

WOOD ANATOMY OF LIMNANTHACEAE AND TROPAEOLACEAE IN RELATION TO HABIT AND PHYLOGENY

SHERWIN CARLQUIST and CHRISTOPHER JOHN DONALD

*Santa Barbara Botanic Garden
1212 Mission Canyon Road
Santa Barbara, CA 93105, U.S.A.*

ABSTRACT

Qualitative and quantitative wood data are provided for *Limnanthes douglasii* R. Brown and *Tropaeolum majus* L.; no descriptions of wood of Limnanthaceae or Tropaeolaceae have been offered hitherto. *Limnanthes douglasii* wood is present in localized zones at the root-stem junction; imperforate tracheary elements are absent; both axial and ray parenchyma are thin-walled. *Tropaeolum majus* has root wood in which all axial tracheary elements are wide or narrow vessels, and no libriform fibers are present; in stems, libriform fibers are present, although narrow vessels predominate in later-formed secondary xylem. The wood patterns of *Limnanthes* and *Tropaeolum* are characteristic of wood of an annual and a vine, respectively. Although both are herbaceous species, wood patterns are quite different, a fact explainable by both habit and systematic position. The concept that both of the families belong to a new expanded Capparales is compatible with wood data.

KEY WORDS: Capparales, ecological wood anatomy, glucosinolate families, Limnanthaceae, secondary xylem, Tropaeolaceae, vine anatomy.

RESUMEN

Se ofrecen datos cualitativos y cuantitativos sobre los leños de *Limnanthes douglasii* R. Brown y *Tropaeolum majus* L.; hasta ahora no existían descripciones de los leños de Limnanthaceae y Tropaeolaceae. El leño de *Limnanthes douglasii* se presenta localizado en la unión entre la raíz y el tallo. Los elementos traqueales sin perforaciones faltan completamente, y tanto el parénquima axial como el radial tienen paredes finas. *Tropaeolum majus* tiene el leño radical con elementos traqueales compuestos por vasos anchos y estrechos; y no hay fibras libriformes presentes. En los tallos existen fibras libriformes, aunque predominan en el xilema secundario formado tardíamente. Los patrones del leño de *Limnanthes* y *Tropaeolum* son característicos de una hierba anual y una trepadora respectivamente. Aunque las dos especies son herbáceas, los modelos del leño son bastante diferentes, hecho explicable tanto por el hábito como por la posición sistemática de las dos especies. Los datos del leño sostienen el concepto de que las dos familias se encuadran en un Capparales nuevo ampliado.

INTRODUCTION

No data on wood anatomy of either Limnanthaceae or Tropaeolaceae have been presented to date (Metcalf & Chalk 1950; Gregory 1994). The wood of these families is interesting with respect to their divergent kinds of habits; all members of both families are herbs. The two families are grouped here because they are the most herbaceous of the families recog-

nized among the glucosinolate families, which may be considered Capparales sensu lato, by Dahlgren (1975), Rodman (1991a, 1991b) and Rodman et al. (1993, 1994). Formerly both Limnanthaceae and Tropaeolaceae were included in Geraniales (e.g., Cronquist 1981; Thorne 1992). In some recent cladistic systems, Tropaeolaceae are a sister group to Akaniaceae and Bretschneideraceae; Limnanthaceae are not far away in the clade of Capparales (s.l.), and among the groups nearest to Limnanthaceae are Batidaceae, Caricaceae, and Moringaceae (Rodman et al. 1993, 1994). Tropaeolaceae and Limnanthaceae are placed close to Capparaceae in the cladogram of Conti et al. (1996), who include fewer of the glucosinolate families in their survey, and who therefore offer less precision in the placement of these two families.

Rodman et al. (1993) concede that marked evolutionary shift in habit must be hypothesized if Tropaeolaceae are close to the tree families Akaniaceae and Bretschneideraceae. However, they do not consider this improbable and invite consideration of how these changes may have occurred. Similar considerations apply to Limnanthaceae. The species of *Tropaeolum* studied, the well known *T. majus*, is an annual herb with vining capabilities. The base of the stem contains a cylinder of secondary xylem 1–2 mm in thickness; the upper portion of the root contains a xylem core 1–3 mm in thickness; these have been used in the present study. *Limnanthes douglasii* is less woody than *Tropaeolum*; *Limnanthes* is an annual with a short basal stem to which numerous thin roots are attached; upwardly, the basal stem branches into several prostrate stems. The patches of secondary xylem in the stem of *Limnanthes* are evidently related to these prostrate stems. These distinctive habits, and the fact that secondary xylem in Limnanthaceae and Tropaeolaceae is minimal in comparison with that of other capparalean families provide reasons for study of wood anatomy of these two families. If marked differences in habit have occurred phylogenetically in the divergence of these two families from their nearest neighbors, we will have new examples of how nature of wood anatomy reflects shift in habit. To be sure, only one species of each family has been used in the present study. The reason for this selection is that for each family, the species studied is the woodiest that could be obtained readily. Further studies are needed, but they may demonstrate more herbaceous modes of structure than do the species in the present paper, judging from the habits described for Limnanthaceae by Ornduff (1971) and Tropaeolaceae by Sparre et al. (1991).

MATERIALS AND METHODS

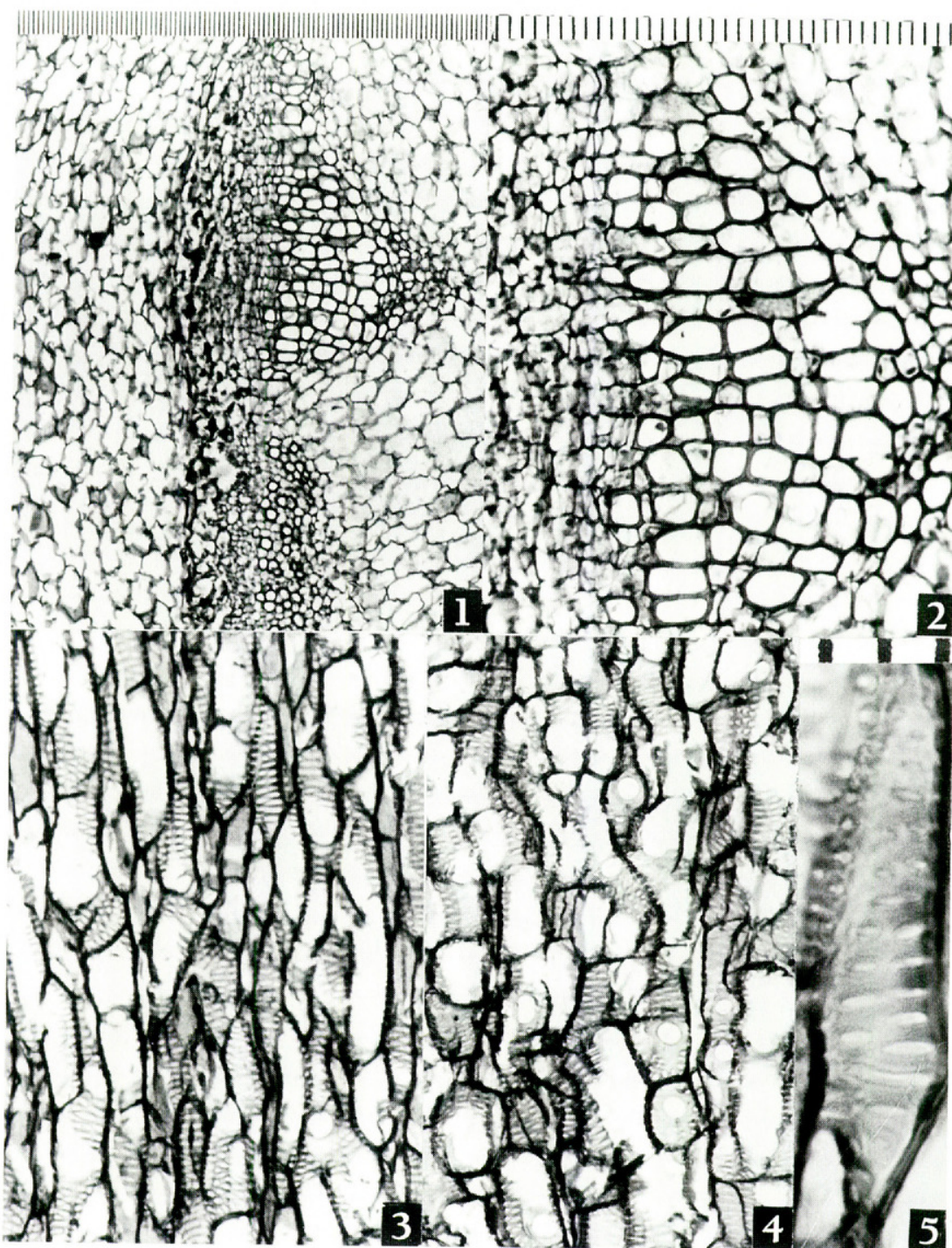
Stems and roots bearing secondary xylem from plants of *Tropaeolum majus* and *Limnanthes douglasii* that were judged to be mature but not yet in decline were collected from plants in cultivation. In the case of the *Tropaeolum*,

plants were collected from a Santa Barbara garden where the species has naturalized. Plants of *Limnanthes douglasii* were collected from Santa Barbara Botanic Garden, where they have become naturalized, with the aid of Mark Stubler. The portions bearing secondary xylem were preserved in 50% aqueous ethyl alcohol. Wood of *Tropaeolum* was softened by immersion in 5% ethylene diamine for two hours. Material was infiltrated and embedded in paraffin according to the usual techniques, sectioned on a rotary microtome; sections mounted on slides were stained with a safranin-fast green combination corresponding to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen 1940). In addition, some sections of unsoftened stems of *T. majus* were sectioned on a sliding microtome, dried between glass slides, sputter coated, and examined with a scanning electron microscope (SEM). Macerations were prepared with Jeffrey's fluid and stained with safranin.

Terminology follows that of the IAWA Committee on Nomenclature (1964). The term "pseudoscalariform" refers to pitting in which pits are horizontally elongate, as in scalariform pitting, but are derived from alternate pits that are markedly widened, and thus the ends of the pits do not correspond to angles of the vessels. Vessels were measured in term of lumen diameter; if oval rather than near-circular in outline, the mean diameter was estimated. The term "intervascular" axial parenchyma refers to a situation in which occasional axial parenchyma cells are scattered among large groupings of vessels, whereas paratracheal parenchyma applies to parenchyma surrounding a vessel or vessel group.

ANATOMICAL RESULTS

Limnanthes douglasii stem (Fig. 1–5). Secondary xylem very limited in extent, and also localized in several segments within the vascular cylinder (Fig. 1, top), intervening parts of the cylinder composed of primary xylem only (e.g., Fig. 1, bottom). Vessels square or polygonal in outline, in large groupings with few intervening axial parenchyma cells (Fig. 1); mean number of vessels per group, 18.1; mean number of vessels per mm² (no areas adjacent to secondary xylem included), 690. Mean vessel diameter, 28.2 μ m. Mean vessel element length, 71.6 μ m. Perforation plates all simple, circular, and appreciably narrower than the vessel diameter (Fig. 4). Vessels irregular in outline, either as seen in tangential (Fig. 3) or radial (Fig. 4) sections. Lateral wall pitting of vessels consisting of pits laterally elongate, alternate to pseudoscalariform (Fig. 5). Lateral wall pits (pit cavity) about 5 μ m as measured vertically (Fig. 5). Imperforate tracheary elements absent. Axial parenchyma sparse, intervascular (Fig. 2), subdivided into strands or two or not subdivided, with thin primary walls only. Rays uniseriate or biseriate (Fig. 3). Mean height of biseriate rays, 238 μ m; mean height of

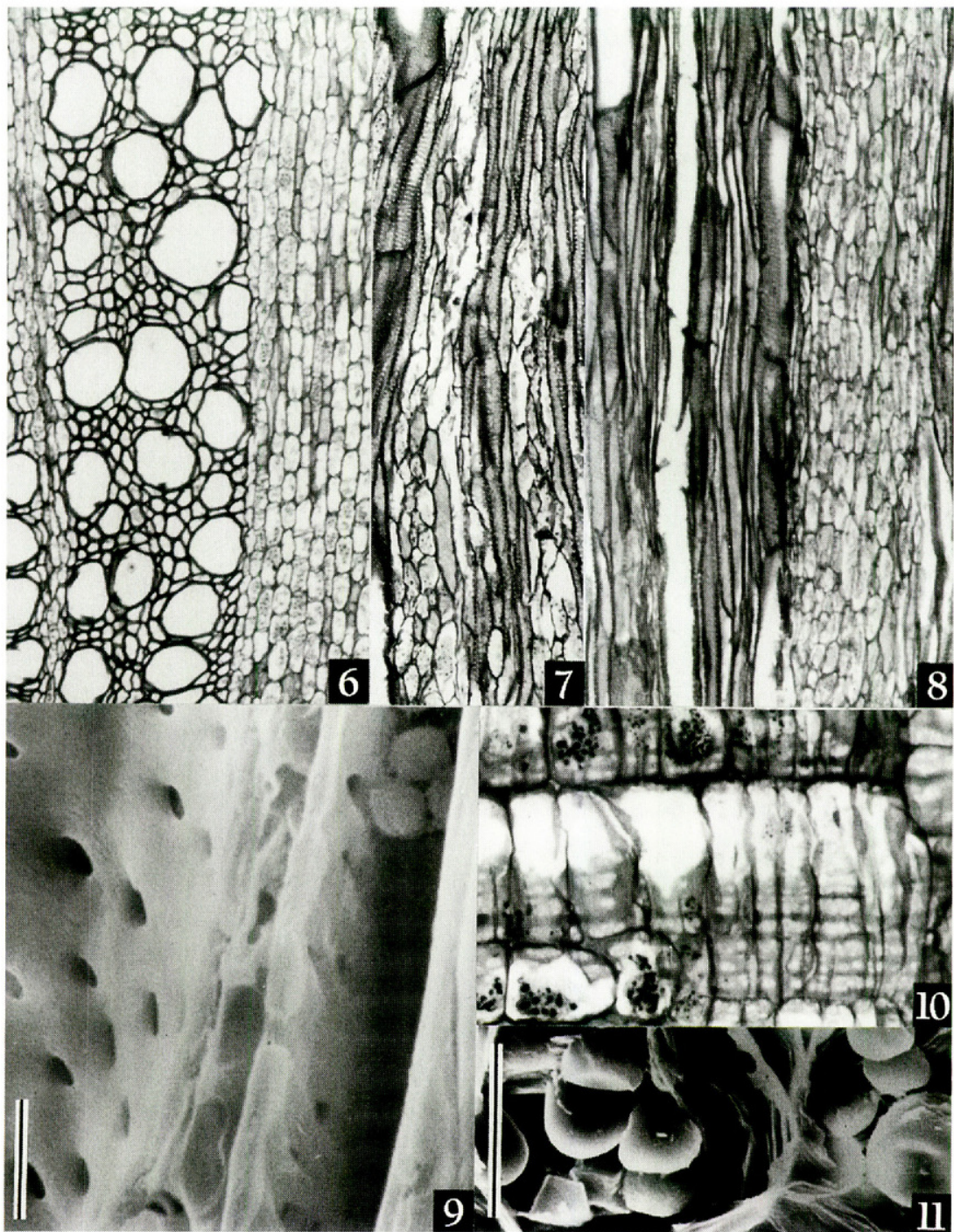


FIGS. 1–5. Wood sections of *Limnanthes douglasii* stems. Fig. 1. Transection; portion of cylinder with secondary xylem, above, portion with only primary xylem below. Fig. 2. Enlarged portion of secondary xylem to show angular nature of vessels; imperforate tracheary elements are absent. Fig. 3. Tangential section; rays are uniseriate or biseriate, composed of upright cells. Fig. 4. Radial section; shortness of vessel elements evident. Fig. 5. Vessel element from tangential section to show pseudoscalariform lateral wall pitting. Fig. 1, scale above Fig. 1 (divisions = 10 μ m); Figs. 2–4, scale above Fig. 2 (divisions = 10 μ m); Fig. 5, scale above Fig. 5 (divisions = 10 μ m).

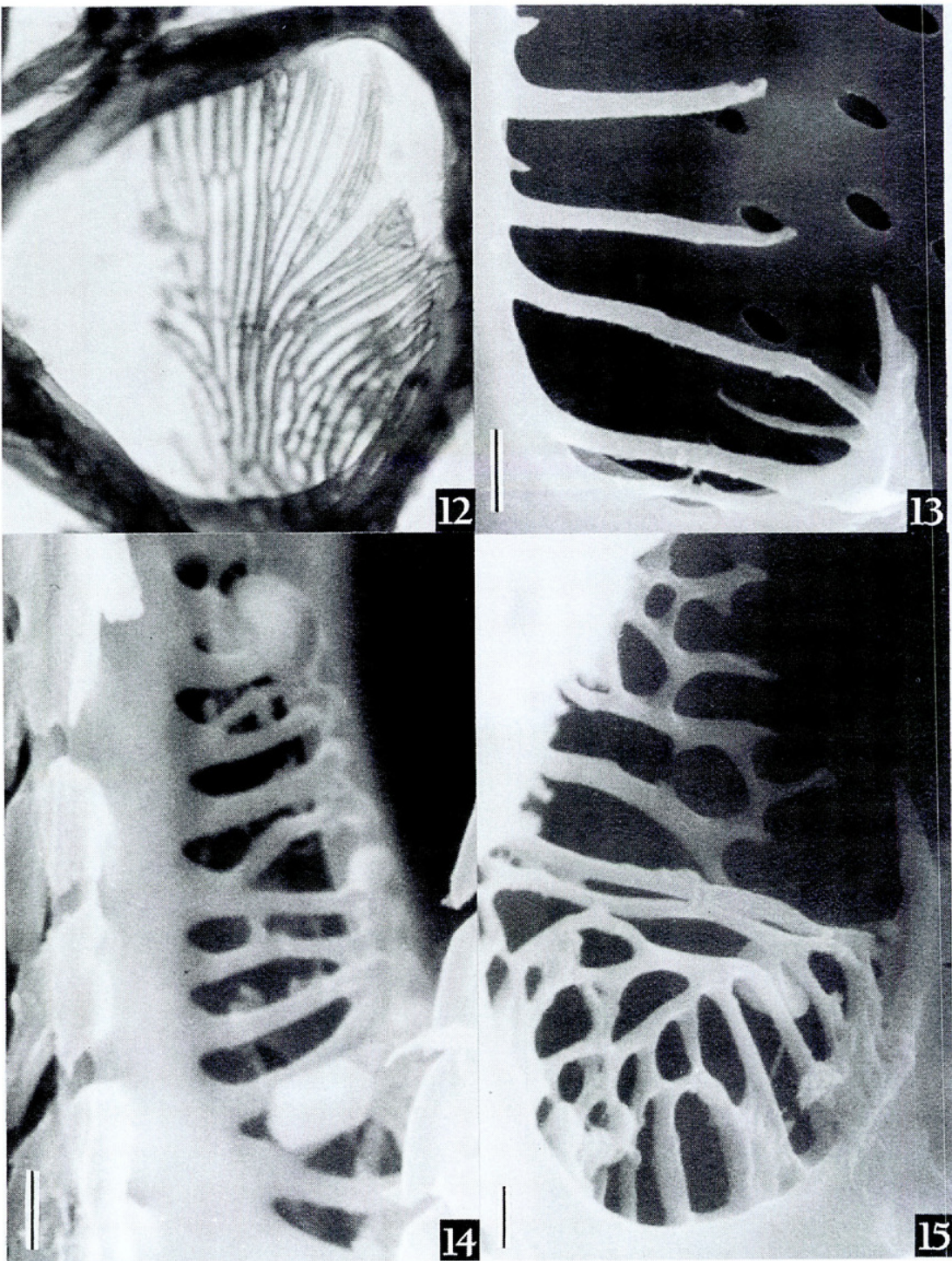
uniseriate rays, 91 μm . Ray cells with thin primary walls. Wood nonstoried (Fig. 3), no starch or crystals observed.

Tropaeolum majus stem (Fig. 6, 8–15). Axial portions of wood consisting largely of vessels dimorphic in diameter (Fig. 6). Wide vessels solitary or in pairs (mean number of vessels per group in nonray areas, 1.8), mean diameter, 81 μm . Narrow vessels comprising the bulk of the remainder of the secondary xylem and therefore in indefinitely large groups; mean diameter of the narrower vessels, 29 μm . Mean length vessel elements (wide and narrow vessel elements combined), 116 μm . Mean wall thickness of vessels varying from 1.8 μm for narrower vessels to 2.5 μm for wider vessels. Perforation plates mostly simple, but occasional scalariform or scalariformlike plates present (Fig. 12–15): some plates with numerous forked or interconnected bars (Fig. 12), some with few bars (Fig. 13), some, on narrow vessels, with wide bars (Fig. 14), some with a condition intermediate between scalariform and multiperforate (Fig. 15). Lateral wall pitting of vessels alternate, pits circular to oval (Fig. 9, left) or elliptical, about 5 μm measured vertically. Libriform fibers present, especially in earlier formed portions of secondary xylem, supplanted in later portions of axial secondary xylem by narrow vessels. Libriform fibers with simple pits, and often containing starch grains (Fig. 9, right). Mean length of libriform fibers, 462 μm ; mean diameter, 24 μm ; mean wall thickness, 2.2 μm . A few vasicentric tracheids and a few cells intermediate in pitting between libriform fibers and vasicentric tracheids present. Axial parenchyma with thin secondary walls, in strands of two cells, adjacent to the larger vessels. Rays multiseriate only, more than 1,000 μm in mean height (Fig. 8, right). Mean width of multiseriate rays, 12 cells. Ray cells with thin primary walls, bearing prominent pit fields on radial walls, separated from each other by horizontal bands of primary wall material (Fig. 10). Ray cells predominantly upright; square and procumbent cells in central portions of rays (Fig. 10). Wood nonstoried (Fig. 8). Starch abundant in ray cells (Fig. 10), starch grains spherical in shape (Fig. 11).

Tropaeolum majus, root (Fig. 7). Axial portions of wood consisting mostly of vessels dimorphic in diameter. Larger vessels mostly solitary, mean number of vessels per group, 1.4. Narrower vessels in groups of indefinite extent. Mean number of larger vessels (ray areas excluded), 44.8. Mean diameter of larger vessels, 96 μm ; mean diameter of narrower vessels, 27 μm . Mean wall thickness of vessels varying from 1.8 to 3.5 μm . Mean length of vessel elements (wide and narrow vessel elements together), 99 μm . Perforation plates and lateral wall pitting as in stems. Libriform fibers very few; a few vasicentric tracheids present. Axial parenchyma in strands of two cells, with secondary walls, adjacent to the larger vessels. Rays multiseriate and uniseriate (Fig. 7). Mean height of multiseriate rays, 1460 μm ; mean



FIGS. 6–11. *Tropaeolum majus*, sections of secondary xylem from stems (Figs. 6, 8–11) and root (Fig. 7). Fig. 6. Transection; marked dimorphism in vessel diameter evident; wide ray at right. Fig. 7. Tangential section; rays narrower, shorter than those of stems. Fig. 8. Tangential section; rays are multiseriate, wide, tall. Fig. 9. SEM photograph of vessel (left) and libriform fiber (right). Fig. 10. Portion of ray from radial section; primary pit fields common on radial walls. Fig. 11. SEM photograph of ray cells from tangential section to show starch grains. Figs. 6–8, scale above Fig. 1; Fig. 10, scale above Fig. 2; Figs. 9, 11, scales at lower left (bar = 5 μ m).



FIGS. 12–15. Perforation plates from vessels of *Tropaeolum majus* stems. Fig. 12. Light micrograph of perforation plate from transection, bars numerous and narrow. Figs. 13–15. SEM photographs of perforation plates from radial section. Fig. 13. Bars few, wide. Fig. 14. Plate from narrow vessel; bars wide. Fig. 15. Plate intermediate between scalariform and multiperforate. Fig. 12, scale above Fig. 5; Figs. 13–15, bars at lower left = 5 μ m.

height of uniseriate rays, 312 μm . Ray cells mostly upright, a few square and procumbent cells present in central portions of multiseriate rays. Mean width of multiseriate rays, 5.1 cells. Ray cells thin-walled, nonlignified. Wood nonstoried, but vague storying visible in tangential sections of secondary phloem. Starch grains abundant in ray cells.

DISCUSSION AND CONCLUSIONS

Limnanthes and *Tropaeolum* differ in a number of salient ways with respect to wood anatomy. *Limnanthes douglasii* has narrow vessels angular in transection, nondimorphic in diameter, with simple perforation plates exclusively and with mostly pseudoscalariform lateral wall pitting; imperforate tracheary elements are entirely absent; axial parenchyma is sparse and with thin nonlignified walls; rays are uniseriate or biseriate, composed of upright cells. *Tropaeolum majus* has markedly dimorphic vessels; the larger are circular in transectional outline, the smaller circular to angular in outline; lateral wall pitting is mostly circular to elliptical; perforation plates are simple, but with an appreciable number of perforation plates that represent alterations of a scalariform pattern; libriform fibers with simple pits are present (somewhat less abundant than the narrow vessels), but a few vasicentric tracheids and cells intermediate between libriform fibers and vasicentric tracheids are present; axial parenchyma has thin lignified walls, is in strands of two cells, and is distributed adjacent to the larger vessels. In *T. majus*, rays are wide and exclusively multiseriate in stems in roots, rays are mostly multiseriate and less wide; ray cells are thin walled, filled with starch, and are mostly upright, but with procumbent and square cells in central ray portions.

The lack of imperforate tracheary elements in *Limnanthes* may be correlated with lack of upright stems, because libriform fibers would be expected where addition of mechanical strength is of selective value. The occurrence of secondary xylem in small restricted patches is related to the short duration of this annual, and the short stem. Secondary xylem apparently connects the branches with the basal stem, and the remainder of the basal stem contains primary xylem only. Thus, habit seems to correspond to those distinctive features. The shortness of vessel elements in *Limnanthes* is likely related to xeromorphy; short vessel elements are found in plants of habitats that dry as a season progresses (Carlquist 1966).

Tropaeolum wood is distinctive in the dimorphism of its vessel diameter, in the sparsity of libriform fibers (supplanted to a large extent by narrow vessels), and in the very wide, tall rays. These are features common in woods of vines and lianas (Carlquist 1985). The relative shortness of vessel elements in *T. majus* is likely related to the drying of soil as the plant reaches its mature size.

Other differences between the wood of *Limnanthus* and that of *Tropaeolum* seem related to phylogenetic relationships. For example, the wood of Tropaeolaceae, placed close to Akaniaceae and Bretschneideraceae (Rodman et al. 1993, 1994), shares with that pair of families a number of wood features (wood of those two families monographed by Carlquist, submitted): perforation plates simple but with an appreciable number of modified scalariform perforation plates; libriform fibers present; axial parenchyma sparse, distributed adjacent to the larger vessels (vasicentric in Akaniaceae and Bretschneideraceae); rays wide and tall, uniseriate rays few or absent (wide rays also a characteristic of vines and lianas, but absence of uniseriate rays is not characteristic of lianas).

On the other hand, some of the features of *Limnanthus* wood can be found in genera of Capparales from which it is not far removed according to the schemes of Rodman et al. (1993, 1994). For example, in Capparaceae, rays are uniseriate or biseriate, rarely multiseriate (Metcalfe & Chalk 1950). The marked difference in habit between the annual *Limnanthus* and genera of Capparaceae, which are trees or shrubs, means that modifications related to habit are likely to be of overriding importance, and similarities related to phyletic relationship are likely to be few. Further studies on wood anatomy of the glucosinolate families, which may tentatively be considered a redefined Capparales, are planned so as to show the relative degrees of influence that habit and phylogenetic relationship have on similarities and differences among the component families of that order.

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