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WOOD ANATOMY OF RESEDACEAE

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ABSTRACT

Quantitative and qualitative data are presented for seven species of four genera of Resedaceae. Newly reported for the family are helical striations in vessels, vasicentric and marginal axial parenchyma, procumbent ray cells, and perforated ray cells. Wood features of Resedaceae may be found in one or more of the families of Capparales close to it (Brassicaceae, Capparaceae, Tovariaceae). Lack of borders on pits of imperforate tracheary elements is likely a derived character state. Wood of *Reseda* is more nearly juvenile than that of the other genera in ray histology; this corresponds to the herbaceousness of *Reseda*. The quantitative features of wood of Resedaceae are intermediate between those of dicotyledonous annuals and those of dicotyledonous desert shrubs. Wood of Resedaceae appears especially xeromorphic in narrowness of vessels, a fact related to the subdesert habitats of shrubby species and to the dry conditions in which annual or short-lived perennial Resedaceae flower and fruit.

Key words: Capparales, ecological wood anatomy, glucosinolate families, systematic wood anatomy, xeromorphy.

INTRODUCTION

The families that contain glucosinolates may be regarded as an expanded version of Capparales (thereby, Capparales *sensu lato*) with the exception of *Drypetes* of the Euphorbiaceae (Rodman 1991a, b; Rodman et al. 1993, 1996). These families have attracted attention in recent years as a spectacular instance of redefinition of a natural group using cladistics and data from DNA studies (Rodman 1991a, b; Rodman et al. 1993; Conti et al. 1996). The traditional Capparales included Brassicaceae, Capparaceae, Resedaceae, and Tovariaceae. To those families these authors have added Akaniaceae (but see Tobe and Raven 1995; Doweld 1996), Bataceae, Bretschneideraceae, Caricaceae, Gyrostemonaceae, Koerberliniaceae, Limnanthaceae, Moringaceae, Pentadiplandraceae, Salvadoraceae, and Tropaeolaceae. A monotypic genus originally described in Capparaceae, *Setchellanthus* Brandege, is currently under study by various workers, and may be treated as a segregate family within Capparales.

Only a little information has hitherto been contributed on wood of Resedaceae (Metcalf and Chalk 1950; Schweingruber 1990). Numerous papers have dealt with wood of Capparaceae (e.g., Stern et al. 1963), but that family is still poorly covered with respect to wood anatomy. There have been recent contributions on wood anatomy of Akaniaceae and Bretschneideraceae (Carlquist 1996); Bataceae and Gyrostemonaceae (Carlquist 1978); Brassicaceae (Carlquist 1971); Koerberliniaceae (Gibson 1979); Limnanthaceae

and Tropaeolaceae (Carlquist and Donald 1996); Salvadoraceae (Den Outer and van Veenendaal 1981); and Tovariaceae (Carlquist 1985). Studies on wood anatomy of Caricaceae and Moringaceae are currently in progress. When the series has been completed, wood data will be summarized and the diversity analyzed. Wood anatomy of Resedaceae is potentially of interest in assessing the closeness of Resedaceae to Brassicaceae, Capparaceae, Gyrostemonaceae, and Tovariaceae, and some aspects of this potential relationship will be considered here.

Capparales *sensu lato* are diverse in habit. Resedaceae range from annuals or facultative perennials (*Caylusea*, *Oligomeris*, *Reseda*), to shrubs (*Ochradenus*, *Randonia*), or subshrubs (*Sesamoides*, formerly known as *Astrocarpus*). Data on habit and many other features of the family are well summarized by Bolle (1936). Resedaceae offer an excellent opportunity to study the differences in wood anatomy between herbs and shrubs.

Most short-lived perennials are considered mesomorphic, but some herbs of short to medium duration, like those in Resedaceae, flower and fruit as soil dries. The shrubs *Caylusea hexandra* and *Ochradenus bacatus* are from semidesert areas of Morocco and Iran, respectively. One might expect such shrubs to have wood more xeromorphic than that of herbs. Quantitative wood data are excellent for showing whether or not this is true, and these are used in comparing Resedaceae to dicotyledons at large.

MATERIALS AND METHODS

The material of *Reseda crystallina* was taken from cultivated specimens and preserved in 50% ethanol.

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Plants of this facultative annual were grown from seeds provided by the Copenhagen Botanical Garden and were cultivated in Santa Barbara, where they survived into a second growing season because of mild conditions.

Although larger wood samples of *Caylusea* and *Ochradenus* could doubtless be obtained from plants in the wild, stems of the cultivated *R. crystallina* and of the herbarium specimens of the remaining species studied here likely represent nearly maximal wood accumulation for these latter species. Dried material was boiled in water and stored in 50% aqueous ethanol. Stems of *R. crystallina* were fixed in 50% aqueous ethanol. Material stored in alcohol was treated with ethylene diamine, infiltrated, embedded in paraffin, and sectioned on a rotary microtome according to the schedule of Carlquist (1982). Sections were mostly mounted on glass slides and stained with a safranin-fast green combination. Some paraffin sections were retained for study by SEM; they were mounted on aluminum stubs, cleansed of paraffin, and sputter coated with gold. Macerations were prepared with Jeffrey's Solution and stained with safranin.

Collection data of the specimens is as follows: *Caylusea hexagyna* (Forsk.) M. L. Green, Ourzazate, Morocco, *Podlech* 42683 (RSA); *Ochradenus baccatus* Delile, 60 km SE of Bastak, canyon in semidesert, 400 m., Fars, Iran, *M. L. Grant* 16893 (RSA); *Oligomeris linifolia* (Vahl) Macbr., Todos Santos, Baja California, Mexico, *M. E. Jones* 24096 (POM); *Reseda alba* L., adventive, Glendora, California, *Ella M. Kennedy* April 2, 1923 (POM); *R. crystallina* Webb & Berth., cultivated, Santa Barbara, California, *Carlquist* 8171 (SBG); *R. lutea* L., limestone slopes, Malo-Sadovoye, ca. 10 km from Bakhchiserai, Crimea, Ukraine, *Elias* 5842 (RSA); *R. luteola* L., adventive, on Highway 395 near Poway Grade, San Diego County, *Gander* 2415 (RSA).

Terms are in accordance with the IAWA Committee on Nomenclature (1964). Number of vessels per group is computed as a solitary vessel = 1, a pair of vessels in contact = 2, etc. Vessel lumen diameter is used rather than outsider diameter of vessels; for vessels oval in transection, an average diameter was estimated. Pseudoscalariform pitting is defined as alternate pitting in which pits are laterally elongate but in which the tips do not correspond to cell angles.

ANATOMICAL RESULTS

Growth Rings

In the shrubby *Caylusea hexagyna* (Fig. 1), growth rings are present, but difficult to define in terms of parenchyma bands or fiber diameter; vessels are narrower in latewood than in earlywood. Narrow vessels are formed during the first year. Some of the axial

parenchyma bands in the species may be related to growth rings. Among the species that can be called biennials, short-lived perennials, or facultative annuals, growth rings may end in terminal parenchyma, as shown for *Reseda crystallina* (Fig. 7, pale band above center) and *R. lutea* (Fig. 13, dark band near top). In *R. alba* (Fig. 9), a band of axial parenchyma in earlywood of the second year's secondary xylem was observed.

Vessel Elements

The mean number of vessels per group (Table 1, column 1) is moderate compared with dicotyledons at large. Solitary vessels and vessels in groups of two or three are about equally abundant (Fig. 1, 5, 7, 9, 10, 13). The greatest degree of vessel grouping is seen in *Ochradenus baccatus* (Fig. 3). There are occasional radial multiples in *R. alba* (Fig. 9, bottom; Fig. 10, center). There are diagonal bands of vessels in *Oligomeris linifolia* (Fig. 5, 6).

Mean vessel diameter (Table 1, column 2) varies to a moderate degree within the family. *Caylusea hexagyna* has notably narrow vessels (Fig. 5); vessels are only slightly wider in *Oligomeris linifolia* (Fig. 5) and *Reseda crystallina* (Fig. 7). Wide vessels occur in earlywood of *R. lutea* (Fig. 13), but mean diameter is diminished by the presence of narrow latewood vessels. The mean lumen diameter for the family, 25 μm , is much smaller than the mean outside vessel diameter for vessels of dicotyledons at large (94 μm), although the sample Metcalfe and Chalk (1950) used to obtain that figure consisted mainly of woodier species, especially trees.

Vessel density (Table 1, column 3) is relatively uniform in the family except for *Ochradenus baccatus* (Fig. 1) and *Oligomeris linifolia* (Fig. 5). The average for the family as a whole (171 μm) is virtually identical to the figure for a sampling of annuals (162 μm : Carlquist 1975, p. 206).

Vessel element length in Resedaceae (Table 1, column 4) ranges from 95 to 197 μm . This span is not unusual considering the divergent habits of the various species and the fact that wood samples of the shrubs are mostly juvenile wood.

Vessel wall thickness (Table 1, column 5) in Resedaceae is rather narrow (range, 2.0–2.7 μm ; family mean = 2.3 μm) compared to that of dicotyledons as a whole. The thinness of vessel walls is evident in Fig. 9–10; larger vessels are thicker walled, as is typical in dicotyledonous woods.

Axial diameter of pits on lateral walls of vessels (Table 1, column 6) ranges from 3 to 5 μm . Pits of the latter size are shown in Figure 15 for *R. lutea*. Pits are generally alternate and circular in outline in Re-

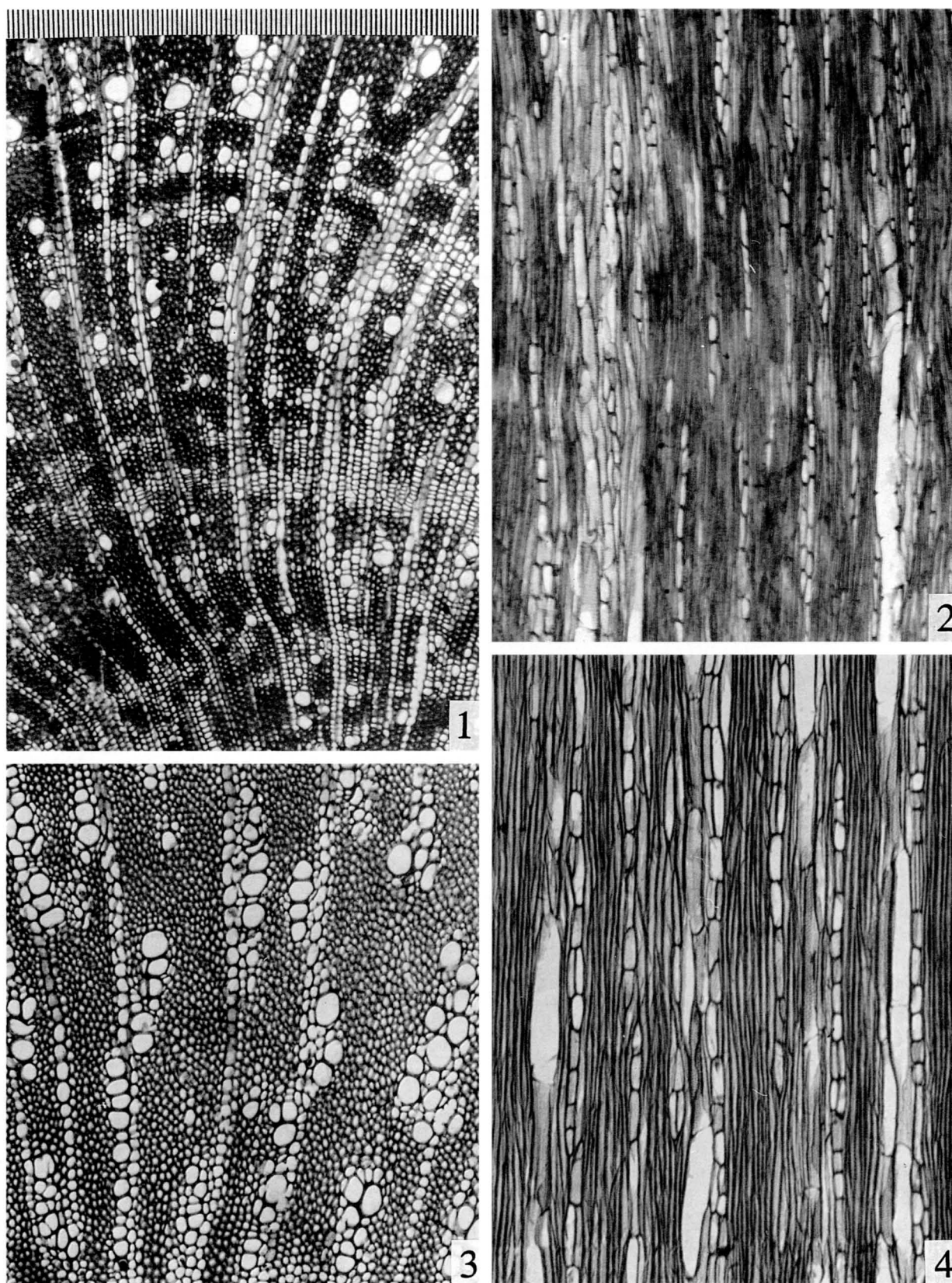


Fig. 1-4. Wood sections of *Caylusea* and *Ochradenus*.—1-2. *C. hexagyna*.—1. Transection; vessels are notably small.—2. Tangential section; rays are mostly uniseriate.—3-4. *O. baccatus*.—3. Transection; vessels are in large radial multiples.—4. Tangential section; rays are biseriate and uniseriate, composed of upright cells. (Fig. 1-4, magnification scale above Fig. 1 [divisions = 10 μ m].)

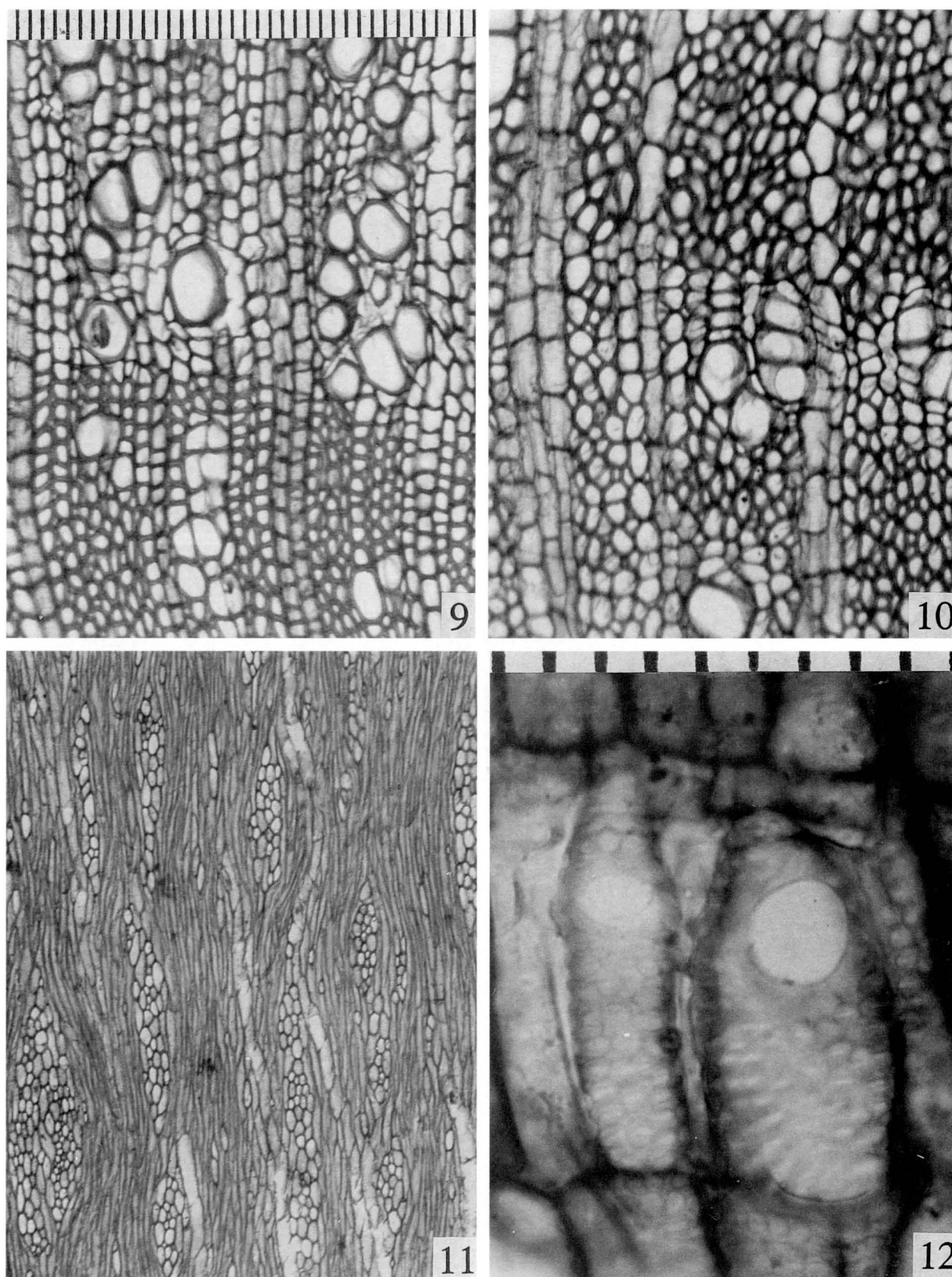


Fig. 9–12. Wood sections of *Reseda alba*.—9–10. Transections.—9. Terminus of first year's growth (center of photograph), beginning of second year's growth; vessels are narrower in the latewood.—10. Area from middle of second year's growth; fibers are wider than in the first year's growth.—11. Tangential section; relatively wide multiseriate rays are common.—12. Two perforated ray cells from a radial section. (Fig. 9–10, scale above Fig. 9 [divisions = 10 μ m]; Fig. 11, scale above Fig. 1; Fig. 12, scale above Fig. 12 [divisions = 10 μ m].)

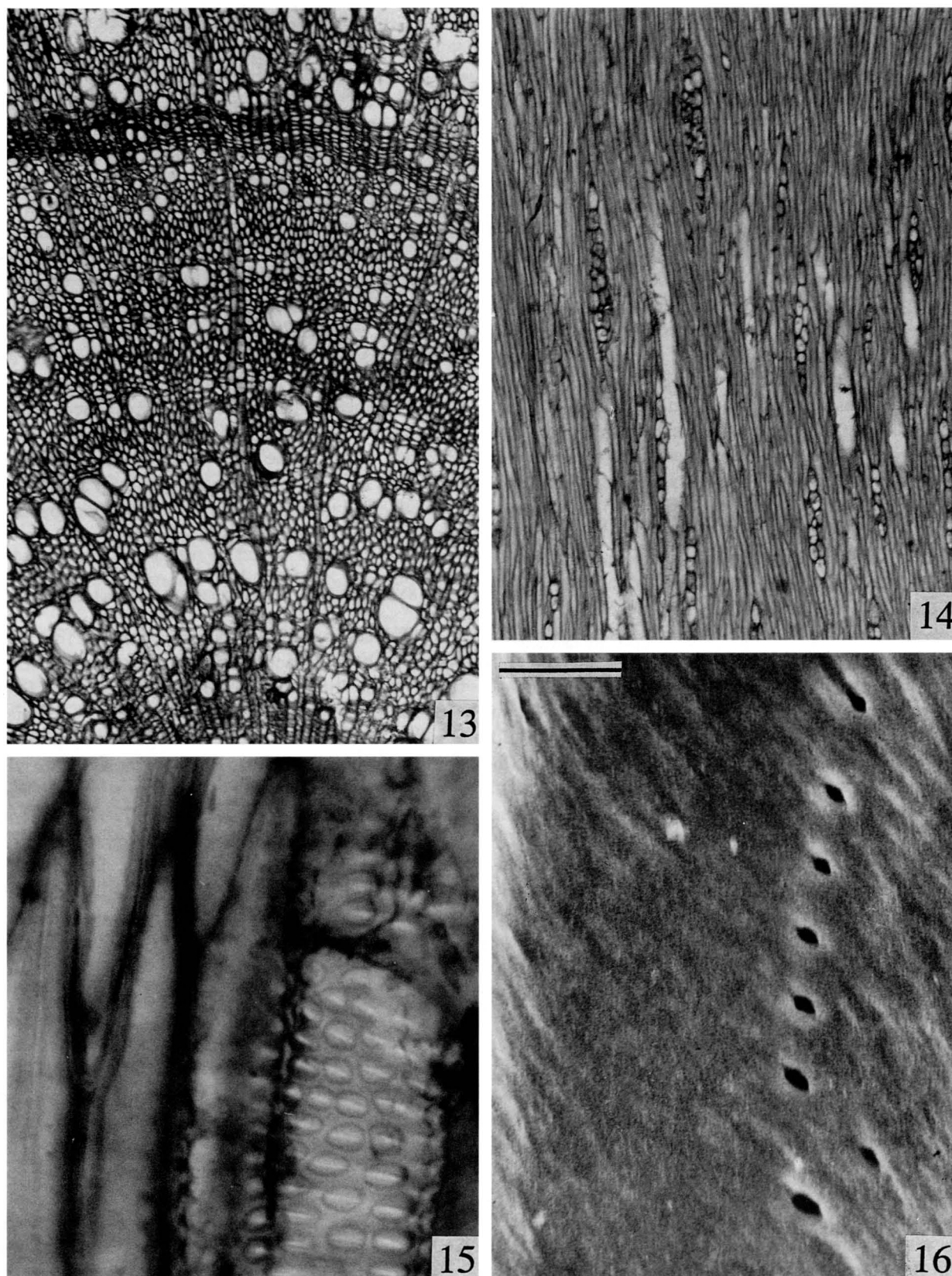


Fig. 13–16. Wood sections of *Reseda lutea* (Fig. 13–15) and *R. luteola* (Fig. 16).—13. Transection; vessels become smaller in diameter in latewood; terminal parenchyma band (top, left) demarcates two years of secondary growth.—14. Tangential section; rays are uniseriate to triseriate.—15. Portion of tangential section to show libriform fibers and, at right, vessel with alternate lateral wall pitting.—16. SEM photograph of vessel wall; striations are present on wall surface. (Fig. 13–14, scale above Fig. 1; Fig. 15, scale above Fig. 12; Fig. 16, bar at upper left = 10 μm .)

observed in imperforate tracheary elements of Resedaceae and Tovariaceae (Carlquist 1985). If the concept that bordered pits are primitive in imperforate tracheary elements of dicotyledons is correct (Metcalf and Chalk 1950, p. xlv), there has been loss of bordered pits in imperforate tracheary elements in the ancestors of Resedaceae and Tovariaceae as well as in the line leading to Akaniaceae and Bretschneideraceae (Carlquist 1996), but borders are preserved in the imperforate tracheary elements of Gyrostemonaceae, Koeberliniaceae (Gibson 1979), and Tropaeolaceae (Carlquist and Donald 1996). Hypothesizing loss of borders on imperforate tracheary elements of Akaniaceae, Bretschneideraceae, Resedaceae, and Tovariaceae would be marginally more parsimonious, because the alternative hypothesis would require acquisition of borders on imperforate tracheary elements of Brassicaceae and Capparaceae (which may be considered as having a common ancestor), as well as in Gyrostemonaceae, Koeberliniaceae, and Tropaeolaceae. Thus far, no evidence has been advanced by wood anatomists for acquisition of borders on pits in imperforate tracheary elements in any phylad of dicotyledons.

Wood features other than vesturing of pits and degree of presence of bordered pits on imperforate tracheary elements are either the same in Resedaceae as in other Capparales (e.g., type of axial parenchyma) or else are features that relate directly to particular habits and habitats (and thus would appear in a cladogram as numerous homoplasies). Additional information on wood of Capparales sensu lato is needed before the phyletic nature of particular character states can be assessed. Such a synthesis will be attempted at the end of this series of papers.

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