

Wood and stem anatomy of *Sarcobatus* (*Caryophyllales*): systematic and ecological implications

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Summary

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Quantitative and qualitative data are given for *Sarcobatus vermiculatus* (Hook.) Torr. stem anatomy in order to provide information relevant to Behnke's segregation of *Sarcobatus* from *Chenopodiaceae* and his idea that *Sarcobataceae* belong in suborder *Phytolaccineae* rather than suborder *Chenopodiineae*. *Sarcobatus* has highly xeromorphic wood such as in xeric *Chenopodiaceae* (presence of vasicentric tracheids, narrow vessels, short vessel elements, numerous vessels per group, helical sculpturing of vessel walls), but these features could have evolved independently in both suborders. Nonbordered perforation plates, present in *Sarcobatus*, are widespread in *Caryophyllales* s.str. and may prove to be a defining feature for the recently expanded *Caryophyllales* together with the neighbouring order *Santalales*. A single-layered lateral meristem occurs in genera of *Chenopodiinae* with successive cambia, but also in genera of *Phytolaccineae*. Likewise, raylessness occurs in both suborders. Stem and wood anatomy does not provide decisive evidence for placement of *Sarcobatus* in *Phytolaccineae*, but it does not provide any evidence against that treatment.

Introduction

Behnke's (1997) discovery of distinctive sieve tube plastids in *Sarcobatus* led him to remove the genus from *Chenopodiaceae*. In an earlier issue of this journal, Behnke (1997) assembled much information about the genus and suggested that the new family he created, *Sarcobataceae*, belongs in close proximity to *Phytolaccaceae*. Behnke (1997) cited evidence from DNA analyses (Clement & Mabry, 1996; Downie & al., 1995, 1997) for this treatment. In the suborder *Phytolaccineae*, Behnke (1997) includes *Achatocarpaceae*, *Agdestidaceae*, *Aizoaceae*, *Barbeuiaceae*, *Nyctaginaceae*, *Phytolaccaceae*, *Rivinaceae*, *Sarcobataceae*, and *StegnospERMATAceae*. This suborder is a modification of *Phytolaccineae* as recognized by Heimerl (1934) and Thorne (in Cronquist & Thorne, 1994). The segregate families were mostly treated as subfamilies of *Phytolaccaceae* by Thorne (in Cronquist & Thorne, 1994).

Information from wood anatomy is often significant with respect to the classification system. Compilations of wood data for *Caryophyllales* have been offered by Metcalfe & Chalk (1950) and by Gibson (1994). A series of monographs on wood of these families is in progress in order to offer more extensive information. These papers include *Caryophyllaceae* (Carlquist, 1995), *Portulacaceae* and *Hectorellaceae* (Carlquist, 1998a), *Petiveria* and *Rivina* (Carlquist, 1998b), *Basellaceae* (Carlquist 1999a), *Agdestis* (Carlquist, 1999b), *Stegno-*

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spermataceae (Carlquist, 1999c), *Barbeuia* (Carlquist, 1999d), and phytolaccoid and rivinoid *Phytolaccaceae* (Carlquist, in press). This survey of families and genera of *Caryophyllales* has been undertaken to supply a more complete data base usable in revising the classification system for the order. The concept of *Caryophyllales* has changed considerably over the past century (Cronquist & Thorne, 1994), but most radically in recent years. The definition of *Caryophyllales* has recently been widened so as to include families with salt glands (*Frankeniaceae*, *Plumbaginaceae*, *Tamaricaceae*) as well as families with digestive glands (*Droseraceae*, *Nepenthaceae*) and some allied families (*Ancistrocladaceae*, *Polygonaceae*) by the Angiosperm Phylogeny Group (APG, 1998), based largely on the data of Williams & al. (1994). If this broader new definition of *Caryophyllales* is adopted, data from wood becomes even more important for comparison to the systematics of the order.

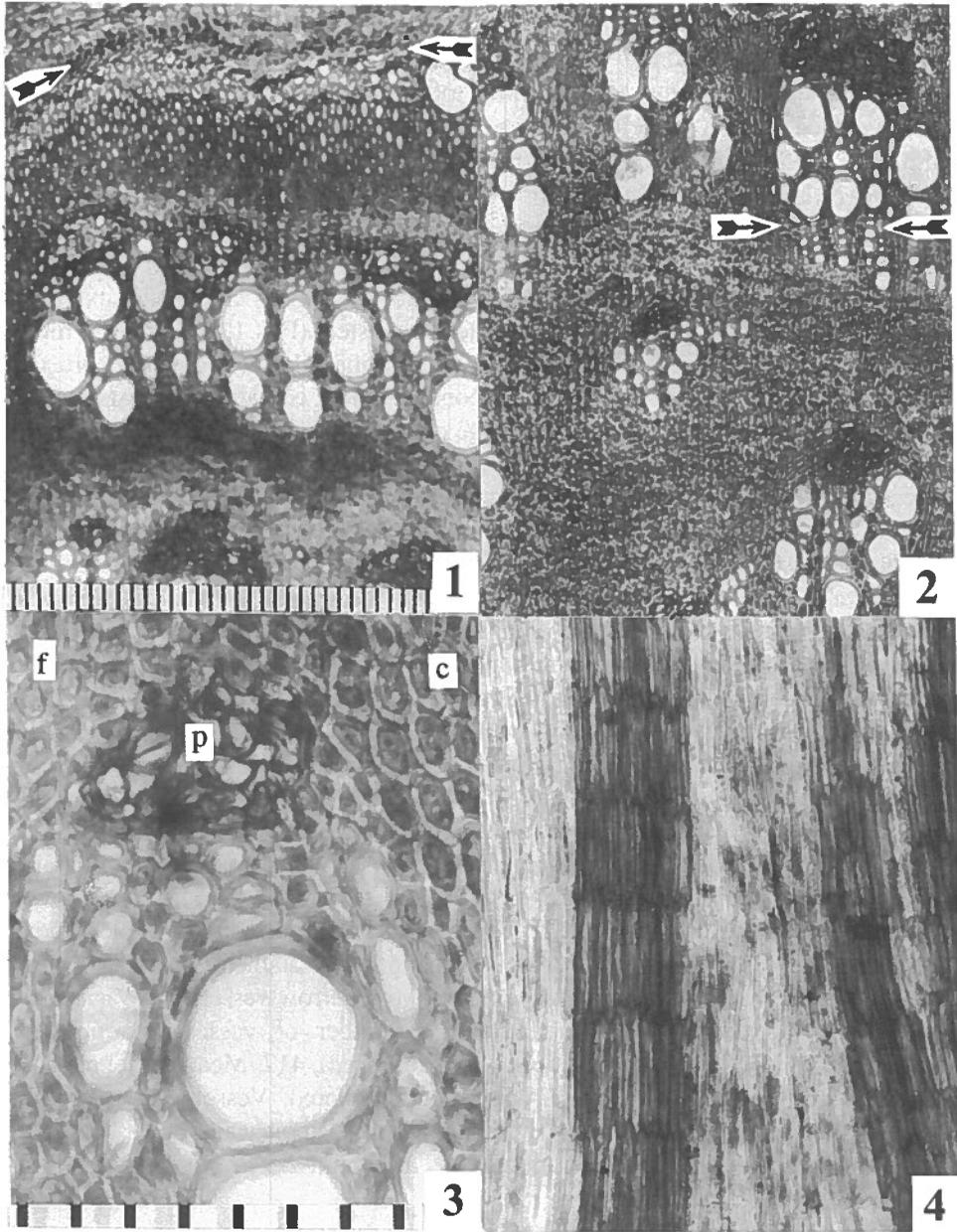
Sarcobatus, like many other families and genera of *Caryophyllales* s.str. (= the order as circumscribed by Behnke & Mabry, 1994), has successive cambia. The successive cambia of these *Caryophyllales*, as well as those of other dicotyledon families, have been subject to various interpretations and terminology. Details from more numerous genera concerning the action and products of these successive cambia, as well as the nature of their origin, are needed from genera outside *Caryophyllales* as well as within the order.

Material and methods

Stem material of *S. vermiculatus*, up to 8 mm in diameter, was collected from plants on the saline margins of Mono Lake, Mono Co., California, 12 Jun 1989, Carlquist 8038 (RSA). The stems were preserved in 50 % aqueous ethanol. Sections were prepared with a sliding microtome. Some sections were stained with a safranin-fast green combination and mounted in Canada Balsam as permanent slides (Figs. 1-4, 9). Other sections were left unstained, dried between clean slides, mounted on aluminium stubs, sputter coated, and examined with a Bausch & Lomb Nanolab scanning electron microscope (SEM). Macerations were prepared by means of Jeffrey's Fluid (equal parts 10 % formalin and 10 % chromic acid) and stained with safranin.

The stems of *Sarcobatus* provide exceptionally challenging microtechnical problems. The fibers of the conjunctive tissue are very hard, yet the phloem strands within the stem are soft; crystals in the conjunctive tissue provide a further impedance. Softening agents proved unsuccessful because any degree of softening that allowed better sectioning also resulted in expansion and distortion of walls, creating numerous artifacts.

Vessel diameter was measured as mean vessel lumen diameter. The figures on vessel diameter are based on random scans of transactions and do not exclude conjunctive tissue. Terms follow the IAWA Committee on Nomenclature (1964); the concept of vasicentric tracheid is based on Carlquist (1985). The sliding microtome sections at best represented only portions of the stem, and the hardness of the conjunctive tissues resulted in small cracks (Fig. 4) plus buckling of softer conjunctive tissue (out of focus band below vessels, Fig. 1).



Figs. 1-4. Sections of stem of *Sarcobatus vermiculatus*. – 1, transection from near surface of stem (top) inward; the lateral meristem is indicated by the pair of arrows; 2, transection of inner portion of stem, showing several vascular strands; arrows indicate terminus of a growth ring; 3, transection of vascular strand and adjacent tissues (f = conjunctive tissue fibers, p = phloem, c = conjunctive tissue parenchyma); 4, tangential section, to show storied nature of phloem (darker vertical strand to left of center) and lack of rays. – Figs. 1, 2, 4, magnification scale below Fig. 1 (divisions = 10 μ m); Fig. 3, divisions = 10 μ m.

Moreover, the conjunctive tissue did not stain readily despite variations in staining methods applied and so is relatively pale in Figs. 3 and 4. Extraordinary difficulties in sectioning and staining of woods like these (e.g., *Chenopodiaceae*) have been experienced by even the best workers (see illustrations by Fahn & al., 1986), and account for the lack of monographic work on woods of *Caryophyllales* with successive cambia.

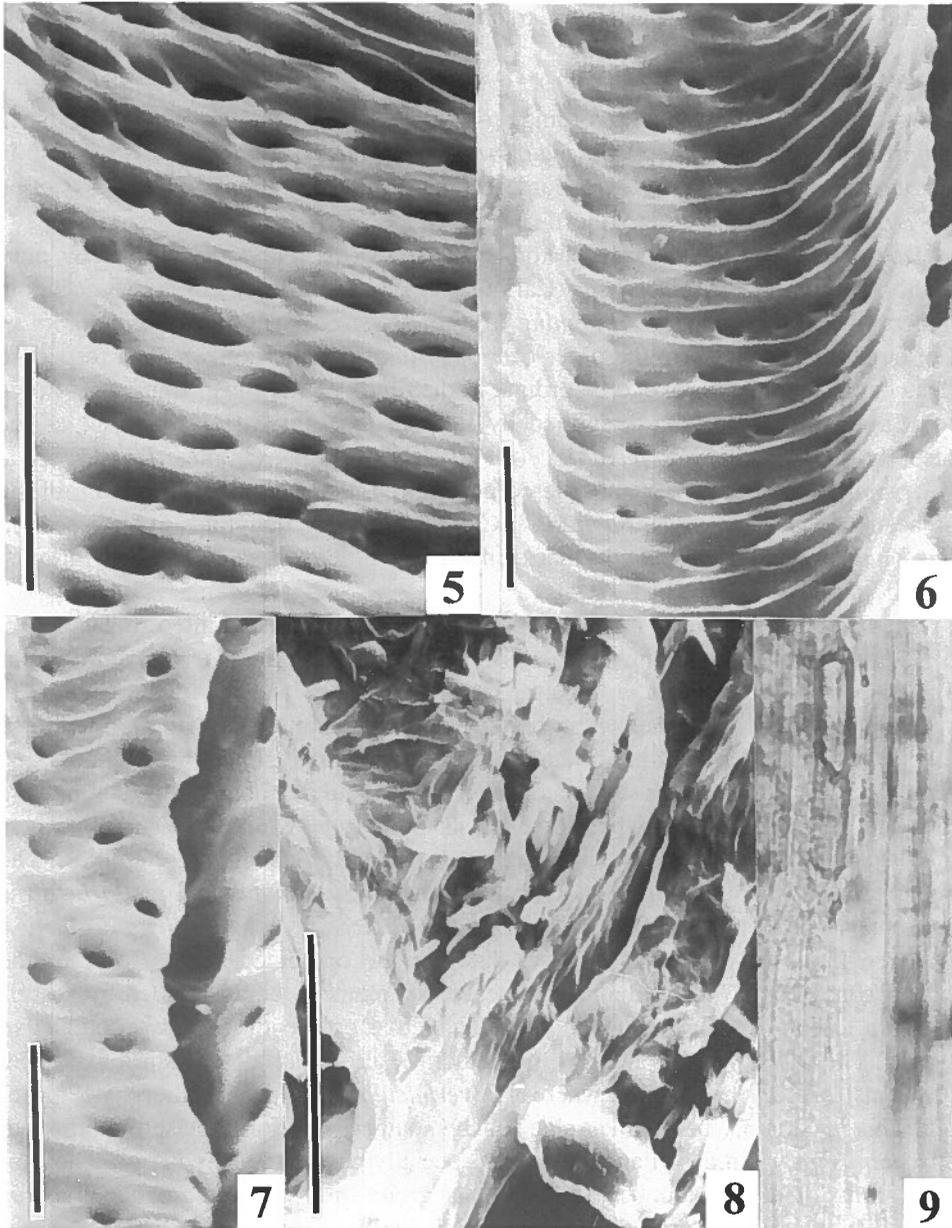
Wood and stem anatomy

At the exterior of the stem, there are remnants of primary cortex, the extent of which depends on the age of the stem. A lateral meristem (Fig. 1, top, arrows) forms in the inner cortex. The lateral meristem produces radial files of secondary cortex to the outside. Like the primary cortex, the secondary cortex contains idioblasts each of which bears either a styloid or an assemblage of separate smaller elongate crystals.

To the interior, the lateral meristem produces conjunctive tissue and, at intervals, (successive) vascular cambia each of which yields secondary phloem and secondary xylem. These vascular strands (Fig. 2) or bands (Fig. 1) are scattered throughout the conjunctive tissue. The conjunctive tissue consists of two kinds of cells: fibers, which have relatively thick lignified walls and contain small amounts of starch; and parenchyma cells, which have thinner lignified walls and contain larger quantities of starch because of their greater lumen diameter (Fig. 3). The parenchyma occurs in the form of tangential bands that interconnect strands of vascular tissue. The parenchyma cells are relatively short (mean = 98 μm) compared to the fibers of the conjunctive tissue (mean = 244 μm). Some of the parenchyma cells contain one to three elongate crystals (Fig. 9).

Sieve tube elements and phloem parenchyma (Figs. 3, 4) are about the same length as the conjunctive tissue parenchyma cells. Phloem parenchyma contains numerous slender elongate crystals (Fig. 8). In the secondary xylem, a few growth rings were observed (arrows, Fig. 2). Vessels are grouped in radial multiples (mean number of vessels per group, 7.3). Vessels range in lumen diameter from 7 to 46 μm (mean lumen diameter, 20 μm). In macerations, very narrow vessels and vasicentric tracheids are about equally abundant. Mean number of vessels per mm^2 of transsection (conjunctive tissue included in area surveyed), 417. Mean vessel element length, 93 μm . Perforation plates all simple, nonbordered. Vessel wall thickness, about 2.0-4.0 μm (wider vessels have thicker walls). Lateral walls of vessels have circular bordered nonvestured pits, pit cavities are about 2.5 μm in diameter (Fig. 7); pit apertures are oval (Fig. 7, right).

Sculpturing on the inner surfaces of vessels and vasicentric tracheids is in the form of grooves interconnecting pit apertures (Figs. 5-7). In many of the vessels, pairs of ridges accompany the grooves (Figs. 5, 6). Axial parenchyma is moderately sparse, all parenchyma cells are in contact with vessels or vasicentric tracheids. Axial parenchyma is not subdivided into strands. Rays are absent (zones of conjunctive tissue fibers or parenchyma between vascular strands do not meet the criteria of rays, as shown in Fig. 4). Sieve tube elements and conjunctive parenchyma tissue with lignified walls are storied (Fig. 4); this storied pattern is



Figs. 5-9. SEM photos (5-8) and light photomicrograph (9) from tangential sections of stem of *Sarcobatus vermiculatus* (5-7 show inside surfaces of vessels). – 5, surface showing grooves interconnecting pit apertures, a pair of ridges parallels most of the grooves; 6, surface showing grooves interconnecting pit apertures and more pronounced ridges paralleling the grooves; 7, surface of vessel with fewer, inconspicuous ridges, outside surface of vessel at right shows nonvestured nature of pits; 8, crystals from a broken phloem parenchyma cell, to show narrow shapes and small sizes; 9, rhomboidal crystal (upper left) in parenchyma of conjunctive tissue. – Figs. 5-8, magnification scales at lower left (bar = 10 μ m); Fig. 9, scale same as below Fig. 3.

shared by the vessels and vasicentric tracheids.

Discussion and conclusions

Sarcobatus is rayless; according to Gibson (1994) raylessness occurs in *Amaranthaceae* and *Chenopodiaceae* (= the suborder *Chenopodiineae*), but also in *Aizoaceae* and *Nyctaginaceae* (suborder *Phytolaccineae*). Behnke (1997) assigned *Sarcobataceae* to the latter suborder.

Sarcobatus has nonbordered perforation plates. This feature, neglected by most authors, occurs in *Phytolaccineae* (Carlquist 1999b-d, in press), but it also occurs in genera of *Portulacineae* (*Alluaudia* of the *Didiereaceae*, and *Chenopodiinae*; Carlquist, unpubl.). When the order *Caryophyllales* is better known with respect to this character, it may prove to be ordinal in distribution, and thus symplesiomorphic for *Caryophyllales* s.str. (as defined by Behnke & Mabry, 1994) as well as the recently expanded *Caryophyllales* (APG, 1998). For example, *Tamaricaceae* (*Caryophyllales* s.l.) have nonbordered perforation plates, as does *Santalum* in the adjacent (APG, 1998) order *Santalales* (Carlquist, unpubl.). Styloids in bark, seen in *Sarcobatus*, occur in bark and other stem tissues of *Phytolaccaceae* s.l. (Carlquist 1998b, in press).

The nature of the lateral meristem in *Sarcobatus* is of unusual interest. Two types of lateral meristems leading to successive cambia occur in *Caryophyllales* s.str. *Stegnosperma* exemplifies a diffuse lateral meristem (radial files of cells in secondary cortex) as a precursor for successive cambium formation (Carlquist, 1999c), whereas *Barbeuia* has a lateral meristem only a single cell in thickness that produces secondary cortex to the outside and vascular cambia plus conjunctive tissue to the inside. Both of these types occur in *Caryophyllales*, and further papers in this series will show the distribution in terms of genera and families. The occurrence of the same type of lateral meristem in *Sarcobatus* and in *Barbeuia* is consonant with Behnke's (1997) idea that *Sarcobataceae* belong in *Phytolaccineae*.

Three kinds of quantitative vessel data can be combined in the form of the Mesomorphy Ratio (vessel diameter times vessel element length divided by vessels per mm²). This ratio reflects not only conductive efficiency but also conductive safety. The Mesomorphy Ratio for southern Californian desert shrubs is 20.9 (Carlquist & Hoekman, 1985), whereas *S. vermiculatus* has a Mesomorphy Ratio of 4.5. This is certainly below the value for the southern California desert shrubs, but *Sarcobatus* grows in desert areas that are especially physiologically xeric because of soil salinity. The high number of vessels per group in *S. vermiculatus* (7.3) also is indicative of a very xeromorphic wood. Qualitative features that indicate xeromorphy in *S. vermiculatus* wood include presence of vasicentric tracheids (Carlquist, 1985) and presence of helical sculpturing on vessel surfaces. This sculpturing takes the form of grooves interconnecting pit apertures often with pairs of ridges accompanying each groove. This, together with other forms of helical sculpturing in vessels, is an indicator of xeromorphy in *Asteraceae*, which occupies a wide range of habitats and is well represented in xeric ones (Carlquist, 1966). Although vessel wall sculpturing also occurs in other *Caryophyllales* such as *Chenopodiaceae* (Gibson, 1994), the occurrence in *Sarcobatus* may be an autapomorphy, developed

independently of the feature in other *Caryophyllales*. The unusually xeromorphic nature of wood of *Sarcobatus* should not be interpreted as indicating close relationship to *Chenopodiaceae* or other *Caryophyllales* with similarly xeromorphic woods. The placement of *Sarcobatus* by Behnke (1997) in suborder *Phytolaccineae* is entirely conceivable on the basis of the stem and wood anatomy data above, even though these data do not decisively place it in that suborder as opposed to placement in the other suborders of *Caryophyllales* s.str.

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