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WOOD ANATOMY AND RELATIONSHIPS OF SANTALACEAE. I. *ACANTHOSYRIS, JODINA,* AND *MYOSCHILOS*

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ABSTRACT

Study of the wood of *Acanthosyris, Jodina,* and *Myoschilos* confirmed a close relationship between Santalaceae and Olacaceae. Features important for defining the three genera and for determining relationships between them and with *Schoepfia,* which belongs to Olacaceae, are reported for the first time: vestured vessel walls, unilaterally compound pits, perforated ray cells, and druses.

Key words: *Acanthosyris, Jodina, Myoschilos,* Santalaceae, systematic wood anatomy.

INTRODUCTION

The objective of this paper is to provide new information about the wood anatomy of the genera *Acanthosyris* Griseb., *Jodina* Hook. & Arn., and *Myoschilos* Ruiz & Pavon, members of Santalaceae. This research is part of a wood anatomical study of the entire family with the goal of understanding phylogenetic relationships. Santalaceae consist of 30 genera with approximately 400 species of trees, shrubs, and semiparasitic herbs widely distributed in tropical and temperate regions of both hemispheres (Willis 1985). *Acanthosyris* is a small genus, with only three species. *Acanthosyris glabrata* (Stapf) H. V. Stauffer is indigenous to Ecuador and Colombia (Stauffer 1961); *A. falcata* Griseb. and *A. spinescens* (Mart. & Eichl.) Griseb. occur in Argentina, Bolivia, Paraguay, and southern Brazil (Dawson 1944; Ulibarri 1987). *Jodina* is monotypic; *J. rhombifolia* (Hook. & Arn.) Reissek is very common in Argentina, Brazil, Uruguay, Paraguay, and Bolivia (Dawson 1944). The genus *Myoschilos* has only one species, *M. oblongum* Ruiz & Pavon distributed in the southern Andean region of Chile and Argentina (Dawson 1984).

MATERIALS AND METHODS

Wood samples were available in dried condition. They were boiled in water, stored in 50% aqueous ethyl alcohol, and softened in ethylenediamine (Kukachka 1977) prior to being sectioned. Sections were prepared on 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, sputtercoated with gold, and examined with an ISI WB-6 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). Terms used in the descriptions follow the IAWA list of microscopic features for hardwood identification (1989). 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, 1991), and then the locality. The sources of the specimens studied are as follows:

Acanthosyris glabrata: *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: *Venturi 952* (*LILw*), Tucumán Prov., Argentina; (*SJRw 1113*), Argentina; *Novarrez s. n.* (*SJRw 15012*), Buenos Aires Prov., Argentina.

Acanthosyris spinescens: Division Forestal (*BAw*), Argentina; *Norverto 16, 17, 18* (*BAw*), Entre Rios Prov., Argentina.

Jodina rhombifolia: *Mantese s. n.* (*BAw 55899, 55901, 55903*), Chaco Prov., Argentina; *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; (*USw 4184*), Catamarca Prov., Argentina.

Myoschilos oblongum: *Brion s. n.* (*BAw 144*), Rio Negro Prov., Argentina; *Rothkugel s. n.* (*SJRw 1744*), Patagonia, Argentina; *Bullock s. n.* (*USw 15356*), Chile.

ANATOMICAL DESCRIPTIONS

Acanthosyris

Growth ring boundaries indistinct or absent (Fig. 1, 7, 11). Wood diffuse porous. Vessels numerous, except in *A. glabrata,* more or less evenly distributed with tendency to radial pattern, especially in young stems. Vessel groupings in radial multiples of 2–7 cells, in clusters and sometimes solitary (Fig. 1, 7, 11). Solitary vessel outline angular to circular. Tangential diameter of vessel lumina small (Table 1). Perforation plates simple, oblique to horizontal. Tails of vessel elements, when present, very short. Intervessel pits opposite, circular, alternate to elliptic and polygonal alternate, large (Fig. 10a), very small in *A. glabrata* (Fig. 3); inner apertures elliptic or slitlike, equaling or exceeding the borders, sometimes coalescent (Fig. 10a, 29, 31). Vessel-to-ray pit pairs larger than the corresponding intervessel pits, often transversely elongate; borders greatly reduced, very nearly simple; unilaterally compound in *A. glabrata* (Fig. 5, 10b, 25, 30, 32). Vessel-to-parenchyma pits similar to vessel-to-ray pits in size and shape (Fig. 4, 5, 10b). Vessel walls helically thickened in *A. glabrata* (Fig. 32), helically thickened and vestured in *A. spinescens* (Fig. 26, 27). Vessel element lengths short to moderate sized (Table 1). Tyloses in *A. falcata* and *A. spinescens* (Fig. 28). Libriform fibers moderate to very long (Table 1), very thick walled, lignified, and with simple pits. Fiber-tracheids thin to thick walled with distinctly bordered pits with elongate apertures. Axial parenchyma different in the three species: in *A. spinescens* diffuse apotracheal and principally scanty paratracheal (Fig. 11), 2–4 cells per parenchyma strand; in *A. falcata* diffuse apotracheal, scanty paratracheal and in terminal bands (Fig. 7), 2–5 cells per parenchyma strand; and in *A. glabrata* confluent paratracheal (Fig. 1). Usually with disjunctive axial parenchyma cell walls. Rays Kribs' Type heterogeneous to homogeneous II in *A. falcata* and *A. spinescens.* In *A. falcata* (Fig. 8) multiseriate rays 3–4 cells wide and 696 μm tall whereas in *A. spinescens* (Fig. 12) rays 4–6 cells wide and 663 μm tall. Rays Kribs' Type heterogeneous to homogeneous I in *A. glabrata,* uniseriate rays 133 μm tall and multiseriate rays

Table 1. Frequency and dimensions of vessels, rays, and fibrous tissue.

Species	1	2	3	4	5	6
A. falcata	10 ± 1.7	75 ± 17	41 ± 14	265 ± 66	696 ± 191	1355 ± 259
A. glabrata	5.2 ± 0.8	76.7 ± 18	31 ± 12	361.2 ± 104.3	$990^m \pm 503^m$ $133.3^u \pm 50^u$	1777 ± 228.3
A. spinescens	10 ± 1.7	57 ± 20	58 ± 20	209 ± 51.3	663 ± 224	1020 ± 307
J. rhombifolia	7 ± 1.4	20 ± 3.9	152 ± 88	266 ± 67.6	1023 ± 454.6	991.2 ± 168
M. oblongum	9 ± 2	32 ± 6.7	127 ± 60	163.5 ± 35.5	$346.2^m \pm 127$ $127.5^u \pm 82$	683.5 ± 89

Key to columns: 1, mean intervessel pit, μm; 2, mean tangential diameter of vessel lumina, μm; 3, mean number of vessels per mm^2; 4, mean vessel element length, μm; 5, mean ray height, μm; 6, mean fiber length, μm (± = Standard Deviation; ^{u} = uniseriate; ^{m} = multiseriate).

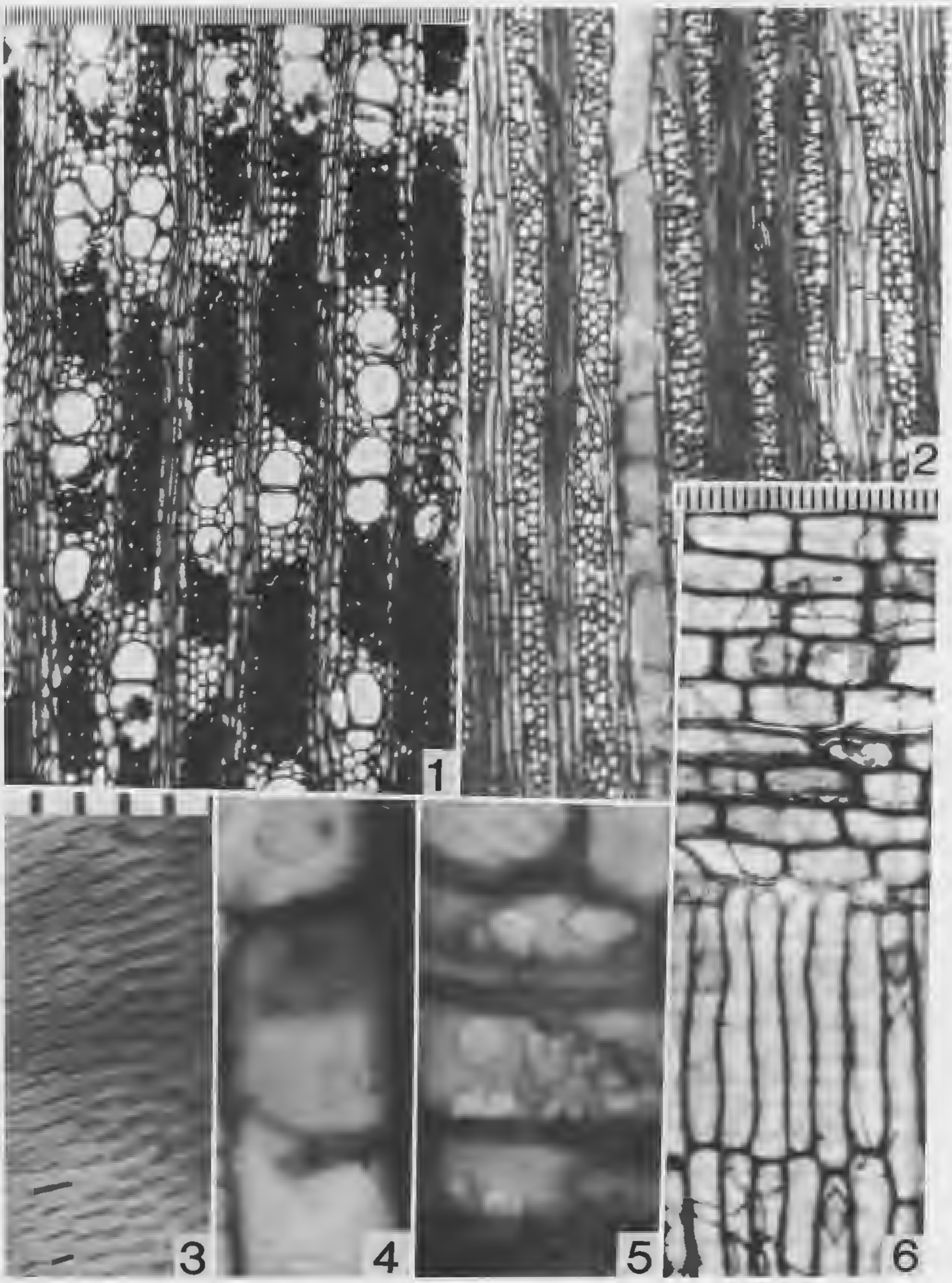

Fig. 1–6. Wood sections of *A. glabrata* (*SJRw 28414*).—1. Transection; axial parenchyma confluent.—2–4. Tangential section.—2. Tall rays.—3. Intervessel pits.—4. Parenchyma-to-vessel pits.—5–6. Radial section.—5. Vessel-to-ray pits.—6. Rhomboidal crystals in axial parenchyma. (Fig. 1–2, magnification scale above Fig. 1 [divisions = 10 μm]; Fig. 3–5, scale above Fig. 3 [divisions = 10 μm]; Fig. 6 [divisions = 10 μm].)

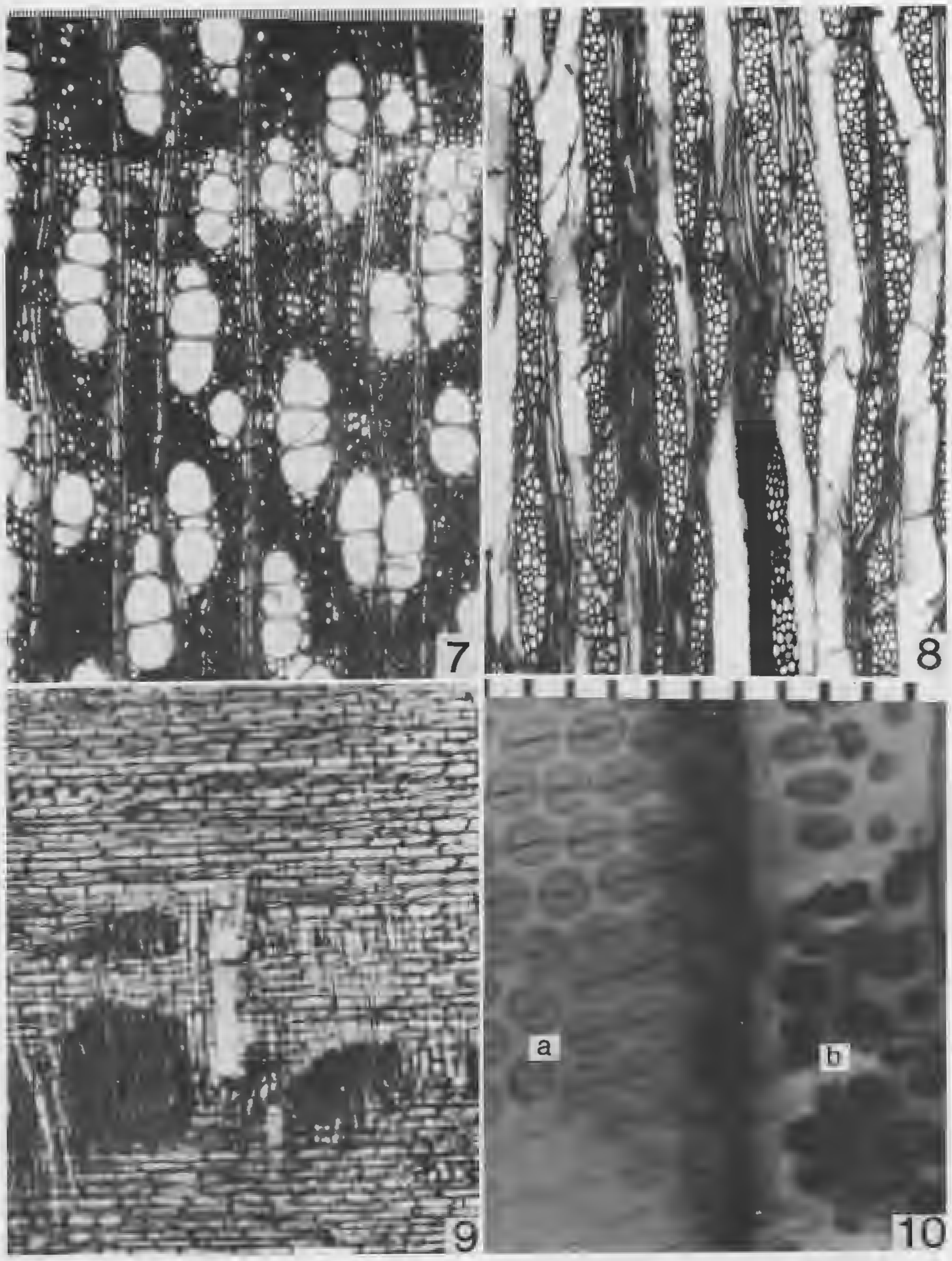

Fig. 7–10. Wood sections of *A. falcata* (*SJRw 15012*).—7. Transection; axial parenchyma in marginal bands.—8. Tangential section; multiseriate rays.—9–10. Radial section.—9. Procumbent cells.—10. a. Intervessel pits with coalescent apertures; b. Vessel-to-vessel ray pits. (Fig. 7–9, magnification scale above Fig. 7 [divisions = 10 μm]; Fig. 10 [divisions = 10 μm].)

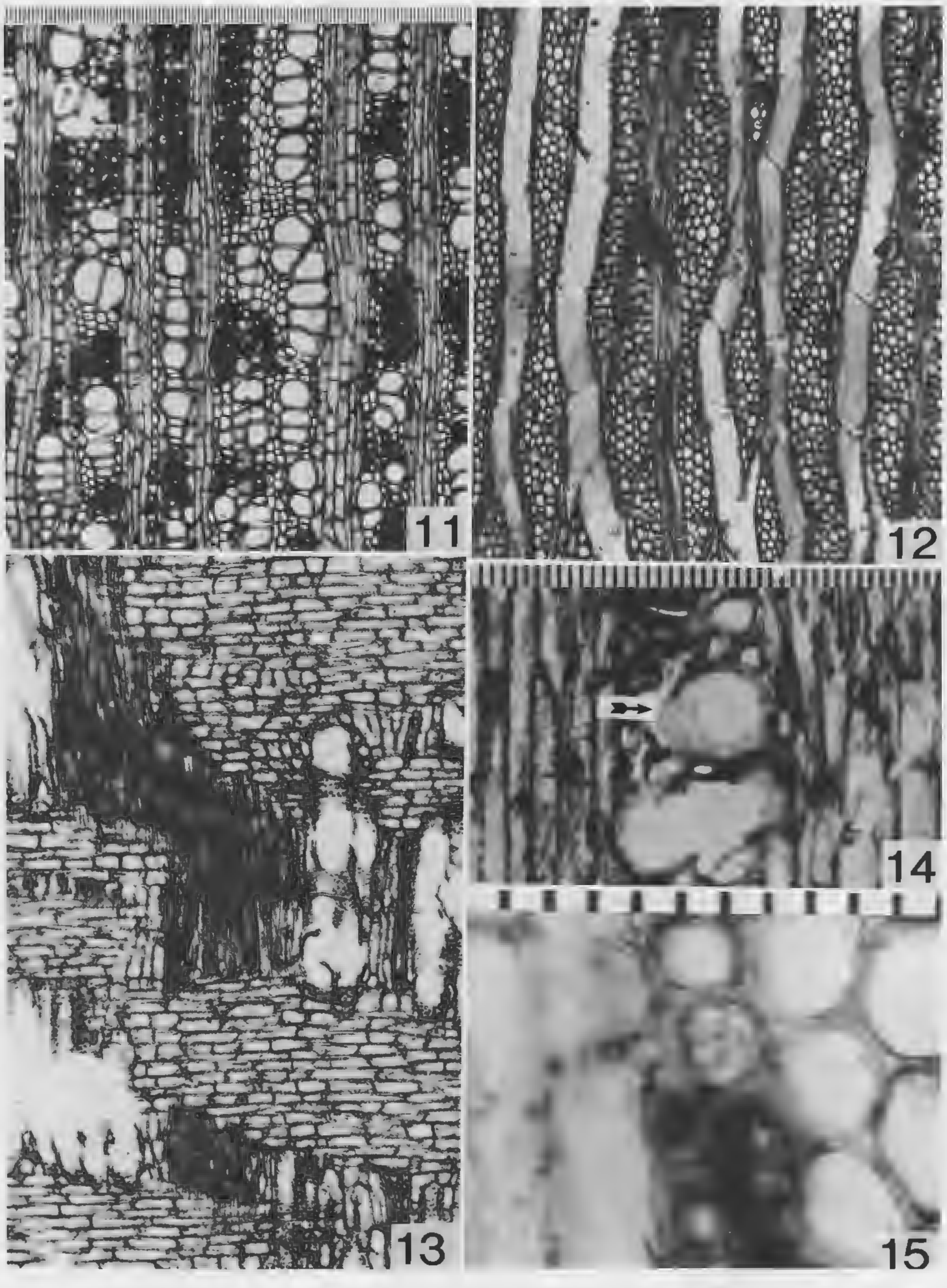

Fig. 11–15. Wood sections of *A. spinescens* (*Norverto 16* [*BAw*]).—11. Transection; vessels are mostly in radial multiples, in clusters and solitary.—12. Tangential section; multiseriate rays.—13–14. Radial section.—13. Procumbent, square and upright cells.—14. Perforated ray cells.—15. Druses in axial parenchyma cells. (Fig. 11–13, magnification scale above Fig. 11 [divisions = 10 μm]; Fig. 14, [divisions = 10 μm]; Fig. 15 [divisions = 10 μm].)

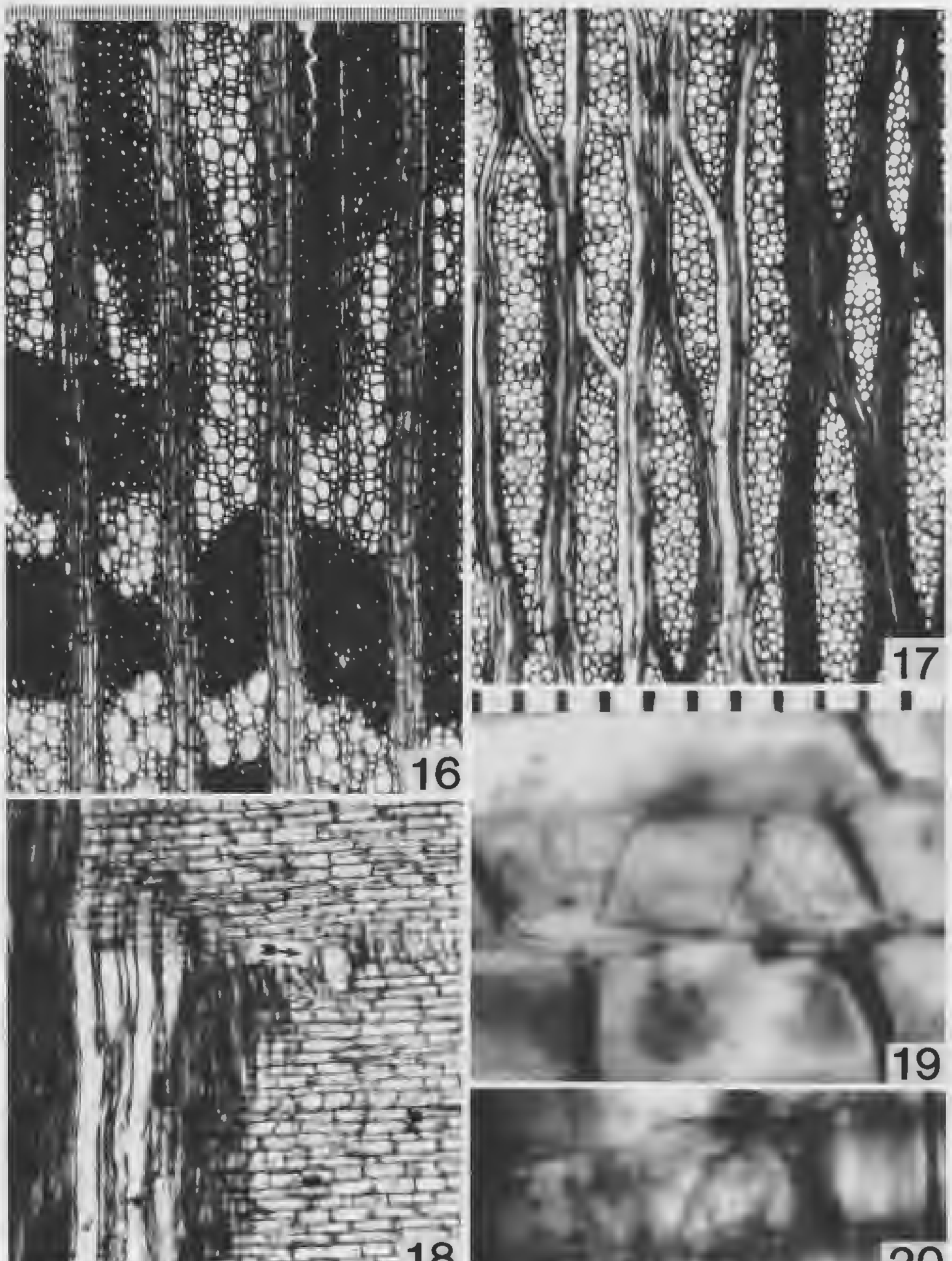

Fig. 16–20. Wood sections of *J. rhombifolia* (Fig. 16–18, *Norverto 18* [*BAw*]; Fig. 19–20, *KW 15425*).—16. Transection; vessels dendritic pattern.—17. Tangential section; tall multiseriate rays.—18. Radial section; perforated ray cell.—19. Rhomboidal (prismatic) crystals and fragments of crystals in procumbent ray cells.—20. Druses in ray parenchyma cells. (Fig. 16–18, magnification scale above Fig. 16 [divisions = 10 μm]; Fig. 19–20, scale above Fig. 19 [divisions = 10 μm].)

2–4 cells wide and 990 μm tall (Fig. 2). Most rays in the three species homocellular, composed exclusively of procumbent cells (Fig. 6, 9). There are also some heterocellular rays composed of procumbent, square and upright cells (Fig. 13). Perforated ray cells very frequent in *A. spinescens* and *A. falcata* (Fig. 14). Rays approximately 1 mm tall, taller in *A. glabrata* (Table 1). Rays and axial elements irregularly storied. In radial parenchyma prismatic calcium oxalate crystals are common in all three species (Fig. 6, 39). In *A. glabrata* crystals also in the axial parenchyma (Fig. 6). In *A. spinescens* druses in axial parenchyma cells (Fig. 15).

Jodina rhombifolia

Growth ring boundaries absent. Wood diffuse porous, sometimes slightly semi-ring-porous (Fig. 16). Vessels in dendritic pattern; very numerous; vessel outline angular (Fig. 16). Perforation plates simple (Fig. 37). Tangential diameter of vessel lumina very small (Table 1). Perforation plates very oblique. Tails present on all vessel elements, moderately long. Intervessel pits opposite to alternate, small; inner apertures elliptic and included. Vessel-to-ray pit pairs larger than the corresponding intervessel pits, often transversely elongate; borders greatly reduced, appearing to be simple. Vessel-to-parenchyma pits similar to vessel-to-ray pits in size and shape. Helical thickenings present in vessel elements (Fig. 35). Vessel element lengths moderate sized (Table 1). Tyloses present. Vasicentric tracheids with helical thickenings in the walls, and bordered pits (Fig. 36). Libriform fiber length moderate (Table 1), very thick walled, lignified and with simple pits. Fiber-tracheids with thin to thick walls and with bordered pits of extended apertures. Axial parenchyma principally scanty paratracheal and diffuse apotracheal (Fig. 16), two cells per parenchyma strand. Rays Kribs' Type heterogeneous to homogeneous II, with multiseriate rays usually 2–4 cells wide, but sometimes 5–6 cells wide, and 1023 μm tall (Fig. 17). Rays heterocellular, composed of procumbent, square and upright cells. Perforated ray cells present (Fig. 18). Rays commonly larger than 1 mm (Table 1). Storied structure absent. Prismatic calcium oxalate crystals and druses present in ray cells (Fig. 19, 20, 38).

Myoschilos oblongum

Growth ring boundaries distinct. Wood semi-ring-porous (Fig. 21). Vessels in dendritic pattern, very numerous. Vessel groupings in short radial multiples of 2–4, clusters, and solitary (Fig. 21). Vessel outline slightly angular. Simple perforation plates. Tangential diameter of vessel lumina very small (Table 1). Perforation plates very oblique. Tails, when present on vessel elements, short to moderately long. Intervessel pits scalariform, opposite and alternate, medium sized (Table 1); inner apertures elliptic (Fig. 34) and included. Vessel-to-ray pit pairs mostly shorter than the corresponding intervessel pits, often unilaterally compound (Fig. 24). Vessel-to-parenchyma pits similar to vessel-to-ray pits in size and shape. Helical thickenings only in narrower vessel elements (Fig. 33). Vessel elements moderately short (Table 1). Vasicentric tracheids with helical thickenings on the walls. Axial parenchyma scanty paratracheal and diffuse apotracheal, two cells per parenchyma strand. Rays Kribs' Type heterogeneous to homogeneous I, with multiseriate rays 4–5 cells wide and 346 μm tall and uniseriate rays 127 μm tall (Fig. 22). Ray composed of procumbent cells, with a few

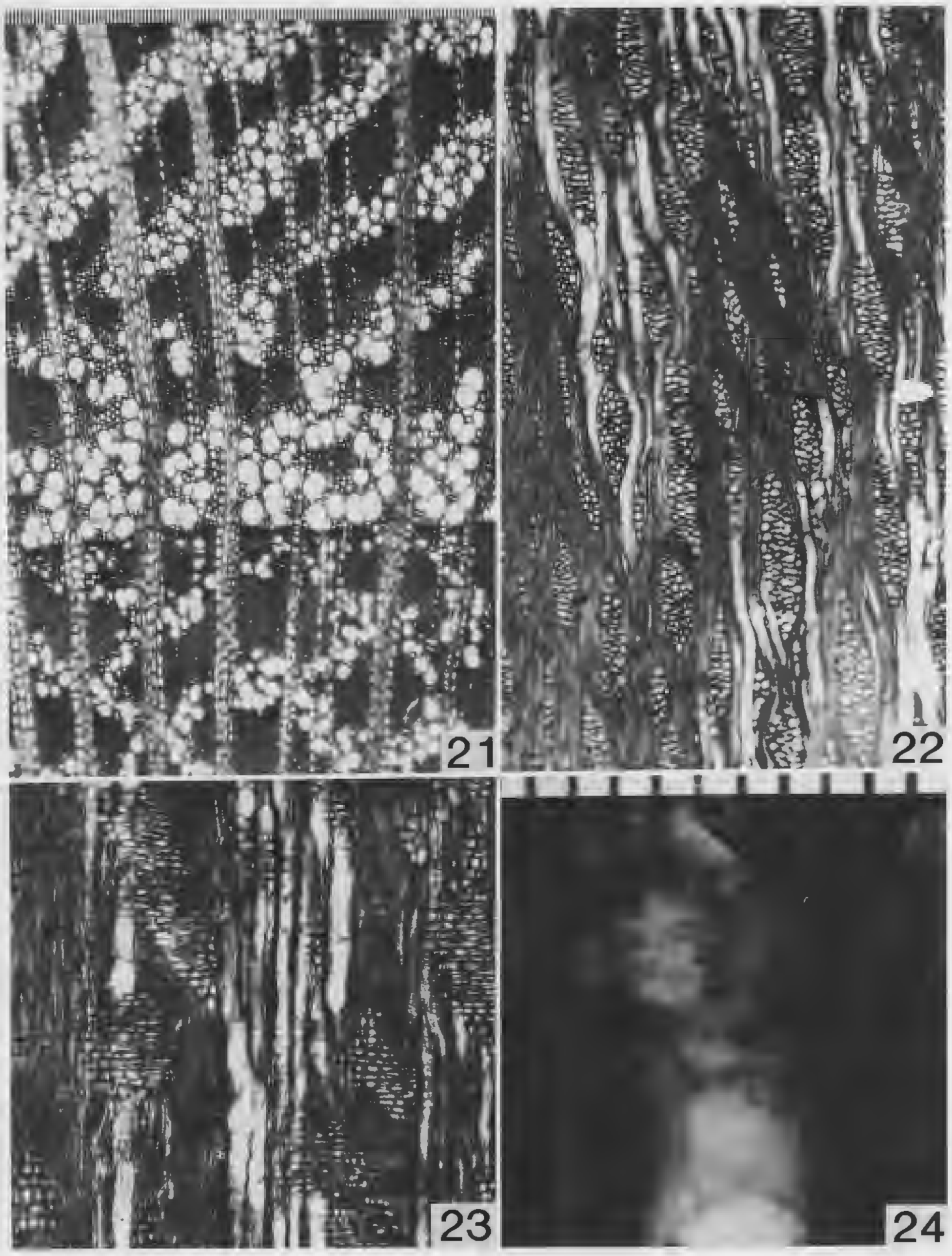

Fig. 21–24. Wood sections of *M. oblongum* (*SJRw 52681*).—21. Transection; semi-ring-porous.—22. Tangential section; both multiseriate and uniseriate rays.—23–24. Radial section.—23. Procumbent, square and upright cells.—24. Vessel-to-ray pits unilaterally compound. (Fig. 21–23, magnification scale above Fig. 21 [divisions = 10 μm]; Fig. 24 [divisions = 10 μm].)

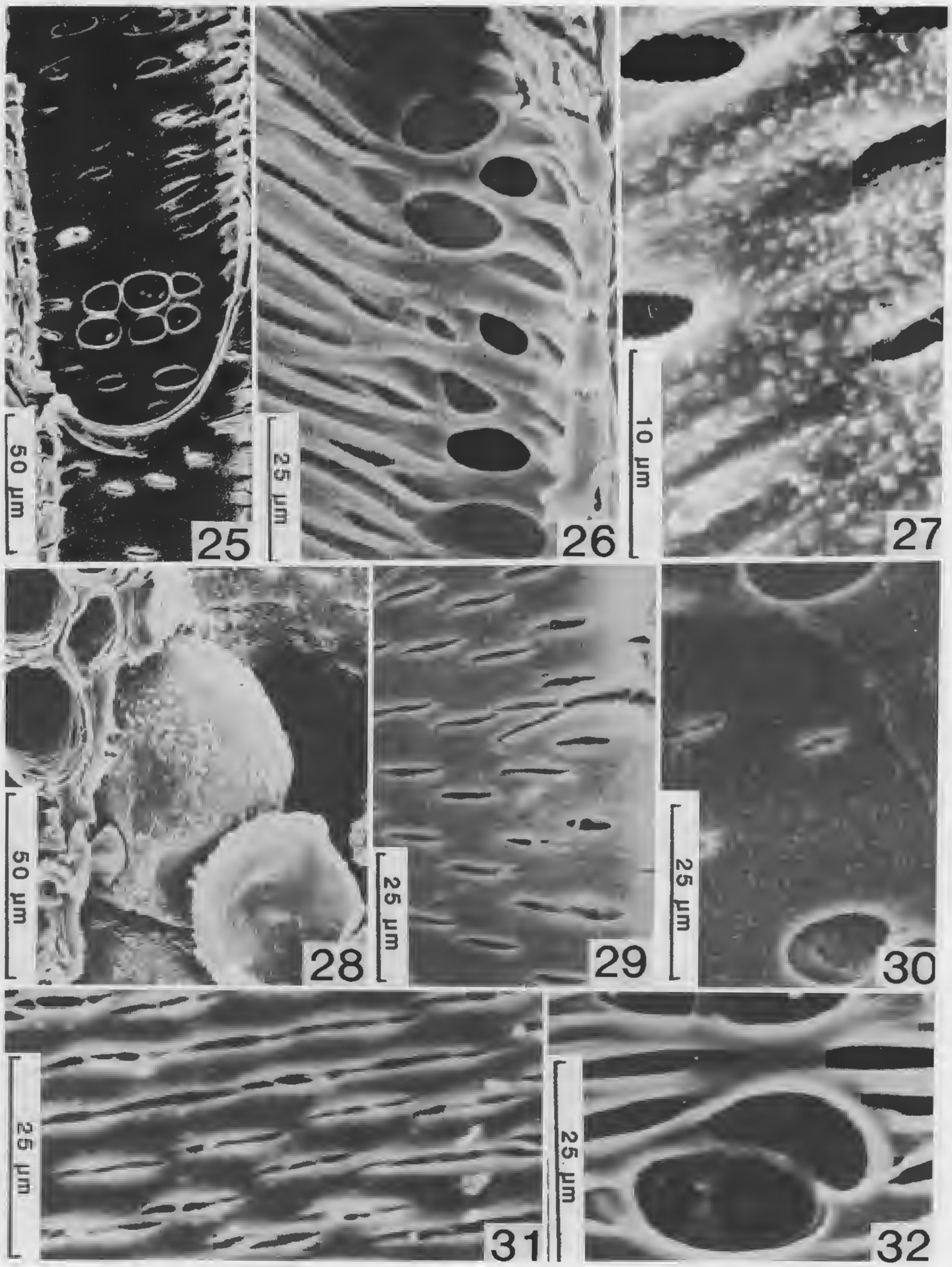

Fig. 25–32. SEM photographs of wood sections of *Acanthosyris* species.—25–28. *A. spinescens* (*Norverto 18* [*BAw*]).—25. Vessels from radial section.—26. Helical thickenings in vessel elements.—27. Vestured walls in vessels.—28. Tyloses in vessel from tangential section.—29–30. *A. falcata* (*MADw 15012*); vessel walls from radial section.—31–32. *A. glabrata* (*SJRw 28414*).—31. Coalescent apertures.—32. Helical thickenings in vessel elements.

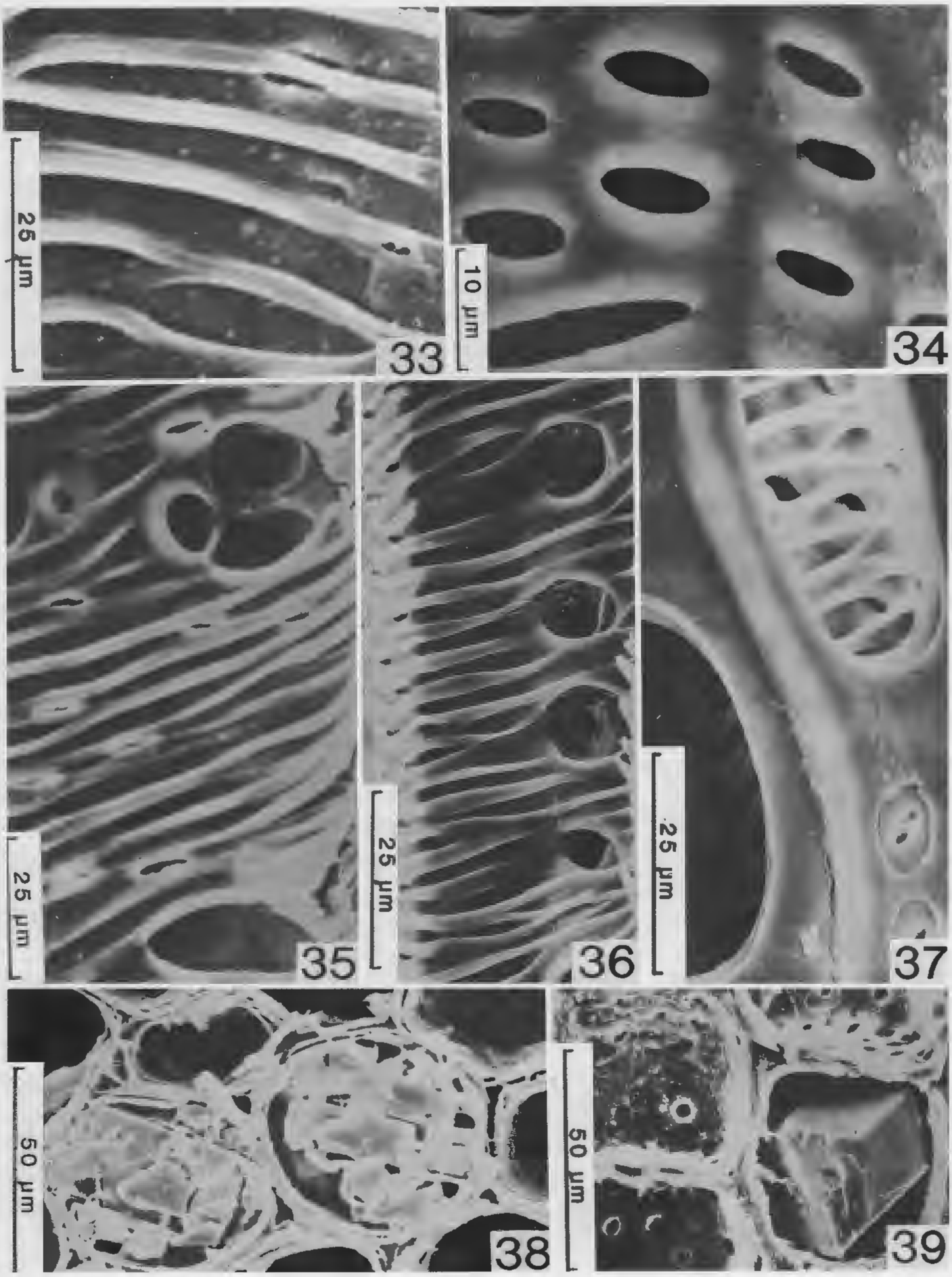

Fig. 33–39. SEM photographs of wood sections.—33–34. *M. oblongum* (*BAw 144*); wall vessels from radial section.—35–38. *J. rhombifolia* (*BAw 75953*).—35. Helical thickenings in vessel elements.—36. Helical thickenings in tracheids.—37. Simple perforation plates.—38. Prismatic crystals and fragments of crystals in ray cells.—39. *A. spinescens* (*Norverto 18* [*BAw*]); rhomboidal crystals in ray cells.

square and upright cells (Fig. 23). Perforated ray cells present. Three rays per mm (Table 1). Storied structure absent. Mineral inclusions absent.

DISCUSSION AND CONCLUSIONS

In this paper the following features are reported for the first time: spiral thickenings in *Acanthosyris glabrata* and *Myoschilos oblongum*; vestured walls in vessels in *A. spinescens*; vessel-to-ray and vessel-to-parenchyma pits unilaterally compound in *A. glabrata* and *M. oblongum*; perforated ray cells in the three genera; and druses in *Jodina rhombifolia* and *A. spinescens*. Of the features listed above those reported for the first time for Santalaceae are: vestures on vessel walls and druses. Perforated ray cells were also reported in *Scleropyrum* Arn. and *Pyrularia* Michx. (Rao, Sharma, and Dayal 1984). These two genera are closely related to *Acanthosyris, Jodina,* and *Myoschilos,* and form a subgroup within Santalaceae (Swamy 1949; Metcalfe and Chalk 1950). According to Swamy (1949), the genus *Calyptosepalum* S. Moore must be excluded from Santalaceae because it has features closer to those of Olacaceae, e.g., vessel-to-parenchyma pits unilaterally compound, vessel elements long (840 μm), and perforation plates scalariform. Patel (1974) also reported scalariform perforation plates in *Mida salicifolia* A. Cunn. These observations together with the new features reported in the present paper appear in several species of Olacaceae. Features reported in both families include: perforated ray cells (Chalk and Chattaway 1933); large vessel-to-ray and vessel-to-parenchyma pits, sometimes unilaterally compound; fiber-tracheids and vasicentric tracheids present (Metcalfe and Chalk 1950). These similarities confirm the strong relationship between Olacaceae and Santalaceae claimed by Kuijt (1968). The genus *Schoepfia* Schreb. is considered the most specialized of Olacaceae (Metcalfe and Chalk 1950). This genus has many anatomical features like those of *A. glabrata* such as confluent axial parenchyma and multiseriate and homogeneous rays.

Acanthosyris is the most specialized of the three genera (Dickison 1975). Within this genus *A. spinescens* and *A. falcata* are very similar.

The vessel-to-ray pits are variable from small and circular to very large and irregular (Record and Hess 1943). This feature was also observed in other species of Santalaceae (Swamy 1949; Metcalfe and Chalk 1950; Meylan and Butterfield 1978). Sheath cells in the rays of *Acanthosyris* were not observed although they were reported by Metcalfe and Chalk (1950). The rays of *Jodina rhombifolia* increase in size during development, as reported in various dicotyledons by Barghoorn (1941) and Carlquist (1988). Cozzo (1946) did not include *J. rhombifolia* in a list of genera with tall rays, very likely because he studied younger wood samples.

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