

# Comparative wood anatomy of *Andromedaeae s.s.*, *Gaultherieae*, *Lyonieae* and *Oxydendreae* (*Vaccinioideae*, *Ericaceae s.l.*)

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The wood anatomical structure of 11 out of 13 genera from four tribes of the *Vaccinioideae*, namely *Andromedaeae s.s.*, *Gaultherieae*, *Lyonieae* and *Oxydendreae* (*Ericaceae s.l.*), is described using light and scanning electron microscopy. Several features of the secondary xylem support the tribal classification based on molecular data: arrangement of vessel-ray pitting, height of multiseriate rays and the shape of the body ray cells. *Oxydendreae* are clearly defined from the other representatives by various wood anatomical features. *Gaultherieae* can be distinguished from *Lyonieae* by differences in vessel perforation plates, vessel-ray pitting, height and structure of multiseriate rays, and occurrence of prismatic crystals, but the wood of *Andromedaeae s.s.* is similar to *Gaultherieae*. Moreover, *Andromedaeae s.s.*, *Oxydendreae* and *Vaccinieae* are characterized by their pith structure, whereas considerable variation in the pith cells is found in *Lyonieae* and *Gaultherieae*. © 2004 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2004, 144, 161–179.

ADDITIONAL KEYWORDS: *Andromedaeae sensu* Stevens – pith structure.

## INTRODUCTION

*Andromedaeae s.s.*, *Gaultherieae*, *Lyonieae* and *Oxydendreae* are four tribes of *Vaccinioideae* (*Ericaceae*) *sensu* Kron *et al.* (2002) comprising about 13 genera and 325 species. All representatives are evergreen shrubs or small trees, which occur in a wide range of geographical areas, ranging from the arctic and temperate regions of the Northern hemisphere to the tropical regions of the Old and New World.

The genera included in the four tribes were previously grouped in the *Andromedaeae sensu* Stevens (1971). The tribe *Andromedaeae* was erected by de Candolle in 1839 and initially comprised 13 genera (Table 1). Hooker (1876) distinguished four subgroups within *Andromedaeae*, without giving them any rank. Drude (1897) divided the group into two tribes, *Andromedaeae* and *Gaultherieae*, both belonging to the subfamily *Arbutoideae* (*Ericaceae*). A significant tax-

onomic contribution to the group was presented by Stevens (1970, 1971), who did not consider the *Gaultherieae* as a separate tribe. This author placed the *Andromedaeae* next to the tribes *Enkiantheae*, *Cassiopeae* and *Vaccinieae* in the subfamily *Vaccinioideae*. On the basis of the indumentum, stamen morphology, seed and phloem anatomy, type of stomata and cytological studies, he distinguished two well-defined groups within *Andromedaeae*, namely the *Lyonia*-group and the *Gaultheria*-group. The three remaining genera (*Andromeda*, *Chamaedaphne* and *Oxydendrum*) were considered to be isolated within the tribe. More recently, however, Stevens (1995) doubted the monophyly of the *Andromedaeae sensu* 1971, because there were no obvious morphological synapomorphies that defined the group. Furthermore, molecular data clearly demonstrated that the study group is a paraphyletic association of genera (Kron, Judd & Crayn, 1999). The most recent classification of *Ericaceae*, based on molecular as well as morphological data, showed that the *Andromedaeae sensu* Stevens fall apart into four well-supported tribes that form together with *Vaccinieae* the subfamily *Vaccinioideae*

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**Table 1.** Historical overview of the study group according to the classifications of de Candolle (1839), Hooker (1876), Drude (1897), Stevens (1971) and Kron *et al.* (2002). Genera in bold type are represented in this study

de Candolle (1839)	Hooker (1876)	Drude (1897)	Stevens (1971)	Kron <i>et al.</i> (2002)
ANDROMEDEAE	ANDROMEDEAE	ANDROMEDEAE	ANDROMEDEAE	ANDROMEDEAE
<b>Andromeda</b>	<b>Diplycosia</b>	<b>Agarista</b>	LYONIA-GROUP	<b>Andromeda</b>
<b>Cassandra</b>	<b>Gaultheria</b>	<b>Agauria</b>	<b>Agarista</b>	<b>Zenobia</b>
<i>Cassiope</i>		<i>Cassiope</i>	<b>Agauria</b>	GAULTHERIEAE
<i>Clethra</i>	<i>Cassiope</i>	<b>Chamaedaphne</b>	<b>Craibiodendron</b>	<b>Chamaedaphne</b>
<b>Diplycosia</b>	<b>Chamaedaphne</b>	<i>Epigaea</i>	<b>Lyonia</b>	<i>Eubotrys</i>
<i>Elliottia</i>	<i>Epigaea</i>	<b>Leucothoe</b>	<b>Pieris</b>	<b>Gaultheria</b> (incl. <b>Pernettya, Diplycosia</b> )
	<b>Leucothoe</b>	<b>Lyonia</b>	GAULTHERIA-GROUP	<b>Leucothoe</b>
<i>Epigaea</i>	<i>Orphanidesia</i>	<i>Orphanidesia</i>	<b>Diplycosia</b>	<i>Pernettyopsis</i>
<b>Gaultheria</b>	<b>Oxydendrum</b>	<b>Oxydendrum</b>	<b>Leucothoe</b>	<b>Tepuia</b>
<b>Leucothoe</b> (incl. <b>Agauria, Agarista</b> )				
<b>Lyonia</b>		<b>Pieris</b>	<b>Gaultheria</b>	LYONIEAE
<b>Oxydendrum</b>	<b>Agauria</b>	<b>Zenobia</b>	<i>Pernettyopsis</i>	<b>Agarista</b> (incl. <b>Agauria</b> )
<b>Pieris</b>	<b>Agarista</b>	GAULTHERIEAE	<b>Tepuia</b>	<b>Craibiodendron</b>
<b>Zenobia</b>	<b>Lyonia</b>	<i>Chiogenes</i>	<b>Zenobia</b>	<b>Lyonia</b>
		<b>Diplycosia</b>		<b>Pieris</b>
	<b>Andromeda</b>	<i>Enkianthus</i>	<b>Andromeda</b>	OXYDENDREAE
	<i>Enkianthus</i>	<b>Gaultheria</b>	<b>Chamaedaphne</b>	<b>Oxydendrum</b>
	<b>Pieris</b>	<b>Pernettya</b>	<b>Oxydendrum</b>	
	<b>Zenobia</b>	<i>Wittsteinia</i>		

(Kron *et al.*, 2002). The monospecific Oxydendreae is sister to the rest of the Vaccinioideae. Lyonieae, including all members of the *Lyonia*-group of Stevens (1970), forms a clade that is sister to Vaccinieae and a clade containing the sister tribes Andromedeae s.s. and Gaultherieae (for further details, see Figs 44–49).

The most important wood anatomical work of the study group was presented by Cox (1948), who studied six genera, namely *Agarista* (incl. *Agauria*), *Andromeda*, *Chamaedaphne*, *Gaultheria* (incl. *Pernettya*), *Diplycosia* and *Chiogenes*), *Leucothoe* and *Oxydendrum*. His observations were based on narrow twigs of herbarium material and the wood anatomical descriptions presented were not very detailed. Metcalfe & Chalk (1950) presented a more complete description in their family treatment, with comments on the genera *Agauria*, *Andromeda*, *Craibiodendron*, *Gaultheria* (incl. *Pernettya*), *Lyonia* and *Oxydendrum*. Furthermore, Suzuki & Noshiro (1988) described the wood structure of *Lyonia* and *Pieris*. A special feature that has been reported so far in a limited number of woody dicots includes the presence of a living protoplast in libriform fibres. These living fibres were also observed in few Vaccinieae species, but the distribution of this feature requires further observations (Braun, 1961; Fahn & Leshem, 1962; Luteyn, 1983).

The above-mentioned studies indicate that a detailed wood anatomical survey of the group is lack-

ing. Therefore, this paper presents data on the wood anatomy of all genera of the Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae recognized by Kron *et al.* (2002), except for *Eubotrys* and *Pernettyopsis*. The variation in the secondary xylem observed is evaluated according to molecular phylogenetic insights in order to reveal possible evolutionary patterns in the wood and to comment on the classification. In addition, we attempt to demonstrate the distribution of living fibres and the results obtained are compared with related taxa within Ericaceae s.l. This study is part of a general wood anatomical survey of Vaccinioideae. An ecological approach to the wood anatomy of this subfamily will be treated elsewhere. As has already been illustrated by Stevens (1971), Judd (1979) and Kron *et al.* (1999), there is also a significant variation in the pith structure of the study group, which will also be investigated here.

## MATERIAL AND METHODS

Wood samples of 55 specimens representing 38 species and 11 genera were investigated using LM and SEM. The wood anatomical terminology follows the 'IAWA list of microscopic features for hardwood identification' (IAWA, 1989). When distinctly bordered vessel-ray pits are mentioned, we actually mean that the pit pairs are half-bordered, because the pit on the paren-

chyma cell side is simple and that on the vessel side is bordered.

Wood sections of about 25 µm were cut using a sledge microtome. After bleaching, staining and dehydrating, the tissues were mounted in euparal. Preparations for macerations and SEM were prepared according to Jansen *et al.* (1998). Nuclei in living fibres were stained using acetocarmine.

All types of non-perforated tracheary elements, namely tracheids, fibre-tracheids and libriform fibres, are present in the wood of Ericaceae *s.l.* (Baas, 1979; Carlquist, 1988; Lens *et al.*, 2003). Accordingly, it may be rather arbitrary to allocate intermediate cell types to one of these categories. Furthermore, the circumscription of tracheids, fibre-tracheids and libriform fibres still remains a matter of dispute (Baas, 1986; Carlquist, 2001). Therefore, we prefer to give a detailed description of these cells. We define tracheids to be long and narrow cells, with dense pitting in both tangential (*c.* more than 15 pits per 100 µm of tracheid length) and radial walls (*c.* 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. Tracheids are rather sparse and randomly distributed within a growth ring. Fibre-tracheids represent the most common cell type of the ground tissue and are abundantly present throughout a growth ring. They are somewhat longer than tracheids, narrow, thin- or thick-walled, and contain a single row of distinctly bordered pits in the tangential walls (*c.* 5–15 pits per 100 µm of fibre-tracheid length) and radial walls (*c.* 8–20 pits per 100 µm of fibre-tracheid length). The mean distance between two fibre-tracheid pits in the tangential wall is longer than the distance between two tracheid pits, although the pit borders do not differ in size (*c.* 3–6 µm). Libriform fibres are sparsely scattered within a growth ring. They are narrow, thin- or thick-walled, generally as long as fibre-tracheids, mostly septate, and show few to very few, indistinctly bordered pits (sometimes also simple pits) in the tangential walls. The pit borders in the libriform fibres are 2–3 µm in size and their density ranges from less than one to four per 100 µm of length in tangential walls, and from two to about ten per 100 µm of length in radial walls. Sometimes, only two or three pits are observed at the tails of libriform fibres. For all measurements of tracheary elements, 25 clearly identifiable cells from maceration slides were taken into account.

The wood samples studied are listed below with reference to the origin, collector and the diameter of the wood sample. *Pernettya* and *Diplycosia*, now included in *Gaultheria*, as well as *Agauria*, now included in *Agarista*, are described separately to investigate whether their inclusion is wood anatomically justified. 'Mature' means that the wood sample is derived from

a mature stem, although the exact diameter could not be traced. An asterisk indicates that the wood sample is preserved in FAA to trace possible nuclei in the libriform fibres. 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 Garden, Edinburgh (E) and The New York Botanical Garden (NY).

*Agarista bracamorensis* G. Don: Peru (Cajamarca), J.L. Luteyn, I. Sánchez-Vega & M. Zapata 15538, 9 mm; *Agarista duckei* (Huber) Judd: Venezuela (Amazonas), B. Maguire *et al.* 42692 (Tw 36848), 58 mm; *Agarista eucalyptoides* (Cham. & Schltdl.) G. Don: Brazil, G.G. Hatschbach & J.C. Lindeman 20935 (Uw 20844), 70 mm; *Agarista organensis* (Gardner) Nied. Brazil, A. Glaziou 2878 (BR), 7 mm; *Agarista populiifolia* (Lam.) Judd: origin and collector unknown (E 19571017), 8 mm; *Agarista pulchella* G. Don: Brazil, R. Kummrow 2048 (BR), 8 mm; *Agarista uleana* (Sleumer) Judd: Brazil, A. Glaziou 3048, 8 mm; *Agauria salicifolia* Oliv.: Eastern Africa, H.-J. Schlieben & Reinbek 1505 (U 15488), 90 mm; *Agauria salicifolia* Oliv.: Rwanda, G. Bouxin 877 (Tw 24171), mature; *Andromeda polifolia* L.\*: Belgium (BR), F. Lens, 4.5 mm; *Chamaedaphne calyculata* Moench: Germany, E. Smets, Botanical Garden of Bochum (Germany), 5 mm; *Craibiodendron stellatum* W.W. Sm.: Thailand (Tunkamang), C.F. Van Beusekom & R. Geesink 4361 (L.), 57 mm; *Diplycosia heterophylla* Blume: Indonesia (Java, Gunong Pangrango), P. Woods 1046 (E 19680830), 9 mm; *Gaultheria anastomosans* (L.) H.B.K.: Colombia (Cauca), J.L. Luteyn, R. Callejas & J.J. Pipoly 10085, 27 mm; *Gaultheria buxifolia* Willd. var. *buxifolia*: Venezuela (Mérida, near Santo Domingo), J.L. Luteyn, M. Lebrón-Luteyn, L. Ruiz-Teran & J.A. Dugarte 5237, 14 mm; *Gaultheria buxifolia* Willd. var. *buxifolia*: Venezuela (Trujillo), J.L. Luteyn, M. Lebrón-Luteyn, L. Ruiz-Teran & J.A. Dugarte 5195, 18 mm; *Gaultheria buxifolia* Willd. var. *ellasantha* (A.C. Sm.) Luteyn: Colombia (Antioquia), J.L. Luteyn & M. Lebrón-Luteyn 7079, 13 mm; *Gaultheria buxifolia* Willd. var. *secunda* (J. Remy) Luteyn: Peru (Cuzco), J.L. Luteyn & M. Lebrón-Luteyn 6376, 8 mm; *Gaultheria erecta* Vent.: Ecuador (Carchi), J.L. Luteyn & M. Lebrón-Luteyn 5739, 8 mm; *Gaultheria erecta* Vent.: Venezuela, Wagener (Kw 11654), 26 mm; *Gaultheria erecta* Vent.: Venezuela (Tachira), J.L. Luteyn, M. Lebrón-Luteyn & L. Ruiz-Teran 6020, 8 mm; *Gaultheria eriophylla* (Persoon) Burt. var. *mucronata* (J. Remy) Luteyn: Peru (Cuzco), J.L. Luteyn & M. Lebrón-Luteyn 6375, 10 mm; *Gaultheria reticulata* H.B.K.: Ecuador (Azuay), J.L. Luteyn & E. Cotton 11158, 18 mm; *Gaultheria rigida* H.B.K.: Colombia, A.M. Cleef 2799 (Uw 20769), 9 mm; *Gaultheria rudis*

Stapf: Sri Lanka, H.P. Nooteboom 3342 (L), 9 mm; *Gaultheria shallon* Pursh: USA (Oregon), R. Dechamps 4308 (Tw 45992), 7 mm; *Gaultheria shallon* Pursh\*: Belgium (BR), F. Lens, 6.5 mm; *Gaultheria strigosa* Benth. var. *strigosa*: Colombia (Antioquia), J.L. Luteyn & M. Lebrón-Luteyn 7101, 10 mm; *Gaultheria strigosa* Benth. var. *strigosa*: Ecuador (Azuay), J.L. Luteyn & M. Lebrón-Luteyn 5777, 12 mm; *Gaultheria tomentosa* H.B.K.: Peru (Amazonas, Chachapoyas), J.L. Luteyn & M. Lebrón-Luteyn 5569, 13 mm; *Leucothoe axillaris* D. Don: USA (Georgia), collector unknown (E 19881623), 13 mm; *Leucothoe fontanesiana* (Steud.) Sleumer\*: Belgium (BR), F. Lens, 5 mm; *Leucothoe grayana* Maxim.: origin and collector unknown (E 1980096), 13 mm; *Lyonia ferruginea* Nutt.: USA (Florida), A. Curtis (Tw 53206), mature; *Lyonia ferruginea* Nutt.: USA, A. Curtis 60 (Kw 11721), 110 mm; *Lyonia heptamera* Urb.: Dominican Republic, J. Pimentel & M. Mejia 993 (MADw 49103), 31 mm; *Lyonia jamaicensis* D. Don: Jamaica, World Colombian Exposition 14997 (MADw 3549), mature; *Lyonia lucida* C. Koch: USA, C.D. Mell (MADw 2951), 22 mm; *Lyonia ovalifolia* (Wall.) Drude: India (Punjab), Birla Institute of Scientific Research (Tw 45182), mature; *Lyonia ovalifolia* (Wall.) Drude: Japan (Kumamoto), For. Exp. Stat. 2244 (Tw 17276), mature; *Lyonia ovalifolia* (Wall.) Drude: Japan, R.E. Regel (Kw 11670), 135 mm; *Lyonia ovalifolia* (Wall.) Drude: India, W. Gamble (Kw 11667); mature; *Lyonia squamulosa* M. Martens & Galeotti: Mexico, D. Breedlove 9683 (MADw 23903), 23 mm; *Oxydendrum arboreum* (L.) DC.: USA (Ohio), A.W. Green 245 (Tw 19787), mature; *Oxydendrum arboreum* (L.) DC.: USA, J.C. Ward 19 (MADw 4550), mature; *Oxydendrum arboreum* (L.) DC.: USA, J.L. Stearns 137 (MADw 9551), mature; *Pernettya mucronata* (L.f.) A. Spreng.: The Netherlands, A.M.W. Mennega (UN 835), 13 mm; *Pernettya mucronata* (L.f.) A. Spreng. var. *angustifolia* (Lindl.) Reiche: Argentina (Rio Negro), P. Dezarbo 433 (BR), 8 mm; *Pernettya rigida* DC.: Chili (Juan Fernandez Islands), Meyer 9490 (Uw 14995), 66 mm; *Pieris formosa* D. Don: India (Meghalaya), Birla Institute of Scientific Research (Tw 45532), mature; *Pieris japonica* (Thunb.) G. Don\*: Belgium (BR), F. Lens, 8 mm; *Pieris japonica* (Thunb.) G. Don: Greece (Crete), L. Rothkegel (BR), 7 mm; *Tepuia venusta* Camp: Venezuela (Bolivar), O. Huber 8581, 2.5 mm; *Zenobia pulverulenta* Pollard\*: Belgium (BR), F. Lens, 7 mm; *Zenobia pulverulenta* Pollard: origin and collector unknown (E 19721932), 10 mm.

## RESULTS

The material studied is described according to the classification of Kron *et al.* (2002). For each genus examined the nominator gives the number of species

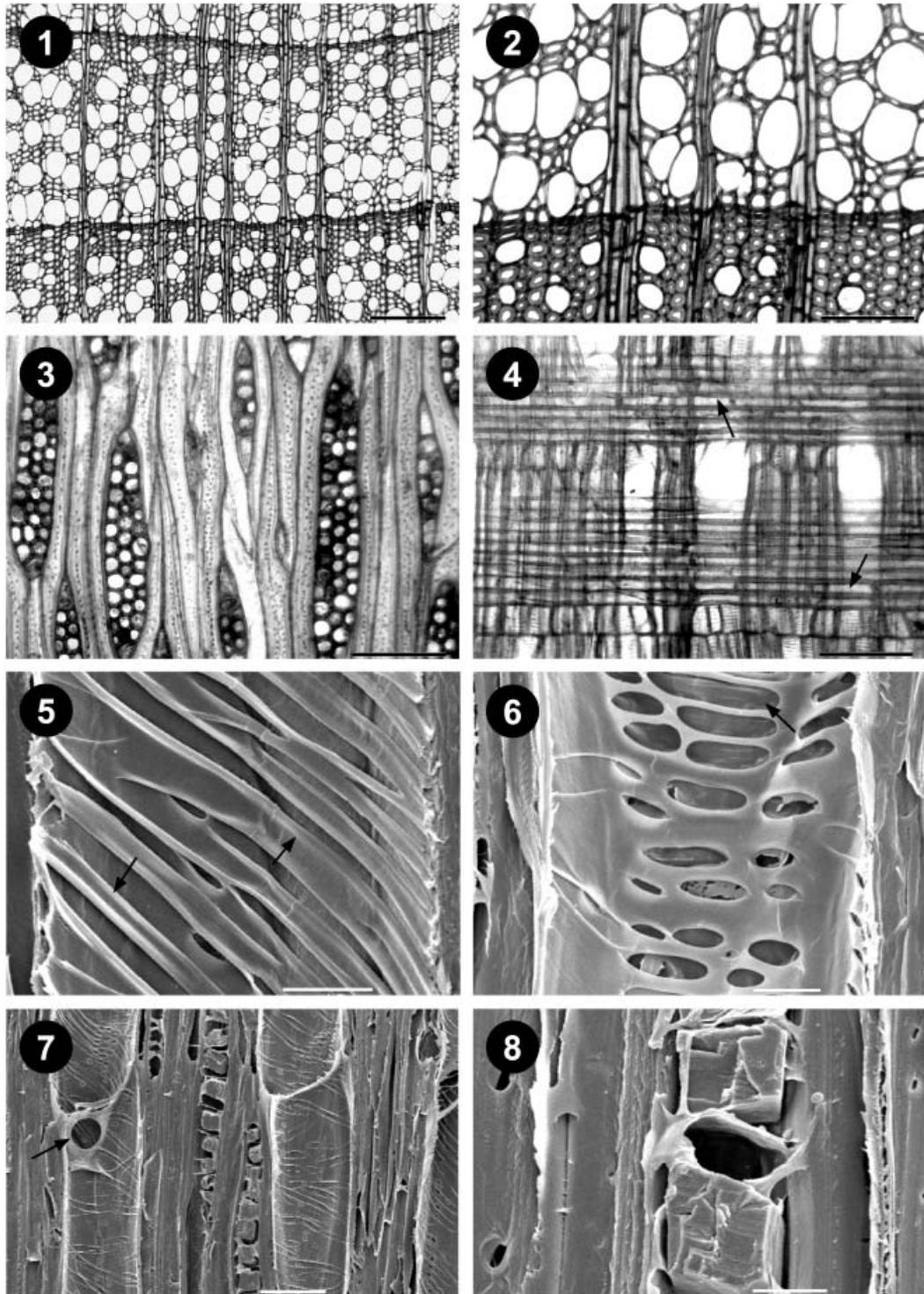
studied and the denominator includes the total number of species. Numbers in parentheses are mean values. A summary of the results is presented in Table 2.

### OXYDENDREAE (*OXYDENDRUM* 1/1; FIGS 1–8)

Growth ring boundaries distinct. Wood usually diffuse-porous, sometimes tendency to semi-ring-porosity. Vessels exclusively solitary or sometimes in small tangential (exceptionally radial) groupings, vessel outline rounded. Vessel perforation plates largely simple, sometimes scalariform with 2–(4)–7 bars. Intervessel pits opposite, 4–6 µm in size, to scalariform, 4–15 µm in size, non-vestured. Vessel-ray pits mostly scalariform, mainly distinctly bordered but sometimes also simple, 8–15 µm in size. Helical sculpturing present throughout body of vessel elements. Tangential diameter of vessel lumina 25–(39)–55 µm, 104–(151)–205 vessels mm<sup>-2</sup>, vessel elements 320–(521)–800 µm long. Tracheids present, 430–(615)–750 µm in length. Fibre-tracheids with distinctly bordered pits, 3–4 µm in diameter, thin- to thick-walled, and 620–(978)–1500 µm long. Occasionally libriform fibres with few simple to indistinctly bordered pits, septate, 350–(577)–780 µm long. Axial parenchyma scanty paratracheal, 2–4 cells per parenchyma strand. Uniseriate rays always present, 80–(145)–300 µm high, consisting of upright cells, 0–(2)–4 rays mm<sup>-1</sup>. Multi-seriate rays often 2–3-seriate, up to 4 cells wide in MADw 9551, 0–(2)–4 rays mm<sup>-1</sup>, consisting of procumbent body ray cells and 1–2 upright marginal ray cells, sheath cells absent. Gummy deposits in ray cells. Prismatic crystals present in axial parenchyma. Pith not seen.

### LYONIEAE (*AGARISTA* 7/30, *AGAURIA* 1/1, *CRAIBIODENDRON* 1/5, *LYONIA* 8/36, *PIERIS* 3/7; FIGS 9–26)

Growth ring boundaries distinct or indistinct. Usually diffuse-porous, but sometimes tendency to semi-ring-porosity in *Agarista uleana*, *Lyonia ferruginea*, *L. heptamera*, *L. ovalifolia* and in *Pieris japonica*. Vessels exclusively solitary, sometimes in small tangential and/or radial groupings in *Agauria salicifolia*, *Lyonia ferruginea*, *L. ovalifolia* and *Pieris formosa*; vessel outline angular, exceptionally rounded in *Lyonia jamaicensis*. Vessel perforation plates mostly scalariform, 1–(15)–59 bars, sometimes mixed scalariform and simple in *Lyonia ovalifolia* Kw 11667 (90% scalariform), *Craibiodendron stellatum* (85% scalariform), *Pieris japonica* (80–50% scalariform) and *Agauria* (30–25% scalariform); perforations exclusively simple in *Lyonia jamaicensis*; sometimes a small percentage of irregular perforations in *Craibiodendron stellatum*. Intervessel pits mainly opposite to



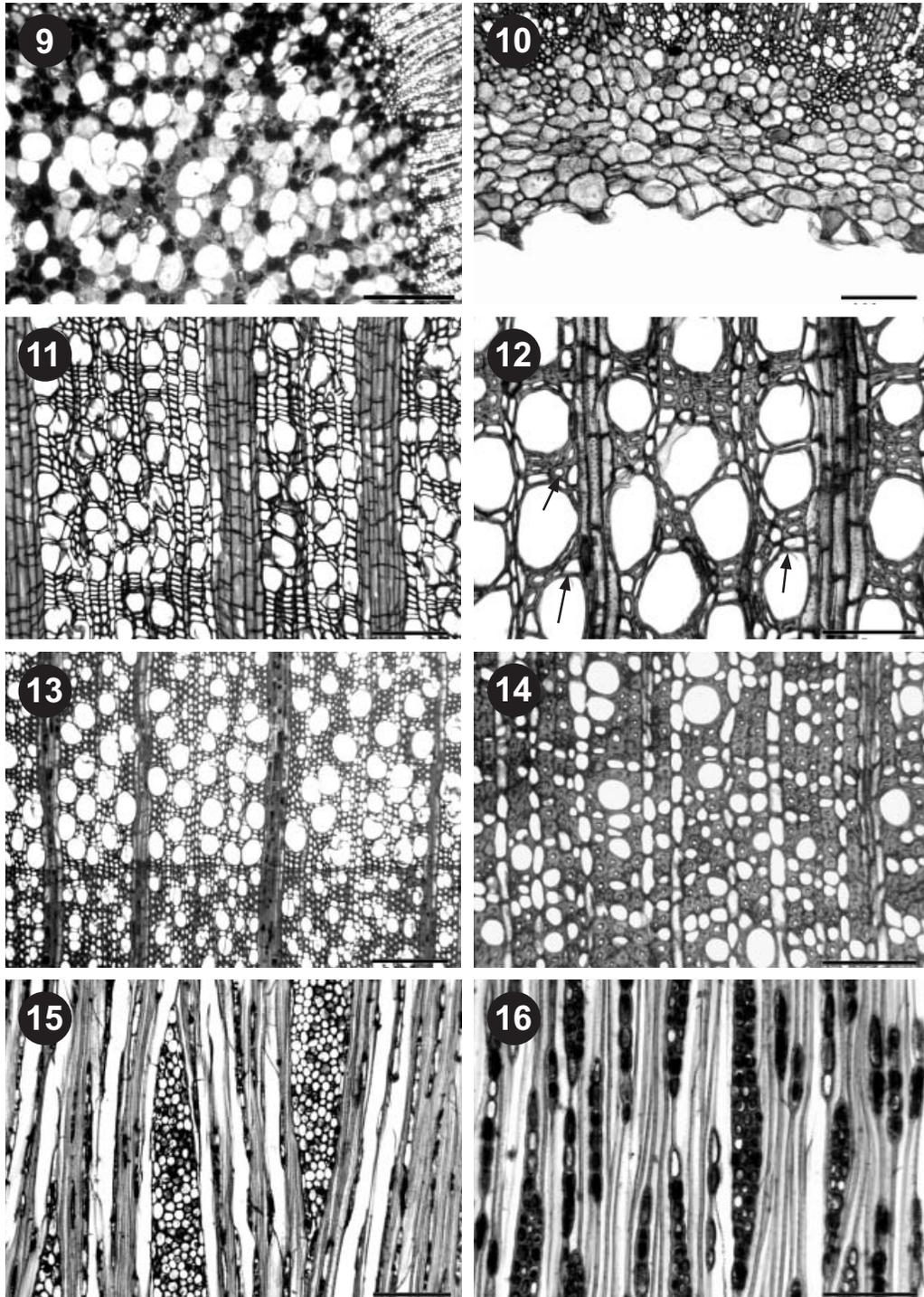
**Figures 1–8.** LM and SEM micrographs showing the wood structure in *Oxydendrum arboreum*. Fig. 1. TS, tendency to semi-ring-porosity with distinct growth rings, overview. Scale bar = 200 µm. Fig. 2. TS, *idem*, detail. Scale bar = 100 µm. Fig. 3. TLS, short, multiseriate rays. Scale bar = 100 µm. Fig. 4. RLS, procumbent body ray cells (arrows). Scale bar = 100 µm. Fig. 5. TLS, helical thickenings on the inner vessel element wall (arrows). Scale bar = 10 µm. Fig. 6. RLS, simple, scalariform vessel-ray pitting (arrow). Scale bar = 10 µm. Fig. 7. RLS, simple vessel perforation (arrow), prismatic crystals in chambered axial parenchyma cells. Scale bar = 50 µm. Fig. 8. RLS, detail of prismatic crystals in chambered axial parenchyma cells. Scale bar = 10 µm.

Table 2. Survey of wood anatomical features of the species studied

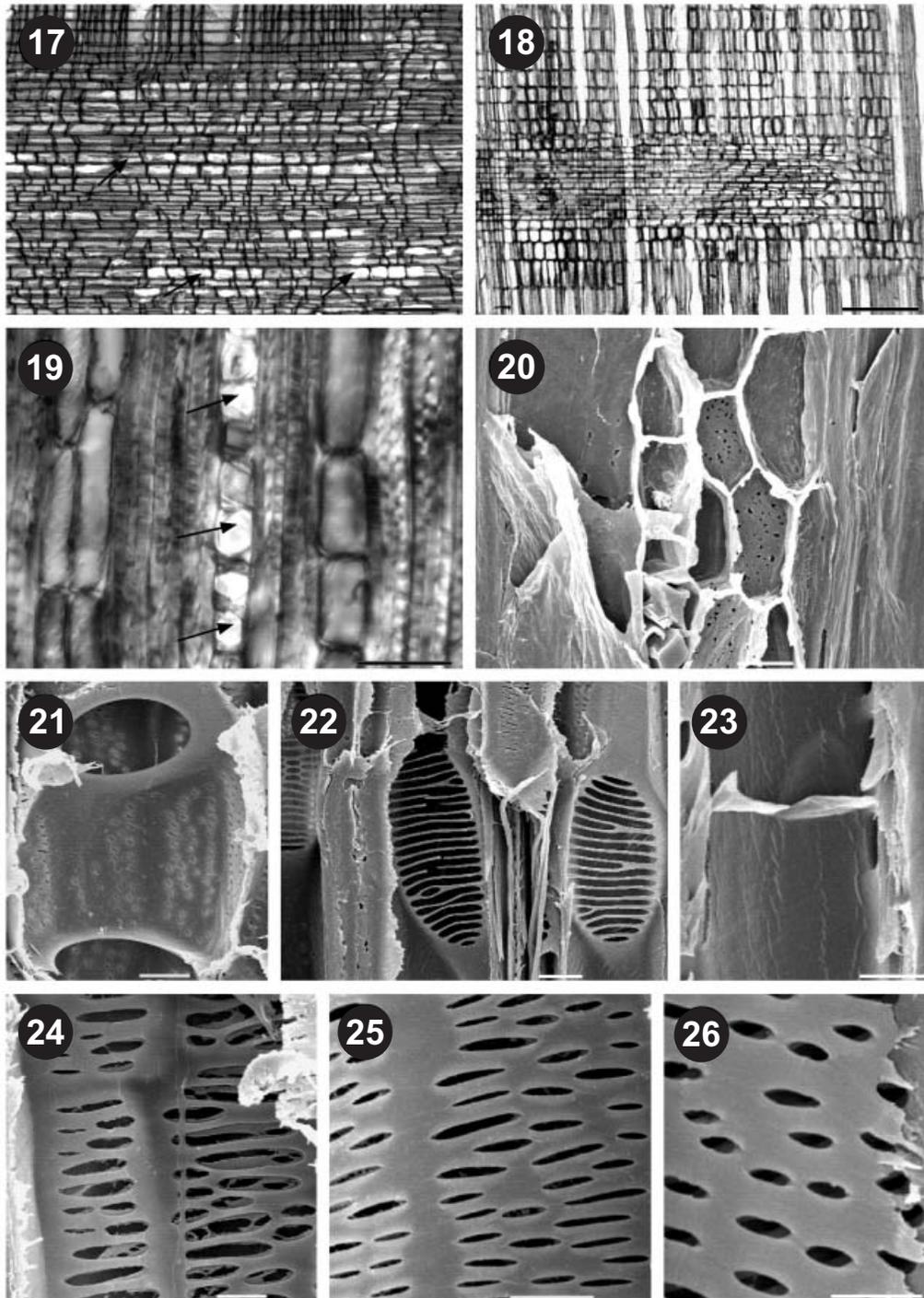
Species	Vessels										Tracheids										Fibres										Rays										Crystals			
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t	u	v	w	x	y	z	aa	bb																
<i>Agarista bracamorensis</i>	100	16	+	(+)	+	+	-	-	23	226	565	575	+	-	807	-	+	4-6	555	2300	14	4	+	-	-	+	-																	
<i>A. duckei</i>	100	19	+	(+)	(+)	-	-	39	101	563	839	839	-	-	1098	-	+	7-9	411	2011	8	3	+	-	-	-	-																	
<i>A. eucalyptoides</i>	100	8	+	+	-	+	-	39	105	546	651	651	+	-	852	-	+	5-9	325	1343	5	3	+	-	-	-	-																	
<i>A. organensis</i>	100	16	+	+	-	+	-	23	229	470	545	545	+	-	704	-	+	3-5	468	1162	7	4	+	-	-	-	-																	
<i>A. populifolia</i>	100	13	+	-	(+)	-	-	21	229	508	490	490	+	-	755	+	-	5-8	474	2207	10	4	+	(+)	-	+	-																	
<i>A. pulchella</i>	100	30	+	+	+	+	-	22	312	430	504	504	-	-	656	-	+	3-6	318	1003	6	4	+	(+)	-	-	-																	
<i>A. uleana</i>	100	16	+	+	+	+	-	24	190	542	763	763	+	-	803	-	+	4-6	326	1097	9	3	+	(+)	-	-	-																	
<i>Agauria salicifolia</i> <sup>1</sup>	30	9	(+)	+	(+)	-	-	53	93	590	883	883	+	-	1190	-	+	5-9	564	2530	4	3	+	-	-	-	-																	
<i>A. salicifolia</i> <sup>2</sup>	30	8	(+)	+	(+)	-	-	51	11	704	1178	1178	+	-	1254	-	+	5-9	580	1789	6	3	+	-	-	-	-	-																
<i>Andromeda polifolia</i>	100	14	+	-	(+)	-	-	17	546	389	320	320	+	-	448	+	-	-	414	-	22	2	?	?	-	-	-	-																
<i>Chamaedaphne calyculata</i>	100	9	+	-	(+)	+	-	16	647	245	225	225	+	-	368	+	-	3-4	315	1410	25	1	+	+	-	-	-	-																
<i>Craibiodendron stellatum</i>	85	4	+	(+)	+	+	-	49	106	654	805	805	-	-	1163	-	+	4-5	325	597	5	5	+	+	-	-	-	-																
<i>Diplycosia heterophylla</i>	100	41	+	(+)	-	-	-	18	179	708	733	733	-	-	891	-	-	2-4	870	1562	15	1	+	+	-	-	-	-																
<i>Gaultheria anastomosans</i>	100	20	+	-	-	+	-	29	89	638	874	874	+	-	1124	+	+	3-4	550	799	16	2	+	+	-	-	-	-																
<i>G. buxifolia</i> <sup>1</sup>	100	23	+	-	(+)	+	-	31	154	700	683	683	+	-	932	-	-	3-4	538	873	10	3	+	+	-	-	-	-																
<i>G. buxifolia</i> <sup>2</sup>	100	16	+	-	(+)	-	-	30	163	510	668	668	+	-	766	-	+	2-3	646	1083	11	4	+	+	-	-	-	-																
<i>G. buxifolia</i> <sup>3</sup>	100	22	+	(+)	-	+	-	28	158	624	680	680	+	-	963	-	+	2-3	382	591	11	3	+	+	-	-	-	-																
<i>G. buxifolia</i> <sup>4</sup>	100	21	+	(+)	-	+	(+)	22	193	485	430	430	+	-	679	-	+	3-4	861	1690	16	3	+	+	-	-	-	-																
<i>G. erecta</i> <sup>1</sup>	100	14	+	(+)	+	+	-	21	284	547	593	593	-	-	808	-	+	2-3	519	750	16	2	+	+	-	-	-	-																
<i>G. erecta</i> <sup>2</sup>	100	19	+	(+)	-	+	-	33	146	740	670	670	-	-	898	-	+	3-4	571	868	14	2	+	+	-	-	-	-																
<i>G. erecta</i> <sup>3</sup>	100	11	+	(+)	-	+	+	16	243	434	481	481	+	-	583	-	+	3-4	504	758	14	3	+	+	-	-	-	-																
<i>G. eriophylla</i>	100	21	+	+	(+)	-	+	20	338	526	663	663	-	-	706	-	+	4	723	1225	21	1	+	+	-	-	-	-																
<i>G. reticulata</i>	100	21	+	-	-	+	-	24	161	582	657	657	+	-	903	+	+	4	845	1044	17	1	+	(+)	-	-	-	-																
<i>G. rigida</i>	100	17	+	+	-	+	+	25	265	608	573	573	+	-	894	+	+	3-4	310	663	16	1	+	(+)	-	-	-	-																
<i>G. rudis</i>	100	16	+	+	(+)	+	+	22	379	696	708	708	-	-	825	-	+	3-4	1017	1989	11	2	+	(+)	-	-	-	-																
<i>G. shallon</i> <sup>1</sup>	100	17	+	-	-	+	+	23	329	681	650	650	-	-	893	-	+	3-4	1010	2967	17	2	+	+	-	-	-	-																
<i>G. shallon</i> <sup>2</sup>	100	14	+	+	-	+	+	21	470	450	516	516	+	-	610	-	+	2-3	897	1794	14	2	+	+	-	-	-	-																
<i>G. strigosa</i> <sup>1</sup>	100	30	+	(+)	-	+	-	23	398	598	682	682	+	-	791	-	+	2-3	712	1891	15	3	+	+	-	-	-	-																
<i>G. strigosa</i> <sup>2</sup>	100	21	+	(+)	-	+	-	21	169	470	476	476	+	-	689	-	+	4-6	627	685	10	4	+	+	-	-	-	-																
<i>G. tomentosa</i>	100	23	+	-	-	+	(+)	18	243	432	465	465	+	-	621	-	+	3-6	250	623	17	1	+	+	-	-	-	-																

<i>Leucothoe axillaris</i>	100	11	+	-	-	-	20	198	352	386	+	-	-	476	+	+	2-4	500	1222	12	4	+	+	-	-
<i>L. fontanesiana</i>	100	12	+	-	-	-	18	240	421	376	+	-	-	597	+	-	2-3	598	1133	19	1	+	+	-	-
<i>L. grayana</i>	100	8	+	-	(+)	-	23	170	438	465	+	+	-	676	-	-	2-4	538	840	12	3	+	(+)	-	-
<i>Lyonia ferruginea</i> <sup>1</sup>	100	20	+	+	+	+	34	209	653	660	+	+	-	954	-	+	(3)-4	369	493	6	6	+	-	-	-
<i>L. ferruginea</i> <sup>2</sup>	100	33	+	+	(+)	-	40	121	712	696	-	+	-	1093	+	+	4-5	355	433	3	6	+	-	-	-
<i>L. heptamera</i>	100	10	+	-	+	+	39	140	670	748	-	+	-	1146	+	+	3-4	271	509	7	6	+	-	-	+
<i>L. jamaicensis</i>	0	0	-	+	+	-	33	73	506	594	-	+	-	772	+	+	2-3	199	330	8	9	+	-	-	+
<i>L. lucida</i>	100	29	+	(+)	+	-	22	360	681	597	+	-	-	1027	+	-	2-4	627	877	11	4	+	-	-	-
<i>L. ovalifolia</i> <sup>1</sup>	100	13	+	-	+	-	31	139	646	814	+	+	-	917	-	+	2-4	492	621	8	7	+	-	-	-
<i>L. ovalifolia</i> <sup>2</sup>	100	17	+	-	+	+	35	164	615	650	+	-	-	1160	-	+	3	441	620	6	8	+	-	-	-
<i>L. ovalifolia</i> <sup>3</sup>	100	16	(+)	-	+	+	31	121	730	630	+	-	-	900	-	+	4-5	559	665	7	4	+	-	-	-
<i>L. ovalifolia</i> <sup>4</sup>	90	24	(+)	-	+	+	28	126	748	898	+	-	-	870	-	+	2-3	541	492	8	5	+	-	-	-
<i>L. squamulosa</i>	100	12	+	-	+	+	32	145	633	685	-	+	-	900	+	+	2-3	375	487	5	7	+	-	-	+
<i>Oxydendrum arboreum</i> <sup>1</sup>	5	4	(+)	+	-	-	46	127	618	646	-	+	-	1188	-	+	2-3	190	335	2	7	+	-	-	+
<i>O. arboreum</i> <sup>2</sup>	5	4	(+)	+	-	-	35	170	442	587	-	+	-	787	-	+	2-3	127	218	3	8	+	-	-	+
<i>O. arboreum</i> <sup>3</sup>	5	5	(+)	+	-	-	37	157	502	613	-	+	-	959	-	+	2-4	118	325	2	8	+	-	-	+
<i>Pernettya mucronata</i> <sup>1</sup>	100	15	+	(+)	-	-	13	277	440	485	+	-	-	581	-	+	3-4	258	545	14	2	+	(+)	-	-
<i>P. mucronata</i> <sup>2</sup>	100	12	+	-	(+)	-	19	416	306	342	+	-	-	456	-	+	3-4	282	494	13	2	+	+	-	-
<i>P. rigida</i>	100	20	+	-	-	-	30	201	753	580	+	-	-	920	+	+	3-4	621	1440	13	2	+	+	-	-
<i>Pieris formosa</i>	100	14	(+)	+	+	-	33	96	725	873	-	+	-	1164	+	+	3-4	497	771	8	4	+	-	-	-
<i>P. japonica</i> <sup>1</sup>	80	8	+	+	(+)	+	18	279	432	440	+	-	-	468	+	+	2-4	264	719	11	3	+	-	-	-
<i>P. japonica</i> <sup>2</sup>	50	14	+	+	(+)	-	17	363	384	454	+	-	-	541	+	+	2-4	325	533	11	6	+	(+)	-	-
<i>Tepuia venusta</i>	100	14	(+)	+	-	-	10	736	622	580	-	+	-	760	+	-	-	353	-	28	-	?	?	-	-
<i>Zenobia pulverulenta</i> <sup>1</sup>	100	10	+	-	(+)	-	25	259	480	485	+	-	-	644	+	-	2	593	750	19	1	?	?	-	-
<i>Z. pulverulenta</i> <sup>2</sup>	100	13	+	-	(+)	-	25	153	434	433	+	-	-	705	+	-	2	421	690	11	5	+	+	-	-

a, Percentage of scalariform perforations. b, Mean number of bars. c, Opposite vessel-ray pitting. d, Scalariform vessel-ray pitting. e, Alternate vessel-ray pitting. f, Helical thickenings only in tail of vessel elements. g, Helical thickenings throughout vessel elements. h, Helical thickenings in fibres and/or tracheids. i, Mean tangential diameter ( $\mu\text{m}$ ). j, Mean density (vessels  $\text{mm}^{-2}$ ). k, Mean length of vessel elements ( $\mu\text{m}$ ). l, Mean length ( $\mu\text{m}$ ). m, Very thin-walled. n, Thin-to-thick-walled. o, Thick-walled. p, Length fibre-tracheids ( $\mu\text{m}$ ). q, Non-septate libriform fibres. r, Septate libriform fibres. s, Multiseriate ray width (number of cells). t, Height uniseriate rays ( $\mu\text{m}$ ). u, Height multiseriate rays ( $\mu\text{m}$ ). v, Uniseriate rays per mm. w, Multiseriate body ray cells. x, Procumbent body ray cells. y, Square body ray cells. z, Upright body ray cells. aa, Present in rays. bb, Present in axial parenchyma. + = present, - = absent,  $\pm$  = sometimes present, + = unknown. Numbers included are all mean values. For specimens from the same species, numbers after the species name refer to the order of the specimen as followed in the species list.



**Figures 9–16.** LM micrographs showing transverse and tangential sections of Lyonieae wood samples. Fig. 9. *Pieris japonica*, heterogeneous pith. Scale bar = 200  $\mu\text{m}$ . Fig. 10. *Agarista populifolia*, TS, *Calluna*-pith type showing a pith cavity at the bottom. Scale bar = 200  $\mu\text{m}$ . Fig. 11. *Agauria salicifolia*, TS, solitary vessels and wide, multiseriate rays. Scale bar = 200  $\mu\text{m}$ . Fig. 12. *Craibiodendron stellatum*, TS, wide, solitary vessels, scanty paratracheal parenchyma (arrows). Scale bar = 100  $\mu\text{m}$ . Fig. 13. *Lyonia ferruginea*, TS, tendency to semi-ring-porous wood. Scale bar = 200  $\mu\text{m}$ . Fig. 14. *Lyonia jamaicensis*, TS, rounded vessel outlines, thick-walled fibres, diffuse-in-aggregates axial parenchyma. Scale bar = 100  $\mu\text{m}$ . Fig. 15. *Agarista duckei*, TLS, wide multiseriate rays. Scale bar = 200  $\mu\text{m}$ . Fig. 16. *Pieris japonica*, TLS, uniseriate rays and narrow multiseriate rays containing tannins. Scale bar = 100  $\mu\text{m}$ .



**Figures 17–26.** LM and SEM micrographs showing the structure of the multiseriate rays, presence of prismatic crystals, vessel perforations, septate fibres and vessel-ray pits. Fig. 17. *Agauria salicifolia*, RLS, procumbent body ray cells (arrows). Scale bar = 200  $\mu\text{m}$ . Fig. 18. *Lyonia lucida*, RLS, *idem*. Scale bar = 200  $\mu\text{m}$ . Fig. 19. *Lyonia jamaicensis*, TLS, prismatic crystals in chambered axial parenchyma cells (arrows). Scale bar = 100  $\mu\text{m}$ . Fig. 20. *Agarista bracamorensis*, TLS, prismatic crystals in ray cells. Scale bar = 10  $\mu\text{m}$ . Fig. 21. *Agauria salicifolia*, RLS, vessel element with simple perforations. Scale bar = 20  $\mu\text{m}$ . Fig. 22. *Agarista duckei*, RLS, scalariform perforations. Scale bar = 20  $\mu\text{m}$ . Fig. 23. *Agarista duckei*, TLS, detail of a libriform fibre wall with a septum. Scale bar = 5  $\mu\text{m}$ . Fig. 24. *Agauria salicifolia*, RLS, scalariform vessel-ray pits with reduced borders to simple. Scale bar = 10  $\mu\text{m}$ . Fig. 25. *Agarista eucalyptoides*, RLS, scalariform to alternate vessel-ray pitting. Scale bar = 10  $\mu\text{m}$ . Fig. 26. *Lyonia squamulosa*, TLS, alternate vessel-ray pitting. Scale bar = 5  $\mu\text{m}$ .

alternate in *Agarista*, *Craibiodendron*, *Lyonia* (but exclusively alternate in *L. jamaicensis*), and *Pieris*, and opposite to scalariform in *Agauria* (sometimes alternate); opposite and alternate pitting 3–5  $\mu\text{m}$  in size, scalariform pitting 8–20  $\mu\text{m}$ , non-vestured. Vessel-ray pits similar to intervessel pits in size and shape, although distinctly bordered scalariform pitting is more abundant; in *Agauria* reduced to even simple scalariform pits. Helical thickenings present throughout the body of vessel elements or only in vessel element tails, but absent in *Agauria* and *L. jamaicensis*. Tangential diameter of vessel lumina 12–(32)–70  $\mu\text{m}$ , 7–(172)–440 vessels  $\text{mm}^{-2}$ , vessel elements 280–(595)–970  $\mu\text{m}$  long. Tracheids present, 340–(695)–1450  $\mu\text{m}$  in length. Fibre-tracheids with distinctly bordered pits, 3–6  $\mu\text{m}$  in diameter, very thin- to thick-walled and 360–(930)–1450  $\mu\text{m}$  in length. Occasionally libriform fibres with few simple to indistinctly bordered pits and mostly septate, 350–(650)–1150  $\mu\text{m}$  long; nuclei observed in libriform fibres of *Pieris japonica* (BR, F. Lens). Axial parenchyma mostly scanty paratracheal, sometimes diffuse-in-aggregates in *Lyonia jamaicensis* and *L. squamulosa*, 2–6 cells per parenchyma strand (6–9 cells per strand in *Lyonia jamaicensis*). Uniseriate rays always present, 80–(422)–1100  $\mu\text{m}$  high, consisting only of upright cells, 1–(8)–19 rays  $\text{mm}^{-1}$ . Multiseriate rays often 2–5-seriate, usually up to 9 cells wide in *Agarista* and *Agauria*, 1–(5)–11 rays  $\text{mm}^{-1}$ , consisting of procumbent body ray cells (sometimes also square in some *Agarista* species) and a variable number of upright or square marginal ray cells, indistinct sheath cells in *Agarista*, *Agauria* and *Craibiodendron*. Gummy deposits in ray cells. Prismatic crystals present in ray cells of *Agarista populifolia* and in axial parenchyma cells of *Lyonia heptamera*, *L. jamaicensis* and *L. squamulosa*. Pith cells of two different forms in *Pieris japonica*: small groups of larger cells with thin walls clustered between smaller cells with thicker walls; pith cells thin-walled and restricted to the periphery of a pith cavity in *Agarista bracamorensis*, *A. organensis*, *A. populifolia*, *A. pulchella* and *A. uleana*. Prismatic crystals in pith cells of *Agarista pulchella* and *A. populifolia*.

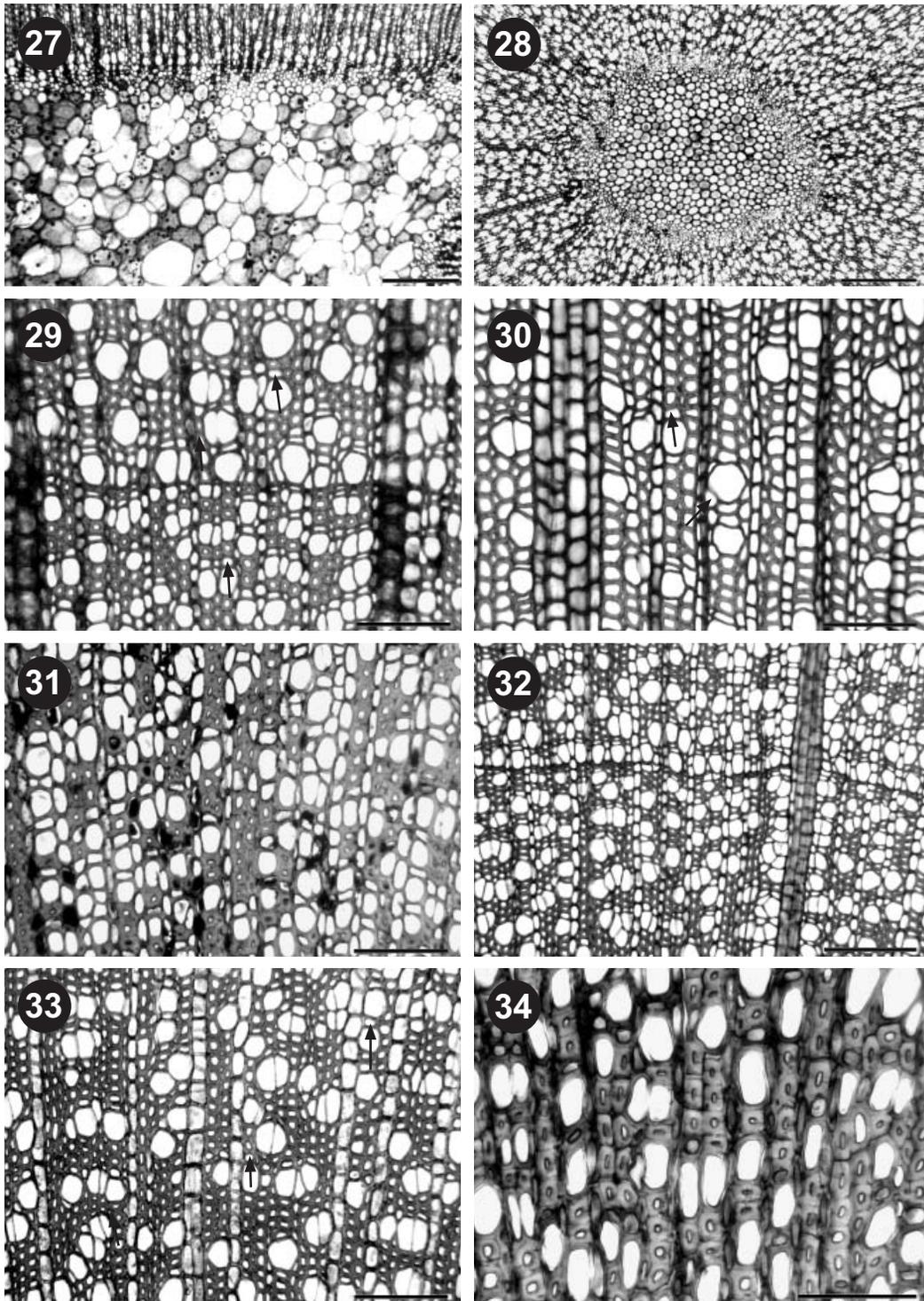
GAULTHERIEAE (*CHAMAEDAPHNE* 1/1, *DIPLYCOSIA* 1/C. 100, *GAULTHERIA* 12/C. 125, *LEUCOTHOE* 3/8, *PERNETTYA* 2/14, *TEPUA* 1/7; FIGS 27–37)

Growth ring boundaries indistinct or distinct. Diffuse-porous. Vessels mostly solitary, sometimes in small tangential or radial groupings, vessel outline angular. Vessel perforation plates exclusively scalariform, with 4–(18)–57 bars. Intervessel pits mainly opposite, sometimes alternate in *Chamaedaphne*, *Gaultheria*, and *Pernettya*, 2–5  $\mu\text{m}$  in size, non-vestured. Vessel-

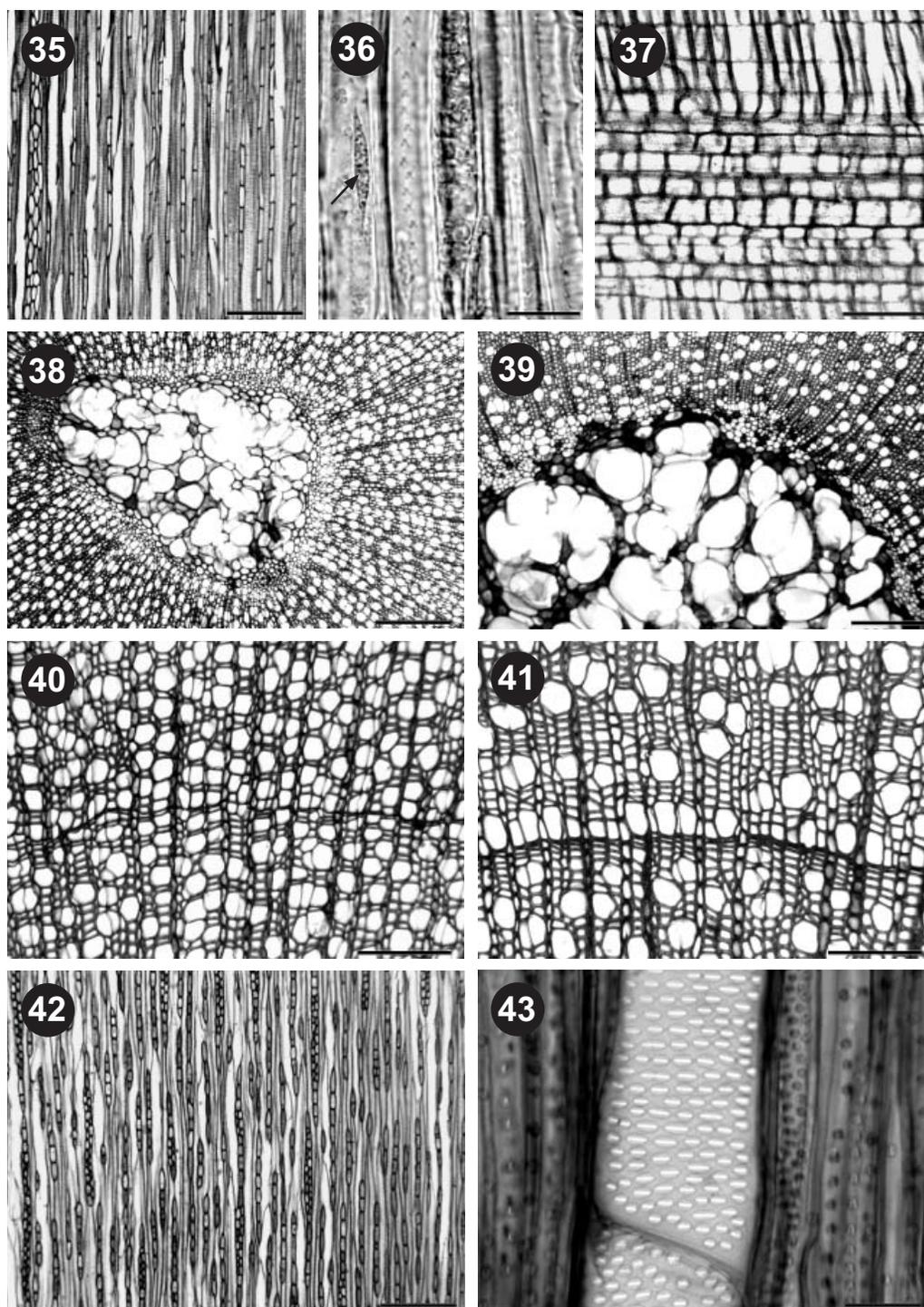
ray pits opposite, 2–5  $\mu\text{m}$  in size, to scalariform, 6–30  $\mu\text{m}$ , mainly scalariform in *Tepuia*, sometimes alternate in *Chamaedaphne*, *Gaultheria* and *Pernettya*, 2–5  $\mu\text{m}$  in size. Helical thickenings in *Chamaedaphne*, *Gaultheria*, *Pernettya* and *Tepuia*, throughout body of vessel elements or only in vessel element tails, but also in fibres and/or tracheids of *Gaultheria* and *Pernettya*. Tangential diameter of vessel lumina 7–(21)–45  $\mu\text{m}$ , 70–(267)–820 vessels  $\text{mm}^{-2}$ , vessel elements 170–(537)–1200  $\mu\text{m}$  long. Tracheids present, 270–(562)–1050  $\mu\text{m}$  in length. Fibre-tracheids mostly with distinctly bordered pits, 3–6  $\mu\text{m}$  in diameter, very thin- to thick-walled, 320–(746)–1400  $\mu\text{m}$  in length. Occasionally libriform fibres with few simple to indistinctly bordered pits (except in *Diplycosia heterophylla*), mostly septate, 220–(624)–1300  $\mu\text{m}$  long; nuclei observed in libriform fibres of *Gaultheria shallon* (BR) and *Leucothoe fontanesiana*. Axial parenchyma scanty paratracheal, 2–4 cells per parenchyma strand. Uniseriate rays always present, 140–(595)–2750  $\mu\text{m}$  high, consisting only of upright cells, 7–(15)–34 rays  $\text{mm}^{-1}$ . Multiseriate rays present except for *Tepuia*, often 2–4-seriate, up to 6 cells wide in *Gaultheria strigosa* var. *strigosa* and *G. tomentosa*, 0–(2)–5 rays  $\text{mm}^{-1}$ , consisting of procumbent and square body ray cells (sometimes also upright in *Gaultheria rudis* and *G. shallon*), and several rows of square or upright marginal ray cells, indistinct sheath cells in *Diplycosia*, *Gaultheria*, *Leucothoe* and *Pernettya*. Gummy deposits in ray cells. Crystals absent. Pith cells of two different forms in *G. buxifolia* var. *secunda*, *G. shallon* and *Pernettya mucronata*: larger cells with very thin walls clustered between smaller cells with thicker walls; all pith cells rounded, similar in size, and thin-walled in *Chamaedaphne* and *Tepuia*. No prismatic crystals in pith cells observed.

ANDROMEDEAE S.S. (*ANDROMEDA* 1/2, *ZENOBIA* 1/1; FIGS 38–43)

Growth ring boundaries distinct. Diffuse-porous. Vessels solitary with an angular vessel outline. Vessel perforation plates exclusively scalariform, with 8–(12)–22 bars. Intervessel and vessel-ray pits mainly opposite, sometimes alternate, 2–3  $\mu\text{m}$  in size, non-vestured. Helical thickenings absent, but sometimes present in vessel element tails of *Zenobia pulverulenta* (BR). Tangential diameter of vessel lumina 12–(22)–35  $\mu\text{m}$ , 128–(319)–660 vessels  $\text{mm}^{-2}$ , vessel elements 270–(434)–620  $\mu\text{m}$  long. Tracheids present, 280–(412)–570  $\mu\text{m}$  long. Fibre-tracheids mostly with distinctly bordered pits, 3–5  $\mu\text{m}$  in diameter, very thin-walled, 360–(599)–830  $\mu\text{m}$  long. Occasionally libriform fibres with few simple to indistinctly bordered pits, non-septate, 370–(541)–730  $\mu\text{m}$  long; nuclei



**Figures 27–34.** LM micrographs showing transverse sections of Gaultherieae wood samples. Fig. 27. *Gaultheria buxifolia* var. *secunda*, TS, heterogeneous pith. Scale bar = 200  $\mu$ m. Fig. 28. *Chamaedaphne calyculata*, TS, homogeneous pith. Scale bar = 200  $\mu$ m. Fig. 29. *Gaultheria shallon*, TS, solitary vessels, scanty paratracheal parenchyma (arrows). Scale bar = 100  $\mu$ m. Fig. 30. *Gaultheria rigida*, TS, *idem* (arrows). Scale bar = 100  $\mu$ m. Fig. 31. *Diplycosia heterophylla*, TS, thick-walled fibres. Scale bar = 100  $\mu$ m. Fig. 32. *Chamaedaphne calyculata*, TS, distinct growth ring, narrow vessels with a high density. Scale bar = 100  $\mu$ m. Fig. 33. *Leucothoe axillaris*, TS, solitary vessels, scanty paratracheal parenchyma (arrows). Scale bar = 100  $\mu$ m. Fig. 34. *Tepuia venusta*, TS, very narrow vessels, thick-walled fibres. Scale bar = 50  $\mu$ m.



**Figures 35–43.** LM micrographs showing the wood structure of Gaultherieae and Andromedeae s.s. Fig. 35. *Gaultheria rudis*, TLS, narrow, high multiseriate ray at left. Scale bar = 200  $\mu$ m. Fig. 36. *Gaultheria shallon*, TLS, living fibre with nucleus (arrow). Scale bar = 20  $\mu$ m. Fig. 37. *Gaultheria strigosa*, RLS, procumbent and square body ray cells. Scale bar = 100  $\mu$ m. Fig. 38. *Andromeda polifolia*, TS, strongly heterogeneous pith. Scale bar = 200  $\mu$ m. Fig. 39. *Zenobia pulverulenta*, TS, strongly heterogeneous pith. Scale bar = 200  $\mu$ m. Fig. 40. *Andromeda polifolia*, TS, narrow vessels with a high density. Scale bar = 100  $\mu$ m. Fig. 41. *Zenobia pulverulenta* (E), TS, distinct growth ring, solitary vessels, very thin-walled fibres. Scale bar = 100  $\mu$ m. Fig. 42. *Zenobia pulverulenta* (E), TLS, narrow, multiseriate rays. Scale bar = 200  $\mu$ m. Fig. 43. *Zenobia pulverulenta* (E), TLS, mainly opposite vessel pitting. Scale bar = 20  $\mu$ m.

observed in libriform fibres of *Andromeda polifolia* and *Zenobia pulverulenta* (BR). Axial parenchyma scanty paratracheal, 2–4 cells per parenchyma strand. Uniseriate rays always present, 110–(476)–1100 µm high, consisting of upright cells, 7–(17)–26 rays mm<sup>-1</sup>. Multiseriate rays present in *Zenobia pulverulenta*, 2-seriate, 0–(3)–17 rays mm<sup>-1</sup>, consisting of procumbent and square body ray cells and 1–3 rows of upright marginal ray cells, 450–(720)–1000 µm high. Gummy deposits in ray cells. Prismatic crystals absent. Pith cells of two different forms: small groups of very large cells with thin walls clustered between smaller cells with thicker walls. No prismatic crystals in pith cells observed.

## DISCUSSION

### CHARACTERISTIC FEATURES OF THE WOOD STRUCTURE OF ANDROMEDEAE S.S., GAULTHERIEAE, LYONIEAE AND OXYDENDREAE

A typical wood sample of the study group shows growth rings and a diffuse porosity. Vessels are mainly solitary, although some tangential vessel groupings are observed in most genera. The tangential diameter is narrow, usually ranging from 15 to 40 µm, and the vessel density usually ranges from 100 to 300 vessels mm<sup>-2</sup>. The length of the vessel elements is commonly between 350 and 800 µm. Vessels often have scalariform perforation plates, but exclusively simple perforations are observed in *Lyonia jamaicensis*; mixed simple and scalariform perforations are found in *Agauria*, *Craibiodendron*, *Lyonia*, *Oxydendrum* and *Pieris*, although usually one type dominates. Intervessel pits are mostly opposite or alternate, except in *Agauria* and *Oxydendrum*, where scalariform intervessel pitting is the main type. Vessel-ray pits are distinctly bordered, but sometimes simple in *Oxydendrum* (Fig. 6), and are similar to intervessel pitting, although more scalariform vessel-ray pitting is observed in some species of *Agarista*, *Gaultheria*, *Lyonia* and *Pieris*. Fibre-tracheids have distinctly bordered pits (3–6 µm in size) and very thin to thick walls. Helical thickenings in fibre-tracheids are seen in *Gaultheria* and *Pernettya*. Occasionally thin-walled libriform fibres, which are nearly always septate with few simple to indistinctly bordered pits, are observed in all species (except for *Diplycosia heterophylla* and *Leucothoe grayana*). Tracheids are always present and occur sparsely throughout the wood, with helical thickenings in several *Gaultheria* and *Pernettya* species. The axial parenchyma is scanty paratracheal, with a tendency to a diffuse-in-aggregates distribution in *Lyonia squamulosa* and especially in *L. jamaicensis* (Fig. 14). Uniseriate rays consisting of upright cells are always present and

occur in combination with heterocellular, multiseriate rays, which consist of exclusively procumbent or procumbent and square body ray cells, and one to several rows of square to upright marginal ray cells. Exclusively uniseriate rays are present in the juvenile stems of *Andromeda polifolia* and *Tepuia venusta*. Multiseriate rays are in general 2–5 cells wide. In *Agauria* and *Agarista*, however, 5–9-seriate rays are observed (Fig. 15). The height of the uniseriate rays mostly ranges from 200 to 1000 µm, whereas multiseriate rays are much higher, mostly between 500 and 3000 µm, with the highest rays in *Agarista*, *Agauria* and *Gaultheria*. Gummy deposits (possibly tannins) are frequently noticed in the ray cells (Fig. 16). Prismatic crystals occur in chambered axial parenchyma cells of *Oxydendrum* (Figs 7, 8) and several *Lyonia* species (Fig. 19), and in ray cells of *Agarista populifolia* and *A. bracamorensis* (Fig. 20).

Our wood anatomical observations largely agree with earlier descriptions and only minor differences can be found (Cox, 1948; Metcalfe & Chalk, 1950; Suzuki & Noshiro, 1988). For example, the presence of relatively narrow vessels and a unique ray type in *Agauria* as mentioned by Cox (1948) are probably due to the juvenile nature of the wood examined. Moreover, some features that were not recorded previously include the presence of simple perforations and helical thickenings in vessel elements of *Lyonia* species, multiseriate rays higher than 1 mm in several genera, sheath cells in some species of *Agarista*, *Diplycosia*, *Leucothoe* and *Pernettya*, and the occurrence of prismatic crystals in *Agarista*, *Lyonia* and *Oxydendrum*. We also noticed few septate and/or non-septate libriform fibres in nearly all genera. The wood samples preserved in FAA (*Andromeda*, *Gaultheria*, *Leucothoe*, *Pieris* and *Zenobia*) demonstrated the presence of nuclei within libriform fibres, thus indicating that a living protoplast occurs in these cells (Fig. 36). It is very likely that septate libriform fibres in *Oxydendrum* and in other genera contain nuclei, because of the general acceptance that septate fibres retain their living protoplasts much longer than fibre-tracheids and tracheids. Likewise, living fibres are also observed within the closely related Vaccinieae (Braun, 1961; Fahn & Leshem, 1962; Giebel, 1983; our observations). However, this can only be determined when looking at non-dried, well-preserved wood samples.

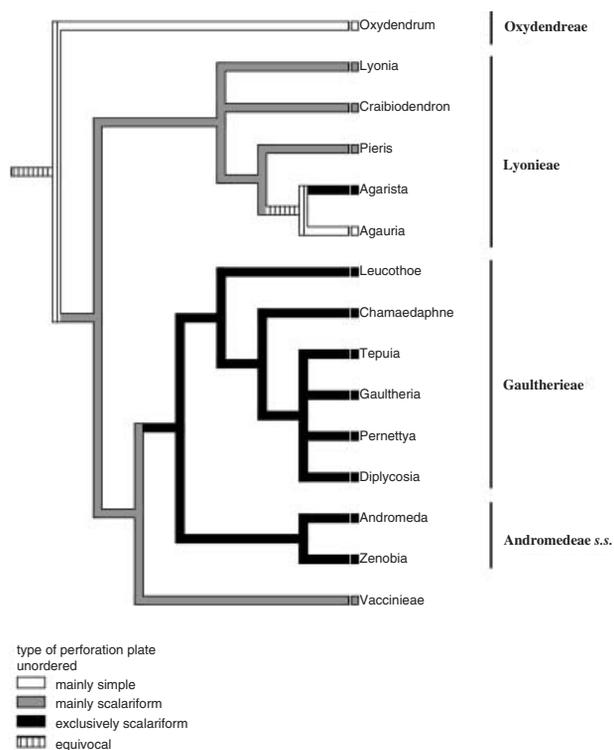
### PHYLOGENETIC WOOD ANATOMY

Although most genera studied cannot be defined by wood anatomical features as such, the secondary xylem provides useful information in confirming or negating already proposed relationships because certain features appear to be consistent at the tribal level. Although the generic relationships within the

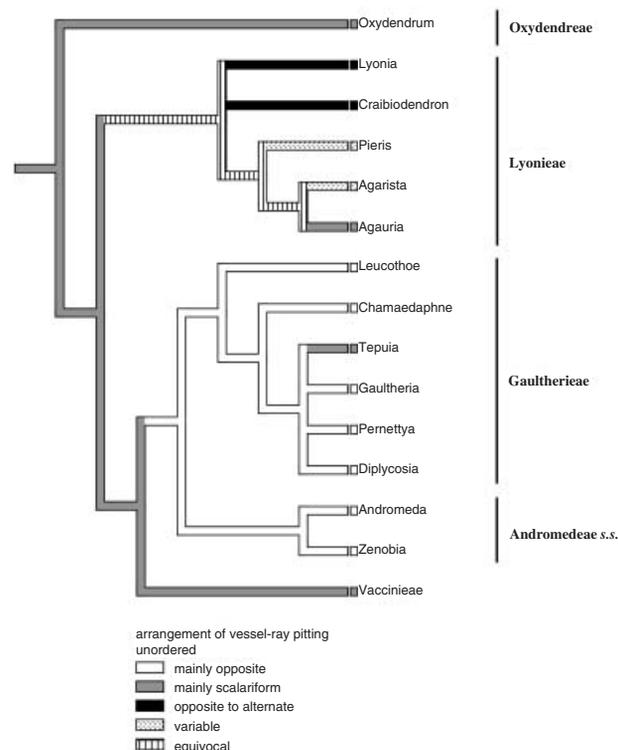
tribes are incompletely understood, we have plotted five important wood anatomical features of the study group on a tree, which is based on the molecular phylogenetic studies of Kron & Judd (1997), Kron *et al.* (1999) and Powell & Kron (2001). The branches of this tree represent all genera examined by us plus one branch forming the Vaccinieae. The five wood characters are the type of vessel perforation plate (Fig. 44), the arrangement of vessel-ray pitting (Fig. 45), the mean height of multiseriate rays (Fig. 46), the shape of body ray cells in multiseriate rays (Fig. 47), and the occurrence and location of prismatic crystals (Fig. 48). These features are selected because of their apparent consistency at the generic and/or tribal level. As for the height of multiseriate rays, four character states are defined based on the overall measurements in the study group as well as on data in Vaccinieae (Table 2; our observations): (1) below 400  $\mu\text{m}$ , (2) between 400 and 1000  $\mu\text{m}$ , (3) between 1000 and 3000  $\mu\text{m}$ , and (4) above 3000  $\mu\text{m}$ . Although there are some genera that cannot be easily categorized into one of these four character states, the character states proposed appear to correspond well with generic and tribal delimitations. A detailed discussion of the wood anatomical

variation within and between the various tribes is presented below.

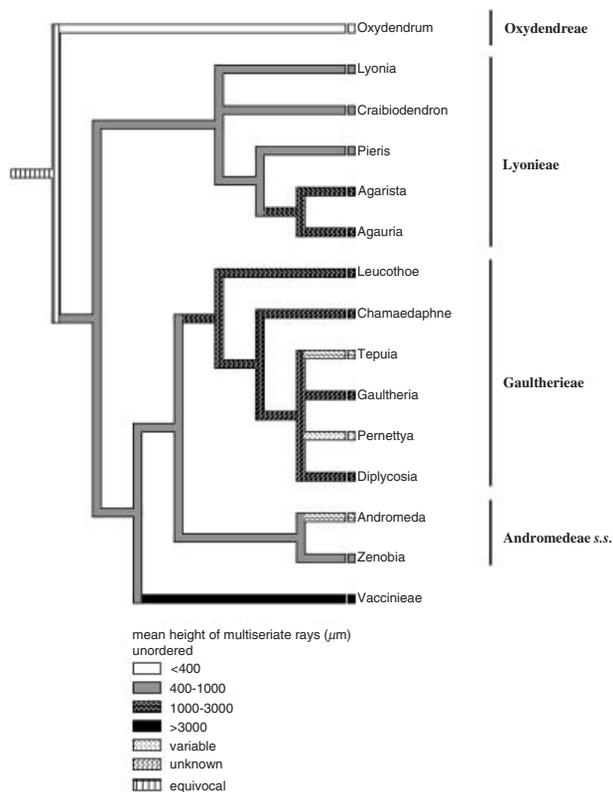
*Oxydendrum* takes the most basal position within Vaccinioideae. Owing to its possession of nearly exclusively simple perforations (Figs 7, 44), mainly scalariform vessel-ray pits that are sometimes simple (Fig. 6), conspicuous helical thickenings (Fig. 5), rare occurrence of low, uniseriate rays, and numerous, low multiseriate rays (Fig. 46), and prismatic crystals in chambered axial parenchyma cells (Figs 7, 8, 48), *Oxydendrum* can clearly be defined on the basis of wood anatomical data alone. Besides these wood anatomical characters, there are also other anatomical features supporting the isolated position of *Oxydendrum* (Palser, 1952; Stevens, 1971). Compared with more primitive Ericaceae clades, it can be suggested that the presence of low and narrow multiseriate rays represents primitive features within Vaccinioideae (Lens *et al.*, 2003). However, these features do not only occur in *Oxydendrum*: low and narrow multiseriate rays are also found in some samples of *Gaultheria* (Fig. 35). By contrast, the presence of scalariform vessel-ray pits with strongly reduced borders, sometimes also observed in *Agauria*, probably represents a derived



**Figure 44.** Type of vessel perforation plates in the wood of Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae plotted on the molecular phylogeny suggested by Kron & Judd (1997), Kron *et al.* (1999) and Powell & Kron (2001).



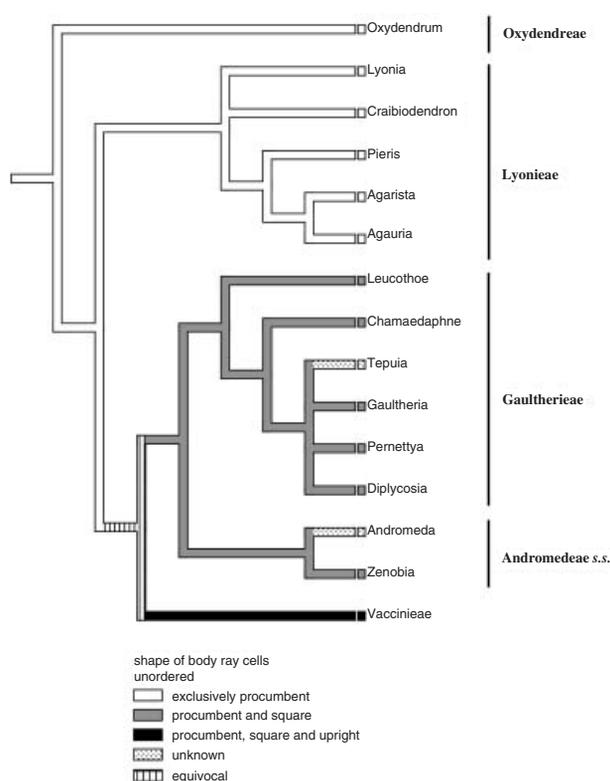
**Figure 45.** Arrangement of vessel-ray pitting in the wood of Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae plotted on the molecular phylogeny suggested by Kron & Judd (1997), Kron *et al.* (1999) and Powell & Kron (2001).



**Figure 46.** Mean height of multiseriate rays in the wood of Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae plotted on the molecular phylogeny suggested by Kron & Judd (1997), Kron *et al.* (1999) and Powell & Kron (2001).

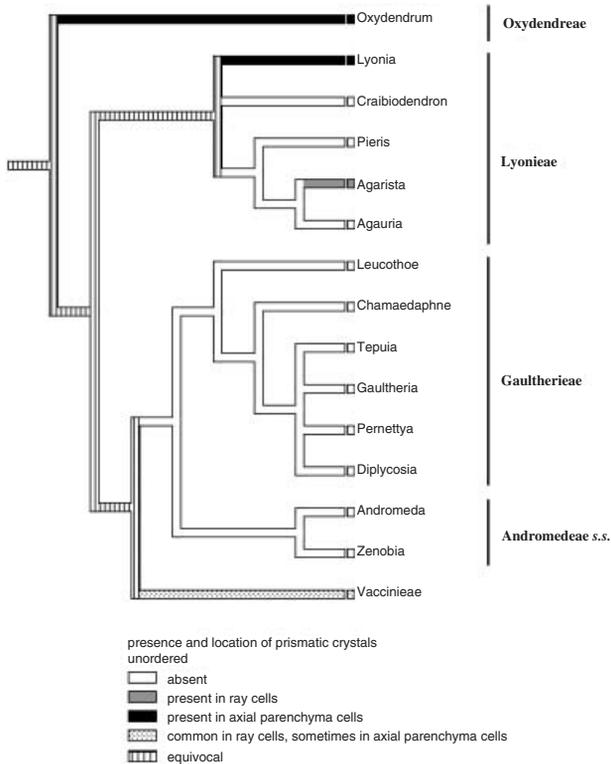
feature because this is commonly observed in Vaccinieae (our observations).

The tribe Lyonieae is characterized by mainly scalariform vessel perforations (Fig. 44; except for *Agauria*, see Fig. 21, and *Lyonia jamaicensis*), mainly opposite to alternate vessel-ray pitting (Figs 26, 45), rather low, multiseriate rays between 400 and 1000 µm high (except for *Agauria* and *Agarista*) showing procumbent body ray cells (Figs 17, 18, 47), and the presence of prismatic crystals in axial parenchyma cells of some *Lyonia* species (Fig. 19). Two features that are not observed in other Lyonieae, namely the presence of scalariform vessel-ray pitting (Figs 24, 25), as well as broad and high rays (sometimes even higher than 3000 µm, Fig. 15), seem to support the close relationship between *Agauria* and *Agarista*. The major difference between the African *Agauria* and the neotropical *Agarista* is the distribution of mainly simple vessel perforation plates in *Agauria* (Fig. 21) and the exclusively scalariform perforations in *Agarista* (Fig. 22), but this could be due to the various ecological conditions. Minor differences include the presence of helical thickenings in vessel



**Figure 47.** Shape of the body ray cells in multiseriate rays in the wood of Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae plotted on the molecular phylogeny suggested by Kron & Judd (1997), Kron *et al.* (1999) and Powell & Kron (2001).

elements, exclusively bordered vessel-ray pitting, and the occurrence of some square body ray cells in *Agarista*. However, the scarce presence of square body ray cells in *Agarista populifolia*, *A. pulchella* and *A. uleana* may be due to the juvenile nature of the wood (see below). Thus, wood anatomical data support the inclusion of *Agauria* as a section within *Agarista* as mentioned by Stevens (1970) and Judd (1984). Another species with a prominent wood structure appears to be *Lyonia jamaicensis* (Fig. 14). This species shows exclusively simple perforations, rounded vessel outlines, exclusively alternate vessel-ray pitting, thick-walled fibres with small, indistinctly to distinctly bordered fibre pits (3 µm in size), and diffuse-in-aggregates axial parenchyma cells, with 6–9 cells per strand. However, the presence of prismatic crystals in chambered axial parenchyma cells links this species with other *Lyonia* species of section *Lyonia*: three of the four species of section *Lyonia* studied, namely *L. heptamera*, *L. jamaicensis* (Fig. 19) and *L. squamulosa*, show prismatic crystals in axial parenchyma cells, whereas other *Lyonia* samples lack crystals in their wood. The



**Figure 48.** Presence and location of prismatic crystals in the wood of Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae plotted on the molecular phylogeny suggested by Kron & Judd (1997), Kron *et al.* (1999) and Powell & Kron (2001).

presence of scalariform vessel-ray pitting within Lyonieae may support the sister relationship between the genera *Pieris* and *Agarista* (incl. *Agauria*), whereas the alternate vessel-ray pits could link *Craibiodendron* with *Lyonia*, as has been pointed out by an analysis of combined morphological and *matK* data (Kron & Judd, 1997).

The secondary xylem of Gaultherieae differs from Lyonieae by the presence of mainly opposite vessel-ray pitting (Fig. 45), relatively rare (often between 0 and 4 rays  $\text{mm}^{-2}$ ), often high, multiseriate rays (between 1000 and 3000  $\mu\text{m}$ ; Fig. 46) with procumbent and square body rays cells (Fig. 37), and the absence of prismatic crystals (Fig. 48). In particular, the shape of the body ray cells within one multiseriate ray may be an important character to distinguish these two tribes from each other (Fig. 47). Heterocellular ray bodies are observed in all Gaultherieae genera, and this type of body ray cell is only seen outside Gaultherieae in *Zenobia pulverulenta*, *Pieris japonica* (L. Rothkegel) and in some *Agarista* species. This may therefore form an argument to include *Chamaedaphne*, which was formerly considered to be isolated, within Gault-

therieae. However, it is worth mentioning that the shape of body ray cells may also depend on the maturity/size of the wood samples studied: in shrubs and small trees, in particular, a higher percentage of upright body ray cells is usually seen near the pith and procumbent cell shapes are more abundant closer to the cambium. Thus, this ontogenetic variation may play a significant role in the study group because the mean diameter of Gaultherieae wood samples studied, all derived from shrubby species, is much smaller than that for the wood samples of Lyonieae, for which shrubs as well as small trees were studied. However, the two Gaultherieae samples with the largest stem diameter, i.e. *Gaultheria anastomosans* (27 mm) and *G. erecta* (Kw 11654, 26 mm), also show square body ray cells, indicating that the structure of multiseriate rays has a phylogenetic signal within the study group. Another feature that could be influenced by ontogenetic variation is the length of tracheary elements. Indeed, the mean length of vessel elements, fibre-tracheids and tracheids in Gaultherieae (respectively 547, 576 and 761  $\mu\text{m}$ ) is somewhat lower than in Lyonieae (respectively 596, 694 and 921  $\mu\text{m}$ ). This difference in length could also be influenced by their habit (shrubs vs. small trees), an important factor in the wood of Vaccinioideae that will be treated elsewhere.

The wood structure of *Leucothoe*, which is the most primitive genus of Gaultherieae, is typical of this tribe, except for the absence of helical thickenings in the vessel elements. Based on the presence of mainly opposite vessel-ray pitting, the absence of conspicuous helical thickenings in vessel elements, and the smaller width and height of the multiseriate rays, it is clear that *Leucothoe* is not closely related to *Agarista*, with which it was formerly associated (Sleumer, 1959). *Leucothoe grayana*, the only species of section *Eubotryoides*, is very similar to the other two *Leucothoe* species observed, which are representatives of section *Leucothoe*, and only small differences can be noticed, such as the presence of occasional helical thickenings in the tails of vessel elements, the thin- to thick-walled fibres, and the absence of libriform fibres in *L. grayana*. *Chamaedaphne calyculata*, which is nested at the basis of the wintergreen group (including *Diplycosia*, *Gaultheria*, *Pernettya* and *Tepuia*), is characterized by several (mainly quantitative) features, namely the small length of the tracheary elements (vessel elements, fibres, tracheids), the very high density of vessels (Fig. 28) and uniseriate rays, and the lack of septate libriform fibres, although some of these features are probably related to its northern boreal distribution. The wood anatomical variation of the taxa studied within the wintergreen group is rather homogeneous. However, the young twig of *Tepuia venusta* studied, an endemic to the tepuis of the Venezuelan Guayana, shows some atypical fea-

tures for this wintergreen group, such as the presence of very narrow vessel elements, a very high vessel density, thick fibre walls (Fig. 34), non-septate libriform fibres and abundant exclusively uniseriate rays. It is interesting to note that some of these features are also found in the wood of *Chamaedaphne*, although the ecological conditions of both genera are rather different. Furthermore, the wood of *Pernettya* and *Gaultheria* is very similar, which may support the results of Middleton & Wilcock (1990) and Powell & Kron (2001), but provides less evidence to consider the two genera as distinct entities (Luteyn, 1995a,b). Indeed, *Gaultheria* and *Pernettya* are the only two genera that are characterized by the presence of helical thickenings throughout the fibres. Although *Diplycosia* is also nested within *Gaultheria* according to molecular data (Powell & Kron, 2001), the only representative of *Diplycosia* studied by us differs from *Gaultheria* by its high number of bars per scalariform perforation plates, the lack of helical thickenings and libriform fibres, and the occurrence of thick-walled fibres (Fig. 31). More wood samples of *Diplycosia* species need to be observed to comment on possible relationships between *Diplycosia* and *Gaultheria*.

Morphological synapomorphies for the two genera of the tribe Andromedeae s.s. have not yet been discovered, but molecular data clearly seem to support this clade (Kron *et al.*, 2002). From a wood anatomical point of view, Andromedeae s.s. is a homogeneous tribe that is similar to its sister tribe Gaultherieae. It is defined by the presence of exclusively scalariform perforation plates, mainly opposite vessel-ray pitting (Fig. 43), relatively low, multiseriate rays (Fig. 42) with procumbent and square body ray cells (although absent in *Andromeda*, but this is probably due to the juvenile wood studied), presence of non-septate libriform fibres, lack of prismatic crystals (Fig. 48) and the presence of a conspicuously heterogeneous pith structure (Figs 38, 39). Apparently, the wood structure of Gaultherieae only differs from Andromedeae s.s. by the mainly septate libriform fibres and higher multiseriate rays (Fig. 46) in Gaultherieae.

#### WOOD ANATOMICAL COMPARISON WITH OTHER ERICACEAE S.L.

The wood structure of the tribes Andromedeae, Gaultherieae, Lyonieae and Oxydendreae show many similarities with other 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 fibre pits (fibre-tracheids), scarcely distributed axial parenchyma and the combination of uniseriate rays with less common multiseriate rays. The study group especially corresponds with the tribe

Vaccinieae, and with the subfamily Styphelioideae, which is the sister group of Vaccinioideae according to molecular data (Kron *et al.*, 2002). As has already been mentioned by Lens *et al.* (2003), the presence of wide and high multiseriate rays, both of which are nearly absent outside Styphelioideae and Vaccinioideae, may support the relationship between both subfamilies. In addition, the sporadic occurrence of libriform fibres and the presence of crystal-bearing axial parenchyma cells is found in both subfamilies, but these two features also occur in the distantly related subfamily Arbutioideae (our observations).

By contrast, there are some wood anatomical features that enable us to distinguish between Andromedeae *sensu* Stevens and Vaccinieae. The most important difference is the abundant presence of procumbent body ray cells in most tribes studied here (Figs 17, 18), whereas Vaccinieae are largely characterized by square and upright body ray cells (Fig. 47; our observations). Procumbent to square body ray cells, however, are characteristic of Gaultherieae (Fig. 47). Other distinguishing features are the height of the multiseriate rays and the presence of prismatic crystals in ray cells: very tall rays of 3000 µm or more and prismatic crystals in ray cells are common in Vaccinieae (Fig. 48; our observations) but rare in other Vaccinioideae.

#### PITH CHARACTERS

The pith structure in Andromedeae *sensu* Stevens shows a significant variation and allows us to define three types (Fig. 49; Judd, 1979; Kron *et al.*, 1999; our observations): (1) a homogeneous pith type with thin- or thick-walled cells, all of more or less the same size (Fig. 28), (2) a heterogeneous pith type with small, thick-walled cells scattered between larger, thin-walled cells (Figs 9, 27) and (3) a *Calluna*-type with small thin- or thick-walled cells at the periphery surrounding a pith cavity (Fig. 10). In this study, we were able to define a fourth pith type, namely a very conspicuously heterogeneous structure in the two genera of Andromedeae s.s.: the very small, thick-walled pith cells strongly contrast with the very large, thin-walled cells, giving the pith structure a reticulate appearance (Figs 38, 39). This 'strongly' heterogeneous pith type could be a first morphological synapomorphy for the Andromedeae s.s. The 'normal', heterogeneous pith type, which is not reticulate at all, is found in representatives of Lyonieae (*Pieris* and *Agauria*) and Gaultherieae (*Gaultheria* and *Pernettya*). The homogeneous pith type characterizes some genera of Lyonieae (*Lyonia* and *Craibiodendron*) and Gaultherieae (*Chamaedaphne*, *Tepuia* and *Diplycosia*). Besides the similar vessel-ray pitting between *Lyonia* and *Craibiodendron*, the homoge-



**Figure 49.** Pith types in Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae plotted on the molecular phylogeny suggested by Kron & Judd (1997), Kron *et al.* (1999) and Powell & Kron (2001).

neous pith type in both genera may give an additional support for their close relationship. The *Calluna*-type is present in *Oxydendrum* (Oxydendreae), *Agarista* (excluding *Agauria*; Lyonieae) and *Leucothoe* section *Leucothoe* (Gaultherieae) (Judd, 1979; Kron *et al.*, 1999).

The different pith types as outlined above become even more striking when compared with the large tribe Vaccinieae, which only have the homogeneous type (Fig. 49). The same pith type is also characteristic of the subfamily Styphelioideae, except for *Richea* and *Dracophyllum* (Richeeae), which show a strongly heterogeneous pith type similar to the Andromedeae s.s. (Lens *et al.*, 2003).

## CONCLUSIONS

Several features in the secondary xylem of Andromedeae s.s., Gaultherieae, Lyonieae and Oxydendreae show a taxonomic significance at the tribal level. In particular, the type of vessel perforation plate, arrangement of vessel-ray pitting, height of multiseriate rays, shape of body ray cells, and the distribution and location of prismatic crystals may be useful in

assigning an unknown specimen to one of the four tribes studied. Living fibres are observed in Andromedeae s.s., Lyonieae and Gaultherieae, and seem to characterize the subfamily Vaccinioideae. It is also demonstrated that the pith structure within Oxydendreae and Andromedeae s.s. is consistent, but there is much more variation in Lyonieae and Gaultherieae.

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