Relationships within balsaminoid Ericales: a wood anatomical approach[1]

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Wood samples of 49 specimens representing 31 species and 11 genera of woody balsaminoids, i.e., Balsaminaceae, Marcgraviaceae, Pellicieraceae, and Tetrameristaceae, were investigated using light microscopy and scanning electron microscopy. The wood structure of Marcgraviaceae, Pellicieraceae, and Tetrameristaceae is characterized by radial vessel multiples with simple perforation plates, alternate vessel pitting, apotracheal and paratracheal parenchyma, septate libriform fibers, and the presence of raphides in ray cells. Tetrameristaceae and Pellicieraceae are found to be closely related based on the occurrence of unilaterally compound vessel-ray pitting and multiseriate rays with long uniseriate ends. The narrow rays in *Pelliciera* are characteristic of this genus, but a broader concept of Tetrameristaceae including *Pelliciera* is favored. Within Marcgraviaceae, wide rays (more than five-seriate) are typical of the genus *Marcgravia*. Furthermore, there is evidence that the impact of altitude and habit plays an important role in the wood structure of this family. The wood structure of Balsaminaceae cannot be compared systematically with other balsaminoids because of their secondary woodiness. Balsaminaceae wood strongly differs due to the presence of exclusively upright ray cells in *Impatiens niamniamensis*, the absence of rays in *Impatiens arguta*, and the occurrence of several additional paedomorphic features in both species.

Key words: Balsaminaceae; balsaminoid clade; Ericales; Marcgraviaceae; paedomorphism; Pellicieraceae; Tetrameristaceae; wood anatomy.

The balsaminoid clade of Ericales comprises Balsaminaceae, Marcgraviaceae, Pellicieraceae, and Tetrameristaceae (Anderberg et al., 2002; Bremer et al., 2002). These families include a total number of 12 genera and about 1130 species, depending on the number of species accepted within *Impatiens* L. (more than 900 and still increasing according to Yuan et al., 2004; about 1000 according to Fischer, 2004). Balsaminaceae, which include the monotypic *Hydrocera* Blume and the huge genus *Impatiens*, are predominantly herbaceous and often grow in montane areas of the tropics and subtropics of the Old World. Only a few *Impatiens* species have a stem with a woody base, while the three other families are all woody. The neotropical Marcgraviaceae, comprising seven genera and about 130 species, include many lianas but also climbing shrubs and some trees (Dressler, 2004). The mangrove tree *Pelliciera rhizophorae* Planch. & Triana, the only representative of Pellicieraceae, grows in tidal swamps along the Pacific coast from Costa Rica to Ecuador (Kobuski, 1951) and more sparsely on the Atlantic coast of Nicaragua, Panama, and Colombia (Roth and Grijalva, 1991). The two genera of Tetrameristaceae have a peculiar distribution pattern: *Tetramerista* Miq. is represented by large trees growing in tropical Southeast Asia, while the monotypic *Pentamerista* Maguire is a shrub or small tree occurring in the Guayana Highlands of Venezuela (Maguire et al., 1972).

The balsaminoid clade, which is sister to all other ericalean families, is one of the few groups in Ericales that is well supported based on molecular sequence data (Savolainen et al., 2000; Soltis et al., 2000; Anderberg et al., 2002; Bremer et al., 2002; Geuten et al., 2004). Marcgraviaceae, Pellicieraceae, and Tetrameristaceae were considered to be closely related by most earlier botanists, and Hallier (1916, 1921) even placed them in one family. On the other hand, the inclusion of Balsaminaceae is surprising because of the aberrant systematic position of this family in previous morphological classifications (Cronquist, 1988; Dahlgren, 1989; Takhtajan, 1997; Thorne, 2000). Furthermore, interfamily relationships within the balsaminoid clade remain obscure. It is clear that *Pelliciera* is closely related to Tetrameristaceae, and should possibly be merged in Tetrameristaceae sensu lato (s.l.) (Bremer et al., 2002; APG II, 2003), but the question of whether this family is more related to Marcgraviaceae than to Balsaminaceae is still a matter of dispute. Anderberg et al. (2002) suggest that Balsaminaceae take the most basal position with Marcgraviaceae sister to Pellicieraceae and Tetrameristaceae, while in the analyses of Bremer et al. (2002) Marcgraviaceae turn out to be the most basal family with Balsaminaceae sister to Tetrameristaceae s.l. In addition, the balsaminoid clade according to Geuten et al. (2004) is divided into two sister clades, a Balsaminaceae-Marcgraviaceae clade and a Pellicieraceae-Tetrameristaceae clade.

Intrafamily relationships of Balsaminaceae and Marcgraviaceae are far from being resolved. Within *Impatiens*, the delimitation of species groups is very difficult due to hybridization processes (Grey-Wilson, 1980). Molecular analyses of ITS sequence data revealed some interesting new relationships

within *Impatiens*, although the basal groups remain poorly understood (Yuan et al., 2004). Within Marcgraviaceae, variation in inflorescences and differences in the shape and position of nectary bracts resulted in three new genera that were recently elevated from the *Norantea* Aubl. s.l. complex, i.e., *Marcgraviastrum* (Wittm. ex Szyszyl.) de Roon & S. Dressler, *Sarcopera* Bedell, and *Schwartzia* Vell. (de Roon and Dressler, 1997). Phylogenetic analyses based on chloroplast sequences supported two subfamilies, Marcgravioideae (including *Marcgravia* L.) and Noranteoideae (including all other genera), but relationships within Noranteoideae were poorly resolved (Ward and Price, 2002).

The wood structure of the balsaminoid clade has received only little attention. Wood samples of *Pelliciera* were studied by Record (1942) and Baretta-Kuipers (1976), and Tetrameristaceae were investigated by Maguire et al. (1972). A wood anatomical comparison of Tetrameristaceae, Pellicieraceae, and Marcgraviaceae was made by Bedell (1980) in her unpublished master's thesis. Consequently, the secondary xylem of Marcgraviaceae is poorly known, and only a few studies deal with some representatives of this family, such as Juel (1887), Beauvisage (1920), Williams (1936), Vestal (1937), Record and Hess (1943), Metcalfe and Chalk (1950), de Roon (1975), and Dressler (1994). Furthermore, as far as we know, only one paper described very briefly the wood structure of an *Impatiens* species (Gerard, 1917).

This study provides detailed wood anatomical descriptions of the poorly known families Balsaminaceae and Marcgraviaceae, which are compared with additional observations of Pellicieraceae and Tetrameristaceae. Wood anatomical variation in Marcgraviaceae will be used to test intrafamily relationships and to determine to what extent differences in habit and altitude may influence the secondary xylem. Within the predominantly herbaceous Balsaminaceae, the possibility of secondary woodiness of two *Impatiens* species is investigated. The wood anatomical variation observed will be used to comment on the difficult interfamily relationships within the balsaminoid clade.

MATERIALS AND METHODS

Wood samples of 49 specimens representing 31 species and 11 genera were investigated using LM and SEM. Transverse and longitudinal sections of approximately 25 μm were cut using a sledge microtome (Reichert, Vienna, Austria). After bleaching, the sections were stained with a mixture of safranin and alcian blue (35 : 65), dehydrated in an ethanol series (50, 75, 96%) and mounted in Euparal (Agar Scientific, Stansted, UK). Macerations were prepared according to Franklin (1945). Sections were observed using a Dialux 20 light microscope (Leitz, Wetzlar, Germany) and photographed with a DP50-CU digital camera (Olympus, Hamburg, Germany). Wood sections for SEM observations were gold-coated with a sputter coater (SPI Supplies, West Chester, Pennsylvania, USA), and observed using a JEOL JSM-5800 LV scanning electron microscope (JEOL, Tokyo, Japan).

The wood anatomical terminology follows the ''IAWA list of microscopic features for hardwood identification'' (IAWA Committee, 1989). In order to investigate the impact of altitude and habit on the wood of Marcgraviaceae, four groups were made. These four groups include 16 climbing lowland specimens (growing under 1000 m), four climbing montane species (occurring above 1000 m), two erect species from the lowlands, and three erect species from the montane regions. Only species with mature wood were taken into account. In general, a stem diameter of 15 mm or more was considered to include mature wood, except for the mature wood specimen *Marcgravia pedunculosa* Triana & Planch. (Uw 4837, 12 mm). In addition, the wood specimen of *Marcgravia brownei* (Triana & Planch.) Krug & Urb. (FR, 15 mm)

was considered to be juvenile because of the large amount of pith parenchyma tissue. The species used in the four categories are indicated in Table 2. Statistical differences were calculated at the 0.5% level using the software program Statistics Calculator version 8.0. (StatPac Inc., Bloomington, Indiana, USA).

In Pellicieraceae and Tetrameristaceae, libriform fibers are obviously present, but in Marcgraviaceae it is sometimes difficult to distinguish between fiber-tracheids and libriform fibers because many intermediate fiber types occur according to the definitions of Baas (1986a) and Carlquist (2001). Therefore, we prefer to give a detailed description of these fibers. For all quantitative data on fibers, 25 measurements based on clearly identifiable cells in maceration slides were taken into account.

The wood samples studied are listed in Table 1 with reference to the origin, collector, and the diameter of the wood sample in millimeters.

RESULTS

The material studied is described according to family. For each genus examined, the numerator gives the number of species studied and the denominator includes the total number of species. Numbers between brackets are extreme values. Values for vessel multiples, pits, bar number, axial parenchyma cells per strand, ray width, and ray density are maximum ranges. A summary of the results is presented in Table 2.

***Balsaminaceae (Impatiens 2/ca. 1000; Figs. 1–7)*—**Growth ring boundaries absent. Wood diffuse-porous. Vessels (10)–30–50–(64)/mm², usually solitary (Figs. 1–2), occasionally in radial multiples of 2–3, vessel outline angular. Vessel perforation plates generally simple (Fig. 5), but very few scalariform perforations with 1–3 bars in *I. arguta* Hook. f. & Thoms. Lateral wall pitting mostly scalariform or sometimes reticulate (Figs. 6–7), minutely bordered, pit cavities 10–75 μm in horizontal size, non-vestured. Tangential diameter of vessels (25)–40–80–(100) μm, vessel elements (130)–210–300–(450) μm long; vessels storied in *I. niamniamensis* Gilg; thin-walled tyloses abundant in vessels of *I. niamniamensis* (Figs. 2, 4). Tracheids absent. Fibers non-septate, thin-walled, and relatively wide, (360)–570–640–(900) μm long, with mostly simple to occasionally minutely bordered pits equally distributed in radial and tangential walls, pits 1–3 μm in diameter, fibers occasionally storied in both species. Axial parenchyma scanty paratracheal in *I. arguta* (Fig. 1), 3–7 cells per strand; abundant in *I. niamniamensis* (Fig. 2), vasicentric or in bands of 2–3 cells wide, sometimes up to 5 cells, 1–2 cells per strand. Rays absent in tiny stem of *I. arguta* (Fig. 3), but exclusively multiseriate in *I. niamniamensis*, ray cells storied (Fig. 4), 11–21 cells wide (Figs. 2, 4), more than 7000 μm high, 1–2 rays/mm, consisting of upright cells only; sheath cells absent; very small simple pits between ray cells, usually 2 μm in horizontal size. Rare occurrence of raphides in tyloses of *I. niamniamensis*.

***Marcgraviaceae (Marcgravia 13/60, Marcgraviastrum 2/15, Norantea 2/2, Ruyschia Jacq. 2/7, Sarcopera 1/10, Schwartzia 4/14, Souroubea Aubl. 3/19; Figs. 8–20)*—**Growth ring boundaries usually indistinct by changes in fiber diameter and wall thickness, growth rings sometimes absent. Wood diffuse-porous. Vessels (2)–4–90–(100)/mm², solitary or in radial multiples of mostly 2–4, sometimes up to seven vessels, vessel outline rounded (Figs. 8–10). Vessel perforation plates predominantly simple in mature wood (Fig. 14), scalariform perforations with 1–11 bars common in metaxylem and sporadic in mature wood (Fig. 15). Intervessel pits alternate,

TABLE 1.   Species list with reference to the family, origin, collector, and the diameter of the wood sample in millimeters. "Mature" means that the wood sample is derived from mature wood with an estimated diameter of at least 30 mm based on the divergence of the rays, although the exact diameter could not be traced. Institutional wood collections and herbaria used in this study are abbreviated according to the Index Xylariorum (Stern, 1988) and Index Herbariorum (Holmgren et al., 1990). Authors of plant names are abbreviated according to Brummitt and Powell (1992).

Species studied	Family	Origin	Collector	Diameter
Impatiens arguta Hook. f. & Thoms.	Balsaminaceae	China	Y.-M. Yuan and X.-J. Ge 2003–57	2 mm
I. niamniamensis Gilg	Balsaminaceae	tropical Africa	unknown (BR)	6 mm
Marcgravia brachysepala Urb.	Marcgraviaceae	Jamaica	Thorne and Proctor 48220 (NY)	10 mm
M. brownei (Triana & Planch.) Krug & Urb.	Marcgraviaceae	Venezuela	F. J. Breteler 3246 (Uw 10998)	58 mm
M. brownei (Triana & Planch.) Krug & Urb.	Marcgraviaceae	Nicaragua	S. Dressler and G. Zizka 325 (FR)	15 mm
M. coriacea Vahl	Marcgraviaceae	Guyana	M. A. Reinders and A. Thom 135 (Uw 34636)	34 mm
M. evenia Krug & Urb. subsp. *evenia*	Marcgraviaceae	Cuba	Flora Cuba Project 52315 (B)	6 mm
M. evenia Krug & Urb. subsp. *calcicola* (Britton) S. Dressler	Marcgraviaceae	Cuba	S. Dressler s.n. (B)	11 mm
M. oligandra Griseb.	Marcgraviaceae	Cuba	Flora Cuba Project 49159 (B)	7 mm
M. pendunculosa Triana & Planch.	Marcgraviaceae	Surinam	R. S. Cowan and J. C. Lindeman 39177 (Uw 4837)	12 mm
M. pendunculosa Triana & Planch.	Marcgraviaceae	Surinam	Land-, Bos- en Bouwbeheer 15302 (Uw 21928)	15 mm
M. pendunculosa Triana & Planch.	Marcgraviaceae	Surinam	J. C. Lindeman 4177 (Uw 3107)	51 mm
M. purpurea I.W. Bailey	Marcgraviaceae	Surinam	J. C. Lindeman et al. 448 (Uw 21819)	34 mm
M. rectiflora Triana & Planch.	Marcgraviaceae	Puerto Rico	P. Sintenis 4461 (MO)	9 mm
M. schippii Standl.	Marcgraviaceae	Panama	R. Mangelsdorff and G. Zizka RMP 1316 (FR)	18 mm
M. sintenisii Urb.	Marcgraviaceae	Puerto Rico	P. Sintenis 5321 (BR)	10 mm
M. sintenisii Urb.	Marcgraviaceae	Puerto Rico	B. Boom 6893 (NY)	8 mm
M. sp.	Marcgraviaceae	Surinam	Schulz 7750 (Uw 5090)	40 mm
M. stonei Utley	Marcgraviaceae	Mexico	S. Dressler s.n. 17.3.2004 (FR)	21 mm
M. tobagensis Urb.	Marcgraviaceae	Tobago	R. S. Cowan 1420 (S)	4 mm
M. umbellata L.	Marcgraviaceae	Dominica	K. L. Chambers 2518 (Uw 15399)	22 mm
M. umbellata L.	Marcgraviaceae	Dominica	W. H. Hodge 1048 (USw)	6 mm
M. umbellata L.	Marcgraviaceae	Saba	I. Boldingh 2275B (U)	6 mm
Marcgraviastrum mixtum (Triana & Planch.) Bedell	Marcgraviaceae	Colombia	A. E. Lawrence 504 (Tw 34691)	13 mm
M. subsessile (Benth.) Bedell	Marcgraviaceae	Panama	R. Mangelsdorff and G. Zizka RMP 1313 (FR)	11 mm
Norantea goyasensis Cambess.	Marcgraviaceae	Brazil	B. Maguire et al. 56587 (Uw 16440)	32 mm
N. guianensis Aubl.	Marcgraviaceae	Surinam	G. Stahel 2998 (Tw 31227)	35 mm
N. guianensis Aubl. subsp. *japurensis* (Mart.) Bedell	Marcgraviaceae	Venezuela	J. J. Wurdack and L. S. Adderley 43256 (USw 17934)	mature
N. guianensis Aubl. subsp. *japurensis* (Mart.) Bedell	Marcgraviaceae	Brazil	B. A. Krukoff 8915 (BR)	9 mm
Pelliciera rhizophorae Planch. & Triana	Pellicieraceae	Colombia	J. Cuatrecasas 19999 (Tw 39723, MADw 17595)	mature
Pelliciera rhizophorae Planch. & Triana	Pellicieraceae	Panama	S. Dressler s.n. 26.2.2004 (FR)	31 mm
Pentamerista neotropica Maguire	Tetrameristaceae	Venezuela	B. Maguire et al. 42865 (Tw 36842)	mature
Pentamerista neotropica Maguire	Tetrameristaceae	Venezuela	J. J. Wurdack and L. S. Adderley 42865 (MADw 23508)	mature
Ruyschia sp.	Marcgraviaceae	Colombia	J. van Rooden et al. 402 (Uw 25576)	32 mm
R. tremadena (Ernst) Lundell	Marcgraviaceae	Venezuela	L. Williams 10021 (Uw 35102)	24 mm
Sarcopera tepuiensis (de Roon) Bedell subsp. *coccinea* de Roon & S. Dressler	Marcgraviaceae	Venezuela	B. Maguire and L. Politi 28537 (Tw 36561)	43 mm
S. tepuiensis (de Roon) Bedell subsp. *tepuiensis*	Marcgraviaceae	Guyana	P. Maas et al. 5712 (Uw 27336)	42 mm
Schwartzia adamantium (Cambess.) Gir.-Cañas	Marcgraviaceae	Brazil	de Haas and de Haas 441 (Uw 14447)	29 mm
S. costaricensis (Gilg) Bedell	Marcgraviaceae	Panama	H. van der Werff and van Hardeveld 6825 (Uw 31172)	23 mm
S. diaz-piedrahitae Gir.-Cañas	Marcgraviaceae	Colombia	J. Cuatrecasas 17214 (Uw 25408)	60 mm
S. spiciflora (A.L. Juss.) Bedell	Marcgraviaceae	Dominica	K. L. Chambers 2648 (USw 33930)	mature
Souroubea guianensis Aubl. subsp. *cylindrica* (Wittm.) de Roon	Marcgraviaceae	Venezuela	B. Maguire and J. J. Wurdack 42076 (Tw 36495)	18 mm
S. guianensis Aubl. subsp. *guianensis*	Marcgraviaceae	Surinam	B. Maguire 24680 (Uw 2652)	35 mm
S. sp.	Marcgraviaceae	unknown	J. C. Lindeman 5382 (Uw 3931)	42 mm
S. sp.	Marcgraviaceae	Panama	S. Dressler s.n., 20.2.2004 (FR)	38 mm
S. sympetala Gilg	Marcgraviaceae	Venezuela	F. J. Breteler 3723 (Uw 11050)	15 mm
S. sympetala Gilg	Marcgraviaceae	Panama	S. Dressler s.n., 28.2.2004 (FR)	12 mm
Tetramerista glabra Miq.	Tetrameristaceae	Borneo	collector unknown (Tw 3836)	mature
Tetramerista glabra Miq.	Tetrameristaceae	Malaysia	H. E. Desch 3750 (MADw 35871)	mature

TABLE 2. Overview of some wood anatomical features within the balsaminoid clade. Numbers between hyphens are mean values. For specimens of the same taxon, superscripted numbers following the species name refer to the order of the specimens as followed in the species list (see Table 1). An asterisk indicates juvenile samples. ALT = altitude (L = lowland, M = montane), DENS = density of vessels (/mm²), DIAM = tangential vessel diameter (μm), DMR = density multiseriate rays (/mm), DUR = density uniseriate rays (/mm), FL = fiber length (μm), HAB = habit (C = climbers, E = erect species), HMR = height multiseriate rays (μm), MRW = multiseriate ray width (no. cells), NB = number of bars per plate, RAP = raphides present in rays, SP = percentage of scalariform perforations, VEL = vessel element length (μm), + = present, − = absent.

Species studied	HAB	ALT	SP	NB	DIAM	DENS	VEL	FL	MRW	HMR	DUR	DMR	RAP
Impatiens arguta*	E	M	<5	1-3	25-46-60	40-48-64	130-207-330	360-568-900	—	—	—	—	—
I. niamniamensis	E	M	0	0	45-76-100	10-29-46	170-296-450	520-640-880	11-21	>7000	—	0-1	—
Marcgravia sp.	C	L	0	0	48-144-248	6-11-15	460-733-925	630-845-1292	5-13	9420->10880	1-2	1-3	+
M. brachysepala*	C	L	0	0	90-176-300	10-13-17	330-494-560	520-681-830	2-4	900->3000	1-4	3-5	+
M. brownei[1]	C	L	0	0	90-206-362	4-6-9	545-786-1300	815-1020-1340	6-42	7350->9600	0-4	2-4	+
M. brownei[2]*	C	L	0	0	45-127-184	11-16-22	570-737-850	680-810-1000	2-5	1300-3507-5825	0-4	3-6	+
M. coriacea	C	L	0	0	100-278-480	3-4-5	650-945-1170	793-1282-1679	2-4	6990->8400	0-4	1-3	+
M. evenia*	C	L	0	0	28-49-72	26-34-46	380-531-860	625-815-1050	3-6	1500-4100-6000	4-5	1-3	+
M. evenia subsp. calcicola*	C	L	0	0	140-182-220	13-16-19	575-715-750	550-806-880	4-13	8700-10167-10300	1-2	1-3	+
M. oligandra*	C	L	<5	2-3	42-52-63	18-27-24	350-624-780	580-835-1070	3	850-2550-4100	0-1	4-6	—
M. pedunculosa[1]	C	L	0	0	75-153-262	3-5-7	518-681-820	450-670-905	4-11	1490-3792-9750	0-2	1-3	+
M. pedunculosa[2]	C	L	0	0	75-110-275	9-12-16	495-598-675	520-615-1410	4-11	2440-3754-6890	0-3	1-3	+
M. pedunculosa[3]	C	L	0	0	89-165-256	8-12-14	545-719-825	430-725-890	5-11	6230->7900	0-2	1-3	+
M. purpurea	C	L	0	0	98-180-294	7-9-11	612-863-1350	550-990-1900	2-37	9545->10150	0-3	1-3	+
M. rectiflora*	C	L	<5	2-3	48-66-90	30-40-52	450-667-910	500-834-1150	2-6	>10000	2-3	3-5	—
M. schippii	C	L	5	1-3	45-71-110	18-26-42	620-764-880	850-1050-1250	3-4	1700->6300	1-2	3-4	—
M. sintenisii[1]*	C	L	5	4-8	30-60-89	28-38-50	535-749-1125	540-850-1200	3-4	1050-2892-9400	0-4	2-5	—
M. sintenisii[2]*	C	L	<5	3-6	45-71-100	28-31-34	500-669-850	600-908-1150	2-4	1100->8500	1-3	3-4	—
M. stonei	C	L	0	0	30-64-95	18-29-46	460-581-720	630-802-950	4-6	>6000	1-2	3-5	—
M. tobagensis*	C	L	0	0	40-56-75	64-88-100	400-533-600	650-785-900	2-4	>4300	2-4	4-6	—
M. umbellata[1]	C	L	0	0	82-204-322	8-11-12	427-658-823	800-955-1190	2-4	1000-2711-6000	2-5	4-7	—
M. umbellata[2]*	C	L	5	3-9	30-57-105	25-36-50	400-558-860	575-724-900	2-6	>9400	4-7	3-4	—
Marcgraviastrum mixtum	C	M	0	0	60-167-282	2-4-7	612-793-995	730-1026-1360	2-4	6270->6300	1-6	1-3	+
M. subsessile*	E	M	30	3-9	25-58-80	24-27-34	730-875-1020	950-1333-1700	3-6	1200-2375-3200	5-13	1-4	—
Norantea goyasensis	E	L	0	0	82-230-458	2-4-6	775-965-1125	820-1310-1680	3-7	1080-2163-4505	0-5	2-6	+
N. guianensis	C	L	10	1-3	119-233-377	2-4-6	995-1104-1362	1145-1628-2285	2-4	2725-3828-6500	1-3	0-3	—
N. guianensis subsp. japurensis[1]	C	L	20	2-5	45-76-140	3-6-9	550-806-1010	700-1100-1500	2-3	1000-1975-3300	0-3	2-5	—
N. guianensis subsp. japurensis[2]*	C	L	10	2-8	42-71-95	12-18-26	605-795-992	650-980-1220	2-4	850-1988-4850	0-3	4-6	—
Ruyschia tremadena	C	M	10	1-11	92-198-331	4-7-11	900-1088-1305	750-1480-1995	2-3	995-2034-4420	2-5	1-3	+
Ruyschia sp.	E	L	5	2-5	37-86-148	7-10-13	650-1044-1300	990-1380-1750	3-6	2095-3090-4080	2-4	2-5	+
S. tepuiensis subsp. coccinea	C	M	0	0	95-232-405	3-5-9	519-815-1005	837-1014-1425	3-6	1010-2887-6705	1-5	2-5	+
S. tepuiensis subsp. tepuiensis	C	M	0	0	88-219-325	3-6-8	670-1025-1259	750-1630-2240	2-5	2150-3650-6800	0-2	3-5	+
Schwartzia adamantium	E	M	10	2-4	53-124-200	6-8-13	442-647-812	550-930-1340	2-7	1550-2436-3780	2-6	2-6	+
S. costaricensis	E	M	20	1-5	56-98-150	9-14-20	421-615-1005	630-1040-1990	2-3	1100-1968-4220	0-4	2-5	+
S. diaz-piedrahitae	C	L	0	0	95-234-373	3-5-7	432-838-1000	620-1020-1300	3-6	3600->5490	0-4	1-3	+
S. spiciflora	E	M	60	5-10	45-76-140	11-19-25	405-852-1159	550-1070-1700	2-3	1300-1855-2315	2-6	1-4	+
Souroubea sp.[1]	C	L	0	0	73-177-312	10-15-21	562-738-942	610-840-1200	2-3	520-1033-2265	1-5	4-7	—
S. sp.[2]	C	L	0	0	100-206-300	5-8-12	600-828-1100	980-1203-1450	3-5	>6000	2-4	2-4	+
S. guianensis subsp. cylindrica	C	L	20	4-7	75-199-282	6-8-10	819-993-1105	910-1250-1580	2-4	1720-3088-6570	2-6	1-4	+
S. guianensis subsp. guianensis	C	L	0	0	144-253-400	3-5-6	415-803-1112	760-1215-1500	2-5	3882->6765	0-8	1-4	+
S. sympetala[1]	C	L	0	0	80-229-355	4-6-7	575-932-1280	820-1250-1600	2-5	8850->9085	1-4	2-5	+
S. sympetala[2]*	C	L	10	5-11	100-131-170	15-18-20	450-683-880	900-1094-1250	3	>6000	2-4	4-5	—
Pelliciera rhizophorae[1]	E	L	0	0	45-60-80	17-23-30	420-588-750	950-1146-1450	2	600-1400-2400	10-16	1-3	+
P. rhizophorae[2]	E	L	0	0	55-65-80	13-18-24	480-669-850	950-1220-1400	2	550-1186-2100	11-15	0-1	+
P. rhizophorae[3]	E	L	0	0	40-56-70	38-49-58	280-498-680	650-950-1100	—	—	10-14	—	+
Pentamerista neotropica[1]	E	M	5	2-5	55-96-175	9-13-18	620-834-1300	1500-2038-2250	3-4	1300-2588-4200	3-6	4-5	+
P. neotropica[2]	E	M	0	0	65-97-120	12-18-22	470-756-1020	1500-1736-1950	3-5	1000-1946-3700	3-5	3-4	+
Tetramerista glabra[1]	E	L	0	0	110-166-225	4-6-9	1080-1446-1950	2650-3071-3500	3-4	1500-2929-4700	3-5	3-6	+
T. glabra[2]	E	L	0	0	110-151-195	3-5-7	800-1148-1500	2050-2444-2900	2-4	1800->6000	6-9	2-3	+
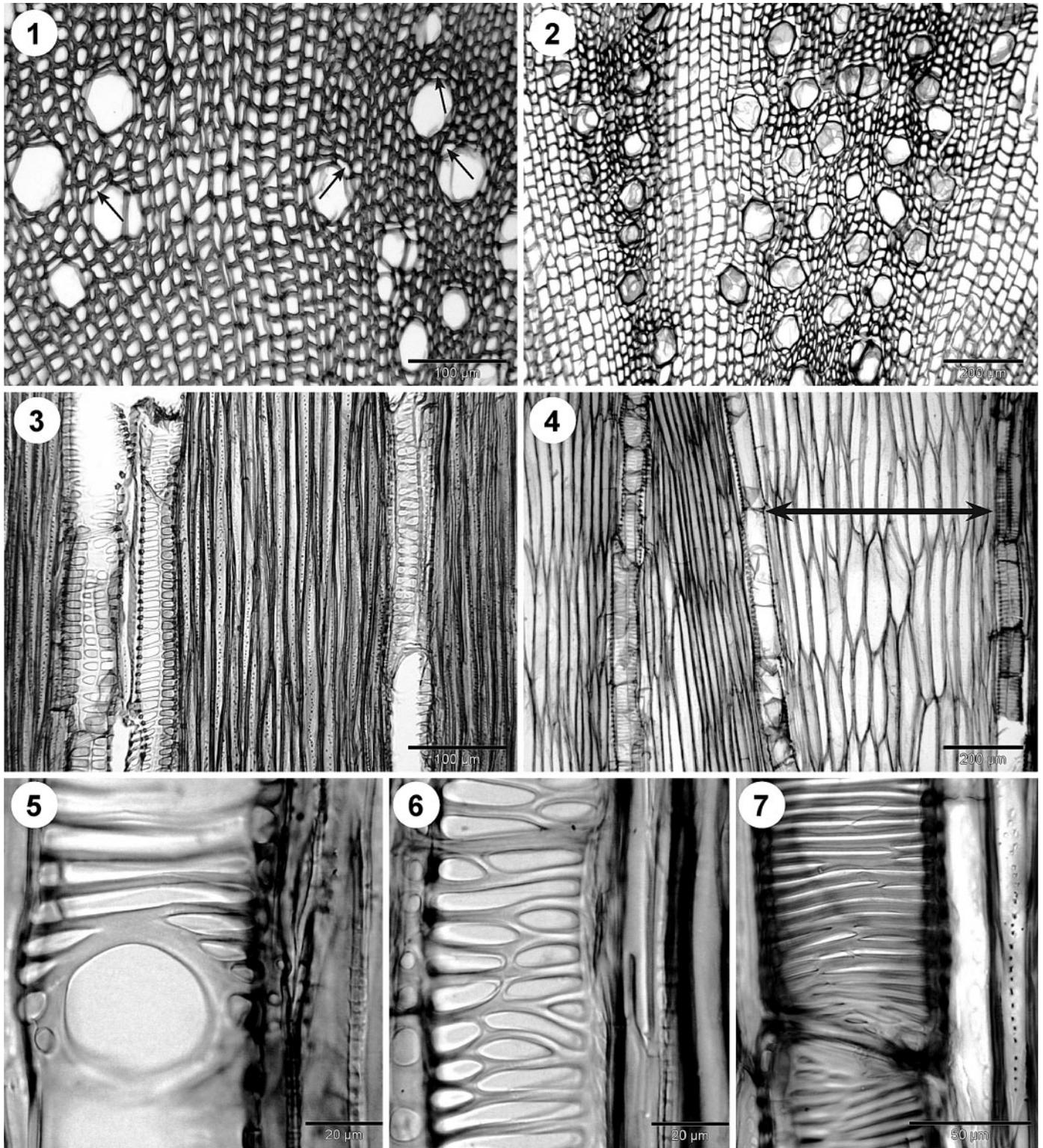
Figs. 1–7. Wood anatomical sections of Balsaminaceae (LM). **1.** *Impatiens arguta*: transverse section (TS), vessels mainly solitary, scanty paratracheal parenchyma (arrows), radial band of wide thin-walled libriform fibers near the center of the image. **2.** *I. niamniamensis*: TS, vessels mainly solitary, wide bands of rays alternating with zones including vessels, thin-walled fibers and parenchyma cells. **3.** *I. arguta*: tangential longitudinal section (TLS), thin-walled fibers, scalariform vessel pitting, and lack of rays. **4.** *I. niamniamensis*: TLS, storied thin-walled fibers (center), wide multiseriate ray with storied ray cells (arrow). **5.** *I. arguta*: radial longitudinal section (RLS), simple vessel perforation. **6.** *I. arguta*: TLS, wide reticulate vessel pitting with strongly reduced borders. **7.** *I. niamniamensis*: TLS, wide scalariform vessel pitting with reduced borders.
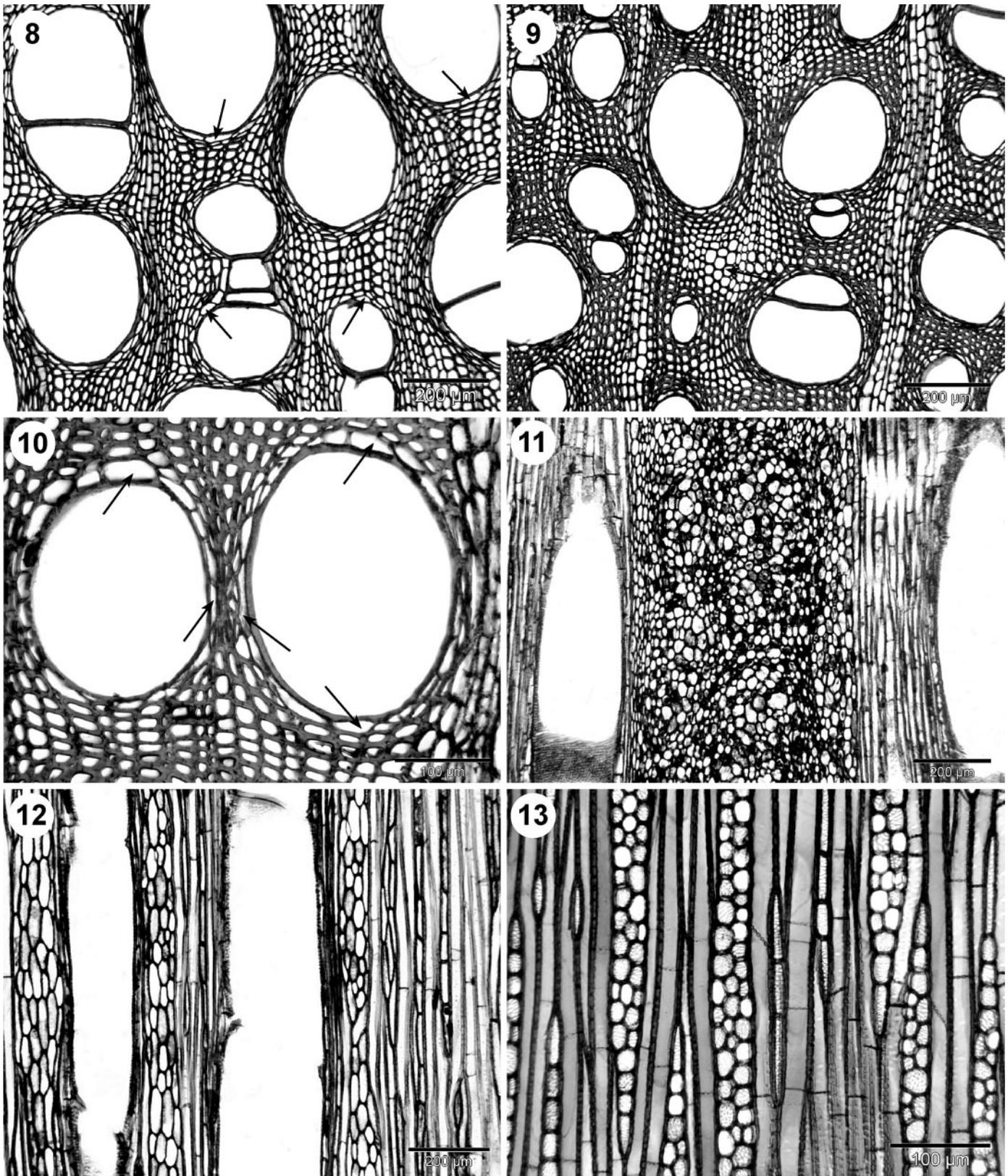
Figs. 8–13.   Transverse and tangential longitudinal sections of Marcgraviaceae (LM). **8.** *Marcgraviastrum mixtum*: TS, vessels solitary or in small radial multiples, scanty paratracheal parenchyma (arrows). **9.** *Marcgravia pedunculosa* Uw 21928: TS, vessels, solitary or in small radial multiples, vasicentric paratracheal parenchyma, and apotracheal parenchyma in clusters (arrows). **10.** *M. pedunculosa* Uw 21928: TS, detail of vessels with vasicentric paratracheal parenchyma (arrows). **11.** *M. purpurea*: TLS, very wide multiseriate ray. **12.** *Sarcopera tepuiensis* subsp. *coccinea*: TLS, relatively narrow, multiseriate rays. **13.** *Souroubea* sp. Uw 3931: TLS, idem.
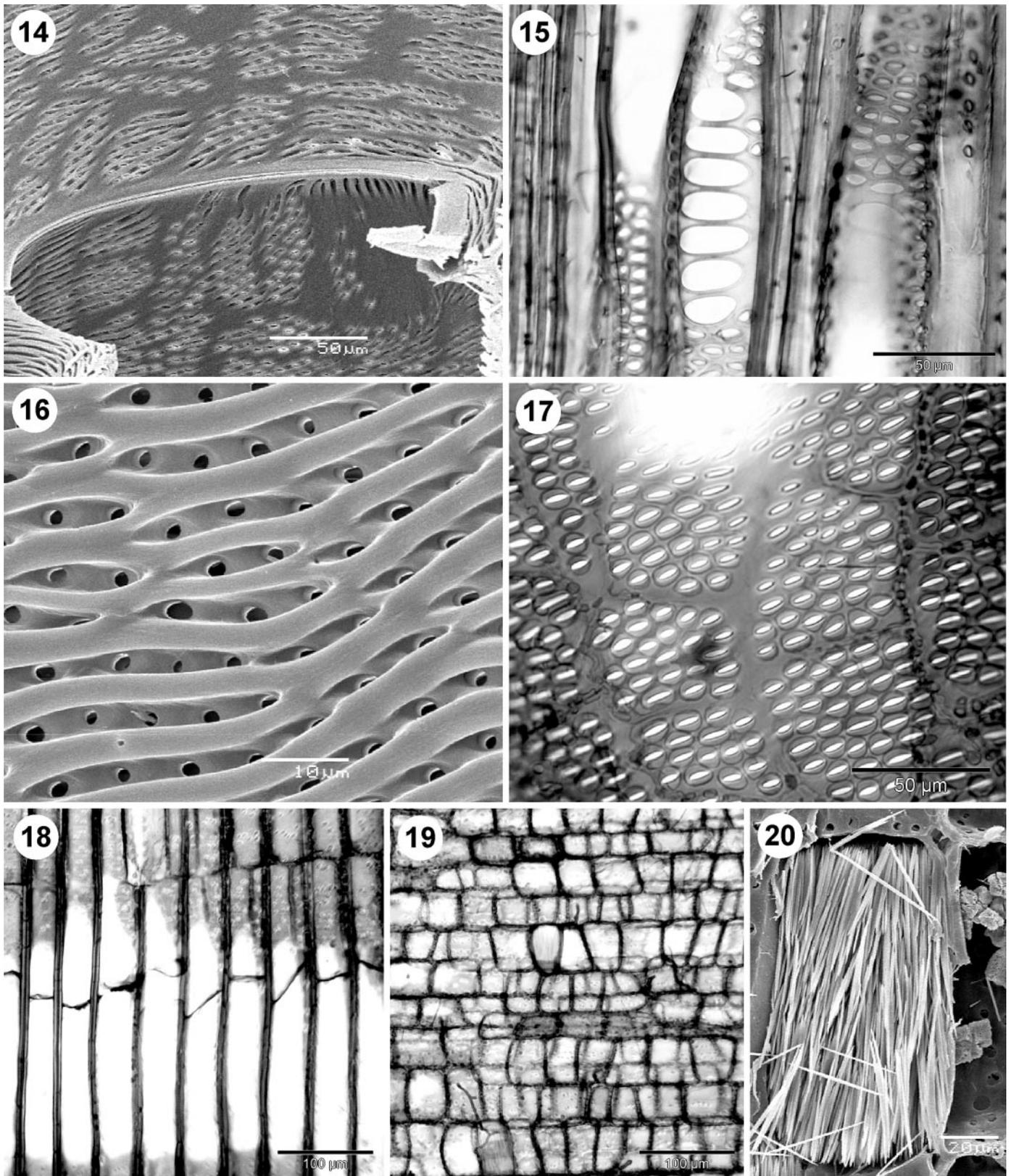
Figs. 14–20. Radial longitudinal surfaces (SEM) and sections (LM) of Marcgraviaceae. **14.** *Marcgravia umbellata* Uw 15399: SEM, simple vessel perforation. **15.** *Schwartzia spiciflora*: LM, scalariform vessel perforation. **16.** *M. umbellata* Uw 15399: SEM, coalescent pits in the inner wall of a vessel element. **17.** *M. umbellata* Uw 15399: LM, alternate vessel-ray pits. **18.** *Sarcopera tepuiensis* subsp. *coccinea*: LM, septate libriform fibers. **19.** *Marcgravia* sp.: LM, heterocellular multiseriate ray consisting of procumbent, square, and upright body ray cells. **20.** *Norantea goyasensis*: SEM, raphides in upright ray cell.

distinctly bordered, sometimes coalescent (Fig. 16), pits (3)–6–10–(20) µm in horizontal diameter, non-vestured. Vessel-ray pits mostly alternate and comparable to intervessel pits in shape and size (Fig. 17), but sometimes scalariform and distinctly bordered, pits (15)–18–25–(45) µm in horizontal diameter. Tangential diameter of vessels (25)–50–280–(480) µm, vessel elements (330)–490–1100–(1362) µm long. Tracheids absent. In *Marcgravia* and *Norantea*, septate fibers with indistinctly to distinctly bordered pits in tangential and radial walls common, pit density between 10–20 pits per 100 µm of fiber length in both walls, fibers thin-walled, (430)–610–1630–(2285) µm long, pit borders (2)–3–4–(6) µm in diameter; in the five other genera studied, septate fibers with simple to minutely bordered pits concentrated in radial walls dominant (Fig. 18), pit density between 10 and 20 pits per 100 µm of fiber length in radial walls and less than 5 pits per 100 µm of fiber length in tangential walls, fibers thin-walled, (550)–840–1630–(2240) µm long, pit borders 2–3 µm in diameter. Axial parenchyma vasicentric forming a one- (at some places two-) layered sheath around the vessels (Fig. 10), sometimes also apotracheal forming clusters in all genera (Fig. 9) in 3–8 celled strands. Uniseriate rays always present (Figs. 12–13), (150)–300–860–(1510) µm high, consisting of upright cells, 0–13 rays/mm. Multiseriate rays mostly 2–5-seriate (Figs. 12–13), but up to 42-seriate in *Marcgravia* (Fig. 11), (520)–1030–10 170–(>11 000) µm high, 0–7 rays/mm, heterocellular consisting mostly of square and upright body ray cells and less frequently procumbent body ray cells (Fig. 19), and two to more than four upright rows of marginal ray cells; sheath cells absent. Gummy deposits, probably tannins, in ray cells. Raphides predominantly present in upright ray cells of most species studied (see Table 2, Fig. 20).

Pellicieraceae (Pelliciera 1/1; Figs. 21–26)—Growth rings absent. Wood diffuse-porous. Vessels (13)–15–50–(58)/mm², sometimes solitary but usually in radial multiples of 2–9 (Figs. 21–22), exceptionally in clusters of 2–7 vessels (in MADw 17595), vessel outline slightly angular. Vessel perforation plates exclusively simple (Fig. 23). Intervessel pits alternate, distinctly bordered, pits 4–5 µm in horizontal diameter, non-vestured (Fig. 23). Vessel-ray pits similar to intervessel pits in shape and size, often unilaterally compound (Fig. 26). Helical sculpturing absent. Tangential diameter of vessels (40)–55–65–(80) µm, vessel elements (280)–500–670–(850) µm long. Tracheids absent. Fibers mostly septate, usually thin- to thick-walled, (650)–950–1220–(1450) µm long, with simple to minutely bordered pits concentrated in radial walls, pit borders 2–3 µm in diameter. Axial parenchyma scarce, diffuse apotracheal and scanty paratracheal (Fig. 22) in 2–3-celled strands. Uniseriate rays always present (Fig. 24), (550)–870–1300–(2250) µm high, consisting of upright cells, 10–16 rays/mm. Multiseriate rays absent in Dressler s.n., but 2–(3)-seriate in MADw 17595 and Tw 39723 (Fig. 24), with long uniseriate tails, (550)–1190–1400–(2400) µm high, 0–2 rays/mm, consisting mainly of square to upright (and sometimes procumbent) body ray cells and more than four rows of upright marginal ray cells (Fig. 25); sheath cells absent. No gummy deposits observed. Raphides present in upright ray cells.

Tetrameristaceae (Pentamerista 1/1, Tetramerista 1/1–3; Figs. 27–32)—Growth ring boundaries absent. Wood diffuse-porous. Vessels (9)–15–(22)/mm² in *Pentamerista* and (3)–5–(9)/mm² in *Tetramerista*, sometimes solitary but more often in radial multiples of 2–4–(6) (Figs. 27–28), occasionally clustered in *Pentamerista*, vessel outline angular. Vessel perforations simple in *Tetramerista*, predominantly simple but sometimes scalariform in *Pentamerista* with 2–5 bars. Intervessel pits alternate, distinctly bordered, pits 4–6 µm in horizontal diameter, non-vestured. Vessel-ray pits similar to intervessel pitting in shape and size, often unilaterally compound. Helical sculpturing absent. Tangential diameter of vessels (55)–100–(175) µm in *Pentamerista* and (110)–150–170–(225) µm in *Tetramerista*, vessel elements (470)–760–830–(1300) µm long in *Pentamerista* and (800)–1150–1450–(1950) µm in *Tetramerista*. Tracheids absent. Fibers sometimes septate, very thick-walled, length (1500)–1740–2040–(2250) µm in *Pentamerista* and (2050)–2440–3070–(3500) µm in *Tetramerista*, with simple to minutely bordered pits concentrated in radial walls, pit borders 2–3 µm in diameter. Axial parenchyma mainly diffuse to diffuse-in-aggregates but also scanty paratracheal (Figs. 27–28) in 4–9 celled strands. Uniseriate rays always present (Figs. 29–30), length (650)–1340–1880–(3200) µm in *Pentamerista* and (650)–1570–2690–(8600) µm in *Tetramerista*, consisting of upright cells, 2–6 rays/mm. Multiseriate rays 2–5-seriate (Figs. 29–30), sometimes connected by long uniseriate tails, length (1000)–1950–2590–(4200) µm in *Pentamerista* and (1500)–3500–(>6000) µm in *Tetramerista*, 2–6 rays/mm, consisting of procumbent and square body ray cells (Figs. 31–32) and more than four rows of upright marginal ray cells; sheath cells absent. Gummy deposits, possibly tannins, observed in *Tetramerista*. Raphides present in procumbent (*Tetramerista*) or procumbent and square ray cells (*Pentamerista*).

DISCUSSION

There are several disagreements between the descriptions given in this work and earlier studies, and this is especially the case for Marcgraviaceae. For example, Vestal (1937) and Metcalfe and Chalk (1950) mentioned that the wood structure of *Norantea* s.l. differs in many aspects from the wood of *Marcgravia* and *Souroubea*, but this is refuted in this study and in some previous studies (de Roon, 1975; Bedell, 1980). Furthermore, Bedell (1980) mentioned several features that could not be supported by us, i.e., vestured, opposite to transitional intervessel pits in *Ruyschia*, fibers with helical thickenings in *Marcgravia*, *Norantea* s.l., and *Souroubea*, predominantly homocellular rays consisting of mainly upright cells, and the presence of secretory canals in *Schwartzia*. This author also reported a lack of axial parenchyma in *Ruyschia* and *Schwartzia* and the absence of uniseriate rays in species of *Marcgravia*, *Ruyschia*, and *Souroubea*, two features that are present in all wood samples that we examined. According to our observations, at least some of these differences may be due to the juvenile nature of the wood. Indeed, some of our juvenile *Marcgravia* samples had very little axial parenchyma, almost no uniseriate rays, and multiseriate rays with exclusively upright ray cells. Previous wood anatomical descriptions of Tetrameristaceae and Pellicieraceae are similar to our results, although Bedell (1980) did not observe uniseriate rays in *Tetramerista*, a feature that was clearly observed by us.

Wood anatomical comparison of Marcgraviaceae, Pellicieraceae, and Tetrameristaceae—The close relationship of Marcgraviaceae, Pellicieraceae, and Tetrameristaceae is supported by several wood anatomical features, such as a high
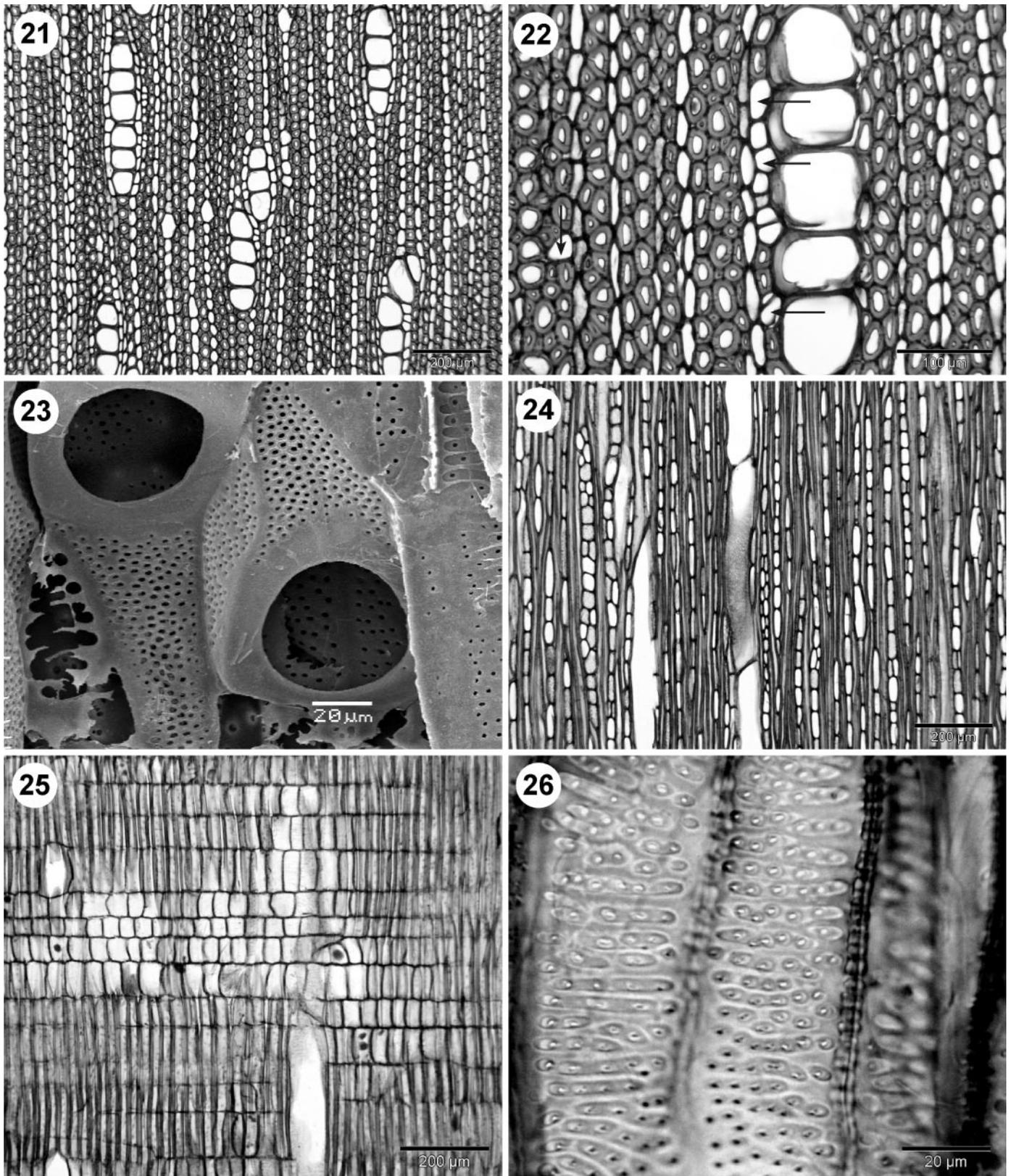
Figs. 21–26.   Wood anatomical sections (LM; Figs. 21–22, 24–26) and a radial longitudinal surface (SEM; Fig. 23) of *Pelliciera rhizophorae*. **21.** Tw 39723: LM, TS, vessels in long radial multiples. **22.** MADw 17595: LM, TS, axial parenchyma scanty paratracheal (horizontal arrows) and diffuse apotracheal (vertical arrow). **23.** Tw 39723: SEM, RLS, simple vessel perforations, alternate intervessel pits. **24.** Tw 39723: LM, TLS, uniseriate and narrow multiseriate rays. **25.** Tw 39723: LM, RLS, heterocellular, multiseriate ray consisting of square and upright cells. **26.** Tw 39723: LM, RLS, unilaterally compound vessel-ray pits.
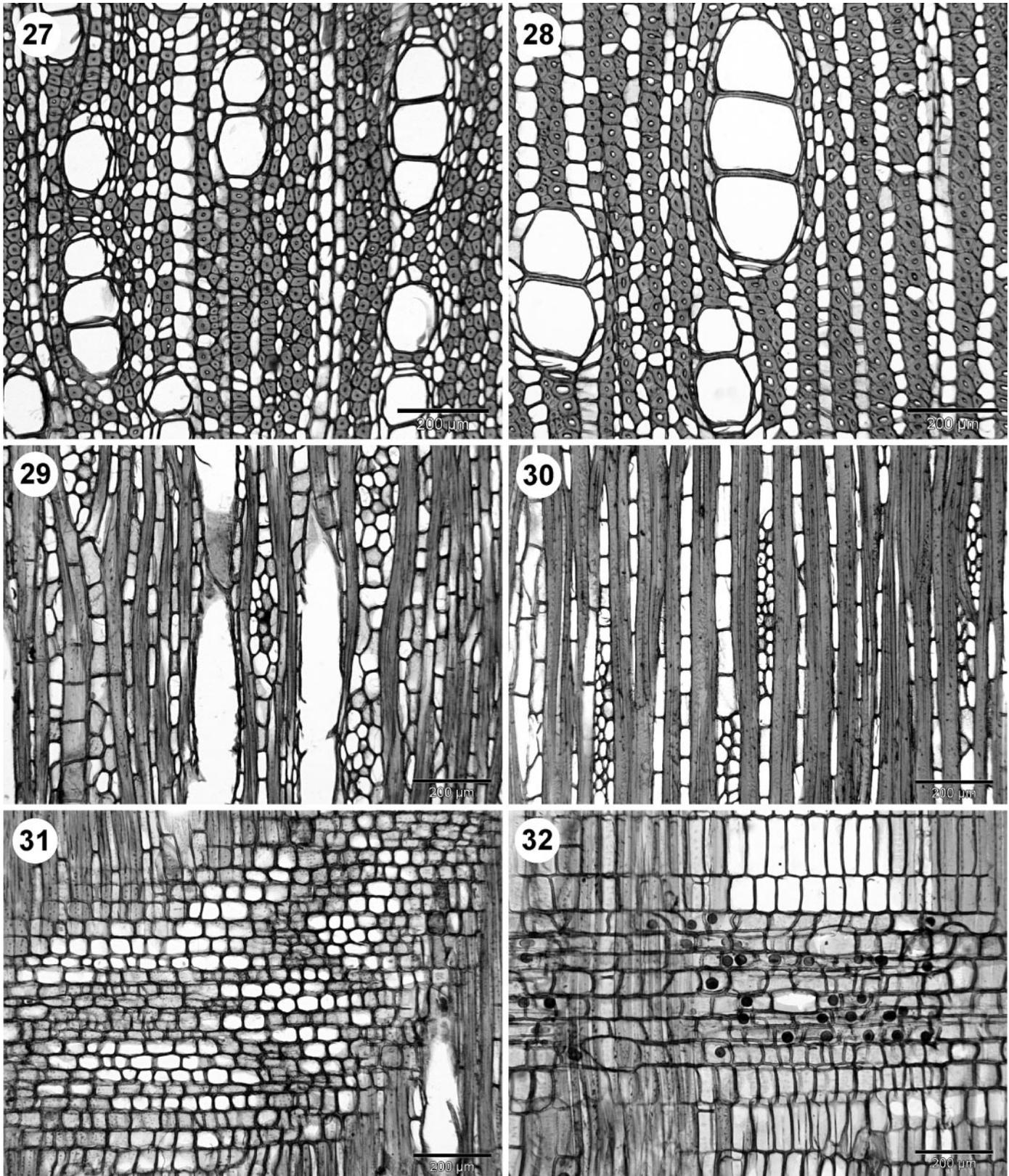
Figs. 27–32. Wood anatomical sections of Tetrameristaceae (LM). **27.** *Pentamerista neotropica* MADw 23508: TS, vessels solitary or in radial multiples, very thick-walled fibers, axial parenchyma diffuse to diffuse-in-aggregates and scanty paratracheal **28.** *Tetramerista glabra* MADw 35871: TS, idem. **29.** *Pentamerista neotropica* MADw 23508: TLS, uniseriate and 3–4-seriate rays. **30.** *Tetramerista glabra* MADw 35871: TLS, uniseriate and 2–3-seriate rays with long uniseriate parts. **31.** *Pentamerista neotropica* MADw 23508: RLS, multiseriate ray consisting of procumbent and square body ray cells. **32.** *Tetramerista glabra* MADw 35871: RLS, multiseriate ray with unknown inclusions (possibly tannins), consisting of procumbent and square body ray cells and upright marginal ray cells.

TABLE 3. Wood anatomical comparison of the balsaminoid families. The values given correspond to extreme rounded means included in Table 2. Numbers in parentheses occur sporadically. + = present, − = absent, ± = sometimes present.

Character	Balsaminaceae	Marcgraviaceae	Pellicieraceae	Tetrameristaceae
Secondary woodiness	+	−	−	−
Scalariform perforations	−	±	−	±
Radial vessel multiples (no. cells)	(2–3)	2–4–(7)	2–9	2–4–(6)
Vessel diameter (μm)	40–80	50–280	55–65	100–170
Vessel element length (μm)	210–300	490–1100	500–670	1150–1450
Unilaterally compound vessel-ray pitting	−	−	+	+
Mean fiber length (μm)	570–640	610–1630	950–1220	1740–3070
Very thick-walled fibers	−	−	±	+
Axial parenchyma diffuse-in-aggregates	−	−	−	+
Axial parenchyma vasicentric	±	+	−	−
Mean multiseriate ray width (no. cells)	− or 10–20	2–15–(42)	2–(3)	2–5
Mean multiseriate ray height (mm)	− or >7	1–10	1.1–1.4	2.0–3.5
Multiseriate rays with long uniseriate ends	−	−	+	+
Raphides	+	+	+	+

frequency of radial vessel multiples, predominantly simple vessel perforation plates, alternate intervascular pitting, a mixed occurrence of apotracheal and paratracheal parenchyma, predominantly septate libriform fibers, co-occurrence of uniseriate and multiseriate rays, and raphides in ray cells (see also Beauvisage, 1920; Baretta-Kuipers, 1976; Bedell, 1980). Most of these characters are also observed in the unrelated woody primuloids, but the presence of raphides in rays is typical of balsaminoids. In addition, two other features that clearly distinguishes woody balsaminoids from primuloids is the general absence of uniseriate rays in Myrsinaceae and Theophrastaceae, and the lack of apotracheal parenchyma in primuloids (Lens et al., 2005).

Despite the anatomical resemblances mentioned, the wood structure allows us to distinguish the three balsaminoid families from each other (Table 3). Tetrameristaceae are defined by exclusively, very thick-walled fibers and diffuse-in-aggregates axial parenchyma, two features that are normally absent in Pellicieraceae and Marcgraviaceae. The low percentage of septate fibers within Tetrameristaceae could be underestimated because of the very thick fiber walls that complicate the observation of septa. Furthermore, the genus *Tetramerista* is characterized by the presence of raphides in procumbent ray cells and by the occurrence of very long fibers, often between 2500 and 3000 μm. Long fibers are not unusual in Ericales; they are also found in Lecythidaceae s.l. (Carlquist, 1988), Symplocaceae (van den Oever, 1981), and Theaceae (Liang and Baas, 1990). Pellicieraceae are defined by long radial vessel multiples of up to nine cells, sparse axial parenchyma (diffuse apotracheal and scanty paratracheal), and narrow multiseriate rays. Typical features of Marcgraviaceae include vasicentric parenchyma, multiseriate rays including upright, square, and procumbent body ray cells, and multiseriate rays with few rows of marginal ray cells. In addition, the presence of very wide vessels (more than 250 μm), which are always rounded in outline, and wide (more than five-seriate) and high multiseriate rays (more than 10 mm) are diagnostic of Marcgraviaceae wood.

From a wood anatomical point of view, it is obvious that *Pentamerista* and *Tetramerista* are closely related. The differences in quantitative features, such as the narrower and shorter vessel elements and shorter fibers in *Pentamerista*, are probably related to their habit (shrub vs. tree). The placement of *Pelliciera* within Tetrameristaceae seems justified because of the presence of unilaterally compound vessel-ray pits and long

uniseriate ends of multiseriate rays interconnecting multiseriate parts, two features that are absent in other balsaminoid representatives (see also Baretta-Kuipers, 1976; Bedell, 1980). However, the wood of *Pelliciera rhizophorae* can be clearly distinguished from Tetrameristaceae by the presence of narrow multiseriate rays. Besides this, *Pelliciera* shows a significantly lower vessel diameter and vessel element length and a higher vessel density. The difference in vessel diameter and vessel density in *Pelliciera* can be explained by the high xylem tensions in mangrove trees due to the physiological dry (saline) environment. Indeed, the mangrove environment often results in a high number of narrow vessels, which increase the safety of the sap stream (Tomlinson, 1986). The shorter vessel elements in *Pelliciera* might have the same effect (Carlquist, 1977), although Panshin (1932) and van Vliet (1976) noticed that the vessel element length of mangrove species does not differ significantly from inland representatives in various families. In conclusion, we think that it is justified to accept the enlarged family concept of Tetrameristaceae with inclusion of *Pelliciera*, as has already been proposed by Bremer et al. (2002) and APG II (2003).

Phylogenetic and ecological wood anatomy of Marcgraviaceae—The wood structure of Marcgraviaceae shows various features that are typical of lianas, such as wide vessel elements in co-occurrence with narrow vessels (vessel dimorphism), simple vessel perforations, paratracheal parenchyma and interspersed apotracheal parenchyma, and wide rays (Carlquist, 1989). However, true tracheids or vasicentric tracheids, which are also common in lianas, were not observed. Although Marcgraviaceae are wood anatomically homogeneous, there is considerable variation in the width of the multiseriate rays. Mature wood of *Marcgravia* is often characterized by wide multiseriate rays (usually 5–15-seriate, sometimes up to 42-seriate), while most species of Noranteoideae have narrower (2–5-seriate) multiseriate rays. This difference remains when *Marcgravia* species, which grow exclusively as lianas, are compared with the other scandent species that characteristically show a more self-supporting, scrambling habit (on average nine-seriate vs. three-seriate, respectively). Therefore, the difference in multiseriate ray width caused by dissimilar growth strategies is phylogenetically important within the family, and it may represent an additional feature to distinguish Marcgravioideae from Noranteoideae, besides other features such as the specific umbellate inflorescence, the tetramery in

TABLE 4. Impact of habit and altitude on the wood structure of Marcgraviaceae. The names of the species in each group and the abbreviations are given in Table 2. Numbers are mean values followed by standard deviations. An asterisk indicates that the values are statistically different at the 0.5% level. N = number of specimens.

Species studied	N	SP	NB	DIAM	DENS	VEL	FL	MRW	HMR
Lowland climbers	16	3 ± 6	1 ± 1	195 ± 65	9 ± 6	810 ± 139	1040 ± 255	7 ± 6	6330 ± 3285
Montane climbers	4	3 ± 5	1 ± 1	205* ± 28	6 ± 1	930 ± 148	1290 ± 315	3 ± 1	3990 ± 2708
Lowland erect species	2	5 ± 7	2 ± 2	160 ± 102	7 ± 4	1005 ± 56	1345 ± 50	4 ± 0	2630 ± 656
Erect montane species	3	35 ± 25	4 ± 2	100* ± 27	14 ± 6	705 ± 129	1010 ± 73	4 ± 1	2090 ± 308

the perianth, and the occurrence of leaf dimorphism in *Marcgravia* (Dressler, 2004). Other ericalean taxa with very wide rays (more than 20-seriate) include the unrelated epacrids (Ericaceae) and primuloids (Theophrastaceae and Myrsinaceae), although lianas are mostly absent in these groups (Lens et al., 2003, 2005).

As mentioned in previous studies, altitudinal ranges may influence the wood structure, although altitudinal trends are less pronounced than latitudinal trends (Van der Graaff and Baas, 1974; van den Oever et al., 1981; Baas, 1986b; Carlquist, 2001; Lens et al., 2004). Within Marcgraviaceae, the most manifest differences between the 16 species representing lowland climbers and the four montane climbing species are the multiseriate ray width (seven-seriate vs. three-seriate, respectively) and height (6330 vs. 3990 μm, respectively) (Table 4). The two erect species from the lowlands differ from the three montane erect species in having a lower percentage of scalariform perforations (5% vs. 35%, respectively), larger vessel diameters (160 vs. 100 m, respectively), a lower vessel density (7 vs. 14, respectively), longer vessel elements (1005 vs. 705 μm, respectively) and fibers (1345 vs. 1010 μm, respectively), and higher multiseriate rays (2630 vs. 2090 μm, respectively). These trends are in agreement with general altitudinal trends reported by the above authors, although none of these trends are significant at the 0.5% level.

Likewise, there are clear signals of the impact of habit on various wood anatomical features in Marcgraviaceae (Table 4), and they corroborate most correlations found in previous studies (Baas and Schweingruber, 1987; Carlquist, 2001; Lens et al., 2004). The mean vessel diameter between climbers and erect species from the montane regions demonstrates the clearest habit trend in our analysis because the values are statistically significant at the 0.5% level (205 vs. 100 μm, respectively; Table 4). Several other trends can be mentioned, such as the higher percentage of scalariform perforations and a higher vessel density in montane erect species compared to montane climbers. Furthermore, climbing species from both lowland and montane regions have higher multiseriate rays than their erect counterparts (Table 4). The data on perforation types explain why scalariform perforations are more common in the *Norantea* s.l. complex because of the abundant occurrence of montane shrubs and treelets among this group (Vestal, 1937; Metcalfe and Chalk, 1950). The impact of habit on the vessel element and fiber lengths is somewhat contradicting (see also Carlquist, 1989). Indeed, montane climbers have longer vessel elements and fibers than montane erect species, but lowland climbers show shorter mean vessel elements and fibers than lowland erect species.

Secondary woodiness in Balsaminaceae—From a wood anatomical point of view, the systematic position of Balsaminaceae is difficult to compare with other balsaminoid members because of the secondary woodiness of this family. Indeed, the few *Impatiens* species with a limited production of secondary xylem are scattered throughout the molecular tree of Yuan et al. (2004), indicating that this phenomenon has evolved multiple times from herbaceous ancestors. Two features that provide wood anatomical evidence for the occurrence of secondary woodiness are the raylessness in *I. arguta* and the presence of exclusively upright ray cells in *I. niamniamensis* (Carlquist, 1992). Furthermore, the wood anatomical search for close relatives of Balsaminaceae is complicated more because of additional paedomorphic features, a term indicating that primitive features from the primary xylem are transferred into the secondary xylem (Carlquist, 1962). The most important evidence for paedomorphism within the two species studied is the gradual decrease of vessel element length from the center of the stem towards the cambium. Indeed, vessel elements in the primary xylem are clearly longer (280–330 μm in *I. arguta*, 380–450 μm in *I. niamniamensis*) than vessel elements that are situated near the cambium (130–170 μm in *I. arguta*, 170–220 μm in *I. niamniamensis*). Other paedomorphic features include wide scalariform to reticulate vessel pits, and thin-walled libriform fibers that are relatively wide. Furthermore, *I. niamniamensis* shows abundant axial parenchyma and wide and high rays, two features that are common in paedomorphic woods (Carlquist, 1962).

As seen in tangential sections of *I. niamniamensis*, the shape and size of the ray cells corresponds fairly well with the libriform fibers (Fig. 4). In *I. arguta*, the difference between ray cells and libriform fibers is vague, resulting in raylessness. This is in agreement with the hypothesis of Carlquist (1970) stating that the increase of xylem production in woody herbs with very short fusiform cambium initials may lead to libriform fibers that are histologically equivalent to ray cells.

Our observations of *I. niamniamensis* resemble the wood of *I. lyallii*, which also shows a high percentage of parenchyma tissue (Gerard, 1917). Nevertheless, major differences in *I. lyallii* are the presence of narrow (1–2-seriate) and low (200–300 μm) rays, and extremely short fibers (150–250 μm). Because raphides are occasionally observed in the wood of *I. niamniamensis*, this character remains the only anatomical–morphological link between Balsaminaceae and the other three balsaminoid families. Besides this observation, Balsaminaceae characteristically show raphides within special cells of the leaves, cortex, and in the anther walls (Cronquist, 1988; Fischer, 2004).

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