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WOOD ANATOMY OF CALYCERACEAE AND VALERIANACEAE, WITH COMMENTS ON ABERRANT PERFORATION PLATES IN PREDOMINANTLY HERBACEOUS GROUPS OF DICOTYLEDONS

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INTRODUCTION

Calyceraceae and Valerianaceae are generally regarded as close to Asteraceae. This treatment can be seen not merely by examining earlier systems, but by comparing the most recent ones as well. Cronquist (1968) and Thorne (1968, 1976) place both Calyceraceae and Valerianaceae in Dipsacales, a group considered to have relationship to Asteraceae, but to have features somewhat more primitive than those of Asteraceae. More recently, Cronquist (1981) segregated Calyceraceae as a monofamilial order, Calycerales, without changing its position in the system. Dahlgren (1980), stressing the presence of iridoid compounds in Calyceraceae as opposed to their absence in Asteraceae and Dipsacales, has relegated Calyceraceae to Gentianales.

Asteraceae, Calyceraceae, Dipsacaceae, and Valerianaceae have many features in common (flowers tetracyclic and pentamerous, stigmas two, calyx reduced to pappus or a pappuslike structure, ovary inferior with a single ovule). In other respects, the four families form a kind of mosaic. Dipsacaceae and Calyceraceae possess endosperm, whereas it is lacking in mature seeds of Asteraceae and Valerianaceae. Calyceraceae and Asteraceae have connate anthers, whereas Dipsacaceae and Valerianceae do not. The ovule in Asteraceae is basal, whereas it is apical in Calyceraceae, Dipsacaceae, and Valerianaceae. The wood of Dipsacaceae (Carlquist 1982a) is less specialized than that of Asteraceae (Carlquist 1966 and the papers cited therein) in having tracheids rather than libriform fibers. The status of wood of Calyceraceae and Valerianaceae in this regard provides an interesting topic for investigation.

Of the four families mentioned, Calyceraceae is comparatively small (60 species according to Cronquist 1968), whereas Asteraceae is quite large and Dipsacaceae (270 spp.) and Valerianaceae (300 spp.) of intermediate size. Calyceraceae can be characterized as exclusively herbaceous, whether perennial or annual. Wood of Calyceraceae is merely that of bases of herbaceous stems. Dipsacaceae and Valerianaceae are somewhat more varied in habit. Dipsacaceae contains some truly shrubby species and may be primitively woody (Carlquist 1982a). Valerianaceae are rarely shrubby, and are at best subshrubs. The latter habit characterizes *Centranthus ruber* (L.) DC. and *Patrinia villosa* Juss., in which stems branch from the basal part of older stems; the new stems root at their bases. These older rooted bases may develop more than one year's accumulation of secondary xylem, and that is what is studied here. The stems studied for *Centranthus ruber* (Fig. 8–10) contained three growth rings. *Valeriana glauca* Poepp. from the matorral of central Chile has little seasonality in growth, and age of stems is difficult to determine. *Valeriana glauca* can be described as semiscandent, sending elongate stems through dense shrubbery and flowering when its stems reach the surface of the shrubs through which they grow.

Because Calyceraceae and Valerianaceae have so little wood, wood anatomy of these families has not been studied very much. Solereder (1906) described vessels of *Centranthus ruber* as having scalariform perforation plates near the primary xylem, with vessels elsewhere provided with simple perforation plates. This description implies study of secondary xylem. Metcalfe and Chalk (1950) add that vessels in Valerianaceae are narrow (less than 25 μm in diameter), vessel elements are short (about 150 μm in length), and vessels as seen in transection occur in radial multiples of 10 or more, rarely in contact with the rays. These authors report large alternate pits in vessels of Valerianaceae. For Calyceraceae, Metcalfe and Chalk report moderately wide circular vessel elements with simple perforations, alternate pitting on lateral walls of vessels, libriform fibers as the imperforate tracheary element type, and wide vascular rays. Secondary growth is evidently absent in *Boopis* (Calyceraceae), in which vascular bundles are embedded in sclerenchyma. Because secondary xylem is very limited in all Calyceraceae in which it occurs to any degree, only a single species was selected for study.

The occurrence of scalariform or aberrant perforation plates in *Patrinia villosa* (Fig. 14–25), with no simple perforation plates in the specimen studied, is curious. The occurrence of these plates recalls similar occurrences in wood of species from predominantly herbaceous groups, such as *Dendroseris* (Asteraceae), *Pentaphragma* (Pentaphragmataceae), and various Campanulaceae. The significance of such perforations in wood of groups of this nature is discussed in a terminal portion of this paper.

MATERIALS AND METHODS

Stems of the species studied were all available in dried form. In view of the tendency of thin-walled ray cells to collapse upon drying (notably in *Centranthus ruber* and *Valeriana glauca*), liquid-preserved material might have resulted in more attractive preparations, but no additional information would likely have been yielded. Wood samples were boiled to remove air. After boiling, the wood sample of *Patrinia villosa* was sectioned on a sliding microtome without any further treatment. The relatively soft texture of woods in the remaining taxa prevented successful sectioning of nonembedded material on a sliding microtome. Therefore, woods of these taxa were softened in ethylenediamine, followed by embedding in paraffin, sectioning on a rotary microtome, and staining of sections in safranin and fast green. This method has been described in detail earlier (Carlquist 1982b).

Herbarium specimens documenting the materials studied for *Calycera sessiliflora* Phil. and *Patrinia villosa* are located at the University of California, Berkeley. Specimens documenting woods of *Centranthus ruber* and *Valeriana glauca* are on file in the herbarium of the Rancho Santa Ana Botanic Garden.

ANATOMICAL DESCRIPTIONS

Calycera sessiliflora (Burkart 18510): Growth ring phenomena not present, but vessels slightly smaller at beginning of secondary growth (Fig. 1). Mean vessel diameter, 53 μm. Vessels solitary or in pairs or small pore multiples, mean number of vessels per group, 1.84. Mean number of vessels per mm^2 = 182. Vessels with simple perforation plates. Lateral walls of vessels with alternate pits, but these pits mostly laterally widened so that a pseudoscalariform pattern may be said to occur (Fig. 4). Mean vessel-element length, 304 μm; mean vessel wall thickness, 2.5 μm. Libriform fibers present as the imperforate tracheary element type. Mean libriform fiber length, 608 μm. Mean diameter of libriform fibers at widest point, 53 μm. Mean libriform fiber wall thickness, 2.5 μm. Axial parenchyma scanty vasicentric. Both multiseriate and uniseriate rays present. Both wider multiseriate rays (derived directly from primary rays) and narrower multiseriate rays present (Fig. 2). Mean height of multiseriate rays in latter category, 902 μm; mean uniseriate ray height, 217 μm. Rays composed of square to upright ray cells only, no procumbent cells present (Fig. 3). Square cells comprising less than 10% of the ray, the balance erect cells. Ray cells thin walled but lignified. Wood nonstoried.

Centranthus ruber (Thorne & Everett 34678): Growth rings present, latewood vessels narrow; a wide band of terminal parenchyma present at the ends of growth rings (Fig. 8). The parenchyma of these growth rings mostly not subdivided and cells the same length as libriform fibers (Fig. 9), very likely the result of the phenomenon known as fiber dimorphism (Carlquist 1958). Mean vessel diameter, 40 μm. Vessels solitary or in small groups; mean number of vessels per group, 1.52. Mean number of vessels per mm^2 = 57. Vessels infrequently in contact with rays, mostly in central part of fascicular areas (Fig. 8). Vessels with simple perforation plates in this material. Lateral walls of vessels with alternate pits. Vessel pits widened laterally so that on some walls (especially narrow ones) a pseudoscalariform appearance is achieved (Fig. 10). Mean vessel-element length, 137 μm; mean vessel wall thickness, 2.5 μm. Libriform fibers present as the imperforate tracheary-element type. Mean libriform fiber length, 196 μm. Mean diameter of li-

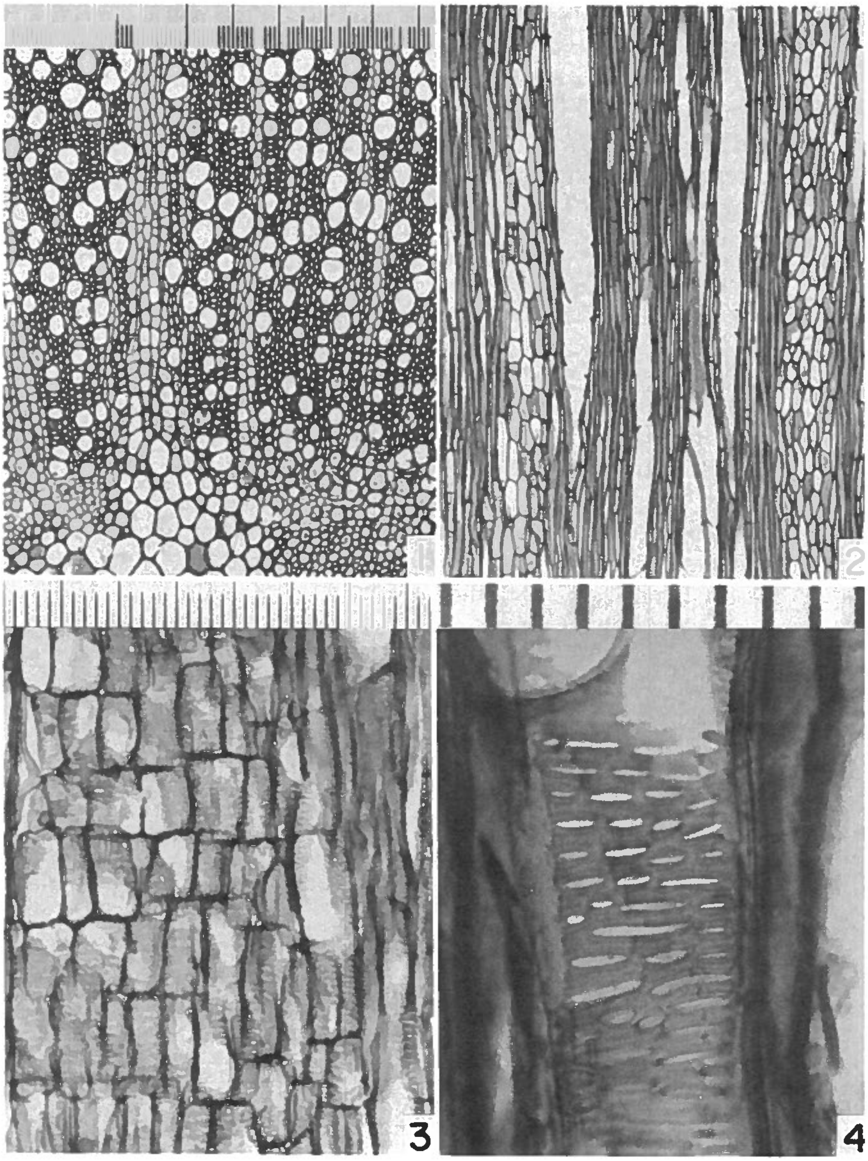

Fig. 1–4. *Calycera sessiliflora* (*Burkart 18510*), wood sections.—1. Transection, pith below.—2. Tangential section; large multiseriate rays which represent little-altered primary rays at left and right.—3. Radial section; all ray cells shown are upright in shape.—4. Vessel wall from radial section; pits are elongate (pseudoscalariform). (Fig. 1, 2, magnification scale above Fig. 1 [finest division = 10 μm]; Fig. 3, scale above Fig. 3 [divisions = 10 μm]; Fig. 4, scale above Fig. 4 [divisions = 10 μm].)

briform fibers at widest point, 1.8 μm. Pits on libriform fibers often elliptical rather than slitlike. Axial parenchyma (other than that of the annual bands) vasicentric scanty. Rays all multiseriate. Most rays more than 5 mm long, representing little-modified primary rays. Ray cell walls thin walled and nonlignified. Wood storied with respect to axial elements (Fig. 9).

Patrinia villosa (Suzuki 445008): Growth rings absent except as minor fluctuations in libriform fiber wall thickness (Fig. 11). Mean vessel diameter, 43 μm. Vessels mostly solitary, mean number of vessels per group, 1.28. Mean number of vessels per mm^2 = 74. Perforations of vessel elements either near-scalariform (Fig. 14, 15) with minor alterations of scalariform conditions (Fig. 16–19, 22–23), considerable alterations of bars (Fig. 20, 21), or with perforations in two rows and pitlike (Fig. 24, 25). No simple perforation plates observed. Perforations slightly bordered to nonbordered. Lateral walls of vessels with alternate pits, many of these widened so that a pseudoscalariform appearance is achieved (Fig. 13). Mean vessel-element length, 443 μm; mean vessel wall thickness, 2.3 μm. Libriform fibers present as the imperforate tracheary element type. Mean libriform fiber length, 649 μm. Mean libriform fiber diameter at widest point, 27 μm. Mean libriform fiber wall thickness, 3.5 μm (thinner in some regions). Axial parenchyma vasicentric scanty, rather infrequent. Rays multiseriate and uniseriate, no wide rays comparable to primary rays in other Valerianaceae present (Fig. 12). Multiseriate rays more abundant than uniseriate rays. Mean height of multiseriate rays, 1239 μm; mean height of uniseriate rays, 256 μm. All ray cells erect (Fig. 12). Ray cells moderately thin but nonlignified. Wood nonstoried.

Valeriana glauca (Carlquist 7260): Growth rings absent (sample with a three-year accumulation of xylem, approximately). Mean vessel diameter, 62 μm. Vessels in large groupings, most of these radially arranged. Mean number of vessels per mm^2 = 243. Vessels mostly in central portion of fascicular areas, infrequently in contact with ray cells. Vessels with simple perforation plates. Lateral walls of vessels with alternate pits, some of these much elongate and mixed with the circular pits (Fig. 7). Mean vessel-element length, 175 μm; mean vessel wall thickness, 1.8 μm. Libriform fibers present as the imperforate tracheary element type. Mean libriform fiber length, 240 μm. Mean libriform fiber diameter at widest point, 37 μm. Most libriform fibers widened in a radial direction (Fig. 5). Mean libriform fiber wall thickness, 2.3 μm. Pits on libriform fibers often elliptical rather than slitlike in shape. Axial parenchyma very scarce, these cells vasicentric. Rays multiseriate exclusively, the rays representing little alteration of the primary rays. Rays chiefly more than 5 mm in height. Ray cells square to erect in shape, the latter more common. Minute rhomboidal crystals, few per cell, observed in ray cells. Ray cells thin walled and nonlignified (Fig. 5, 6). Libriform fibers vaguely storied, the wood otherwise nonstoried.

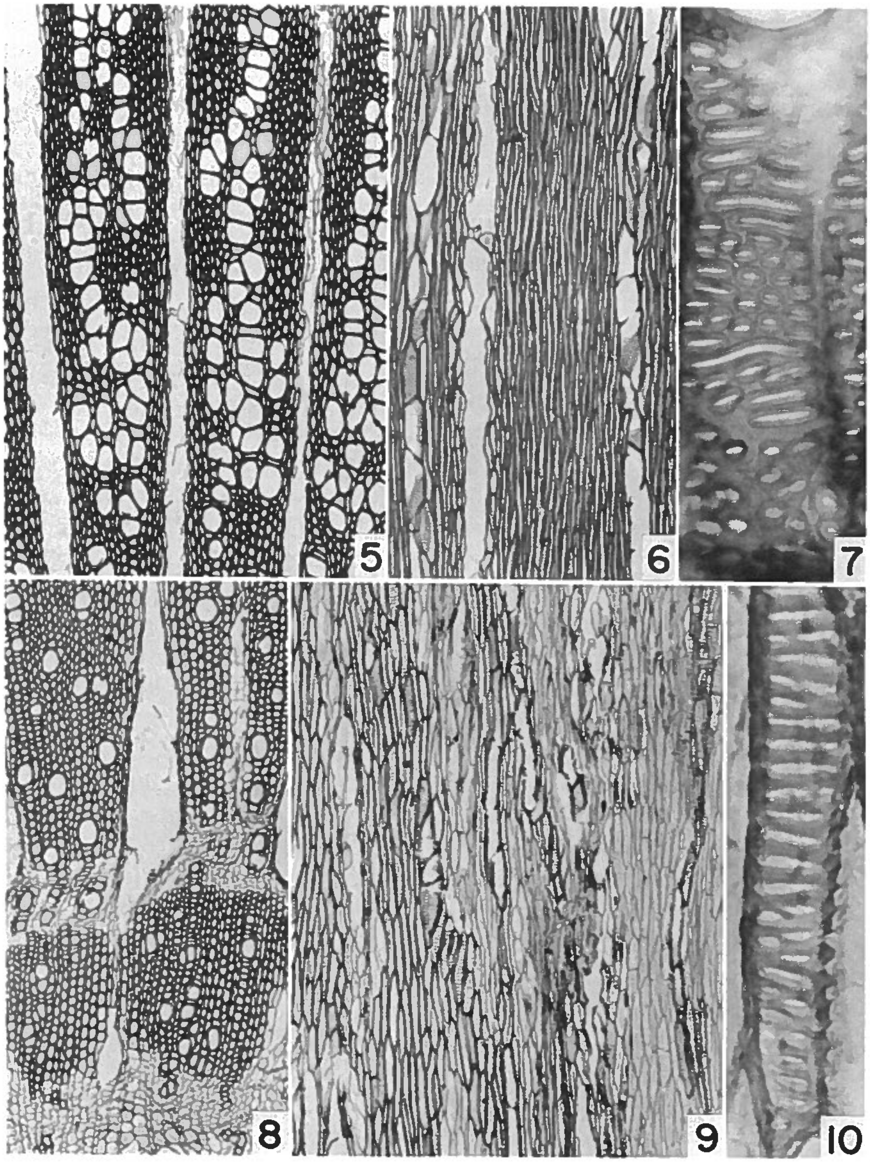

Fig. 5–10. Wood sections of Valerianaceae.—5–7. *Valeriana glauca* (*Carlquist 7260*).—5. Transection; ray cells thin walled, mostly collapsed.—6. Tangential section; incipient storied condition visible.—7. Vessel wall from radial section; pitting pseudoscalariform.—8–10. *Centranthus ruber* (*Thorne & Everett 34678*).—8. Transection; two bands of fiber-free (parenchymatous) xylem seen; thin-walled large rays with shrunken cells.—9. Tangential section; libriform fibers at left, parenchyma at right; storying evident.—10. Vessel wall from parenchymatous portion of radial section. (Fig. 5–6, 8–9, magnification scale above Fig. 1; Fig. 7, 10, scale above Fig. 4.)

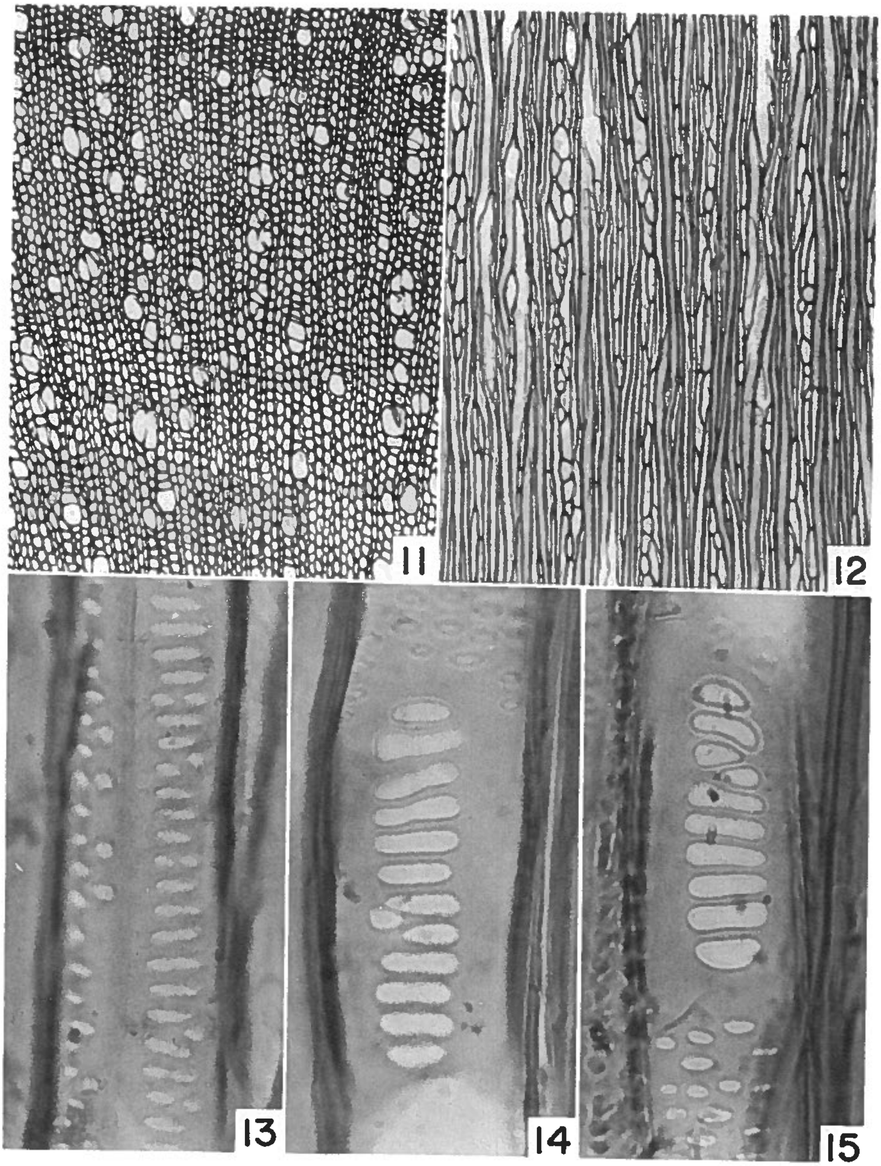

Fig. 11–15. *Patrinia villosa* (*Suzuki 445008*), wood sections.—11. Transection; no growth rings evident.—12. Tangential section; rays mostly multiseriate.—13. Vessel wall from radial section. Elongate pits evident.—14–15. Perforation plates from radial section, illustrating near-scalariform conditions. (Fig. 11–12, magnification scale above Fig. 1; Fig. 13–15, scale above Fig. 4.)

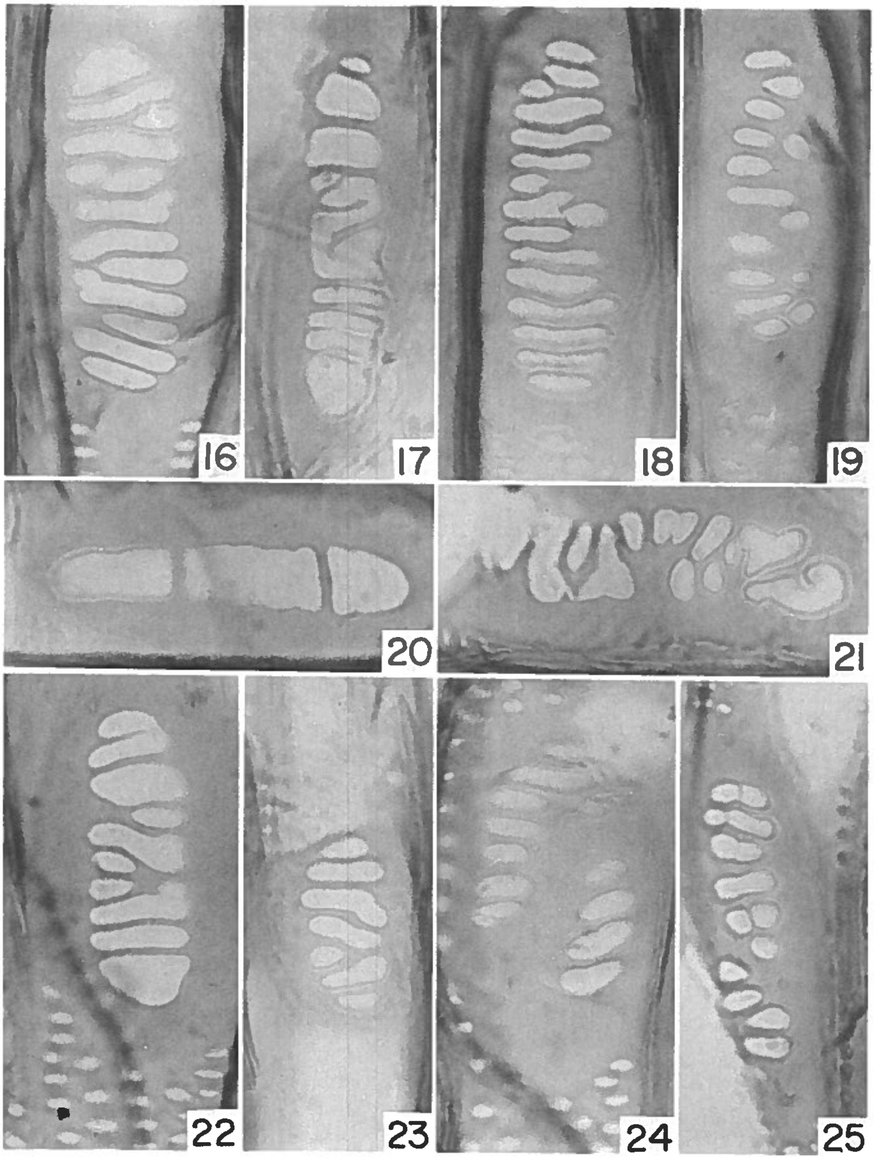

Fig. 16–25. *Patrinia villosa* (*Suzuki 445008*), perforation plates of vessels from radial sections of wood.—16–19, 22–23, near-scalariform perforation plates.—20. Elongate perforation plate bearing only two bars.—21. Perforation plate (one perforation sliced away, at left) intermediate between barlike and pitlike configurations.—24–25. Perforation plates each with two rows of pitlike perforations. (Magnification scale for all above Fig. 4.)

ECOLOGICAL CONCLUSIONS

Based on formulae offered earlier (Carlquist 1977) one may calculate values for the indices "Vulnerability" and "Mesomorphy" for the species studied here.

	Vulnerability	Mesomorphy
Calycera sessiliflora	0.29	88
Centranthus ruber	0.70	96
Patrinia villosa	0.58	257
Valeriana glauca	0.26	45

The figures given here seem an accurate reflection of the habitats occupied by these species. *Patrinia villosa,* from moist montane areas of Japan, China, Korea, and Manchuria is more mesic in its site preferences than the other Valerianaceae studied here. *Valeriana glauca* is from a matorral area (Parque Nacional La Campaña) near Santiago where summers are hot and dry; the wood is correspondingly xeromorphic, as the figures indicate. That the wood has narrow vessels indicates that xeromorphic construction overrides the tendency of vessels in scandent plants to be wide; the wide, thin-walled rays in *Valeriana glauca* may be related to that habit, however. The rocky areas of southern Europe and adjacent Mediterranean coast areas where *Centranthus ruber* occurs may not be much more mesic than the matorral areas near Santiago, but the specimen of *Centranthus* studied here was from cultivation, and therefore very likely has wood somewhat more mesomorphic than that of plants in wild.

Calycera sessiliflora is a montane annual. The figures given above suggest its wood to be rather xeromorphic. However, annuals in general may be termed xeromorphic in wood structure, a fact related to termination of annuals under water stress conditions. If the figures given for a group of annuals by Carlquist (1975, p. 206) are used, those annuals have a vulnerability value of 0.38 and a mesomorphy value of 61, figures very close to those given above for *Calycera sessiliflora.* Vessel elements of all four species studied in this paper are notably short. Extremely short vessel elements tend to characterize annuals and herbaceous perennials, especially those of dry climates.

TAXONOMIC CONCLUSIONS

Calyceraceae has been placed close to Asteraceae with great uniformity, the only disagreements among authors being the degree of closeness stressed. In wood anatomy, *Calycera sessiliflora* is well within the range described for Asteraceae (see Carlquist 1966). Notable in this regard is the rather high ratio in length between libriform fibers and vessel elements (2.0), occurrence of simple pits on imperforate elements (which are thereby libriform fibers), scanty vasicentric parenchyma, presence of both uniseriate and multiseriate rays (with histological features like those of Asteraceae), and the occurrence of vessels more commonly grouped than solitary (on the average 1.84 vessels per group). In no feature could the wood of *Calycera sessiliflora* be identified as distinct from wood of Asteraceae.

Wood of Valerianaceae likewise is very close to that of Asteraceae. Vessel groupings may be small (*Patrinia villosa,* Fig. 11) or extensive (*Valeriana glauca,* Fig. 5). Pits on imperforate tracheary elements are all simple. Axial parenchyma is scanty vasicentric. The annual bands of parenchyma, produced at the ends of growing seasons, in *Centranthus ruber* (Fig. 8, 9) are of significance with regard to the growth form. Such bands occur in herbaceous perennials in strongly seasonal climates, plants in which branching occurs from the base—for example, *Hemizonia minthornii* Jepson (Carlquist 1958).

The tendency for vessels to occur in the central portion of fascicular areas, and therefore for vessels not to be in contact with ray cells (Fig. 5, 8), was noted for unspecified Valerianceae by Metcalfe and Chalk (1950). It is a tendency I have not observed in Asteraceae. *Patrinia villosa* contrasts with *Centranthus ruber* and *Valeriana glauca* in lacking this feature; it also contrasts with those two taxa by having relatively short multiseriate rays. Uniseriate rays are present in *Patrinia villosa,* but absent in *Centranthus ruber* and *Valeriana glauca.* The ray cells of the latter two taxa are thin walled and nonlignified. The contrast in rays may be related to presence of greater mechanical strength in stems of *Patrinia villosa,* which bear tall inflorescences. The wood of *Centranthus* is from perennial stems at ground level; the stems of *Valeriana glauca* lean on branches of shrubs; these two taxa might therefore be expected to have lesser degrees of mechanical strength (connoted by large multiseriate rays composed of thin-walled cells) in stems.

Patrinia villosa lacks storied structure (Fig. 12). Storying is vaguely present in *Valeriana glauca* (Fig. 6) but clearly expressed in *Centranthus ruber* (Fig. 9). Storied structure characterizes an appreciable proportion of Asteraceae, although the majority of that family has nonstoried wood (Carlquist 1966).

If Asteraceae, Calyceraceae, and Valerianaceae form a close group on the basis of wood anatomy, they do contrast with Dipsacaceae in a feature often thought to be of basic importance. Dipsacaceae have tracheids (Carlquist 1982a) whereas Asteraceae, Calyceraceae, and Valerianaceae have only libriform fibers. However, the four families just mentioned tend to form a mosaic in terms of primitive and specialized characters, a fact cited in the introduction. Some other families of tubiflorous dicotyledons also have tracheids rather than libriform fibers, notably Hydrophyllaceae (Carlquist, Eckhart, and Michener 1983) and Goodeniaceae (Carlquist 1969a).

Perforation plates ranging from near-scalariform to much modified are illustrated for *Patrinia villosa* (Fig. 13–25). No simple perforation plates were observed in material of this species. Solereder (1906) reported scalariform perforation plates near the primary xylem in *Centranthus ruber*; while noting this exception, Metcalfe and Chalk (1950) cite simple perforation plates for Valerianaceae. In the sample studied of *Patrinia villosa,* no truly simple perforation plates were seen. Should one conclude that the occurrence of scalariform perforation plates in a family with predominantly simple perforation plates denotes a primitive condition, as Shulkina and Zikov (1980) conclude for Campanulaceae? The situation is not so simple, because an ontogenetic dimension must be included. Families such as Calyceraceae, Campanulaceae, and Valerianaceae have wood highly juvenilistic in many respects, a fact correlated with the high degree of herbaceousness in these families. Indeed, such indicators of juvenilism as erect ray cells (Fig. 3) and laterally widened pits (Fig. 4, 7, 10, 13) are characteristic in these families, as they are in other groups showing paedomorphosis (Carlquist 1962, 1969b).

Campanulaceae (including lobelioids) probably have scalariform perforation plates commonly in metaxylem, although not often in secondary xylem. Bierhorst and Zamora (1965) report scalariform plates for metaxylem of *Lobelia syphilitica* L. They also mention a curious primary xylem sequence incorporating tracheids in *Lobelia cardinalis* L. *Patrinia villosa* does prove to have scalariform pitting in protoxylem and metaxylem vessels, and Solereder's report of scalariform perforation plates in *Centranthus ruber* very likely refers to metaxylem also. A few scalariform perforation plates have been found in Asteraceae (Bierhorst and Zamora, 1965, report them in *Aster novae-angliae* L., *Centaurea cineraria* L., *C. nigra* L., and *Hieracium aurantiacum* L.). Aberrant versions of scalariform perforation plates occur in secondary xylem in some Asteraceae, notably two species of *Dendroseris* sect. *Phoenicoseris* (Carlquist 1960) and one species of *Crepidiastrum* (Carlquist 1983), both genera of the tribe Lactuceae. Another remarkable example which must belong to this pattern is *Pentaphragma,* a curious tubiflorous herb in which secondary xylem has exclusively scalariform perforation plates, as does its metaxylem (Carlquist 1975). The above patterns can only be described as types of paedomorphosis in which the relictual occurrence of scalariform perforation plates in primary xylem is expressed occasionally or frequently in the secondary xylem.

However, what controls when scalariform perforation plates occur in secondary xylem of such groups and when they are absent? In all of the above-mentioned groups (except perhaps *Pentaphragma*), the ability to form simple perforation plates in secondary xylem certainly exists. One must hypothesize that scalariform plates are formed in species of more mesic sites. Of the Valerianaceae studied here, *Patrinia villosa* occurs in the most mesic sites, and also is the only one in which secondary xylem regularly forms scalariform or aberrant plates. The species of *Dendroseris* sect. *Phoenicoseris* grow in quite moist Juan Fernandez rain forest. *Crepidiastrum ameristophyllum* (Koidz.) Nakai occurs only at the cloud-covered summit of Hahajima I., Bonin Islads. The Campanulaceae for which Shulkina and Zikov (1980) figure scalariform plus simple perforation plates are all mesophytes: *Canarina canariensis* Kuntze, *Musschia aurea* Dum., and *M. wollastonii* Lowe are understory elements of Macaronesian laurel forest; *Platycodon grandiflorum* (Jacq.) A. DC. occurs in Japan, China, and Korea on slopes much like those where *Patrinia villosa* grows. *Pentaphragma* is an understory element of moist Malesian forest. Scalariform perforation plates (or aberrant types) can be hypothesized—for these groups and under these ecological conditions—to be expressed in secondary xylem because they are not of negative selective value. This was concluded earlier in the case of *Pentaphragma* (Carlquist 1975, p. 157), but the abovementioned instances also seem referable to this concept. Under more highly seasonal climates, higher flow rates in xylem during short moist seasons—as in the Mediterranean type climate where *Centranthus ruber* grows—would make presence of simple perforation plates exclusively (or nearly so) in secondary xylem a feature of positive selective value.

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