

Comparative Wood Anatomy of the Primuloid Clade (Ericales s.l.)

FREDERIC LENS,^{1,3} STEVEN JANSEN,^{2,1} PIETER CARIS,¹ LIESBET SERLET,¹ and ERIK SMETS¹

¹Laboratory of Plant Systematics, Institute of Botany and Microbiology, Katholieke Universiteit Leuven, Kasteelpark Arenberg 31, B-3001 Leuven, Belgium

²Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS, U.K.

³Author for Correspondence (frederic.lens@bio.kuleuven.ac.be)

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ABSTRACT. The wood structure of 78 species from 27 genera representing the woody primuloids (Maesaceae, Myrsinaceae, and Theophrastaceae) was investigated using light microscopy (LM) and scanning electron microscopy (SEM). Results indicated that the ray structure, the nature of mineral inclusions, and the occurrence of breakdown areas in rays can be used to separate the three primuloid families from each other. Within Ericales, the presence of exclusively multiseriate rays is synapomorphic for Myrsinaceae and Theophrastaceae, and the occurrence of breakdown areas in rays is synapomorphic for Myrsinaceae. Within Myrsinaceae, the wood structure of the mangrove genus *Aegiceras* differs because it has short vessel elements that are storied, non-septate fibers, a combination of low uni- and multiseriate rays, and multiseriate rays with exclusively procumbent body ray cells. The aberrant wood anatomy of *Coris* and *Lysimachia* can be explained by their secondary woodiness. Within Theophrastaceae, *Clavija* and *Theophrasta* can be distinguished from *Bonellia*, *Jacquinia*, and *Deherainia*. The recent division of *Jacquinia* s.l. into *Jacquinia* s.s. and *Bonellia* is supported by a difference in mineral inclusions.

The primuloid clade is one of the few groups within the newly circumscribed Ericales that is well supported based on molecular sequence data (Anderberg et al. 2002; Bremer et al. 2002). The clade comprises five families, Maesaceae, Myrsinaceae, Primulaceae, Samolaceae, and Theophrastaceae, and about 65 genera and 2600 species (Kubitzki 2004). More than half of the primuloid representatives are woody, mostly small to medium-sized trees or shrubs, and sometimes lianas. The genus *Samolus* L. (Samolaceae), all Primulaceae, and a few Myrsinaceae taxa, representing ca. 20 genera and 1100 species, are herbs and therefore omitted from this study. The distribution of woody primuloids is mainly tropical: Myrsinaceae are pantropical with several taxa extending to tropical montane habitats, Theophrastaceae are restricted to the neotropics, and Maesaceae are concentrated in the palaeotropics. Primulaceae, on the other hand, grow in the temperate regions of the Northern Hemisphere, and Samolaceae have their main distribution in saline habitats of the Southern Hemisphere (Källersjö et al. 2000).

All representatives of the primuloid clade have long been placed in the former Primulales (Pax 1889; Mez 1902, 1903), which were characterized by a set of floral characteristics: (1) sympetalous flowers with functional stamens as many as and opposite to the corolla lobes, (2) a compound, mainly hypogynous ovary with one style, and (3) few to many tenuinucellate, usually anatropous, bitegmic ovules set on a free-central to basal placenta (Cronquist 1988). Family concepts within the primuloid clade have changed considerably during the last 10 years. Based on molecular and morphological data, the genus *Maesa* Forssk. was removed from Myrsinaceae and elevated to family level (Anderberg and Ståhl 1995; Anderberg et al. 1998, 2000; Caris et al. 2000; Ståhl and Anderberg 2004a). Now, Maesaceae are

considered sister to all other primuloids (Källersjö et al. 2000). In addition, Källersjö et al. (2000) and Anderberg et al. (2001) proposed to place the former Primulaceae genera *Ardisiandra* Hook. f., *Anagallis* L., *Asterolinon* Hoffmannsegg & Link, *Coris* L., *Cyclamen* L., *Glaux* L., *Lysimachia* L., *Pelletiera* A. St.-Hil., *Stimpsonia* C. Wright ex A. Gray, and *Trientalis* L. within the sister family Myrsinaceae. Furthermore, another genus of Primulaceae, *Samolus*, was placed as sister to the remaining Theophrastaceae by the same authors. The monophyly of the family Theophrastaceae excluding *Samolus* is morphologically well supported (Ståhl 2004a, b). Also floral ontogenetic work supported the family level for *Samolus* as sister to Theophrastaceae (Caris and Smets 2004). These two families in turn are sister to the Primulaceae-Myrsinaceae clade (Källersjö et al. 2000).

Besides these renewed family concepts, generic realignments within primuloid families were proposed. For instance, the monophyly of various Myrsinaceae genera is still a matter of dispute (Ståhl and Anderberg 2004b), and recent molecular sequence data from Theophrastaceae suggest that the orange-red flowered *Jacquinia* L. species together with *Jacquinia paludicola* Standl. and *J. longifolia* Standl. should be recognized as a separate genus *Bonellia* Colla in order to maintain the monophyly of the morphologically well supported genera *Deherainia* Decaisne and *Votschia* Ståhl (Källersjö and Ståhl 2003; Ståhl and Källersjö 2004).

The wood anatomy of primuloid families is poorly known. The most detailed overview was presented by Metcalfe and Chalk (1950), based on nine Myrsinaceae genera, four Theophrastaceae genera, and *Maesa*. Other noteworthy studies that included a restricted number of primuloids were presented by Moll and Janssonius (1926), Williams (1936), Détienne et al. (1982), Suzuki

and Noshiro (1988), Ogata and Kalat (1997), and Sosef et al. (1998).

This work aims to present a detailed wood anatomical overview of Maesaceae, Myrsinaceae, and Theophrastaceae, using light microscopy (LM) and scanning electron microscopy (SEM). The anatomical variation observed will be compared with the recent familial and generic realignments within the primuloid clade, taking ecological and physiological aspects into account. In addition, some selected wood features will be plotted on a simplified molecular tree to trace evolutionary patterns. This study also addresses the possibilities of secondary woodiness within primuloids, since Anderberg et al. (2001) suggested that the ancestor of the Samolaceae-Theophrastaceae-Primulaceae-Myrsinaceae clade could be herbaceous.

MATERIALS AND METHODS

In total, 92 wood specimens representing 78 species and 27 genera were investigated using LM and SEM (Appendix 1). Twenty one genera of Myrsinaceae sensu Ståhl and Anderberg (2004b), five genera of Theophrastaceae (including *Bonellia*) and the genus *Maesa* were included.

Wood sections of about 25 μm thick were cut using a sledge microtome. After bleaching, staining and dehydrating, the tissues were mounted in euparal. Preparations for macerations and SEM are according to Jansen et al. (1998). The wood anatomical terminology follows the "IAWA list of microscopic features for hardwood identification" (IAWA Committee 1989), except for the term 'breakdown areas in rays' which is illustrated by *Aegiceras* Gaertn. in the CSIRO family key for hardwood identification (Ilic 1987). According to Webber (1938), these structures are 'intercellular cavities possibly of normal occurrence' and were called 'gum cysts' by Panshin (1932) or 'schizogenous secretory cavities' by Metcalfe and Chalk (1950). Breakdown areas in rays often contain orange to dark brown substances including neutral lipids and hydrobenzoquinones, a typical compound that is observed in five Myrsinaceae genera and in *Maesa*. Hydrobenzoquinones are also present in epithelial cells surrounding secretory cavities in both vegetative and reproductive tissues, and in groups of cells in the placental epidermis, and possibly function as a defense mechanism against insects (Otegui et al. 1997).

Wood features were optimized on trees using the program MacClade 4.04 (Maddison and Maddison 2002).

RESULTS

The material studied is presented according to the classification of Källersjö et al. (2000). For each genus examined the number of species studied is provided before the slash mark and the total number of species in the genus follows the slash mark. Numbers between brackets are extreme values. A summary of the results is presented in Table 1.

Maesaceae. Taxa studied: *Maesa* 5/100 (Fig. 1). Growth ring boundaries absent or distinct. Diffuse-porous. Vessels usually solitary and in short radial multiples of 2–4 (Figs. 1A–B; up to 8 cells in Uw 15537), or exceptionally in vessel clusters of 3–5 cells; vessel outline mostly angular. Vessel perforation plates simple (Fig. 1C), but few scalariform perforations with 5–7

bars in *M. lanceolata*. Intervessel pits alternate (Fig. 1D), 4–6 μm in size, non-vestured. Vessel-ray pits similar to intervessel pits in shape and size, sometimes having scalariform pits with distinct borders in *M. indica*, *M. ramentacea*, and *M. schweinfurthii*; vessel ray-pits mainly scalariform with strongly reduced to nearly simple pits in *M. lanceolata* (Fig. 1H) and *M. macrothyrsa*, 10–30 μm in size. Helical sculpturing indistinctly present throughout body of vessel elements, or restricted to tails of vessel elements. Tangential diameter of vessels (30–)40–100(–120) μm , (18–)20–90(–101) vessels per mm^2 , vessel elements (330–)460–850(–1070) μm long. Tracheids absent. Fibers septate, thin- or thin- to thick-walled, (520–)870–1270(–1560) μm long, with simple to minutely bordered pits concentrated in radial walls, pit borders 2–3 μm in diameter. Axial parenchyma scanty paratracheal (Figs. 1A, B); 2–4 cells per parenchyma strand. Uniseriate rays always present (Figs. 1E, F), (160–)330–1430(–2100) μm high, consisting of upright cells, 0(–2)–6 rays per mm. Multiseriate rays 2–5(–8)–seriate, (200–)470–2590(–7000) μm (and even more) high, 0(–4)–6 rays per mm, consisting of predominantly procumbent body ray cells (Fig. 1G) or a mixture of procumbent, square, and upright body ray cells, and 1–4 upright rows of marginal ray cells; sheath cells present. Breakdown areas in rays absent. Gummy deposits in ray cells. Very few prismatic crystals in procumbent and upright ray cells of *M. indica*. Pith cells homogeneous.

Myrsinaceae. Taxa studied: *Aegiceras* 1/2, *Afrardisia* Mez 1/16, *Ardisia* Sw. 4/250, *Badula* Juss. 1/17, *Coris* 1/2, *Ctenardisia* Ducke 1/2, *Cybianthus* Mart. 7/150, *Discocalyx* (A. DC.) Mez 2/50, *Embelia* Burm. f. 4/130, *Geissanthus* Hook. f. 2/30, *Grammadenia* Benth. 2/7, *Heberdenia* Banks ex A. DC. 1/1, *Lysimachia* 2/150, *Myrsine* L. 3/4, *Oncostemum* A. Juss. 4/100, *Parathesis* (A. DC.) Hook. f. 6/75, *Rapanea* Aubl. 6/300, *Stylogyne* A. DC. 4/60, *Synardisia* (Mez) Lundell 1/1, *Tapeinosperma* Hook. f. 1/4, *Wallenia* Sw. 2/20 (Figs. 2–6). Growth ring boundaries generally indistinct, but distinct in *Coris monspeliensis* (Figs. 6A, B), *Grammadenia parasitica* (Fig. 2B), and in *Oncostemum venulosum*. Diffuse-porous. Vessels mostly solitary (Fig. 2A) and in short radial multiples of 2–4 (Figs. 2B–E, 6B–D; of up to 8 vessels in *Ardisia cauliflora*), few vessel clusters of 3–9 cells occasionally observed in most genera (Figs. 2F, H, 3A), exceptionally short tangential vessel multiples in *Discocalyx* and *Embelia*; vessel outline angular. Vessel perforation plates mostly simple (Figs. 3E, F, 6G, H), some scalariform perforations with 2–5 bars observed in *Afrardisia staudti*, *Ctenardisia stenobotrys*, *Discocalyx insignis*, *Stylogyne venezuelana*, and *Tapeinosperma nectandroides*; vessel elements storied in *Aegiceras* (Fig. 4A). Intervessel pits alternate (Figs. 3G, H), 3–6 μm in size, non-vestured. Vessel-ray pits usually similar to intervessel pitting in shape and size, but mainly scalariform

TABLE 1. Survey of wood anatomical features of the species studied. Numbers between hyphens are mean values. For specimens from the same species, numbers after the species name refer to the order of the specimen as followed in the species list. *Specimens with juvenile wood. BA = Breakdown areas in rays, DENS = Density of vessels (per mm²), DIAM = Tangential diameter of vessels (µm), DM = Density of multiseriate rays (per mm), DU = Density of uniseriate rays (per mm), HMR = Height of multiseriate rays (µm), HUR = Height of uniseriate rays (µm), LFL = Length of libriform fibers (µm), MW = Multiseriate ray width (no. cells), PC = Prismatic crystals, SF = Septate fibers, SB = Silica bodies, SF = Septate fibers, UR = Uniseriate rays, VEL = Length of vessel elements (µm); + = present, - = absent, ± = sometimes present.

Species studied	Vessels			Fibers			Rays							Mineral inclusions		
	DIAM	DENS	VEL	LFL	SF	UR	MW	HUR	HMR	DU	DM	BA	PC	SB		
<i>Agaveceres majus</i> *	10-22-35	256-306-352	150-207-240	275-364-460	-	+	2	75-127-250	100-188-250	2-5	0-1	+	+	-		
<i>A. majus</i> ²	30-36-50	38-59-66	160-221-270	360-452-550	-	+	2-3	100-156-250	250-342-430	0-2	2-5	+	-	-		
<i>Afrardisia strudtit</i> *	20-27-40	70-88-114	380-519-670	450-617-860	+	+	2-3	-	500-1280-2100	-	1-2	+	-	-		
<i>Ardisia cauliflora</i>	40-51-60	22-26-30	300-485-690	600-958-1220	+	-	5-6	-	>8000	-	2-3	+	-	-		
<i>A. copelandii</i>	45-78-125	7-10-15	520-683-850	670-1185-1540	+	-	8-10	-	2400-3080-4300	-	1-3	+	-	-		
<i>A. mangillo</i>	50-70-90	24-28-33	300-430-650	490-750-830	+	-	3-4	-	2500-5333-6200	-	2-3	+	+	-		
<i>A. obtusifolia</i> *	15-20-35	84-99-118	300-423-500	570-697-840	+	-	4-9	-	1900->9000	-	1-3	+	+	-		
<i>Badula barthisia</i>	30-48-65	18-29-56	390-543-660	680-799-920	+	-	10-17	-	1600-2080-2600	-	1-2	+	+	+		
<i>Bonellia frutescens</i> ¹	40-54-75	18-29-37	170-229-269	420-475-560	+	-	17-22	-	1600-2511-4200	-	0-2	+	+	+		
<i>B. frutescens</i> ²	38-53-70	13-27-41	170-231-320	350-392-480	+	-	9-22	-	1200-1963-2900	-	0-2	+	+	+		
<i>B. frutescens</i> ³	35-50-68	26-35-40	170-220-320	380-763-540	+	-	6-12	-	>4000	-	1-2	+	+	+		
<i>B. macrocarpa</i> *	30-42-60	30-118-140	150-172-260	175-248-290	-	-	15-25	-	2100-3920-5500	-	1	-	-	+		
<i>B. cf. macrocarpa</i>	35-60-80	14-34-44	160-202-300	350-450-520	-	-	9-12	-	1600-2686-3200	-	2	-	-	+		
<i>B. stueferi</i>	20-32-50	44-52-58	180-198-240	340-408-450	-	-	8-16	-	1500-2278-3700	-	1-2	+	+	-		
<i>B. umbellata</i>	20-33-45	39-46-64	120-213-320	400-480-550	-	-	9-15	-	1900-3208-6400	-	2-3	-	-	-		
<i>B. umbellata</i>	30-41-60	28-35-46	150-232-280	320-398-470	-	-	6-10	-	1400-3327-5500	-	1-3	-	-	+		
<i>Clavia lancifolia</i> ¹	15-21-30	42-64-81	190-327-480	310-526-650	+	-	5-12	-	1350-3275-6700	-	1-3	-	+	+		
<i>C. lancifolia</i> ²	12-19-25	63-75-96	320-436-520	450-641-790	+	-	11-14	-	1900-3500-5000	-	1-2	-	+	+		
<i>C. longifolia</i>	25-37-55	32-43-60	240-385-550	620-785-920	+	-	2-9	-	500-2589-5000	-	1-2	-	-	+		
<i>C. nutans</i> *	20-29-35	94-114-128	210-401-530	470-621-750	+	-	6-8	-	1600-2350-4500	-	1-3	-	-	+		
<i>C. nutans</i> ²	15-27-40	50-69-82	200-310-410	500-577-700	+	-	3-14	-	1700-3456-7900	-	1-3	-	-	+		
<i>C. proera</i>	25-31-40	92-118-154	220-337-470	470-550-650	+	-	7-10	-	3100-4385-6000	-	1-3	-	-	+		
<i>C. tarapotana</i>	25-30-40	56-71-88	320-412-540	370-637-800	+	-	10-14	-	3100->10000	-	1-3	-	+	+		
<i>C. umbrosa</i> ¹	25-37-45	62-71-82	150-267-350	350-416-520	+	-	6-11	-	3500->12000	-	1-3	-	+	+		
<i>C. umbrosa</i> ²	30-37-45	62-73-84	300-376-440	520-623-700	+	-	6-12	-	750-2345-3900	-	2-3	-	+	+		
<i>C. weberbaueri</i> *	12-16-25	84-103-130	240-359-510	490-585-650	+	-	8-13	-	2100-3513-4900	-	2-3	-	+	+		
<i>C. weberbaueri</i> ²	20-27-35	39-65-90	240-414-620	530-664-810	+	-	-	-	-	-	-	-	-	-		
<i>Coris nonspatiensis</i>	10-13-19	90-114-145	60-158-330	180-278-450	-	-	4-6	-	1800-5800-8700	-	2-3	-	+	-		
<i>Ctenardisia stenobotrys</i>	38-45-50	34-47-57	580-745-880	700-990-1120	+	-	4-8	-	>6000	-	1-2	-	-	-		
<i>Cybianthus conperuvianus</i>	45-64-75	26-32-44	500-682-900	850-1067-1200	+	-	4-9	-	1500-3617-5300	-	1-2	+	+	-		
<i>C. magnifolia</i>	25-51-80	22-38-73	290-330-370	550-667-700	+	-	2-4	-	1300-2422-3500	-	2-3	-	-	-		
<i>C. multiflorus</i>	25-35-45	20-34-52	370-487-620	590-728-930	+	-	3-5	-	1900-2944-4500	-	2-3	-	-	-		
<i>C. peruvianus</i>	50-63-80	16-21-24	380-604-780	800-1148-1300	+	-	2-3	-	500-2239-4500	-	1-3	-	+	-		
<i>C. priurei</i>	20-29-40	33-41-52	650-838-1160	920-1198-1520	+	-	3-7	-	4050-6163-8900	-	1-2	-	+	-		
<i>C. psychotriaefolius</i>	30-50-70	32-42-68	310-465-580	560-730-900	+	-	5-11	-	1600->7000	-	2-3	-	-	-		
<i>Deherania smaragdina</i>	25-33-45	70-89-105	180-293-490	340-396-450	-	-	2-4	-	1500-4030-8200	-	2-3	-	-	-		
<i>Discolalyx megacarpa</i>	20-27-40	29-36-44	380-642-920	630-914-1080	+	-	-	-	-	-	-	+	-	-		

TABLE 1. Continued.

Species studied	Vessels			Fibers			Rays					Mineral inclusions		
	DIAM	DENS	VEL	LFL	SF	UR	MW	HUR	HMR	DU	DM	BA	PC	SB
<i>D. insignis</i>	25-38-50	38-46-62	305-411-550	510-749-900	+	-	2-4	-	1500-4229-8000	-	3-4	+	+	-
<i>Embelia kilimandscharica</i>	80-146-200	10-16-22	320-532-700	560-750-930	+	-	12-38	-	>10000	-	1-2	+	+	-
<i>E. multiflora</i>	43-66-100	29-35-50	380-420-495	445-619-860	+	-	3-4	-	>4000	-	3-4	-	-	-
<i>E. schimperii*</i>	30-51-75	49-61-76	300-520-650	475-827-980	+	-	2-5	-	>7300	-	2-3	-	+	-
<i>E. upembensis</i>	36-59-98	18-27-37	440-782-1080	990-1215-1560	+	-	12-18	-	4800-4850-1900	-	1-2	+	+	-
<i>Ceasanthus angustiflorus</i>	60-84-120	8-10-15	350-589-910	880-1107-1420	+	-	6-10	-	>12000	-	2	+	+	-
<i>G. quinadensis¹</i>	50-85-110	11-18-25	240-471-600	530-686-840	+	-	10-12	-	6400-7629-8700	-	1-2	-	-	-
<i>G. quinadensis²</i>	65-77-105	9-14-22	370-507-670	530-761-920	+	-	17-21	-	>10000	-	1-2	+	+	-
<i>G. parasitica</i>	35-40-65	16-21-27	250-395-540	410-549-800	+	+	2-4	130-220-250	800-1390-2900	0-1	1-2	-	-	-
<i>G. parviflora</i>	44-54-55	14-18-26	270-453-700	670-853-1010	+	+	2-7	170-210-250	700-1600-2600	0-2	1-2	-	-	-
<i>Heberdenia bahamensis</i>	30-51-75	50-60-72	240-374-500	600-756-1080	+	-	5-8	-	2600-5080-9500	-	1-2	+	+	-
<i>Jacquinia arborea¹</i>	40-54-70	33-35-52	240-273-330	470-557-730	+	-	10-18	-	2200-3200-4300	-	1-3	+	+	-
<i>J. arborea²</i>	35-45-60	18-32-50	200-263-300	420-543-620	+	-	10-17	-	1500->8000	-	1-2	-	+	-
<i>J. cf. armillaris</i>	35-54-75	18-30-44	150-208-300	320-416-480	+	-	4-10	-	400-1771-3700	-	2-3	-	+	-
<i>J. berterii¹</i>	35-49-60	26-39-62	190-240-280	440-495-530	+	-	7-21	-	2000-4013-6000	-	1-2	-	+	-
<i>J. berterii^{2*}</i>	15-25-35	92-119-134	150-202-260	350-450-520	+	-	6-12	-	1300->4000	-	1-3	-	+	-
<i>J. keyensis¹</i>	25-41-50	20-42-70	160-193-270	370-414-570	+	-	8-18	-	1300-3009-5300	-	1-2	-	+	-
<i>J. keyensis²</i>	15-27-35	28-58-75	130-167-210	280-353-400	+	-	12-36	-	1400-4480-9000	-	1-2	-	+	-
<i>Lysimachia katalauensis</i>	10-24-40	88-97-109	240-433-520	410-586-680	+	-	-	-	-	-	-	-	-	-
<i>L. vulgaris</i>	15-22-35	120-176-188	220-321-520	480-577-760	+	-	-	-	-	-	-	-	-	-
<i>Marsa indica</i>	40-57-80	30-39-53	350-686-900	1000-1230-1560	+	+	2-6	160-342-680	600-1311-240	0-2	3-6	-	-	-
<i>M. lanceolata¹</i>	45-71-95	18-21-24	500-668-800	750-1135-1250	+	+	3-8	200-439-600	200-958-1300	3-4	3-5	-	-	-
<i>M. lanceolata²</i>	40-60-100	31-42-55	330-458-650	520-979-1390	+	+	4	170-325-525	400-563-1000	0-2	4-6	-	-	-
<i>M. macrothyrsa</i>	60-95-120	32-37-43	450-623-820	830-1036-1200	+	+	3-4	300-533-1100	2100-7000	0-2	4-6	-	-	-
<i>M. ramentacea</i>	50-76-105	36-46-56	650-853-1070	1050-1271-1450	+	+	2-4	400-1000-2100	600-2586-4800	4-6	2-3	-	-	-
<i>M. schweinfurthii*</i>	30-43-60	76-88-101	360-526-670	590-866-1100	+	+	2-4	950-1425-1800	300-467-900	0-2	0-2	-	-	-
<i>Myrsine angustifolia</i>	35-48-60	30-37-41	370-512-620	500-664-820	+	-	4-8	-	900-2720-6000	-	1-3	+	+	-
<i>M. lessertiana</i>	20-34-50	124-148-184	275-348-450	310-438-545	+	-	2-4	-	1000-2420-3500	-	2-3	+	+	-
<i>M. sandwicensis</i>	40-47-50	18-23-29	350-539-680	510-819-1120	+	-	4-5	-	1200->10000	-	2-3	+	+	-
<i>Oncostenium botryoides</i>	45-60-80	24-37-50	310-438-630	670-911-1080	+	-	4-8	-	3700->7600	-	2-3	+	+	-
<i>O. cauliflorum</i>	19-29-50	49-63-80	450-599-690	750-1010-1220	+	-	2-5	-	>9000	-	2-4	-	+	-
<i>O. leptosium</i>	50-64-85	26-33-44	620-727-820	1020-1217-1380	+	-	6-10	-	>10000	-	2	-	+	-
<i>O. renulosum</i>	30-40-50	42-57-68	300-534-670	600-745-950	+	-	3-5	-	>7000	-	2-3	+	+	-
<i>Parathesis chiapensis</i>	40-52-60	32-40-58	370-495-620	650-792-900	+	-	4-8	-	2800-3900-6100	-	2-3	+	+	-
<i>P. chrysophylla</i>	60-91-115	10-19-27	380-494-650	670-802-970	+	-	20-26	-	>8000	-	1-2	+	-	-
<i>P. crenulata</i>	35-50-70	18-24-34	380-597-720	900-1095-1360	+	-	6-7	-	>9000	-	0-2	+	+	-
<i>P. cubana</i>	30-54-75	39-46-54	250-399-510	480-678-840	+	-	4-6	-	2100-3360-4800	-	2-3	-	-	-
<i>P. leptopa</i>	40-52-80	22-35-42	400-630-750	800-1044-1200	+	-	6-8	-	>8500	-	2-4	-	+	-
<i>P. rekoii</i>	30-56-80	20-25-32	450-718-910	950-1207-1380	+	-	5-11	-	2900->6000	-	0-2	+	+	-
<i>Rapanea australis</i>	25-41-50	38-50-61	300-400-520	540-682-830	+	-	7-17	-	1900-3438-7600	-	2	-	+	-
<i>R. dependens petandra</i>	30-45-60	28-35-48	320-515-650	700-856-1140	+	-	4-8	-	2400-3700-6000	-	1-2	-	+	-

TABLE 1. Continued.

Species studied	Vessels				Fibers				Rays				Mineral inclusions	
	DIAM	DENS	VEL	LFL	SF	UR	MW	HUR	HMR	DU	DM	BA	PC	SB
<i>R. gracicolor</i>	50-62-80	24-30-38	350-590-720	750-952-1170	+	-	5-10	-	1900->12000	-	1-2	-	+	-
<i>R. guianensis</i>	30-42-50	112-124-150	340-468-610	425-552-650	+	-	2-4	-	>5500	-	2-3	+	+	-
<i>R. melanophloeos</i>	50-79-110	14-19-23	370-416-720	650-762-920	+	-	4-5	-	4300-8250-11900	-	2	+	+	-
<i>R. quaternata</i>	25-41-55	56-66-79	440-537-700	670-833-970	+	-	5-10	-	1400-4017-8800	-	1-3	+	+	-
<i>Stylogyne amplifolia</i> ¹	30-50-70	19-22-26	320-575-810	760-903-1100	+	-	4	-	>7300	-	1-3	-	+	-
<i>S. amplifolia</i> ²	40-58-75	24-32-36	320-540-700	820-1052-1240	+	-	4-5	-	1600->8000	-	2-3	-	+	-
<i>S. latifolia</i>	55-68-90	7-16-24	500-751-960	900-1137-1280	+	-	5-8	-	>14000	-	3-4	-	+	-
<i>S. standleyi</i>	25-49-75	14-20-28	220-443-600	920-1044-1280	+	-	3-4	-	1400-3538-5100	-	2-3	-	+	-
<i>S. venezuelana</i>	35-53-65	10-17-24	250-475-620	750-953-1160	+	-	4-11	-	>9000	-	2-3	+	+	-
<i>Synardisia venosa</i>	30-64-105	22-25-48	340-546-900	900-1054-1330	+	-	5-7	-	>7000	-	1-3	+	+	-
<i>Tapeinosperma nectandroides</i>	50-78-105	15-26-34	700-847-980	800-1153-1510	+	-	8-10	-	>11000	-	1-2	-	+	-
<i>Theophrasta americana</i>	15-20-25	48-66-85	210-299-430	450-541-730	+	-	7-13	-	2200-3643-6000	-	2-3	-	+	-
<i>Wallenia grisebachii</i>	45-56-70	20-28-40	420-621-870	750-992-1240	+	-	6-12	-	>6000	-	1-2	+	+	-
<i>W. laurifolia</i>	30-46-60	28-42-60	330-471-620	600-790-1100	+	-	7-9	-	>6000	-	2-4	+	+	-

with distinct borders in *Discocalyx*, *Embelia* (Fig. 3I), *Geissanthus*, and *Stylogyne*, 10-30 μm in size. Helical sculpturing restricted to the tails of vessel elements in *Ctenardisia stenobotrys*. Tangential diameter of vessels (10-)10-150(-200) μm, (7-)10-310(-352) vessels per mm², vessel elements (60-)160-850(-1160) μm long. Tracheids absent. Fibers usually septate (Figs. 5A, B) except in *Aegiceras*, *Coris*, and *Lysimachia*, thin- to thick-walled, (180-)280-1220(-1560) μm long, with simple to minutely bordered pits concentrated in both tangential and radial walls, pit borders 2-3 μm in diameter, slit-like apertures sometimes elongated (Fig. 5B); fibers storied in *Aegiceras* (Fig. 4A). Axial parenchyma scanty paratracheal or vasicentric (Fig. 2), 2-8 cells per parenchyma strand. Sometimes undivided (fusiform) axial parenchyma cells observed in *Ardisia*, *Badula*, *Cybianthus*, *Discocalyx*, *Embelia*, *Geissanthus*, *Oncostemum*, *Rapanea*, and *Stylogyne*, fusiform cells 550-950 μm in length. Rays entirely absent in *Coris* and *Lysimachia* (Figs. 6E, F). Uniseriate rays clearly present in *Aegiceras* (Fig. 4A) and occasionally in *Grammadenia* (Fig. 4B), (75-)210-220(-250) μm high, consisting of upright cells, 0(-1)5 rays per mm. Multiseriate rays often 2-6-seriate (Figs. 4C, D), more than 10 cells wide in species of *Embelia* (Fig. 4E), *Geissanthus* (Fig. 4F), *Parathesis*, *Rapanea*, *Stylogyne*, and *Wallenia*, (100-)190-8250(-14000) μm (and even more) high, 0(-2)5 rays per mm, usually consisting of a mixture of procumbent, square and upright body ray cells (Figs. 5C, D) and a variable number of upright marginal ray cell rows; multiseriate rays often dissected (Fig. 4E), sheath cells present (Figs. 4C, D) except in *Aegiceras*. Groups of sclereids in rays concentrated near the end of a growth ring in *Grammadenia parasitica* (Fig. 4B) and *Oncostemum venulosum*. Breakdown areas in rays confined to one normal-sized (Figs. 3B, D) or enlarged cell (Figs. 4G, H), or to two or more adjacent ray cells (Figs. 3A, C, 4A, D, 5C, E, F); areas usually with a brown substance, in *Parathesis chiapensis* sometimes sclereid-like (Fig. 4H), or areas empty giving the appearance of secretory ducts in *Ardisia copelandii* (Fig. 4D); breakdown areas in rays absent in species of *Coris*, *Ctenardisia*, *Embelia*, *Geissanthus*, *Grammadenia*, *Heberdenia*, *Lysimachia*, and *Oncostemum*. Gummy deposits present in ray cells. Single prismatic crystals (Figs. 5G, H) mostly present in non-chambered procumbent and upright ray cells, or exceptionally in chambered ray cells; sometimes styloids present in procumbent and upright ray cells. Pith including solitary or groups of sclereids, sometimes with secretory ducts in *Ardisia* (Fig. 2A), *Embelia*, *Myrsine*, and *Oncostemum*; pith containing many intercellular spaces in *Lysimachia vulgaris* (Fig. 6C).

Theophrastaceae. Taxa studied: *Bonellia* 5/22, *Clavija* Ruiz & Pav. 10/50, *Deherainia* 1/2-3, *Jacquinia* 4/13, *Theophrasta* L. 1/2 (Figs. 7-9). Growth ring boundaries indistinct. Diffuse-porous. Vessels solitary and in short

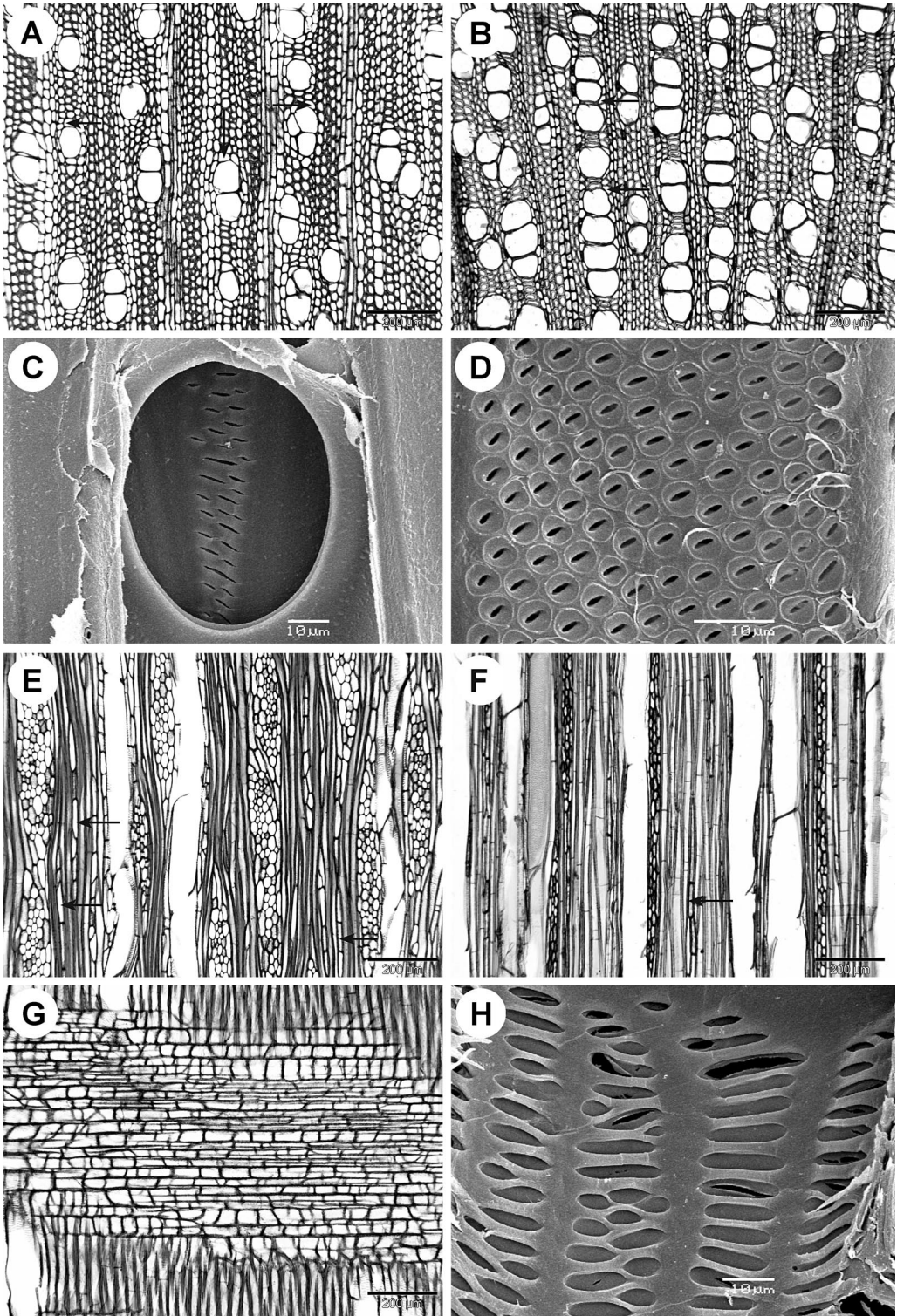


FIG. 1. Wood anatomical illustrations of Maesaceae (TS: transverse section, TLS: tangential section, RLS: radial section). A. *Maesa lanceolata* (Tw), TS, short radial vessel multiples and scanty paratracheal parenchyma (arrows). B. *M. ramentacea*, TS, short radial vessel multiples and scanty paratracheal parenchyma (arrows). C. *M. ramentacea*, RLS, simple vessel perforation. D. *M. ramentacea*, TLS, alternate vessel pitting. E. *M. lanceolata* (Tw), TLS, co-occurrence of uniseriate (arrows) and multiseriate rays. F. *M. ramentacea*, TLS, co-occurrence of uniseriate (arrow) and multiseriate rays. G. *M. lanceolata* (Tw), RLS, multiseriate ray showing mainly procumbent body ray cells. H. *M. lanceolata* (Uw), RLS, scalariform vessel-ray pitting.

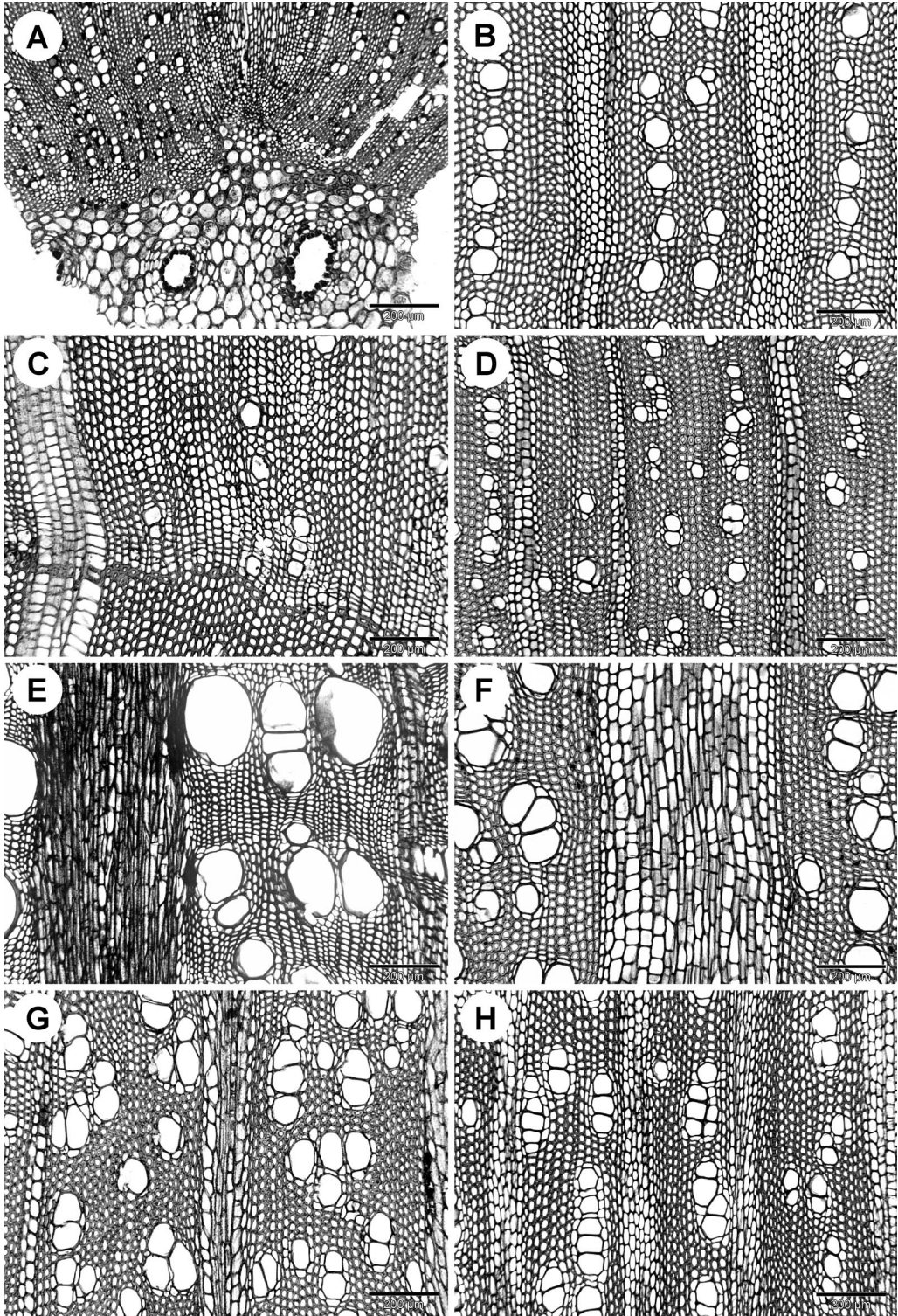


FIG. 2. Transverse sections of Myrsinaceae. A. *Ardisia obovata*, secretory ducts in pith. B. *Stylogyne latifolia*, vessels mostly solitary, scanty paratracheal parenchyma. C. *Grammadenia parasitica*, thick-walled sclereids at the end of a growth ring, scanty paratracheal parenchyma. D. *Ctenardisia stenobotrys*, vessels solitary or in short radial multiples, scanty paratracheal parenchyma. E. *Embelia kilimandscharica*, vessels solitary or in short radial multiples, scanty paratracheal parenchyma. F. *Geissanthus quindiensis* (MADw), vessels solitary, in short radial multiples or in clusters, axial parenchyma scanty to vasicentric paratracheal. G. *Oncostenum leprosum*, vessels solitary, in short radial multiples or in clusters, axial parenchyma scanty paratracheal. H. *Ardisia cauliflora*, vessels in radial multiples or exceptionally in clusters, axial parenchyma scanty to vasicentric paratracheal.

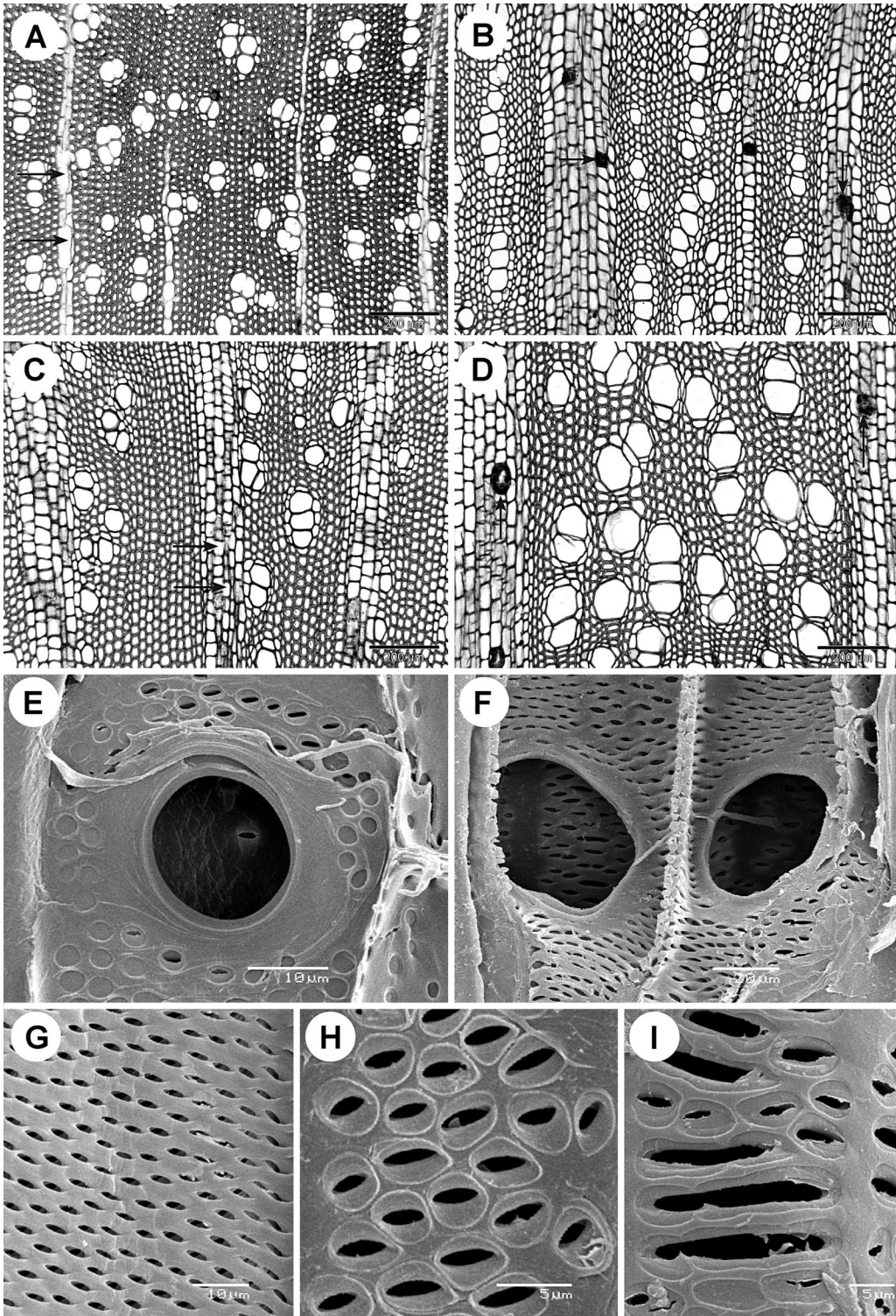


FIG. 3. Wood anatomy of Myrsinaceae showing breakdown areas in rays, vessel perforations, and vessel pitting. A. *Aegiceras majus* (MADw), TS, breakdown areas in rays (arrows). B. *Wallenia laurifolia*, TS, breakdown areas in rays (arrows). C. *Badula barthesia*, TS, breakdown areas in rays (arrows). D. *Parathesis chrysophylla*, TS, breakdown areas in rays (arrows). E. *Cybianthus priurei*, RLS, one simple vessel perforation. F. *Ardisia cauliflora*, RLS, two simple vessel perforations. G. *Geissanthus angustiflorus*, TLS, alternate vessel pitting (inner pit apertures) shown from inside of vessel element. H. *Stylogyne amplifolia* (MADw), TLS, alternate vessel pitting (pit borders and outer pit apertures). I. *Embelia kilimandscharica*, RLS, tendency to scalariform vessel-ray pitting with distinct borders.

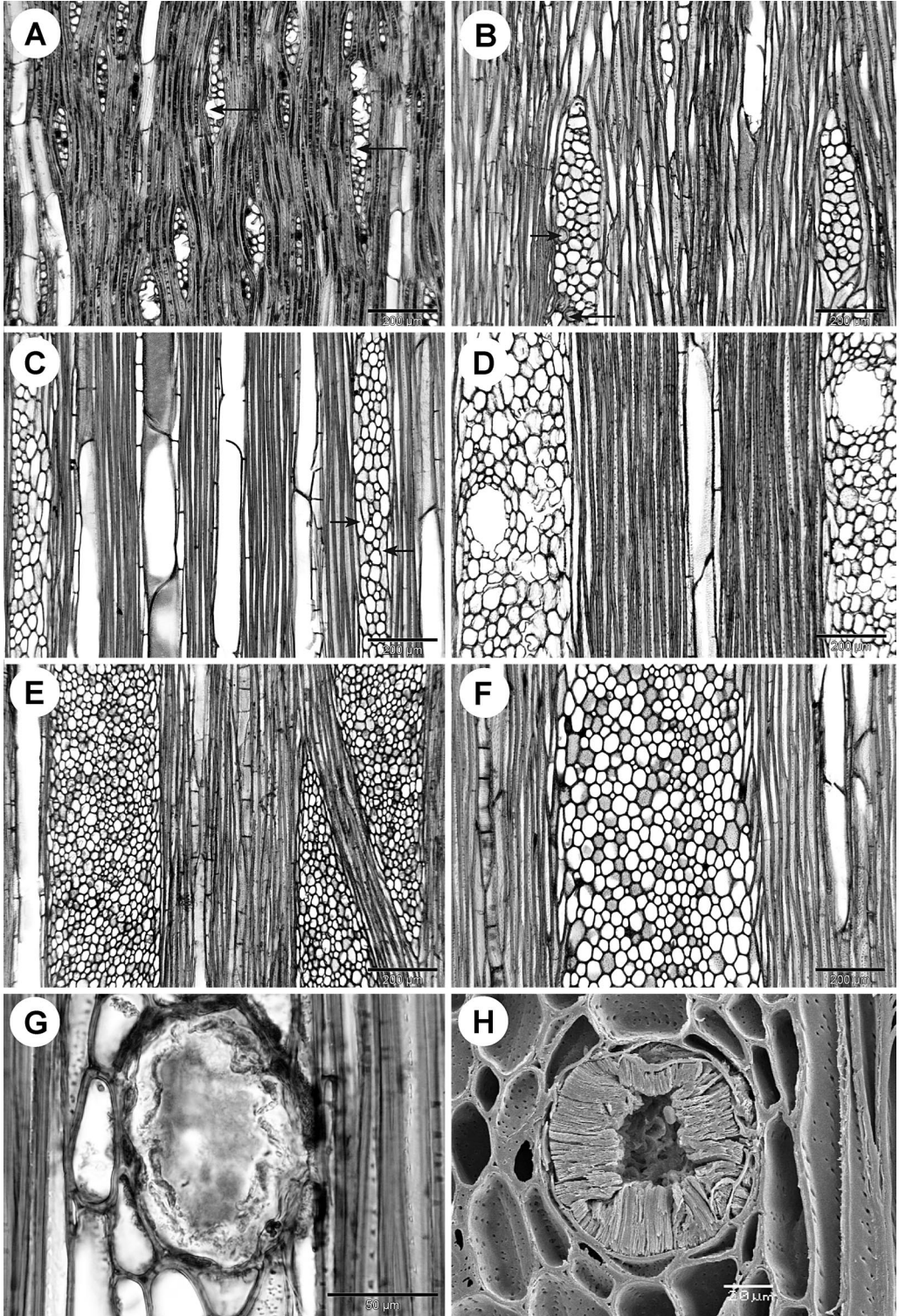


FIG. 4. Tangential sections of Myrsinaceae. A. *Aegiceris majus* (MADw), co-occurrence of uniseriate and narrow, low multiseriate rays with breakdown areas in rays (arrows). B. *Grammadenia parasitica*, multiseriate rays with few sclereids (arrows), occasionally uniseriate rays. C. *Cybianthus comperuvianus*, high multiseriate rays with indistinct sheath cells (arrows). D. *Ardisia copelandii*, empty breakdown ray areas. E. *Embelia upembensis*, wide multiseriate rays. F. *Geissanthus quindensis*, wide multiseriate ray. G. *Parathesis crenulata*, detail of breakdown ray area. H. *Parathesis chiapensis*, detail of breakdown ray area containing a sclereid-like substance.

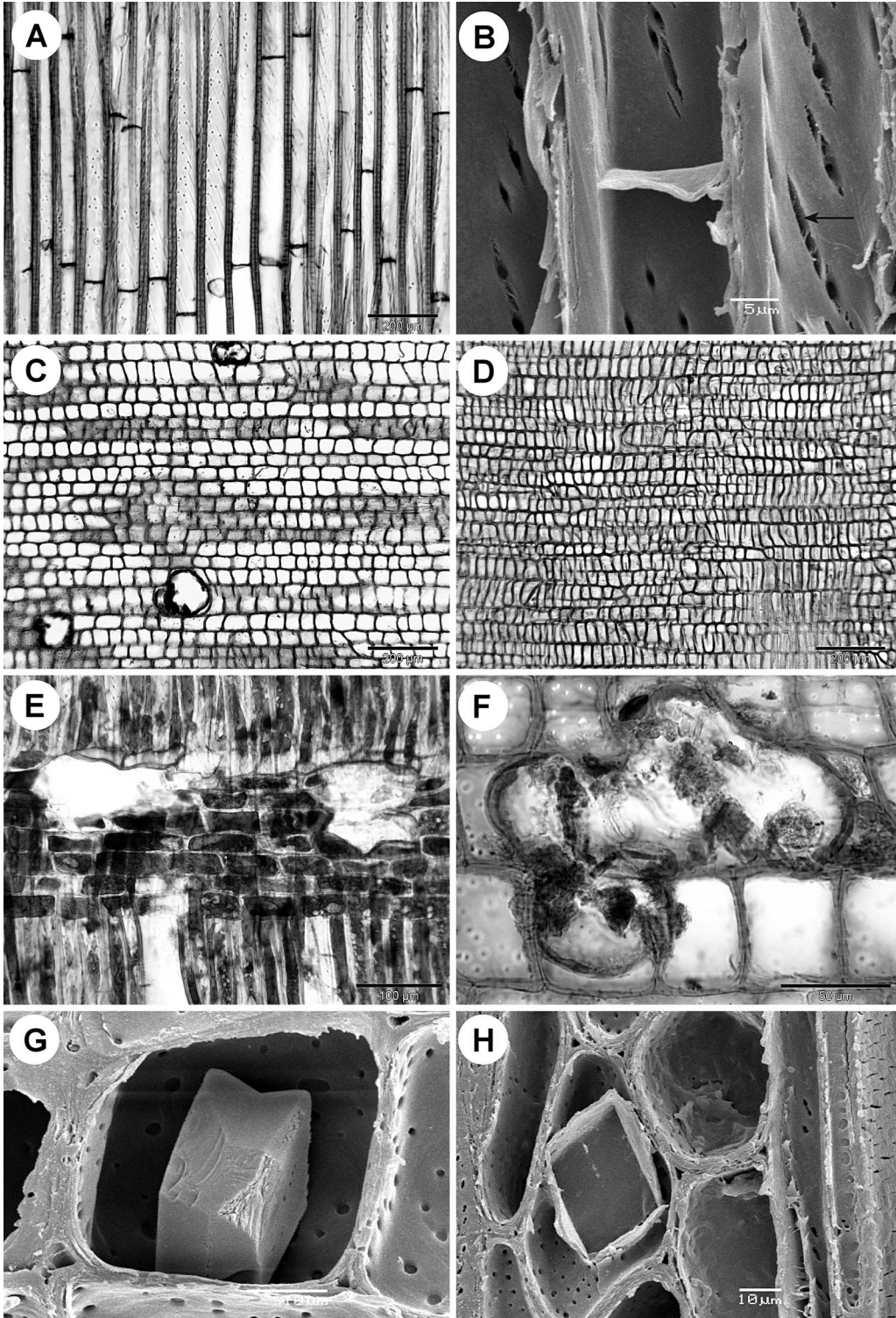


FIG. 5. Radial (A-G) and tangential (H) sections of Myrsinaceae. A. *Stylogyne latifolia*, septate libriform fibers. B. *Parathesis chiapensis*, detail of septate libriform fiber pits, slit-like apertures sometimes elongated (arrow). C. *Cybianthus magniifolia*, ray with procumbent, square and upright body ray cells, and breakdown areas in rays. D. *Ctenardisia stenobotrys*, ray with square to upright body ray cells. E. *Aegiceras majus* (MADw), ray with procumbent body ray cells and large breakdown areas in rays. F. *Cybianthus magniifolia*, detail of breakdown area in ray. G. *Parathesis chiapensis*, prismatic crystal in ray cell. H. *Ctenardisia stenobotrys*, prismatic crystal in ray cell.

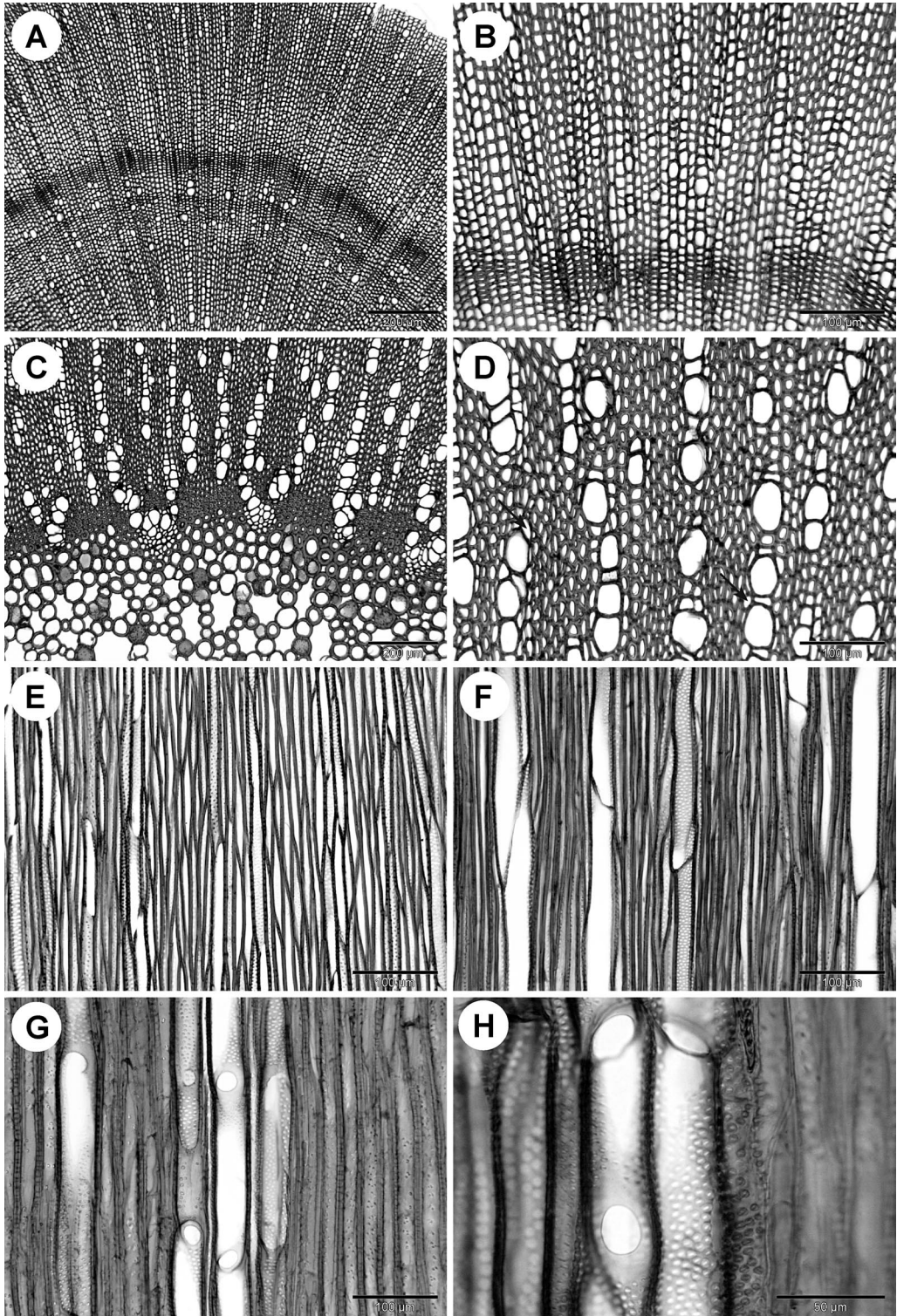


FIG. 6. Secondary woodiness in Myrsinaceae. A. *Coris monspeliensis*, TS, distinct growth rings and very narrow vessel elements. B. *C. monspeliensis*, TS, detail, narrow vessels solitary or in short radial multiples. C. *Lysimachia vulgaris*, TS, pith, primary xylem and first formed secondary xylem. D. *L. vulgaris*, TS, detail, vessels in solitary or in short radial multiples, axial parenchyma scanty paratracheal (arrows). E. *C. monspeliensis*, TLS, absence of rays. F. TLS, *L. vulgaris*, absence of rays. G. *L. kalalauensis*, RLS, simple vessel perforations. H. *L. vulgaris*, RLS, simple vessel perforations.

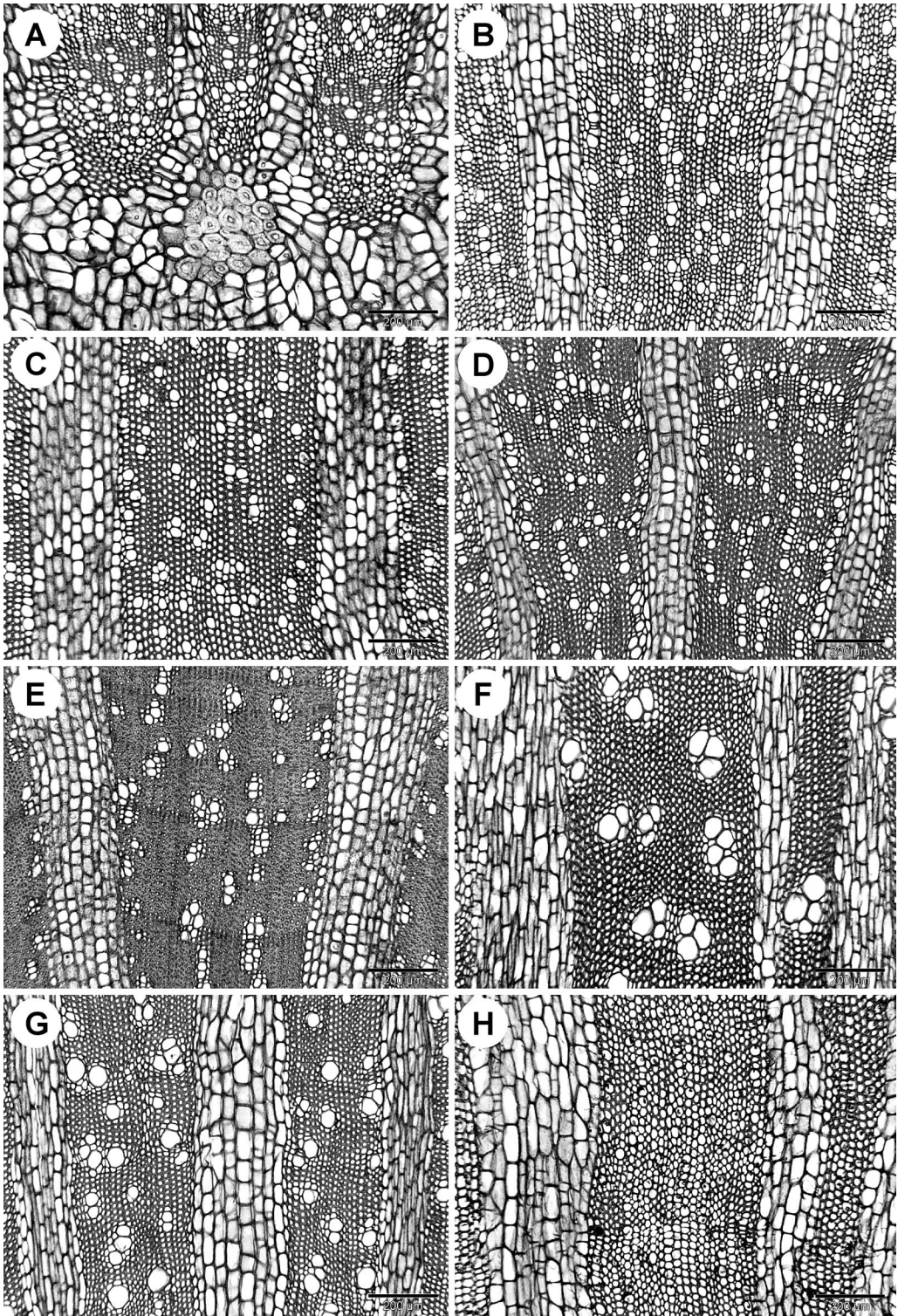


FIG. 7. Transverse sections of Theophrastaceae showing vessel arrangement, paratracheal parenchyma and wide multiseriate rays. A. *Clavija procera*, pith with a group of sclereids, primary xylem and first formed secondary xylem. B. *C. nutans*, vessels solitary or in short radial multiples, very thin-walled fibers. C. *C. reflexiflora*, vessels solitary or in short radial multiples, very thin-walled fibers. D. *Deherainia smaragdina*, vessels solitary, in radial or tangential multiples, or exceptionally in clusters. E. *Jacquinia berterii*, vessels in clusters, thick-walled fibers. F. *Bonellia frutescens*, vessels in clusters, thick-walled fibers. G. *B. umbellata*, vessels solitary, in short radial multiples or in clusters. H. *Theophrasta americana*, very narrow vessels solitary or in short radial multiples.

radial multiples (*Clavija* (Figs. 7A–C) and *Theophrasta* (Fig. 7H)), while vessel clustering is observed in *Deherainia* (Fig. 7D) and especially in *Jacquinia* (Fig. 7E) and *Bonellia* (Figs. 7F, G); vessel outline angular. Vessel perforation plates exclusively simple (Fig. 8A). Intervessel pits alternate (Fig. 8B), 3–5 μm in size, non-vestured. Vessel-ray pits similar to intervessel pitting in shape and size, sometimes unilaterally compound in *Bonellia* and *Jacquinia*. Helical sculpturing absent. Tangential diameter of vessels (12-)20–60(-80) μm , (13-)30–120(-154) vessels per mm^2 , vessel elements (120-)170–440(-620) μm long. Tracheids absent. Fibers septate in *Clavija* (Fig. 9A) and *Theophrasta*, but non-septate in *Deherainia*, *Jacquinia* (few septate fibers in *J. arborea*), and *Bonellia* p.p. (septate in *B. frutescens*), thin to thick-walled, (175-)250–790(-920) μm long, with simple to indistinctly bordered pits concentrated in radial walls, pit borders 2–3(-4) μm in diameter, slit-like apertures sometimes elongated. Axial parenchyma scanty paratracheal with a tendency to vasicentric parenchyma in *Bonellia* and *Jacquinia*, 2–4 cells per parenchyma strand. Rays exclusively multiseriate, often 6–10-seriate (Figs. 8C–E, 8H), up to more than 15 cells wide in many species of *Jacquinia* (Figs. 8F, G) and *Bonellia*, (400-)1770–4480(-12000) μm (and even more) high, 0(-2)-4 rays per mm, consisting of mainly procumbent body ray cells (*Bonellia*, *Jacquinia* (Fig. 9D), and *Theophrasta*) or procumbent and square body ray cells (*Clavija* (Fig. 9B) and *Deherainia* (Fig. 9C)), and 1–2 rows of square to upright marginal ray cells; multiseriate rays often dissected (Figs. 8F–H), sheath cells sometimes present (Figs. 8C, F, H). Groups of sclereids in rays concentrated near the end of a growth ring in *Deherainia smaragdina* (Fig. 9C). Breakdown areas in rays absent. Gummy deposits in ray cells. Solitary prismatic crystals, navicular crystals and styloids present in procumbent and square ray cells of *Jacquinia* (Fig. 9G), solitary prismatic calcium oxalate crystals in procumbent and square ray cells of *Bonellia frutescens* (MADw 35912; Uw 35592), and spherical clusters of needle-shaped calcium oxalate crystals frequently observed in non-chambered procumbent ray cells of *Theophrasta* (Fig. 9H), and less common in *Clavija longifolia*, *C. umbrosa*, and *C. weberbaueri* (MADw 35911). Silica bodies mostly present in non-chambered procumbent to square ray cells of *Clavija* (Fig. 9E), *Bonellia frutescens* (Fig. 9F), *B. macrocarpa*, and *B. shaferi*. Pith including groups of sclereids (Fig. 7A); druses present in the pith of *Jacquinia berterii*, silica bodies in *Clavija*.

DISCUSSION

Our observations agree with most of the earlier wood anatomical studies, although some differences are notable. Examples of features that could not be confirmed here are the short tangential vessel multiples and very wide rays in *Aegicerias*, non-septate fibers in

Clavija, uniseriate rays in *Cybianthus*, very small multiseriate rays in *Deherainia*, and druses in rays of *Maesa*, and silica bodies in Myrsinaceae (Metcalf and Chalk 1950; Welle 1976; Suzuki and Noshiro 1988). In addition, our scarce observations of scalariform perforations and helical thickenings in the wood of Myrsinaceae are most likely caused by our limited sampling in montane regions. Additional scalariform perforations in this family were recorded in largely montane species of *Ardisia*, *Myrsine*, and *Cybianthus* (Moll and Janssonius 1926; Metcalf and Chalk 1950; Versteegh 1968), and helical thickenings were observed in *Myrsine* and *Rapanea* by Meylan and Butterfield (1978a, b).

Wood Anatomical Diversity of Primuloids within Ericales. The wood structure of primuloid families is rather homogeneous and can be characterized by a set of anatomical features, i.e. radial multiples of vessels in combination with solitary vessels, vessels with simple perforation plates and alternate vessel pitting, libriform fibers which are usually septate, scanty to vasicentric paratracheal parenchyma, and heterocellular rays (Figs. 1–9). Nevertheless, the secondary xylem can be used to define the three woody primuloid families primarily based on the ray structure, the occurrence of calcium oxalate crystals and silica bodies, and the presence of breakdown areas in rays (Figs. 10–12; Table 2). Within Ericales, the overall wood structure of primuloids can be compared with the non-related Marcgraviaceae, Tetrameristaceae, and Pelliceraceae, although these three families could clearly be distinguished from primuloids by the occurrence of apotracheal and paratracheal axial parenchyma, raphides in ray cells, and the abundance of uniseriate rays. Baas et al. (2000) did not emphasize similarities between Marcgraviaceae and primuloids in their wood anatomical comparison of Ericales. Instead, they considered the wood structure of Marcgraviaceae to be more or less primitive, linking it with other ericalean families such as Actinidiaceae, Cyrillaceae and Ericaceae. However, this is contradicted by our ongoing studies (F. Lens, pers. obs.).

According to Geuten et al. (2004), the sister group of the primuloid clade consists of Pentaphylacaceae sensu APG II (including *Sladenia*, *Ficalhoa*, and the former Ternstroemiaceae). From a wood anatomical point of view, this is surprising because Pentaphylacaceae are totally different in having solitary vessels, long vessel elements with exclusively scalariform perforations containing many bars, opposite to scalariform vessel pitting, fibers with distinctly bordered pits, diffuse apotracheal parenchyma, and co-occurrence of uniseriate and relatively low multiseriate rays (Baretta-Kuipers 1976; Carlquist 1984; Liang and Baas 1990). The genus *Sladenia* is somewhat aberrant in Pentaphylacaceae due to the occurrence of vessels in radial multiples and the tendency to alternate intervessel pitting,

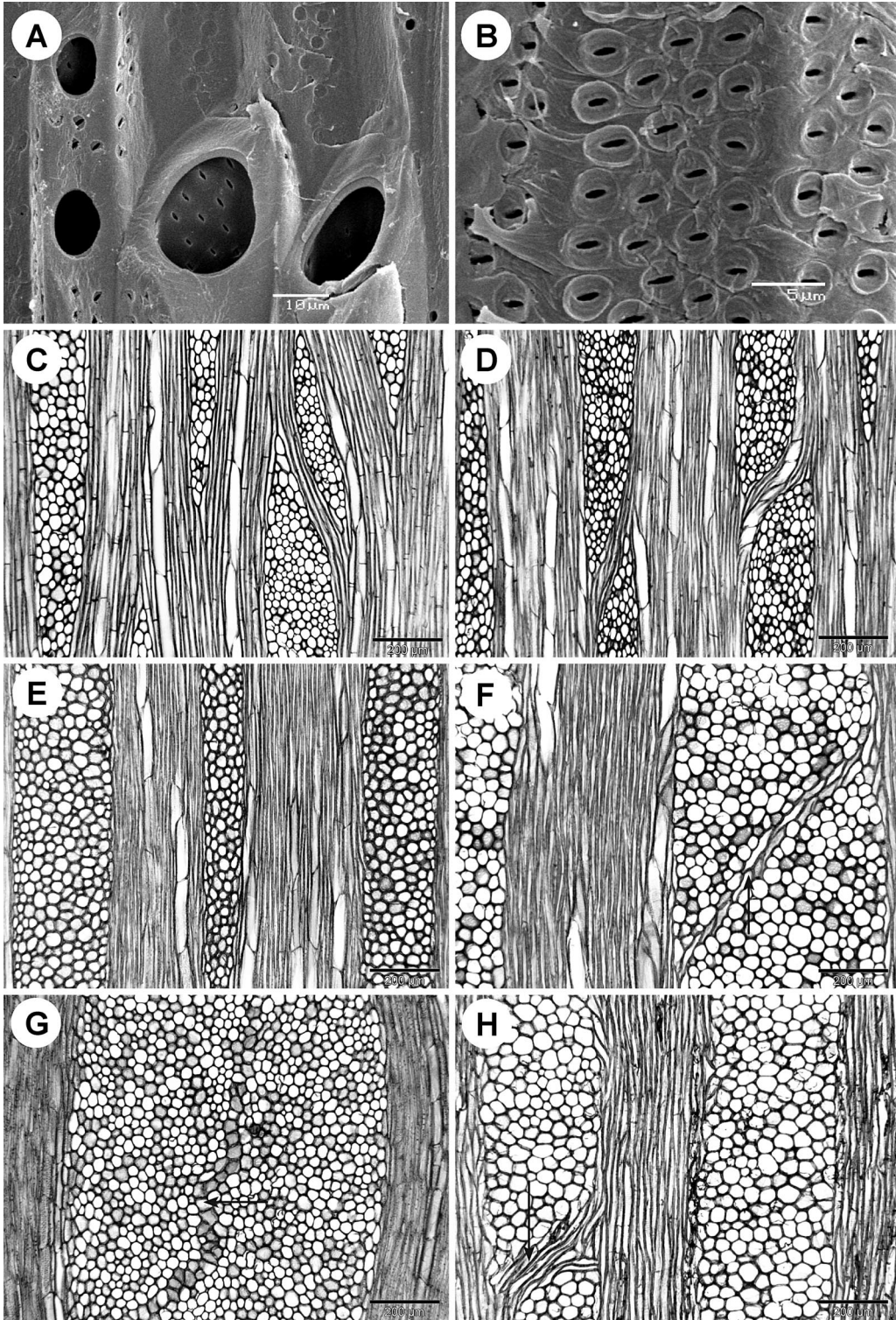


FIG. 8. Wood anatomical variation in Theophrastaceae showing vessel perforations, vessel pitting and rays. A. *Clavija procera*, RLS, simple vessel perforations. B. *Deherainia smaragdina*, RLS, alternate vessel pitting (outer pit apertures). C. *C. nutans*, TLS, wide multiseriate rays. D. *C. procera*, TLS, wide multiseriate rays. E. *Deherainia smaragdina*, TLS, wide multiseriate rays. F. *Jacquinia arborea*, TLS, detail of multiseriate ray dissection (arrow). G. *J. keyensis*, TLS, detail of multiseriate ray dissection (arrow). H. *Theophrasta americana*, TLS, detail of multiseriate ray dissection (arrow).

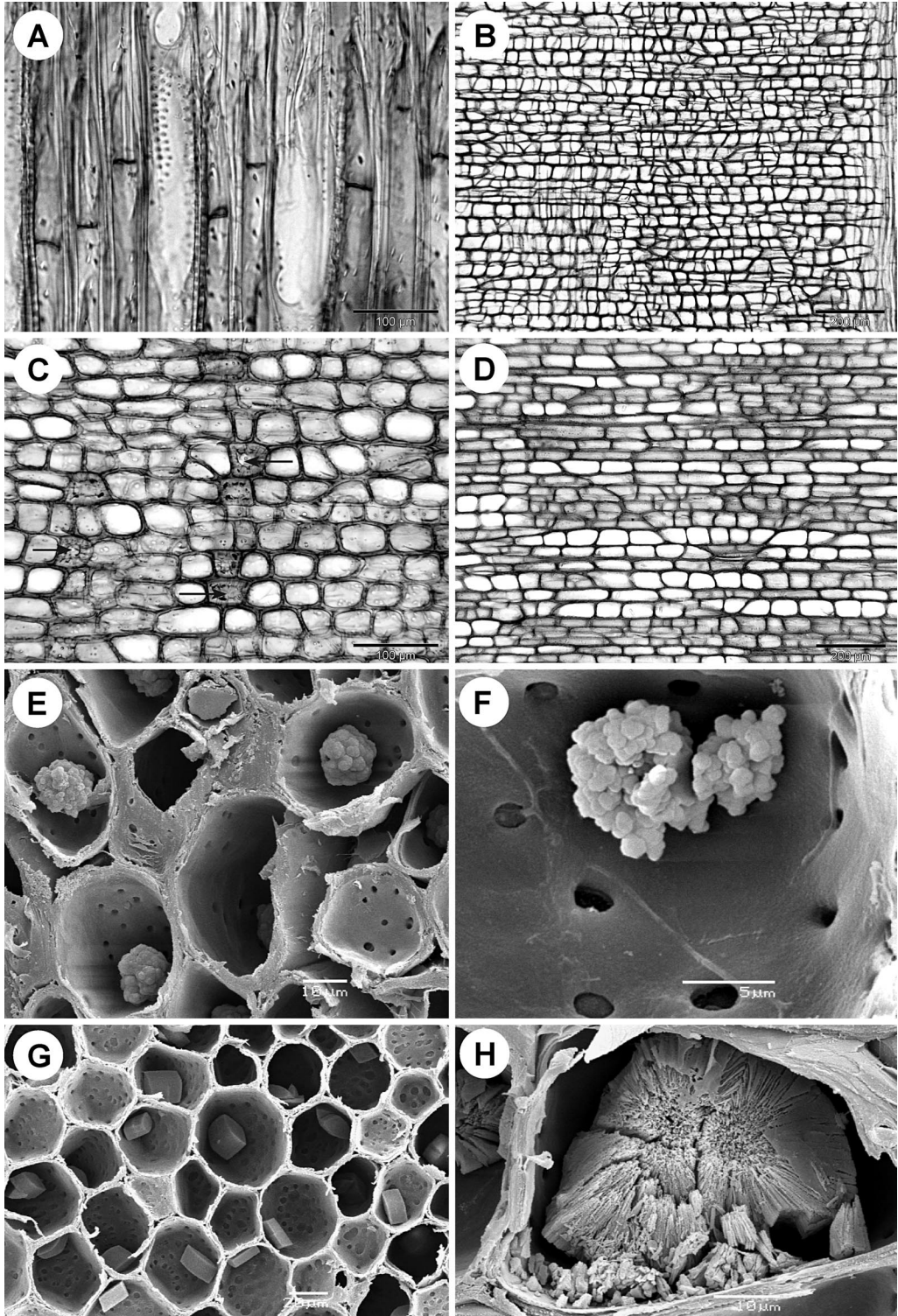
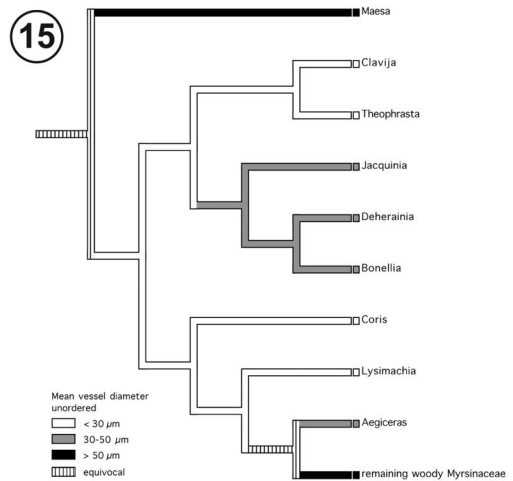
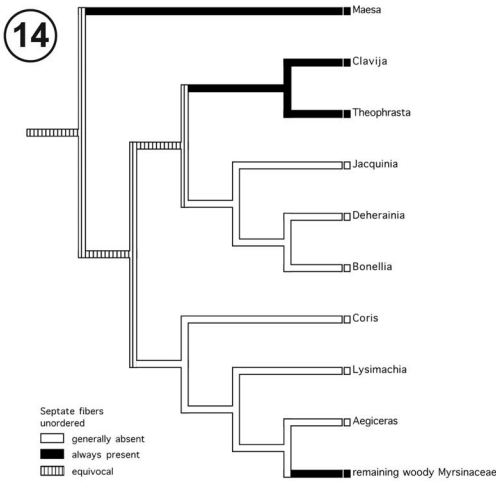
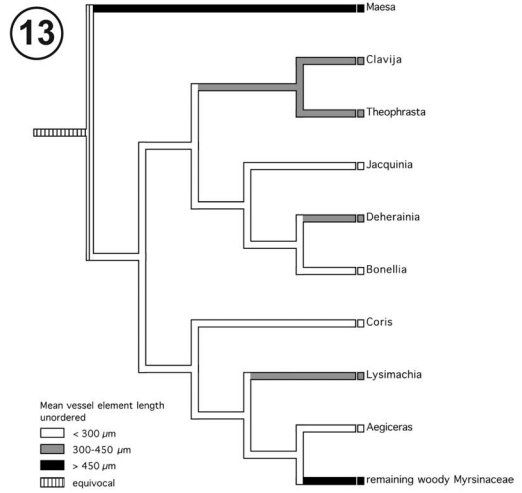
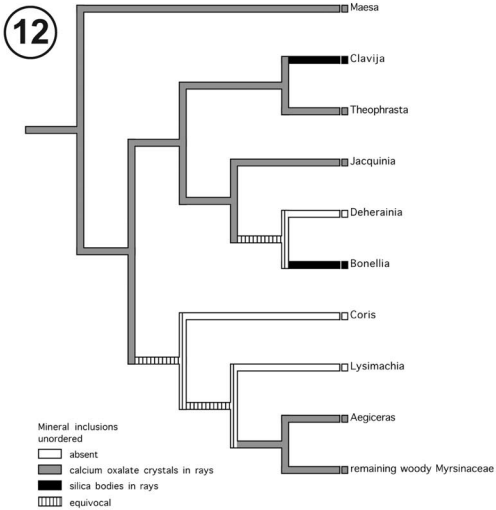
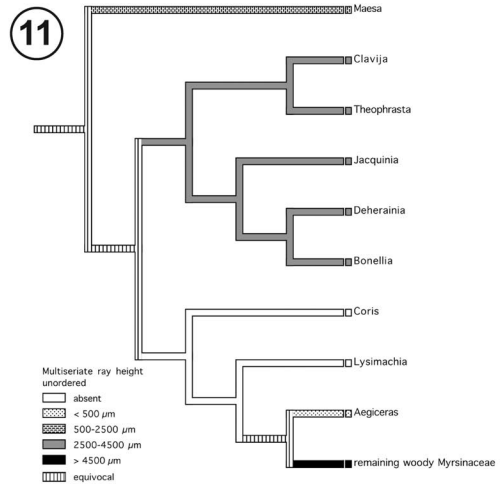
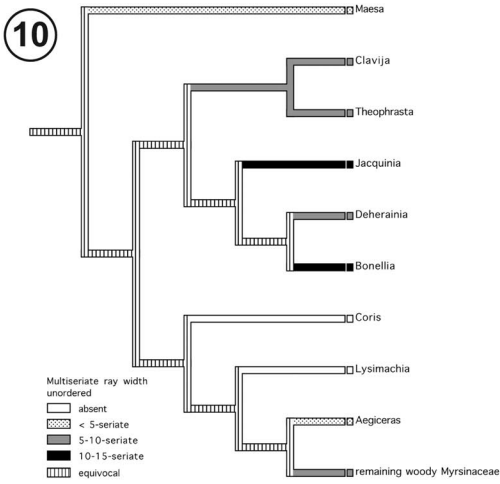


FIG. 9. Wood anatomical variation in Theophrastaceae showing fibers, rays, and mineral inclusions. A. *Clavija lancifolia* subsp. *lancifolia*, RLS, septate libriform fibers. B. *C. nutans*, RLS, multiseriate ray with square and procumbent body ray cells. C. RLS, *Deherainia smaragdina*, multiseriate ray including sclereids (arrows). D. *Jacquinia arborea*, RLS, multiseriate ray containing mainly procumbent body ray cells. E. *C. lancifolia* (Tw), TLS, silica bodies in ray cells. F. *Bonellia frutescens*, RLS, silica bodies in ray cells. G. TLS, *J. armillaris*, navicular, rectangular and prismatic crystals in ray cells. H. *Theophrasta americana*, RLS, spherical cluster of needle-shaped crystals in a ray cell.



FIGS. 10–15. Simplified trees based on the molecular studies of Källersjö et al. (2000) and Källersjö and Ståhl (2003), showing the distribution of characters in woody primuloids. 10. Distribution of multiserial ray width. 11. Distribution of multiserial ray height. 12. Distribution of mineral inclusions. 13. Distribution of vessel element length. 14. Distribution of septate fibers. 15. Distribution of vessel diameter.

TABLE 2. Wood anatomical comparison of the primuloid families. Only specimens with mature wood are included. *Within Myrsinaceae, the genera *Coris* and *Lysimachia* are not included because of secondary woodiness. BA = Breakdown areas in rays, HMR = Mean height of multiseriate rays (μm), LFL = Mean length of libriform fibers (μm), MW = Mean width of multiseriate rays (no. cells), PC = Prismatic crystals, SB = Silica bodies, SF = Fibers usually septate, SP = Scalariform vessel perforations, UC = Upright body ray cells, UR = Uniseriate rays, VEL = Mean length of vessel elements (μm); + = present, - = absent, \pm = sometimes present.

Family	SP	VEL	LFL	SF	UR	MW	HMR	UC	BA	PC	SB
Maesaceae	\pm	460–850	980–1270	+	+	2–5	560–2590	\pm	-	\pm	-
Myrsinaceae*	\pm	220–850	440–1220	+	\pm	5–10	340–8250	+	+	+	-
Theophrastaceae	-	170–440	250–790	\pm	-	5–15	1770–4480	-	-	\pm	\pm

two features that are characteristic of the primuloid clade (Liang and Baas 1990). Therefore, this genus could represent a link between the enlarged Pentaphylacaceae and primuloids, but the position of *Sladenia* within Pentaphylacaceae remains uncertain.

Maesaceae. Typical of Maesaceae is the occurrence of uniseriate as well as multiseriate rays (Figs. 1E–F), although this combination is also present in *Aegiceras* (Fig. 4A) and rarely in *Grammadenia* (Fig. 4B) (Moll and Janssonius 1926). Because of the high percentage of uniseriate rays in *Maesa*, vessels are nearly always adjacent to rays, a condition which is unique within the primuloid clade (Moll and Janssonius 1926). In addition, Maesaceae show relatively long vessel elements and fibers (460–850 μm and 820–1270 μm , respectively), low multiseriate rays (470–2590 μm), and prismatic crystals are very few to absent (Figs. 1, 11–13; Table 2). The basal position of Maesaceae within primuloids might be supported by the secondary xylem. Indeed, based on the current sister relationship with Pentaphylacaceae s.l., ancestral wood features in Maesaceae are long vessel elements (sometimes with scalariform perforations) and fibers, and a co-occurrence of uniseriate and multiseriate rays.

Myrsinaceae. This family is defined by libriform fibers showing a dense pitting in both radial and tangential walls, and by multiseriate rays that are often very high (usually more than 4500 μm , Fig. 11), usually consisting of procumbent, square and upright body ray cells with solitary calcium oxalate crystals (Figs. 5G–H), but always without silica bodies (Fig. 12). Furthermore, the presence of breakdown areas in rays (Figs. 3–5) is a typical feature in the wood of Myrsinaceae, although it is not observed in *Coris*, *Embelia*, *Geissanthus*, *Grammadenia*, *Heberdenia*, *Lysimachia*, and *Oncostemum*. According to Metcalfe and Chalk (1950), these structures also occur in the leaves (see also Große 1908), pith, and cortex of additional taxa, for instance *Embelia*, *Grammadenia*, *Heberdenia*, and *Maesa*. Until further research is carried out on the development of these cavities, discussion of their possible homology is too preliminary (Otegui et al. 1997). Breakdown areas in rays are a specialized structure that is not found in other ericalean families. Therefore, it is reasonable to believe that breakdown ray areas repre-

sent a synapomorphic feature in Myrsinaceae. The so-called breakdown areas in the rays of *Piper* (Ilic 1987) are undoubtedly different in origin.

Generic boundaries within woody Myrsinaceae remain a matter of dispute (Coode 1976; Pipoly 1987; Anderberg and Ståhl 1995; Ricketson and Pipoly 1997; Ståhl and Anderberg 2004b). It is impossible to distinguish the genera from each other by their wood anatomy, except for *Aegiceras*, *Coris*, and *Lysimachia* (see below). The only suprageneric group that could be supported is *Cybianthus* (including *Conomorpha* and *Weigeltia*) and *Grammadenia*, which is placed within *Cybianthus* by Pipoly (1987). These taxa exhibit relatively low multiseriate rays (often between 1000 and 5000 μm , except for *Cybianthus comperuvianus*), a feature that is rare in other Myrsinaceae.

Aegiceras can easily be distinguished from other Myrsinaceae by the presence of relatively narrow vessels, a relatively high vessel density, short vessel elements and fibers (which are both storied), non-septate fibers, a combination of low uni- and multiseriate rays (about 100–400 μm), and multiseriate rays with exclusively procumbent body ray cells and without sheath cells (Figs. 11, 13–15). On the other hand, the characteristic breakdown areas in rays are clearly present (Figs. 3A, 4A, 5E) (Moll and Janssonius 1926; Panshin 1932; Metcalfe and Chalk 1950). At least some of these differences are related to the mangrove habit of *Aegiceras*. Tomlinson (1986) noted that the wood of mangrove species typically has a high number of narrow vessels, which are less vulnerable to cavitation, causing a safer sap stream. Furthermore, short vessel elements could also contribute to the safety of the sap stream in mangroves, which experience strongly negative pressures in their vessels due to the saline, physiologically dry, environment (Carlquist 1977). However, Panshin (1932) and van Vliet (1976) mentioned that the vessel element length of mangrove inhabitants does not differ considerably from the inland representatives. There are also other morphological features in *Aegiceras* that are atypical of Myrsinaceae, such as the presence of versatile anthers, viviparous fruits with exalbuminous seeds, and unitegmic ovules (Ståhl and Anderberg 2004b). According to some authors, it seems highly unlikely that all these differences can be ex-

plained by the mangrove habit, supporting the idea to elevate *Aegiceras* to family level (de Candolle 1844; Dahlgren 1989). However, molecular data show that *Aegiceras* falls within a well supported clade including all other woody taxa of Myrsinaceae studied (Källersjö et al. 2000).

Theophrastaceae. The genera *Bonellia* and *Clavija* of Theophrastaceae can be distinguished from Myrsinaceae, Maesaceae, and other Theophrastaceae genera studied by the presence of silica bodies (Figs. 9E, F, 12; ter Welle 1976). Spherical clusters of needle-shaped calcium oxalate crystals are only observed in *Clavija* and *Theophrasta* (Fig. 9H). *Jacquinia* shows solitary calcium oxalate crystals (Fig. 9G), which are typical of Myrsinaceae, while *Deherainia* lacks mineral inclusions (Fig. 12). Generally, the wood of Theophrastaceae is characterized by very short vessel elements and fibers (on average 170–440 μm and 250–790 μm , respectively), values that are also found within primuloids in *Aegiceras*, *Coris*, and *Lysimachia* (Fig. 13). In addition, the family often exhibits wide multiseriate rays with few sheath cells (sometimes more than 20 cells wide; Fig. 8G), although 20-seriate rays or wider are also observed in some Myrsinaceae taxa, such as *Embelia*, *Geisanthus*, and *Parathesis* (see also Metcalfe and Chalk 1950).

Within Theophrastaceae, there are two major clades: a pachycaulous group containing *Clavija*, *Neomezia*, and *Theophrasta*, and a richly branching group of *Bonellia*, *Deherainia*, *Jacquinia*, and *Votschia* (de Candolle 1844; Ståhl 1991, 2004b; Källersjö and Ståhl 2003). The species studied of the pachycaulous group differ from the richly branched clade in vessel diameter (usually < 30 and 30–50 μm , respectively, Fig. 15), vessel density (on average often 60–80 and 30–60 vessels per mm^2 , respectively), length of vessel elements (usually 300–450 and < 300 μm , respectively, Fig. 13), fiber length (often 500–700 and 400–500 μm , respectively), and the width of multiseriate rays (less than 15-seriate vs. more than 10-seriate, Fig. 10). Furthermore, some features are typical of the pachycaulous clade, such as septate fibers (Fig. 14) and spherical clusters of calcium oxalate crystals (*Theophrasta americana* and some *Clavija* species), while the richly branched clade is characterized by pronounced vessel clustering.

Most pachycaulous *Clavija* and *Theophrasta* species are unbranched or sparsely branched shrubs or treelets with a rather thin main stem, mostly reaching only a few meters in height (Ståhl 1987, 1991). Their habit is clearly different from the thick pachycaulous bottle trees, which are anatomically characterized by a higher quantity of parenchyma tissue, wider vessels, and a lower vessel density (Olson and Carlquist 2001; Olson 2003). The narrow vessels of the pachycaulous clade can functionally be interpreted by the presence of a single bunch of terminal leaves, which require a small-

er number of wide vessels than stems supplying a fully branched crown (Fig. 15). Apparently, the influence of the single-stemmed or sparsely branched habit on vessel diameter exceeds the ecological impact in *Clavija*. Indeed, most *Clavija* species grow in wet evergreen forests (Ståhl 2004), a habitat in which plants characteristically show wide vessels, low vessel densities and long vessel elements. On the other hand, ecological influences are much clearer in the wood of *Bonellia* and *Jacquinia*, which typically occur in seasonally dry thorn scrub vegetation (Ståhl 2004). The secondary xylem of the two genera shows several features that are in agreement with other taxa growing in similar seasonally dry vegetation types, such as the presence of very short vessels with simple perforations, relatively narrow vessel diameters, and an increase of vessel multiples (Carlquist and Hoekman 1985).

The presence of silica grains in *Bonellia* and the absence of silica in *Jacquinia* supports the decision to divide *Jacquinia* s.l. into two genera (Ståhl and Källersjö 2004, Fig. 12), but in other respects the wood structure of *Jacquinia* is almost identical to *Bonellia*. The difference in mineral inclusions and corolla color between both genera might possibly reflect different metabolic pathways.

Relationship Between Myrsinaceae and Theophrastaceae. Within woody Ericales, Myrsinaceae and Theophrastaceae are the only two families that lack uniseriate rays, although *Aegiceras* represents an interesting exception. Since the absence of uniseriate rays in Ericales is most likely a derived condition, and because these two families are without doubt closely related, uniseriate rays probably have been lost in the woody common ancestor of Myrsinaceae, Theophrastaceae, and the herbaceous Primulaceae, indicating a plausible synapomorphy for Myrsinaceae and Theophrastaceae. Besides the wood features that are typical of the primuloid clade, other characters linking both families are the presence of vessel clusters and relatively wide multiseriate rays (more than 10-seriate) in some Myrsinaceae species and in the majority of Theophrastaceae species studied. Furthermore, ray dissection is common (Otegui 1994). The wide rays and wide vessels in *Embelia* are probably correlated with the scandent habit.

Secondary Woodiness. *Coris* and *Lysimachia* show an aberrant wood structure compared to other woody Myrsinaceae. Notable differences are the short and narrow vessel elements, short and non-septate fibers, and the absence of rays (Aymard 1968). Furthermore, the length of vessel elements decreases significantly from the centre of the stem towards the periphery, a phenomenon often observed in pedomorphic woods (i.e. woods that remain permanently juvenile; Carlquist 1962). These anomalies are most likely caused by secondary woodiness, a term that is used for woody

plants (often asterids) that evolved from herbaceous ancestors (Carlquist 1992). As a result, wood anatomy cannot provide evidence for the systematic position of these two genera (Carlquist 1962). The possible presence of secondary woodiness in *Coris* and *Lysimachia* is supported by molecular analyses of Källersjö et al. (2000) and Anderberg et al. (2001), since these genera are closely related to herbaceous genera. Woody Myrsinaceae on the other hand (except for *Coris* and *Lysimachia*), form a monophyletic group and are derived within a larger clade including the rest of Myrsinaceae and Primulaceae. However, the hypothesis of Anderberg et al. (2001) that the common ancestor of the clade formed by Samolaceae-Theophrastaceae-Myrsinaceae-Primulaceae is herbaceous seems unlikely because all woody primuloids investigated (except for *Coris* and *Lysimachia*) do not show clear signs of secondary woodiness.

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APPENDIX

The wood samples studied are listed below with reference to the origin, collector, and the diameter of the wood sample in mm. "Mature" means that the wood sample is derived from mature wood, although the exact diameter could not be traced. Institutional wood collections used in this study are abbreviated according to the Index Xylariorum (Stern 1988). The other institution that was used to collect wood samples is the National Botanic Garden of Belgium (BR).

Aegiceras majus Gaertn.; Australia: Narrabeen, E.F. Constable 24199 (BR), 6 mm. *A. majus* Gaertn.; Philippines, Philippine Bureau of Forestry 10260 (MADw 5198), mature. *Afrardisia staudtii* Mez; R. D. Congo, J. Louis 3647 (BR), 10 mm. *Ardisia cauliflora* Mart. & Miq.; Brazil, B.A. Krukoff 5662 (Uw 20106), 55 mm. *A. copelandii* Merr.; Northern Borneo, S. Herb 26792 (Tw 17538), mature. *A. manglillo* Cuatrec.; Colombia, J. Cuatrecasas 16304 (Tw 39542), mature. *A. obovata* Desv. ex J.C.Hassk.; Puerto Rico: Nanauta, R.A. Howard 16802 (BR), 7 mm. *Badula barthesia* A.D.C.; Sri Lanka, Kramer 9441 (Uw 33647), 14 mm. *Bonellia frutescens* (Mill.) B.Stähl & Källersjö; Venezuela, L. Williams 12185 (MADw 35912; Uw 35592), 30 mm. *B. frutescens* (Mill.) B.Stähl & Källersjö; Venezuela, H. Pittier 12425 (MADw 36654), 32 mm. *B. cf. macrocarpa* (Cav.) B.Stähl & Källersjö; Mexico: Quiroga, A. Curtis s.n. (Tw 45664), mature. *B. macrocarpa* (Cav.) B.Stähl & Källersjö subsp. *pungens* (A.Gray) B.Stähl & Källersjö; Mexico: Sonora, P. Fryxell 3070 (BR), 4 mm. *B. shaferi* (Urb.) B.Stähl & Källersjö; Cuba: Camagüey, Maragaoa, R. Dechamps 12718 (Tw 51964), mature. *B. stenophylla* (Urb.) B.Stähl & Källersjö; Cuba, A.J. Fors 985 (MADw 14446), mature. *B. umbellata* (A.D.C.) B.Stähl & Källersjö; Puerto Rico, G. Caminero et al. 485 (MADw 47821), 23 mm. *Clawija lancifolia* Desf. subsp. *lancifolia*; Surinam,

- Lindeman 4463 (Tw 26168), 24 mm. *C. lancifolia* Desf. subsp. *chermontiana* (Standl.) B.Stähl; Guyana, *M. Jansen-Jacobs et al.* 1518 (Uw 33202), 16 mm. *C. longifolia* Ruiz & Pav.; Peru, *J. Schunke* 4884 (MADw 39288), 29 mm. *C. nutans* (Vell.) B.Stähl; Brazil, *Lindeman et al.* 1486 (Uw 13101), 11 mm. *C. nutans* (Vell.) B.Stähl; Bolivia, *M. Nee* 40976 (MADw 46866), 16 mm. *C. procerata* B.Stähl; Ecuador, *W. Palacios* 1339 (Kw 49865), 21 mm. *C. tarapotana* Mez; Peru, *J. Schunke* 4239 (MADw 39072), 23 mm. *C. umbrosa* Regel; Brazil, *B.A. Krukoff* 6742 (Uw 7908, MADw 34206), 40 mm. *C. weberbaueri* Mez; Peru, *Ellenberg* 2523 (Uw 8723), 11 mm. *C. weberbaueri* Mez; Brazil, *B.A. Krukoff* 8136 (MADw 35911), 26 mm. *Coris monspeliensis* L.; Spain: Almeria, *P. Auquier et al.* 6765 (BR), 4 mm. *Ctenardisia stenobotrys* (Standl.) Lundell & Pipoly; Venezuela, *M. Nee* 30825 (MADw 44258), 31 mm. *Cybianthus comperuvianus* Pipoly; Bolivia, *B.A. Krukoff* s.n. (SJRw 39748), 44 mm. *C. magnifolia* (Mez) G.Agostini; Venezuela: Amazone, *B. Maguire et al.* 42702 (Tw 38185), 18 mm. *C. multiflorus* (A.C.Sm.) G.Agostini; Brazil, *B.A. Krukoff* 7290 (MADw 36606), 23 mm. *C. peruvianus* Miq.; origin and collector unknown (SJRw 46505), 27 mm. *C. priourei* A.DC.; Guyana, *Stoffers et al.* 138 (Uw 30091), 24 mm. *C. psychotriaefolius* Rusby; Brazil: Acre, *B.A. Krukoff* 5753 (Tw 34513), 20 mm. *Deherainia smaragdina* Decne.; Mexico, collector unknown (BR 1972-6256), 14 mm. *Discocalyx megacarpa* Merr.; Philippines, *H.A. Miller and Ponape* 6692 (Uw 16699), 14 mm. *D. insignis* Merr.; Philippines: Surigao, *C.A. Wenzel* 3326 (BR), 10 mm. *Embelia kilimandscharica* Gilg; East Africa, *Reinbek* 1703 (Uw 15919), 24 mm. *E. multiflora* Taton; origin unknown, *A. Leonard* 2049 (BR), 8 mm. *E. schimperii* Vatke; Ethiopia, *J.J.E. De Wilde* 6157 (BR), 6 mm. *E. upembensis* Taton; Democratic Republic of Congo: Shaba, *F. Malaisse* 9393 (Tw 31827), 21 mm. *Geissanthus angustiflorus* Cuatrec.; Colombia, *J. Cuatrecasas* 14872 (Uw 25110), 55 mm. *G. quindensis* Mez; Colombia, *J. Cuatrecasas* 20064 (Tw 39724, MADw 17622), mature. *Grammadenia lineata* Benth.; Venezuela: Amazone, *B. Maguire et al.* 37052 (Tw 36547), 12 mm. *G. parasitica* Griseb.; Dominica, *W. Stern and Wasshausen* 2554 (MADw 24234), 16 mm. *Heberdenia bahamensis* Sprague; Spain: Madeira, collector unknown (Tw 22947), mature. *Jacquinia arborea* Vahl; Dominica, *Chambers* 2634 (Uw 2634), 32 mm. *J. arborea* Vahl; Puerto Rico, *M. Nee* 44191 (MADw 47975), 48 mm. *J. cf. armillaris* Jacq.; USA, *Fairchild Tropical Garden* 61493 (MADw 43800), 33 mm. *J. berterii* Spreng.; Guadeloupe, *Rollet* 1137 (Uw 29675), mature. *J. berterii* Spreng.; Puerto Rico, *Knudsen and B. Stähl* 67, 12 mm. *J. keyensis* Mez; USA: Florida, *W. Stern et al.* 3063 (Uw 20284), 48 mm. *J. keyensis* Mez; USA, *W. Stern* 123 (MADw 16890), 40 mm. *Lysimachia kalalauensis* Skotts.; USA: Hawaii, *W. Stern* 2998 (Tw 24160), 7 mm. *L. vulgaris* L.; Spain: Begonte, *Lugo et al.* s.n. (BR), 6 mm. *Maesa indica* Wall.; India: Amla, *Sikkim* 551 (Tw 47058), mature. *M. lanceolata* Forssk.; Africa, *Reinbek* 1598 (Uw 15537), 45 mm. *M. lanceolata* Forssk. var. *rufescens* (A.DC.) Taton; Democratic Republic of Congo: Kivu, *J. Lebrun* 5412 (Tw 910), mature. *M. macrothyrsa* Miq.; Malaysia, *W. Meijer* 122550 (MADw 48614), 15 mm. *M. ramentacea* Wall.; Brunei, *Ogata et al.* 317 (MADw 48458), 15 mm. *M. schweinfurthii* Mez; Democratic Republic of Congo: Zemio, *R. Boutique* 163 (BR), 8 mm. *Myrsine angustifolia* (Mez) Hosaka; USA: Hawaii, *W. Stern* 2931 (Tw 24104), mature. *M. lessertiana* A.DC.; USA: Hawaii, *S.H. Lamb* 26 (BR), 36 mm. *M. sandwicensis* A.DC.; USA: Hawaii, *S.H. Lamb* 24 (Tw 35928), 36 mm. *Oncostemum botryoides* Baker; Madagascar, *L.J. Dorr et al.* 3584 (MADw 44414), 24 mm. *O. cauliflorum* H.Perrier; Madagascar: Tamatave, *J.L. Dorr* 3136 (Tw 44790), 19 mm. *O. leprosum* Mez; Madagascar, *Thouvenot* 133 (MADw 34230), mature. *O. venulosum* Baker; Madagascar, *L.J. Dorr and L.C. Barnett* 3193 (MADw 44367), 11 mm. *Parathesis chiapensis* Fernald; Mexico, *D. Breedlove* 9658 (MADw 23890), 40 mm. *P. chrysophylla* Lundell; Guatemala, *C. Galluser* 3 (MADw 34231), 47 mm. *P. crenulata* Hemsl.; Panama, *G.P. Cooper* 464 (MADw 34232), 28 mm. *P. cubana* (A.DC.) Molinet & B.A.Gomes; Cuba: Pinar del Rio, *R. Dechamps* 12458 (Tw 49932), 17 mm. *P. leptota* Lundell; Mexico, *D. Breedlove* 9724 (MADw 23924), 48 mm. *P. rekoii* Standl.; Guatemala, *S.J. Record and H. Kuylen* 44 (MADw 10989), 50 mm. *Rapanea australis* (A.Rich.) W.R.B.Oliv.; New Zealand, *A.M. Greeb* 1467 (Tw 19867), mature. *R. dependens* (Spreng.) Mez var. *petandra* Cuatrec.; Colombia, *J. Cuatrecasas* 20138 (Tw 39726), mature. *R. gracicolor* Mildbr.; Africa: near Tanganyika, *Reinbek* 1660 (Uw 15570), 35 mm. *R. guianensis* (Aubl.) Kuntze; Surinam, *H.P. Bottelier* 2605 (BR), 18 mm. *R. melanophloeos* (L.) Mez; Rwanda, *G. Troupin* 14490 (Tw 26067), mature. *R. quaternata* Hassl.; Paraguay, *Lindeman et al.* 1496 (Uw 13111), 35 mm. *Stylogyne amplifolia* Macbr.; Peru, *Mathias and Taylor* 5469 (Uw 27158), 38 mm. *S. amplifolia* Macbr.; Peru, *J. Schunke* 4374 (MADw 38788), 30 mm. *S. latifolia* A.C.Sm.; Guyana, *M. Jansen et al.* 5662 (Uw 30535), 45 mm. *S. standleyi* Lundell; Panama, *M. Nee* 9472 (MADw 32560), 51 mm. *S. venezuelana* Mez; Venezuela, *L. Williams* 11984 (MADw 34251), mature. *Synardisia venosa* (Donn.Sm.) Lundell; Mexico, *D. Breedlove* 15400 (MADw 23969), 60 mm. *Tapeinosperma nectandroides* Mez; New Caledonia, *P. Sarlin* 132 (Tw 30578), 12 mm. *Theophrasta americana* L.; Dominican Republic: Hispaniola, *W.L. Abbott* s.n. (SJRw 7447), 30 mm. *Wallenia grisebachii* Mez; Jamaica, *Miller* 1365 (MADw 20765), 40 mm. *W. laurifolia* Sw.; Dominican Republic, *Abbott* 2519 (MADw 19894), 42 mm.