

Under the microscope: plant anatomy and systematics.

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Pollen morphology and wood anatomy of the *Crudia* group (Leguminosae, Caesalpinioideae, Detarieae)

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Pollen from all 12 and wood from 11 genera in the *Crudia* group have been examined using light, scanning electron and transmission electron microscopy. This group is currently of systematic interest because it is part of a tribe undergoing taxonomic revision. The pollen grains fall into four groups: (1) *Oxystigma*, *Kingiodendron*, *Gossweilerodendron*, *Bathiaea*, *Neopaloxylon*, *Stemonocoleus*, *Guibourtia* and *Prioria* have pollen of a widespread and generalized caesalpinoid type that are small to medium sized, spheroidal to prolate, tricolporate and with a perforate exine, with some variation in surface ornamentation, aperture margins and ultrastructure. (2) *Crudia* pollen is tricolporate, coarsely striate with a coarsely scabrate to vermiculate aperture membrane. (3) *Augouardia* is tricolporate and coarsely reticulate. (4) *Hardwickia* and *Colophospermum* are pantoporate and reticulate or microreticulate-rugulate. The wood of *Prioria*, *Oxystigma*, *Kingiodendron* and *Gossweilerodendron* has diffusely arranged axial canals, and these are four genera that have recently been merged into *Prioria*. *Bathiaea* has tangentially arranged axial canals. The other genera lack normal axial canals. *Crudia* is distinct, with banded parenchyma and variably storied short rays, *Augouardia* has much less abundant axial parenchyma that is mainly scanty paratracheal and vasicentric, *Guibourtia* has mainly aliform parenchyma and rays variable in height and width, and *Colophospermum* and *Hardwickia* have similar paratracheal parenchyma patterns, although the rays tend to be wider in the latter. Our conclusion is that the *Crudia* group is not monophyletic.

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ADDITIONAL KEY WORDS:—*Augouardia* – *Bathiaea* – *Colophospermum* – *Gossweilerodendron* – *Guibourtia* – *Hardwickia* – *Kingiodendron* – *Neopaloxylon* – *Oxystigma* – *Prioria* – *Stemonocoleus*.

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INTRODUCTION

The *Crudia* group comprises 12 genera according to Cowan & Polhill (1981a) and Polhill (1994) (Table 1). Breteler *et al.* (1997) combined *Colophospermum* under *Hardwickia*, reducing the number of genera in the group to 11, but Smith, Timberlake & van Wyk (1998) proposed conservation of the name *Colophospermum*, and Léonard (1999) provided evidence that the two genera should remain separate. This paper

TABLE 1. Genera in the *Crudia* group (Cowan & Polhill, 1981a)

Genus	Number of species	Pollen No. of species examined	Wood No. of species examined	Distribution
<i>Crudia</i> Benth. & Hook.	c. 55	7	2	10 tropical America (mostly Amazonian), 8 Guinea/Congo, rest Asia, mostly Malaya-Malesia and New Guinea
<i>Oxystigma</i> Harms	5	4	1	4 Guinea/Congo, 1 Tanzania
<i>Kingiodendron</i> Harms	6	5	2	India, Philippines, Moluccas and New Guinea to Solomon Is. and Fiji
<i>Gossweilerodendron</i> Harms	2	2	1	Gulf of Guinea
<i>Bathiaea</i> Drake	1	1	1	Madagascar
<i>Neopaloxylon</i> S. Rauschert	2	2	1 (twig)	Madagascar
<i>Prioria</i> Benth. & Hook.	1	1	1	Panama, Costa Rica, Jamaica, Colombia
<i>Augouardia</i> Pellegr.	1	1	1	Gabon
<i>Stemonocoleus</i> Harms	1	1	1 (in lit.)	Guinea/Congo
<i>Hardwickia</i> Roxb.	1	1	1	Western India
<i>Guibourtia</i> Benn.	c. 17	8	8	13 tropical Africa, 3 or 4 West Indies and South America
<i>Colophospermum</i> Kirk ex Benth.	1	1	1	Low rainfall areas of southern tropical Africa

surveys the pollen morphology and wood anatomy, and provides two lines of evidence that can be used in future taxonomic decisions on the *Crudia* group. A survey of the pollen and wood of these genera is timely, in view of current work on the morphological and molecular systematics of the Caesalpinioideae by an international group of researchers, and the recent revision by Breteler (1999) combining four genera (*Prioria*, *Kingiodendron*, *Oxystigma* and *Gossweilerodendron*) into one (*Prioria*).

Several authors have described caesalpinoid and Detarieae pollen, but not in the same accounts in a systematic context. Pollen of ten of the 12 genera in the *Crudia* group has previously been described. Using light microscopy (LM), Fiebner (1959) examined *Crudia*, *Kingiodendron* and *Prioria*. LM and scanning electron microscopy (SEM) were used to describe pollen of *Bathiaea*, *Neoapaloxylon* and *Guibourtia* (Senesce, 1980) in a survey of taxa from Madagascar and the Mascarenes. Because pantoporate pollen is not found in any other taxa in the Caesalpinioideae, *Colophospermum* and *Hardwickia* were described in an account of unique pollen types in the Caesalpinioideae by Graham, Barker & da Silva (1980) using SEM. Using SEM, Graham & Barker (1981) described the pollen of *Prioria* as coarsely scabrate. Ferguson (1987) described the pollen of *Oxystigma*, *Stemonocoleus*, *Crudia*, *Hardwickia*, *Colophospermum* and *Guibourtia* using SEM and transmission electron microscopy (TEM), and found the exine stratification of the *Crudia* group to be very heterogeneous. In this study, the pollen of 34 taxa from 12 genera was examined with LM, SEM, and, selectively, with TEM.

The wood anatomy of 11 of the 12 genera has been described in previous literature, but in some cases the published information is very limited. Wood descriptions are dispersed throughout the literature, and are mainly in books describing the woods from a region rather than for systematic purposes. This is the first time that these genera have been combined in a systematic survey of wood anatomy.

MATERIAL AND METHODS

The wood anatomy of 11 and pollen of all 12 of the genera currently constituting the *Crudia* group in the tribe Amherstieae/Detarieae (Cowan & Polhill, 1981a,b; Polhill, 1994) are discussed in this paper. Pollen material was obtained from the herbaria of the Royal Botanic Gardens, Kew (K), Utrecht (U), Leiden (L) and Wageningen (WAG) (see Table 2 for specimens examined). Pollen was not available for *Kingiodendron tenuicarpum* (only known in fruit) and *Oxystigma mannii*. Mature, unopened buds were dissected in a 1% solution of the wetting agent Libsorb under a Leica Wild M8 microscope. Pollen was prepared for study using acetolysis (Erdtman, 1960). Acetolysed pollen was prepared for LM by mounting in glycerol jelly. Measurements were recorded using a Nikon Labophot light microscope with a $\times 100$ oil immersion objective lens. Specimens examined, together with pollen measurements, are given in Table 2. For SEM, acetolysed pollen exines in 95% ethanol were pipetted onto specimen stubs and allowed to air dry under an inverted glass beaker. They were then sputter-coated with platinum and examined in a Hitachi S-2400 SEM. For TEM, acetolysed material was fixed with a 2% solution of osmium tetroxide in cacodylate buffer and pre-stained with 0.5% uranyl acetate,

TABLE 2. Collection details of pollen samples. LM measurements taken from at least 10 grains per sample

Genera	Species	Authority	P*E (µm)	P/E	Shape	Wall thickness (µm)	Country of origin	Collector	Collector number	Herbaria of origin
<i>Augouardia</i>	<i>telestui</i>	Pellegr.	(37-)46.0(-49) × (33-)37.1(-42)	1.24	Subprolate	3	Gabon	Wieringa <i>et al.</i>	2898	WAG
<i>Augouardia</i>	<i>telestui</i>	Pellegr.	(47-)49.8(-52) × (34-)37.3(-44)	1.33	Prolate	2-3	Gabon	Wieringa <i>et al.</i>	2848	WAG
<i>Augouardia</i>	<i>telestui</i>	Pellegr.	(35-)43.1(-47) × (32-)37.3(-40)	1.55	Prolate	3	Gabon	White	1496	WAG
<i>Bathiaea</i>	<i>rubriflora</i>	Drake	(31-)34.4(-40) × (31-)33.7(-37)	1.02	Spheroidal	1.5-2	Madagascar	Du Puy <i>et al.</i>	MB403	K
<i>Bathiaea</i>	<i>rubriflora</i>	Drake	(28-)39.4(-43) × (30-)37.2(-39)	1.05	Spheroidal	1.5	Madagascar	Capuron	11266SF	WAG
<i>Colophospermum</i>	<i>mopane</i>	(Kirk ex Benth.)	(43-)47.2(-55) in diameter		Spheroidal	1-1.5	Mozambique	Torre	7326	K
<i>Colophospermum</i>	<i>mopane</i>	Kirk ex Léon (Kirk ex Benth.)	(44-)49.4(-55) in diameter		Spheroidal	1-1.5	Botswana	Lugard	243	K
<i>Crudia</i>	<i>caudata</i>	Prain ex King	(45-)50.4(-55) × (39-)41.6(-44)	1.21	Subprolate	2	Thailand	Niyomdham	1664	K
<i>Crudia</i>	<i>curtisii</i>	Prain ex King	(39-)41.4(-43) × (21-)27.6(-30)	1.49	Prolate	2	Malaysia	unknown	7457	K
<i>Crudia</i>	<i>glaberrima</i>	Macbride	(39-)41.6(-45) × (30-)34.0(-39)	1.22	Subprolate	2	Surinam	Lanjour + Lindeman	9231	K
<i>Crudia</i>	<i>senegalensis</i>	Planche. ex Benth.	(48-)49.1(-51) × (29-)31.6(-35)	1.55	Prolate	2	Guinea	Lisowski	51389	K
<i>Crudia</i>	<i>spicata</i>	Planche. ex Benth.	(43-)45.5(-49) × (31-)34.8(-38)	1.31	Prolate	2	Brazil	Ducke	5630	K
<i>Crudia</i>	<i>tenuipes</i>	Merrill	(33-)41.1(-45) × (34-)39.2(-42)	1.05	Spheroidal	2	Malaysia	Shea	75635	K
<i>Crudia</i>	<i>tomentosa</i>	Macbride	(46-)42.3(-47) × (28-)32.5(-36)	1.30	Subprolate	2	Brazil	Daly <i>et al.</i>	D251	K
<i>Gossweilerodendron</i>	<i>balsamiferum</i>	(Verm.) Harms	(22-)24.5(-28) × (23-)25.4(-28)	0.97	Spheroidal	1.5-2	Congo	Donis	1524	K
<i>Gossweilerodendron</i>	<i>balsamiferum</i>	(Verm.) Harms	(31-)33.5(-37) × (25-)26.4(-32)	0.93	Spheroidal	1.5-2	Nigeria	Kenudy	554	K
<i>Gossweilerodendron</i>	<i>joveri</i>	Normand ex Aubrev.	(25-)26.1(-28) × (25-)25.9(-28)	1.0	Spheroidal	2	unknown	Reitsma <i>et al.</i>	2595	WAG
<i>Guibourtia</i>	<i>coleosperma</i>	(Benth.) J. Léonard	(30-)33.8(-36) × (28-)36.7(-37)	0.92	Spheroidal	1-2	Zambia	Brummitt	14179	K
<i>Guibourtia</i>	<i>conjugata</i>	(Bolle) J. Léonard	(31-)33.5(-36) × (29-)33.0(-36)	1.01	Spheroidal	2	Mozambique	Barbosa/de Demos	8152	K
<i>Guibourtia</i>	<i>conjugata</i>	(Bolle) J. Léonard	(26-)30.1(-34) × (28-)31.0(-34)	0.97	Spheroidal	1	Mozambique	Mendoca	3242	K
<i>Guibourtia</i>	<i>copaifera</i>	(Harms) Léonard	(35-)38.0(-43) × (35-)38.0(-42)	1.00	Spheroidal	2	Guinea/Sudan	Felix	7120	K
<i>Guibourtia</i>	<i>demeusei</i>	(Harms) Léonard	(40-)42.0(-45) × (34-)37.2(-40)	1.13	Spheroidal	2	Cameroon	Villers	689	K
<i>Guibourtia</i>	<i>gossweilerii</i>	(M.A. Exell) Torre & Hillc.	(36-)37.2(-39) × (36-)38.6(-40)	0.96	Spheroidal	2	Angola	Grandvaux-Barbosa	11.322	K
<i>Guibourtia</i>	<i>hymenifolia</i>	(Moric.) J. Léonard	(40-)46.1(-51) × (38-)47.0(-50)	0.98	Spheroidal	1	Paraguay	Bernardi	1896	U
<i>Guibourtia</i>	<i>pellegriniana</i>	J. Léonard	(26-)29.4(-31) × (26-)28.3(-37)	1.04	Spheroidal	1	Angola	Gossweiler	6893	K
<i>Guibourtia</i>	<i>tessmannii</i>	(Harms) J. Léonard	(28-)34.6(-38) × (30-)33.2(-39)	1.04	Spheroidal	1	Cameroon	Mildbraedi	7770	K
<i>Hardwickia</i>	<i>binata</i>	Roxb.	(39-)42.7(-46) in diameter		Spheroidal	1-1.5	India	Gamble	874	K
<i>Hardwickia</i>	<i>binata</i>	Roxb.	(36-)43.1(-46) in diameter		Spheroidal	1-1.5	India	Gamble	15258	K
<i>Hardwickia</i>	<i>binata</i>	Roxb.	(38-)41.6(-47) in diameter		Spheroidal	1-1.5	India	Khan	2319	K
<i>Kingiodendron</i>	<i>alternifolium</i>	(Elm.) Merr. & Rolfe	No measurements available				Guinea	Katik	NGF46873	K
<i>Kingiodendron</i>	<i>novoguineensis</i>	Verdc.	No measurements available				Guinea	NGF	36784	WAG
<i>Kingiodendron</i>	<i>micranthum</i>	Burr	(24-)25.1(-27) × (24-)24.9(-26)	1.0	Spheroidal	1-1.5	unknown	Beers	B.S.I.P6730	L
<i>Kingiodendron</i>	<i>pinnatum</i>	Roxb. ex DC	(22-)25.6(-29) × (22-)24.8(-29)	1.0	Spheroidal	1.5-2	India	Bourdillon	26	K
<i>Kingiodendron</i>	<i>pinnatum</i>	(Roxb. ex DC) Harms	(28-)29.5(-31) × (21-)23.7(-27)	1.25	Subprolate	1	unknown	s.n.	5807	K

continued

TABLE 2. — continued

Genera	Species	Authority	P/E (µm)	P/E	Shape	Wall thickness (µm)	Country of origin	Collector	Collector number	Herbaria of origin
<i>Kingia</i>	<i>kingiana</i>	(Roxb. ex DC.) Harms	(22-25.0) × (27) × (20) (21.4) (24)	1.17	Subprolate	1.5-2	India	Wallich	5807	K
<i>Kingia</i>	<i>platycaulam</i>	Burt	(23) (27.5) (32) × (22) (25.4) (29)	1.08	Spheroidal	1.5-2	Solomon Islands	B.S.L.P.	3635	K
<i>Kingia</i>	<i>platycaulam</i>	Burt	(25) (27.4) (30) × (25) (28.4) (30)	0.96	Spheroidal	1.5-2	Solomon Islands	Beer	6730	K
<i>Neona</i>	<i>neonana</i>	(R. Viguier) S. Rauschert	(31) (33.3) (35) × (27) (30.1) (32)	1.11	Spheroidal	1.5-2	Madagascar	Du Puy <i>et al.</i>	M519	K
<i>Neona</i>	<i>madagascariensis</i>	(Drake del Castillo) S. Rauschert	(29) (31.2) (34) × (25) (29.9) (31)	1.04	Spheroidal	1.5-2	Madagascar	Perrier de la Bathie	885	K
<i>Oxydigma</i>	<i>humboldtii</i>	Harms	(27) (31.3) (34) × (24) (25.5) (28)	1.23	Subprolate	1.5-2	Gabon	Le Testu	8776	K
<i>Oxydigma</i>	<i>nanum</i>	Harms	(24) (27.1) (30) × (24) (26.8) (29)	1.10	Spheroidal	1.5-2	Tanzania	Kisumu	538	K
<i>Oxydigma</i>	<i>oxydigma</i>	(Harms) J. Leonard	(25) (30.5) (32) × (25) (27.2) (31)	1.21	Subprolate	1.5-2	Zaire	Jean-Louis Dubois	9490	K
<i>Oxydigma</i>	<i>gibberita</i>	J. Leonard	(23) (26.7) (29) × (23) (25.8) (30)	1.03	Spheroidal	1.5-2	Zaire	Dubois	195	WAG
<i>Prinia</i>	<i>copajera</i>	Griseb.	(25) (29.4) (35) × (22) (24.7) (28)	1.19	Subprolate	1.5	Trinidad	Broadway	5833	K
<i>Prinia</i>	<i>copajera</i>	Griseb.	(27) (30.5) (34) × (21) (24.1) (28)	1.27	Subprolate	1	Panama	Cooper	345	K
<i>Prinia</i>	<i>copajera</i>	Griseb.	(27) (29.4) (31) × (22) (24.2) (26)	1.21	Subprolate	1	Trinidad and Tobago	s.n.	?	K
<i>Prinia</i>	<i>copajera</i>	Griseb.	(27) (29.7) (32) × (21) (23.5) (26)	1.26	Subprolate	1	Panama	Castroviejo <i>et al.</i>	7136MV	K
<i>Prinia</i>	<i>copajera</i>	Griseb.	(29) (30.5) (31) × (24) (25.1) (26)	1.22	Subprolate	1	Trinidad and Tobago	Broadway	9250	K
<i>Prinia</i>	<i>copajera</i>	Griseb.	(30) (32.7) (36) × (24) (26.5) (28)	1.23	Subprolate	1	Trinidad and Tobago	Broadway	5833	K
<i>Stemmatoclelea</i>	<i>micrantha</i>	Harms	(40) (44.3) (47) × (29) (33.9) (40)	1.31	Prolate	2-3	Ivory Coast	Oldeman	303	K
<i>Stemmatoclelea</i>	<i>micrantha</i>	Harms	(36) (40.1) (43) × (28) (34.7) (39)	1.16	Subprolate	2	Nigeria	Chesters	OBS182	K

before embedding in Epon-araldite resin (Skvarla, 1966). The pollen was thin-sectioned using a diamond knife, post-stained with uranyl acetate and lead citrate in an LKB 2168 Ultrastainer, and examined in a Hitachi H-300 TEM. Terminology follows Punt *et al.* (1994).

Some wood samples were obtained from F. Breteler (Wageningen) and H.G. Richter (Hamburg). Permanent microscope slides already in the reference collection in the Jodrell Laboratory were also examined, as was one of *Bathiaea* lent by A.M.W. Mennega (Utrecht). Details of wood samples are given in the generic descriptions (see also Stern, 1988). Permanent slides 18–25 µm thick were prepared using a Reichert sliding microtome, stained in 1% aqueous Alcian Blue and 1% Safranin in 50% ethanol, taken through an alcohol series, cleared in Histoclear and mounted in Euparal. Photographs were taken using a Leica Diaplan. Where available in the literature, information on density or specific gravity is given at the end of the wood description.

POLLEN MORPHOLOGY

Pollen grains isopolar, spheroidal to prolate, with circular to triangular equatorial outline in polar view. Size: P=(22–)26.3–46.3(–55); E=(21–)24.6–48.8(–55) µm (Table 2). Tricolporate (most genera) or pantoporate (*Hardwickia* and *Colophospermum*). In tricolporate species apertures long, approximately equal to polar length, apocolpium small. In porate species, diameter of pores 5–7 µm (*Hardwickia* and *Colophospermum*, Figs 34, 36). Aperture membrane smooth to finely granular. Colporate apertures folding inwards when dehydrated (Figs 10, 44), or aperture margins prominent and mesocolpial areas becoming concave when dehydrated (Figs 25, 47). Endoapertures circular (Figs 1, 4, 22). Mesocolpial exine 1–3 µm thick (Table 2). Stratification of wall variable between taxa (Figs 3, 6, 9, 12, 17, 21, 24, 27, 30, 33, 36, 39), although endexine usually thin under mesocolpial area, thickened under aperture margins (Fig. 24). Granular layer present in infratectum just below tectum in *Prioria*, *Gossweilerodendron* and *Stemonocoleus* (Figs 12, 17, 24), a sporopollenin layer is present in infratectum in *Augouardia* (Fig. 33). Surface tectate and perforate (Figs 2, 5, 8, 13–15, 18), striate (Fig. 29) or reticulate (Figs 32, 35, 38). Ornamentation of perforate pollen psilate, microreticulate, scabrate, rugulate or shallowly striate. See Table 2 for measurements.

Key to pollen

- 1. Tricolporate 2
 Pantoporate *Hardwickia*, *Colophospermum*
- 2. Reticulate *Augouardia*
 Coarsely striate *Crudia*
 Perforate 3
- 3. Aperture margins protruding 4
 Aperture margins not protruding 5
- 4. Microperforate, granular-rugulate *Guibourtia*
 Perforate, shallowly striate *Stemonocoleus*

5. Perforate, rugulate-vermiculate *Kingiodendron*
 Perforate, rugulate, psilate, microreticulate or scabrate 6
6. Layer of granules present in the infratectum *Prioria*, *Gossweilerodendron*
 Granules absent *Oxystigma*, *Bathiaea*, *Neopaloxylon*

Oxystigma, *Bathiaea*, *Neopaloxylon*
 (Figs 1–9, 40–42)

Spheroidal to subprolate. Size: $P = (23 -)33.4(-43)$; $E = (23 -)34.7(-39)$ μm ; $P/E = 0.96$. Aperture membrane smooth to finely granular. Aperture margins smooth. Exine 1.5–2 μm thick at mesocolpium; tectum 0.3–0.7 μm ; infratectum 0.4–0.6 μm , columellae densely packed; foot layer 0.4–0.7 μm ; endexine 0.1–0.2 μm in mesocolpial areas, thickening under apertures. Tectum perforate and psilate to finely rugulate.

Prioria, *Gossweilerodendron*
 (Figs 10–18, 43, 44)

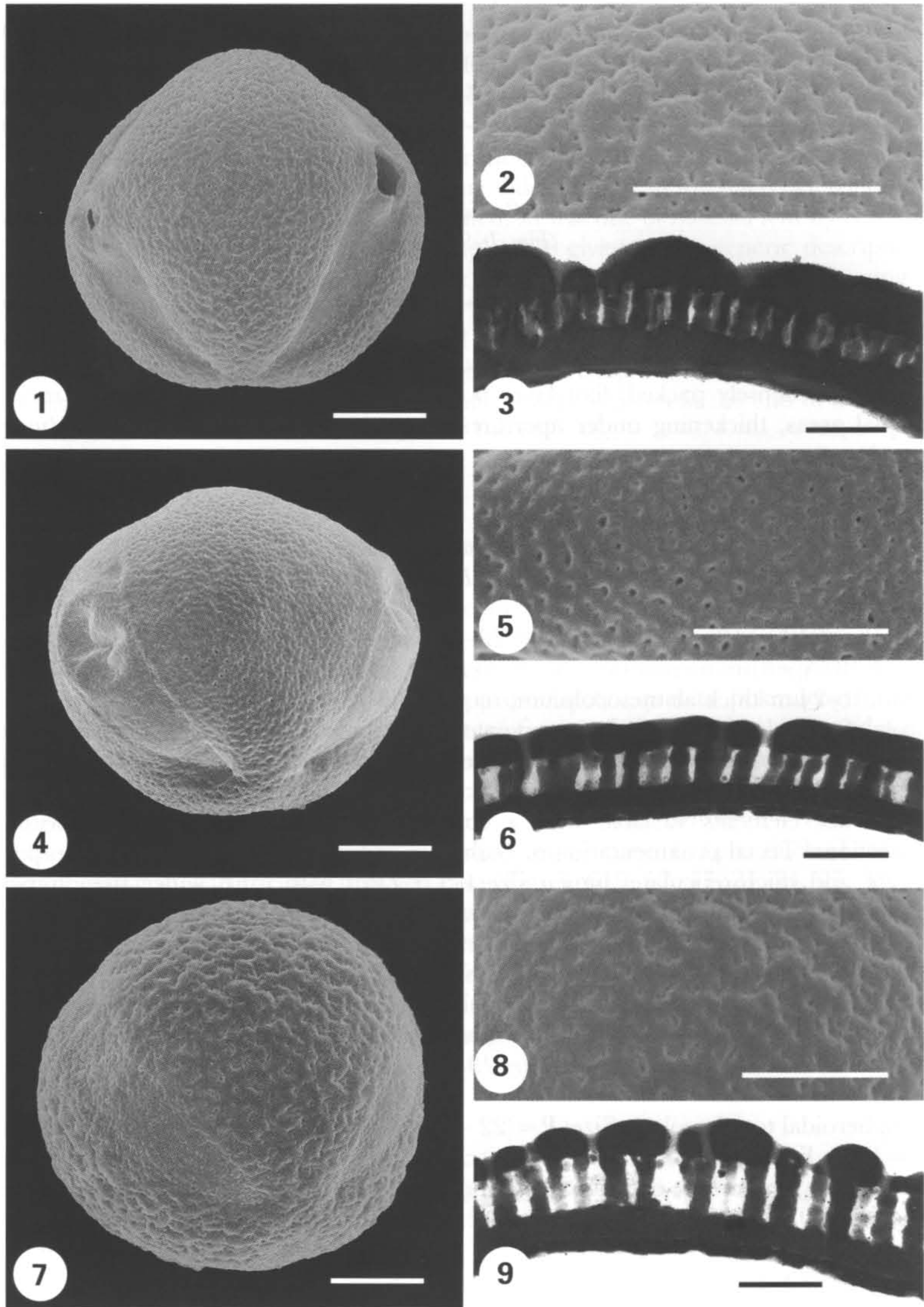
Spheroidal to subprolate. Size: $P = (22 -)29.6(-37)$; $E = (21 -)25.1(-32)$ μm ; $P/E = 1.18$. Aperture membrane smooth to finely granular. Aperture margins smooth. Exine 1–2 μm thick at mesocolpium; tectum 0.3–0.8 μm ; infratectum 0.5–0.8 μm , layer of granules just beneath tectum extends to about a quarter of the width of the infratectum; foot layer 0.4–0.5 μm ; endexine 0.1 μm , thickened under apertures. Tectum perforate and psilate, microreticulate, scabrate or rugulate, presence/size of surface elements variable with a continuous gradation between and within collections. Tectal ornamentation of *Gossweilerodendron joveri* borderline between perforate and microreticulate, lumen size 0.5–1.2 μm with muri wider than lumen diameter (definitions according to Punt *et al.*, 1994). A continuum is seen between all extremes of ornamentation (Figs 13–15, 18).

Kingiodendron
 (Figs 19–21, 45)

Spheroidal to subprolate. Size: $P = (22 -)26.3(-31)$; $E = (20 -)24.6(-30)$ μm ; $P/E = 1.07$. Exine 1–2 μm thick at mesocolpium; tectum 0.3–0.6 μm ; infratectum 0.3–0.8 μm , columellae occasionally branching under tectum; foot layer 0.6–1.2 μm ; endexine 0.1–0.2 μm , thickening under apertures. Tectum perforate, rugulate-vermiculate.

Stemonocoleus
 (Figs 22–24, 46)

Prolate. Size: $P = (40 -)44.3(-47)$; $E = (29 -)33.9(-40)$ μm ; $P/E = 1.31$. Aperture membrane finely granular. Endoapertures conspicuous circular pores. Aperture margins prominent, mesocolpial wall buckles inwards on dehydration. Exine



Figures 1–9. Figs 1–3. *Oxystigma*. Fig. 1. SEM *O. buchholzii* (*Le Testu* 8776) Equatorial view showing mesocolpium. Scale bar = 10 μm . Fig. 2. SEM *O. buchholzii* (*Le Testu* 8776) mesocolpial surface. Scale bar = 5 μm . Fig. 3. TEM *O. msoo* (*Kisena* 538) mesocolpial exine. Scale bar = 1 μm . Figs 4–6. *Bathiaea*. Fig. 4. SEM *B. rubriflora* (*Du Puy et al.* MB403) Oblique equatorial view showing mesocolpial and polar area. Scale bar = 10 μm . Fig. 5. SEM *B. rubriflora* (*Du Puy et al.* MB403) mesocolpial surface. Scale bar = 5 μm . Fig. 6. TEM *B. rubriflora* (*Du Puy et al.* MB403) mesocolpial exine. Scale bar = 1 μm .

1.5–3 μm thick at mesocolpium; tectum 0.3–0.5 μm ; infratectum 0.5–1.0 μm thick, columellae sparse, thick and sometimes branched beneath tectum, layer of granules present in infratectum just below tectum; foot layer thin, 0.1–0.2 μm thick; endexine 0.2–0.3 μm , thickening under apertures. Tectum perforate and shallowly striate, striae short, narrow and multidirectional.

Guibourtia
(Figs 25–27, 47)

Spheroidal. Size: $P=(26-36.1(-51))$; $E=(26-35.9(-50))$ μm ; $P/E=1.01$. Aperture membrane finely granular. Endoapertures conspicuous circular pores, equal to or larger than width of ectoaperture, occasionally lalongate. Aperture margins prominent, fastigium present between foot layer and endexine in margins adjacent to endoapertures. Mesocolpial wall buckles inwards on dehydration. Exine 1–2 μm thick at mesocolpium; tectum 0.3–0.6 μm , perforated with many microchannels; infratectum 0.6–0.8 μm , columellae densely packed; foot layer 0.6–1.2 μm ; endexine 0.1–0.5 μm , thickening under apertures. Tectum microperforate and granular-rugulate.

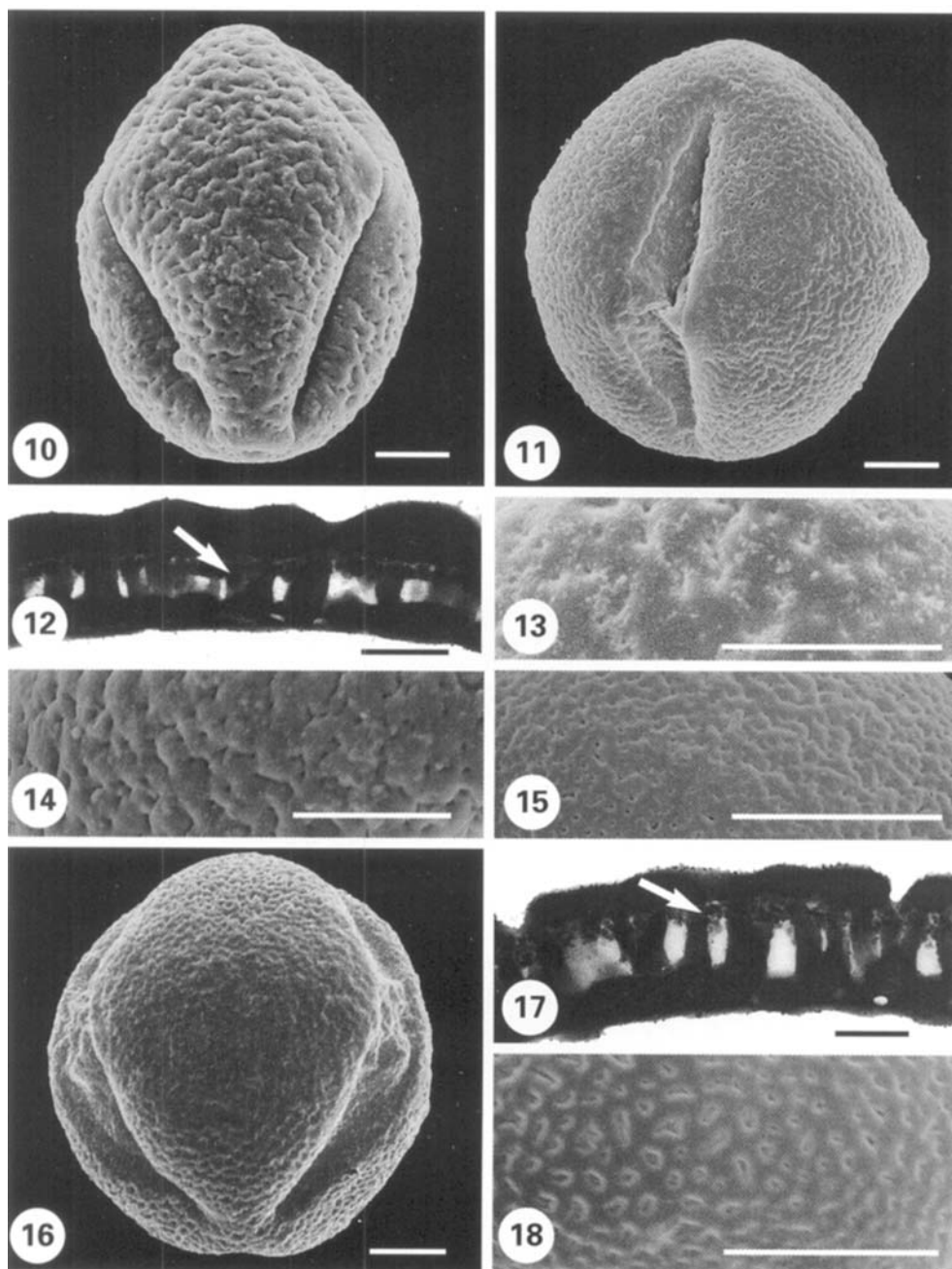
Crudia
(Figs 28–30, 48)

Spheroidal to prolate. Size: $P=(33-37.4(-55))$; $E=(21-34.5(-44))$ μm ; $P/E=1.0$. Tricolporate, colpi long, approximately equal to polar length, aperture membrane coarsely scabrate to vermiculate. Exine 2 μm thick at mesocolpium; tectum 0.8–1.2 μm including supracteal striae which are mushroom-shaped; infratectum 0.3–0.4 μm , columellae short and widely spaced; foot layer thin and broken or rudimentary, less than 0.1 μm ; endexine 0.1–0.2 μm , thickening under apertures. Tectum coarsely striate, striae long, running pole to pole.

Augouardia
(Figs 31–33, 49)

Subprolate to prolate. Size: $P=(35-46.3(-52))$; $E=(32-37.2(-44))$ μm ; $P/E=1.25$. Tricolporate, colpi long, approximately equal to polar length, aperture membrane finely granular. Endoapertures generally conspicuous circular pores. Exine 2–3 μm thick at mesocolpium; tectum 0.5–0.8 μm ; infratectum 0.8–1.3 μm , with an acetolysis-resistant layer at mid-infracteal level to just above foot layer height; foot layer 0.3–0.5 μm ; endexine 0.1–0.2 μm , thickening under apertures. Tectum reticulate, simplicolumellate, heterobrochate, lumen size decreasing towards aperture margins. Dense, free standing bacules present in lumina.

Figs 7–9. *Neopaloxylon tuberosum* (Du Puy et al. M519). Fig. 7. SEM oblique equatorial view showing mesocolpial and polar area. Scale bar = 10 μm . Fig. 8. SEM mesocolpial surface. Scale bar = 5 μm . Fig. 9. TEM mesocolpial exine. Scale bar = 1 μm .



Figures 10–18. Figs 10–15. *Prioria copaiifera*. Fig. 10. SEM (*Broadway* 5833) Equatorial view showing mesocolpium. Scale bar = 5 μm . Fig. 11. SEM (*Cooper* 345) mesocolpial surface. Scale bar = 5 μm . Fig. 12. TEM (*Broadway* 5833) mesocolpial exine with fine granules in infratectum. Scale bar = 1 μm . Fig. 13. SEM (*Castroviejo et al.* 7136MV) mesocolpial surface. Scale bar = 5 μm . Fig. 14. SEM *P. copaiifera* (*Broadway* 5833) mesocolpial surface. Scale bar = 5 μm . Fig. 15. SEM (*Cooper* 345) mesocolpial surface. Scale bar = 5 μm . Figs 16–18. *Gossweilenodendron*. Fig. 16. SEM *G. balsamiferum* (*Kenudy* 554) Equatorial view. Scale bar = 5 μm . Fig. 17. TEM *G. balsamiferum* (*Donis* 1524) mesocolpial exine with fine granules in infratectum. Scale bar = 1 μm . Fig. 18. SEM *G. juveni* (*Reitsma et al.* 2595) mesocolpial surface perforate to microreticulate. Scale bar = 5 μm .

Colophospermum, Hardwickia
(Figs 34–39, 50, 51)

Spheroidal, (40–)44.8(–50) μm in diameter. Pantoporate with 8–12 pores 5–7 μm in diameter, pores with a granular or rugulate membrane. Exine 1–1.5 μm thick at mesocolpium; tectum 0.3–0.5 μm ; infratectum 0.2–0.3 μm ; foot layer 0.1–0.2 μm thick in *Colophospermum*, thin and broken in *Hardwickia*; endexine less than 0.1 μm , no thickening under apertures (Fig. 51). Tectum reticulate or microreticulate/rugulate. Lumen size *c.* 3 μm in *Colophospermum* and 1–2 μm in *Hardwickia*.

WOOD ANATOMY

Prioria copaiifera
(Figs 52–55)

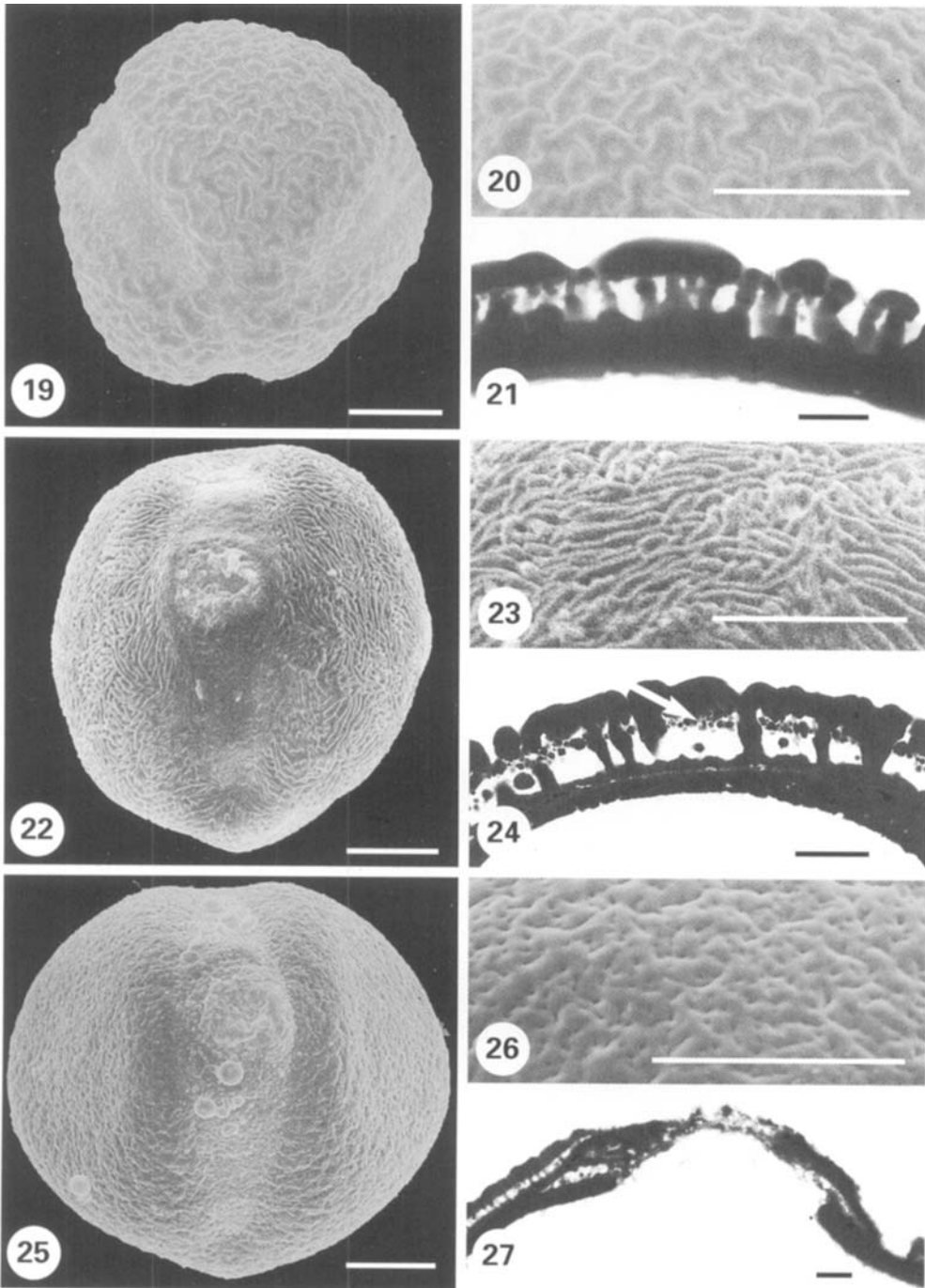
There are numerous descriptions and photographs in the wood anatomical literature, including: Kribs (1959), Brazier & Franklin (1961), Sudo (1963), McKenzie (1972), Gaiotti de Peralta & Edlmann Abbate (1981), D tienne & Jacquet (1983), Wiemann (1987), Anon (1986), Ilic (1991), Nardi Berti & Edlmann Abbate (1992). Two samples were examined here: IFI 3412, Panama (from Oxford Forestry Institute); W-16558 (USNM, Smithsonian).

Growth rings present but indistinct. Vessels solitary, in pairs and clusters and radial multiples up to 5. Intervessel pitting fine (3–8 μm), vessel ray pitting the same. Fibres thin-walled and short, irregularly storied and often difficult to distinguish from fusiform axial parenchyma cells. Axial parenchyma scanty paratracheal, vasicentric, aliform and confluent, also some straight bands up to 3 or 4 cells wide. Axial parenchyma strands mainly 2 and 3–4-celled, some fusiform. Rays 1–3 cells wide and up to 37 cells high, many rays uniseriate. Rays heterocellular, with many upright cells. Axial canals larger than vessels. In IFI3412 there are some crystals in axial parenchyma strands and especially in epithelial cells of axial canals. In W-16558 the epithelial cells have been destroyed which is possibly why no crystals were seen. Density 450 kg m^{-3} at 15% moisture content (BSI, 1991).

Oxystigma
(Figs 56–60)

Wood anatomical references include Huber & Schmidt (1938), Normand (1948), Jentsch *et al.* (1936–9), Fouarge, G rard & Sacr  (1953), Lebacq (1957), Kribs (1959) (*O. mannii* & *O. oxyphyllus*), Fouarge & G rard (1964), Brazier & Franklin (1961), Ferreirinha (1962), Lebacq & Dechamps (1964), Sudo (1963), Bierna (1963), Monteiro (1967), Lebacq & Dechamps (1967), Wagenf hr & Scheiber (1974), Normand & Paquis (1976/7), Nardi Berti & Edlmann Abbate (1988), Park (1987), Ogata (1989), Ilic (1991), Wicmann (1994). One species was examined here: *O. oxyphyllus*, Tropical Africa 1953.

Growth rings present but indistinct. Vessels solitary, in pairs and radial multiples up to 3, some with dark-staining contents. Intervessel pitting fine (3–4 μm), alternate,



Figures 19–27. Figs 19–21. *Kingiodendron*. Fig. 19. SEM *K. pinnatum* (*s.n.*5807). Slightly oblique equatorial view showing mesocolpium and part of one pole. Scale bar = 10 μm . Fig. 20. SEM *K. pinnatum* (*s.n.*5807) surface rugulate-vermiculate. Scale bar = 5 μm . Fig. 21. TEM *K. pinnatum* (*s.n.*5807) mesocolpial exine with thick foot layer. Scale bar = 1 μm . Figs 22–24. *Stemonocoleus*. Fig. 22. SEM *S. micranthus* (*Chesters* OBS182) Equatorial view with prominent endoaperture and aperture margins. Scale bar = 10 μm . Fig. 23. SEM *S. micranthus* (*Chesters* OBS182) mesocolpial area. Scale bar = 5 μm . Fig. 24. TEM *S. micranthus*

polygonal and vested, vessel-ray pitting similar. Fibres thin-walled. Axial parenchyma paratracheal and in indistinct bands up to 5 cells wide, including marginal bands (described as terminal in Kribs, 1959). Axial parenchyma strands 2–4-celled, a few fusiform and 5-celled, not storied. Axial canals about the same diameter as vessels are diffusely scattered and often present in tangential parenchyma bands. Rays 1–3 cells wide, uniseriate rays up to 10 cells high and wider rays up to *c.* 35 cells high, not storied, heterocellular, with mixed procumbent, square and upright cells, many with dark contents. Prismatic crystals abundant in chambered axial parenchyma cells, sometimes adjacent to rays. Some ray cells, especially upright cells, have chambered crystals. Density 610 kg m^{-3} at 15% moisture content (BSI, 1991).

Gossweilerodendron
(Figs 61–64)

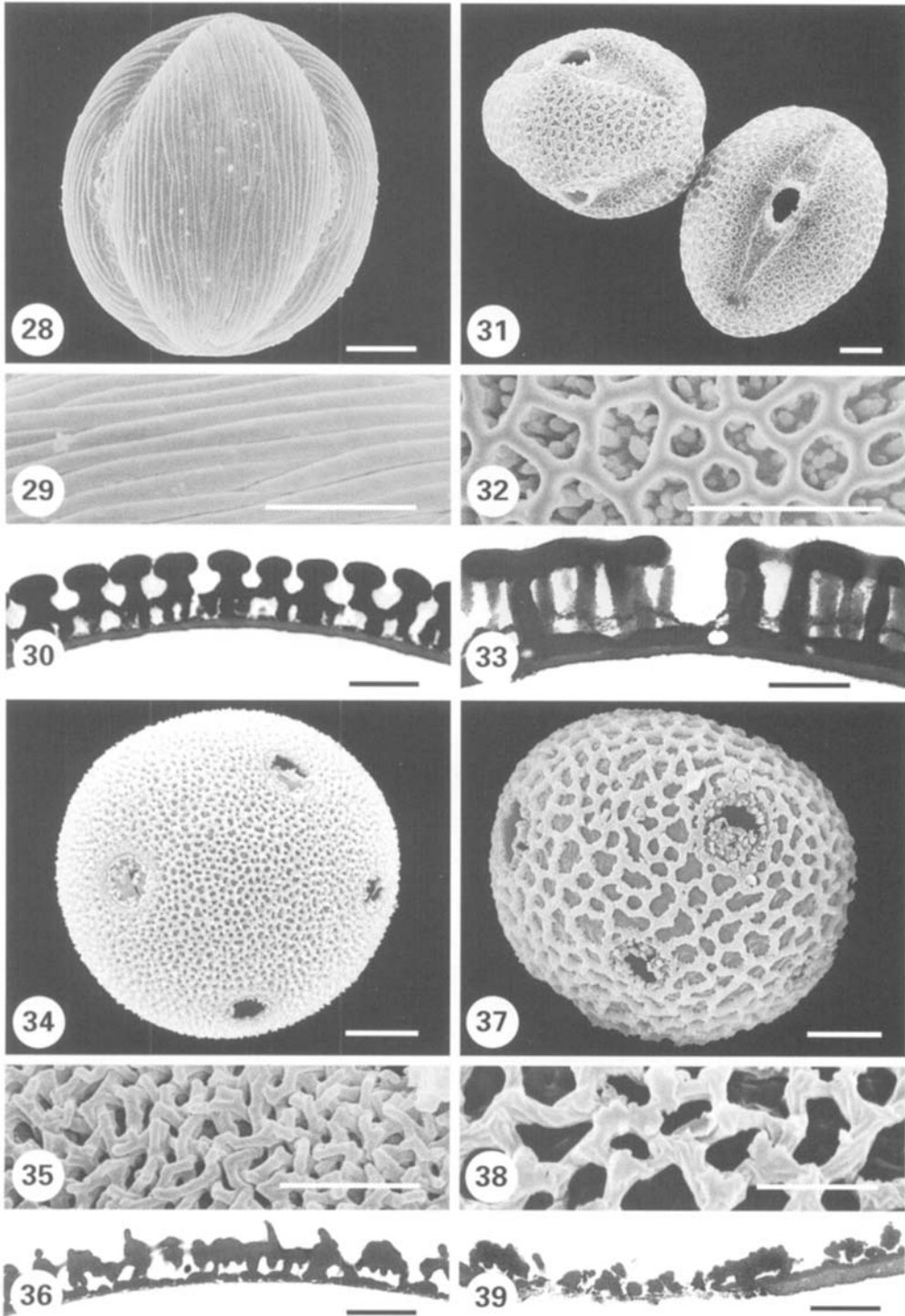
There are many references to *Gossweilerodendron* wood anatomy, including: Normand (1948), Lebacq (1957), Kribs (1959), Chattaway (1956), Scott (1950), Eeckhout (1951), Schmidt (1951–2), Spalt & Stern (1956/7/9), Seabra & Ferreirinha (1960), Anon (1963), Fouarge & Gérard (1964), Brazier & Franklin (1961), Lebacq & Dechamps (1964), Sudo (1963), Bierna (1963), de Freitas (1965), Lebacq & Dechamps (1967), Wagenführ & Scheiber (1974), Normand & Paquis (1976/7), Gill, Onuja & Husaini (1983), Nardi Berti & Edlmann Abbate (1988), Anon (1986), Ogata (1987), Ilic (1991), Wiemann (1994). *G. balsamiferum* is described here from three wood samples: IFI 5138 Nigeria, Trade 1949, 1962.

Growth rings indistinct. Vessels solitary, in pairs and threes. Intervessel pitting fine (4–8 μm), alternate, vested, vessel-ray pitting the same. Fibres mostly thin-walled. Axial parenchyma abundant, initial, scanty paratracheal, vasicentric, confluent, diffuse and diffuse in aggregates, poorly defined and not always clearly distinct from the thin-walled fibres in TS. Axial parenchyma strands irregularly storied, occasionally fusiform, but mainly 2–4-celled. Axial canals diffuse, with some tendency towards arrangement in short tangential bands in places. Rays 1–3, occasionally 5 cells wide, multiseriate rays to at least 40 cells high, uniseriate rays shorter. Rays heterocellular, with most cells procumbent, but some square and upright. Prismatic crystals in chambered axial parenchyma cells and possibly also chambered fibres, sometimes very rare. Crystals also sometimes in epithelial cells of the axial canals. Density 510 kg m^{-3} at 15% moisture content (BSI, 1991).

Kingiodendron
(Figs 65–72)

K. pinnatum was once known as *Hardwickia pinnata*, and the wood was described under this name by Pearson & Brown (1932). There are also many other wood

Chesters OBS182) aperture margin with sparse columellae and granules in infractum. Scale bar = 1 μm . Figs 25–27. *Guibourtia*. Fig. 25. SEM *G. tessmannii* (*Mildbraedi* 7770) Equatorial view. Scale bar = 10 μm . Fig. 26. SEM *G. demeusei* (*Villers* 689) mesocolpial surface. Scale bar = 5 μm . Fig. 27. TEM *G. conjugata* (*Mendoca* 3242) apertural area showing fastigium and thickening of endexine under aperture margins. Scale bar = 1 μm .



Figures 28–39. Figs 28–30. *Crudia*. Fig. 28. SEM *C. spicata* (Ducke 5630). Equatorial view. Scale bar = 10 μm . Fig. 29. SEM *C. spicata* (Ducke 5630) mesocolpial surface. Scale bar = 5 μm . Fig. 30. TEM *C. senegalensis* (Lisowski 51389) mesocolpial exine with suprategical striae. Scale bar = 2 μm . Figs 31–33.

anatomical references, including: Sosef, Hong & Prawirohatmodjo (1998), Kanehira (1924), Kribs (1959), Chattaway (1956), Sudo (1963), Meniado, Robillos & Zamuco (1970), Meniado, Valbucna & Tamolang (1974), Knaap van Meeuwen (1970), Ramesh Rao & Purkayastha (1972), Furuno (1979), Lalitha & Prakash (1980), Gill & Ogunlowo (1986), Awasthi & Prakash (1986), Sudo (1988), Ilic (1991), Awasthi (1992). *K. pinnatum* (syn. *Hardwickia pinnata*) and *K. alternifolium* (syn. *H. alternifolia*) have been examined here: three samples of *K. alternifolium*, Philippines 139-1908, Philippines 1951, Philippines 1808; one sample of *K. pinnatum*, Hay's collection, Kew.

K. alternifolium: Growth rings indistinct. Vessels solitary, in pairs, small clusters and radial multiples up to 5. Intervessel pitting very fine (4–6 µm), alternate, polygonal and vested, vessel-ray pitting the same. Fibres thin to thick-walled. Axial parenchyma scanty paratracheal, vasicentric, occasionally aliform and often confluent and banded. Axial parenchyma strands 2–4-celled, not storied. Axial canals about the same size as vessels, diffusely arranged, occasionally in tangential pairs, associated with axial parenchyma. Rays 1–5 cells wide, uniseriate rays up to 10 cells high, multiseriate rays up to c. 60 cells high. Rays heterocellular, cells procumbent, square and upright. Vessels, rays and axial parenchyma often have dark contents. Prismatic crystals abundant in chambered axial parenchyma in Philippines 1808, where also present singly in some non-chambered ray cells, as in 139-1908.

K. pinnatum is similar, but axial parenchyma is scanty paratracheal and in narrow bands 2–3 cells wide, rays generally shorter, up to c. 21 cells high. Occasional crystals present in ray cells, some in chambered upright ray cells.

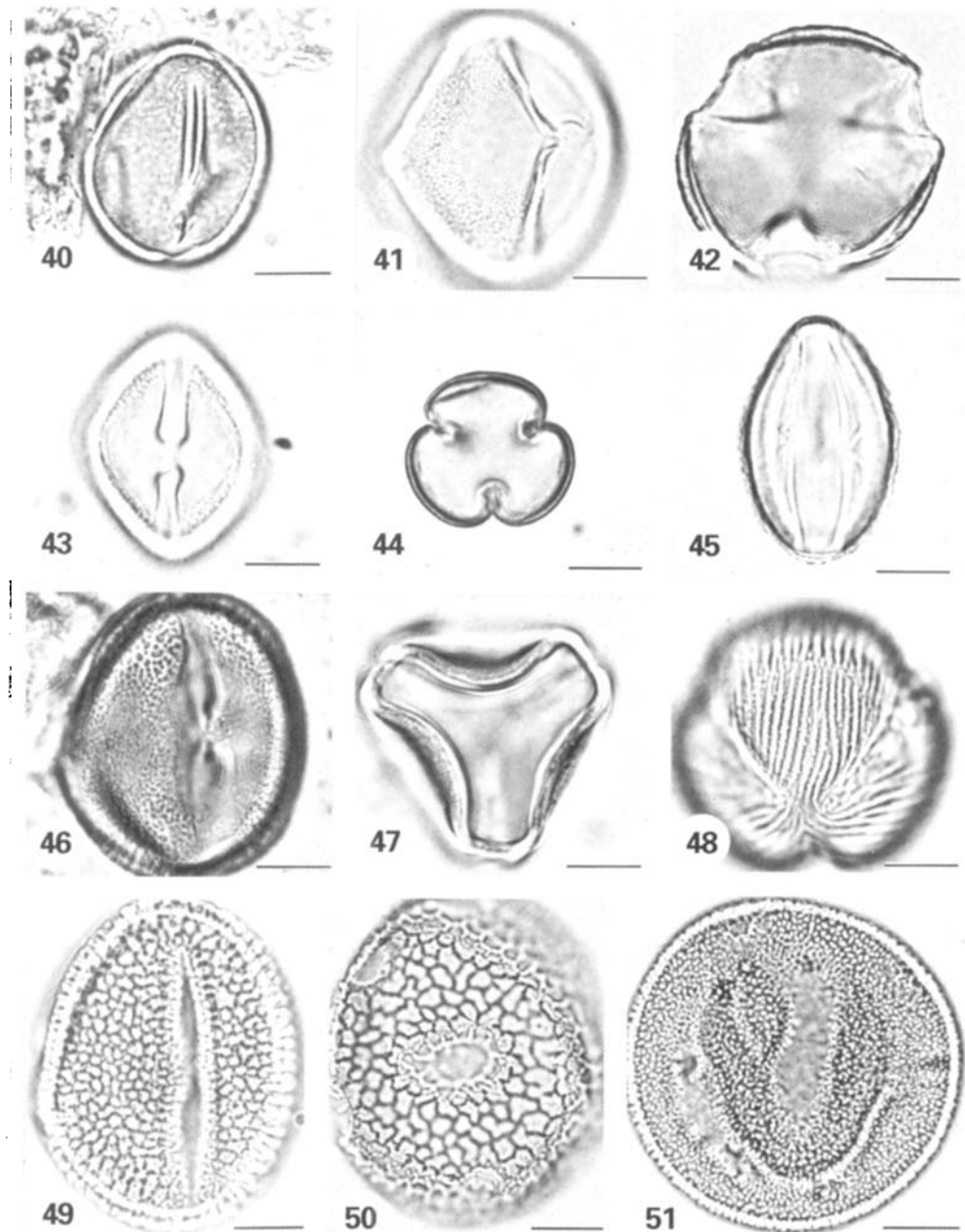
Density for *K. pinnatum* is 450–760 kg m⁻³ at 15% m.c. (Sosef *et al.*, 1998), specific gravity 0.55–0.70 (as *H. pinnata* in Pearson & Brown, 1932). Fibres are thickest walled in this genus. There is some diffuse parenchyma, but not nearly as much as in *Gossweilerodendron*.

Bathiaea rubriflora
(Figs 73–78)

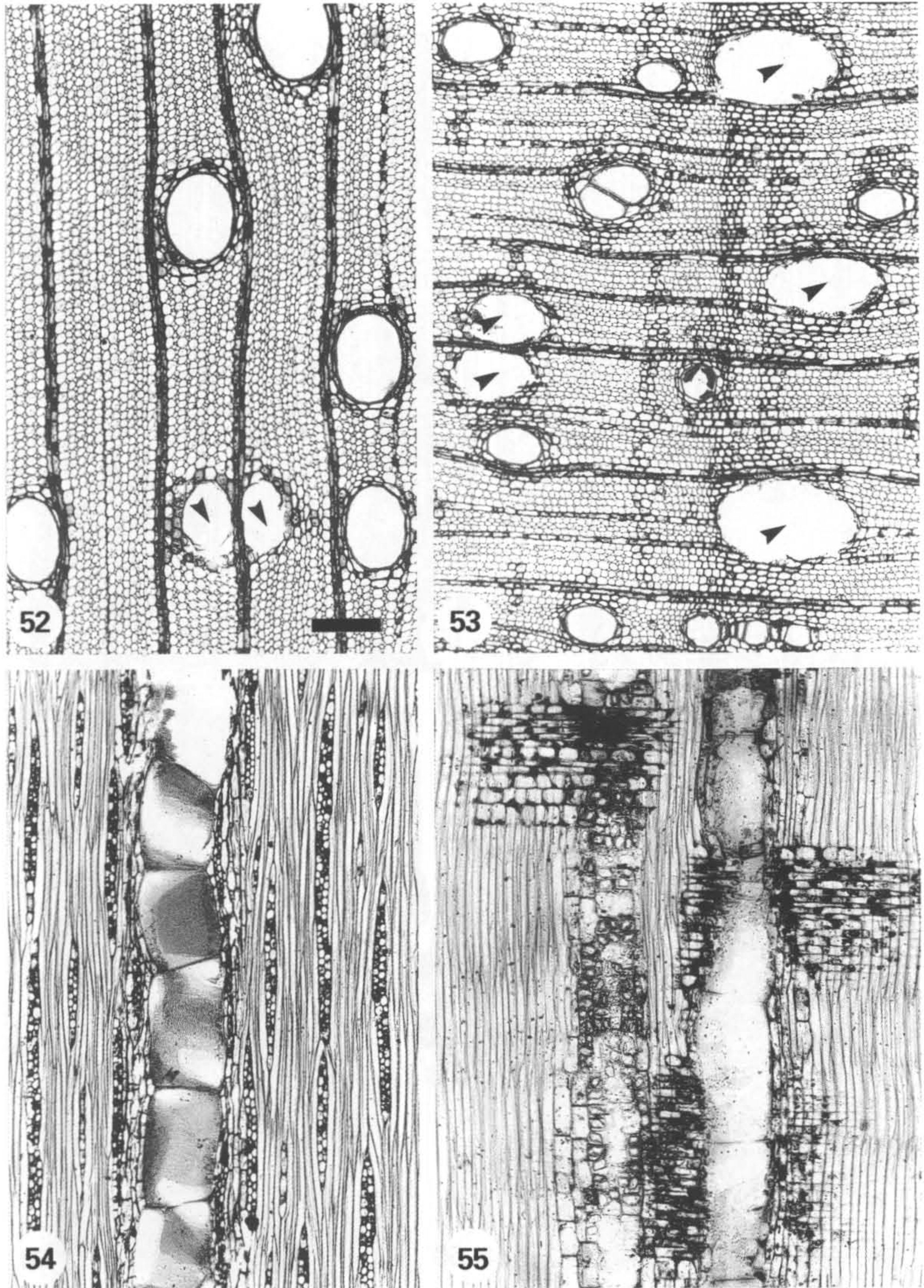
The wood anatomy of this genus appears not to have been studied in detail, although it is mentioned by Baretta-Kuipers (1981) who is quoted in Gasson (1994). One wood sample was examined: RBHw 10233, Paris Herbarium SF 15807.

Growth rings indistinct or absent. Vessels solitary, in pairs and occasionally in threes and radial multiples of 4. Intervascular pitting fine (6–9 µm), alternate, vested. Fibres very short, only slightly longer than adjacent axial parenchyma strands. Axial parenchyma vasicentric to aliform, rarely confluent, also in bands,

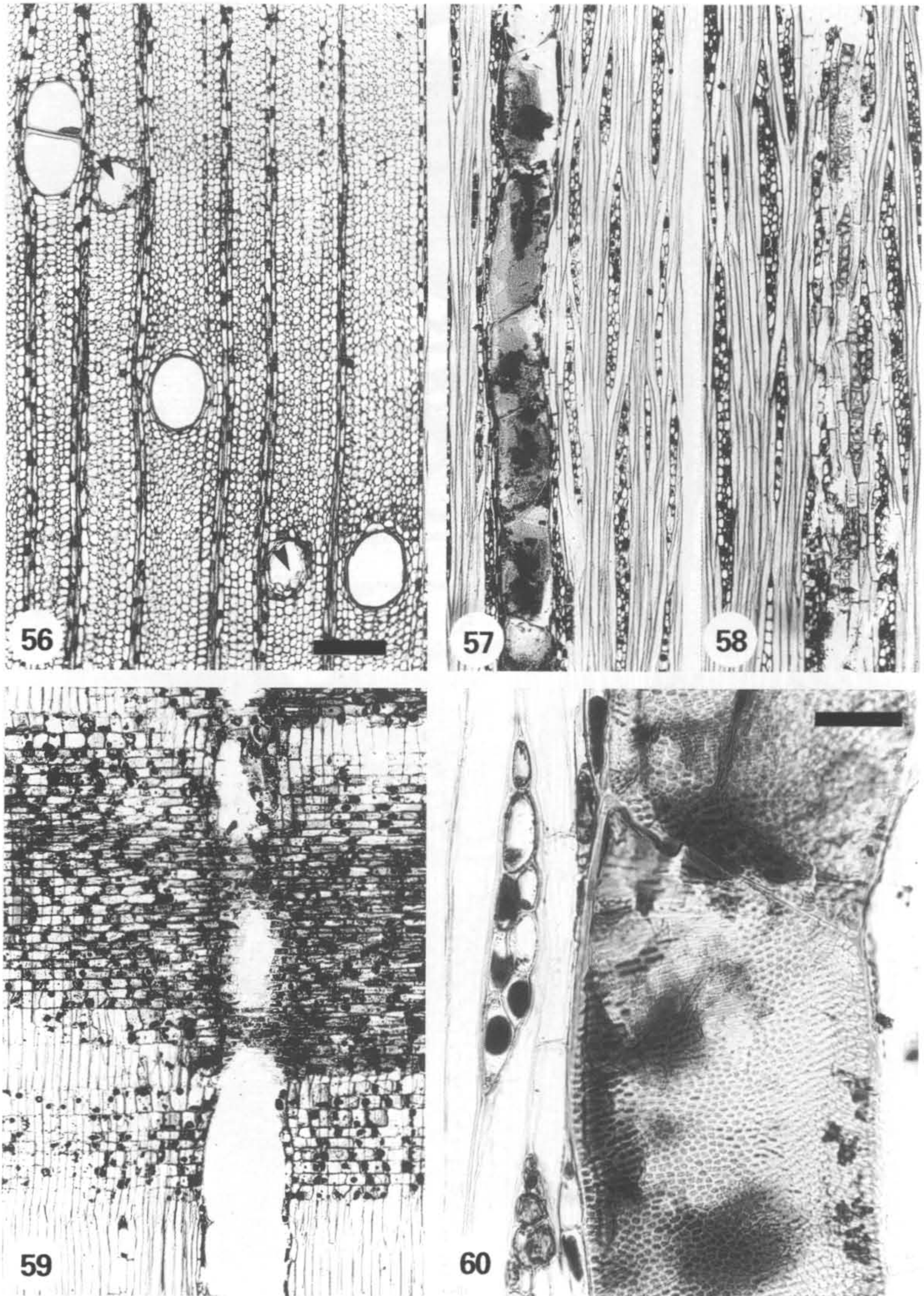
Augouardia. Fig. 31. SEM *A. tetestui* (Wieringa *et al.* 2898) equatorial view. Scale bar = 10 µm. Fig. 32. SEM *A. tetestui* (Wieringa *et al.* 2898) mesocolpial surface. Scale bar = 5 µm. Fig. 33. TEM *A. tetestui* (White 1496) mesocolpial exine with layer in infratectum. Scale bar = 2 µm. Fig. 34. SEM *Hardwickia binata* (Khan 2319) whole grain. Scale bar = 10 µm. Fig. 35. SEM *Hardwickia binata* (Khan 2319) surface. Scale bar = 5 µm. Fig. 36. TEM *Hardwickia binata* (Khan 2319) exine. Scale bar = 2 µm. Fig. 37. SEM *Colophospermum mopane* (Lugard 243) whole grain. Scale bar = 10 µm. Fig. 38. SEM *Colophospermum mopane* (Lugard 243). Scale bar = 5 µm. Fig. 39. TEM *Colophospermum mopane* (Lugard 243) apertural area. Scale bar = 2 µm.



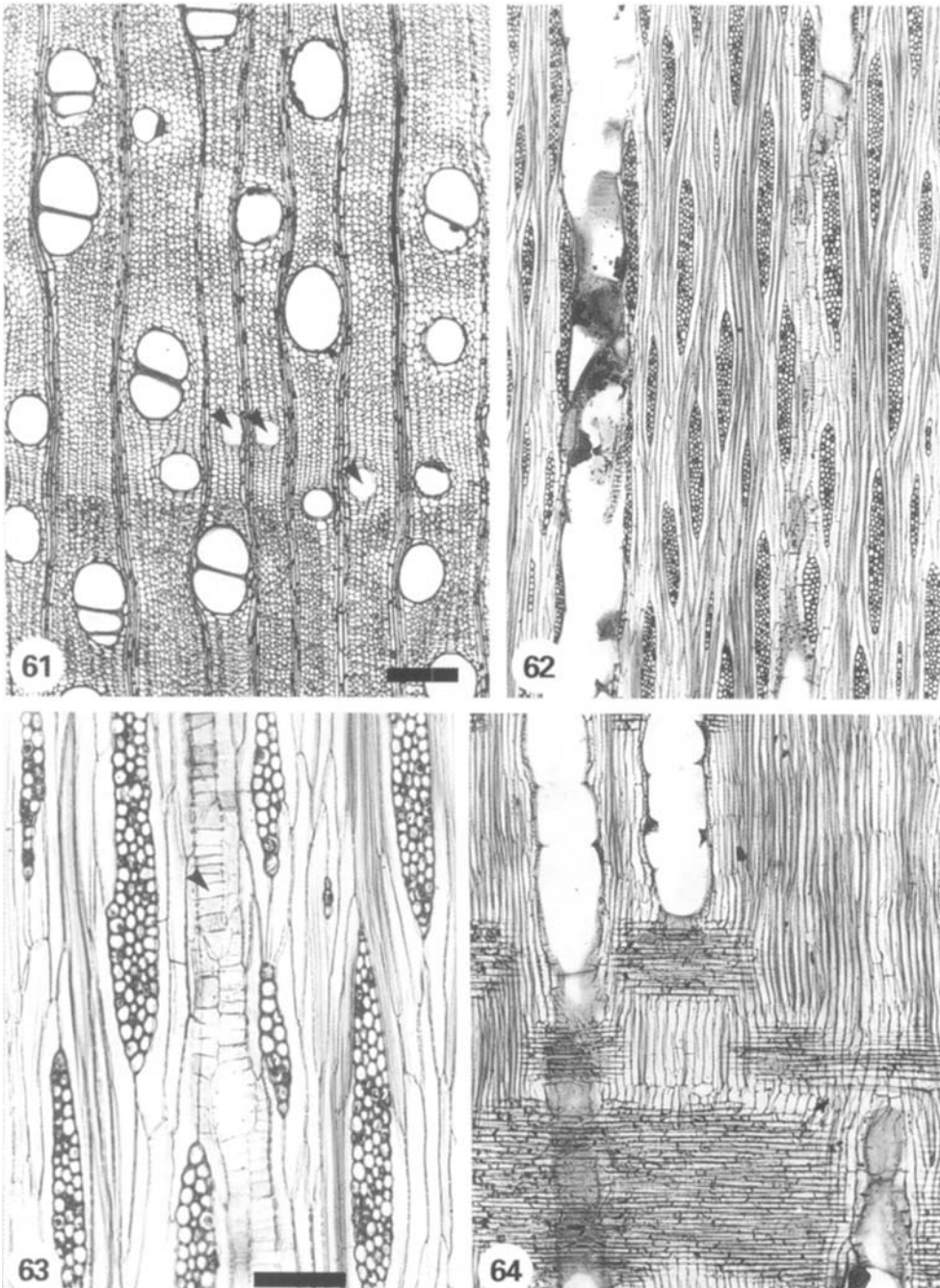
Figures 40–51. Scale bar = 10 μm in all Figs. Fig. 40. *Oxystigma oxyphyllum* (Jean-Louis 9490) equatorial view. Fig. 41. *Bathiaea rubriflora* (Du Puy et al. MB403) equatorial view. Fig. 42. *Neopaloxylon tuberosum* (Du Puy et al. M519) polar view. Fig. 43. *Gossweilerodendron balsamiferum* (Kenedy 554) equatorial view. Fig. 44. *Prioria copaifera* (Castroviejo et al. 7136MV) polar view showing shape of mesocolpial wall in dehydrated grain compared with *Guibourtia* (Fig. 47). Fig. 45. *Kingiodendron pinnatum* (Wallich 5807) equatorial view. Fig. 46. *Stemonocoleus micranthus* (Oldeman 383) equatorial view. Fig. 47. *Guibourtia gossweileri* (Grandvaux-Barbosa 11.322) polar view of whole grain with mesocolpial wall caving inwards in dehydrated grain. Fig. 48. *Crudia tenuipes* (Shea 75635) slightly oblique polar view. Fig. 49. *Augouardia letestui* (Wieringa et al. 2848) equatorial view. Fig. 50. *Colophospermum mopane* (Torre 7326) whole grain. Fig. 51. *Hardwickia binata* (Gamble 874) whole grain.



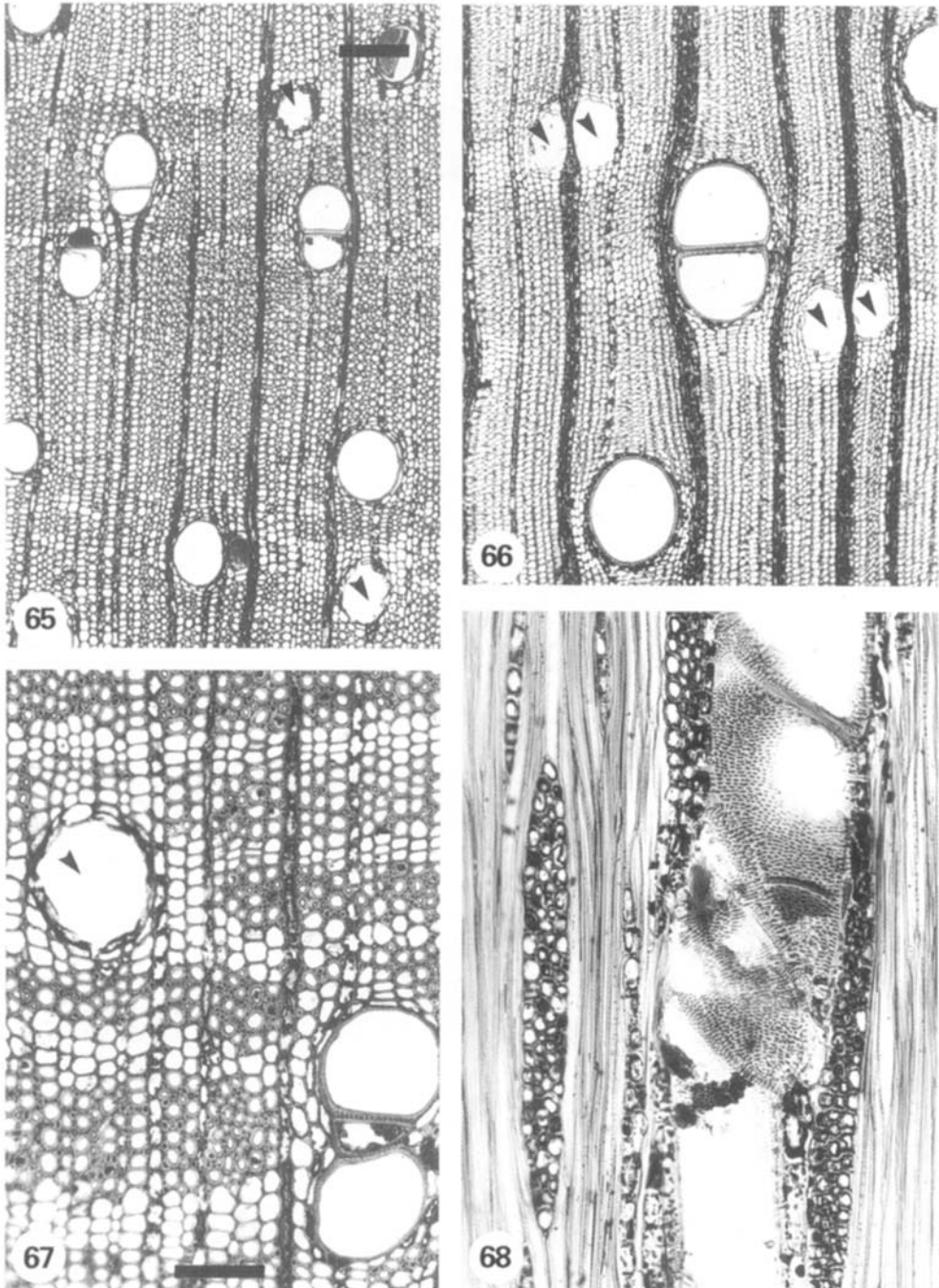
Figures 52–55. *Prioria copaifera*. Figs 52, 53. TS, wide axial canals (arrowed), diffusely arranged but often in pairs or short tangential lines. Orientation of Fig. 53 is at 90° to Fig. 52 to show three canals. Fig. 54. TLS, fine intervessel pitting, tall narrow rays. Fig. 55. RLS, heterocellular ray and abundant prismatic crystals in axial parenchyma. Scale bar = 200 μ m for all (on Fig. 52).



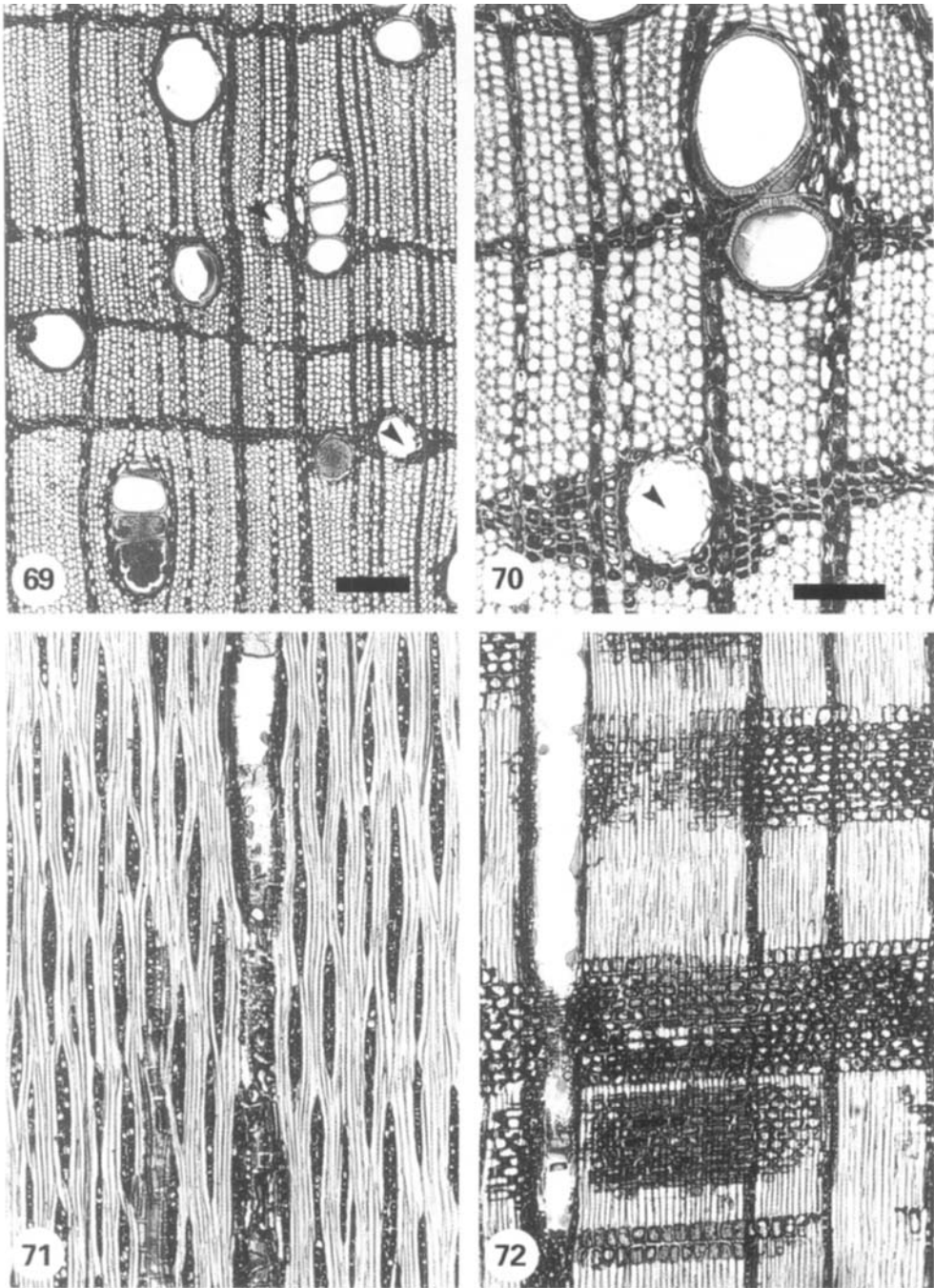
Figures 56–60. *Oxystigma oxyphyllus*. Fig. 56. TS, narrow diffusely arranged axial canals (arrowed). Scale bar = 200 μm . Figs 57, 58. TLS, fine intervessel pitting, tall narrow rays. Scale as per Fig. 56. Fig. 59. RLS, heterocellular ray. Scale as per Fig. 56. Fig. 60. TLS, alternate, vestured intervessel pitting. Scale bar = 25 μm .



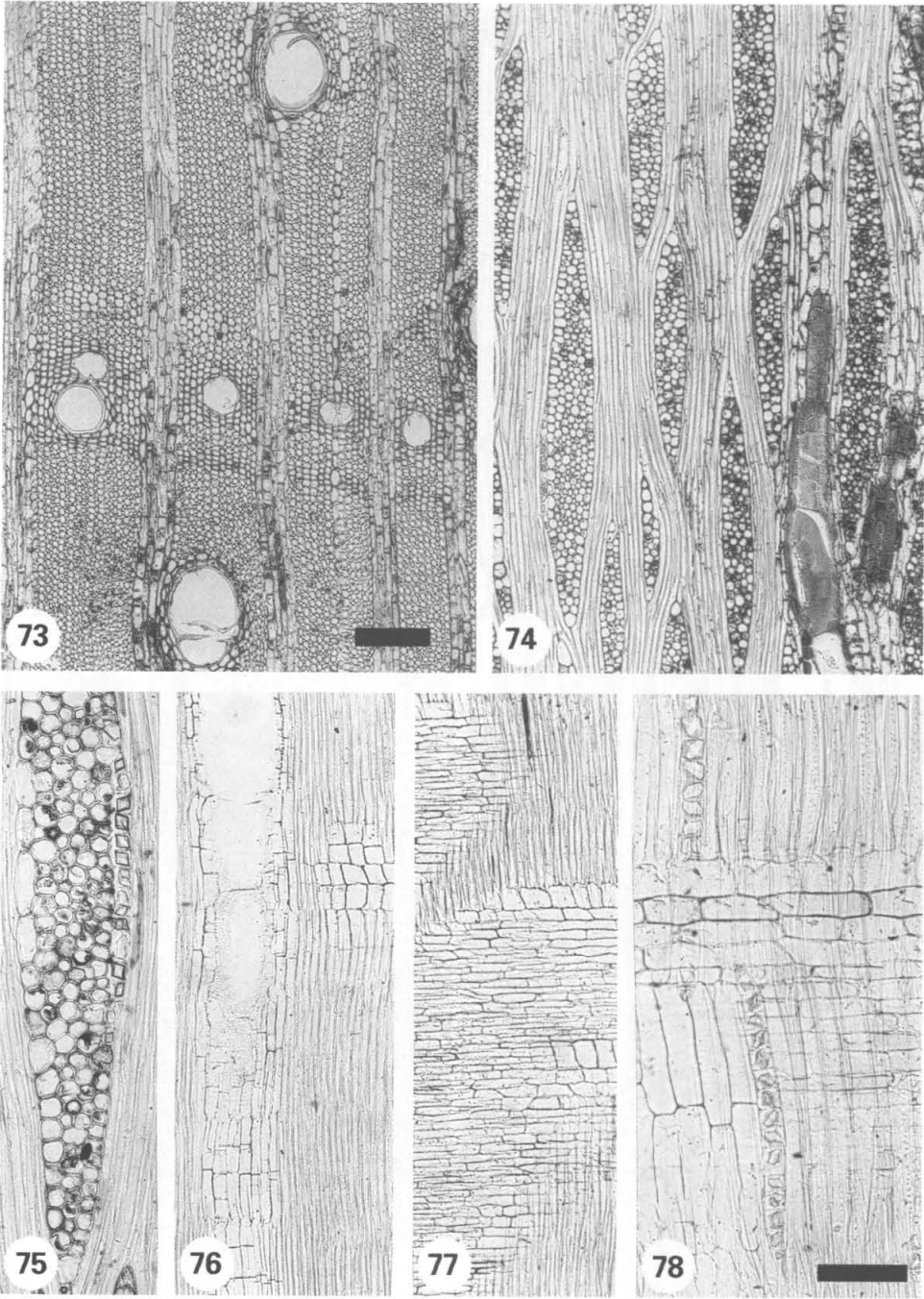
Figures 61–64. *Gossweilerodendron balsamiferum*. Fig. 61. LS, indistinct axial parenchyma pattern, diffusely arranged narrow axial canals (arrowed). Scale bar = 200 μm . Fig. 62. TLS, fine intervessel pitting, fairly tall wide rays. Scale as per Fig. 61. Fig. 63. TLS, epithelial cells to axial canal are arrowed. Scale bar = 100 μm . Fig. 64. RLS, homocellular rays. Scale as per Fig. 61.



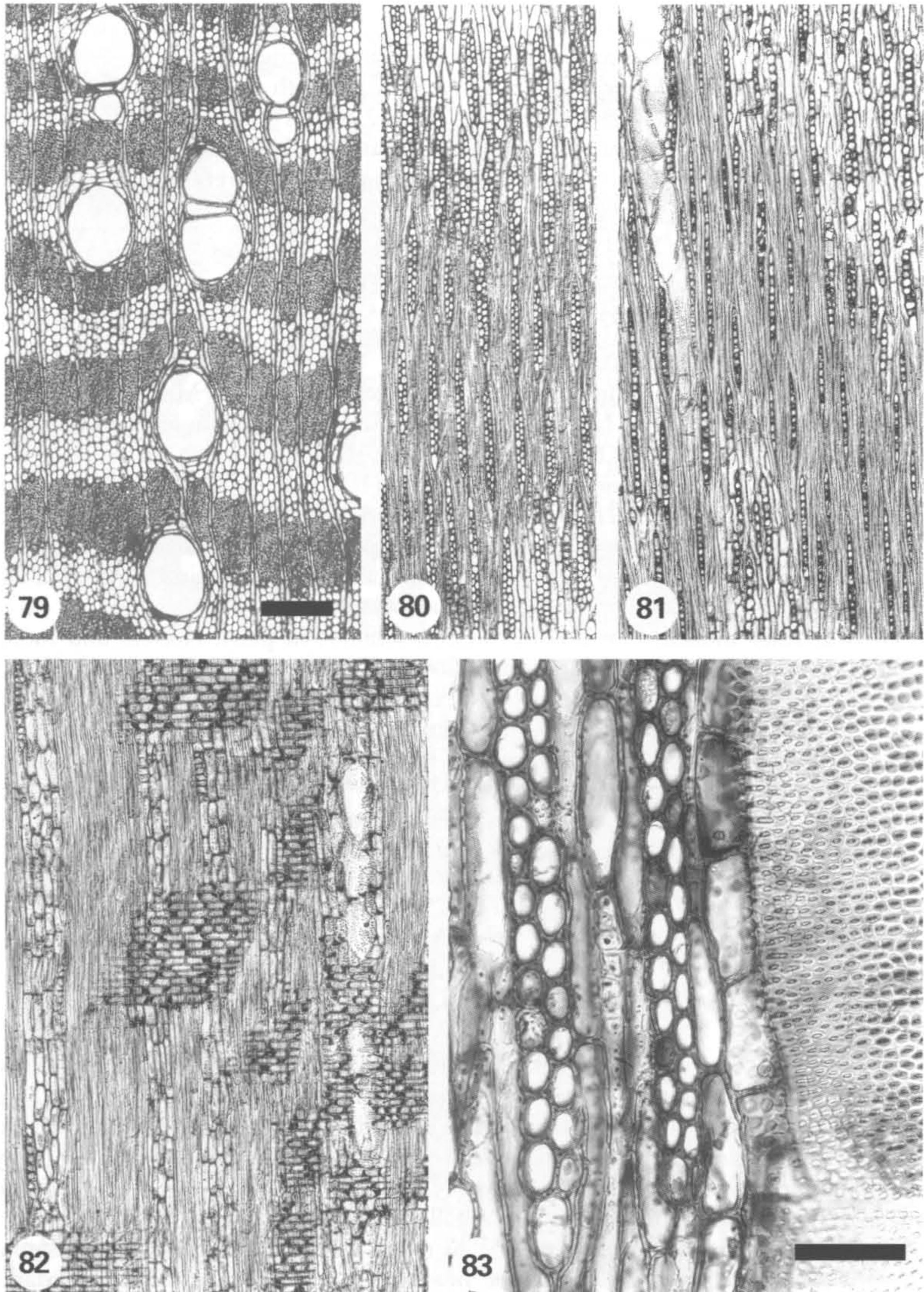
Figures 65–68. *Kingiodendron alternifolium*. Figs 65–67. TS, fairly indistinct axial parenchyma pattern, diffusely arranged narrow axial canals (arrowed). Scale bar = 200 μ m for Figs 65, 66 (on Fig. 65), 100 μ m on Fig. 67. Fig. 68. TLS, fine intervessel pitting. Scale as per Fig. 67.



Figures 69–72. *Kingiodendron pinnatum*. Figs 69, 70. TS, narrow bands of axial parenchyma, diffusely arranged narrow axial canals. Scale bar = 200 μm on Fig. 69, 100 μm on Fig. 70. Fig. 71. TLS, fairly short narrow rays. Scale as per Fig. 69. Fig. 72. RLS, heterocellular rays. Scale as per Fig. 69.



Figures 73–78. *Bathiaea rubriflora*. Fig. 73. TS, fairly indistinct axial parenchyma pattern, axial canals in a tangential line. Scale bar = 200 μm . Figs 74, 75. TLS, fairly tall wide rays, fine intervessel pitting. Scale for Fig. 74 as per Fig. 73, scale for Fig. 75 as per Fig. 78. Figs 76, 77. RLS, rays heterocellular. Scale as per Fig. 73. Fig. 78. RLS, prismatic crystals in chambered axial parenchyma or fibres. Scale bar = 100 μm .



Figures 79–83. *Crudia*. Figs 79, 80, 83, *C. glaberrima*; Figs 81, 82, *C. gabonensis*. Fig. 79. TS, wide bands of confluent parenchyma, no axial canals. Scale bar = 200 μ m. Fig. 80. TLS, rays irregularly storied. Scale as per Fig. 79. Fig. 81. TLS, rays not storied. Scale as per Fig. 79. Fig. 82. RLS, rays slightly heterocellular, prismatic crystals in chambered axial parenchyma cells. Scale as per Fig. 79. Fig. 83. TLS, storied rays, alternate, vestured intervessel pitting. Scale bar = 50 μ m.

sometimes apparently marginal containing tangentially arranged axial canals narrower than most vessels. Axial parenchyma strands storied in places, 2–4-celled. Rays 1–8 cells wide, more or less of two distinct sizes, with short rays 1–3 cells wide and up to *c.* 20 cells high, and larger rays up to *c.* 8 cells wide and *c.* 70 cells high, with one to several rows of upright ray cells at the margins. Rays not storied. Prismatic crystals in chambered fibres, not alongside axial parenchyma strands.

Crudia
(Figs 79–83)

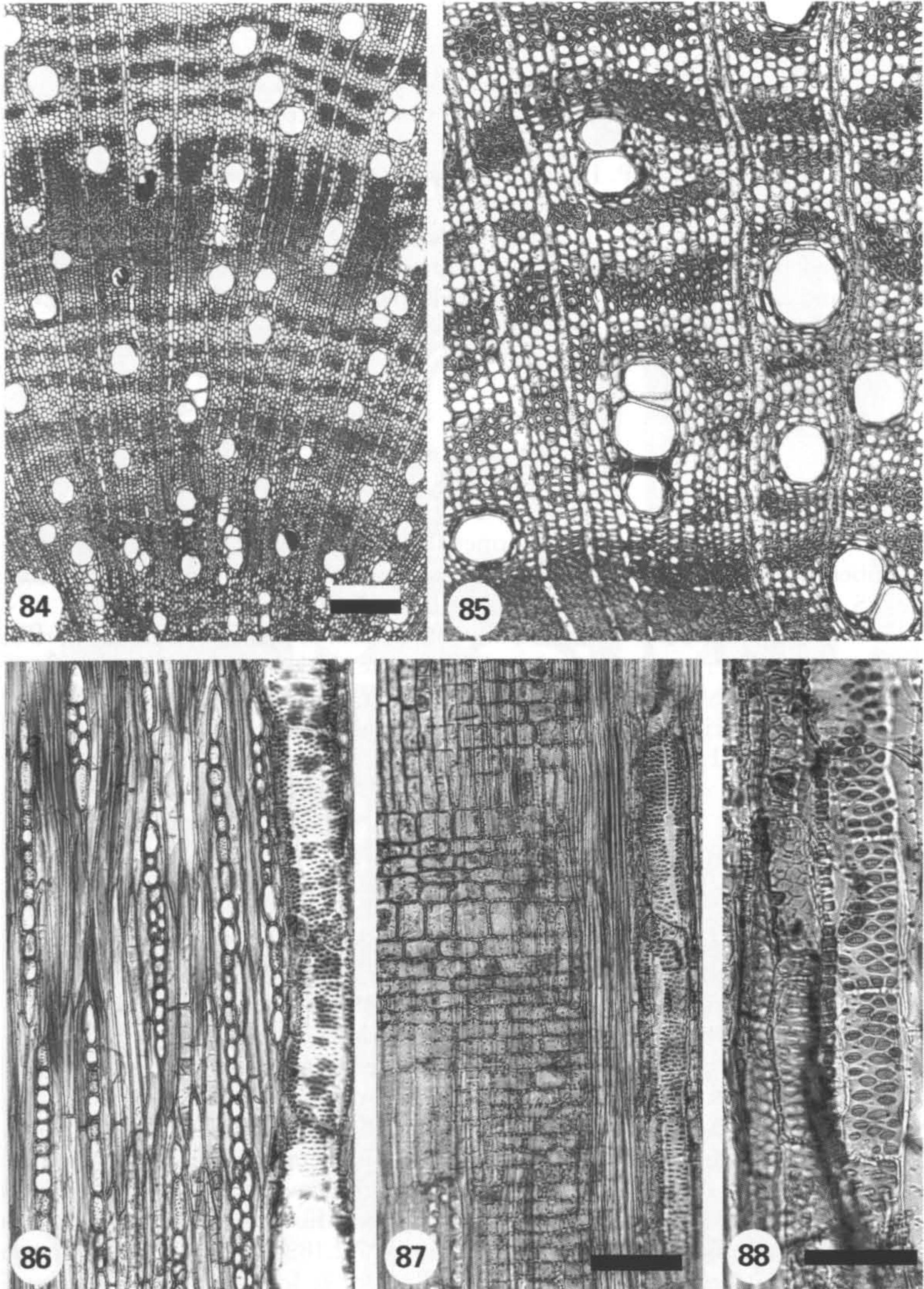
Several publications include information on wood anatomy: Moll & Janssonius (1906–36), Williams (1936), Normand (1950a), Lebacq (1957), Lindeman, Mennega & Hekking (1963), Lebacq & Dechamps (1964, 1967), Loureiro & Silva (1973), Lebacq *et al.* (1973), Normand & Paquis (1976/7), D tienne, Jacquet & Mariaux (1982), Dechamps (1980), D tienne & Jacquet (1983), Ilic (1991), Tanaka & Bernard (1995). Sosef *et al.* (1998) provided wood descriptions of two Asian species. Two species were examined here: *C. gabonensis* F.J. Breteler & C. Jongkind 10808, Gabon and *C. glaberrima* F.J. Breteler 5118, Venezuela.

Growth rings indistinct or absent. Vessels solitary, in pairs, clusters and radial multiples up to 5. Intervascular pitting fine (4–7 µm), alternate, vested. Fibres thick-walled. Axial parenchyma in bands up to *c.* 6 cells wide, strands mainly in fours, storied in *C. glaberrima*. Rays uniseriate, occasionally with biseriate portions and up to *c.* 36 cells high in *C. gabonensis*, biseriate and up to 20 cells high in *C. glaberrima*, clearly storied in latter, less so in former. Heterocellular, with one or two rows of square or upright cells at margins of rays. Many prismatic crystals in chambered axial parenchyma cells in *C. gabonensis*.

Neopaloxylon
(Figs 84–88)

We could not find any published information on the wood anatomy of this genus, and were unable to obtain mature wood samples. We did, however, examine a twig (8 mm in diameter including bark, 6.2 mm excluding bark) from a Kew herbarium specimen of *N. tuberosum* (R. Viguier) Rauschert, collected by D.J. & B.P. Du Puy and J. Andriantiana, M519, Madagascar 31.iii.1990. The wood was therefore juvenile, but yielded information for the following description.

Growth rings absent. Vessels solitary, in radial multiples up to 6 and occasional clusters. Some longer radial multiples near pith. Some vessels containing dark-staining contents. Intervessel pitting fine. Many fibres gelatinous. Axial parenchyma in bands up to 5 cells wide, scanty paratracheal in some areas near pith, becoming confluent and banded. Axial parenchyma strands in twos, storied, often containing abundant chambered crystals. Rays 1–2 cells wide, from very few to at least 40 cells high, heterocellular, with mixed square and upright cells, with one to many rows of upright cells at margins. Axial canals absent. Prismatic crystals in chambered axial parenchyma cells.



Figures 84–88. *Neopaloxylon tuberosum*. Figs 84, 85. TS, axial parenchyma confluent and banded, no axial canals. Scale bar on Fig. 84 = 200 μm , scale for Fig. 85 as per Fig. 87. Fig. 86. TLS, rays 1–2 cells wide, axial parenchyma storied. Scale as per Fig. 87. Figs 87, 88. RLS, rays heterocellular, intervessel pits vestured in Fig. 88. Scale bar on Fig. 87 = 100 μm , on Fig. 88 = 50 μm .

Augouardia letestui
(Figs 89–93)

The wood anatomy was described but not illustrated by Normand & Paquis (1996/7), and is also described briefly here. One wood sample was examined: J.J. Wieringa, F.I. van Nek, J.P. Hedin & Moussavou 2898, Gabon.

Growth rings present, marked by initial parenchyma. Vessels solitary, in pairs and radial multiples up to 6. Intervascular pitting fine (4–5 µm). Fibres thick-walled. Axial parenchyma scanty paratracheal, vasicentric to aliform, and in places confluent. Rays 1 and 2 cells wide and up to *c.* 14 cells high, heterocellular, with many rows of square and upright cells. Axial canals absent. Prismatic crystals in chambered axial parenchyma and possibly fibres.

Stemonocoleus micranthus

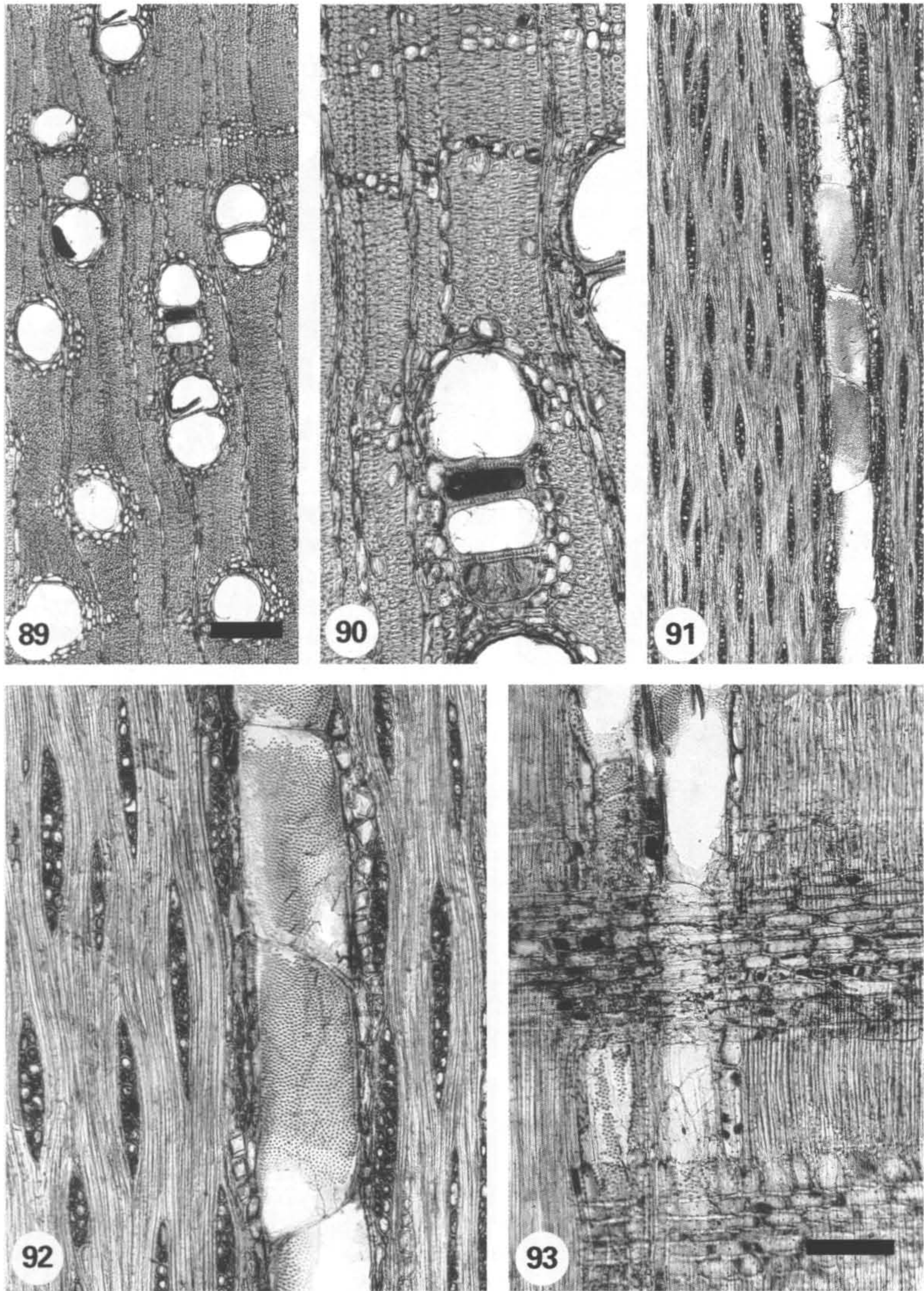
Normand (1950a) and Normand & Paquis (1976/7) have briefly described and illustrated the wood anatomy. The former showed plates of TS and TLS, the latter described a few vessel, ray and axial parenchyma characters and illustrated only the TS. The following description is taken from these two publications.

Growth rings indistinct. Vessels mainly solitary and in pairs, occasionally in radial multiples of 3. Intervessel pitting fine. Fibres quite thick-walled. Axial parenchyma vasicentric, with a slight tendency towards lozenge aliform and confluent. Rays uniseriate and biseriate, up to *c.* 20 cells high. Axial canals absent. Prismatic crystals in chambered axial parenchyma cells.

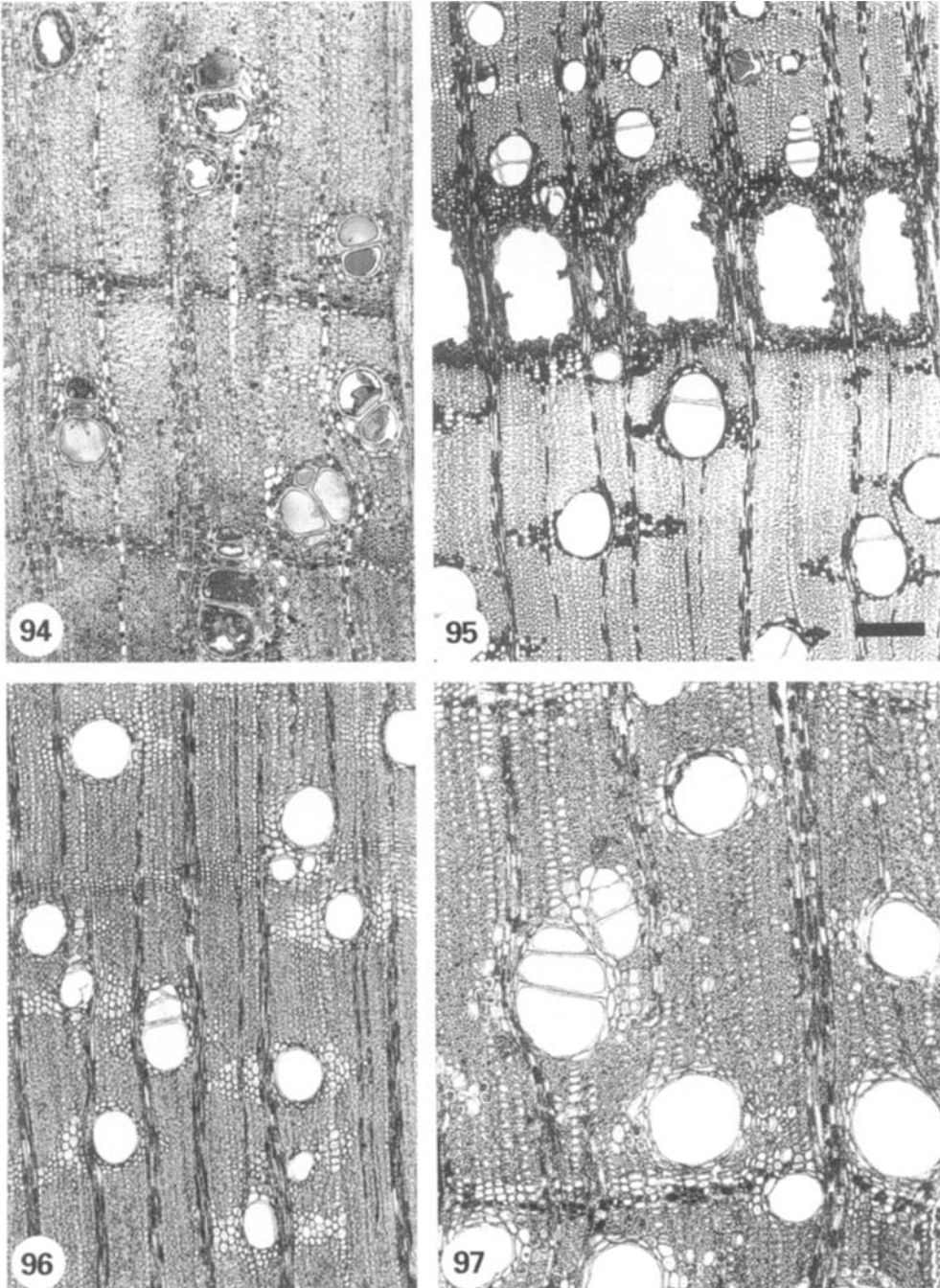
Guibourtia
(Figs 94–105)

Wood anatomy is described in many publications: Normand (1950a,b); Brazier (1955, 1957/8); Lebacq (1957); Kribs (1959); Eeckhout (1951); Brazier & Franklin (1961); Ferreirinha (1962); Lebacq & Dechamps (1964); Sudo (1963); Bierna (1963); Laming (1966); Monteiro & Franca (1965); Ferreirinha & Reis (1969); Freitas (1965); Lebacq & Dechamps (1967); Wagenführ & Scheiber (1974); Gottwald & Schwab (1978); Normand & Paquis (1976/7); Tsoumis, Voulgaridis & Nouloupoulos (1977); Kromhout (1975); Miwa *et al.* (1981); Richter (1988); Nardi Berti & Edlmann Abbate (1988); Anon (1986); Park (1987); Ogata (1988); Wiemann (1994). The wood of eight species (none American) was examined here: *G. arnoldiana* FPRL15301 Middle Congo, Trade 1954 Belgian Congo; *G. coleosperma* Milne-Redhead 989 Rhodesia; *G. conjugata* Rhodesia 12.1954; *G. demeusii* Basoko 7.2.1896 Belgian Congo, Breteler 13041 Gabon; *G. ehie* FHI 37053 Nigeria, Breteler & Jongkind 10505 Gabon; *G. leonensis* Jordan 2083 & 2169 Sierra Leone, IFI 12746; *G. pellegrimiana* Breteler 12562 Gabon; *G. tessmannii* Victoria Botanic Gardens, Cameroon.

Growth rings usually present and distinct, marked by marginal bands of axial parenchyma. Vessels solitary, in pairs and clusters and radial multiples up to 5, sometimes with dark contents. Intervessel pitting fine (6–9 µm), alternate, vested. Fibres thick-walled. Axial parenchyma mainly aliform and confluent. Rays 1–5 cells wide in most species, up to 6–8 cells wide in *G. coleosperma*, *G. demeusii* and *G.*



Figures 89–93. *Augouardia letestui*. Figs 89, 90. TS, axial parenchyma mainly scanty paratracheal and vasicentric, fibres thick-walled. Scale bar for Fig. 89 = 200 μm , scale for Fig. 90 as per Fig. 93. Figs 91, 92. TLS, fine intervessel pitting, rays very short and narrow, not storied, prismatic crystals in chambered axial parenchyma cells in Fig. 92. Scale for Fig. 91 as per Fig. 89, for Fig. 92 as per Fig. 93. Fig. 93. RLS, rays slightly heterocellular. Scale bar = 100 μm .



Figures 94–97. *Guibourtia* TS. Fig. 94. *G. coleosperma*, narrow tangential bands of axial parenchyma delimiting growth rings. Fig. 95. *G. demeusei*, very wide traumatic axial canals in tangential line. Fig. 96. *G. ehie*, mainly aliform axial parenchyma. Fig. 97. *G. pellegriniana*, axial parenchyma scanty paratracheal to aliform, also narrow band at growth ring boundary. Scale bar = 200 μm for all (on Fig. 95).

pellegriniana, generally up to *c.* 40 cells high, up to 50 cells in *G. coleosperma* and 75 cells in *G. arnoldiana*. Rays homocellular, but some species with a very slight tendency towards heterocellular with one or two rows of larger, but still usually procumbent cells at ray margins. Prismatic crystals usually present in chambered axial parenchyma cells or fibres. A tangential line of large traumatic resin canals was found in *G. demeusii*. Specific gravity of *G. ehie* and *G. tessmannii* is 0.80 (Kribs, 1959; Gottwald & Schwab, 1978). Density of *G. arnoldiana* is 0.80–1.00 g cm⁻³ (Laming, 1966), of *G. coleosperma* is 0.67 g cm⁻³ (Kromhout, 1975).

Colophospermum mopane
(Figs 106–109)

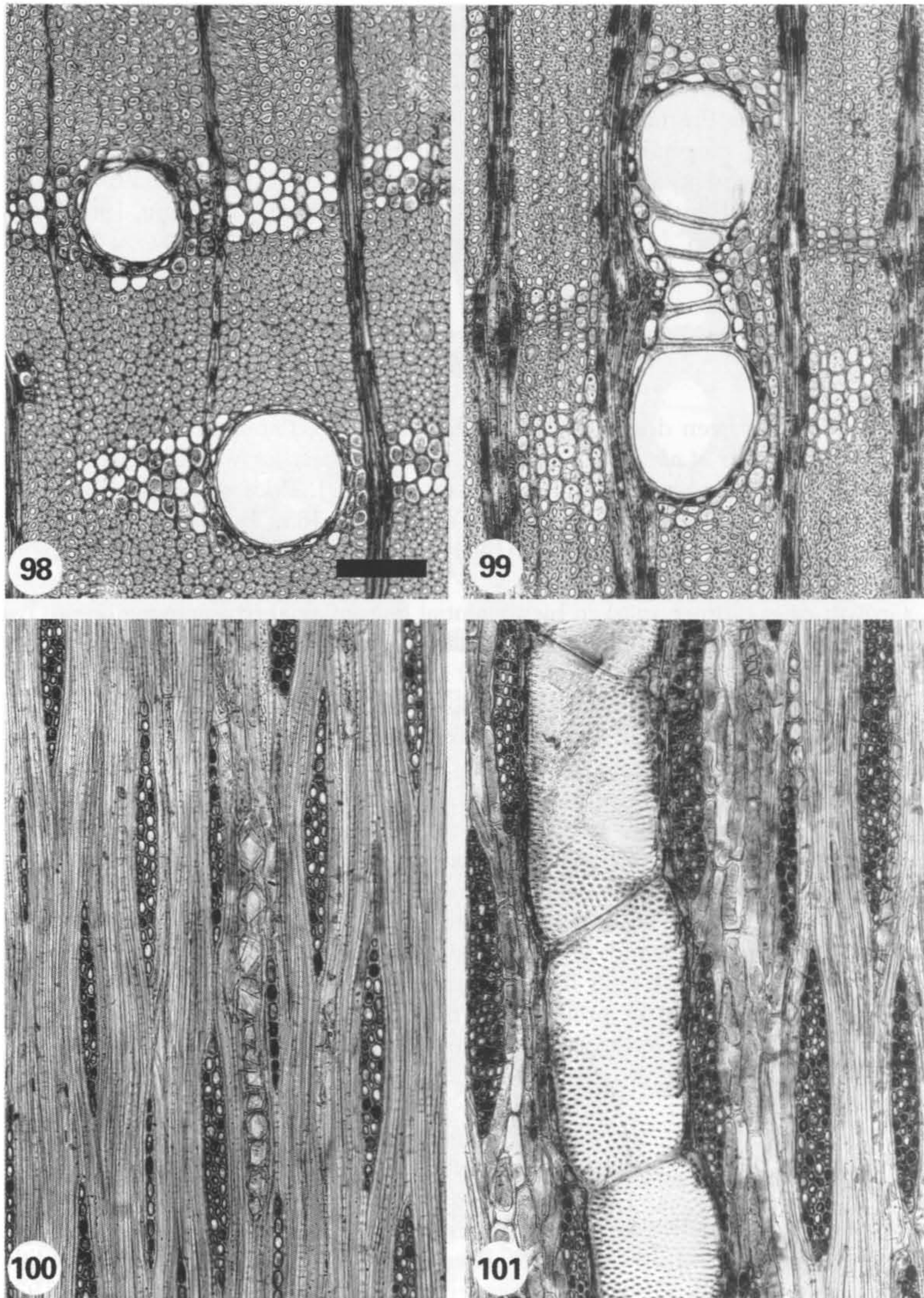
The wood has been described in Ferreirinha (1955), Laming (1966), Kromhout (1975) and Breteler *et al.* (1997). It is said to be the best fuelwood in Africa (Prior & Cutler, 1992). Six wood samples were examined: J. Prior s.n., Zimbabwe; Kw 7103, Rhodesia 12.1954; Kw 72242, Terry *et al.* 185, Botswana; Uw 23528, Dechamps *et al.* 1194, Angola; RBHw 14016, Pettinen s.n., Namibia; RBHw 15178, South Africa.

Growth rings distinct, marked by tangential lines of axial parenchyma one to two cells wide. Vessels diffuse, some solitary, usually in radial multiples of 2–4, occasionally to at least 12, sometimes in 2 immediately adjacent rows, or in irregular clusters of 2–6. Intervascular pits alternate, vested, round or oval to polygonal, sometimes elongated, often with coalescent apertures, 2–5 µm. Vessel-ray and vessel-parenchyma pits similar, but half-bordered. Yellow to dark-brown organic deposits common to abundant. Fibres thick-walled, with simple pits, more frequent on the radial than the tangential walls. Very few fibres gelatinous. Axial parenchyma scanty paratracheal, incompletely vasicentric, vasicentric-aliform (lozenge-type), some diffuse, and terminal tangential bands one to two cells wide. Crystalliferous chambered parenchyma strands with prismatic crystals abundant, strands often in contact with the rays. Strands 2–4 cells long. Rays 2(–3)-seriate, few uniseriate, the uniseriate rays up to 7–8 cells high, the multiseriate rays up to 16–27 cells high, homocellular, composed of procumbent cells. Yellow to brown organic deposits common to abundant. Density is 1.09 g cm⁻³ (Kromhout, 1975).

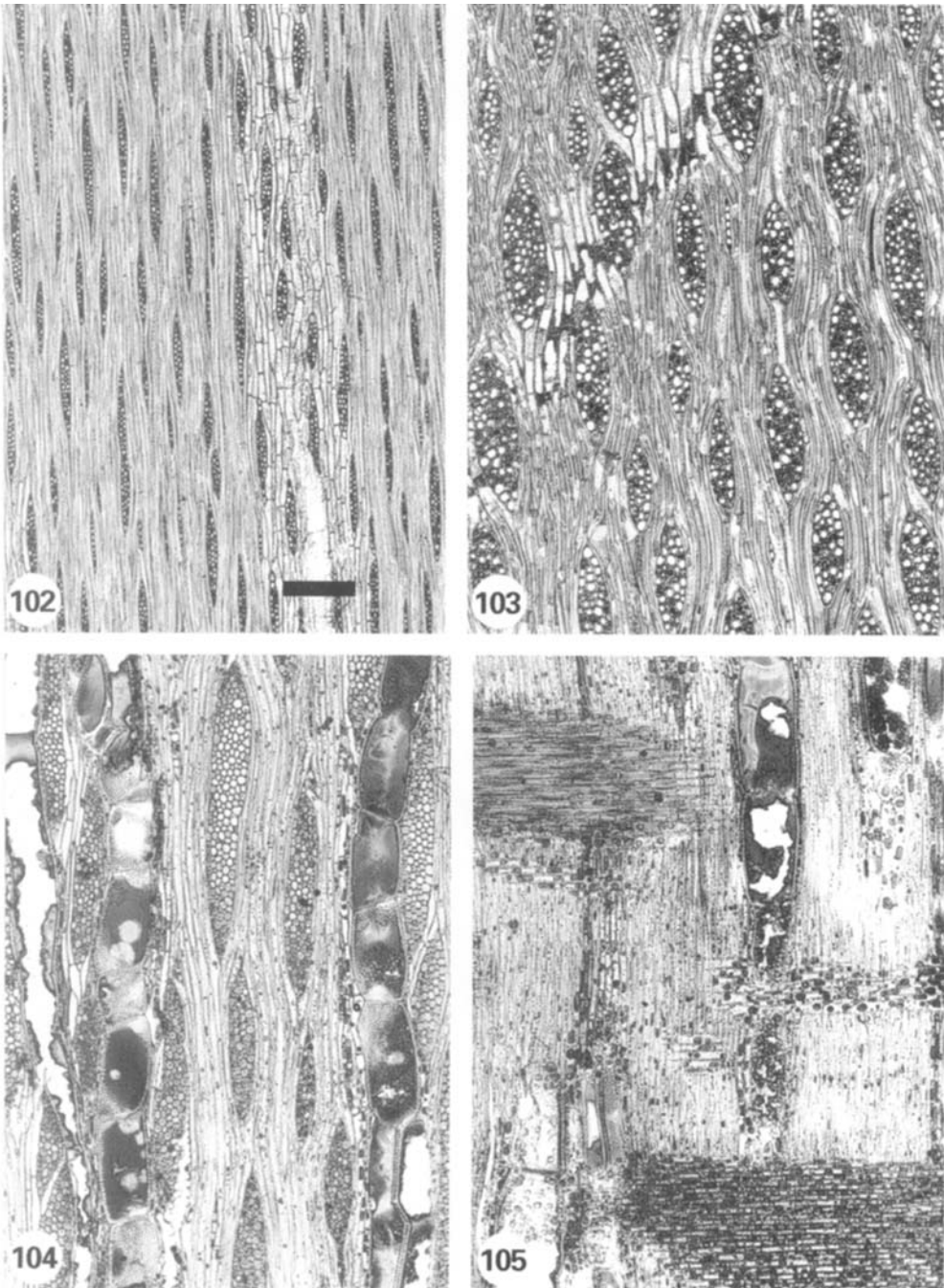
Hardwickia binata
(Figs 110–113)

The wood anatomy of this species has been described by Pearson & Brown (1932), Jutte in Knaap Van Meeuwen (1970), Ramesh Rao & Purkayastha (1972), Lalitha & Prakash (1980), Ilic (1991) and Breteler *et al.* (1997). Pearson & Brown (1932) refer to Kanehira (1924) reporting horizontal (i.e. radial) gum canals in the wood. Three wood samples were examined here: Kw 7306, Royal Botanic Gardens, Calcutta, Anderson 1868; Kw 21523, Madhya Pradesh, Gamble 143; Kw 21524, Gamble 4020, Coimbatore.

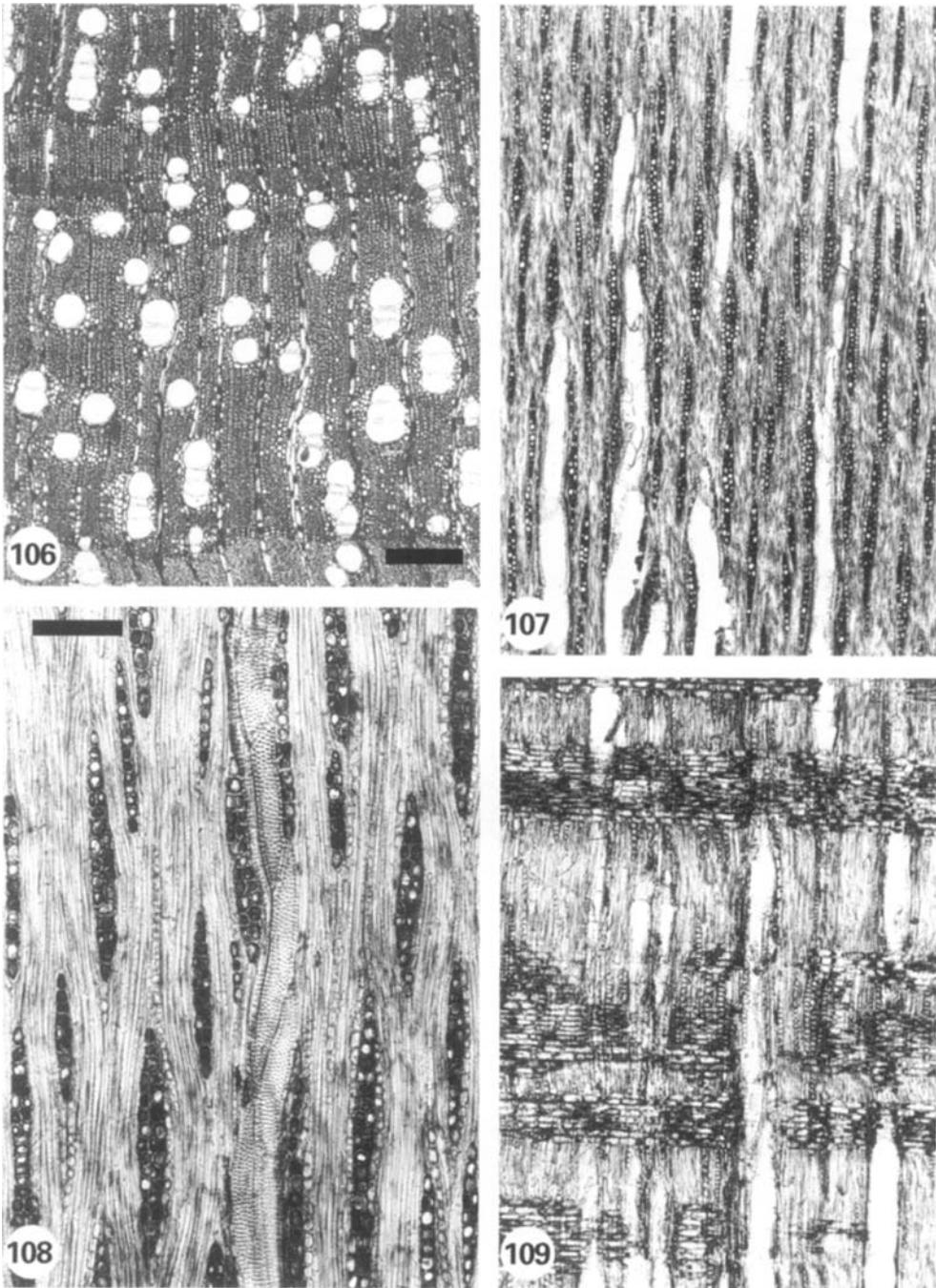
Growth rings distinct, marked by tangential lines of axial parenchyma one to several cells wide. Vessels diffuse, solitary and in radial multiples of 2–3, occasionally up to 6. Intervascular pits alternate, vested, round to oval, occasionally with



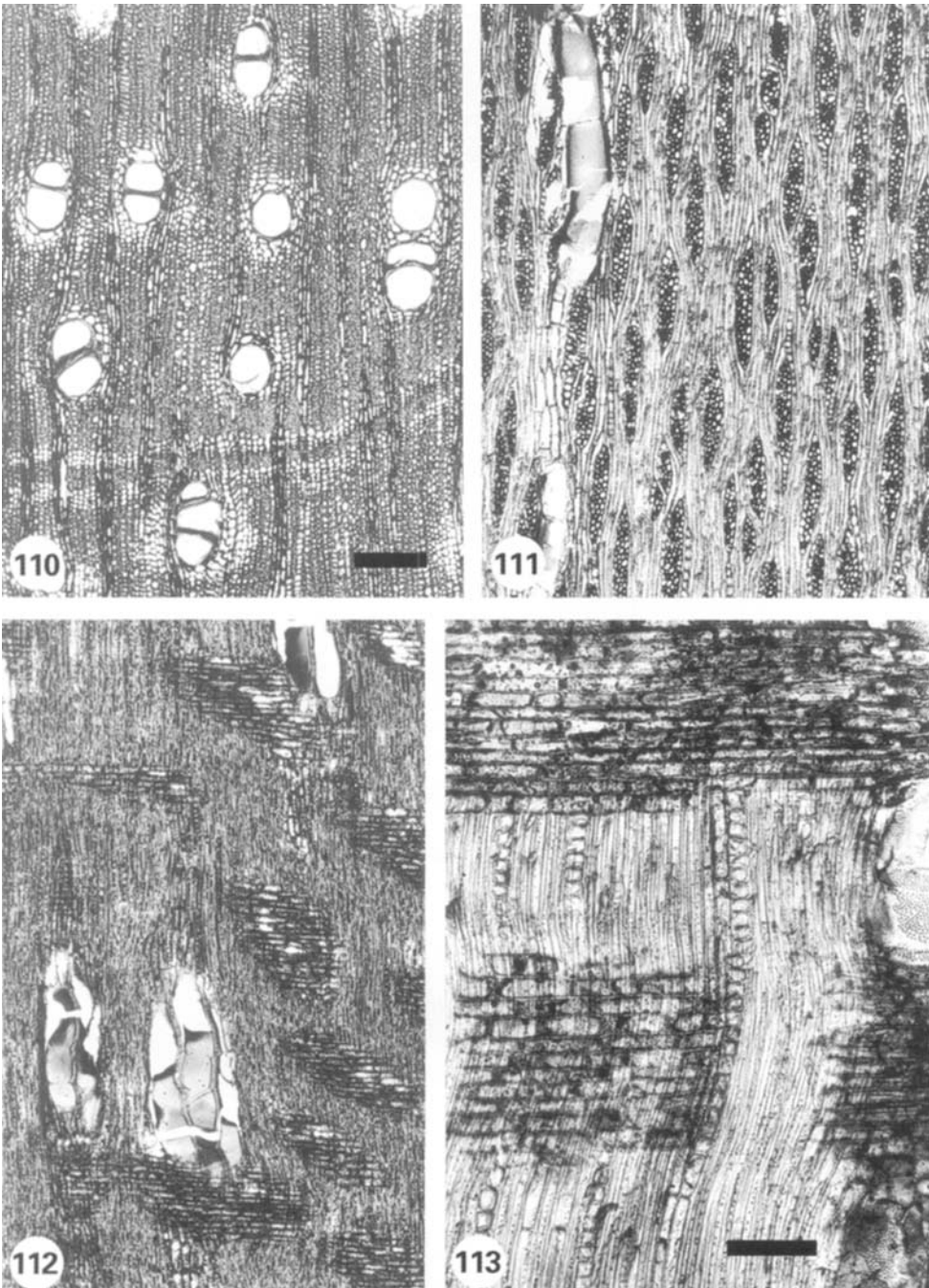
Figures 98–101. *Guibourtia*. Fig. 98. *G. demeusei* TS, aliform parenchyma, gelatinous fibres predominate above the top vessel, normal fibres below it. Fig. 99. *G. ehie* TS, scanty paratracheal and aliform parenchyma, fibres all normal. Fig. 100. *G. demeusei* TLS, fairly short, narrow, irregularly storied rays, prismatic crystals in chambered fibres. Fig. 101. *G. ehie* TLS, intervessel pitting, wider rays than Fig. 100. Scale bar = 100 μ m for all (on Fig. 98).



Figures 102–105. *Guibourtia*. Figs 102–104 TLS, 105 RLS. Fig. 102. *G. demusei* TLS, rays fairly short and narrow, irregularly storied. Fig. 103. *G. pellegriniana* TLS, rays short and wide, irregularly storied. Fig. 104. *G. coleosperma* TLS, intervessel pitting fine, rays fairly tall and wide. Fig. 105. *G. coleosperma* RLS, rays homocellular. Scale bar = 200 μ m for all (on Fig. 102).



Figures 106–109. *Colophospermum mopane*. Fig. 106. TS, axial parenchyma scanty paratracheal and in very narrow tangential lines. Scale bar = 200 μm . Figs 107, 108. TLS, rays narrow and fairly short, fine intervessel pitting and crystals in chambered axial parenchyma. Scale for Fig. 107 as per Fig. 106, scale bar for Fig. 108 = 100 μm . Fig. 109. RLS, rays homocellular. Scale as per Fig. 106.



Figures 110–113. *Hardwickia binata*. Fig. 110. TS, axial parenchyma scanty paratracheal and irregularly vasicentric, also in narrow tangential lines. Scale bar = 200 μm . Fig. 111. Rays fairly short. Scale as per Fig. 110. Fig. 112. RLS, rays homocellular. Scale as per Fig. 110. Fig. 113. RLS, rays homocellular, fine intervessel pitting, crystals in chambered axial parenchyma. Scale bar = 100 μm .

coalescent apertures, 2–5 μm . Reddish-brown deposits common. Fibres thick-walled, with simple pits, more frequent on the radial than the tangential walls. Fibres often gelatinous, but not found in Kw7306. Axial parenchyma scanty paratracheal and incompletely vasicentric, occasionally forming lateral wings (i.e. winged aliform), also diffuse and in terminal tangential lines, in Kw 21524 many tangential bands up to 10 cells wide. Crystalliferous chambered parenchyma strands with prismatic crystals abundant, these strands usually bordering the rays. Strands 2–4 cells long. Rays 3–4-seriate, up to 22 cells high, homocellular, composed of procumbent cells. Brown organic deposits common. Probably the hardest and heaviest Indian wood, with a specific gravity of *c.* 1.08 (Pearson & Brown, 1932; Ramesh Rao & Purkayastha, 1972).

DISCUSSION

Pollen morphology

Within the *Crudia* group, *Prioria*, *Oxystigma*, *Gossweilerodendron*, *Kingiodendron*, *Guibourtia*, *Stemonocoleus*, *Neoapaloxylon* and *Bathiaea* have perforate, tricolporate pollen with little variation in surface ornamentation. In contrast, *Crudia* pollen is tricolporate and coarsely striate, that of *Augouardia* is tricolporate and reticulate, and *Hardwickia* and *Colophospermum* have pantoporate pollen with distinctive ornamentation (Breteler *et al.*, 1997; this paper). Graham & Barker (1981) stated that “the perforate tectum is the most common structural feature of angiosperm pollen, and is especially widespread throughout the Leguminosae”. More specifically, Ferguson (1987) added that “tricolporate perforate pollen is widespread throughout the Caesalpinioideae”. Lack of derived pollen morphological characters does not automatically imply a close relationship with other taxa with non-specialized, tricolporate, perforate types of pollen. In the tribe Detarieae *Cynometra*, *Umtiza*, *Eurypetalum*, *Leucostegane*, *Hymenaea*, *Peltogyne*, *Goniorrhachis*, *Gilletiodendron* and *Phyllocarpus* all have unspecialized pollen (Graham & Barker, 1981; Ferguson, 1987; Banks, unpublished), and its occurrence does not correspond with taxonomic groupings.

The species with perforate pollen have a wide range of surface ornamentation, which is difficult to use for taxonomic or systematic purposes in this group. However, wall and aperture structure can be used to characterize some of these taxa. Exine stratification in *Oxystigma*, *Kingiodendron*, *Guibourtia*, *Neoapaloxylon* and *Bathiaea* is of the generalized caesalpinoid type described by Ferguson (1987); however, *Gossweilerodendron*, *Prioria* and *Stemonocoleus* differ by having a layer of fine granules in the interstitium just below the tectum (Table 3). Ferguson (1987) thought this character to be randomly scattered throughout the Caesalpinioideae, for example in *Campsiandra* (Caesalpinieae), *Cercis* (Cercideae) and *Martiodendron* (Cassieae), but in the absence of data on all caesalpinoid genera we cannot confirm homoplasy. The significance and function of these granules is unknown, although a granular infratectum is suggested to resist compressive forces caused by certain types of harmomegathic movements better (Crane, 1986). The ontogeny of exines with and without this structure would be an interesting topic for further study, to ascertain whether it is developmentally similar to layers seen in the infratectum of other taxa such as *Eperua* and *Goniorrhachis* (Banks & Rico, 1999). Exine stratification provides important

TABLE 3. Summary of observations on pollen morphology and wood anatomy

Genus	Many pores	Tricolporate	Granular layer in wall	Aperture margins prominent	Striate/ reticulate/ perforate	Endexine thicker under aperture margins	Supratracheal structures present	Normal axial canals diffuse/ tangential	Rays storied	Banded parenchyma	Axial parenchyma in distinct pattern
<i>Crudia</i> Benth. & Hook.	-	+	-	-	S	+	+	-	+	+	+
<i>Oxydigma</i> Harms	-	+	-	-	P	+	-	-	-	-	-
<i>Kingiodendron</i> Harms	-	+	-	-	P	+	-	+	-	+	+
<i>Gossweilendendron</i> Harms	-	+	+	-	P	+	-	+	-	-	-
<i>Bathiaea</i> Drake	-	+	-	-	P	+	-	-	-	-	-
<i>Neopaloxylon</i> S. Rauschert	-	+	-	-	P	+	-	+	-	+	+
<i>Prioria</i> Benth. & Hook.	-	+	+	-	P	+	-	+	-	+	+
<i>Anguaratia</i> Pellegr.	-	+	-	-	R	+	-	-	-	-	+
<i>Stemonocoleus</i> Harms	-	+	+	-	P(-S)	+	-	-	?	-	+
<i>Hantwickia</i> Roxb.	+	+	-	-	R	-	-	-	-	-	+
<i>Guthourtia</i> Benn.	-	+	-	+	P	+	-	-	-	-	+
<i>Colaphospermum</i> Kirk ex Benth.	+	-	-	-	R	-	-	-	-	-	+

characters in the tribe Detarieae. Exine sculpturing may be correlated more with pollination syndromes than phylogeny (Guinet & Ferguson, 1989), and similar surface ornamentation can overlie different ultrastructure. For example, striate ornamentation is common throughout the Amherstieae/Detarieae (*sensu* Cowan & Polhill, 1981a,b), but the supratectal striae seen in *Crudia* are not seen in any other Detarieae, although they are common in pollen of Amherstieae.

Stemonocoleus and *Guibourtia* differ from all other taxa in the *Crudia* group by having prominent aperture margins (Table 3). In *Guibourtia*, where this phenomenon is more pronounced, TEM has revealed a fastigium in sections taken from the aperture margins adjacent to the endoapertures. The aperture margins are prominent, and in dehydrated grains the apertures do not collapse inwards. Instead, the reduction in volume is accounted for by the mesocolpial regions caving inwards (compare Figure 44 with 47). This may have a profound effect on the relative compressive and tensile stresses that the exine wall is subjected to during variations in levels of hydration (Crane, 1986). Further investigation using fresh pollen would be desirable to study the harmomegathic mechanisms (Wodehouse, 1935) involved (Blackmore & Barnes, 1986). *Stemonocoleus* and *Guibourtia* differ in their thickness of endexine, foot layer, infratectum and density of columellae, relative to each other and to all other taxa in the *Crudia* group.

Augouardia has coarsely reticulate ornamentation which is quite different from any other taxa in the *Crudia* group. In Amherstieae and Detarieae, similar ornamentation occurs in *Afzelia*, *Intsia*, *Baikiaea*, *Brachystegia*, *Brodrugesia*, *Paramacrolobium* and some species of *Eperua* (Banks & Rico, 1999), and is widespread in Caesalpinieae. Exine stratification of *Augouardia* reveals an acetolysis-resistant layer in the infratectum similar to that in *Eperua* and *Goniorrhachis* (Banks & Rico, 1999). Whether this structure is related to the granular layer seen in *Gossweilerodendron*, *Prioria* and *Stemonocoleus* requires further investigation.

Hardwickia and *Colophospermum* have unique pollen found nowhere else in the Detarieae (Table 3), and are similar to each other in both surface and ultrastructural features. They are the only known wind pollinated taxa in the Caesalpinioideae (Graham *et al.*, 1980; Breteler *et al.*, 1997). Reduction of the apertural area to pores is common in wind pollinated taxa. This reduces dehydration, which is most extreme in wind dispersal (Crane, 1986; Linder, 1998). In Leguminosae, pantoporate pollen occurs only in one or two species of *Bauhinia* and in two genera of Papilionoideae (Breteler *et al.*, 1997).

Wood anatomy

The wood anatomy of the *Crudia* group is heterogeneous (Table 3, Figs 52–108). Four genera (*Prioria*, *Oxystigma*, *Gossweilerodendron* and *Kingiodendron*) are uniform, and all have diffusely arranged axial canals. Baretta-Kuipers (1981) stated that *Daniella*, which also has diffusely arranged axial canals, could belong to this group, but differs in having storied rays. The axial canals are small in *Gossweilerodendron*, *Oxystigma* and *Kingiodendron* (see Baretta-Kuipers, plate II), but much larger in *Prioria*. *Bathiaea* has tangential bands of small axial canals and slightly wider rays, but is otherwise similar to the above genera. Most genera of the *Crudia* group lack normal axial canals (Table 3), although one specimen of *Guibourtia* has traumatic axial canals. The similarity of wood features suggests that *Prioria*, *Oxystigma*, *Gossweilerodendron* and

Kingiodendron are closely related, but no firm conclusion can be reached on whether the genera should be combined or remain separate on the basis of wood anatomy or pollen morphology without testing in a broader context.

General comments

A preliminary molecular analysis of the Caesalpinioideae based on cp *trnL* intron sequences (Bruneau *et al.*, pers comm.) has shown that *Gossweilerodendron*, *Kingiodendron*, *Colophospermum* and *Oxystigma* group closely together (*Prioria*, *Bathiaea*, *Hardwickia* and *Neopaloxylon* were not in the analysis), *Guibourtia* is in a separate clade with *Augouardia*, *Stemonocoleus* and several other genera with unresolved relationships, and *Crudia* has unresolved relationships with a large number of genera in a third clade. These observations, taken with ours, strongly suggest that the *Crudia* group is not monophyletic. Both the wood and pollen of *Hardwickia* and *Colophospermum* are particularly similar, although only the latter was included by Bruneau *et al.* The close relationship of these two genera is discussed in Breteler *et al.* (1997), who combined them, and Smith *et al.* (1998) and Léonard (1999) who keep them separate.

CONCLUSIONS

Our observations on pollen morphology and wood anatomy indicate that the *Crudia* group is not a natural one, a conclusion supported by the work of Anne Bruneau *et al.* (pers comm.). The inclusion of our data in analyses of a wider range of taxa and data sets should help to improve phylogenetic resolution in the Detarieae/Amherstieae.

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