

STUDY OF THE COMPARATIVE WOOD ANATOMY OF THE SPECIES OF AMPHOROGENACEAE, CERVANTESIACEAE, NANODEACEAE, SANTALACEAE, AND THESIACEAE

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ABSTRACT

This work compares the anatomy of the secondary xylem of 56 species of 19 genera belonging to Amphorogynaceae, Cervantesiaceae, Nanodeaceae, Santalaceae, and Thesiaceae according to the new classification (Nickrent et al. 2010). Anatomical characters typical for each species were identified and two wood anatomical groups were recognized: Group A with vessel groupings with few solitary vessels, vessels in dendritic pattern (only *Jodina rhombifolia*, *Pyrularia*, *Myoschilos oblongum* and *Mida salicifolia*), long fibers with simple to bordered pits, vasicentric tracheids (except in *Acanthosyris*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Pyrularia* and *Scleropyrum*), fiber-tracheids (except in *Pyrularia*, *Okoubaka aubrevillei*, *Scleropyrum* and *Pilgerina madagascariensis*). Group B with solitary vessels, vasicentric tracheids, fiber-tracheids. Most species of Group A belong to Cervantesiaceae according to the new classification, except for the species of *Scleropyrum* that according to their anatomical characters belong to Group B. *Myoschilos oblongum* is part of Santalaceae (Group B) but anatomical characters are same as Cervantesiaceae. The wood anatomy of species in Group A shows more xeromorphic characters than the species of Group B. *Myoschilos oblongum* is adapted to cold regions where there is no water in the winter season.

RESUMEN

El presente trabajo compara la anatomía del xilema secundario de 56 especies de 19 géneros pertenecientes a Amphorogynaceae, Cervantesiaceae, Nanodeaceae, Santalaceae, y Thesiaceae de acuerdo a la nueva clasificación (Nickrent et al. 2010). Se identificaron caracteres anatómicos típicos para cada especie, pudiéndose establecer dos grandes grupos de acuerdo a dichos caracteres: Grupo A con vasos agrupados y algunos solitarios, dispuestos de manera dendrítica (solamente en *Jodina rhombifolia*, *Pyrularia*, *Myoschilos oblongum* and *Mida salicifolia*), fibras largas con puntuaciones simples a rebordeadas, traqueidas vasicéntricas con paredes muy engrosadas y puntuaciones rebordeadas (excepto en *Acanthosyris*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Pyrularia* y *Scleropyrum*), fibro-traqueidas (excepto en *Pyrularia*, *Okoubaka aubrevillei*, *Scleropyrum* y *Pilgerina madagascariensis*). Grupo B con vasos solitarios, sin traqueidas vasicéntricas y con fibras liberiformes con puntuaciones simples. La mayoría de las especies del Grupo A pertenece a Cervantesiaceae según la nueva clasificación, con excepción de las especies de *Scleropyrum* que de acuerdo con sus caracteres anatómicos pertenecen al Grupo B. *Myoschilos oblongum* es parte de Santalaceae (Grupo B), pero sus caracteres anatómicos son los mismos que Cervantesiaceae. La anatomía de la madera de las especies del Grupo A muestra más caracteres xeromórficos que las especies del Grupo B. *Myoschilos oblongum* está adaptada a regiones frías donde no hay agua en invierno.

INTRODUCTION

The objective of this paper is to provide new information about the wood anatomy of the species belonging to the families Cervantesiaceae Nickrent & Der, Thesiaceae Vest, Nanodeaceae Nickrent & Der, Amphorogynaceae (Stauffer ex Stearn) Nickrent & Der, and Santalaceae R. Br., with the aim of providing a better understanding of the relationships between these plants, according to the new classification of the order Santalales (Nickrent et al. 2010). This classification is based on results from molecular phylogenetic investigations and brings together currently available information that contributes to our understanding of relationships among these plants. The species studied are *Acanthosyris falcata*, *A. spinescens*, and *A. glabrata* of temperate South America; *Cervantesia tomentosa* of Andean South America; *Jodina rhombifolia* of southern Brazil, Uruguay, and Argentina; *Okoubaka aubrevillei* of tropical Africa; *Pilgerina madagascariensis* of Madagascar; *Pyrularia pubera* of the southeastern U.S. and *P. edulis* of India; *Scleropyrum walichianum* and *Scleropyrum maingayi* of India, southeast Asia, and Malesia; *Buckleya distichophylla* of eastern U.S.; *Thesium lineatum* of Namibia and South Africa; *Mida salicifolia* disjunct from New Zealand to the Juan Fernandez Islands; *Dendromyza reinwardtiana* of Papua New Guinea; *Dendrotrophe varians* from the Himalayas to the Philippines and Malaysia, Indonesia; *Colpoon compre-*

sum of South Africa; *Eubrachion ambiguum* of South America (Argentina, Uruguay, and south Brazil); *Exocarpos brachystachys*, *E. bidwillii*, *E. cupressiformis*, *E. vitensis* of southeast Asia and Malaysia to Hawaii; *Leptomeria billardieri* and *L. spinosa* of Australia; *Myoschilos oblongum* of Argentina and Chile; *Osyris* L., 6 species of Europe, Mediterranean, Africa, and China; and *Santalum* L., 16 taxa from Indomalaya to Australia and Hawaii.

MATERIALS AND METHODS

In total, 56 species of Cervantesiaceae Nickrent & Der, Thesiaceae Vest, Nanodeaceae Nickrent & Der, Amphorogynaceae (Stauffer ex Stearn) Nickrent & Der, and Santalaceae, representing 19 genera, were investigated using light microscopy (LM) and scanning electron microscopy (SEM).

Wood samples were available in dried condition. They were boiled in water, stored in 50% aqueous ethyl alcohol, and softened for 3 days in ethylenediamine (Kukachka 1977) prior to being sectioned; sections were prepared with a sliding microtome. Some sections were stained with safranin and counterstained with fast green before being mounted on slides. Other sections were dried between clean glass slides, sputter coated with gold, and examined with a scanning electron microscope. Macerations were prepared with Jeffrey's fluid (Jeffrey 1917) and stained with safranin-fast green combination.

All quantitative data are based on 25 measurements per feature. Terminology follows that of the IAWA Committee on Nomenclature (1964). For each sample, the collector name is listed first, followed by the wood collection number preceded by a code from Stern's *Index Xylariorum* (1988), and then the locality. The sources of the specimens studied are in Table 1 (some codes, localities and collectors are not known).

RESULTS

Descriptions of the anatomical characters are based on mature wood samples. A summary of selected anatomical features for the 56 species is shown in Table 2.

Growth ring boundaries generally indistinct or absent, but distinct growth rings observed in *Pyrularia pubera* (Fig. 1A), *Exocarpos bidwillii*, *Santalum spicatum* (Fig. 1B), *Buckleya distichophylla*, and *Myoschilos oblongum* (Fig. 1C).

Porosity diffuse in most of the species, except *Jodina rhombifolia* (Fig. 1D), *Pyrularia* (Fig. 1A), *Myoschilos oblongum* (Fig. 1C), and *Buckleya distichophylla* (Fig. 7E) semi-ring porous.

Vessels small to very small, average tangential diameter (20–100 μm). *Jodina rhombifolia* and *Leptomeria* have the narrowest vessels (20–22 μm) and *Scleropyrum* the widest (86 μm). Vessel element length is short (100–300 μm): *Leptomeria* (243 μm) had the longest vessel elements, followed by *Scleropyrum* (163 μm); *Myoschilos oblongum* (127 μm) had the shortest. *Scleropyrum* has the least number of vessels per mm^2 (12 vessels per mm^2) (Fig. 1E) and *Leptomeria* has the largest number of vessels per mm^2 (244 vessels per mm^2) (Fig. 1F).

Exclusively solitary vessels occur in most of the species (Fig. 1E, 2A), but *Acanthosyris* (Fig. 2B), *Okoubaka aubrevillei* (Fig. 7A), and *Mida salicifolia* (Fig. 2D) have vessels in radial multiples; *Cervantesia tomentosa* (Fig. 2C) and *Buckleya distichophylla* have vessels in short radial multiples and in clusters. *Myoschilos oblongum* is the only species of the Santalaceae that does not have exclusively solitary vessels and vessels occur in short radial multiples of 2–4 (Fig. 1C). *Mida salicifolia* has radial multiples of 4 or more and clusters (Fig. 2D).

Jodina rhombifolia (Fig. 1D), *Pyrularia* (Fig. 1A), *Myoschilos oblongum* (Fig. 1C), and *Mida salicifolia* (Fig. 2D) have vessels in dendritic pattern.

Simple perforation plates in all species; only rimmed perforation plates in *Buckleya distichophylla*, *Leptomeria*, and *Santalum hendersonense* (Fig. 2E). *Mida salicifolia* has a few scalariform perforation plates with 10–20 anastomosing bars (Fig. 2F).

Vessel outline was angular (Fig. 1F), circular (Fig. 3A) or oval (Fig. 3B) and the position of the perforation plates can be very oblique (Fig. 3C), oblique or horizontal (Fig. 3D) depending on each species.

Intervessel pits are opposite and/or alternate in all species (Fig. 3E). *Cervantesia tomentosa* and *Acanthosyris glabrata* have also polygonal alternate pits (Fig. 3F). *Dendromyza reinwardtiana*, *Myoschilos oblongum*, *Thesium*

TABLE 1. Sources of specimens studied. Collector's name/no. is listed first, followed by the wood collection number preceded by a code from Stern's *Index Xylariumum* (1988), and locality.

Taxon	Collector & No.	Index Xylariumum	Locality
		Code	
Acanthosyris glabrata (Stapf) Stauffer	Dugand s.n.	(SJRw 27095)	Colombia
	Dugand s.n.	(SJRw 28474)	Colombia
	Dugand s.n.	(SJRw 29686)	Colombia
	Dugand s.n.	(SJRw 32393)	Colombia
Acanthosyris falcata Griseb.	Venturi 952	(LILw)	Tucumán Prov., Argentina
		(SJRw 1113)	Argentina
Acanthosyris spinescens (Mart. & Eichler) Griseb.	Novarrez s.n.	(SJRw 15012)	Buenos Aires Prov., Argentina
	División Forestal	(Baw)	Argentina
Buckleya distichophylla (Nutt.) Torr.	Norverto 16, 17, 18	(BAw)	Entre Ríos Prov., Argentina
Cervantesia tomentosa Ruiz & Pav.	L.J. Musselman		Virginia, U.S.A.
Colpoon compressum P.J. Bergius	A. Dugand s.n.	(SJRw 28474)	Colombia
	A. Dugand s.n.	(SJRw 29686)	Colombia
	A. Dugand s.n.	(SJRw 32393)	Colombia
	Pappe s.n.	(Kw 15407)	South Africa
Dendromyza reinwardtiana (Blume ex Korth.) Danser	B. Hyland 9519,	(SMHI 1739)	
Dendrotrophe varians Miq.	Susanne Kaplan s.n.		
Eubrachion ambiguum (Hook. & Arn.) Engl.		(DLN 4017)	
Exocarpos bidwillii Hook. f.	Nickrent 2699		
Exocarpos brachystachys Hillebr.	Carlquist 5545		
Exocarpos cupressiformis Lab.	Carlquist 1899	(USw 38946)	Hawaii, U.S.A.
	Forbes s.n.	(SJRw 26283)	W. Maui, Hawaii, U.S.A.
		(Kw 15416)	Victoria, Australia
		(USw 949)	New South Wales, Australia
Exocarpos vitensis A.C. Sm.	Div. of Forest Products	(SJRw 19446)	New South Wales, Australia
	Col. A.C. Simth s.n.	(SJRw 33466)	Victoria, Australia
		(USw 30483)	Fiji
		(BAw 55899,	Chaco Prov., Argentina
Jodina rhombifolia Hook. & Arn.	Mantese s.n.	55901, 55903)	
	Venturi 388b	(LILw)	Tucumán Prov., Argentina
	Cozzo s.n.	(Baw 52256)	Córdoba Prov., Argentina
	Norverto 20, 21, 22	(BAw)	Buenos Aires Prov., Argentina
	Del Vitto 994	(Baw)	San Luis Prov., Argentina
	Schuel s.n.	(Kw 15425)	northern Argentina
Leptomeria billardieri R. Br.		(Usw 4184)	Catamarca Prov., Argentina
		(Kw 15427)	Hobart, Tasmania
Leptomeria spinosa A. DC.	Walker s.n.	(DLN 3081)	
Mida salicifolia A. Cunn. (= <i>Fusanus cunninghamii</i> Benth. et Hook.		(USw W13905)	New Zealand. DLN 4307
Myoschilos oblongum Ruiz et Pav.	Brion s.n.	(BAw 144)	Río Negro Prov., Argentina
	Rotkugel s.n.	(SJRw 1744)	Patagonia, Argentina
	Bullock s.n.	(Usw 15356)	Chile. DLN 4504B
Okoubaka aubrevillei Pellegr. & Normand		Xylariumum 158	Odi, Ghana, Africa
Osyris abyssinica Hochst.		(SJRw 31899)	East Africa
Osyris alba L.		(MADw 4856)	South Africa
	Playfair s.n.	(Kw 15428)	Algeria
Osyris lanceolata Hochst. & Steud.		(PPFw 5143)	Pretoria, South Africa
Osyris lanceolata Hochst. & Steud. (= <i>Osyris quadripartita</i> Salzm. ex Decne	Schweingruber s.n.	(SMHI s.n.)	Murcia, España
Osyris tenuifolia Engl.		(USw V11836)	Tanganyika, East Africa
Osyris wightiana Wall.		(SJRw 29410)	Kilimandscharo, Tanganyika, East Africa
Pilgerina madagascariensis Z.S. Rogers, Nickrent & Malécot	Rabenatoandro et al. 315A		
Pyralaria edulis A. DC.		(Kw 15431)	Darjeeling, India
Pyralaria pubera Michx.		(MADw 15725)	West Virginia, U.S.A.
Santalum album L.		(Kw 15434)	Mysore, India
		(USw 37761)	India

TABLE 1. Continued.

Taxon	Collector & No.	Index Xylarium	Locality
		Code	
<i>Santalum austrocaledonicum</i> Vieill.		(USw w4760)	New Caledonia
		(SJRw 13991)	
		(SJRw 14316)	
<i>Santalum cuneatum</i> Rock		(SJRw 29753)	Hawaii, U.S.A.
<i>Santalum ellipticum</i> Gaud.		(SJRw 1902)	
<i>Santalum fernandezianum</i> F. Phil.	Meyer s.n.	(USw 34036)	Juan Fernandez Islands
<i>Santalum freycinetianum</i> Gaud.	Carlquist 1918	(USw 38950)	Hawaii, U.S.A.
		(SJRw 1902)	Hawaii, U.S.A.
	Carlquist	(USw 15344)	
<i>Santalum freycinetianum</i> var. <i>pyrularium</i> (Gray) L. Stemmermann	Carlquist 598 (RSA) Stern & Carlquist 1278	(USw 25976)	
	522 (RSA)		
<i>Santalum freycinetianum</i> var. <i>lanaiense</i> Rock		(SJRw 26249)	
<i>Santalum haleakalae</i> Hillebr.	Carlquist 548	(USw 15319)	Maui, Hawaiian Islands
<i>Santalum hendersonense</i> F. Br.	Bishop s.n.	(SJRw 37304)	Henderson Is.
<i>Santalum insulare</i> var. <i>raiateense</i> (J. Moore) Fosberg & Sachet		(SJRw 24861); (SJRw 24295)	
<i>Santalum insulare</i> var. <i>marchionense</i> (Skotts.) Skotts.		(SJRw 24369)	
<i>Santalum lanceolatum</i> R. Br.		(USw 21172)	
<i>Santalum paniculatum</i> Hook. & Arn.		(USw w5630)	Hawaiian Islands
<i>Santalum yasi</i> Seem.		(USw30349)	
<i>Santalum spicatum</i> A. DC. = <i>Eucarya</i> <i>spicata</i> (R. Br.) Spr. et Summerh	F. du s.n.	(Kw 15409)	Western Australia
		(Kw 15424)	Western Australia
	Baron F. von Mueller s.n.	(Kw 15412)	S.W. Australia
	Forestry Commission s.n.	(USw 22403)	Western Australia
		(USw 4031)	Western Australia
		(USw W-8802)	Western Australia
<i>Scleropyrum walichianum</i> Ait.	Wright	(Kw 15452)	Ceylon
	Ridsdale 485	(USw s.n.)	South India
<i>Scleropyrum maingayi</i> Hook. f.		(USw 28364)	
<i>Thesium lineatum</i> L.f.		(RSA 4627a)	South Africa

lineatum, and *Mida salicifolia* also have scalariform intervessel pits (Fig. 4A). Apertures are sometimes coalescent (Fig. 3E; 4B).

Vessel-ray pits are of two distinct sizes and types in the same ray cell, distinctly bordered pits and other large pits with much reduced borders to apparently simple, pits rounded (Fig. 4C). There are also vessel-ray pits with distinct borders, similar to intervessel pits (Fig. 4D). Vessel-ray pits with much reduced borders to apparently simple; pit outline rounded present in *Okoubaka aubrevillei* (Fig. 7B). *Acanthosyris glabrata* has vessel-pits unilaterally compound and coarse (Norverto 1993).

Tails are present or absent on vessels. Various species have helical thickenings in vessel elements (Fig. 4E). Vessel walls helically thickened and vested in *A. spinescens* (Norverto 1993). There are also species with unusual thickenings surrounding vessel pits (Metcalf & Chalk 1950; Patel 1974) (Fig. 4F). Some species have tyloses (Fig. 1B).

Parenchyma. Most of the species have diffuse apotracheal axial parenchyma (Fig. 1E). Some species of *Exocarpos*, *Santalum*, and *Okoubaka aubrevillei* have diffuse in aggregates axial parenchyma (Fig. 5A; 7A). Absence of axial parenchyma was observed in *Buckleya distichophylla* (Fig. 7 F), *Osyris alba*, and *O. wightiana*. Generally, the species have scanty paratracheal axial parenchyma. *Acanthosyris glabrata*, *Osyris alba*, *O. lanceolata* and *O. wightiana* have axial parenchyma confluent (Fig. 5B). *Acanthosyris falcata* and *Cervantesia tomentosa*

TABLE 2. Overview of selected wood anatomical characters within species of Amphorogynaceae, Cervantesiaceae, Nanodeaceae, Santalaceae, and Thesiaceae.

Family/Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Cervantesiaceae																									
<i>Acanthosyris glabrata</i>	1	2	2	1	0&1	1	1	1	1	1	0	1	1	2	1	0	2	0	0&1	0	2	0	0&1	1	0
<i>Acanthosyris falcata</i>	1	2	2	1	0&1	1	0	1	1&2	0	0	1	1	1	1	0	1	1	0&1	0	0	1	0&1	1	0
<i>Acanthosyris spinescens</i>	1	2	2	1	0&1	1	1	1	2	0	0	1	1	1	1	0	1	0	1	0	0	1	0	0	1
<i>Cervantesia tomentosa</i>	1	2	2	1&2	0	1	1	0&1	1	0	0	1	1	2	1	0	1	1	0	1	1	0	0&1	1	0
<i>Okoubaka aubrevillei</i>	1	2	2	1&2	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0&1	0	1
<i>Jodina rhombifolia</i>	1	1	3	1&2	0	0	1	0	0	0	0	1	1	0&1	1	0	1	0	0&1	0	1	1	0	1	1
<i>Pyralaria edulis</i>	1	1	3	1&2	0	0	1	1&2	0	0	0	1	1	1	1	0	0	0	0	1	0	1	0	0	0
<i>Pyralaria pubera</i>	0	1	3	1&2	0	0&1	0	1&2	0	0	0	1	1	1	1	0	1	0	0	1	0	1	0	0	0
<i>Scleropyrum wallichianum</i>	1	2	0	0	1	1	0	1	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0	1	0
<i>Scleropyrum ridleyi</i>	1	2	0	0	1	1	0	1	0	0	0	0	1	1	1	0	1	0	1&2	0	1	1	0	1	0
<i>Scleropyrum maingayi</i>	1	2	0	0	1	1	0	1	0	0	0	0	1	1	1	1	1	1	1&2	0	0	1	0	1	0
<i>Pilgerina madagascariensis</i>	1	2	0	0	1	0&1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	1
Amphorogynaceae																									
<i>Dendromyza reinwardtiana</i>	1	2	0	0	1	1	1	2	1	0	1	1	0	0	1	0	1	0	0&1	1	0	0	0	1	1
<i>Dendrotrophe varians</i>	1	2	0	0	1	1	1	2	1&2	0	1	1	0	0	1	0	1	0	0	0	0	0	1	1	0
<i>Leptomeria billardieri</i>	1	2	1&2	0&1	0	0&1	0	0	1&2	0	1	1	0	0	1	0	1	0	0&1	1	2	1	0	0	0
<i>Leptomeria spinosa</i>	1	2	1&2	0&1	0	0&1	0	0	1&2	0	1	1	0	0	1	0	1	0	0&1	1	2	1	0	0	0
Santalaceae																									
<i>Colpoon compressum</i>	1	2	0	0	0&1	1	0	0&1	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0
<i>Eubrachion ambiguum</i>	1	2	0	0	0	0&1	0	0&1	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Exocarpos brachystachys</i>	1	2	0	0	0&1	0&1	0	0&1	1&2	0&1	1	1	0	0&1	1	0	0&1	1	0	0	0	0	0	1	0
<i>Exocarpos cupressiformis</i>	1	2	0	0	1	1	0	0&1	1&2	0	1	1	0	0&1	1	0	0&1	1	0	0	0	0	1&2	1	0
<i>Exocarpos bidwillii</i>	1	2	0	0	0&1	0&1	1	0&1	2	0	1	1	1	1	1	0	0&1	1	0	0&1	0	0	1&2	1	0
<i>Exocarpos latifolius</i>	1	2	0	0	0	0&1	0	0&1	1	0	1	1	0	0&1	1	0	1	0	0	0	0	1	1	1	0
<i>Exocarpos vitensis</i>	1	2	0	0	1	1	0	0&1	1&2	0	1	1	0	0&1	1	0	0&1	1	0	0	0	0	1	1	0
<i>Myoschilos oblongum</i>	0	1	3	1	0	0	1	0	0&1&2	0	1	1	1	1	1	0	1	1	1	0	2	1	0	0	0
<i>Osyris abyssinica</i>	1	2	0	0	0&1	1	0	0&1	1&2	0&1	1	1	0	0&1	1	0	1	0	0	0	0	1	0	0	0
<i>Osyris alba</i>	0	2	0	0	0&1	0	1	0	2	0	1	1	0	0	0	0	0	0	0&1	0	2	0	0	0	0
<i>Osyris lanceolata</i>	1	2	0	0	0&1	0&1	0&1	0&1	1&2	0	1	1	0	0&1	1	0	0&1	0	0	0	2	0	0	0	0
<i>Osyris tenuifolia</i>	1	2	0	0	1	1	0	0&1	1&2	0	1	1	0	0&1	1	0	1	0	0	0	2	0	0	1	0
<i>Osyris wightiana</i>	1	2	0	0	0&1	1	1	0&1	1&2	0	1	1	0	0&1	1	0	0	0	0	0	2	0	0	0	0
<i>Santalum album</i>	1	2	0	0	1	1	1	0&1	1&2	0&1	1	1	0	0&1	1	0	0&1	1	0	0&1	0	0	1	1	0
<i>Santalum insulare</i> var. <i>raiateense</i>	1	2	0	0	1	1	1	0	1&2	1	1	1	0	0	1	0	0&1	1	0	0	0	0	1	1	0
<i>Santalum insulare</i> var. <i>marchionense</i>	1	2	0	0	1	1	0	0&1	1&2	0	1	1	0	0&1	1	0	0&1	1	0	0	0	0	0	1	0
<i>Santalum austro-caledonicum</i>	1	2	0	0	1	0&1	1	0&1	1&2	0	1	1	0	0&1	1	0	0&1	1	0	0	0	0	0	1	0
<i>Santalum cuneatum</i>	1	2	0	0	1	0&1	0	0&1	1&2	0	1	1	0	0&1	1	0	0&1	1	0	0	1	0	0	1	0
<i>Santalum fernandezianum</i>	1	2	0	0	1	1	0	1	0	0	1	1	0	0&1	1	0	1	0	0	0	0	0	1	1	0
<i>Santalum freycinetianum</i>	1	2	0	0	1	1	0	0&1	1&2	0	1	1	0	0&1	1	0	1	0	0	0	0	0	1	1	0

TABLE 2. Continued.

Family/Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Santalaceae (cont.)																										
<i>Santalum freycinetianum</i> var. <i>pyrularium</i>	1	2	0	0	1	1	0	0&1	1&2	0	1	1	0	0&1	1	0&1	1	0	0	0	0	0	0	0	1	0
<i>Santalum freycinetianum</i> var. <i>lanaiense</i>	1	1	0	0	0&1	1	0	0&1	1&2	0	1	1	0	0&1	1	0	1	0	0	0	0	0	0	0	1	0
<i>Santalum haleakalae</i>	1	2	0	0	0&1	1	0	2	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0
<i>Santalum hendersonense</i>	1	2	0	0	0&1	1	0	0&1	1&2	0	1	1	0	0&1	1	1	1	0	0	0	0	0	0	1	1	0
<i>Santalum paniculatum</i>	1	2	0	0	1	1	0	1	1	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0
<i>Santalum pyrularium</i>	1	2	0	0	1	1	0	0	1	0	1	1	0	1	1	0&1	1	0	0	0	0	0	0	0	1	0
<i>Santalum spicatum</i>	1	2	0	0	0	1	0	0&1	1&2	0	1	1	0	0&1	1	0	1	0	0	0	0	0	0	1	1	0
<i>Santalum yasi</i>	1	2	0	0	1	1	0	0&1	1&2	0	1	1	0	0&1	1	0	1	0	0	0	0	0	0	0	1	0
<i>Santalum ellipticum</i>	1	2	0	0	0&1	1	0	0&1	1&2	0	1	1	0	0	1	0&1	1	0	0	0	0	0	0	0	1	0
<i>Santalum spicatum</i> (R. Br.) A. DC. (= <i>Eucarya spicata</i>)	0	1	0	0	0	1	1	1	2	0	1	1	0	0	1	0	1	0	0	1	2	1	1	1	0	0
Thesiaceae																										
<i>Buckleya distichophylla</i>	0	0	3	0&1	0	1	0	0	2	1	1	1	0	0&1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thesium lineatum</i>	1	2	0	1	0	1	0	0	2	0	1	1	0	0&1	1	0	1	0	0	0	2	0	1	0	1	0
Nanodeaceae																										
<i>Mida salicifolia</i> A. Cunn (= <i>Fusanus cunnighamii</i>)	1	2	2&3	1&2	0	0&1	1	0	2	1	1	1	1	1	1	0&1	1	2	0	0	0	0	1	0	1	0

GROWTH RING—1. **Growth ring:** 0- boundaries distinct; 1- boundaries indistinct or absent.

VESSELS—2. **Porosity:** 0- Wood ring-porous, 1- Wood semi-ring-porous, 2- Wood diffuse-porous. 3. **Vessel arrangement:** 0- absent, 1- in tangential bands, 2- in diagonal and/or radial pattern, 3- in dendritic pattern. 4. **Vessel grouping:** 0- exclusively solitary (90% or more), 1- in radial multiples, 2- clusters common. 5. **Solitary vessel outline:** 0- angular, 1- circular or oval. 6. **Perforation plate position:** 0- very oblique, 1- slightly oblique or horizontal. 7. **Helical thickenings:** 0- absent, 1- present in vessel elements. 8. **Mean tangential diameter of vessel lumina:** 0- ≤ 50 μm, 1- 50-100 μm, 2- 100-200 μm. 9. **Vessels per square mm:** 0- 5-20 per mm², 1- 20-100 per mm², 2- ≥ 100 per mm². 10. **Mean vessel element length:** 0- ≤ 350 μm, 1- 350-800 μm.

TRACHEIDS AND FIBERS—11. **Vascular/vasicentric tracheids:** 0- Absent, 1- Present. 12. **Fiber-tracheids:** 0- absent, 1- present. 13. **Fibers:** 0- absent, 1- present. 14. **Mean fibers lengths:** 0- ≤ 900 μm, 1- 900-1600 μm, 2- ≥ 1600 μm.

AXIAL PARENCHYMA—15. **Axial parenchyma:** 0- absent or extremely rare, 1- present. 16. **Apotracheal axial parenchyma:** 0- diffuse, 1- diffuse in aggregates. 17. **Paratracheal axial parenchyma:** 0- absent, 1- scanty paratracheal, 2- confluent. 18. **Axial parenchyma banding:** 0- absent, 1- bands more than three cells wide, 2- in narrow bands or lines up to 3 cells wide.

RAY—19. **Ray width:** 0- 1 to 3 cells, 1- 4 to 10-seriate for larger rays, 2- > 10-seriate for larger rays. 20. **Ray with multiseriate portion(s) as wide as uniseriate portions:** 0- absent, 1- present. 21. **Ray height:** 0- ≤ 1 mm, 1- > 1 mm, 2- of two distinct sizes. 22. **Perforated ray cells:** 0- absent, 1- present. 23. **Rays per mm:** 0- ≤ 4/mm, 1- 4-12 / mm, 2- ≥ 12 / mm.

MINERAL INCLUSIONS—24. **Prismatic crystals:** 0- absent, 1- present. 25. **Druses:** 0- absent, 1- present.

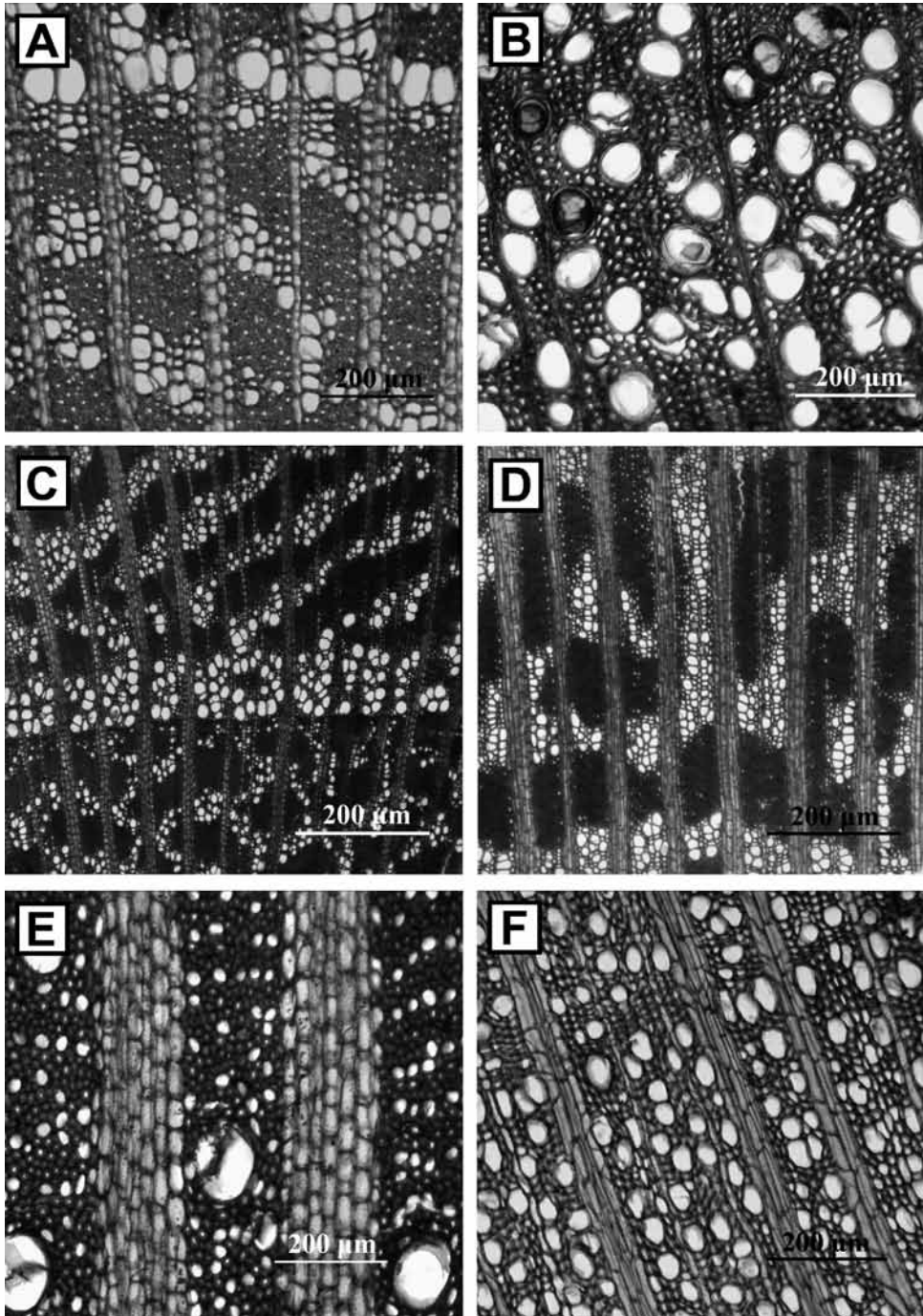


FIG. 1. LM micrographs of the wood structure in Santalaceae. A, *Pyralia pubera*, growth ring boundaries distinct and wood ring-porous, vessels in dendritic pattern, transverse section (TS); B, *Santalum spicatum*, growth ring boundaries indistinct, tyloses in vessels, TS; C, *Myoschilos oblongum*, growth ring boundaries distinct and wood ring-porous and to semi-ring-porous, vessels in diagonal to dendritic pattern, TS; D, *Jodina rhombifolia*, vessels in dendritic pattern, TS; E, *Scleropyrum walchianum*, solitary vessel outline oval, axial parenchyma diffuse, and wide rays, TS; F, *Leptomeria billiardieri*, solitary vessel outline angular, TS.

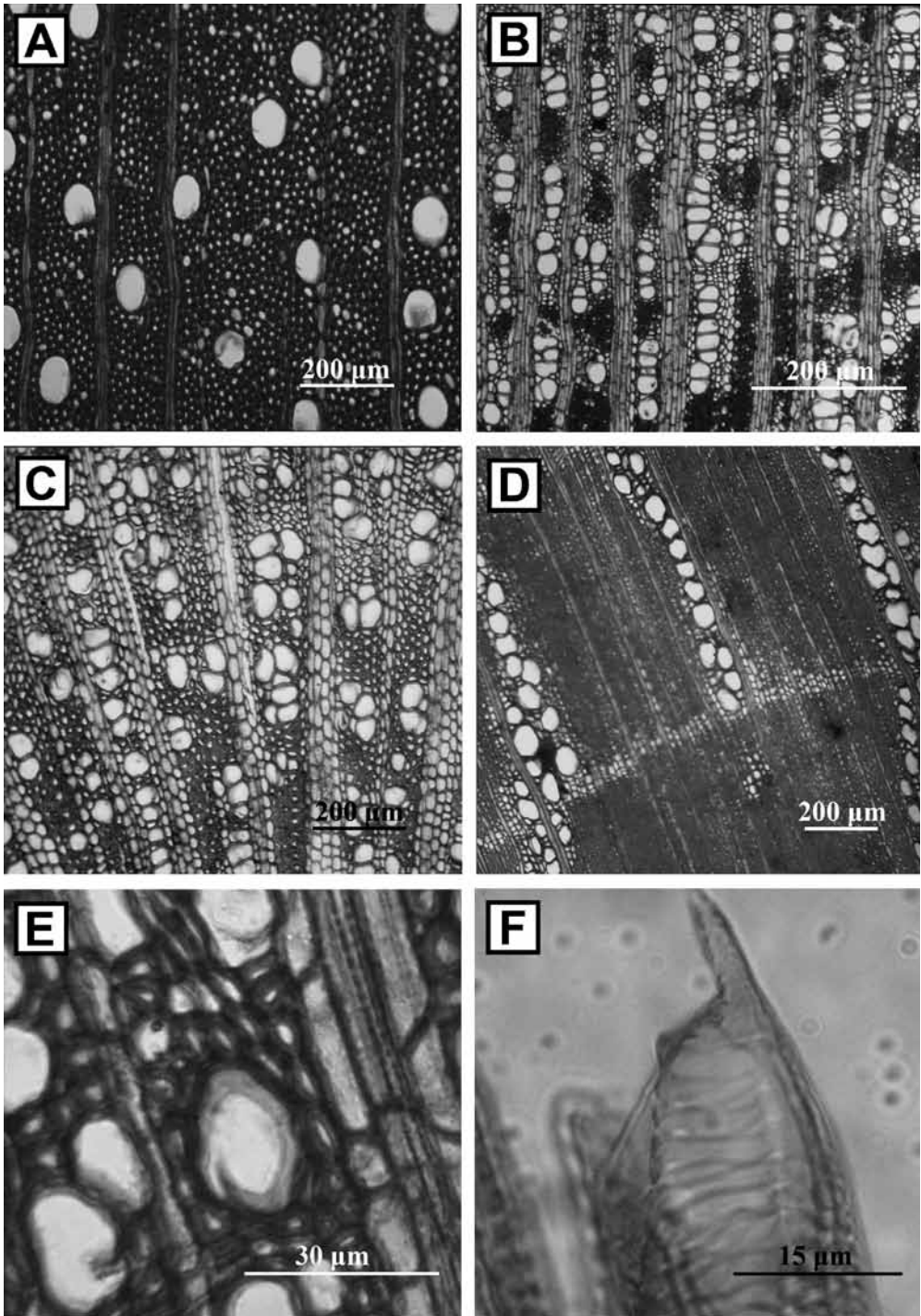


FIG. 2. LM micrographs of the wood structure in Santalaceae. A, *Santalum freycinetianum* var. *pyrularium*, solitary vessel outline oval, TS; B, *Acanthosyris spinescens*, vessels in radial multiples, TS; C, *Cervantesia tomentosa*, vessels in radial multiples, TS; D, *Mida salicifolia*, vessels in radial dendritic pattern TS; E, *Leptomeria billardieri*, rimmed perforation plate, TS; F, *Mida salicifolia*, scalariform perforation plate, maceration.

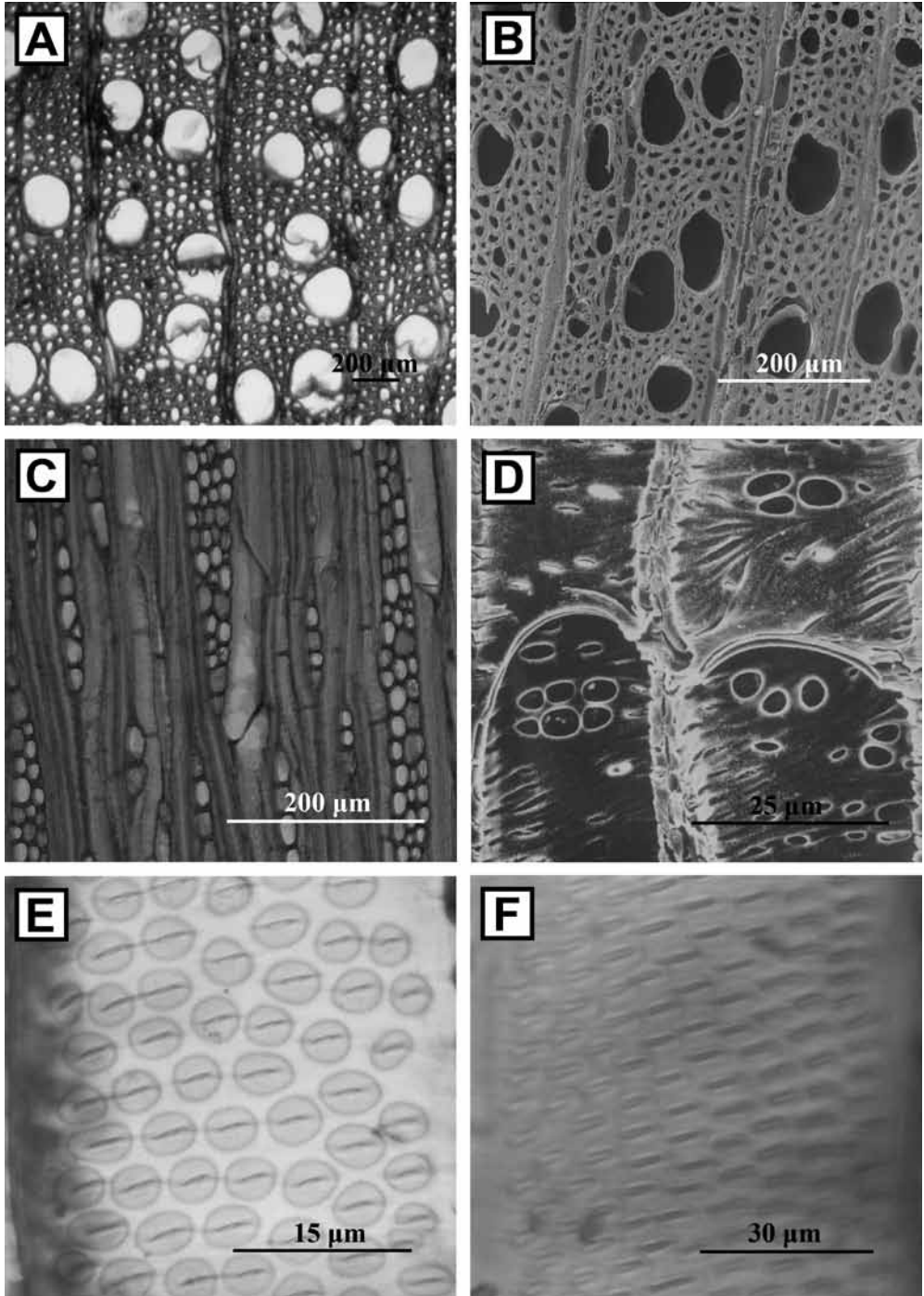


FIG. 3. LM micrographs (A–C–F) and SEM micrographs (B–D) of the wood structure in Santalaceae. A, *Santalum insulare* var. *raiateense*, solitary vessel outline circular, TS; B, *Osyris abyssinica*, solitary vessel outline oval, TS; C, *Leptomeria billarderi*, perforation plates oblique, tangential longitudinal section (TLS); D, *Acanthosyris spinescens*, perforation plates horizontal and pits with borders greatly reduced to very nearly simple, radial longitudinal section (RLS); E, *Acanthosyris falcata*, intervessel pits alternate, RLS; F, *Acanthosyris glabrata*, intervessel pits, shape of alternate pits polygonal, TLS.

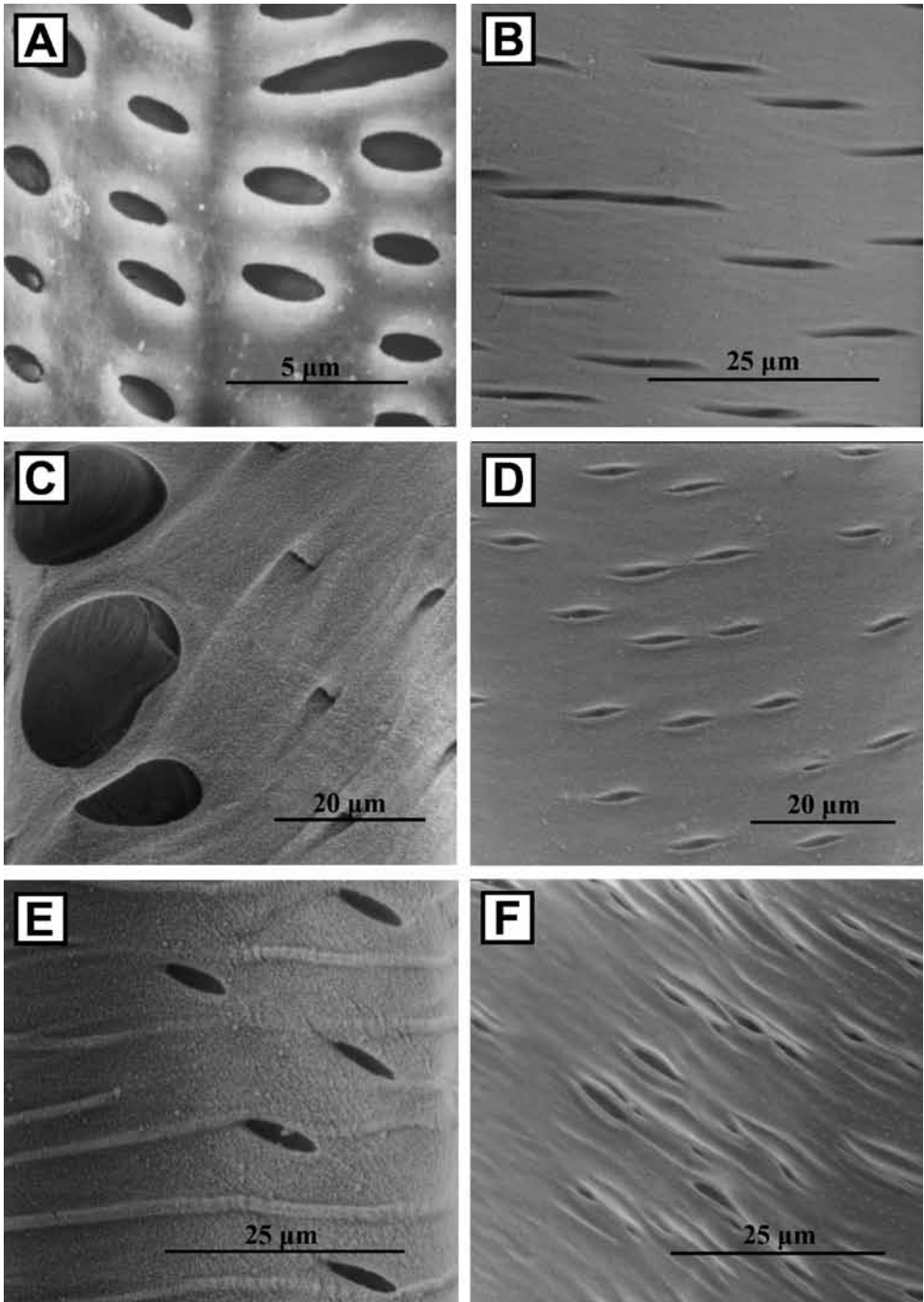


FIG. 4. SEM micrographs of the wood structure in Santalaceae. A, *Myoschilos oblongum*, intervessel pits scalariform, RLS; B, *Santalum album*, included and coalescent apertures; C, *Cervantesia tomentosa*, vessel-ray pits of two distinct sizes and types in the same ray cell, TLS; D, *Santalum freycinetianum* var. *lanaiense*, vessel-ray pits with distinct borders, similar to intervessel pits in size, RLS; E, *Pyralaria edulis*, helical thickenings in vessel element, TLS; F, *Santalum insulare* var. *raiateense*, thickenings around bordered pits, RLS.

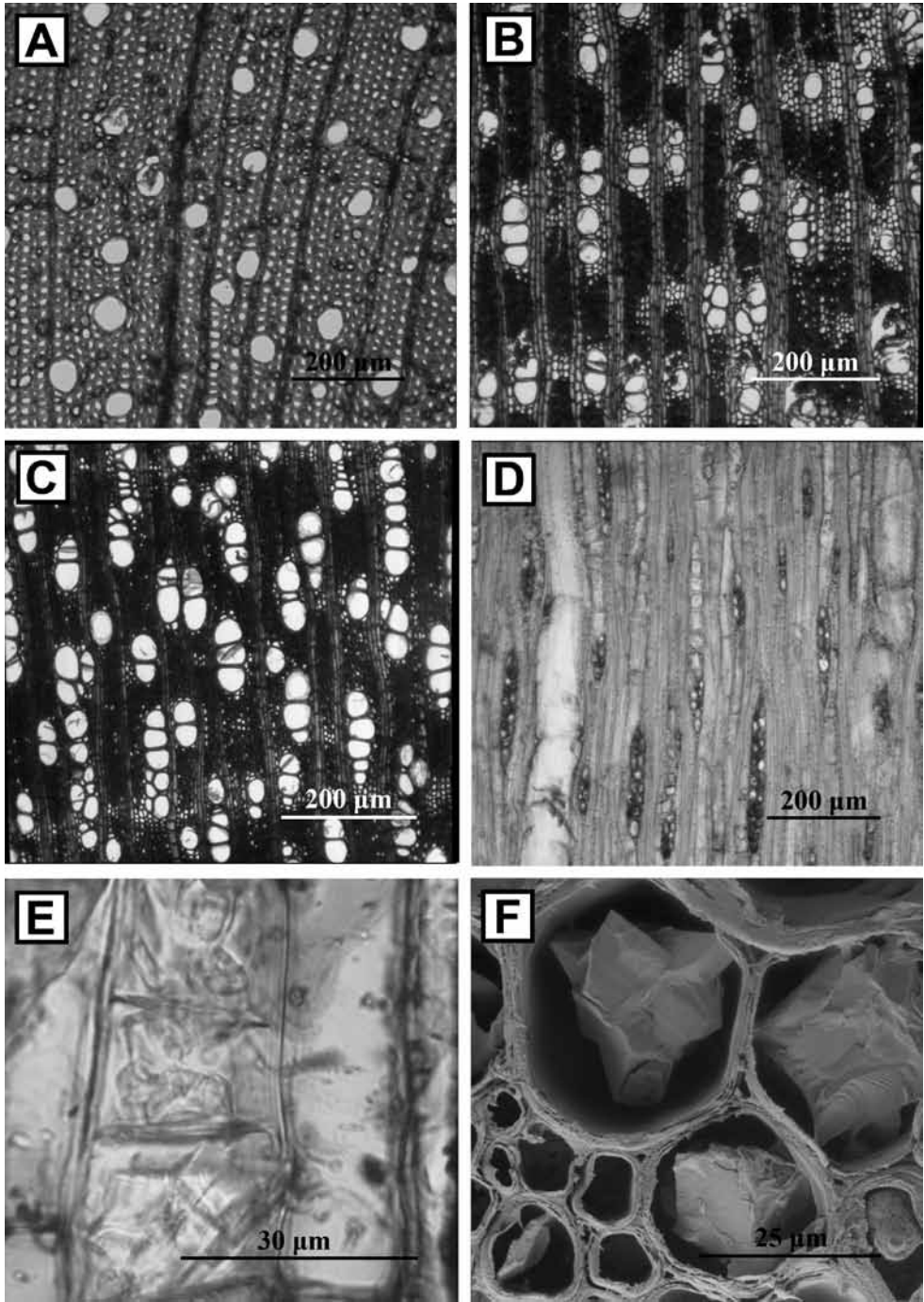


FIG. 5. LM micrographs (A–E) and SEM micrographs (F) of the wood structure in Santalaceae. A, *Exocarpos brachystachys*, solitary vessels, axial parenchyma diffuse-in-aggregates, TS; B, *Acanthosyris glabrata*, vessels commonly in radial multiples, axial parenchyma confluent, TS; C, *Acanthosyris falcata*, parenchyma axial bands and scanty paratracheal parenchyma, TS; D, *Exocarpos vitensis*, narrow rays, prismatic crystal in chambered axial parenchyma cells, TLS; E, *Dendromyza reinwardtiana*, druses in axial parenchyma cells, RLS; F, *Dendromyza reinwardtiana*, druses in axial parenchyma cells, TS.

have axial parenchyma bands with more than 3 cells wide (Fig. 5C). *Mida salicifolia* has axial parenchyma narrow bands from 1 to 2 cells wide (Fig. 2D).

Parenchyma of the species is usually 2 to 4 cells per parenchyma strand. Fusiform parenchyma cells are found in *Scleropyrum walichianum* and *Eubracion ambigunn*. *Acanthosyris*, *Okoubaka aubrevillei*, *Dendrotrophe varians*, *Exocarpos*, *Santalum yasi*, and *Mida salicifolia* have 5 or more parenchyma cells per strand. In *Acanthosyris* and *Cervantesia tomentosa*, disjunctive axial parenchyma cell walls were observed.

Prismatic crystals in axial parenchyma cells of *A. glabrata*, *Dendromyza reinwardtiana* and *Colpoon compressum*. Prismatic crystals in chambered axial parenchyma cells of *Exocarpos brachystachys*, *E. cupressiformis*, *E. latifolius*, *E. vitensis*, and *Santalum* (Fig. 5D). Druses in axial parenchyma cells of *Acanthosyris spinescens*, *Dendromyza reinwardtiana*, and *Pilgerina madagascariensis* (Fig. 5E, F). Crystals in idioblasts were observed in *Colpoon compressum* and *Santalum spicatum*.

Rays usually 1 to 3 cells wide. Rays 4 to 10 cells wide in *Acanthosyris*, *Buckleya distichophylla*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Scleropyrum*, *Exocarpos bidwillii*, *Myoschilos oblongum*, *Osyris alba*, and *Santalum album* (Fig. 6A). *Scleropyrum maingayi* and *S. walichianum* may have rays more than 10 cells wide (Fig. 1E).

Dendromyza, *Dendrotrophe*, *Leptomeria*, *Pyralaria*, *Santalum spicatum*, and *Santalum cuneatum* have rays with uniseriate portions as wide as multiseriate portions (Fig. 6B). *Okoubaka aubrevillei* has rays with procumbent body cells and over 4 rows of upright marginal cells (Fig. 7C). Aggregate rays were only observed in *Cervantesia tomentosa* (Fig. 6C). Type heterogeneous (Kribs II) to homogeneous (Kribs I). All species have rays irregularly storied (Fig. 6D).

Perforated rays cells in *Acanthosyris falcata*, *A. spniescens*, *Scleropyrum*, *Leptomeria*, *Exocarpos latifolius*, *E. bidwillii*, *Myoschilos oblongum*, *Osyris abyssinica*, *Pyralaria*, and *Santalum spicatum* (Fig. 6E) (Rao et al. 1984).

Prismatic crystals in ray parenchyma cells in *Acanthosyris falcata*, *A. glabrata*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Scleropyrum*, *Dendromyza reinwardtiana*, *Dendrotrophe varians*, and *Osyris tenuifolia* (Fig. 6F). Prismatic crystals in chambered ray parenchyma cells in *Dendrotrophe varians*. Druses in ray parenchyma cells present in *Jodina rhombifolia* (Norverto 1993) and *Okoubaka aubrevillei* (Fig. 7D).

Libriform fibers present in *Acanthosyris*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Pyralaria*, *Okoubaka aubrevillei*, *Scleropyrum*, and *Pilgerina madagascariensis*. Septate fibers were found in *Cervantesia tomentosa* (Fig. 6G) and observed by Butterfield et al. (1976) in some species of genus *Mida*.

Fiber-tracheids present in most of the species except *Pyralaria*, *Okoubaka aubrevillei*, *Scleropyrum*, and *Pilgerina madagascariensis*.

Vasicentric tracheids present in most of the species, except in *Acanthosyris*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Pyralaria*, and *Scleropyrum*. Vasicentric tracheids thin-walled, lumen wide and with distinctly bordered pits in *Myoschilos oblongum* and *Buckleya distichophylla*. The rest with vasicentric tracheids thick-walled, lumen narrow and small to medium bordered pits and included apertures.

DISCUSSION

Most species are characterized by the absence of growth rings but some species do have growth rings. Swamy (1949) observed growth rings in *Mida salicifolia* and *Santalum*, and Patel (1974) indicated absence in *Exocarpos bidwillii*, unlike what was observed in this study.

The diameter and density of vessels have consequences in conductive efficiency and safety (Carlquist 1977, 1988). Most species have vessel diameters that are very narrow to narrow. The narrowest vessels and highest number per mm² occur in *Leptomeria*, *Jodina rhombifolia*, *Thesium lineatum*, and *Myoschilos oblongum*; wider vessels and fewer number per mm² are present in *Scleropyrum*. *Santalum* and *Osyris*, with the greatest number of species distributed in diverse habitats, have vessels with tangential diameter between 30 to 60 µm, and a density of 23 to 80 vessels per mm².

The taxa with solitary vessels are *Santalum*, *Exocarpos*, *Osyris*, *Colpoon*, *Thesium lineatum*, *Leptomeria*, and *Scleropyrum*, and those with vessel groupings include *Acanthosyris*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Buckleya distichophylla*, *Pyralaria*, *Myoschilos oblongum*, and *Mida salicifolia* (Metcalf 1935; Swamy 1949;

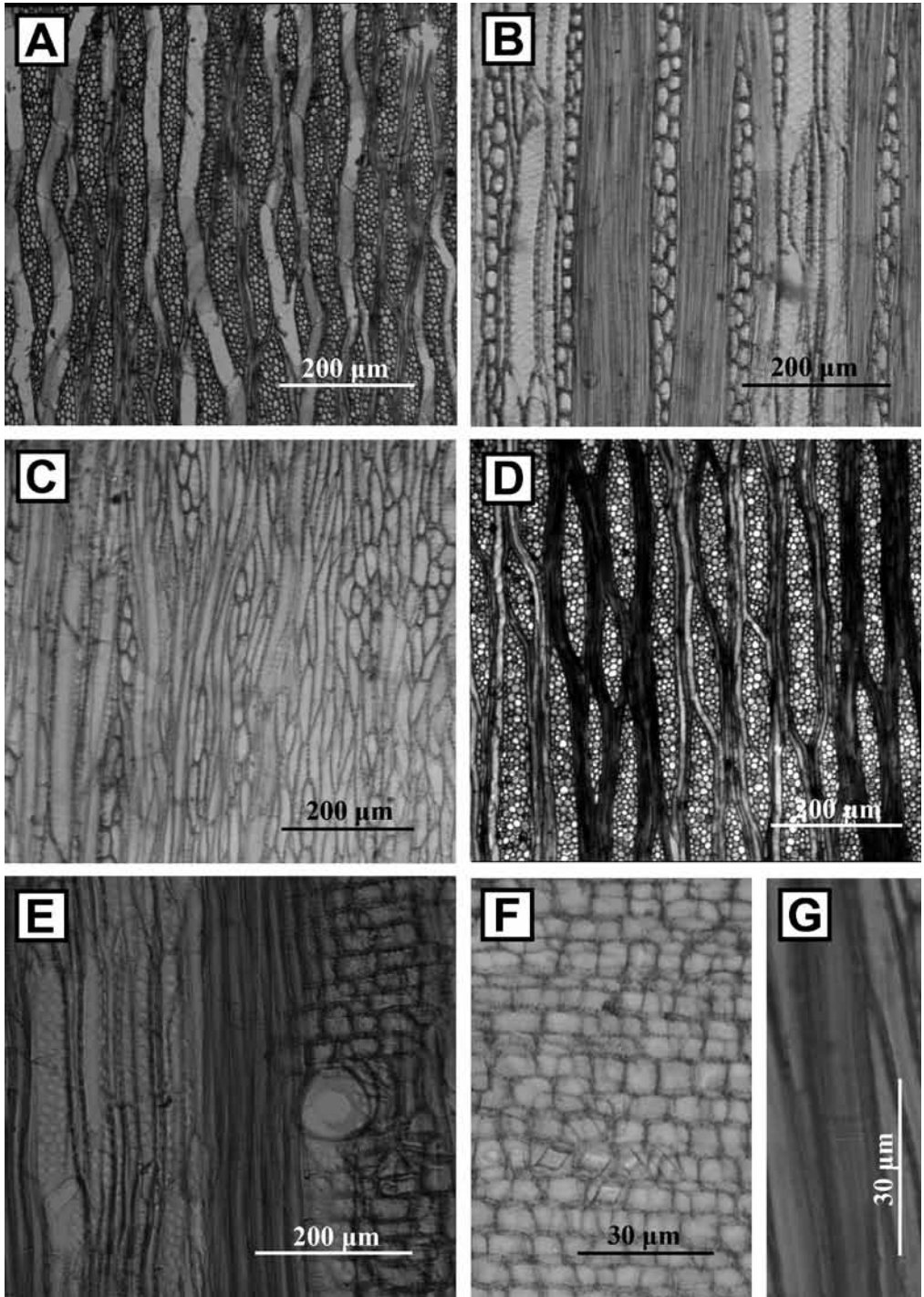


FIG. 6. LM micrographs of the wood structure in Santalaceae. A, *Acanthosyris spinescens*, larger rays commonly 4 to 10-seriate, TLS; B, *Pyrularia pubera*, rays 1–2 seriate, TLS; C, *Cervantesia tomentosa*, aggregate rays, TLS; D, *Jodina rhombifolia*, rays irregularly storied, TLS; E, *Pyrularia edulis*, perforated ray cell RLS; F, *Scleropyrum walichianum*, prismatic crystals in cells, RLS; G, *Cervantesia tomentosa*, fiber walls, TLS.

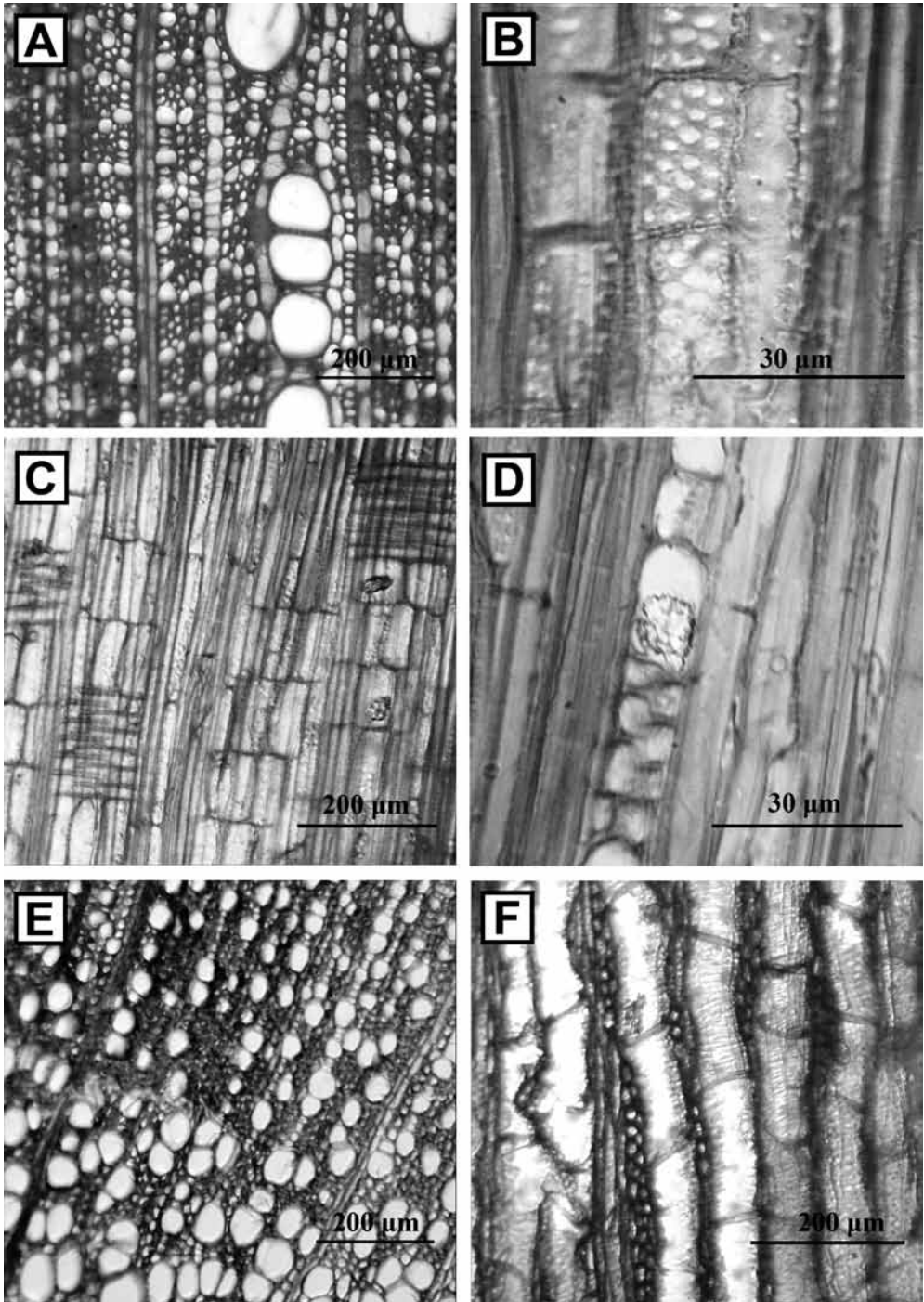


FIG. 7. LM micrographs of the wood structure in Santalaceae. A, *Okoubaka aubrevillei*, vessels in radial multiples, axial parenchyma diffuse-in-aggregates, in fine lines, TS; B, *Okoubaka aubrevillei*, Vessel-ray pits with reduced borders to apparently simple, pit outline rounded, (RLS); C, *Okoubaka aubrevillei*, rays with procumbent body ray cells and over 4 rows of upright marginal cells, RLS; D, *Okoubaka aubrevillei*, druse in radial parenchyma cells, TLS; E, *Buckleya distichophylla*, semi-ring porous, TS; F, *Buckleya distichophylla*, Absence of axial parenchyma, TLS.

Metcalfe & Chalk 1950). The presence of vessel groupings and lack of solitary vessels is a xeromorphic character (Chalk et al. 1937; Baas et al. 1983; Carlquist 1966, 1977, 1980, 1984; Webber 1936). Carlquist (1966) describes some families with a vessel groupings increase with increasing aridity.

Perforation plates are simple in all species and in *Mida salicifolia* there are also scalariform plates (Patel 1974). The species with solitary vessels, except *Scleropyrum*, have more oblique perforation plates.

Tails on vessel elements may be present and/or absent depending on the species. Swamy (1949) showed absence of tails for *Exocarpos*, but they were observed by Patel (1974) and in the present study.

Helical thickenings in vessel elements were observed in *Acanthosyris glabrata*, *A. spiniscens*, *Cervantesia tomentosa*, and *Jodina rhombifolia* (Record & Hess 1943), *Pyrularia* (Swamy 1949), *Dendrotrophe varians*, *Exocarpos bidwillii* (Patel 1974), *Myoschilos oblongum*, *Osyris alba*, *O. quadripartita*, *Santalum album*, *S. insulare*, *S. austrocaledonicum*, *S. haleakalae*, *Santalum spicatum*, and *Mida salicifolia*. Helical thickenings in vessel elements are typical of species that develop in dry and cold temperate regions (Carlquist 1988).

Patel (1974) identified helical thickenings in vessel element tails of *Exocarpos bidwillii* and unusual thickenings that surround the pits and extend laterally. Metcalfe and Chalk (1950) mention striations due to the coalescent pits in Santalaceae. In the present study unusual thickenings around pits were observed for the first time in *Santalum album* and *S. insulare* (Fig. 4F).

The families generally have diffuse apotracheal axial parenchyma, which Kribs (1937) considered to be a primitive feature. *Acanthosyris glabrata*, *Osyris alba*, *O. lanceolata*, and *O. wightiana* have confluent axial parenchyma. *Scleropyrum walichianum* and *Eubracion ambiguum* have fusiform parenchyma cells.

The species in relation to the fibers might be considered primitive, because the specialization indicating that fiber-tracheids are the most common primitive character; a few species have libriform fibers (Metcalfe & Chalk 1950, 1983; Vliet et al. 1981).

There is a correlation between the occurrence of exclusively solitary vessels and vascentric tracheids (Carlquist 1984). Only *Acanthosyris*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Okoubaka aubrevillei* (Normand 1944), and *Pyrularia* lack vascentric tracheids, and they have vessel groups.

CONCLUSIONS

Based on the characters of vessels, vascentric tracheids, fibers, and the axial and ray parenchyma, the studied species are divided in two groups:

GROUP A: Present vessel groupings with few solitary, vessel outline circular; vessels in dendritic pattern (only *Jodina rhombifolia*, *Pyrularia*, *Myoschilos oblongum*, and *Mida salicifolia*); long fibers with simple to bordered pits, vascentric tracheids (except in *Acanthosyris*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Pyrularia*, and *Scleropyrum*), fiber-tracheids (except in *Pyrularia*, *Okoubaka aubrevillei*, *Scleropyrum*, and *Pilgerina madagascariensis*), with uniseriate and multiseriate rays (width 3 to 6 cells) Heterogeneous (Kribs Type II) with one or more square marginal cells and/or upright to Homogeneous (Kribs Type I).

Species in Group A: *Acanthosyris falcata*, *A. spiniscens*, *A. glabrata*, *Buckleya distichophylla*, *Cervantesia tomentosa*, *Jodina rhombifolia*, *Myoschilos oblongum*, *Okoubaka aubrevillei*, *Pyrularia edulis*, *P. pubera*, and *Pilgeria madagascariensis*.

GROUP B: This group consists of a large number of species with solitary vessel, outline angular, oval, and circular; vascentric tracheids very thick-walled, elongated and with bordered pits; fiber-tracheids with bordered pits and coalescent apertures; uniseriate and multiseriate rays (2 to 4 cells wide), Heterogeneous (Kribs Type II) to Homogeneous (Kribs Type I).

Species in Group B: *Colpoon compressum*, *Dendromyza reinwardtiana*, *Dendrotrophe varians*, *Eubracion ambiguum*, *Exocarpos bidwillii*, *E. brachystachys*, *E. cupressiformis*, *E. vitensis*, *Leptomeria billardieri*, *L. spinosa*, *Mida salicifolia*, *Osyris abyssinica*, *O. alba*, *O. lanceolata*, *O. quadripartita*, *O. tenuifolia*, *O. wightiana*, *Santalum album*, *S. austrocaledonicum*, *S. cuneatum*, *S. ellipticum*, *S. fernandezianum*, *S. freycinetianum*, *S. freycinetianum* var. *pyrularium*, *S. freycinetianum* var. *lanaiense*, *S. haleakalae*, *S. hendersonense*, *S. insulare* var. *raiateense*, *S. insulare* var. *marchionense*, *S. lanceolatum*, *S. paniculatum*, *S. yasi*, *S. spicatum*, *Scleropyrum walichianum*, *S. main-*

gayi, and *Thesium lineatum*.

The wood anatomy of Group A species shows more xeromorphic characters than the species of Group B. Most species of Group A belong to Cervantesiaceae (Nickrent et al. 2010) based on the new classification except for species of *Scleropyrum* that according to their anatomical characters, belong to Group B. These differences were also observed by Swamy (1949) and Metcalfe and Chalk (1950). *Okoubaka* has affinity with *Pyrularia* and *Scleropyrum* based on habit, fruit, and wood anatomy (Stauffer 1957). In the present study, *Okoubaka aubrevillei* has affinity with *Pyrularia*, *Acanthosyris*, and *Jodina*.

Myoschilos oblongum is part of Group A but the wood anatomy characters are completely different from the rest of the species of Santalaceae (Group B) according to the new classification (Nickrent et al. 2010). *Myoschilos oblongum* is adapted to cold regions where there is no water in the winter season.

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