

*Dedicated to Professor Dr. Gerhard Wagenitz
on his 60th birthday on May 31, 1987*

Wood anatomy and relationships of Stackhousiaceae

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With 4 figures and 1 table in the text

Abstract

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Quantitative and qualitative features are described for five species of *Stackhousia*. The imperforate tracheary elements are all tracheidlike fiber-tracheids. Very narrow fusiform vessel elements are present. All other vessel elements are relatively narrow, and numerous per mm² of transection. All of these features connote xeromorphy. Quantitatively the xeromorphy is not extreme, a fact thought to relate to the habit in *Stackhousia* of stems to die back to a woody base annually, as well as to drought-deciduous nature of foliage and short-lived nature of plants. Wood features of *Stackhousia* are compatible with the concept that the family belongs to Celastrales. Possession of fiber-tracheids, as well as other features, favor this hypothesis over the idea of relationship to Scrophulariaceae or Lobeliaceae.

1. Introduction

Stackhousiaceae can be said to consist of three genera: *Macgregoria* and *Tripterooccus* are monotypic, whereas *Stackhousia* has about 20 species (CRONQUIST 1981). *Stackhousia* is primarily Australian, although the genus is represented on New Zealand, the Philippines, and some Malesian islands (HEYWOOD 1978). *Stackhousia* is at most a subshrub with moderate wood accumulation. For that reason, comparative wood anatomy of the family has not been studied hitherto. The information offered by METCALFE & CHALK (1950) and STANT (1951) is minimal.

Stackhousia is a short-lived perennial in which most commonly stems die back annually to a woody caudex. Stems appear rarely to exceed about five

years in duration. The root-stem juncture, which is thereby the woodiest part of the plant, has been used as the source of the wood studied here, except for *S. viminea* Sm., in which some stems accumulate secondary xylem for several years before dying back to ground level. The species selected for study represent among the woodiest of the family, and the omission of most taxa has been based on their minimal accumulation of wood.

Study of wood anatomy of *Stackhousia* is desirable in view of uncertainty over systematic affinities of the family. The majority view, from BENTHAM & HOOKER (1862–1883) to recent phylogenists, such as CRONQUIST (1981), DAHLGREN (1980), THORNE (1976), and TAKHTAJAN (1980) regards Stackhousiaceae as a member of Celastrales. Embryological data reinforces this view (MAURITZON 1936, NARANG 1953). However, STANT (1951) finds affinities between Stackhousiaceae and such tubiflorous families as Scrophulariaceae and Lobeliaceae. Because wood anatomy of celastralean families differs rather markedly from that of Scrophulariaceae and Lobeliaceae, one might use wood anatomy to place Stackhousiaceae in one group or the other.

With respect to ecological aspects of wood anatomy, *Stackhousia* is of potential interest. *Stackhousia* grows in the Mediterranean-type areas of southwestern Australia (*S. brunonis* Benth., *S. huegelii* Endl., *S. pubescens* A. Rich.) or other areas of Australia with prolonged dry seasons. The specimen of *S. viminea* studied is from near Ayer's Rock in the central desert of Australia, where rainfall tends to occur in summer, but rainfall amounts are small and irregular from year to year. The specimen of *S. monogyna* Labill. is from sclerophyll woodland in the Grampian Mountains of Victoria. However, one should not expect wood anatomy of *Stackhousia* to be a direct indicator of habitat conditions. Because stems can die back to a woody base, and because *Stackhousia* is a short-lived perennial, any given stem or root may die partially or wholly in an unfavorable season, so that wood structure need not be expected to provide as ultimate a degree of safety as would xylem of a long-lived shrub of these regions. Drought-deciduous nature of foliage in *Stackhousia* may also lessen the necessity for wood to be maximally xeromorphic.

2. Materials and methods

Wood samples were obtained from dried specimens or, in the case of *S. pubescens*, collected in the field and dried. The largest of these specimens, that of *S. pubescens*, was about 6 mm in diameter. The specimens documenting the work are all located in the herbarium of the Rancho Santa Ana Botanic Garden (RSA) and are as follows: *S. brunonis*, Thorne 24242; *A. huegelii*, Carlquist 5524; *S. monogyna*, Hegi 454; *S. pubescens*, Carlquist 927; *S. viminea*, Donner 4381.

Wood samples were boiled in water and stored in 50% ethyl alcohol. They were then sectioned on a sliding microtome. Sections were stained with safranin and counterstained with fast green. Macerations were prepared from boiled specimens by means of treatment with JEFFREY's fluid and stained with safranin.

Quantitative data (Table 1) are presented in terms of means; these means are based upon 20 measurements except for vessel wall thickness, fiber-tracheid wall thickness, and fiber-tracheid wall diameter, in which typical conditions were selected for measurement.

3. Results

The *Stackhousia* species studied have wood features that correspond to a basic plan, and differ from each other only in quantitative features (Table 1). Therefore a generic description is offered below, followed by a few comments on features observed in particular species.

Growth rings are present, characterized by presence of wider vessels, and, to various degrees, wider fiber-tracheids and presence of initial parenchyma (Fig. 1). Vessels are mostly solitary, but an appreciable degree of vessel grouping does occur. Some vessels that appear in pairs are actually overlapping tips of vessel elements with fusiform ends. Fusiform vessel elements comprise an appreciable proportion of the vessel elements; fusiform vessel elements are difficult to differentiate from wider fiber-tracheids in transection. Perforation plates are mostly simple, but a few double perforation plates (the pair interconnecting two vessel elements, not relating to a vessel branching) were observed in all species (Fig. 4). Lateral wall pits of vessels are alternate, 3–5 μm in diameter, the pit apertures narrowly elliptical (Fig. 4). Imperforate tracheary elements are all fiber-tracheids. The pits of fiber-tracheids are similar in size and morphology to those of lateral vessel walls, but are scattered and thus not as dense; for this reason, the imperforate tracheary elements have been termed fiber-tracheids rather than tracheids here. Axial parenchyma occurs in the form of thin-walled cells not subdivided into strands (these form the dark band, Fig. 3, left). Axial parenchyma is absent in latewood and in some growth rings; where present, axial parenchyma occurs most abundantly in earlywood and decreases during the transition to latewood. Axial parenchyma tends to be more common in outer growth rings of a stem than in inner growth rings, and is

Table 1. Quantitative wood features in *Stackhousia*.

| Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---------------------|----|-----|-----|-----|----|-----|-----|-----|-----|-----|
| <i>S. brunonis</i> | 42 | 198 | 198 | 2.5 | 20 | 3.8 | 333 | 239 | 310 | 2.7 |
| <i>S. huegelii</i> | 33 | 328 | 200 | 2.3 | 10 | 3.2 | 239 | 244 | 177 | 2.5 |
| <i>S. monogyna</i> | 25 | 540 | 220 | 2.2 | 9 | 2.3 | 327 | 275 | 107 | 2.3 |
| <i>S. pubescens</i> | 24 | 600 | 304 | 2.2 | 7 | 2.3 | 353 | 469 | 164 | 2.2 |
| <i>S. viminea</i> | 43 | 260 | 212 | 2.4 | 9 | 3.5 | 334 | 270 | 116 | 2.2 |

Legends for columns: 1, mean vessel diameter, μm . 2, mean number of vessels per mm^2 . 3, mean vessel element length, μm . 4, vessel wall thickness, μm . 5, fiber-tracheid diameter, μm . 6, fiber-tracheid wall thickness, μm . 7, mean fiber-tracheid length, μm . 8, mean height multiseriate rays, μm . 9, mean height uniseriate rays, μm . 10, mean width multiseriate rays, cells. Collections given in Materials and Methods.

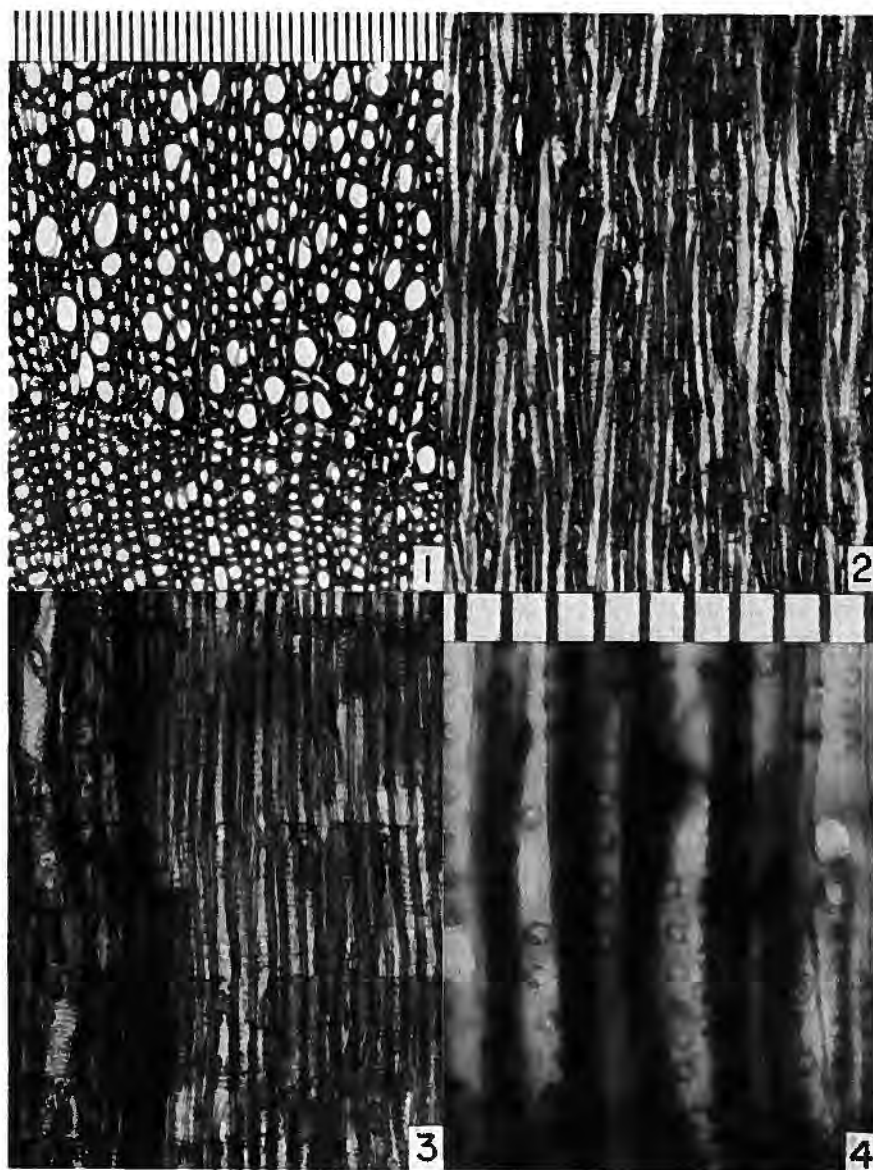


Fig. 1—4. Wood sections of *Stackhousia pubescens*, Carlquist 927 (RSA). — 1, transection; beginning of a new growth ring is about 1/3 from bottom of photograph; some axial parenchyma is present in earlywood. — 2, tangential section; rays are uniseriate or biseriate; the ray cells are erect and contain a dark-staining material. — 3, radial section; earlywood (left 1/3) contains several vessels, abundant dark-staining parenchyma. — 4, portion of radial section, showing pitting of the narrow vessels; a double perforation plate can be seen in the vessel at right. Fig. 1—2, magnification scale above Fig. 1 (divisions = 10 μ m). Fig. 4, scale above Fig. 4 (divisions = 10 μ m).

quite common (to the exclusion of imperforate tracheary elements) in a few narrow growth rings, evidently those formed just prior to cessation of the stem. Both multiseriate and uniseriate rays are present (Fig. 2), but multiseriate rays very rarely exceed three cells in width. Ray cells are predominantly erect (Fig. 2); square and procumbent cells are present only infrequently and are absent from most rays. Dark-staining compounds are present in ray cells (Fig. 2) and in axial parenchyma (Fig. 3) in most collections. No crystals were observed. Wood is nonstoried.

4. Discussion

4.1. Wood characterizations

METCALFE & CHALK (1950) noted the presence of circular bordered pits on imperforate tracheary elements of *Stackhousia*; the definition of fiber-tracheids (IAWA Committee on Nomenclature 1964) seems applicable to them. METCALFE & CHALK report raylessness in *Stackhousia*, but my material does not confirm this.

The nature of growth rings deserves comment. Some earlier growth rings may be devoid of axial parenchyma, but later-formed growth rings show progressively more axial parenchyma. In fig. 3, one sees at the left a dark zone composed of parenchyma in which some vessels (extreme left) are embedded; fiber-tracheids were absent in that growth ring. Such growth rings were seen in several of the species where three or more growth rings were present. This parenchymatization of the secondary xylem seems to characterize stems or roots reaching maximal diameter. Ray cells have thin primary walls in such highly parenchymatous growth rings, whereas elsewhere ray cells normally have moderately thin lignified walls. The axial parenchyma cells, by virtue of lacking subdivision into strands, seem more an innovation than a modification of typical axial parenchyma cells. Parenchymatous bands of this nature do occur in a number of herbaceous perennials (CARLQUIST & ECKHART 1984). In highly parenchymatized growth rings in *Stackhousia*, vessels have laterally widened pits, in accordance with such vessels in other families (CARLQUIST & ECKHART 1984).

4.2. Relationships

As noted in the Introduction, the majority of workers have considered *Stackhousia* related to Celastraceae and to other Celastrales. Is this view consonant with wood anatomy? One important feature is the occurrence of tracheidlike fiber-tracheids rather than libriform fibers as the imperforate tracheary element type. Tracheids or tracheidlike fiber-tracheids are characteristic

of most Celastraceae (METCALFE & CHALK 1950). The occurrence of numerous vessels per mm², some fibriform, can be found in a genus recently transferred to Celastraceae, *Empleuridium* (GOLDBLATT et al. 1985). *Empleuridium* is also pertinent because it is a short-lived shrub with small stems; this limited wood accumulation is like that of *Stackhousia* and may be related to the fact that in both genera ray cells are erect or essentially so. Production of procumbent cells is a consequence of continued ontogeny (BARGHOORN 1941), and both *Empleuridium* and *Stackhousia* show foreshortened ontogeny. *Empleuridium* should not be regarded as the genus closest to *Stackhousia*, however. The rays of *Stackhousia* demonstrate this, for *Empleuridium* has uniseriate rays exclusively, whereas *Stackhousia* has both uniseriate and multiseriate rays. The multiseriate rays of *Stackhousia* are relatively narrow, mostly biseriate, whereas many Celastraceae have wider multiseriate rays. However, METCALFE & CHALK (1950) list nine genera of Celastraceae in which multiseriate rays are most often biseriate. Axial parenchyma in *Stackhousia* is unusual in being essentially absent, with various degrees of parenchymatization of initial portions of growth rings. Axial parenchyma is typically diffuse in Celastraceae, but absence of axial parenchyma is listed for nine genera of Celastraceae by METCALFE & CHALK (1950).

STANT's (1951) idea that *Stackhousia* is related to Scrophulariaceae or Lobeliaceae is not confirmed by wood anatomy. Both of those families have libriform fibers (fiber-tracheids in a scattering of Scrophulariaceae, but these have at most much reduced pit borders); both families have vascentric scanty parenchyma (METCALFE & CHALK 1950). The occurrence of tracheidlike fiber-tracheids and absence of axial parenchyma (except as initial parenchyma) are the most important features that would tend to contradict the relationship proposed by STANT; narrowness of rays is not characteristic of Scrophulariaceae or Lobeliaceae.

Predominance of erect cells in rays of *Stackhousia* is related to juvenility, since the cambium is finite in duration and procumbent ray cells tend to become more common later in ontogeny (BARGHOORN 1941). Predominance of erect cells is characteristic of a number of "woody herbs" with habits similar to *Stackhousia* (CARLQUIST 1962). Thus ray cell shape is not a consideration in determining relationships of *Stackhousia*.

4.3. Ecological correlations of wood anatomy

The narrow vessels, numerous per mm², and occurrence of well-marked growth rings are xeromorphic features which can be related to the occurrence of prolonged dry seasons in the habitats of the *Stackhousia* species studied. The figures for vessels per mm² in Table 1 may be conservative because narrow fibriform vessels are not easily identified as seen in transection and can easily be counted as fiber-tracheids. Dieback during dry periods and drought-decidu-

ous nature of foliage probably account for the fact that wood of *Stackhousia* is only moderately xeromorphic, quantitatively, compared to wood of longer-lived woody shrubs in comparable habitats. Mesomorphy values (vessel diameter times vessel element length divided by number of vessels per mm²) for the five *Stackhousia* species are 42, 20, 10, 12, and 35, respectively (mean for the five species, 24). These figures are higher than, for example, in *Empleuridium* (Mesomorphy = 2.4), but *Empleuridium* is a shrub that does not experience summer dieback, and thus *Empleuridium*, also from a Mediterranean-type climate, should be expected to have more xeromorphic wood. Leaves of *Stackhousia* are, as might be expected from its dry-season dieback habit, drought-deciduous whereas the leaves of *Empleuridium* are evergreen and needlelike.

Vessels of *Stackhousia* are grouped to a moderate extent. This is an indicator of xeromorphy (CARLQUIST 1984). In a paper dealing with vessel grouping (CARLQUIST 1984), *Stackhousia* was said to have solitary vessels and tracheids on the basis of insufficient material; species in the present study show that the mean number of vessels per group exceeds 2.5 and that imperforate tracheary elements are fiber-tracheids; an attempt has not been made here to develop exact figures for number of vessels per group in the various species because narrow vessels are so very similar to fiber-tracheids as seen in transection. *Stackhousia* wood validates the theory in my 1984 paper, but Stackhousiaceae should be transferred from the first list to the second in that paper.

References

- BARGHOORN, E. S. 1941: The ontogenetic and phylogenetic specialization of rays in the xylem of dicotyledons. II. Modification of the multiseriate and uniseriate rays. — *Amer. J. Bot.* 28: 273—282.
- BENTHAM, G. & HOOKER, J. D. 1862—1883: *Genera plantarum*. — 3 vols. London.
- CARLQUIST, S. 1962: A theory of pedomorphosis in dicotyledonous woods. — *Phytomorphology* 12: 30—45.
- 1984: Vessel grouping in dicotyledon wood: significance and relationship to imperforate tracheary elements. — *Aliso* 10: 505—525.
- CARLQUIST, S. & ECKHART, V. M. 1984: Wood anatomy of Hydrophyllaceae. II. Genera other than *Eriodictyon*, with comments on parenchyma bands containing vessels with large pits. — *Aliso* 10: 527—546.
- CRONQUIST, A. 1981: An integrated system of classification of flowering plants. — New York: Columbia Univ. Press.
- DAHLGREN, R. M. T. 1980: A revised system of classification of the angiosperms. — *J. Linn. Soc., Bot.* 80, 91—124.
- GOLDBLATT, P., TOBE, H., CARLQUIST, S. & PATEL, V. C. 1985: Familial position of the Cape genus *Empleuridium*. — *Ann. Missouri Bot. Gard.* 72: 167—183.
- HEYWOOD, V. H. (ed.) 1978: *Flowering plants of the world*. — New York: Mayflower Books.
- IAWA Committee on Nomenclature 1964: Multilingual glossary of terms used in wood anatomy. — Verlagsanstalt Buchdruckerei Winterthur: Konkordia.

- MAURITZON, J. 1936: Embryologische Angaben über Stackhousiaceae, Hippocrateaceae und Icacinaceae. — Svensk. Bot. Tidsskr. 30: 541—550.
- METCALFE, C. R. & CHALK, L. 1950: Anatomy of the dicotyledons. — Oxford: Clarendon Press.
- NARANG, N. 1953: The life history of *Stackhousia linariaefolia* A. Cunn. with a discussion on its systematic position. — Phytomorphology 3: 485—493.
- STANT, M. Y. 1952: Notes on the systematic anatomy of *Stackhousia*. — Kew Bull. 1951: 309—318.
- TAKHTAJAN, A. L. 1980: Outline of a classification of flowering plants (Magnoliophyta). — Bot. Rev. 46: 225—359.
- THORNE, R. F. 1976: A phylogenetic classification of the Angiospermae. — Evol. Biol. 9: 35—106.

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