COMPARATIVE WOOD ANATOMY OF THE BLUEBERRY TRIBE (VACCINIEAE, ERICACEAE S.L.)[1]

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Abstract

Wood samples of 111 Vaccinieae specimens (Vaccinioideae, Ericaceae s.l.) representing 98 species and 26 genera are investigated with light microscopy and scanning electron microscopy. The wood structure of Vaccinieae delivers taxonomically important characters that can be used to define some subclades within the tribe. The wood of the large polyphyletic genus *Vaccinium* strongly resembles non-vaccinioid members of the family, which are characterized by bordered vessel-ray pits and relatively narrow (2- to 4-seriate) and low multiseriate rays (often less than 1000 μm) with exclusively or mainly procumbent body ray cells. The East Malesian clade, Meso-American/Caribbean clade, and the Andean clade show a combination of wood anatomical features that is lacking in other representatives of the family. These features include scalariform vessel-ray pits with strongly reduced borders, a high portion of upright body ray cells, wide (4- to 14-seriate) and high multiseriate rays (often more than 3000 μm), and prismatic crystals in chambered ray cells (although absent in *Symphysia racemosa*). The presence of secretory ducts in the primary xylem and in the pith tissue may represent a synapomorphy for the Andean clade. Furthermore, the presence of undivided axial parenchyma cells, usually ranging from 500 to 900 μm, seems to be unique in the subfamily.

Key words: blueberries, comparative wood anatomy, Ericaceae, Neotropics, secretory ducts, systematics, Vaccinieae.

The tribe Vaccinieae Rchb. (Ericaceae Juss. s.l.) comprises about 35 genera and more than 1000 species. Most representatives are evergreen shrubs, many occurring as epiphytes and occasionally as lianas. The vast majority of the taxa (about 30 genera and 900 species) are concentrated in the cooler, moist, montane areas of South America between 1500 and 3000 m (Luteyn, 2002). The remaining taxa are concentrated in the montane regions of southeast Asia and Malesia, and a few species are restricted to southeast Africa and Madagascar. *Vaccinium* L., the only genus that occurs in the tropics of the Old and New World, is by far the largest of the tribe (ca. 450 species), but it does not seem to be monophyletic according to molecular data (Kron et al., 2002b).

Hooker (1876) considered the blueberry tribe as a separate family, Vacciniaceae Gray, particularly because of the inferior ovary and the fleshy fruit. Based on the overwhelming similarities between Vacciniaceae and Ericaceae, most authors placed the study group as a tribe within the subfamily Vaccinioideae Arn. of the Ericaceae (Drude, 1897; Stevens, 1971). In the classification of Stevens (1971), the circumscription of Vaccinioideae was greatly enlarged by the inclusion of Arbuteae Meisn., Andromedeae Klotzsch, Cassiopeae P. F. Stevens, and Enkiantheae P. F. Stevens. In the most recent classification of Kron et al. (2002a), based on molecular as well as morphological data, Vaccinieae are sister to Andromedeae s. str. and Gaultherieae Nied., which form together with Lyonieae Kron & Judd and Oxydendreae H. T. Cox the rest of the subfamily Vaccinioideae.

Within the study group, the systematic relationships are far from resolved. Many earlier botanists divided Vacciniaceae into two tribes, namely Vaccinieae and Thibaudieae Benth. & Hook.f., based

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on flower morphology and leaf anatomy (Hooker, 1876; Niedenzu, 1890; Drude, 1897). Nevertheless, the two tribes could not be clearly distinguished from each other because of the variation in the flowers and leaves of some genera. Also the generic boundaries within the study group, traditionally based on flower, fruit, seed, and vegetative characters, caused many problems (Sleumer, 1941; Luteyn, 1991). Nowadays, our knowledge of Vaccinieae has increased significantly, although several genera still remain poorly studied (Stevens, 1985). This can be illustrated, for instance, by molecular sequence data, which show that only few Vaccinieae genera seem to be monophyletic (Kron et al., 2002b). On the other hand, five major evolutionary lines within Vaccinieae could be established, i.e., a large Andean clade with the majority of genera, a Meso-American/Caribbean clade, an East Malesian clade, an *Agapetes* G. Don clade with some Asian *Vaccinium* and *Agapetes* species, and a *Vaccinium* clade with members of *Vaccinium* sections *Bracteata* and *Oarianthe.*

The wood anatomy of the blueberry tribe is only fragmentarily known. Metcalfe and Chalk (1950) commented on the wood anatomy of a few species of *Agapetes, Gaylussacia* Kunth, *Macleania* Hook., *Paphia* Seem., *Psammisia* Klotzsch, and *Vaccinium.* Other authors investigated the secondary xylem of several species belonging to only one genus. For instance, Giebel (1983) studied the wood anatomy of *Cavendishia* Lindl., Suzuki and Noshiro (1988) investigated *Agapetes,* and species of *Vaccinium* were treated by, for instance, Flint (1918), Moll and Janssonius (1926), Greguss (1959), Weingartner (1969), Baas (1979), Carlquist (1985, 1988), Odell et al. (1989), Queiroz and Van Der Burgh (1989), Stuzková et al. (2003), and Edwards and Axe (2004).

This work aims to present a detailed wood anatomical overview of the tribe Vaccinieae, including most genera except for *Anthopteropsis* A. C. Sm., *Costera* J. J. Sm., *Didonica* Luteyn & Wilbur, *Gonocalyx* Planch. & Lindl., *Paphia, Pellegrinia* Sleumer, *Rusbya* Britton, and *Utleya* Wilbur & Luteyn. Special emphasis is paid to comparison of the wood anatomical variation with recent taxonomic insights based on molecular sequence data in order to reveal possible evolutionary patterns and to look for wood anatomical support in one or more evolutionary lines. The presence of fibers with a living protoplast, as has been discovered previously by several authors in Vaccinioideae (Braun, 1961; Fahn & Leshem, 1962; Giebel, 1983; Lens et al., 2004a), will also be discussed briefly. This manuscript is part of a general wood anatomical survey of Vaccinioideae (Lens et al., 2004a). The ecological wood anatomy of the subfamily is treated elsewhere (Lens et al., 2004b).

Material and Methods

Wood samples of 111 specimens representing 98 species and 26 genera (cf. Index, Table 1) were investigated using light microscopy (LM) and scanning electron microscopy (SEM). For LM observations, transverse and longitudinal sections of about 25 μm were cut using a sledge microtome (Reichert, Vienna, Austria), after softening the wood samples in hot water; a previous warming of the knives is not necessary. Transverse sections of tiny samples were cut using two pieces of polystyrene foam. In order to make tangential and radial longitudinal sections of these thin stems, the sample was mounted with superglue on a rectangular piece of wood that was clamped in the microtome holder. The entire thickness of the wood sample could then be used to produce longitudinal sections. All the sections were bleached with sodium hypochlorite and stained with a mixture of safranin and alcian blue (35:65). The safranin was prepared as a 1% solution in 50% ethanol, while the 1% alcian blue stain was dissolved in pure water. Afterward, the tissues were dehydrated with 50%–75%–96% ethanol and mounted in Euparal. LM observations were carried out using a Dialux 20 light microscope (Leitz, Wetzlar, Germany), and pictures were taken using a DP50-CU digital camera (Olympus, Hamburg, Germany). Preparations for macerations were made using a hot mixture of glacial acetic acid and hydrogen peroxide (Franklin, 1945). For SEM observations, wood samples were softened in hot water. Longitudinal wood sections were made using a razor blade. The sections were bleached with sodium hypochlorite and dehydrated with 50%–75%–96% ethanol. Afterward, the sections were gold-coated with a sputter coater (SPI Supplies, West Chester, Pennsylvania, U.S.A.) and observed using a JEOL JSM-5800 LV scanning electron microscope (JEOL Ltd., Tokyo, Japan), which is situated in the National Botanic Garden of Belgium.

The wood anatomical terminology follows the “IAWA list of microscopic features for hardwood identification” (IAWA Committee, 1989). Because of the difficulties in determining the type of non-perforated tracheary elements, a description is given below.

All types of non-perforated tracheary elements, i.e., tracheids, fiber-tracheids, and libriform fibers, are present in the wood of Ericaceae s.l. (Baas, 1979; Carlquist, 1988; Lens et al., 2003). It may

Table 1. Survey of selected wood anatomical features within Vaccinieae. + = present, − = absent, ± = sometimes present, ? = unknown. [1,2,3,4]Numbers after the names of specimens refer to the order used in the material list. Minimum and maximum values are shown in parentheses. ">" means that the height of the multiseriate ray exceeds the length of the section.

		Vessels									
Species studied	Secretory ducts in pith or primary xylem	Percentage of scalariform perforations	Number of bars	Opposite vessel-ray pitting	Scalariform vessel-ray pitting	Alternate vessel-ray pitting	Simple vessel-ray pitting	Helical thickening throughout vessel elements	Helical thickenings in fibers and/or tracheids	Tangential diameter of vessel lumina (μm)	Vessels per square mm
Agapetes flava	−	10	(1–)4(–6)	±	−	+	−	+	−	(12–)18(–25)	(210–)288(–390)
A. hosseana	−	100	(7–)14(–24)	±	−	+	−	−	−	(10–)18(–30)	(140–)194(–240)
A. mannii	−	100	(6–)9(–11)	±	−	+	−	+	+	(10–)13(–18)	(300–)379(–440)
A. moorei	−	85	(2–)9(–15)	±	−	+	−	−	−	(15–)18(–22)	(120–)145(–200)
A. sikkimensis	−	20	(2–)8(–13)	±	−	+	−	−	−	(19–)25(–30)	(140–)169(–200)
A. variegata	−	20	(7–)10(–12)	±	−	+	−	−	−	(20–)26(–35)	(96–)122(–160)
Anthopterus wardii[1]	?	100	(8–)12(–20)	+	+	−	+	−	−	(15–)20(–30)	(92–)129(–178)
A. wardii[2]	+	90	(1–)7(–15)	+	+	−	+	−	−	(25–)31(–50)	(156–)199(–231)
Cavendishia bracteata	+	70	(1–)5(–9)	−	+	−	+	−	−	(25–)37(–50)	(70–)93(–126)
C. duidae	?	25	(1–)3(–8)	±	+	−	+	−	−	(22–)29(–35)	(140–)166(–192)
C. compacta	?	60	(2–)5(–9)	−	+	−	+	−	−	(30–)39(–50)	(126–)155(–178)
C. lindauiana	+	90	(2–)5(–7)	−	+	−	+	−	−	(25–)39(-50)	(92–)111(–135)
C. pubescens	?	100	(2–)8(–12)	−	+	−	+	−	−	(35–)47(–60)	(36–)44(–58)
C. urophylla	?	70	(3–)5(–8)	−	+	−	+	−	−	(20–)30(–40)	(100–)126(–142)
Ceratostema reginaldii[1]	?	95	(2–)5(–7)	−	+	−	+	−	−	(20–)27(–40)	(54–)91(–122)
C. reginaldii[2]	?	100	(5–)9(–13)	−	+	−	+	±	−	(20–)28(–35)	(32–)51(–95)
Demosthenesia spectabilis	+	100	(2–)5(–7)	+	+	−	+	−	−	(15–)25(–32)	(160–)178(–210)
Dimorphanthera collinsii	?	10	3–4	+	+	−	+	−	−	(110–)163 (–220)	(10-)18(–24)
D. cornuta var. *cornuta*	?	0	0	−	+	−	+	−	−	(60–)103 (–140)	(22–)27(–32)
D. dekockii var. *pubiflora*	?	0	0	−	+	−	+	−	−	(60–)110 (–160)	(16–)24(–32)
D. kempteriana	?	10	9–10	+	+	−	+	−	−	(110–)164 (–205)	(8–)12(–18)
Diogenesia floribunda	−	95	(1–)9(–15)	−	+	−	+	−	−	(20–)30(–40)	(66–)95(–114)
D. tetrandra	+	80	(2–)7(–18)	−	+	−	+	−	−	(20–)27(–40)	(61–)73(–82)
Disterigma. sp. indet.[1]	−	100	(6–)10(–16)	+	+	−	−	+	+	(12–)17(–25)	(240–)362(–415)
D. sp. indet.[2]	?	100	(4–)12(–25)	±	+	−	−	+	+	(12–)17(–20)	(168–)223(–272)
D. alaternoides	−	70	(1–)8(–17)	−	+	−	±	−	−	(25–)35(–45)	(70–)91(–120)
D. cryptocalyx	−	90	(1–)5(–9)	±	+	−	±	−	−	(15–)22(–25)	(120–)152(–180)
Gaylussacia baccata	−	90	(2–)7(–12)	+	+	−	±	+	−	(10–)16(–22)	(215–)307(–370)
G. decipiens var. *decipiens*	−	90	(1–)6(–10)	+	+	−	+	+	−	(15–)20(–30)	(230–)271(–362)

Table 1. Extended.

Vessels	Tracheids	Fibers	Rays			Crystals	
Length of vessel elements (μm)	Length of tracheids (μm)	Length of fiber tracheids (μm)	Multiseriate ray width (number of cells)	Height of uniseriate rays (μm)	Height of multiseriate rays (μm)	Present in rays	Present in axial parenchyma
(370–)472(–580)	(380–)437(–480)	(480–)580(–640)	3–15	(280–)459(–790)	(1300–)2816(–4600)	−	−
(350–)548(–700)	(430–)532(–610)	(620–)724(–910)	4–5	(400–)739(–1300)	(950–)1327(–2150)	−	−
(330–)437(–550)	(350–)481(–570)	(520–)634(–750)	6–9	(600–)850(–1200)	(1100–)1689(–3900)	−	−
(370–)579(–740)	(570–)638(–680)	(700–)783(–970)	6–12	(450–)744(–1000)	1500->8500	±	−
(460–)765(–940)	(670–)805(–900)	(750–)1013(–1180)	5–11	(450–)993(–1600)	>11500	−	−
(530–)704(–840)	(670–)740(–810)	(880–)937(–1070)	6–10	(650–)1766(–3500)	(2400–)3280(–4600)	−	−
(450–)596(–750)	(460–)576(–800)	(600–)829(–1000)	4–5	(600–)936(–1800)	>6000	+	−
(480–)613(–770)	(550–)619(–690)	(680–)823(–930)	4–6	(450–)1069(–2700)	>8000	+	±
(470–)613(–850)	(570–)645(–720)	(690–)941(–1150)	4–5	(250–)577(–1300)	(1000–)2123(–3000)	+	±
(400–)548(–660)	(600–)645(–700)	(670–)833(–970)	4–6	(300–)592(–950)	650->5000	−	−
(270–)657(–880)	(600–753(–950)	(640–)892(–1150)	2–3	(300–)600(–950)	2400->5400	+	±
(280–)590(–820)	(690–)734(–770)	(650–)802(–920)	3–4	(350–)600(–800)	1300->6000	+	+
(450–)619(–820)	(560–)656(–850)	(900–)1060(–1320)	4–5	(550–)744(–850)	(1200–)2036(–2400)	+	−
(390–)598(–750)	(670–)730(–820)	(750–)956(–1140)	3–4	(200–)450(–1000)	(800–)1473(–2200)	+	+
(450–)645(–870)	(580–)693(–1000)	(770–)921(–1100)	3–4	(400–)763(–1400)	(1100–)2605(–5500)	−	−
(450–)635(–830)	(480–)530(–670)	(680–)995(–1160)	4–5	(350–)807(–1400)	(900–)1569(–2700)	−	−
(350–)529(–690)	(450–)619(–750)	(560–)695(–820)	4–9	(450–)735(–1200)	(1600–)2267(–3500)	−	−
(550–)754(–1000)	(800–)1016(–1200)	—	3	(300–)605(–1200)	(7000–)8100(–9500)	+	−
(400–)560(–700)	(550–)686(–780)	—	4–6	(200–)406(–550)	(800–)2086(–3600)	+	−
(420–)608(–790)	(630–)823(–970)	(820–)990(–1120)	6–11	(300–)492(–950)	(1800–)2843(–5000)	+	−
(700–)930(–1150)	(1100–)1396(–1600)	(800–)990(–1200)	4–7	(300–)804(–1300)	(4000–)6050(–8400)	+	−
(420–)684(–820)	(640–)728(–820)	(720–)889(–1050)	4	(500–)1122(–1750)	>9200	−	−
(350–)548(–750)	(500–)608(–700)	(600–)790(–950)	4–5	(350–)780(–1400)	(800–)3920(–6000)	−	−
(250–)364(–550)	(350–)463(–640)	(400–)565(–750)	3	(200–)416(–650)	(500–)643(–1000)	+	−
(300–)330(–450)	(300–)460(–580)	(400–)502(–650)	3	(200–)365(–650)	(400–)693(–1000)	+	−
(400–)720(–950)	(560–)752(–900)	(700–)938(–1050)	8–12	(400–)500(–650)	900->5000	±	+
(680–)1006(–1250)	(450–)690(–800)	(1120–)1252(–1880)	3–4	(600–)2357(–5100)	>17500	+	−
(280–)393(–500)	(320–)375(–430)	(440–)500(–620)	3–5	(650–)789(–1000)	(800–)1520(–3500)	−	−
(230–)460(–600)	(320–)478(–650)	(560–)688(–960)	4–5	(350–)572(–850)	(2100–)1963(–2700)	−	−

Table 1. Continued.

Species studied	Secretory ducts in pith or primary xylem	Vessels: Percentage of scalariform perforations	Number of bars	Opposite vessel-ray pitting	Scalariform vessel-ray pitting	Alternate vessel-ray pitting	Simple vessel-ray pitting	Helical thickening throughout vessel elements	Helical thickenings in fibers and/or tracheids	Tangential diameter of vessel lumina (μm)	Vessels per square mm
Lateropora ovata	+	100	(5–)10(–17)	−	+	−	+	−	−	(15–)23(–30)	(148–)194(–220)
Macleania crassa	?	10	(2–)5(–9)	−	+	−	+	−	−	(35–)49(–60)	(32–)54(–80)
M. ericae	+	85	(2–)5(–9)	−	+	−	+	−	−	(20–)29(–40)	(90–)110(–130)
M. hirtiflora	+	95	(2–)7(–13)	−	+	−	+	−	−	(20–)26(–30)	(83–)108(–148)
M. loeseneriana	?	90	(3–)7(–10)	−	+	−	+	−	−	(20–)33(–50)	(48–)69(–90)
M. pentaptera	?	0	0	−	+	−	+	−	−	(27–)33(–40)	(32–)58(–98)
M. rupestris	?	0	0	−	+	−	+	−	−	(25–)51(–75)	(44–)55(–68)
M. stricta	+	45	(2–)6(–10)	−	+	−	+	−	−	(25–)34(–40)	(91–)105(–123)
Mycerinus chimantensis	−	100	(1–)5(–7)	−	+	−	+	−	−	(20–)25(–35)	(105–)132(–160)
Notopora cardonae	−	15	(3–)6(–11)	−	+	−	+	−	−	(35–)45(–60)	(68–)85(–105)
N. schomburgkii	−	0	0	−	+	−	+	−	−	(30–)46(–65)	(46–)61(–80)
Oreanthes ecuadorensis	+	100	(3–)6(–12)	−	+	−	+	−	−	(20–)26(–30)	(180–)250(–290)
Orthaea fimbriata	+	80	(2–)6(–13)	−	+	−	+	−	−	(20–)31(–40)	(51–)62(–78)
Plutarchia ecuadorensis	−	100	(3–)4(–6)	−	+	−	+	−	−	(15–)20(–35)	(130–)145(–172)
P. rigida	−	95	(2–)4(–6)	−	+	−	+	−	−	(20–)25(–30)	(120–)146(–170)
Polyclita turbinata	+	25	(1–)3(–6)	−	+	−	+	−	−	(25–)28(–40)	(81–)96(–120)
Psammisia sp. indet.	?	0	0	−	+	−	+	−	−	(65–)85(–120)	(24–)33(–40)
P. ecuadorensis	+	75	(1–)5(–8)	−	+	−	+	−	−	(25–)38(–55)	(53–)74(–90)
P. ferruginea	?	25	(3–)8(–13)	−	+	−	+	−	−	(50–)73(–120)	(34–)41(–52)
P. graebneriana	+	95	(1–)7(–14)	−	+	−	+	−	−	(15–)26(–35)	(83–)97(–110)
P. guianenis	+	20	(8–)10(–15)	−	+	−	+	−	−	(25–)37(–60)	(60–)72(–90)
P. guianensis	+	85	(1–)8(–13)	±	+	−	+	−	−	(25–)42(–65)	(58–)79(–106)
P. penduliflora	+	100	(3–)4(–9)	−	+	−	+	−	−	(20–)31(–40)	(80–)97(–118)
P. cf. *ulbrichiana*	+	50	(1–)7(–15)	−	+	−	+	−	−	(30–)50(–70)	(32–)42(–50)
Satyria sp. indet.[1]	?	95	(1–)5(–10)	−	+	−	+	−	−	(28–)41(–60)	(34–)52(–66)
S. sp. indet[2]	?	0	0	−	+	−	+	−	−	(65–)93(–115)	(22–)26(–32)

Table 1. Extended. Continued.

Vessels	Tracheids	Fibers	Rays			Crystals	
Length of vessel elements (μm)	Length of tracheids (μm)	Length of fiber tracheids (μm)	Multi-seriate ray width (number of cells)	Height of uniseriate rays (μm)	Height of multiseriate rays (μm)	Present in rays	Present in axial paren-chyma
(430–)567(–670)	(520–)577(–620)	(620–)819(–920)	4–6	(550–)950(–1550)	>8000	+	−
(560–)795(–920)	(670–)844 (–1100)	(970–)1117 (–1290)	4–5	(600–)1200 (–1700)	1300->7300	+	+
(460–)653(–750)	(690–)760(–830)	(890–)1012 (–1150)	2–3	(500–)669(–900)	(1100–)2343(–3400)	−	−
(340–)586(–830)	(550–)655(–750)	(850–)974(–1170)	4–5	(550–)821(–1750)	4900->12000	+	+
(400–)617(–800)	(550–)675(–940)	(800–)994(–1200)	3	(300–)446(–1200)	(800–)1645(–3500)	+	−
(270–)551(–770)	(440–)520(–600)	(530–)789(–1060)	4–7	(500–)860(–1300)	(1050–)1628(–1950)	+	+
(510–)837 (–1000)	(910–)1109 (–1340)	—	3–5	(350–)1465 (–2700)	3600->10500	+	−
(340–)630(–840)	(520–)590(–650)	(830–)928(–1020)	3–4	(1100–)1643 (–2100)	(1800–)4760(–7200)	−	−
(480–)697(–860)	(260–)678(–750)	(720–)864(–1000)	2–3	(550–)1063 (–1900)	(950–)1704(–3200)	+	−
(500–)697(–940)	(600–)648(–750)	(580–)862(–1100)	5–7	(550–)983(–1350)	2250->8000	+	−
(520–)700(–960)	(550–)725(–850)	(750–)925(–1250)	4–5	(350–)850(–1800)	(600–)2208(–3000)	+	−
(420–)649(–979)	(520–)580(–670)	(540–)743(–1040)	4	(450–)700(–1300)	>8500	−	−
(550–)680(–850)	(540–)745(–880)	(700–)979(–1250)	4–5	(350–)700(–900)	(1100–)3488(–7500)	+	−
(390–)558(–670)	(450–)480(–520)	(600–)716(–850)	7–9	(400–)483(–650)	>2500	−	−
(400–)556 (–810)	(450–)519(–600)	(550–)749(–860)	4	(650–)1350 (–2000)	>5700	−	−
(320–)561(–780)	(500–)664(–750)	(650–)760(–980)	6–7	(500–)729(–1050)	(1350–)2908(–4950)	+	−
(530–)726(–880)	(750–)938 (–1050)	(750–)1095 (–1230)	3–4	(250–)600(–1000)	500->4000	+	+
(520–)694(–870)	(650–)740(–850)	(840–)981(–1260)	3–5	(300–)900(–1500)	1400->8000	+	−
(620–)748(–930)	(730–)871 (–1120)	(870–)1146 (–1380)	4–6	(400–)745(–1100)	5900->10.000	+	−
(340–)579(–770)	(470–)595(–760)	(600–)844(–1060)	4–7	(620–)2478 (–2100)	(5200–)8600 (–10800)	+	−
(700–)900 (–1150)	(650–)939 (–1150)	(1150–)1286 (–1650)	3–4	(250–)696(–1300)	2100->6000	+	−
(580–)696(–880)	(570–)650(–740)	(840–)995(–1170)	6–8	(750–)1710 (–4100)	>13500	+	−
(440–)630(–810)	(580–)639(–680)	(630–)815(–980)	4–5	(1350–)1583 (–2000)	8700->16500	+	−
(500–)668(–800)	(700–)777(–870)	(850–)1005 (–1170)	3–4	(700–)1122 (–1700)	>11000	+	+
(470–)680(–850)	(500–)612(–820)	(720–)967(–1170)	5–6	(500–)740(–1100)	3000->8700	+	−
(450–)684(–870)	(750–)913 (–1100)	(780–)999(–1170)	4–7	(400–)771(–1500)	(1150–)2771(–5300)	+	−

Table 1. Continued.

		Vessels									
Species studied	Secretory ducts in pith or primary xylem	Percentage of scalariform perforations	Number of bars	Opposite vessel-ray pitting	Scalariform vessel-ray pitting	Alternate vessel-ray pitting	Simple vessel-ray pitting	Helical thickening throughout vessel elements	Helical thickenings in fibers and/or tracheids	Tangential diameter of vessel lumina (μm)	Vessels per square mm
S. sp. indet.[3]	?	0	0	−	+	−	+	−	−	(60–)81(–100)	(40–)49(–68)
S. sp. indet.[4]	+	40	(1–)5(–9)	−	+	−	+	−	−	(30–)40(–50)	(66–)87(–120)
S. carnosiflora	+	20	(2–)5(–11)	−	+	−	+	−	−	(30–)41(–60)	(59–)79(–110)
S. meiantha	?	15	(2–)4(–6)	−	+	−	+	−	−	(30–)49(–60)	(50–)62(–82)
S. panurensis	?	0	0	+	+	−	+	−	−	(60–)96(–140)	(24–)28(–30)
S. warszewiczii	+	25	(3–)5(–8)	−	+	−	+	−	−	(20–)35(–40)	(81–)121(–167)
S. warszewiczii	+	70	(2–)6(–11)	−	+	−	+	−	−	(30–)37(–45)	(32–)65(–106)
Semiramisia pulcherrima	+	100	(7–)10(–15)	+	+	−	+	−	−	(14–)21(–27)	(87–)95(–105)
Siphonandra elliptica	?	20	3–4	−	+	−	+	−	−	(25–)36(–50)	(74–)86(–108)
Sphyrospermum sp. indet.	−	95	(2–)9(–20)	−	+	−	+	−	−	(15–)19(–22)	(180–)249(–320)
S. buxifolium	−	100	(8–)10(–12)	+	+	−	+	−	−	(20–)26(–31)	(240–)318(–360)
S. sodiroi	−	100	(8–)11(–14)	−	+	−	+	−	−	(11–)16(–25)	
Symphysia racemosa	−	90	(9–)13(–20)	−	+	−	+	−	−	(20–)33(–40)	(95–)103(–114)
Themistoclesia epiphytica	+	100	(7–)13(–16)	−	+	−	+	−	−	(25–)30(–35)	(120–)153(–170)
T. pendula	+	0	0	−	+	−	+	−	−	(30–)61(–85)	(62–)75(–102)
T. vegasana	+	20	(1–)7(–11)	−	+	−	+	−	−	(15–)30(–45)	(130–)156(–192)
Thibaudia angustifolia	+	95	(1–)4(–9)	±	+	−	+	−	−	(20–)31(–40)	(125–)159(–230)
T. floribunda	+	30	(1–)6(–13)	−	+	−	+	−	−	(20–)36(–45)	(42–)64(–80)
T. formosa	?	90	(1–)7(–11)	−	+	−	+	−	−	(20–)34(–55)	(38–)70(–110)
T. jahnii	+	90	(1–)6(–10)	−	+	−	+	−	−	(20–)35(–45)	(76–)107(–141)
T. martiniana	?	100	(4–)8(–10)	−	+	−	+	−	−	(40–)53(–70)	(36–)69(–84)
T. pachypoda	+	35	(1–)4(–8)	−	+	−	+	−	−	(30–)43(–50)	(100–)144(–185)
T. parvifolia	?	95	(1–)7(–11)	−	+	−	+	−	−	(20–)25(–30)	(112–)141(–168)
T. rigidiflora	?	95	(1–)5(–13)	−	+	−	+	−	−	(30–)43(–60)	(64–)81(–100)
Vaccinium sp. indet.	?	50	(1–)8(–18)	±	+	−	−	+	−	(15–)23(–40)	(160–)228(–280)
V. africanum	?	75	(1–)8(–20)	±	+	−	+	+	−	(25–)32(–40)	(95–)138(–170)
V. angustifolium	−	80	(1–)8(–12)	+	+	+	−	+	−	(12–)18(–29)	(200–)267(–310)
V. arboreum	?	75	(7–)26(–53)	+	+	+	−	+	+	(18–)25(–40)	(89–)109(–150)
V. atrococcum	?	85	(4–)10(–16)	+	+	±	±	+	−	(15–)23(–35)	(170–)200(–240)
V. bancanum	?	0	0	±	+	+	−	−	−	(35–)46(–60)	(52–)65(–88)

Table 1. Extended. Continued.

Vessels	Tracheids	Fibers	Rays			Crystals	
Length of vessel elements (μm)	Length of tracheids (μm)	Length of fiber tracheids (μm)	Multiseriate ray width (number of cells)	Height of uniseriate rays (μm)	Height of multiseriate rays (μm)	Present in rays	Present in axial parenchyma
(580–)833(1080)	(850–)1069(–1190)	(990–)1146(–1300)	4–7	(400–)711(–1200)	1600->6000	+	−
(420–)637(–900)	(460–)713(–780)	(850–)1000(–1180)	3–4	(250–)764(–1300)	(1300–)2793(–5400)	−	−
(300–)522(–650)	(400–)543(–660)	(600–)740(–900)	3	(250–)485(–90)	(800–)2845(–7000)	+	−
(490–)744(–990)	(650–)756(–850)	(900–)1150(–1500)	5–6	(350–)644(–1200)	1900->9000	+	−
(640–)789(–1000)	(840–)938(–1100)	(800–)1053(–1260)	9–14	(450–)881(–1500)	2700->12000	+	−
(570–)745(–930)	(630–)758(–810)	(870–)1004(–1210)	4–8	(300–)647(–1450)	4000->11000	−	−
(430–)688(–800)	(620–)711(–800)	(780–)910(–1250)	5–8	(400–)700(–1600)	(1900–)2600(–3300)	+	−
(430–)649(–880)	(620–)685(–740)	(800–)912(–1000)	4–5	(400–)1456(–4200)	(1450–)2983(–3950)	−	−
(270–)430(–510)	(450–)546(–730)	(500–)662(–810)	4–7	(200–)466(–900)	(600–)1013(–1950)	−	−
(370–)512(–600)	(390–)477(–570)	(540–)707(–930)	3	(450–)883(–1500)	1100->4100	+	−
(340–)452(–600)	(370–)457(–550)	(450–)586(–670)	5–8	(150–)402(–600)	(1200–)1668(–2300)	−	−
(400–)620(–800)	(400–)442(–520)	(630–)778(–950)	2–4	(250–)444(–600)	?	−	−
(420–)620(–850)	(430–)508(–650)	(800–)1010(–1150)	4	(350–)564(–900)	(600–)1511(–2400)	−	−
(480–)696(–890)	(560–)648(–720)	(720–)888(–1050)	4–12	(900–)1406(–1800)	>10.000	−	−
(280–)473(–730)	(520–)594(–720)	(650–)821(–930)	5–7	(400–)535(–850)	1500–>4900	+	+
(400–)538(–650)	(480–)593(–720)	(600–)766(–950)	3–5	(300–)538(–1100)	2400->6000	+	−
(570–)733(–930)	(600–)702)(–780)	(780–)881(–1050)	3–5	(700–)1459(–3000)	(1200–)3350(–6300)	−	−
(410–)508(–680)	(570–)637(–690)	(630–)767(–830)	5–11	(200–)437(–650)	(950–)2123(–4500)	+	−
(350–)534(–800)	(430–)628(–920)	(700–)940(–1150)	5–7	(300–)527(–900)	(1200–)2475(–5500)	+	−
(330–)608(–850)	(580–)662(–760)	(760–)957(–1170)	4–5	(350–)850(–1450)	(1800–)2775(–6300)	+	+
(560–)836(–1000)	(750–)891(–960)	(1000–)1177(–1350)	3–4	(450–)929(–1500)	(1300–)2777(–4500)	+	−
(570–)763(–930)	(700–)851(–1160)	(930–)1109(–1270)	3–12	(500–)1000(–1450)	(900–)3600(–6700)	+	+
(210–)539(–650)	(570–)628(–700)	(600–)783(–920)	4–6	(550–)830(–1150)	(1100–)2510(–2900)	−	−
(370–)636(–870)	(750–)790(–850)	(930–)1041(–1170)	4–6	(350–)633(–1800)	(1300–)2511(–5200)	+	+
(160–)393(–520)	(420–)455(–470)	(450–)523(–600)	3–4	(250–)421(–1050)	(550–)924(–1555)	−	−
(490–)649(–840)	(540–)590(–700)	(670–)835(–1070)	5–8	(450–)658(–900)	(950–)2046(–3200)	−	−
(210–)296(–390)	(300–)318(–350)	(390–)456(–520)	3–4	(250–)383(–750)	(350–)700(–1200)	−	−
(450–)642(–850)	(560–)764(–880)	(1100–)1324(–1650)	5–6	(300–)556(–900)	(500–)1397(–2400)	−	−
(210–)381(–500)	(420–)467(–550)	(500–)690(–830)	4–6	(100–)243(–400)	(200–)730(–1400)	−	−
(380–)696(–950)	(620–)824(–950)	(920–)1150(–1370)	3–5	(200–)323(–450)	(450–)1458(–2050)	+	−

Table 1. Continued.

	Vessels										
Species studied	Secretory ducts in pith or primary xylem	Percentage of scalariform perforations	Number of bars	Opposite vessel-ray pitting	Scalariform vessel-ray pitting	Alternate vessel-ray pitting	Simple vessel-ray pitting	Helical thickening throughout vessel elements	Helical thickenings in fibers and/or tracheids	Tangential diameter of vessel lumina (μm)	Vessels per square mm
V. barandanum var. *barandanum*	?	20	(1–)3(–5)	+	+	−	±	−	−	(30–)40(–50)	(31–)53(–65)
V. berberidifolium	−	90	(9–)12(–14)	±	+	+	−	+	−	(11–)16(–21)	(240–)294(–210)
V. bracteatum	?	50	(6–)9(–13)	+	+	−	±	+	−	(20–)32(–50)	(165–)210(–260)
V. calycinum	?	90	(1–)15(–33)	±	+	−	−	−	−	(20–)25(–40)	(190–)242(–360)
V. consanguineum	?	25	(5–)13(–15)	+	+	+	±	+	−	(30–)38(–45)	(81–)107(–124)
V. corymbodendron	?	80	(4–)12(–18)	+	+	+	±	−	−	(20–)30(–40)	(76–)106(–126)
V. corymbosum	−	80	(2–)9(-19)	±	+	−	−	+	−	(12–)16(–22)	(380–)430(–495)
V. cumingianum	?	5	(1–)3(–5)	±	+	−	±	−	−	(15–)30(–45)	(72–)79(–88)
V. exaristatum	?	50	(2–)8(–15)	±	+	−	±	−	−	(30–)38(–50)	(52–)73(–102)
V. exul	?	80	(3–)8(–12)	+	−	+	−	−	−	(23–)42(–60)	(42–)61(–83)
V. floccosum	?	30	(3–)6(–9)	±	+	−	−	−	−	(25–)37(–60)	(82–)103(–140)
V. floribundum	—	90	(1–)9(–18)	+	+	+	−	+	−	(10–)14(–20)	(280–)334(–380)
V. globulare	?	0	0	±	−	+	−	+	+	(15–)19(–30)	(160–)297(–360)
V. leschenaultii	?	40	(2–)9(–14)	+	±	+	−	−	−	(25–)34(–40)	(66–)83(–100)
V. leucanthum	?	60	(1–)7(–10)	+	±	+	−	+	−	(15–)31(–40)	(92–)107(–128)
V. maderense	?	75	(1–)3(–6)	±	+	−	−	+	−	(15–)25(–35)	(170–)210(–240)
V. membranaceum	?	85	(6–)11(–16)	+	+	−	−	+	−	(15–)21(–30)	(220–)273(–360)
V. meridionale	?	0	0	±	−	+	−	−	−	(70–)83(–105)	(20–)23(–26)
V. myrtillus	—	90	(5–)10(–14)	+	+	−	−	−	−	(15–)18(–25)	(285–)344(-400)
V. occidentale	?	60	(4–)8(–11)	+	−	+	−	−	−	(13–)18(–25)	(290–)403(–448)
V. ovatum	?	100	(8–)12(–15)	+	+	−	±	+	+	(15–)22(–30)	(200–)238(–289)
V. parvifolium	?	100	(6–)9(–12)	+	+	−	−	+	−	(15–)17(–20)	(210–)263(–300)
V. puberulum var. *subcrenulatum*	?	90	(2–)6(–11)	±	+	−	±	−	−	(25–)32(–40)	(80–)100(–120)
V. scoparium	?	50	(2–)4(–8)	+	+	−	−	−	−	(12–)16(–25)	(310–)336(–390)
V. stanleyi	−	70	(2–)7(–10)	±	+	−	±	−	−	(15–)21(–30)	(250–)280(–310)
V. uliginosum	−	15	(1–)4(–6)	+	−	+	−	−	−	(10–)14(–20)	(360–)421(–480)

Table 1. Extended. Continued.

Vessels	Tracheids	Fibers	Rays			Crystals	
Length of vessel elements (μm)	Length of tracheids (μm)	Length of fiber tracheids (μm)	Multi-seriate ray width (number of cells)	Height of uniseriate rays (μm)	Height of multiseriate rays (μm)	Present in rays	Present in axial paren-chyma
(470–)695(–960)	(430–)663(–830)	(860–)999(–1120)	4–7	(200–)400(–650)	(500–)1217(–1800)	−	−
(370–)517(–650)	(430–)507(–570)	(510–)648(–810)	2–5	(400–)583(–800)	(700–)986(–1600)	−	−
(300–)487(–600)	(470–)687(–970)	(900–)1081 (–1300)	5–6	(350–)563(–1100)	(700–)1408(–3000)	−	−
(270–)422(–520)	(390–)508(–600)	(450–)598(–700)	3–4	(150–)286(–450)	(300–)617(–1100)		
(520–)721(–920)	(700–)776(–850)	(840–)1042 (–1210)	4–5	(250–)554(–1200)	(400–)1059(–1600)	−	−
(450–)640(–850)	(440–)650(–800)	(750–)965(–1100)	5–7	(250–)441(–600)	(800(–)1079(–1500)	−	−
(200–)298(–400)	(310–)368(–520)	(350–)526(–650)	3	(200–)486(–1150)	(500–)1388(–4200)	+	−
(410–)596(–830)	(500–)644(–750)	(840–)930(–1160)	5–7	(400–)586(–900)	(800–)1837(–3300)	+	−
(360–)539(–690)	(430–)678(–830)	(680–)943(–1170)	4–7	(250–)463(–1050)	(400–)1055(–2100)	−	−
(570–)910 (–1170)	(890–)942 (–1050)	(1020–)1408 (–1970)	6–12	(350–)750(–1100)	(800–)1725(–3700)	−	−
(370–)907(–830)	(530–)640(–720)	(900–)1108 (–1133)	3–6	(450–)886(–1700)	(900–)2661(–6800)	−	−
(360–)389(–880)	(290–)423(–490)	(440–)549(–670)	5–7	(150–)275(–450)	(500–)728(–850)	−	−
(260–)387(–570)	(300–)383(–520)	(330–)435(–520)	?	?	?	−	−
(520–)737(–930)	(750–)942 (–1020)	(1020–)1198 (–1450)	4–6	(300–)585(–1050)	(1000–)1710(–2500)	+	−
(320–)536(–880)	(450–)506(–600)	(830–)1043 (–1250)	3-6	(350–)522(–700)	(500–)868(–1200)	−	−
(250–)448(–570)	(400–)545(–510)	(480–)622(–740)	4–9	(200–)275(–400)	(450–)933(–1300)	−	−
(230–)366(–470)	(200–)250(–280)	(370–)493(–580)	3	(300–)479(–750)	(500–)643(–1050)	−	−
(430–)739 (–1040)	(900–)1013 (–1150)	(1320–)1516 (–1800)	4–5	(350–)581(–1050)	(750–)1844(–3900)	+	−
(300–)471(–580)	(220–)300(–350)	(370–)564(–680)	4–5	(200–)305(–400)	(350–)725(–950)	−	−
(150–)220(–320)	(140–)210(–250)	(220–)302(–380)	3–4	(150–)263(–350)	(350–)685(–1150)	−	−
(330–)558(–800)	(270–)394(–520)	(630–)771(–950)	4–5	(500–)610(–800)	(650–)912(–1500)	+	−
(300–)403(–510)	(270–)414(–560)	(450–564(–710)	2–3	(300–)383(–500)	(350–)538(–950)	−	−
(570–)697(–860)	(350–)450(–600)	(890–)1042 (–1340)	4–5	(450–)715(–1200)	(1100–)1930(–2700)	+	−
(170–)256(–400)	(200–(251) (–280)	(280–)330(–370)	3	(150–)207(–300)	(250–)475(–650)	−	−
(230–)438(–600)	(480–)522(–620)	(680)–)783 (–1030)	4–5	(250–)367(–650)	(500–)1045(–1700)	−	−
(130–)242(–350)	(270–)341(–410)	(370–)400(–450)	4–5	(200–)275(–400)	(400–)575(–1050)	−	−

be rather arbitrary to distinguish intermediate cell types to one of these categories, because their definition remains a matter of dispute (Baas, 1986; Carlquist, 2001). Therefore, we prefer to give a detailed description of these cells. We consider tracheids to be long and narrow cells, with dense pitting in tangential walls (more than 15 pits per 100 µm of tracheid length) and radial walls (more than 20 pits per 100 µm of tracheid length). These pits are distinctly bordered and form two or three longitudinal rows in the radial and tangential walls (see Fig. 3H). Fiber-tracheids represent the most common cell type of the ground tissue. They are somewhat longer than tracheids, narrow, thin- or thick-walled, and contain one single row of distinctly bordered pits in tangential walls (ca. 5 to 15 pits per 100 µm of fiber-tracheid length) and radial walls (ca. 5 to 20 pits per 100 µm of fiber-tracheid length). The mean distance between two fiber-tracheid pits in the tangential wall is longer than the distance between two tracheid pits, although the pit borders do not differ in size (ca. 3–6 µm). Libriform fibers are generally as long as fiber-tracheids. They are narrow, mostly thin-walled and septate, and show few to very few, minutely bordered to simple pits in the tangential walls. The pit borders in the libriform fibers are 2–3 µm in size, and their density ranges from less than 1 to 4 per 100 µm of length in tangential walls, and from 2 to about 10 per 100 µm of length in radial walls. Sometimes only two or three pits are observed near the end of libriform fibers. Septate fiber-tracheids and intermediate cells between septate libriform fibers and fiber-tracheids are also seen in most species. For all measurements of tracheary elements, only clearly identifiable cells were taken into account.

Wood features were plotted on trees using the program MacClade 4.04 (Maddison & Maddison, 2002).

Results

Woods of most species have indistinct growth rings and are diffuse-porous (Figs. 1, 2), although a few species of *Cavendishia, Satyria* Klotzsch, *Thibaudia* J. St.-Hil., and *Vaccinium* (Fig. 1C) show a tendency to semi-ring-porous wood. Vessels are angular and mainly solitary (Figs. 1, 2), although some tangential vessel groupings of 2 to 4 cells are reported in several genera. The mean tangential vessel diameter ranges from 14 µm in *Vaccinium uliginosum* to 164 µm in *Dimorphanthera kempteriana* with an overall average of 35 µm. Likewise, the two species mentioned show extreme mean vessel density values (421 and 12 vessels per square mm, respectively), while the mean value for the entire tribe is 145 vessels per square mm. The mean length of the vessel elements is 600 µm and varies from 220 µm in *Vaccinium occidentale* to 1006 µm in *Disterigma cryptocalyx.*

Vaccinieae often have mixed simple and scalariform perforation plates, although the scalariform type usually dominates. Genera with species having mostly scalariform perforations include *Anthopterus* Hook., *Ceratostema* Juss., *Demosthenesia* A. C. Sm., *Diogenesia* Sleumer, *Disterigma* (Klotzsch) Nied., *Lateropora* A. C. Sm., *Gaylussacia, Mycerinus* A. C. Sm., *Plutarchia* A. C. Sm., *Oreanthes* Benth. (Fig. 3D), *Orthaea* Klotzsch (Fig. 3C), *Semiramisia* Klotzsch, *Symphysia* C. Presl, and *Sphyrospermum* Poepp. & Endl., while simple perforations dominate in *Dimorphanthera* F. Muell., *Notopora* Hook. f., *Polyclita* A. C. Sm., and *Siphonandra* Klotzsch; the other genera show more variation in the type of vessel perforation between the species observed, for example, *Agapetes* (Figs. 3A, E) and *Vaccinium* (Figs. 3B, F). Intervessel pits are scarce and mostly opposite (2–5 µm in size) to scalariform (6–20 µm in size), except in *Agapetes* and *Vaccinium,* which often show alternate intervessel pitting (2–5 µm in size). Vessel-ray pits are scalariform with strongly reduced borders in most genera (Figs. 4E–H) except for *Agapetes, Gaylussacia,* and most *Vaccinium* species, and range from rather small (6 µm in size) to very large (40 µm in size in species with wide vessels). Alternate vessel-ray pits with distinct borders are typical of *Agapetes* (2–5 µm in size, Fig. 4D), while in *Vaccinium* all types of vessel-ray pitting is observed.

Helical thickenings are nearly always present in the tails of vessel elements; their presence throughout the body of vessel elements is restricted to species of *Agapetes, Disterigma, Ceratostema, Gaylussacia,* and is especially common in *Vaccinium* (Fig. 3G). Helical thickenings were also observed in some fibers and/or tracheids of *Agapetes, Disterigma,* and *Vaccinium.*

The ground tissue of the wood consists of fiber-tracheids, except for *Dimorphanthera collinsii, D. cornuta,* and *Macleania rupestris,* in which tracheids form the ground tissue. The fiber-tracheids have very thin to thick walls. The mean length of the fiber-tracheids is 865 µm with a minimum mean value of 302 µm in *Vaccinium occidentale* and a maximum mean length of 1516 µm in *Vaccinium meridionale.* Occasionally thin-walled libriform fibers, which are usually septate with few simple to indistinctly bordered pits, were reported in all species, except for *Dimorphanthera kempteriana, Macleania crassa, M. rupestris, Satyria* sp. in-

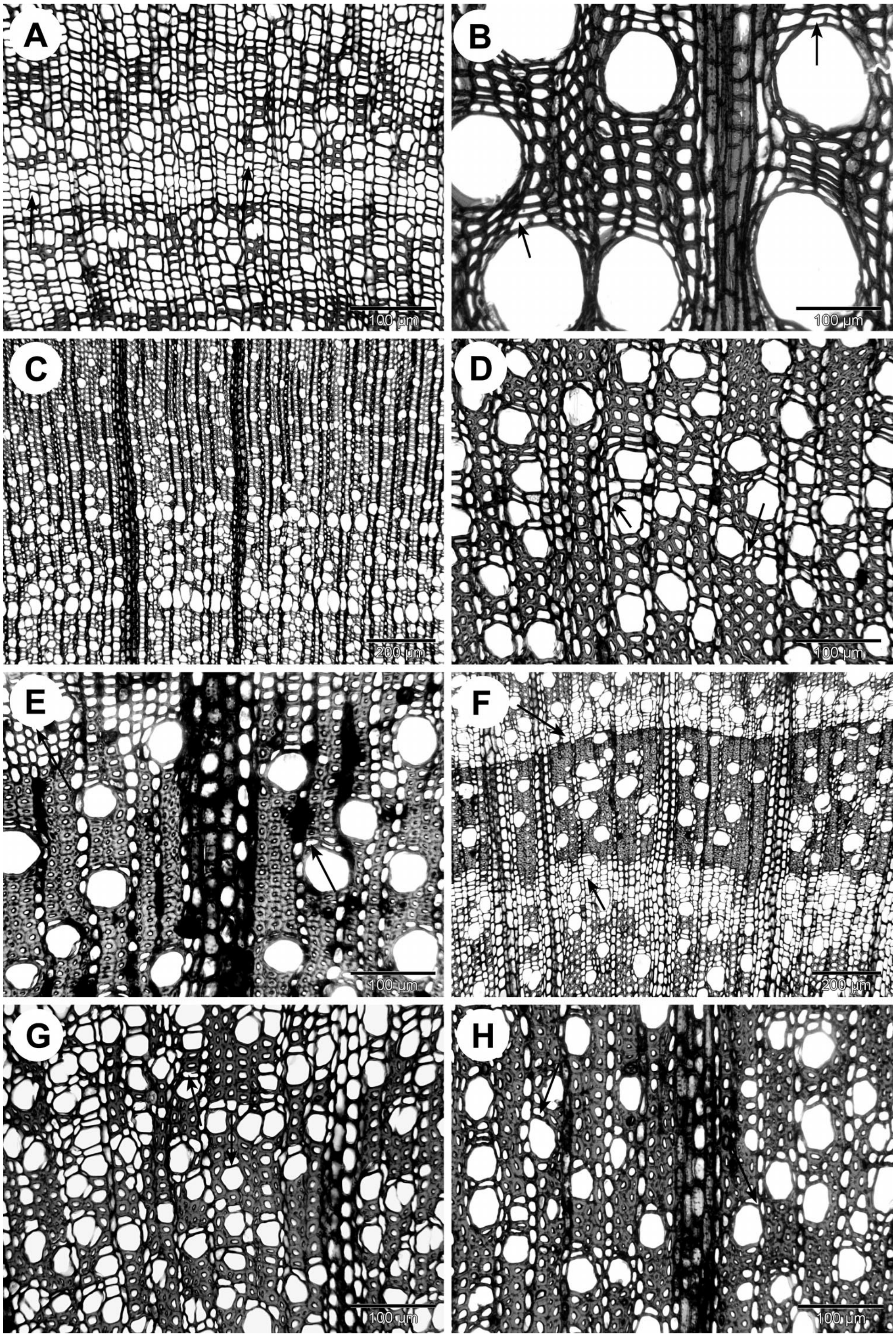

Figure 1. A–H. Transverse sections showing arrangement of vessels, distribution of axial parenchyma (arrows), and thickness of fiber walls. —A. *Agapetes flava* (*Grierson & Long 3076,* E 19822403). —B. *Dimorphanthera dekockii* var. *pubiflora* (*Vink 17307,* Kw 11639). —C. *Vaccinium calycinum* (*Stern 2950,* Tw 24121). —D. *Vaccinium puberulum* var. *subcrenulatum* (*Maas et al. 5733,* Uw 27342). —E. *Notopora schomburgkii* (*Maas et al. 5808,* Uw 27397). —F. *Psammisia* cf. *ulbrichiana* (*Luteyn & Lebrón-Luteyn 6532,* NY). —G. *Lateropora ovata* (*Luteyn 15294,* NY). —H. *Diogenesia tetrandra* (*Luteyn et al. 7388,* NY).

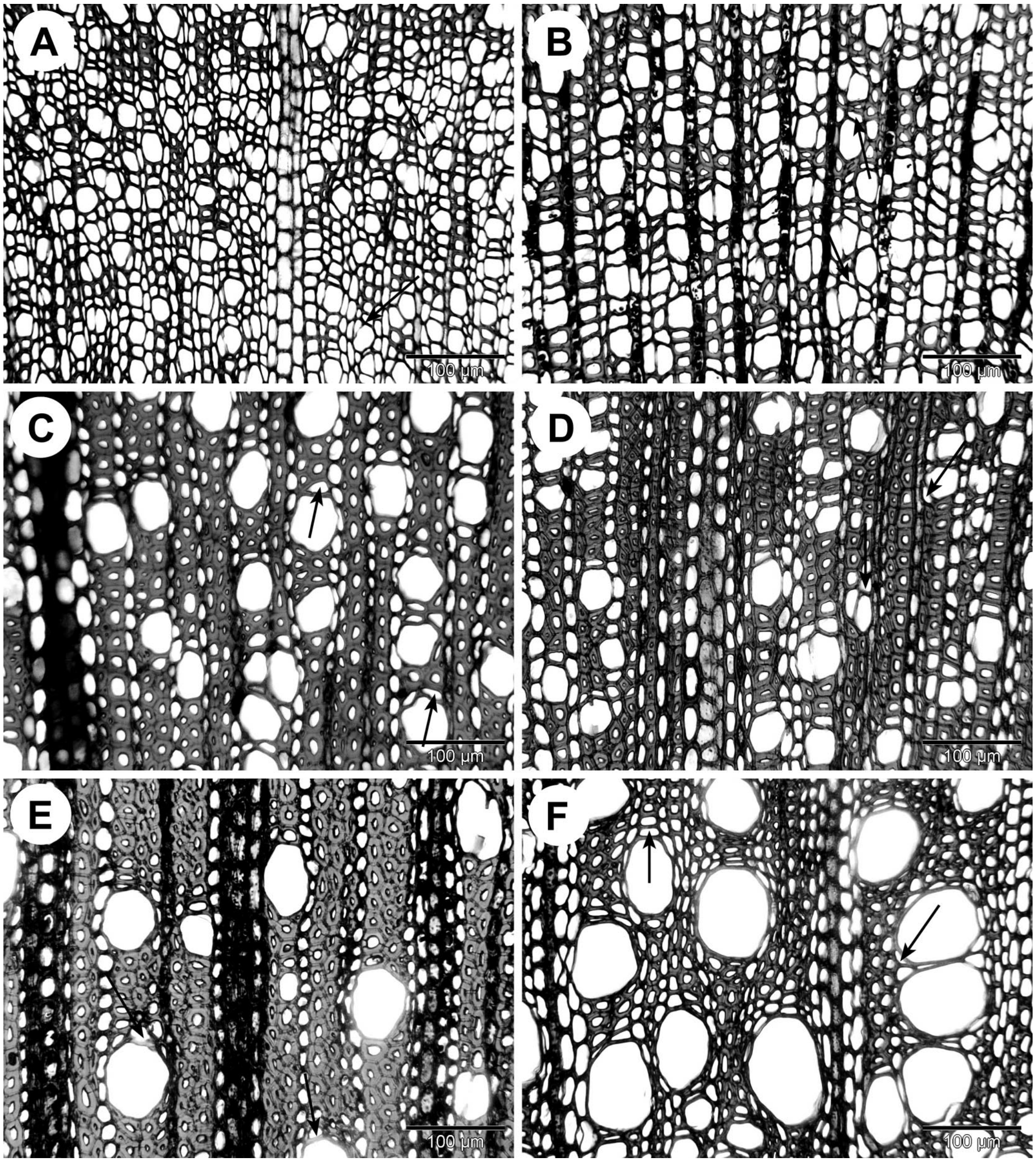

Figure 2. A–F. Transverse sections showing arrangement of vessels, distribution of axial parenchyma (arrows), and thickness of fiber walls. —A. *Sphyrospermum* sp. indet. (*Argent*, E 19762390). —B. *Demosthenesia spectabilis* (*Luteyn 6452*, NY). —C. *Cavendishia bracteata* (*Dorr et al. 6890*, Lw). —D. *Macleania stricta* (*Luteyn & Lebrón-Luteyn 5744*, NY). —E. *Orthaea fimbriata* (*Luteyn & Lebrón-Luteyn 5794*, NY). —F. *Satyria meiantha* (*Breedlove 9746*, MADw 23933).

det. (Uw 17005), *Siphonandra elliptica*, *Themistoclesia pendula*, *T. vegasana*, and *Vaccinium meridionale*. The libriform fibers are somewhat shorter than fiber-tracheids (on average 700 μm) and contain nuclei (Fig. 5H). Also septate fiber-tracheids and cells intermediate between septate libriform fibers and fiber-tracheids were observed in most species. In general, tracheids are present (Fig. 3H), although they were not observed in *Disterigma cryptocalyx*, *Vaccinium membranaceum*, *V. myrtillus*, *V. occidentale*, and *V. puberulum*. In *Dimorphanthera collinsii* and *D. cornuta*, the ground tissue is formed by tracheids only, which show large, bordered pits usually between 6 and 9 μm in size.

The main distribution type of the axial paren-

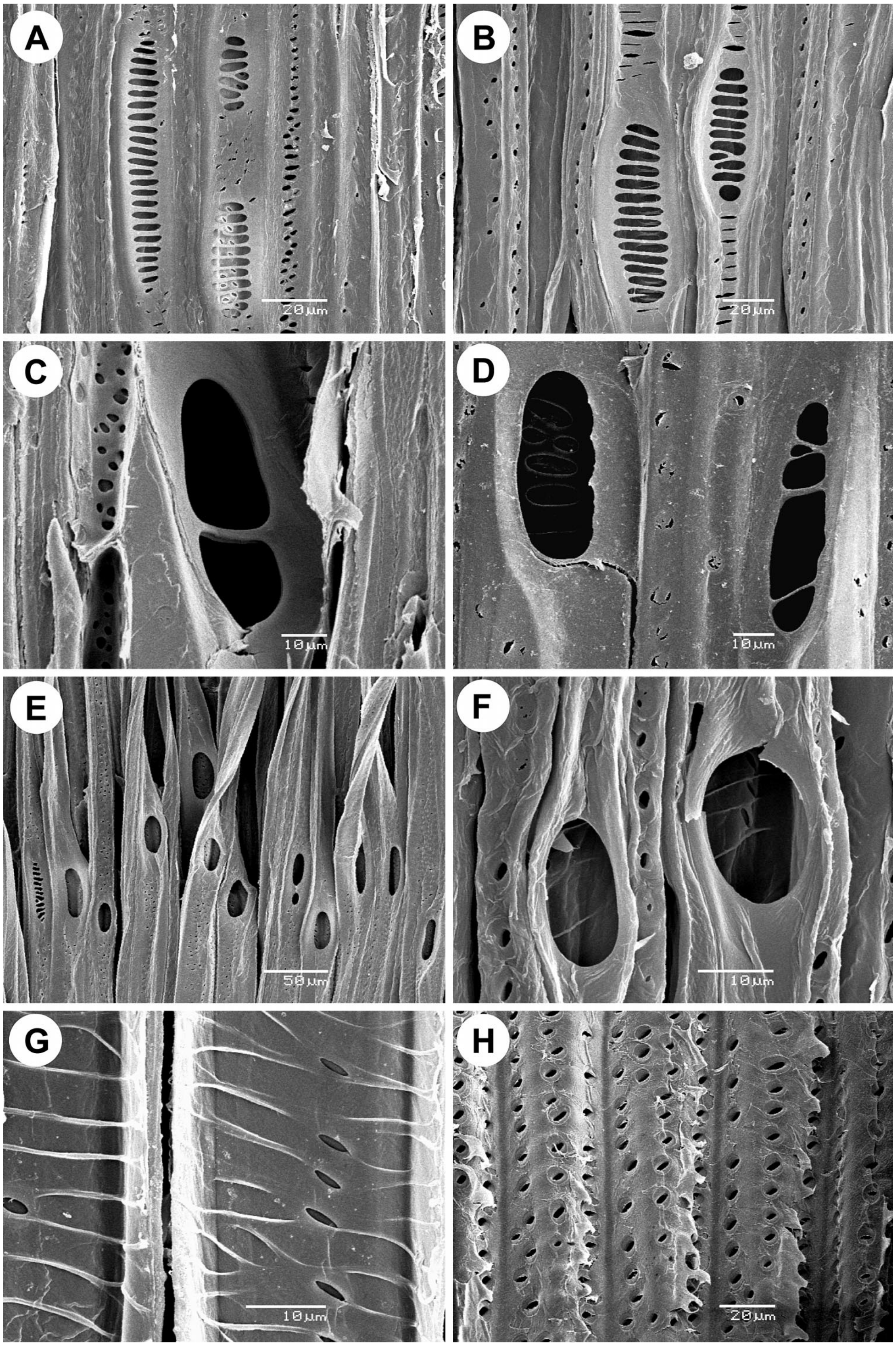

Figure 3. A–C. Scalariform vessel perforations. —A. *Agapetes hosseana* (*Burtt 958*, E 19672592). —B. *Vaccinium angustifolium* (*Lens*, BR). —C. *Orthaea fimbriata* (*Luteyn & Lebrón-Luteyn 5794*, NY). —D. Vessel perforation mixed scalariform and simple: *Oreanthes ecuadorensis* (*Luteyn 15394*, NY). E–F. Simple vessel perforations. —E. *Agapetes sikkimensis* (*Sinclair & Long 5778*, E 19842032). —F. *Vaccinium globulare* (*Dechamps 4460*, Tw 46335). —G. Helical thickenings throughout vessel element: *Vaccinium ovatum* (*Dechamps 4418*, Tw 46267). —H. Tracheids: *Dimorphanthera kempteriana* (*Vink 16888*, Tw 23733).

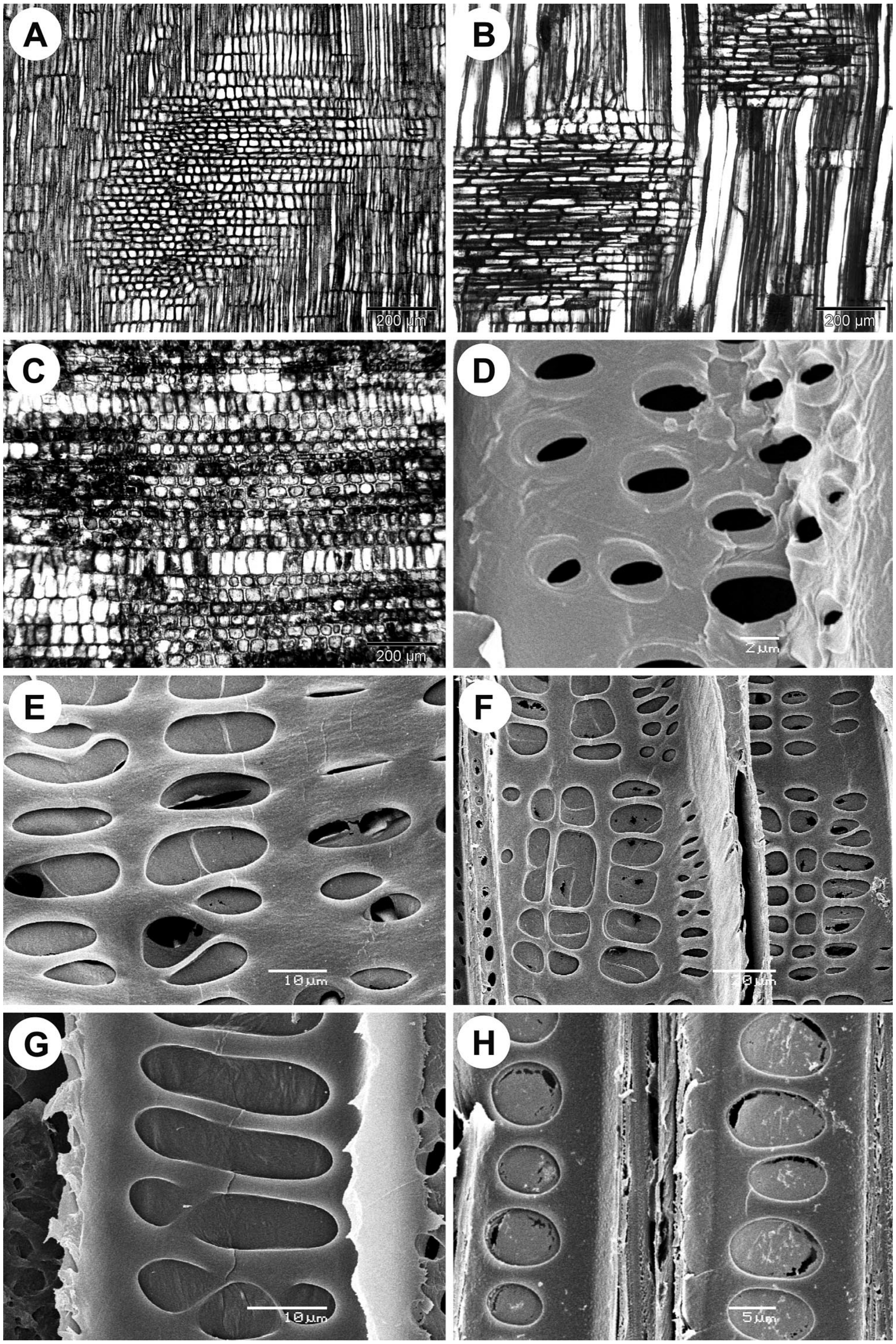

Figure 4. A–C. Radial sections showing structure of multiseriate rays. —A. Procumbent, square and upright body ray cells: *Agapetes mannii* (*Kingdon-Ward 19097*, E 19500046). —B. Exclusively procumbent body ray cells: *Vaccinium consanguineum* (*Wiemann 13*, Uw 30897). —C. Mainly upright and square body ray cells: *Macleania pentaptera* (*Luteyn & Lebrón-Luteyn 6957*, NY). D–H. Vessel-ray pitting. —D. Vessel-ray pits bordered: *Agapetes sikkimensis* (*Sinclair & Long 5778*, E 19842032). E–H. Vessel-ray pitting scalariform with much reduced borders. —E. *Dimorphanthera kempteriana* (*Vink 16888*, Tw 23733). —F. *Orthaea fimbriata* (*Luteyn & Lebrón-Luteyn 5794*, NY). —G. *Macleania loeseneriana* (*Luteyn & Lebrón-Luteyn 5726*, NY). —H. *Oreanthes ecuadorensis* (*Luteyn 15394*, NY).

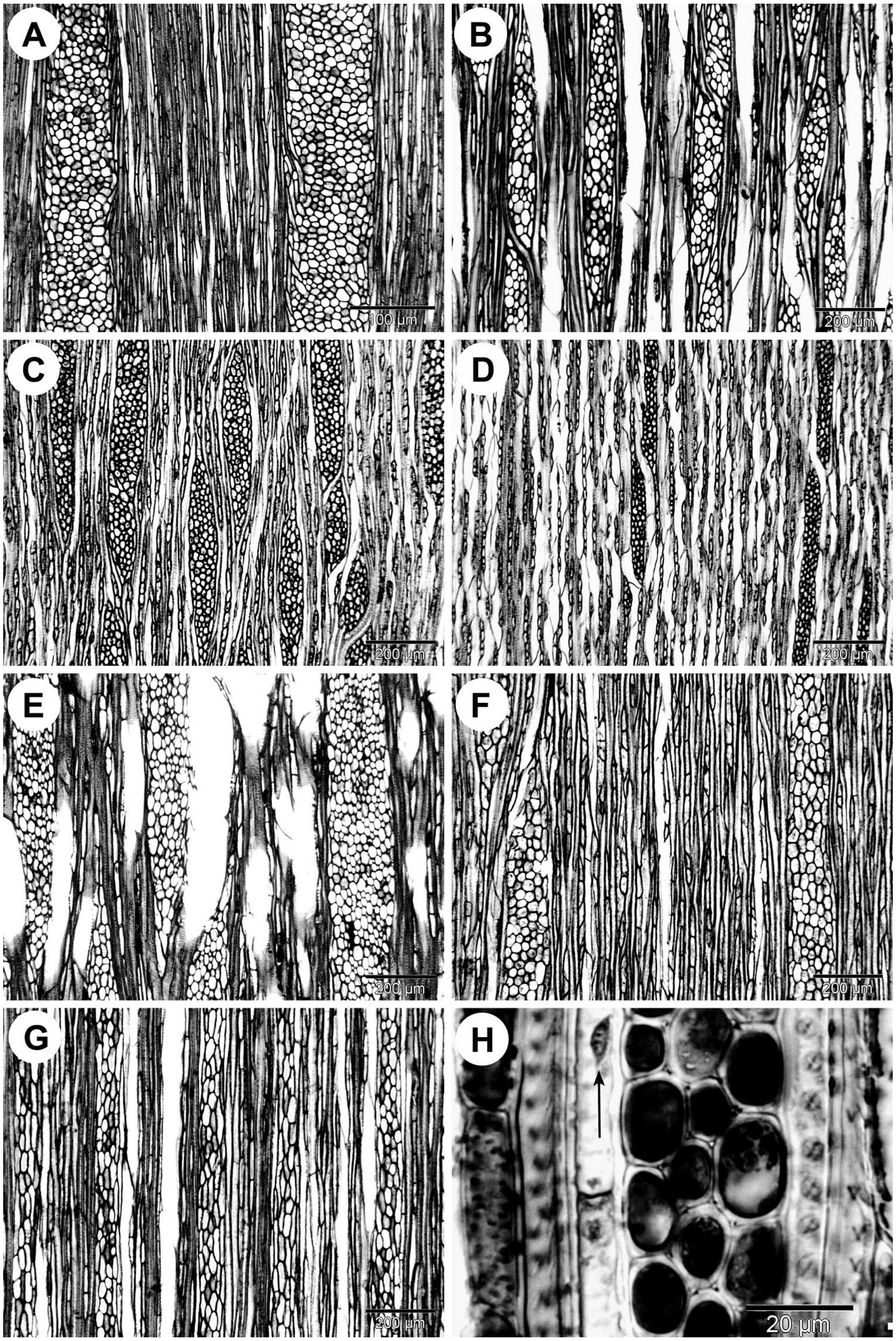

Figure 5. Tangential sections showing the width of multiseriate rays. —A. *Agapetes flava* (*Grierson & Long 3076*, E 19822403). —B. *Vaccinium barandanum* var. *barandanum* (*Jacobs 7249*, Uw 33743). —C. *Vaccinium floribundum* (*De Sloover 399*, BR). —D. *Vaccinium uliginosum* (*Dechamps 6033*, Tw 38581). —E. *Satyria* sp. indet. (*Maguire et al. 48650*, Uw 16976). —F. *Polyclita turbinata* (*Luteyn 15453*, NY). —G. *Psammisia* cf. *ulbrichiana* (*Luteyn & Lebrón-Luteyn 6532*, NY). —H. Nucleus (arrow) in septate libriform fiber: *Gaylussacia baccata* (*F. Lens*, BR).

chyma is scanty paratracheal (Figs. 1, 2); sparsely diffuse apotracheal parenchyma was also seen in species of *Agapetes, Cavendishia, Ceratostema, Dimorphanthera, Orthaea, Psammisia, Satyria, Thibaudia,* and *Vaccinium,* while diffuse-in-aggregates parenchyma was observed in some *Vaccinium* species. Banded marginal parenchyma was seen in a few species, viz. *Agapetes flava* (Fig. 1A), *Mycerinus chimantensis, Notopora schomburgkii, Psammisia* cf. *ulbrichiana* (Fig. 1F), *Satyria* sp. indet. (*Luteyn & Lebrón-Luteyn 7177,* NY), and *Sphyrospermum* sp. indet. Axial parenchyma strands usually consist of 2 to 4 cells, although strands with up to 8 cells were also observed. In almost all genera, except for *Gaylussaccia* and most species of *Vaccinium,* undivided (fusiform) axial parenchyma cells were seen, ranging from 350 μm to 1050 μm with an average length of 600 μm. Intermediate types between fusiform axial parenchyma cells and libriform fibers also occur.

Uniseriate rays consist of predominantly upright cells. The mean height of the uniseriate rays varies greatly from 207 μm in *Vaccinium uliginosum* to 2478 μm in *Psammisia graebneriana,* with an average height of 740 μm for all species studied. Chambered cell types and prismatic crystals are always absent within uniseriate rays.

Multiseriate rays are heterocellular and usually consist of procumbent, square and/or upright body ray cells and several rows of upright marginal ray cells. In *Agapetes, Dimorphanthera, Disterigma, Gaylussacia,* and *Vaccinium,* however, upright body ray cells are rare while procumbent and/or square body ray cells dominate (Figs. 4A, B). Multiseriate rays are in general 3 to 7 cells wide (Fig. 5). Narrow rays (2- to 3-seriate) were observed in juvenile stems of *Cavendishia compacta, Macleania ericae,* and *Mycerinus chimantensis,* while wide multiseriate rays (sometimes more than 10 cells wide) were seen in several *Agapetes* species (Fig. 5A) and in *Dimorphanthera dekockii, Disterigma alaternoides, Satyria panurensis, Themistoclesia epiphytica, Thibaudia floribunda, Thibaudia pachypoda,* and *Vaccinium exul.* Multiseriate rays are much higher than uniseriate rays, mostly between 1000 and 7500 μm, with an average height of 4020 μm. Multiseriate rays in some species are without doubt much higher than indicated by the measurements in Table 1, since the height of the multiseriate rays often exceeds the length on the section. Very high rays (more than 10,000 μm) were observed in species of *Agapetes, Disterigma, Macleania, Psammisia, Satyria,* and *Themistoclesia* Klotzsch. Sheath cells are mostly present, but not always clearly developed. Gummy deposits (possibly tannins) were frequently noticed in the ray cells (Figs. 4B, C, 5H).

Prismatic crystals occur in non-chambered ray cells (Fig. 6A) or in chambered ray cells (Figs. 6B, C), but they were absent in species investigated of *Ceratostema, Demosthenesia, Diogenesia, Gaylussacia, Oreanthes, Plutarchia, Semiramisia, Siphonandra,* and *Symphysia.* Sometimes they are observed in chambered axial parenchyma cells of *Anthopterus, Cavendishia, Disterigma, Macleania* (Fig. 6E), *Psammisia* (Fig. 6D), *Themistoclesia,* and *Thibaudia.*

The pith structure of the Vaccinieae species investigated is homogeneous. In *Demosthenesia, Gaylussacia, Oreanthes, Plutarchia,* and *Symphysia* no crystals were observed in the pith, but the remaining genera show prismatic crystals and/or druses. In *Notopora cardonae* and *Polyclita turbinata* (Fig. 6I), thick-walled sclereids are observed among the pith cells. Secretory ducts at the border of the primary xylem and the pith, but sometimes also in the pith, were observed in species of *Cavendishia, Demosthenesia, Diogenesia, Lateropora, Macleania, Oreanthes* (Fig. 6H), *Orthaea* (Fig. 6F, G), *Polyclita, Psammisia, Satyria, Semiramisia, Themistoclesia,* and *Thibaudia.*

Discussion

Our wood anatomical observations largely agree with the earlier description of Vaccinieae by Metcalfe and Chalk (1950), although some differences can be found. For instance, the width of the vessels is generally reported to be between 25 and 50 μm and only slightly larger in *Paphia.* We have observed several species with a mean tangential vessel diameter of more than 80 μm. Furthermore, Metcalfe and Chalk (1950) mentioned that helical thickenings throughout vessel elements are restricted to *Vaccinium,* but this study has shown that these thickenings are also present in species of *Agapetes, Ceratostema, Disterigma,* and *Gaylussacia.* In addition, helical thickenings are found throughout fiber-tracheids and/or tracheids in *Agapetes mannii, Disterigma* sp. indet., *Vaccinium arboreum, V. globulare,* and *V. ovatum.* The abovementioned authors also underestimated the height of the multiseriate rays (commonly more than 1000 μm), but Giebel (1983) found a more correct value for the height of multiseriate rays in *Cavendishia,* i.e., often between 1073 and 7021 μm. The most striking new character is the observation of secretory ducts in the primary xylem and pith of 13 genera belonging to the Andean clade, which has not been recorded previously as far as we know. The

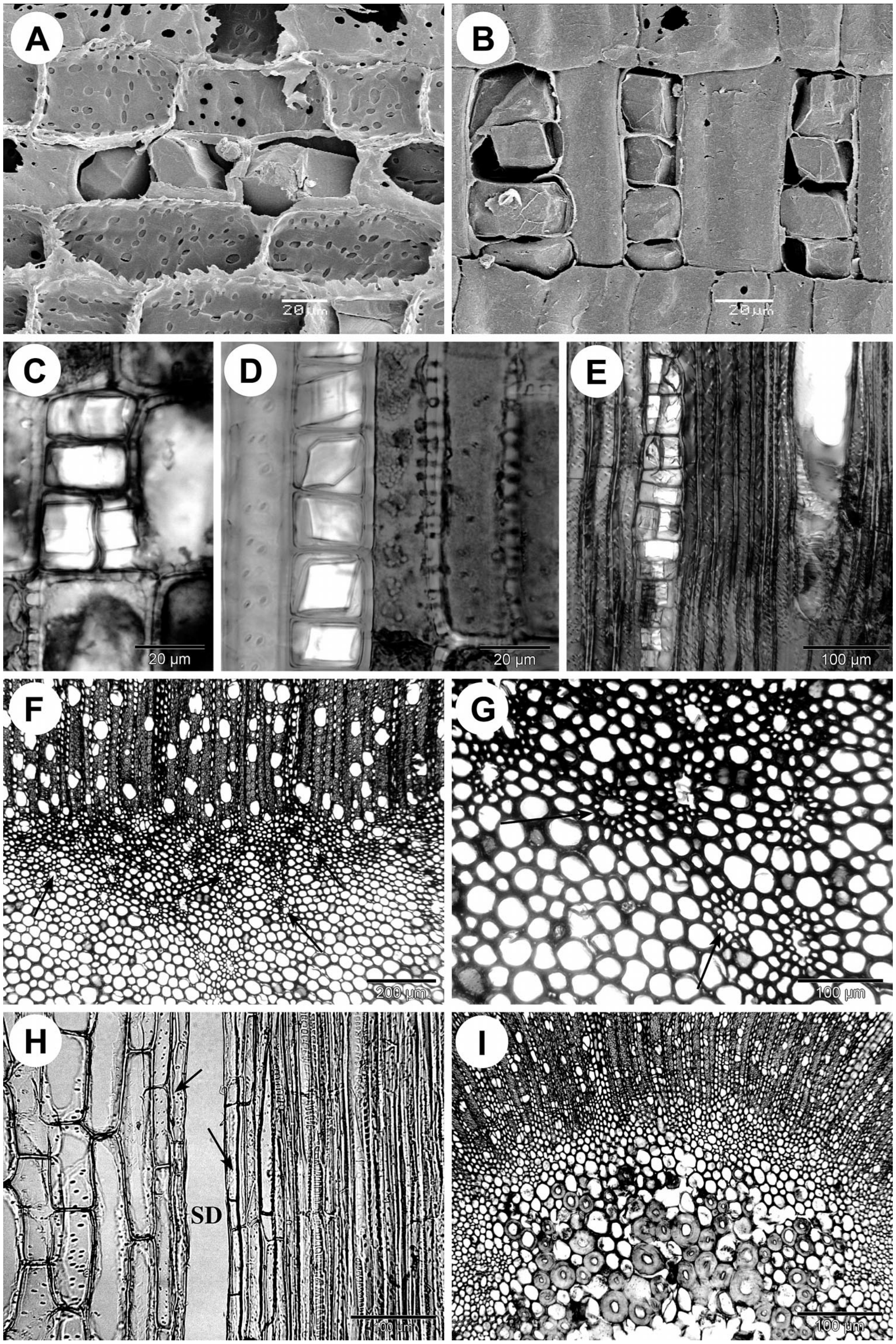

Figure 6. A–C. Prismatic crystals in ray cells. —A. Non-chambered ray cells: *Dimorphanthera kempteriana* (*Vink 16888*, Tw 23733). B, C. Chambered ray cells. —B. *Mycerinus chimantensis* (*O. Huber 9010*, NY). —C. *Notopora schomburgkii* (*Maas et al. 5808*, Uw 27397). D, E. Prismatic crystals in chambered axial parenchyma cells. —D. *Psammisia* sp. indet. (*van Rooden et al. 359*, Uw 25565). —E. *Macleania crassa* (*Luteyn et al. 7378*, NY). F–H. Secretory ducts in primary xylem and pith. —F, G. Transverse section (arrows): *Orthaea fimbriata* (*Luteyn & Lebrón-Luteyn 5794*, NY). —H. Longitudinal section showing secretory cells (arrows) around a secretory duct (SD): *Oreanthes ecuadorensis* (*Luteyn 15394*, NY). —I. Sclereids in pith: *Polyclita turbinata* (*Luteyn 15453*, NY).

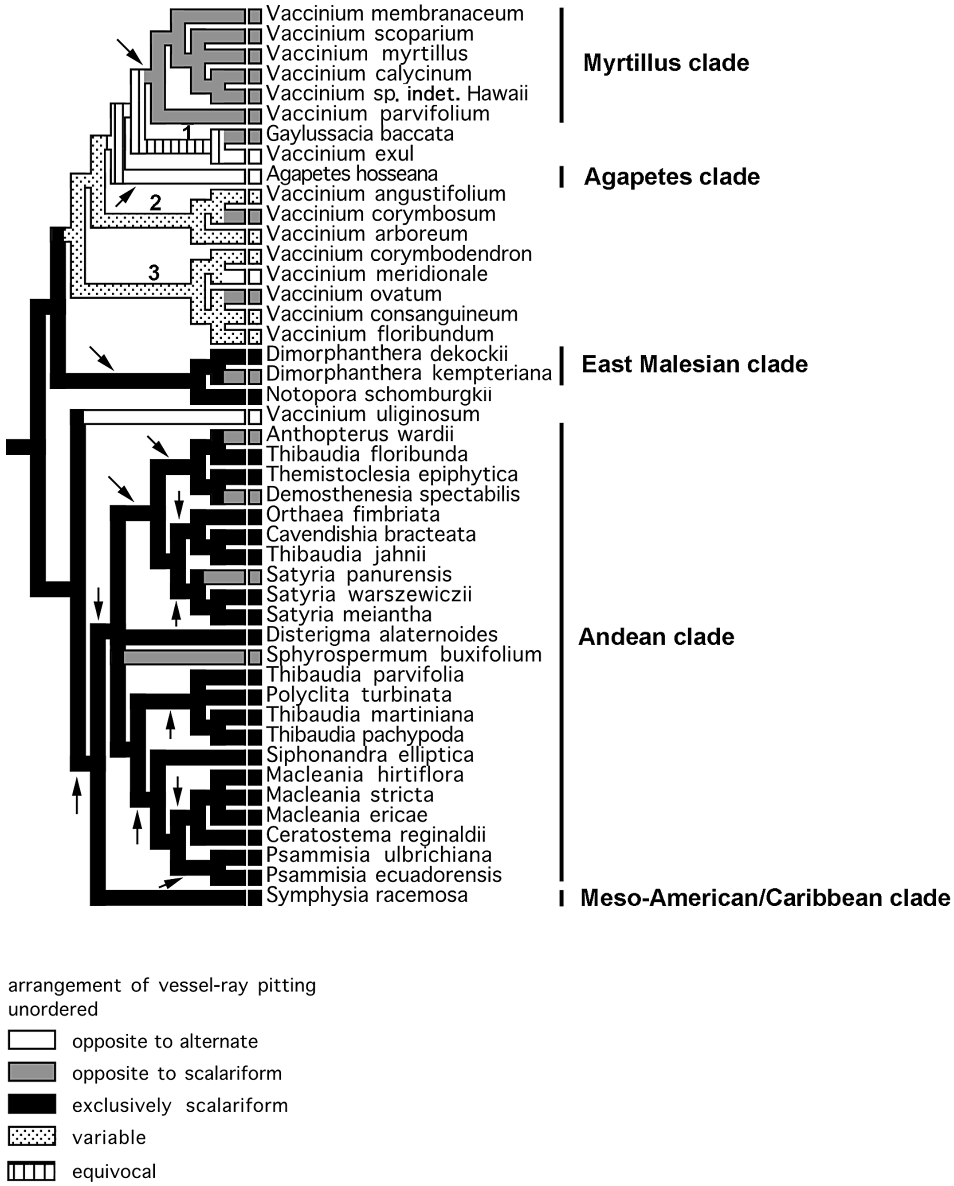

Figure 7. Modified tree based on the molecular analyses of Kron et al. (2002b) and Powell and Kron (2002, 2003) showing the arrangement of vessel-ray pits in Vaccinieae. Clades one, two, and three represent an intermediate group based on their wood structure. Arrows indicate bootstrap values of at least 85%.

exact contents of these secretory ducts is unknown. When unbleached, longitudinal sections were observed, a brown substance was sometimes seen, but the secretory duct also seems to be empty in many cases (Fig. 6H). It is also unclear whether these secretory ducts are present in other vegetative tissues.

We also found nuclei in septate libriform fibers of the two species that were stored in FAA, namely *Gaylussacia baccata* and *Vaccinium angustifolium.* Besides these two species, it is known that other Vaccinieae species contain living fibers, namely *Vaccinium myrtillus, V. varingiaefolium,* and species of *Cavendishia* (Wolkinger, 1970; Giebel, 1983). It is generally accepted that nuclei in septate fibers persist much longer than in fiber-tracheids and tracheids. Nuclei in septate fibers are likely to be found in Vaccinieae, if fresh material

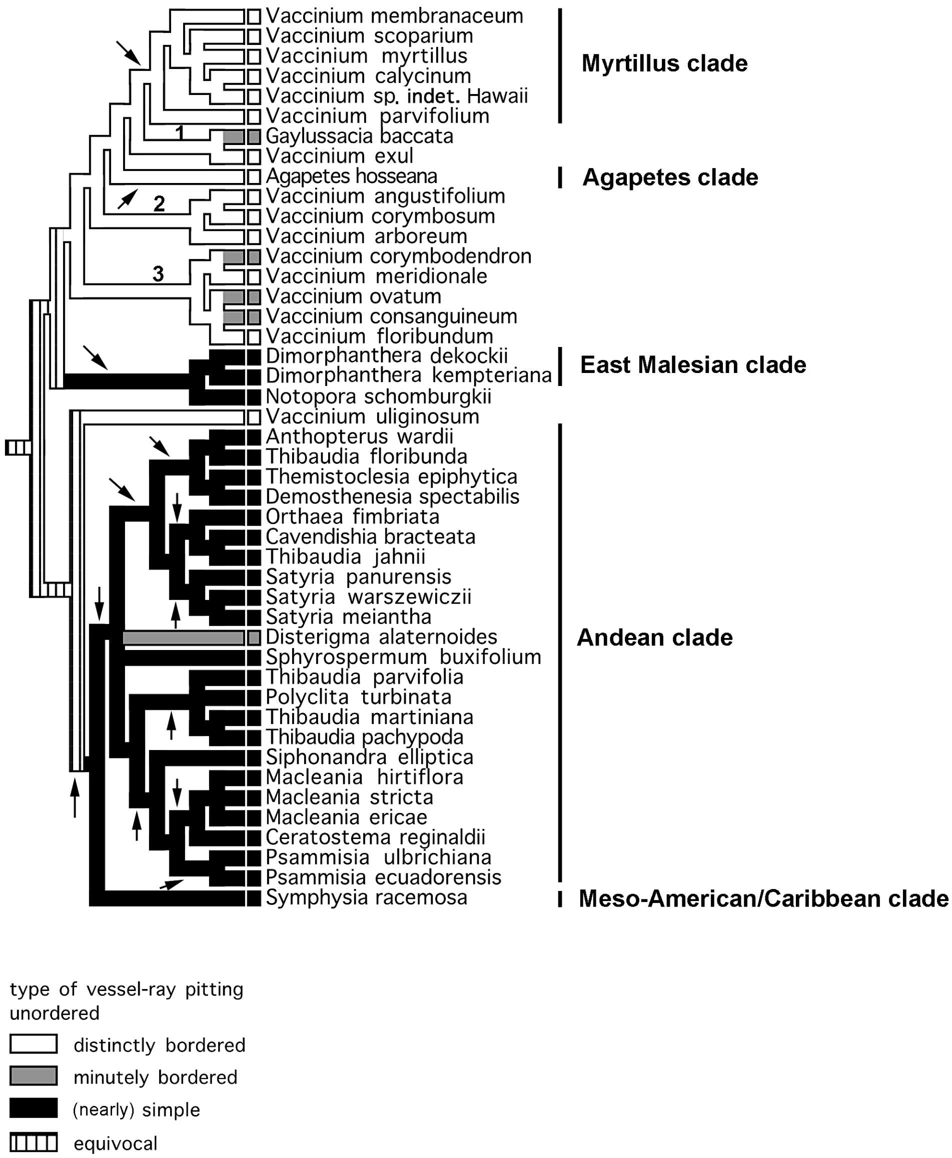

Figure 8. Modified tree based on the molecular analyses of Kron et al. (2002b) and Powell and Kron (2002, 2003) showing the type of vessel-ray pits in Vaccinieae. Clades one, two, and three represent an intermediate group based on their wood structure. Arrows indicate bootstrap values of at least 85%.

is preserved in FAA. Since Vaccinieae and the subfamily Vaccinioideae as a whole is characterized by septate fibers, it is expected that nucleate fibers are typical of the subfamily. Indeed, several authors have noticed the presence of living fibers in Vaccinieae (Braun, 1961; Fahn & Leshem, 1962; Giebel, 1983) and other tribes of the subfamily (Lens et al., 2004a). However, there are also records in Arbutoideae, another subfamily of Ericaceae, in which septate fibers are found (Wolkinger, 1970).

PHYLOGENETIC WOOD ANATOMY

In order to comment on the recent generic realignments within the tribe and to trace the evolution of some important wood anatomical characters, we have created a tree, based on the molecular phylogenetic studies of Kron et al. (2002b) and

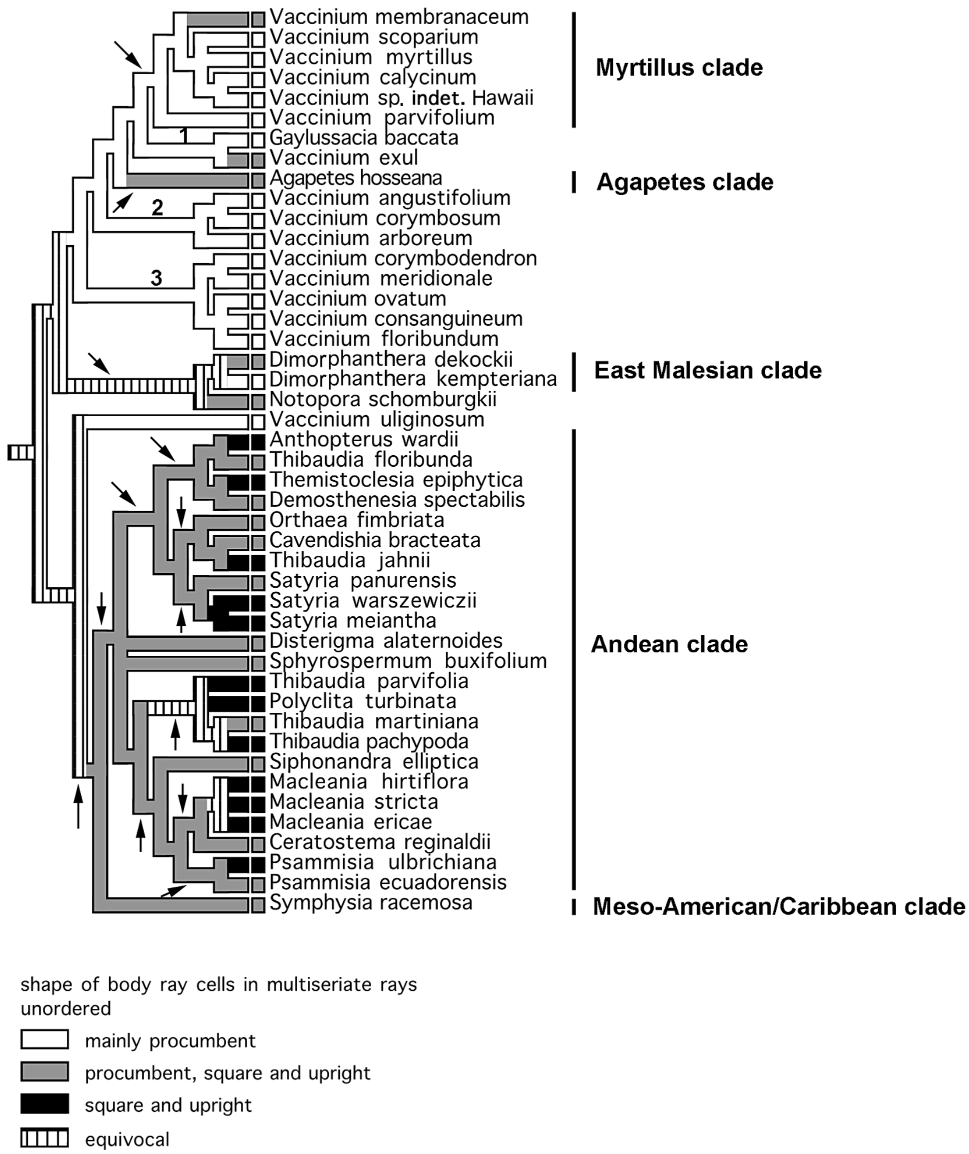

Figure 9. Modified tree based on the molecular analyses of Kron et al. (2002b) and Powell and Kron (2002, 2003) showing the shape of body ray cells in multiseriate rays of Vaccinieae. Clades one, two, and three represent an intermediate group based on their wood structure. Arrows indicate bootstrap values of at least 85%.

Powell and Kron (2002, 2003). The tree contains 45 species and 20 genera that are included in this study and represents all major evolutionary lines in Vaccinieae, except for the Bracteata–Oarianthe clade. This clade, comprised of species of *Vaccinium* from New Guinea and Borneo, was omitted from this study due to lack of material. As indicated by arrows, the subclades with an informal name have bootstrap values of at least 85%, but relationships between these clades are poorly supported (Figs. 7–10). Therefore, our discussion of the relationships within Vaccinieae is focused on the named subclades.

Four wood characters are plotted on the tree, i.e., arrangement of vessel-ray pitting (Fig. 7), the type of vessel-ray pitting (Fig. 8), the shape of body ray cells in multiseriate rays (Fig. 9), and the presence of secretory ducts (Fig. 10). These features are chosen based on their apparent consistency within the various subclades of Vaccinieae and on previous studies within the family (Lens et al., 2003, 2004a).

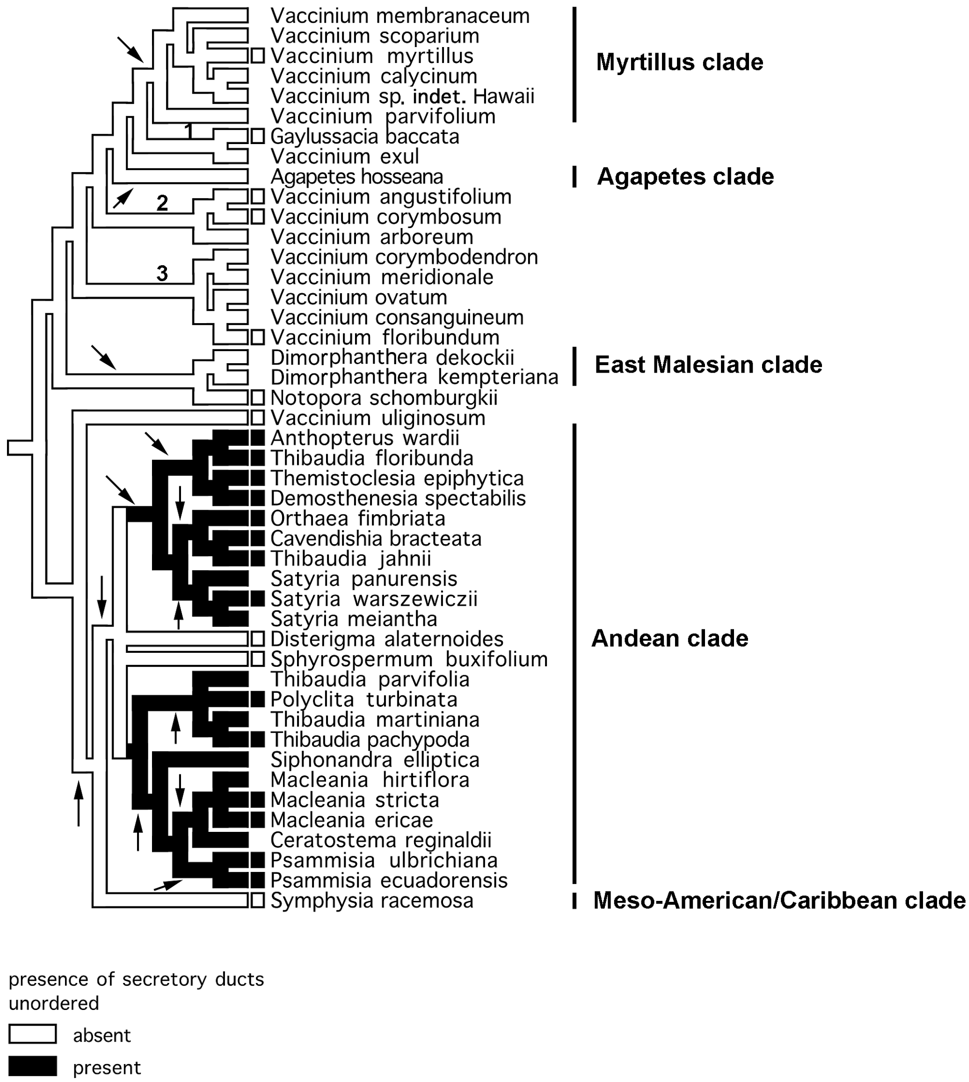

Figure 10. Modified tree based on the molecular analyses of Kron et al. (2002b) and Powell and Kron (2002, 2003) showing the presence of secretory ducts in the primary xylem and the pith of Vaccinieae. Clades one, two, and three represent an intermediate group based on their wood structure. Arrows indicate bootstrap values of at least 85%. Missing blocks indicate that the pith and primary xylem tissue was not available.

Myrtillus Clade (represented by Vaccinium calycinum, V. membranaceum, V. myrtillus, V. parvifolium, V. scoparium, *and* V. *sp. indet. Hawaii)*

The enlarged Myrtillus clade sensu Powell and Kron (2002) mostly occurs along the Pacific Rim from Japan to Mexico (Powell & Kron, 2002). The species studied are wood anatomically defined by the presence of exclusively or mainly scalariform perforations, opposite to scalariform vessel-ray pitting with distinctly bordered pits (Figs. 7, 8), and narrow (2- to 5-seriate) and low multiseriate rays (often lower than 1000 μm) with mainly procumbent body ray cells (Fig. 9). It is remarkable that this set of characters is common in non-vaccinioid Ericaceae (see also Cox, 1948; Suzuki & Noshiro, 1988).

Agapetes Clade (represented by Agapetes hosseana *only)*

This clade contains temperate and tropical Asian *Vaccinium* species and species of *Agapetes* (Kron et al., 2002b). Although we have studied several *Agapetes* species, only *A. hosseana* is included in the molecular tree. This species shows some features that resemble the Myrtillus clade, for instance, the presence of distinctly bordered vessel-ray pitting (Fig. 8), and the relatively narrow and low multiseriate rays. On the other hand, other *Agapetes* species investigated are characterized by very broad (3- to 15-seriate) and high multiseriate rays (sometimes more than 10,000 μm in *A. sikkimensis* and *A. moorei*). The only characters that seem to distinguish this group from the Myrtillus clade are (1) the presence of alternate vessel-ray pitting, which is also seen outside the Agapetes clade in a few *Vaccinium* species and in many non-vaccinioid Ericaceae, and (2) the occurrence of procumbent, square and upright body ray cells in the multiseriate rays, although this type of ray composition is also seen in *Vaccinium membranaceum* (Figs. 7, 9).

East Malesian Clade (represented by Dimorphanthera dekockii *and* D. kempteriana*)*

The East Malesian clade comprises species belonging to *Dimorphanthera* and *Paphia* (Kron et al., 2002b). The two *Dimorphanthera* species that are used in this study differ from the Agapetes and Myrtillus clades by the presence of wide vessel elements (ranging from 60 μm to 205 μm) with almost exclusively simple perforation plates, mainly scalariform vessel-ray pits with strongly reduced borders (Figs. 7, 8), and the occurrence of prismatic crystals in multiseriate rays. Furthermore, the two species studied are also defined by an abundant presence of tracheids and a small amount of fiber-tracheids, and broad (4- to 11-seriate) and high multiseriate rays (1800–8400 μm). The high percentage of wide vessels with simple perforations and the abundant occurrence of tracheids is likely due to the climbing habit of *Dimorphanthera* (see also Lens et al., 2004b).

Meso-American/Caribbean Clade (represented by Symphysia racemosa *only)*

This is a well-supported clade that contains species generally found in Central America and the Caribbean (Kron et al., 2002b). The species examined in this study shows mainly scalariform vessel perforations, exclusively scalariform vessel-ray pits with strongly reduced borders, and relatively narrow multiseriate rays (4-seriate) with procumbent, square and upright body ray cells (Figs. 7–9). It is worth mentioning that similar vessel-ray pits are found in the East Malesian clade and the Andean clade.

Andean Clade (represented by Anthopterus wardii, Cavendishia bracteata, Ceratostema reginaldii, Demosthenesia spectabilis, Disterigma alaternoides, Macleania ericae, M. hirtiflora, M. stricta, Orthaea fimbriata, Polyclita turbinata, Psammisia ecuadorensis, P. *cf.* ulbrichiana, Satyria meiantha, S. panurensis, S. warszewiczii, Siphonandra elliptica, Sphyrospermum buxifolium, Themistoclesia epiphytica, Thibaudia floribunda, T. jahnii, T. parvifolia, T. pachypoda, *and* T. martiniana*)*

The Andean clade shows by far the highest species diversity within Vaccinieae, and is concentrated in the moist, montane forests of the northern Andes. This group has evolved very recently, about 20 million years ago when the Andes began to rise (Luteyn, 2002). This can also be illustrated by its homogeneous wood structure. Species of the Andean clade are characterized by scalariform vessel-ray pits with strongly reduced borders (Figs. 7, 8), and by broad (4- to 14-seriate) and high (often more than 3000 μm) multiseriate rays with a high percentage of square and upright body ray cells (Fig. 9). Furthermore, prismatic crystals often occur in ray cells as well as in axial parenchyma cells. The most distinguishing character, however, is the occurrence of secretory ducts near the primary xylem and the pith tissue. All specimens with secretory ducts are included in the Andean clade (Table 1), but this character is sometimes lacking in, for instance, the two unplaced species, i.e., *Disterigma alaternoides* and *Sphyrospermum buxifolium* (Fig. 10).

Within the Andean clade, wood anatomical support for the division into the two major subclades is lacking. Nevertheless, the sister relationship of the Andean clade with the Meso-American/Caribbean clade seems justified according to wood anatomical data: both clades show mainly scalariform vessel perforations, scalariform vessel-ray pits with strongly reduced borders, and distinctly upright body ray cells (Figs. 7–9).

Remaining Subclades (represented by Gaylussacia baccata, Notopora schomburgkii, Vaccinium angustifolium, V. arboreum, V. consanguineum, V. corymbodendron, V. corymbosum, V. exul, V. floribundum, V. meridionale, V. ovatum, *and* V. uliginosum*)*

Because the monophyly and the taxonomic position of the remaining subclades is still debatable, it is difficult to speculate on the wood anatomical trends in these groups. Wood anatomically, it seems that clades one to three, comprising several *Vaccinium* species and *Gaylussacia baccata* (Figs. 7–10, clades 1–3), form an intermediate group between the Myrtillus clade and the group including the East Malesian clade, the Meso-American/Caribbean clade and the Andean clade. Wood features that illustrate the intermediate position of clades one to three include the presence of (1) minutely bordered pits in *Gaylussacia baccata, Vaccinium corymbodendron, V. consanguineum,* and *V. ovatum* (Fig. 8), (2) prismatic crystals in ray cells of *V. corymbosum, V. meridionale,* and *V. ovatum,* and (3) relatively broad (6–12-seriate in *V. exul*) and high multiseriate rays in some species (up to 4200 μm in *V. corymbosum*). The taxonomic position of *Vaccinium uliginosum,* which is placed as sister to the Andean clade and the Meso-American/Caribbean clade, is not supported wood anatomically because none of the above-mentioned intermediate characters are present.

The taxonomic position of *Notopora schomburgkii* as sister to the East Malesian clade is wood anatomically supported by the occurrence of simple vessel perforations, scalariform vessel-ray pits with strongly reduced borders (Figs. 7, 8), and the occurrence of prismatic crystals in the rays. Furthermore, the same features are also present in some representatives of the Andean clade, as in, for instance, *Satyria meiantha, S. panurensis, Thibaudia floribunda,* and *T. pachypoda.*

The possible relationship of *Dimorphanthera* and *Satyria* as suggested by Stevens (1974) is wood anatomically disputable: the two genera share several similar wood features, like scalariform vessel raypits with much reduced borders, high multiseriate rays and prismatic crystals in ray cells, but these features are very common in the Andean clade. In addition, the two genera show a high percentage of simple vessel perforations in their wood, a feature that is relatively rare in the Andean clade, but this is probably due to the climbing habit of *Dimorphanthera* and *Satyria.*

Structure of multiseriate rays

The taxonomic value of multiseriate rays with mainly square and upright body ray cells in Vaccinieae is somewhat unexpected in a family containing many shrubs with relatively thin stems. It is known that upright body ray cells are abundantly present near the pith while more procumbent cell shapes are found closer to the cambium. Indeed, the mean stem diameter of the *Vaccinium* species studied is larger than the stem diameter of the Andean clade species. This could explain the presence of exclusively procumbent body ray cells in *Vaccinium* in regard to the mainly square to upright body ray cells in the wood of the Andean clade species. However, thick wood samples of the Andean clade (e.g., *Ceratostema reginaldii, Satyria meiantha,* and *S. panurensis*) and the East Malesian clade (*Dimorphanthera kempteriana*) also show many upright and square body ray cells. Moreover, only mature stems of species belonging to the Andean clade were collected during various field trips. This indicates that the shape of body ray cells contains a phylogenetic signal within Vaccinioideae, as mentioned by Lens et al. (2004a).

Wood anatomical comparison with other Ericaceae s.l.

The wood structure of Vaccinieae shows many similarities with that of Ericaceae s.l. Examples include the diffuse-porosity, narrow and solitary vessels with an angular vessel outline, high vessel frequency, scalariform and/or simple vessel perforations, tracheids, distinctly bordered fiber pits (fiber-tracheids), scarcely distributed axial parenchyma, and the combination of uniseriate rays with less common multiseriate rays. The study group corresponds especially to other tribes of the subfamily Vaccinioideae as well as to the related epacrids (subfamily Styphelioideae). As mentioned by Lens et al. (2003, 2004a), the presence of wide and high multiseriate rays, which are nearly absent outside Styphelioideae and Vaccinioideae, may support the relationship between both subfamilies. In addition, the sporadic occurrence of libriform fibers and the presence of crystal-bearing axial parenchyma cells are found in both subfamilies, but these two features also occur in the distantly related subfamily Arbutoideae (Lens, pers. obs.).

Most genera of Vaccinieae, except for the large genus *Vaccinium,* can easily be distinguished from other Ericaceae by a set of wood anatomical features. These features include the presence of scalariform vessel-ray pits with strongly reduced borders, high multiseriate rays (often more than 3000 μm) with mainly square to upright body ray cells containing prismatic crystals, and the occurrence of undivided axial parenchyma cells, which usually range from 500 to 900 μm.

Conclusions

The wood structure of the tribe Vaccinieae, considered to be a derived tribe within the Ericaceae, fits well within the family and shows some taxonomically important characters. Many species of *Vaccinium* show several wood features that correspond with a typical Ericaceae wood sample: distinctly bordered vessel-ray pits, and narrow (2- to 4-seriate) and low (often less than 1000 μm) multiseriate rays, which mainly consist of procumbent body ray cells. Other clades within Vaccinieae, represented by the East Malesian clade, the Meso-American/Caribbean clade, and the Andean clade, show a set of characters that are absent in other members of the family, viz. scalariform vessel-ray pits with strongly reduced borders, a high portion of upright body ray cells (although exclusively procumbent in *Dimorphanthera kempteriana*), wide (4- to 14-seriate) and high multiseriate rays (often more than 3000 μm), and prismatic crystals in chambered ray cells (but absent in *Symphysia racemosa*). Furthermore, the presence of secretory ducts in the primary xylem and in the pith, which is frequently observed in the Andean clade, seems to represent a feature otherwise lacking in the family. In addition, the presence of long, non-divided axial parenchyma cells in most species of Vaccinieae distinguishes this tribe from the rest of the subfamily.

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Index to Specimens Examined

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 a mature branch, although the exact diameter could not be traced. Authors of plant names are according to Brummit and Powell (1992). Two samples were preserved in FAA to investigate living substances in fibers. Institutional wood collections used in this study are abbreviated according to the *Index Xylariorum* (Stern, 1988). Other institutions that were used to collect wood samples are The National Botanic Garden of Belgium (BR), The Royal Botanic Gardens, Edinburgh (E), and The New York Botanical Garden (NY).

Agapetes flava (Hook. f.) Sleumer: BHUTAN. **Chukka,** *A. Grierson & D. Long 3076* (E 19822403), 10 mm; *A. hosseana* Diels: THAILAND. **Chiang Mai,** *B. L. Burtt 958* (E 19672592), 7 mm; *A. mannii* Hemsl.: MYANMAR. *F. Kingdon-Ward 19097* (E 19500046), 10 mm; *A. moorei* Hemsl.: origin and collector unknown (E 19696069), 10 mm; *A. sikkimensis* Airy Shaw: BHUTAN. **Phuntsholing,** *I. Sinclair & D. Long 5778* (E 19842032), 12 mm; *A. variegata* G. Don: INDIA. **Meghalaya,** *D. F. Chamberlain 106* (E 19751313), 9 mm.

Anthopterus wardii Ball: COLOMBIA. **Nariño,** *J. L. Luteyn & M. Lebrón-Luteyn 6865* (NY), 8 mm; *A. wardii* Ball: COLOMBIA. *van Rooden et al. 443* (Uw 25586), 7 mm.

Cavendishia bracteata (J. St.-Hil.) Hoerold: BOLIVIA. **La Paz,** *L. J. Dorr et al. 6890* (Lw), 12 mm; *C. compacta* A. C. Sm.: COLOMBIA. *van Rooden et al. 555* (Uw 25619), 15 mm; *C. callista* Donn. Sm.: SURINAM. **Lely Mountains,** *Lindeman & Stoffers 502* (Uw 21835), 11 mm; *C. lindauiana* Hoerold: COLOMBIA. *van Rooden et al. 630* (Uw 25642), 15 mm; *C. pubescens* (Kunth) Hemsl.: VENEZUELA. *L. Williams 10020* (Uw 35101), 43 mm; *C. urophylla* A. C. Sm.: COLOMBIA. *van Rooden et al. 371* (Uw 25568), 21 mm.

Ceratostema reginaldii (Sleumer) A. C. Sm.: ECUADOR. **Loja,** *G. P. Lewis 3345* (Kw 74944), 20 mm; *C. reginaldii* (Sleumer) A. C. Sm.: ECUADOR. **Loja,** *L. J. Dorr & I. Valdespino 6562* (Lw), 15 mm.

Demosthenesia spectabilis (Rusby) A. C. Sm.: PERU. **Cuzco,** *J. L. Luteyn 6452* (NY), 7 mm.

Dimorphanthera collinsii Sleumer var. *collinsii*: INDONESIA. **Irian,** *Kalkman 4902* (Tw 23696), 60 mm; *D. cornuta* J. J. Sm. var. *cornuta*: EAST NEW GUINEA. *Vink 17084* (Kw 11639, Uw 18298), 51 mm; *D. dekockii* J. J. Sm. var. *pubiflora* Sleumer: EAST NEW GUINEA. *Vink 17307* (Kw 11639, Uw 18316), 45 mm; *D. kempteriana* Schltr.: INDONESIA. **East Irian,** *Vink 16888* (Tw 23733), 44 mm.

Diogenesia floribunda (A. C. Sm.) Sleumer: ECUADOR. **Napo-Pastaza,** *J. L. Luteyn & M. Lebrón-Luteyn 5675* (NY), 9 mm; *D. tetrandra* (A. C. Sm.) Sleumer: COLOMBIA. **Cauca,** *J. L. Luteyn et al. 7388* (NY), 11 mm.

Disterigma sp. indet.: PERU. **Loreto,** collector unknown (Tw 31380), 10 mm; *D.* sp. indet.: PERU. **Cajamarca,** *C. Carton 54* (BR), 8 mm; *D. alaternoides* Nied.: COLOMBIA. **Cauca,** *J. L. Luteyn et al. 7400* (NY), 11 mm; *D. cryptocalyx* A. C. Sm.: COLOMBIA. **Huila**, *J. L. Luteyn & M. Lebrón-Luteyn 7545* (NY), 7 mm.

Gaylussacia baccata K. Koch (preserved in FAA): BELGIUM. *F. Lens* (BR), 7 mm; *G. decipiens* Cham. var. *decipiens*: BRAZIL. *P. Clausen 1840* (BR), 6 mm.

Lateropora ovata A. C. Sm.: PANAMA. **Chiriquí,** *J. L. Luteyn 15294* (NY), 9 mm.

Macleania crassa A. C. Sm.: COLOMBIA. **Cauca,** *J. L. Luteyn et al. 7378* (NY), 20 mm; *M. ericae* Sleumer: ECUADOR. **Pichincha,** *J. L. Luteyn & M. Lebrón-Luteyn 5639* (NY), 15 mm; *M. hirtiflora* (Benth.) A. C. Sm.: COLOMBIA. **Cauca,** *J. L. Luteyn et al. 7386* (NY), 13 mm; *M. loeseneriana* Hoerold: ECUADOR. **Carchi,** *J. L. Luteyn & M. Lebrón-Luteyn 5726* (NY), 18 mm; *M. pentaptera* Hoerold: COLOMBIA. **Valle,** *J. L. Luteyn & M. Lebrón-Luteyn 6957* (NY), 19 mm; *M. rupestris* (Kunth) A. C. Sm.: VENEZUELA. *L. Williams 10904* (Uw 35316), 18 mm; *M. stricta* A. C. Sm.: ECUADOR. **Carchi,** *J. L. Luteyn & M. Lebrón-Luteyn 5744* (NY), 10 mm.

Mycerinus chimantensis Maguire, Steyerm. & Luteyn: VENEZUELA. **Bolívar,** *O. Huber 9010* (NY), 7 mm.

Notopora cardonae A. C. Sm.: VENEZUELA. **Bolívar,** *J. L. Luteyn 9596* (NY), 10 mm; *N. schomburgkii* Hook. f.: VENEZUELA. *Maas et al. 5808* (Uw 27397), 10 mm.

Oreanthes ecuadorensis Luteyn: ECUADOR. **Loja,** *J. L. Luteyn 15394* (NY), 4 mm.

Orthaea fimbriata Luteyn: ECUADOR. **Morona-Santiago,** *J. L. Luteyn & M. Lebrón-Luteyn 5794* (NY), 15 mm.

Plutarchia ecuadorensis Luteyn: ECUADOR. **Azuay,** *J. L. Luteyn & M. Lebrón-Luteyn 5778* (NY), 13 mm; *P. rigida* (Benth.) A. C. Sm.: COLOMBIA. **Cauca,** *J. L. Luteyn 10108* (NY), 5 mm.

Polyclita turbinata (Kuntze) A. C. Sm.: BOLIVIA. **Cochabamba,** *J. L. Luteyn 15453* (NY), 10 mm.

Psammisia sp. indet.: COLOMBIA. *van Rooden et al. 359* (Uw 25565), 30 mm; *P. ecuadorensis* Hoerold: ECUADOR. **Pichincha,** *J. L. Luteyn & M. Lebrón-Luteyn 5621* (NY), 7 mm; *P. ferruginea* A. C. Sm.: ECUADOR. *Maas et al. 3041* (Uw 23589), 20 mm; *P. graebneriana* Hoerold: COLOMBIA. **Nariño,** *J. L. Luteyn & M. Lebrón-Luteyn 6809* (NY), 10 mm; *P. guianensis* Klotzsch: VENEZUELA. **Amazonas,** *B. Maguire et al. 42397* (Tw 36530), 11 mm; *P. guianensis* Klotzsch: ECUADOR. **Azuay,** *Camp 4367* (Uw 10655), 11 mm; *P. penduliflora* (Dunal) Klotzsch: VENEZUELA. **Trujillo,** *J. L. Luteyn et al. 5223* (NY), 8 mm; *P.* cf. *ulbrichiana* Hoerold: ECUADOR. **Pichincha,** *J. L. Luteyn & M. Lebrón-Luteyn 6532* (NY), 12 mm.

Satyria sp. indet.: COLOMBIA. **Antioquia,** *J. L. Luteyn et al. 7017* (NY), 16 mm; *S.* sp. indet.: BRAZIL. *B. Maguire et al. 48650* (Uw 16976), 35 mm; *S.* sp.

indet.: BRAZIL. *B. Maguire et al. 46784* (Uw 17005), 22 mm; *S.* sp. indet.: COLOMBIA. **Antioquia,** *J. L. Luteyn & M. Lebrón-Luteyn 7177* (NY), 15 mm; *S. carnosiflora* Lanj.: VENEZUELA. **Amazonas,** *B. Maguire et al. 42061* (Tw 36580), 15 mm; *S. meiantha* Donn. Sm.: MEXICO. *D. Breedlove 9746* (MADw 23933), mature; *S. panurensis* (Meisn.) Nied.: BRAZIL. *B. Maguire et al. 48650* (MADw 20301), mature; *S. warszewiczii* Klotzsch: MEXICO. **Veracruz,** *R. T. Cedillo & J. I. Calzada 170* (BR), 10 mm; *S. warszewiczii* Klotzsch: origin unknown, *Warszewicz,* (BR), 12 mm.

Semiramisia pulcherrima A. C. Sm.: COLOMBIA. **Nariño,** *J. L. Luteyn 15210* (NY), 9 mm.

Siphonandra elliptica Klotzsch: PERU. **Cuzco,** *J. L. Luteyn & M. Lebrón-Luteyn 6377* (NY), 14 mm.

Sphyrospermum sp. indet.: ECUADOR. **Pichincha,** *G. Argent* (E 19762390), 11 mm; *S. buxifolium* Poepp. & Endl.: ECUADOR. *G. Argent* (E 19762390), 6 mm; *S. sodiroi* A. C. Sm.: ECUADOR. **Pichincha,** *G. Argent 526* (E 19762398), 6 mm.

Symphysia racemosa (Vahl) Stearn: DOMINICA. *Chambers 2555* (Uw 15385), 22 mm.

Themistoclesia epiphytica A. C. Sm.: COLOMBIA. *A. M. Cleef 2652* (Uw 20767), 5 mm; *T. pendula* Klotsch: VENEZUELA. **La Mucuy,** *Breteler 3476* (Uw 11013), 35 mm; *T. vegasana* A. C. Sm.: COLOMBIA. **Boyacá,** *J. L. Luteyn et al. 7590* (NY), 13 mm.

Thibaudia angustifolia Hook.: PERU. **Amazonas,** *J. L. Luteyn & M. Lebrón-Luteyn 5528* (NY), 13 mm; *T. floribunda* HBK: ECUADOR. **Carchi,** *J. L. Luteyn & M. Lebrón-Luteyn 5725* (NY), 14 mm; *T. formosa* (Klotzsch) Hoerold: VENEZUELA. **Amazonas,** *B. Maguire et al. 27673* (Tw 36552), 20 mm; *T. jahnii* S. F. Blake: VENEZUELA. **Mérida,** *J. L. Luteyn et al. 6185* (NY), 15 mm; *T. martiniana* A. C. Sm.: ECUADOR. **Pichincha,** *J. L. Luteyn & M. Lebrón-Luteyn 5654* (NY), 24 mm; *T. pachypoda* A. C. Sm.: COLOMBIA. *Cuatrecasas 19876* (Uw 25099), 11 mm; *T. parvifolia* Hoerold: COLOMBIA. **Cauca,** *J. L. Luteyn & M. Lebrón-Luteyn 6897* (NY), 14 mm; *T. rigidiflora* A. C. Sm: COLOMBIA. **Valle,** *J. L. Luteyn & M. Lebrón-Luteyn 6985* (NY), 23 mm.

Vaccinium sp. indet.: U.S.A. **Hawaii,** *W. Stern 2980* (Tw 24148), 33 mm; *V. africanum* Britton: AFRICA. *H. Brown 52* (Kw 11707), 70 mm; *V. angustifolium* Benth. (preserved in FAA): BELGIUM. *F. Lens* (BR), 6 mm; *V. arboreum* Marshall: U.S.A. **Texas,** *H. Nogle 258* (Tw 18270), mature; *V. atrococcum* A. Heller: U.S.A. **Maryland,** collector unknown (Kw 11706), mature; *V. bancanum* Miq.: BRUNEI. Collector unknown, (Kw 74737), 67 mm; *V. barandanum* Vidal var. *barandanum*: PHILIPPINES. *M. Jacobs 7249* (Uw 33743), 45 mm; *V. berberidifolium* (A. Gray) Skottsb.: U.S.A. **Hawaii,** *Stern & Herbst 496* (Uw 18579), 9 mm; *V. bracteatum* Thunb.: CHINA. **Guangdong,** *Forest Research Institute 1623* (Tw 42071), mature; *V. calycinum* Sm.: U.S.A. **Hawaii,** *W. Stern 2950* (Tw 24121), 17 mm; *V. consanguineum* Klotzsch: COSTA RICA. **San José,** *M. Wiemann 13* (Uw 30897), mature; *V. corymbodendron* Dun.: COLOMBIA. *J. Cuatrecasas 20784* (Tw 20784), mature; *V. corymbosum* L.: CANADA. **Québec,** *R. Dechamps 5003* (Tw 33895), 8 mm; *V. cumingianum* Vidal: PHILIPPINES. *M. Jacobs 7270* (Uw 33746), 36 mm; *V. exaristatum* Kurz: INDIA. **Assam,** Lushai Hills, *N. E. Parry 45* (Kw 11747), 36 mm; *V. exul* Bolus: SOUTH AFRICA. *J. Prior 464,* 23 mm; *V. floccosum* (L. O. Williams) Wilbur & Luteyn: PANAMA. **Chiriquí.** *Maas et al. 4957* (Uw 26277), 33 mm; *V. floribundum* HBK: BOLIVIA. **Cumba de Sama,** *J. R. De Sloover 399* (BR), 5 mm; *V. globulare* Rydb.: U.S.A. **Washington,** *R. Dechamps 4460* (Tw 46335), 15 mm; *V. leschenaultii* Wight: INDIA. Collector unknown (Kw 70598), mature; *V. leucanthum* Schltdl.: MEXICO. **Puebla,** *L. Lebacq 73* (Tw 24590), adult; *V. maderense* Link: SPAIN. **Madeira,** *N. H. Mason* (Kw 11745), mature; *V. membranaceum* Hook.: U.S.A. **Oregon,** *R. Dechamps 4325* (Tw 46029), 9 mm; *V. meridionale* Sw.: VENEZUELA. *L. Williams 10896* (Uw 35314), mature; *V. myrtillus* L.: BELGIUM. **Luik,** *R. Dechamps* (Tw 43142), 8 mm; *V. occidentale* A. Gray: U.S.A. **Oregon,** *R. Dechamps 4414* (Tw 46260), mature; *V. ovatum* Pursh: U.S.A. **Oregon,** *R. Dechamps 4418* (Tw 46267), 23 mm; *V. parvifolium* Sm.: U.S.A. **Oregon,** *R. Dechamps 4310* (Tw 45996), 27 mm; *V. puberulum* C. F. W. Meissn. var. *subcrenulatum* Maguire, Steyerm. & Luteyn: GUYANA. *Maas et al. 5733* (Uw 27342), 13 mm; *V. scoparium* Leiberg: U.S.A. **Oregon,** *R. Dechamps 4383* (Tw 46187), 6 mm; *V. stanleyi* Schweinf.: DEMOCRATIC REPUBLIC OF CONGO. **Kivu,** P. Deuse 55 (BR), 9 mm; *V. uliginosum* L: NORWAY. **Hordaland,** *R. Dechamps 6033* (Tw 38581), 6 mm.