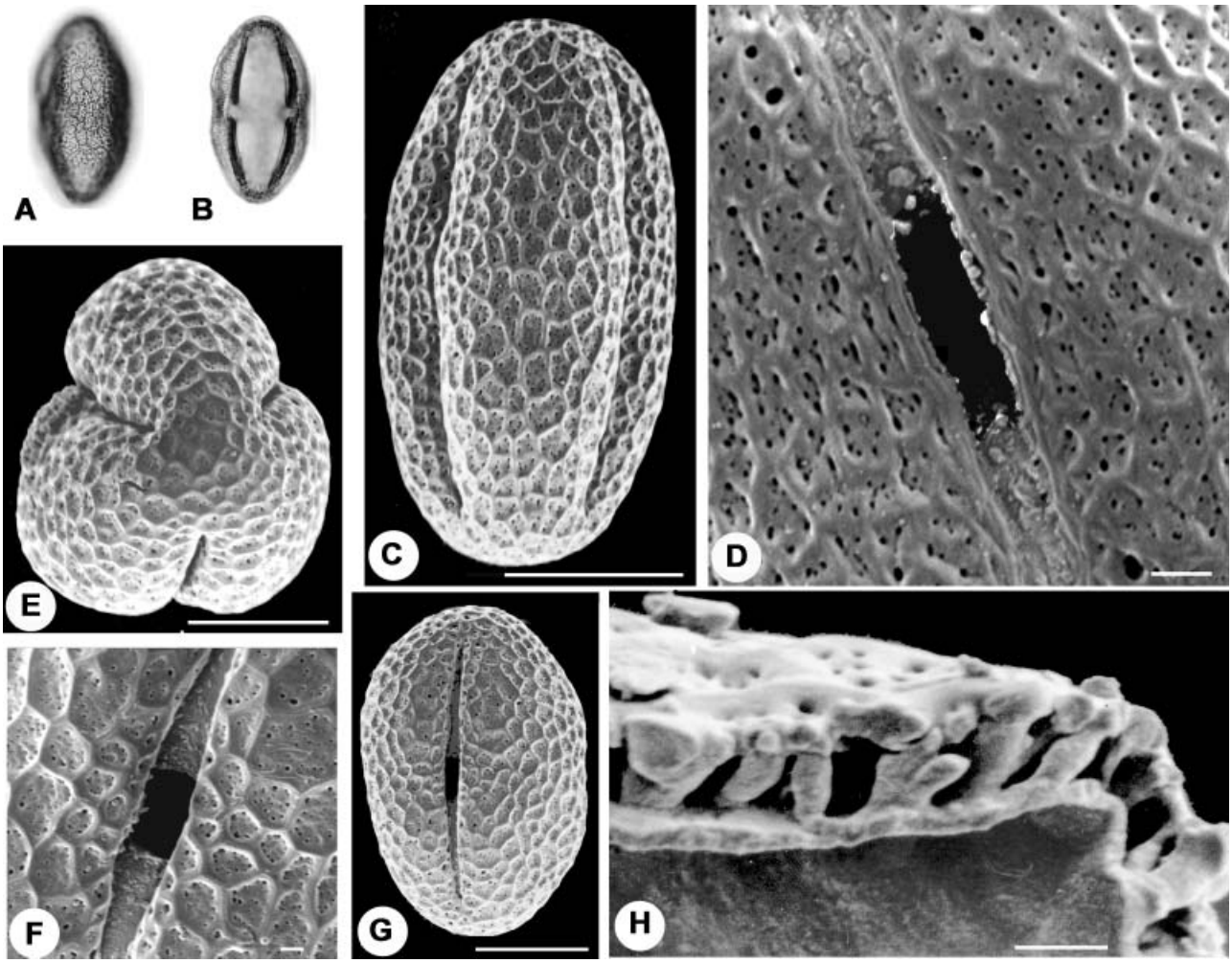

Fig. 11. A – D. *Goethalsia meiantha* (Wilbur 27398, F) (A) Pollen grain, equatorial view, high focus, LM. (B) Equatorial view, low focus, LM. (C) Pollen grain, equatorial view, showing mesocolpium, SEM. (D) Detail of exine pattern, showing coarsely reticulate tectum with perforated lumina, SEM. E – H. *Grewia forbesii* (Semsei 4251, BR). (E) Pollen grain, polar view, SEM. (F) Detail of exine pattern, SEM. (G) Pollen grain equatorial view, SEM. (H) Fragmented pollen, showing branched collumellae, SEM. All LM — × 1000. Scale bar — 1 μm (*D, F, H*); 10 μm (*C, E, G*).

trilobed with convex mesocolpia, equatorial view transverse elliptical. 3-colporate. Colpi short, 15 μm. Ora lalongate, not clear. Exine 1.9 – 2 μm thick. Sexine thicker than nexine, nexine 0.3 – 0.9 μm.

SEM (Fig. 3 D, E; Hainania trichosperma)

Exine sculpturing is rugulate-reticulate with irregular pattern of muri. Colpi short, tapering ends. Colpal membrane granulated.

Heliocarpus L.

LM (Fig. 12 E – G; Heliocarpus terebinthinaceus)

Pollen grains single, isopolar, prolate. P = (33 –)38.5 (– 44) μm. E = (22 –)24(– 26) μm. P/E ratio: 1.56. Amb trilobed-triangular with slightly convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 30 – 38 μm. Ora lalongate, 1.9 – 5 × 8 – 11 μm. Exine 2 – 3 μm thick. Sexine thicker than nexine, nexine ca. 1 μm.

SEM (Fig. 12 C, D, H, I; Heliocarpus americanus and H. terebinthinaceus)

Exine sculpturing coarsely reticulate, more or less irregular pattern of muri. Lumina variable in shape and size, 0.5 – 1 μm in diameter. Lumina perforated, perforations 0.01 – 0.2 μm in diameter; perforations more distinct towards the margins. Colpi long, narrow with tapering ends.

Luehea Willd.

LM (Fig. 13 A, B; Luehea conwentzii)

Pollen grains sub-prolate, isopolar. P = (25 –)39(– 53) μm, E = (18 –)29.5(– 41) μm. P/E ratio: 1.24 – 1.56. Amb trilobed with convex mesocolpia, equatorial view elliptical.

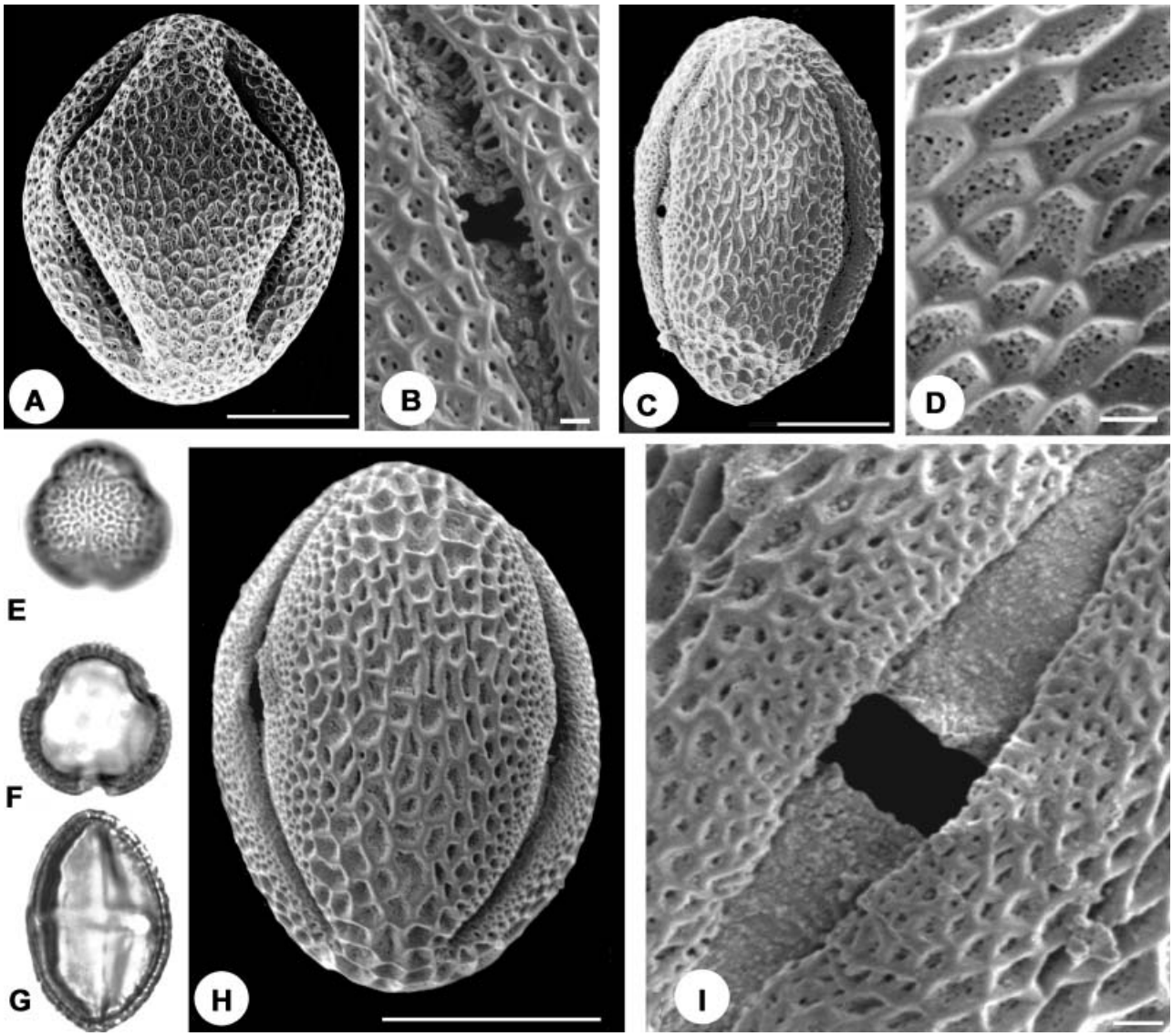

Fig. 12. A – B. *Grewia villosa* (Bamps & Martins 4396, BR). (A) Pollen grain, equatorial view, SEM. (B) Detail of colpus with granulated colpal membrane, SEM. C, D *Heliocarpus americanus* (Bourgeau 1574, L) (C) Pollen grain, equatorial view, SEM. (D) Detail of exine pattern, showing coarsely reticulate tectum with perforated lumina, SEM. E – I. *H. terebinthinaceus* (Purpus 3062, L). (E) Pollen grain, polar view, high focus, LM. (F) Polar view, low focus, LM. (G) Equatorial view, mid focus, LM. (H) Pollen grain, equatorial view, SEM. (I) Detail of colpus with distinct endoaperture, SEM. All LM — × 1000. Scale bar — 1 μm (*G, M*); 10 μm (*E, F, L*).

3-colporate. Colpi long, narrow, 24 – 37 μm. Ora lalongate, 4 × 4 μm. Exine 1.2 – 1.9 μm thick. Sexine thicker than nexine, nexine 0.2 – 0.8 μm.

SEM (Fig. 13 C, D; Luehea conwentzii)

In *Luehea conwentzii* exine sculpturing is coarsely rugulate-reticulate. More or less irregular pattern of muri. Colpal membrane subpsilate. Lumina variable in shape and size, 0.1 – 1.2 μm in diameter. Colpal margin subpsilate.

In *L. divaricata* exine sculpturing is coarsely reticulate. More or less irregular pattern of muri, lumina variable in shape and size, 0.4 – 1.4 μm in diameter, gradually reduced towards the colpus, forming distinct colpus margin. Lumina perforated, perforations 0.01 – 0.35 μm in diameter. Colpi long, narrow with tapering ends, colpal membrane granulated.

***Lueheopsis* Burret.**

LM (Fig. 13 E, F; Lueheopsis althaeiflora)

Pollen grains isopolar, single, prolate or prolate-spheroidal. P = (29 −)35.5(−42) μm, E = (25 −)29.5(−34) μm. P/E ratio: 1.16 – 1.24. Amb triangular with convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 32 – 36 μm. Ora lalongate, 2.5 − 5 × 6 − 10 μm. Exine ca.

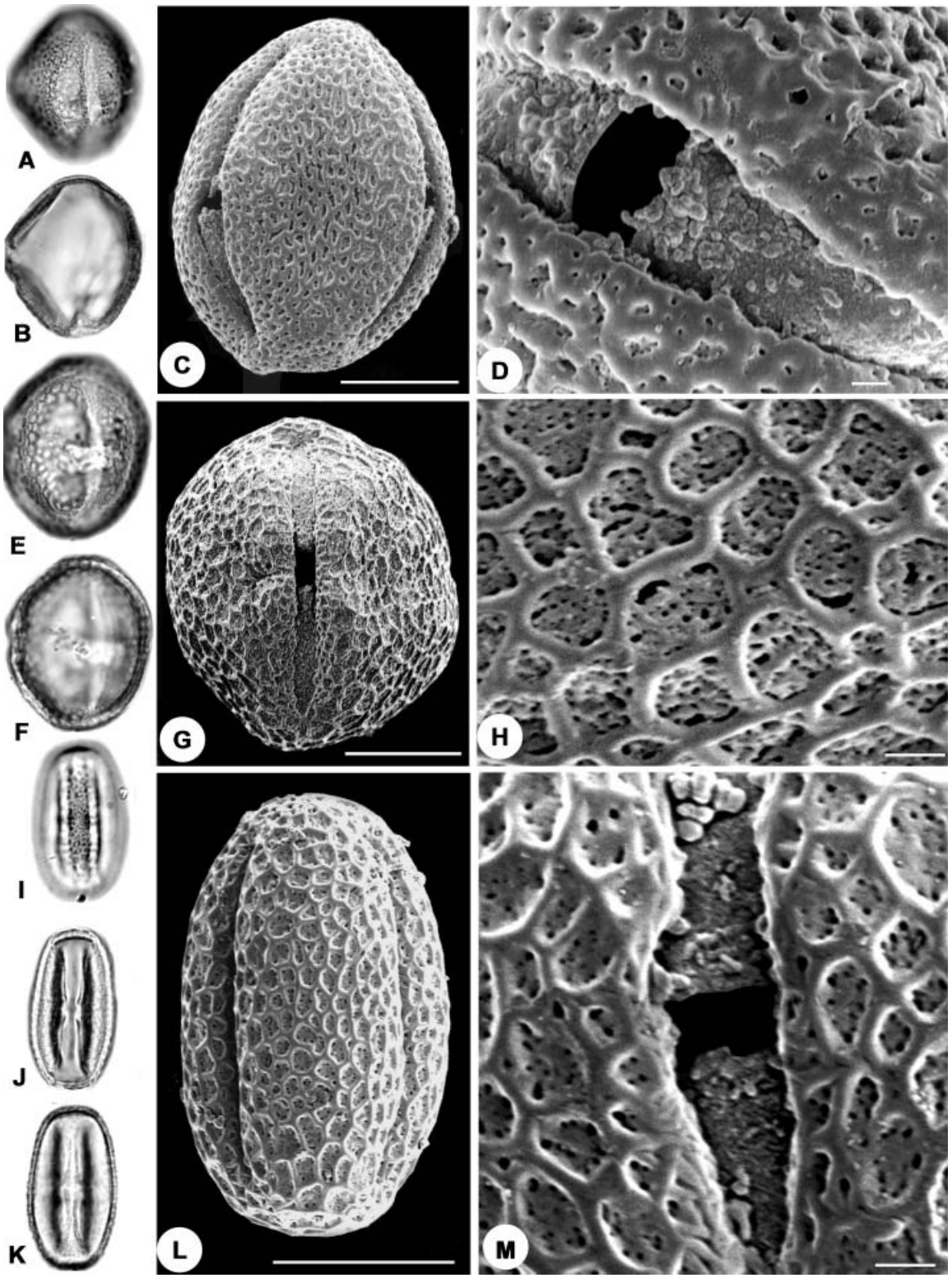

Fig. 13. A – D. *Luehea conwentzii* (Parana 29.12.1987, Kummrov 2959, HBG). (A) Pollen grain, equatorial view, high focus, LM. (B) Equatorial view, low focus, LM. (C) Pollen grain, equatorial view, SEM. (D) Lalongate endoaperture, SEM. E – H. *Lueheopsis althaeiflora* (San Carlos de Rio Negro no date. Stergois et al. 13093, INPA). (E) Pollen grain, equatorial view, high focus, LM. (F) Equatorial view, low focus, LM. (G) Pollen grain, equatorial view, SEM. (H) Detail of exine pattern, SEM. I – M. Microcos coriacea (Thomas & Nemba 5930, BR). (I) Pollen grain, equatorial view, high focus, LM. (J) Equatorial view, mid focus, LM. (K) Equatorial view, low focus, LM. (L) Pollen grain, equatorial view, SEM. (M) Exine pattern in the aperture area SEM. All LM — × 1000. Scale bar — 1 μm (*D, H, M*); 10 μm (*C, G, L*).

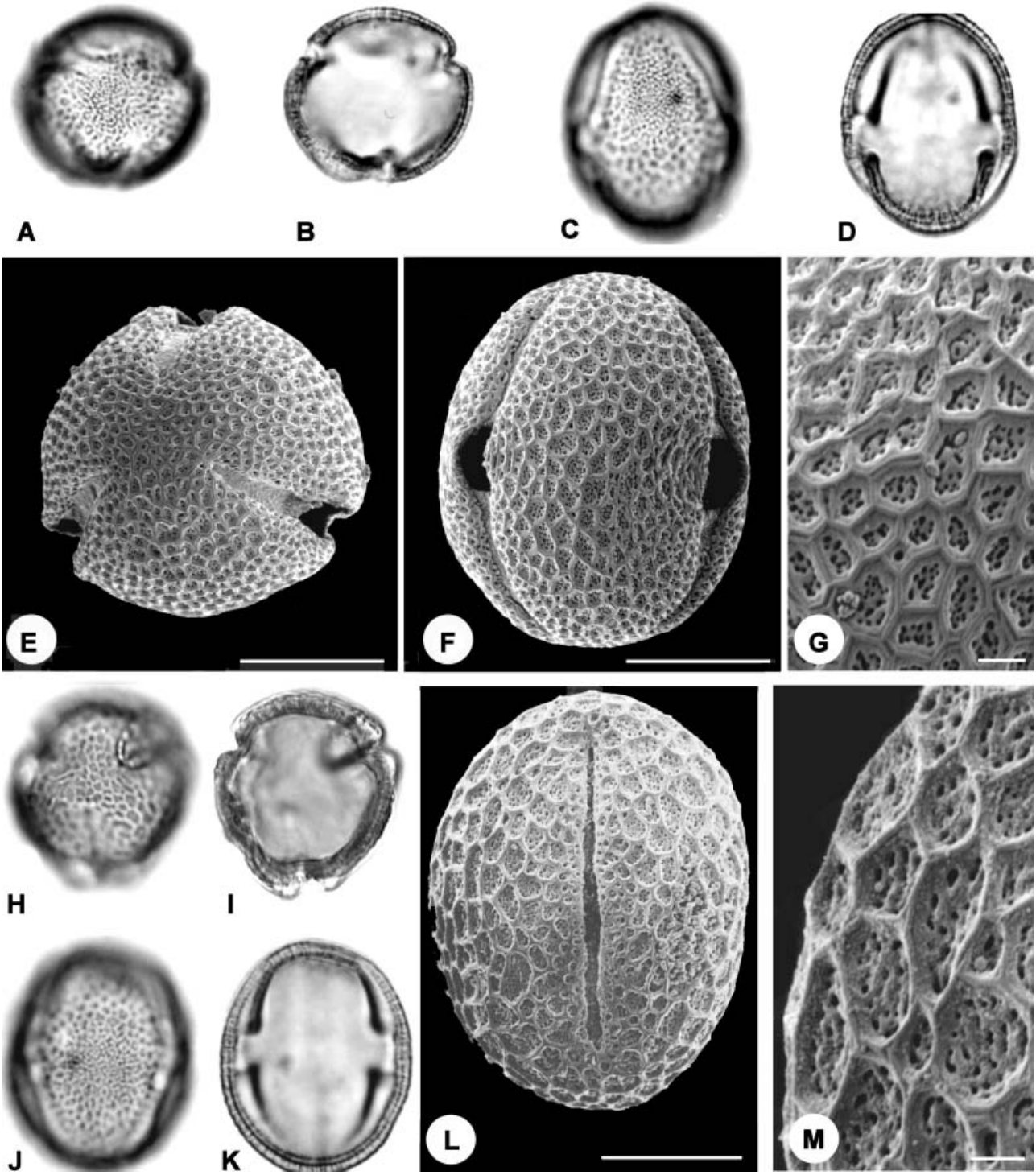

Fig. 14. A – G. *Sparmannia abyssinica* (Vokens 414, HBG). (A) Pollen grain, polar view, high focus, LM. (B) Polar view, mid focus, LM. (C) Pollen grain, equatorial view, high focus, LM. (D) Equatorial view, SEM. (E) Pollen grain, polar view, SEM. (F) Pollen grain, equatorial view, SEM. (G) Detail pattern of exine, showing reticulate tectum, SEM. H – K. *Tetralix brachypetalus* (Wright 1993, P). (H) Pollen grain, polar view, high focus, LM. (I) Polar view, low focus, LM. (J) Pollen grain, equatorial view, high focus, LM. (K) Equatorial view, low focus, LM. L – M. *Tetralix jaucoensis* (Bisse 20129, JE). (L) Pollen grain equatorial view, SEM. (M) Reticulate tectum, SEM. All LM — × 1000. Scale bar — 1 μm (*G, M*); 10 μm (*E, F, L*).

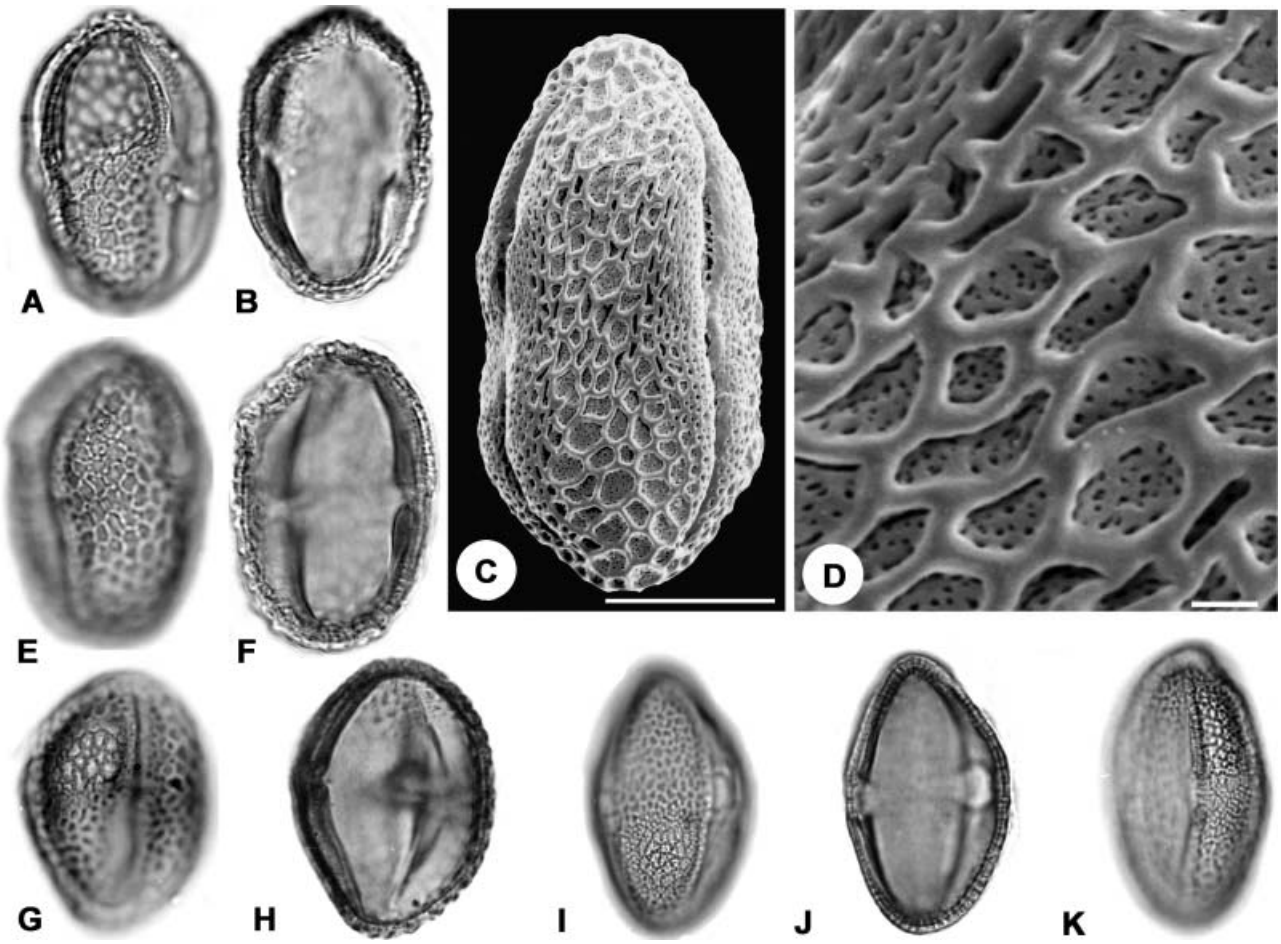

Fig. 15. A – D. *Trichospermum arachnoideum* (Burn-Murdochs Coll. BSIP). (A) Pollen grain, equatorial view, high focus, LM. (B) Equatorial view, low focus, LM. (C) Pollen grain, equatorial, view, SEM. (D) Detail of exine patten, SEM. E – F. *T. eriopodum* (Rames B.Sc 17659, L). (E) Pollen grain, equatorial view, high focus, LM. (F) Equatorial view, low focus, LM. G – H. *Vasivaea alchorneoides* (Piers 3535, L). (G) Pollen grain, equatorial view, high focus, LM. (H) Equatorial view, low focus, LM. I – K. *Triumfetta cana* (Mousseh s.n. HBG). (I) Pollen grain, equatorial view, high focus, LM. (J) Equatorial view, mid focus, LM. (K) Equatorial view, low focus, LM. All LM — × 1000. Scale bar — 10 μm (*C, D*).

2 μm thick. Sexine slightly thicker than nexine, nexine ca. 1 μm.

SEM (Fig. 13 G, H; Lueheopsis althaeiflora)

Exine sculpturing coarsely reticulate with sparsely scabrate, more or less irregular pattern of muri, lumina variable in shape and size, 0.4 – 2.35 μm in diameter. Lumina perforated, perforations 0.01 – 0.45 μm in diameter, perforations evenly distributed. Colpi long, narrow with tapering ends, colpal membrane granulated.

Microcos L.

LM (Fig. 13 I, K; Microcos coriacea)

Pollen grains single, isopolar, prolate to subprolate. P = (19 –)28(– 37) μm. E = (13 –)21.5(– 30) μm. P/E ratio: 1.30. Amb trilobed-triangular with slightly convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 14 – 36 μm. Ora lalongate, 1 – 5 × 4 – 10 μm. Exine 1.8 – 3 μm thick. Sexine thicker than nexine, nexine 0.8 – 1.2 μm.

SEM (Fig. 13 L, M; Microcos coriacea)

In *Microcos barambiensis, M. conocarpoides* and *M. coriacea* exine sculpturing is coarsely reticulate-rugulate, more or less irregular pattern of muri. Lumina variable in shape and size 0.1 – 1.33 μm in diameter, lumina perforated, perforations 0.01 – 0.11 μm in diameter; perforations more distinct towards the margins, perforations evenly distributed within the lumina. Colpi long, narrow with tapering ends. In *M. floribunda* exine sculpturing is coarsely reticulate-rugulate, sparsely scabrate, lumina variable in shape and size, 0.4 – 1.33 μm in diameter,

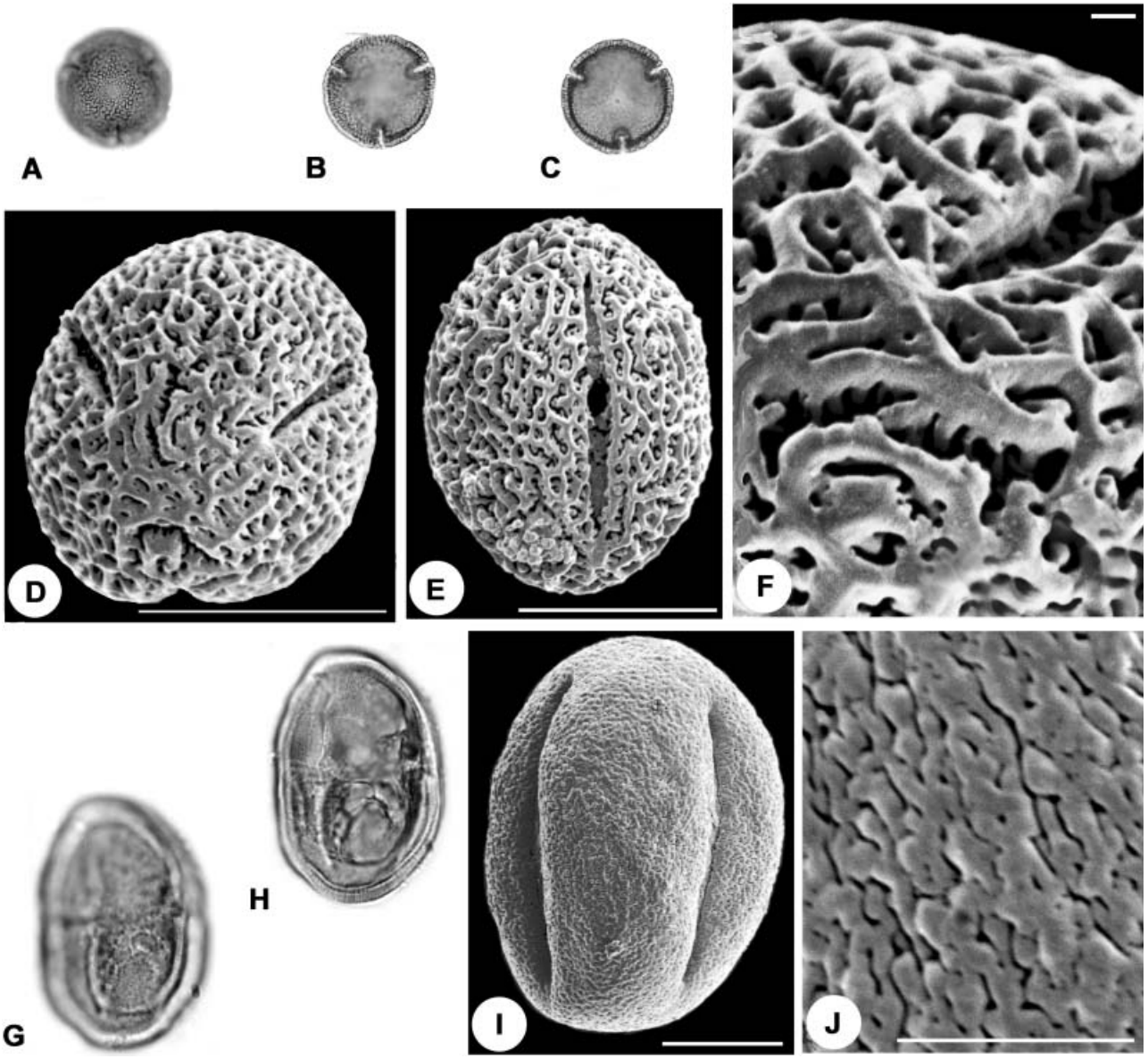

Fig. 16. A–F. *Duboscia macrocarpa* (Mildbraed 4320, HBG). (A) Pollen grain, polar view, high focus, LM. (B) Polar view, mid focus, LM. (C) Polar view, low focus, LM. (D) Pollen grain, polar view, SEM. (E) Pollen grain, equatorial view, SEM. (F) Detail of exine pattern, note coarsely rugulate tectum, SEM. G–J *Mollia grandiflora* (Maguier 41684, JAN). (G) Pollen grain, equatorial view, high focus, LM. (H) Equatorial view, mid focus, LM. (I) Pollen grain, equatorial view, showing mesocolpium, SEM. (J) Detail pattern of exine, showing fossulate-rugulate tectum; SEM. All LM — × 1000. Scale bar — 1 μm (*D, E, I*); 10 μm (*F, J*).

lumina perforated. Colpi long, narrow, with tapering ends, colpal membrane granulated.

3-colporate or tetracolporate. Ora lalongate, long, narrow, 30–40 μm. Colpi narrow with costae. Sexine thicker than nexine. Nexine 1.0 μm. Exine 3.2–4.1 μm.

Mollia C. Martius

LM (Fig. 16 G, H; Mollia grandiflora)

Pollen grains prolate, single, isopolar. P= (25−)35.5 (−46) μm. E= (18−)25.5(−33) μm. P/E ratio: 1.39. Amb with convex mesocolpia, equatorial view elliptical.

SEM (Fig. 16 I, J; Mollia grandiflora)

Exine sculpturing densely rugulate-reticulate.

Colpi long, narrow with tapering ends, colpal membrane granulated.

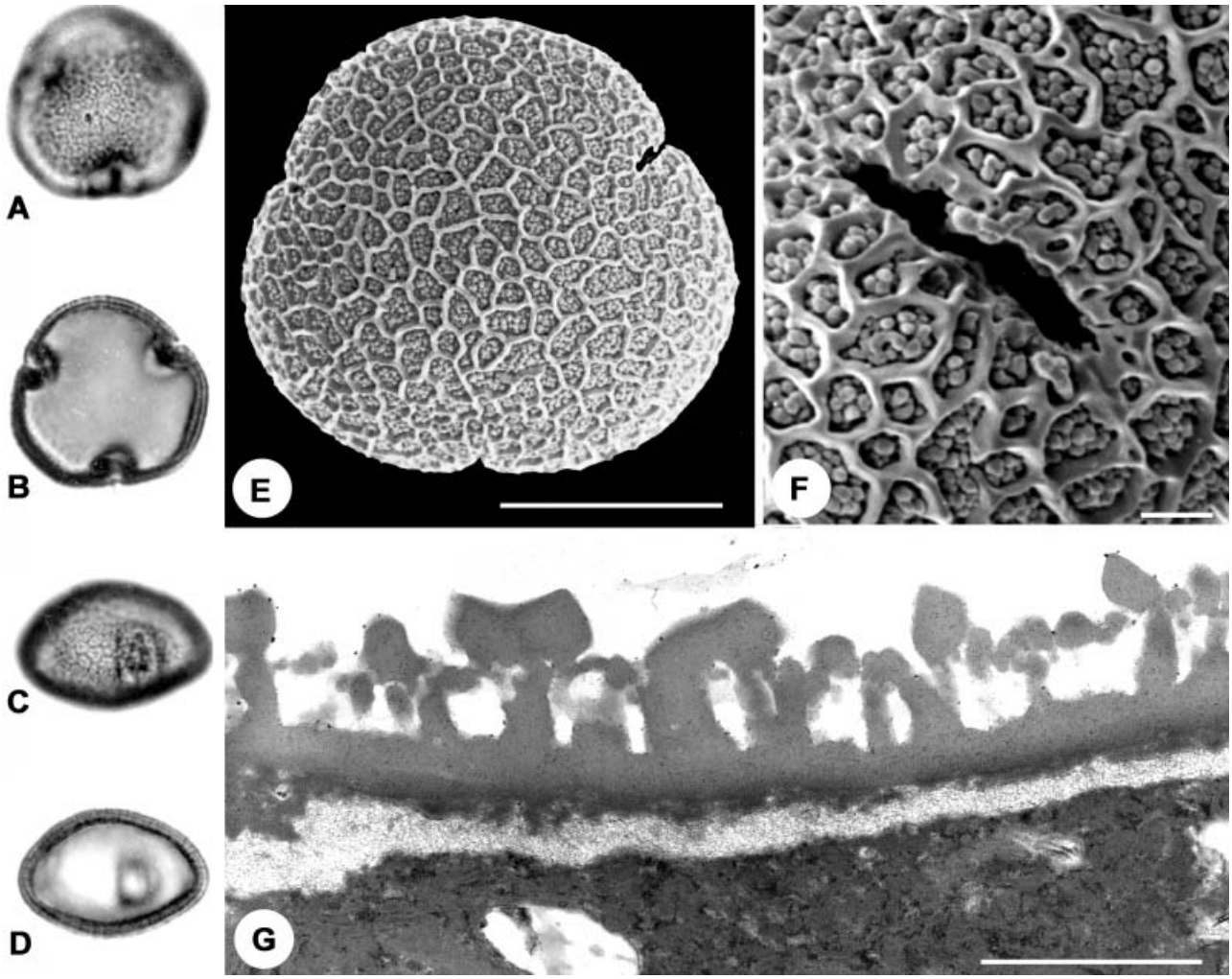

Fig. 17. A–F. *Mortoniodendron costaricense* (Haber et al. 4937, MO). (A) Pollen grain, polar view, high focus, LM. (B) Polar view, low focus, LM. (C) Pollen grain, equatorial view, high focus, LM. (D) Equatorial view, low focus, LM. (E) Pollen grain, polar view, SEM. (F) Detail of exine surface, showing coarsely reticulate tectum, SEM. (G) *M. guatemalense* (W.Haber & E.Bello C.1598, MO). Cross-section of exine consisting of supratectal reticulum, muri and lumina. Lumina filled with granules. Muri supported by relatively slim columellae on a compact foot-layer subtended by irregular endexine, and intine, TEM. All LM — × 1000. Scale bar — 1 μm (*F, G*); 10 μm (*E*).

***Mortoniodendron* Standley & Steyerm.**

LM (Fig. 17 A–D; Mortoniodendron costaricense)

Pollen grains single, isopolar, oblate. P= (16−)18.5 (−21) μm, E= (25−)28(−31) μm. P/E ratio: 0.66. Amb trilobed with convex mesocolpia, equatorial view transverse elliptical. 3-colporate. Colpi short, narrow, 6–10 μm. Ora lalongate. Exine 1.5–2 μm thick. Sexine thicker than nexine, nexine 0.5–1.0 μm.

SEM (Fig. 17 E, F; Mortoniodendron costaricense)

Exine sculpturing coarsely reticulate, lumina variable in shape and size, 0.3–2 μm in diameter, lumina coarsely perforated with granules, colpi short, narrow, with tapering ends, colpal membrane granulated.

TEM (Fig. 17 G; Mortoniodendron guatemalense)

Exine consisting of supratectal reticulum. Muri and lumina supported by relatively slim columellae on a compact foot-layer subtended by irregular endexine and intine. Muri filled with granules.

***Pentace* Hassk.**

LM (Fig. 3 F–H; Pentace borneensis)

Pollen grains single, isopolar, oblate. P= (15−)20.5 (−26) μm, E= (11−)26(−41) μm. P/E ratio: 0.63–1.55. Amb rounded-triangular or trilobed triangular with convex mesocolpia, equatorial view transverse elliptical. 3-colporate. Colpi short, narrow, 5–11 μm. Ora lalongate. Exine 2–2.5 μm thick. Sexine thicker than nexine, nexine 0.2–1 μm.

SEM (Fig. 3 I–K; Pentace borneensis)

Exine sculpturing rugulate-reticulate with perforated lumina. Colpi short, with rough ends, colpal membrane granulated.

Sparmannia L.

LM (Fig. 14 A–D; Sparmannia abyssinica)

Pollen grains sub-prolate, isopolar. P= (36−)40.5(−45) μm E= (30−)33(−36) μm. P/E ratio: 1.23. Amb triangular with convex mesocolpia, equatorial view elliptical.

Pollen grains 3-colporate. Colpi long, narrow, 6–7 μm with costae. Ora lalongate, 5.5−7×4−9 μm. Exine 2–3.2 μm thick. Sexine slightly thicker than nexine, nexine 0.5–1 μm.

SEM (Fig.14 E–G; Sparmannia abyssinica)

Exine sculpturing coarsely reticulate, ora rectangular, more or less irregular pattern of lumina and muri, variable in shape and size, 0.4–1.9 μm in diameter, lumina perforated, lumina 0.05–0.2 μm in diameter. Colpi long, with acute ends, colpal membrane granulated.

Tetralix Griseb.

LM (Fig. 14 H–K; Tetralix brachypetalus)

Pollen grains prolate, isopolar, single. P= (38−)42.5 (−47) μm, E= (26−)30.5(−35) μm.

P/E ratio: 1.37. Amb trilobed with convex mesocolpia, equatorial view elliptical.

Pollen 3-colporate. Colpi long, 6–7 μm, narrow, with costae. Ora lalongate, 4×8 μm. Exine 1.9–2.6 μm thick. Sexine slightly thicker than nexine, nexine 0.2–1 μm.

SEM (Fig. 14 L, M; Tetralix jaucoensis)

In *Tetralix brachypetalus* and *T. jaucoensis* exine pattern is coarsely reticulate.

Tilia L.

LM (Fig. 4 A–D; Tilia platyphyllos)

Pollen grains single, oblate. P= (25−)27(−29) μm, E= (43−)47.5(−52) μm. P/E ratio: 0.57. Slightly paraisopolar, oblate. Amb circular, equatorial view transverse elliptical. 3-colp(or)ate. Colpi short, 10×2 μm, ora circular or lalongate with somewhat irregularly shaped margin, surrounded by considerably thickened, lamellated nexine. Exine ca. 2 μm thick. Sexine as thick as nexine or slightly thicker, with circular or polygonal funnel-like, tectal concavities, in surface view appearing as finely reticulate or pitted. Intine thin, except beneath the apertures, where it is markedly thickened to form onci.

SEM (Fig. 4 E–G; Tilia platyphyllos)

Exine perforate to microreticulate. Muri sparsely perforated.

TEM (Fig. 4 H; Tilia platyphyllos)

The tectum and footlayer are about of the same thickness. Tectum is interrupted by polygonal funnel-like concavities which end with compact columellae.

Trichospermum Blume

LM (Fig. 15 A, B, E, F; Trichospermum arachnoideum and T. eriopodum)

Pollen grains single, isopolar, prolate. P= (30−)37.5 (−45) μm. E= (20−)27.5(−35) μm. P/E ratio: 1.33–1.71. Amb triangular with convex mesocolpia, equatorial view transverse elliptical. 3-colporate. Colpi long, narrow, 30–41 μm with costae. Ora lolongate, ca. 3.1 μm. Exine 2–3 μm thick. Sexine slightly thicker than nexine, nexine ca. 1 μm.

SEM (Fig. 15 C, D; Trichospermum arachnoideum)

Exine sculpturing coarsely reticulate. More or less irregular pattern of muri, variable in shape and size, 0.4–3 μm in diameter, lumina perforated between the muri, lumina 0.01–0.2 μm in diameter. Colpi long, with tapering ends, colpal membrane granulated.

Triumfetta L.

LM (Fig. 15 I–K; Triumfetta cana)

Pollen grains single, isopolar, prolate. P= (37−)44.5 (−52) μm. E= (22−)26.5(−31) μm. P/E ratio: 1.78. Amb triangular-trilobed with slightly convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 30–45 μm. Ora lalongate, 2.4–1.9 μm in diameter. Exine 2–3 μm thick. Sexine thicker than nexine, nexine 0.2–1.0 μm.

SEM

Exine sculpturing coarsely reticulate. More or less irregular pattern of muri, variable in shape and size, 0.4–1.2 μm in diameter. Lumina perforated; 0.01–0.1 μm in diameter. Colpi long, with tapering ends, colpal membrane granulated.

Vasivaea Baill.

LM (Fig. 15 G, H; Vasivaea alchorneoides)

Pollen grains single, isopolar, sub-prolate. P= (42−)44 (−46) μm, E= (26−)33.5(−41) μm. P/E ratio: 1.31. Amb trilobed-triangular with convex mesocolpia, equatorial view elliptical. 3-colporate. Colpi long, narrow, 34–40 μm. Ora lalongate, 2.4×1.9 μm. Exine 2–2.9 μm thick. Sexine thicker than nexine, nexine 0.5–1.0 μm.

SEM

Exine sculpturing coarsely reticulate. More or less irregular pattern of lumina and muri, variable in shape and size, 0.4–1.2 μm in diameter, lumina perforated with dense

granules. Colpi long, rounded ends, colpal membrane granulate.

GENERAL POLLEN DESCRIPTION

Light microscopy (LM)

Figs 1 A–C, F–G; 2 C–E; 3 B, C, F, G, J; 4 A–D; 5 E–G; 6 A–B; 7 A, B, F– H; 8 A, E–G; 9 A–C, F, G; 10 C, D; 11 A–B; 12 E–G; 13 A, B, E, F, I–K; 14 A–D, H–K; 15 A, B, E–K; 16 A–C, G, H; 17 A–D.

Pollen grains shed as monads. Isopolar or often apolar, radially symmetrical, fossaperturate (trilobed), less frequently angulaperturate, tricolporate, occasionally tetracolporate (*Clappertonia ficifolia)* and rarely colp(or)rate. Almost all types of shape classes are found. Prolate-subprolate or suboblate to oblate are the more common, P = 15−77 (17−72.5) μm, E = 16−54 (18−53); shape in polar view rounded triangular or trilobed triangular with convex mesocolpia; shape in equatorial view elliptic or broadly elliptic, rarely circular.

Colpi short or long, narrow to broad, with rounded or pointed apices and sometimes with a distinct colpus margin.

Ora are 0.9−9 × 1−11 μm in diameter, lalongate, circular to rectangular. Exine 0.2–4.1 μm thick, sexine partially discontinuous (semitectate), often continuous (tectate), sexine usually thicker than nexine, rarely thinner than nexine. Endexine 0.1–1.9 μm, often striate-rugulate, microreticulate, rugulate-reticulate or spinulose.

Scanning electron microscopy (SEM)

Figs 1 D, E, H, I; 2 A, B, F–I; 3 A, D, E, H, I, K; 4 E–G; 5 A–D, H–I; 6 C–E, H, I; 7 C–E, I, J; 8 B–D, H, I; 9 D, E, H–J; 10 A, B, E, F; 11 C–H; 12 A–D, H, I; 13 C, D, G, H, L, M; 14 E–G, L, M; 15 C, D; 16 D–F, I, J; 17 E, F.

Sexine usually reticulate, varying from finely to coarsely reticulate or reticulate-rugulate, regulate-reticulate, often regulate-foveolate or striate-rugulate, rarely spinulose. In the reticulate tectum lumina varies in shape and size, 0.1–6.6 μm in diameter.

Lumina are sometimes reduced towards the colpus, forming a distinct colpal margin. Lumina perforated, perforations 0.01–1.2 μm in diameter, colpus usually more distinct towards the margin. Colpus membrane granulated.

Transmission electron microscopy (TEM)

Figs 4 H; 6 F, G; 17 G.

The ectexine is stratified into tectum, infratectum and foot layer. Thickness of each stratum varies between the genera. The tectum is compact. The infratectal stratum is always columellate and generally well-defined, and varies in thickness between genera. The foot layer has a compact structure. The foot layer is conspicuously thickened at the aperture margin. The endexine is inconspicuous, in some taxa slightly lamellate.

The intine is structured and varies in thickness.

POLLEN TYPES

Berrya-type

Apeiba albiflora, A. burchelli, Berrya cordifolia, *B. mollis*, *Brownlowia argentatai*, *B. tabularis, Carpodiptera africana, C. floribunda*, *C. cubensis, Christiana africana*, *C. eburnea*, *Diplodiscus hookerianus*, *D. longifolius*, *D. paniculatus, D. parviflorus, Hainania trichosperma, Pentace borneensis, P. curtisii, P. chartacea, P. laxiflora, P. rigida, P. cordata* and *Tilia platyphyllos*.

LM (Figs 1 A–C, F, G; 2 C–E; 3 B, C, F, G, J; 4 A–D; 5 E–G)

Isopolar, radially symmetrical: P = (15−) 26 (−37) μm, E = (18−) 29,5 (−41) μm. P/E = ratio: 0.70–0.86. Suboblate, rarely oblate-spheroidal. 3-colporate, colpi short (3–8 μm) and narrow, costae ora not always distinct, circular to slightly lalongate. Amb rounded-triangular with slightly convex mesocolpia, equatorial view oblate. Ora lalongate, Exine 1.5–3 μm thick. Sexine thinner or thicker than nexine, microreticulate to coarsely reticulate. Endexine 0.6 μm thick.

SEM (Figs 1 D, E, H, I; 2 A, B, F–I; 3 A, D, E, H, I, K; 4 E–G; 5 A–D, H, I)

Exine medium reticulate or rugulate to microreticulate, lumina 0.1–0.5 μm in diameter.

TEM (Fig. 4 H)

Tectum and footlayer are about of the same thickness. Tectum is interrupted by polygonal funnel-like concavities which end with compact columellae.

Two subtypes are recognized, based on exine pattern:

***Berrya*-subtype A**
Apeiba albiflora, A. burchelli
SEM (Fig. 5 A–C)

Exine medium reticulate or rugulate to reticulate (irregular pattern of muri) with spinulose muri (generally scabrate). Lumina 0.1–0.5 μm in diameter.

***Berrya*-subtype B**
Carpodiptera africana
SEM (Fig. 5 D, H, I)

Exine sculpturing coarsely rugulate-reticulate with subpsilate lumina.

Corchorus-type

Ancistrocarpus bequaertii, *A. comperei, A. densispinosus, Clappertonia ficifolia*, *C. polyandra, Colona auriculata*, *C. javanica*, *C. scabra, C. serratifolia, C. velutina*, *Corchorus aestuans, C. asplenifolius, C. hirsutus, C. pongolensis, Christiana eburnea, Desplatsia chrysochlamys*, *D. dewevrei D. subericarpa, Duboscia macrocarpa, D. viridiflora, Eleutherostylus renistipulata, Entelea ,arborescens, Erinocarpus nimmonii, Glyphaea brevis, G. tomentosa, G. lateriflora,*

Goethalsia meiantha, Grewia carpinifolia, G. forbesii, G. flavescens, G. louisii, G. orientalis, G. villosa, Heliocarpus americanus, H. americanus var. *popayanensis, H. terebinthinaceus, Luehea conwentzii, L. divaricata, L. paniculata, Lueheopsis althaeiflora, L. rosea, Microcos barombiensis, M. conocarpoides, M. coriacea, M. floribunda, Mollia grandiflora, Sparmannia abyssinica, Tetralix brachypetalus, T. jaucoensis, Trichospermum arachnoideum, T. calyculatum, T. fletcheri, T. discolor, T. eriopodium, T. incaniopsis, T. tripyxis, Triumfetta cana, T. semitriloba* and *Vasiavea alchorneoides*.

LM (Figs 6 A–B; 7 A, B, F–H; 8 A, E–G; 9 A–C, F, G; 10 C, D; 11 A, B; 12 E–G; 13 A, B, E, F, I–K; 14 A–D, H–K; 15 A, B, E–K; 16 A–C, G, H)

Isopolar, radially symmetrical. P=(19−) 45.5 (−72) µm. E=(13−) 33 (−53) µm. P/E ratio: 1.46–1.36. Prolate to subprolate, rarely prolate-spheroidal or perprolate. Amb triangular or triangular-trilobed with convex mesocolpia, equatorial view elliptical. 3-colporate, rarely 4-colporate. Colpi long, narrow with costae, 14–52 µm, Ora lalongate, rarely lolongate, 2−8 × 5−9 µm. Exine 1–5 µm thick. Sexine thicker than nexine, rarely thinner than nexine, nexine 0.2–2 µm thick.

SEM (Figs 6 C–E, H, I; 7 C–E, I, J; 8 B–D, H, I; 9 D, E, H–J; 10 A, B, E, F; 11 C–H; 12 A, D, H, I; 13 C, D, G, H, L, M; 14 E–G, L, M; 15 C, D; 16 D–F, I, J)

Exine coarsely reticulate, more or less regular pattern of muri, lumina variable in shape and size, 0.1–10 µm in diameter, lumina sometimes perforated between the muri, perforations 0.01–0.2 µm; perforations evenly distributed on the lumina, in some species perforations restricted to the margin. In most species lumina size gradually reduced towards the colpus forming distinct colpus margin. Colpus membrane granulated.

TEM. Ancistrocarpus bequaertii (Fig. 6 F, G)

The exine consists of a supratectal reticulum with perforated lumina, supported by stout columellae on an equally solid foot-layer. Endexine appears absent.

Two subtypes are recognized on the basis of exine pattern.

***Corchorus*-subtype A**
Duboscia macrocarpa
SEM (Fig. 16 D–F)

Colpi long, approx. 15 µm, narrow with tapering ends, colpus membrane granular, margin more or less psilate. Exine reticulate, lumina with perforations or irregular holes. Crest of muri keeled, sloped.

***Corchorus*-subtype B**
Mollia grandiflora
SEM (Fig. 16 I, J)

Colpi long, approx. 30 µm, narrow with tapering ends, colpus membrane granular. Exine densely regulate-reticulate.

***Mortoniodendron*-type**

Mortoniodendron anisophyllum, M. costaricense, M. guatemalense

LM (Fig. 17 A–D)

Isopolar, radially symmetrical; P=(16−) 18.5 (−21) µm, E=(25−) 28 (−31) µm. P/E ratio: 0.84–0.67, oblate. Amb trilobed with convex mesocolpia. 3-colporate. Colpi short, narrow, 6–10 µm. Ora lalongate. Sexine thicker than nexine. Endexine 0.5–1.0 µm. Exine 1.5–2 µm thick.

SEM (Fig. 17 E, F)

Exine coarsely reticulate, lumina variable in shape and size 0.3–2 µm in diameter, lumina coarsely perforated with granules, colpi with tapering ends, colpus membrane granulated.

TEM (Fig. 17 G)

The exine consists of supratectal elements: reticulum and lumina which are filled with granules. Columellae relatively slender, foot-layer compact, subtended by irregular endexine.

KEY TO THE POLLEN TYPES AND SUBTYPES

1. Pollen grains usually oblate-suboblate, rarely oblate-spheroidal 2
1. Pollen grains prolate-subprolate, rarely prolate-spheroidal 5
2. Tectum coarsely reticulate with granular lumina ***Mortoniodendron*-type**
2. Tectum not as above 3
3. Tectum not coarsely reticulate without granular lumina ***Berrya*-type**
3. Tectum not as above 4
4. Tectum medium reticulate or rugulate with spinulose muri ***Berrya*-subtype A**
4. Tectum coarsely reticulate-rugulate ***Berrya*-subtype B**
5. Tectum coarsely reticulate with sometimes perforated lumina ***Corchorus*-type**
5. Tectum not coarsely reticulate 6
6. Tectum reticulate-rugulate, lumina with sparse perforations or irregular holes ***Corchorus*-subtype A**
6. Tectum densely regulate-reticulate ***Corchorus*-subtype B**

DISCUSSION

General pollen morphology

Pollen grains are generally isopolar. Shape varies from suboblate to prolate or subprolate. Less common shape class is oblate-spheroidal (*Apeiba albiflora*) or prolate-spheroidal (*Christiana eburnea*). The shape seems to be of diagnostic character between the genera.

Shape in polar view is usually rounded triangular or trilobed-triangular or trilobed with more or less convex mesocolpia in spheroidal pollen. The equatorial outline is elliptic to subelliptic, or circular in spheroidal pollen. Size varies widely, from P = 15 µm in *Pentace chartacea* to 77.5 µm in *Clappertonia ficifolia*. However, the majority of the taxa have medium size pollen ranges from 21 – 35 µm.

Tricolporate pollen grains are most frequent, occasionally 4-colporate in *Clappertonia ficifolia*. In colporate pollen grains the colpi varies widely in length. Oblate to suboblate pollen grains have small, broad colpi (4 – 15 µm) with acute ends. In sub-prolate to prolate pollen grains, length range of colpi usually is 16 – 63 µm, with tapering or pointed ends.

Ora are lalongate, mostly narrow to broad, sometimes rarely lolongate. In oblate and suboblate pollen ora are broad. Sexine is thicker than nexine, collumellae are distinct or indistinct, exine 2 – 4 µm thick, and endexine 0.1 – 2 µm. Exine is usually perforate. Exine pattern shows a wide range of variation. However, the supra-reticulate pattern is the most dominant, found in the majority of species examined. The reticulum varies from fine to coarse. In some species combinations of other patterns are also found like reticulate-rugulate, regulate-reticulate, reticulate to foveolate (*Brownlowia tabularis*, Fig. 1 F – I), and reticulate-striate (*Mollia grandiflora*, Fig. 16 I, J). Most of the reticulate species have a distinct colpus margin. Lumina size is gradually reduced towards colpus, forming a distinct colpal margin. Lumina variable in shape and size, 0.1 – 6.6 µm, lumina perforated between muri, perforations 0.01 – 1.2 µm.

In the present study, symmetry, aperture types, and in particular shape class and exine ornamentation are significant pollen characters. On this basis 3 pollen types and 4 subtypes are recognized. Each subfamily is palynologically quite heterogeneous, however, they share some distinct pollen characters and can be assigned to the different pollen types recognized. Tricolporate pollen grains, oblate to suboblate pollen with short colpi are commonly found in most of the genera in subfamily Brownlowioideae (*Berrya*-type pollen). In the subfamily Grewioideae tricolporate, prolate pollen grains with long colpi occur in almost all genera (*Corchorus*-type pollen). However, radially symmetrical, tricolporate pollen grains with reticulate tectum are also frequent. In the subfamily Grewioideae two pollen subtypes are found: prolate with long colpi (*Ancistrocarpus, Clappertonia, Colona, Corchorus, Desplatsia, Duboscia, Eleutherostylis, Entelea, Erinocarpus, Glyphaea, Goethalsia, Grewia, Heliocarpus, Luehea*, *Lueheopsis*, *Microcos, Mollia, Sparmannia, Tetralix, Trichospermum, Triumfetta* and *Vasivea*) and oblate to suboblate pollen with short colpi (*Apeiba*). Although *Apeiba* is nested within subfamily Grewioideae in molecular analyses (Alverson et al. 1999, Bayer et al. 1999), pollen of *Apeiba* is more similar to many of the genera in subfamily Brownlowioideae.

The genus *Mortoniodendron* has been thought to have an isolated position (e.g., Miranda 1956). Bayer & Kubitzki (2002) noted that *Mortoniodendron* might be related to either Tilioideae or Brownlowioideae. Analyses with information of molecular data and of combined molecular and morphological data strengthen the support for the inclusion of *Mortoniodendron* within Tilioideae (Judd & Manchester 1997, Alverson et al. 1999, Nyffeler et al.: submitted). Exine pattern of *Mortoniodendron* pollen indicate an affinity with the subfamily Grewioideae, whereas its pollen shape suggests a closer relationships with Brownlowioideae or Tilioideae. Thus, pollen characters do not allow for any conclusive suggestions concerning the phylogenetic placement of *Mortoniodendron*.

In the genus *Tilia* of Tilioideae, *Berrya*-type pollen occur and therefore an isolated systematic position of *Tilia* as suggested by Bayer et al. (1999) is not supported by our study. Pollen morphology of this genus rather points to a close affinity with the subfamily Brownlowioideae. In all the genera of the subfamily Brownlowioideae, such as *Christiana, Brownlowia, Diplodiscus, Hainania, Berrya, Christiana* and *Pentace*, tricolporate (short colpi), suboblate or oblate pollen with usually reticulate tectum occur. Thorne (1983) treated the genus *Tetralix* as a distinct subfamily. But in the genus *Tetralix, Corchorus*-type pollen is observed.

The pollen types recognized from the three subfamilies appear to fall out more or less along phylogenetic lines with the *Corchorus*-type pollen being found within the Grewioideae clade and the *Berrya*-type within Brownlowioideae. However, *Berrya*-subtype A pollen is found in Tilioideae suggesting it may be more widespread. Further taxon sampling from the subfamilies not investigated and molecular investigations incorporating taxa documented in this study will be required to confirm whether pollen morphology can be phylogenetically informative.

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APPENDIX

LIST OF PREVIOUS STUDIES ON POLLEN MORPHOLOGY IN MALVACEAE P.P. (BROWNLOWIOIDEAE, GREWIOIDEAE AND TILIOIDEAE).

Anderson 1976
Andrew 1971
Banerjee 1976
Barth & Barbosa 1973
Browicz 1968
Cathary 1968
Chambers & Godwin 1971
Chaudhuri 1965
Christensen & Blackmore 1988
Datta & Bose 1964
Datta & Panda 1961
Datta & Roy 1963
Datta 1956

De Castellis et al. 1985
Dnyansagar & Gaoli 1965
Fisher 1890
Guggenheim 1975
Hesse 1978
Jain & Nanda 1966
Kasartseva 1982
Mai 1961
Mittre 1970
Moore & Webb 1978
Patel & Datta 1958
Qaiser & Perveen 1997
Rao & Rao 1952
Sharma 1969
Srivastava 1976
Stockmarr 1973
Tang & Gao 1993
Tarnavschi & Serbanescu-Jitariu 1968
Tirel et al. 1996
Wang 1960
Zhang & Chen 1984
Zhuge 1990

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