ANATOMY AND MORPHOLOGY

Stem anatomy is congruent with molecular phylogenies placing *Hypericopsis persica* in *Frankenia* (Frankeniaceae): comments on vasicentric tracheids

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Stem and root anatomy of *Hypericopsis persica* is evaluated in light of molecular data reconstructing *Hypericopsis* within a clade of Asian *Frankenia*. No anatomical information contradicts the idea that *Hypericopsis* should be subsumed within *Frankenia*. Anatomy in the two genera is comparable, taking into account the unusual habit of *Hypericopsis*, which consists of slender, short-lived shoots from a long-lived caudex, whereas most species of *Frankenia* are small shrubs with long-lived shoots. Wood of the slender stems of *Hypericopsis* is similar to twig wood of the related *Frankenia hirsuta* in qualitative and quantitative features but differs from mature wood of other species of *Frankenia* described in previous studies in having smaller cells and little storying. Wood of *Hypericopsis* is rayless and is made up mostly of libriform fibers and vessel elements associated with vasicentric tracheids. Axial parenchyma is occasional at the margins of growth rings. We briefly evaluate wood characters in the context of Caryophyllales s.l. and suggest characters that may be synapomorphies of clades within this group, e.g., minute lateral wall pits apparently characterize the clade comprising Plumbaginaceae, Polygonaceae, Frankeniaceae, and Tamaricaceae. That vasicentric tracheids elongate considerably beyond the lengths of the vessel elements with which they are associated is cited as a distinct ontogenetic difference between these cell types. Likewise, numerous vessel elements comparable in diameter to vasicentric tracheids were observed. These observations are offered as reasons to reject the concept of vasicentric tracheids as simply vessel elements that are too narrow for the formation of perforation plates.

KEYWORDS: Caryophyllales, central Asia, Frankeniaceae, systematics, vasicentric tracheids, wood anatomy.

INTRODUCTION

The evaluation of morphological similarities among taxa is particularly aided by a robustly-supported molecular phylogenetic hypothesis. The associations suggested by molecular studies are effectively complemented by searching for morphological variation that is congruent with the molecular phylogeny. In this paper, we present an account of the wood and bark anatomy of *Hypericopsis persica* Boiss. (Fig. 1) in the context of recent molecular phylogeny reconstructions showing that this taxon is nested within *Frankenia* (Frankeniaceae). Shortly after its description (Boissier, 1846), the single species of *Hypericopsis* was subsumed into *Frankenia* (Jaubert & Spach, 1847). The newer combination was not widely accepted, and the generic name *Hypericopsis* has been the most commonly applied (e.g., Chrtek, 1972). The separation of *Hypericopsis* from *Frankenia* has traditionally been justified by the higher number of stamens in *Hypericopsis* (16–24 vs. 3–12 in *Frankenia*). Likewise, sepal and carpel numbers are higher in *Hypericopsis* than in most *Frankenia* (Niedenzu, 1925).

However, recent molecular phylogeny reconstruction based on a combined parsimony analysis of DNA sequence variation in three loci (18S, *rbcL*, and tRNA Ser/Gly spacer) shows that *Hypericopsis* is nested well within an Asian clade of *Frankenia* (Cuénoud & al., 2002; Gaskin & al., unpubl.). Because of the diversity of cell types in stems, wood and bark are a potentially rich source of phylogenetically useful characters. Therefore, we compare wood and bark anatomy of *Hypericopsis* with *Frankenia hirsuta* L., an Asian species shown to be closely related and possibly sister to *Hypericopsis* (Gaskin & al., unpubl.). We expect to find no difference between the genera except for features associated with the unusual habit of *Hypericopsis*. Most species of *Frankenia* are small shrubs with long-lived stems. In contrast, *Hypericopsis* forms a long-lived caudex from

Fig. 1. *Hypericopsis* (*Frankenia*) *persica.* A, small plants near Shiraz, Iran, showing narrow stems (photograph by F. Ghahremani-nejad); B, detail of flowering shoots, scale bar = 1 cm (photograph by J. Gaskin).

which arise slender, cane-like twigs that periodically die back. Thus it is of particular interest to compare the wood of *Hypericopsis* stems with twigs of *Frankenia*. We also examine the wood of the long-lived root of *Hypericopsis* to see if there are major differences that contrast with the short-lived stems, and review wood anatomy of *Frankenia* in the context of the greater Caryophyllales. Frankeniaceae are plants of dry or saline environments in which very low water potentials are regular occurrences. In light of this, we consider selected adaptive aspects of *Frankenia* xylem, and propose a potential reason for raylessness in Frankeniaceae.

Frankeniaceae also provide an opportunity to examine the nature of vasicentric tracheids. We provide comments on the ontogenetic differences between vessel elements and vasicentric tracheids, observations provided in part to refute the idea that vasicentric tracheids are simply vessel elements that are so small as to preclude formation of a perforation plate, a position taken by many authors (e.g., Esau, 1977).

MATERIALS AND METHODS

Samples of *Hypericopsis persica* stem and root were collected on the shores of the saline lake Daryacheh-Ye-Tashk (Iran: Fars province; between the villages of Gomban and Tashk, east of Shiraz, 29º 48' 26" N, 53º 35' 29" E, 1579 m, 18 May 2000, *Gaskin 995*, MO). *Frankenia hirsuta* stem samples were collected from an area of sand dunes along a small salt lake (Turkmenistan. Balkan province; near the city of Balkanabad, formerly Nebit-Dag, 39º 38' 34" N, 54º 10' 29" E, 0 m, 2 Jun 2000, *Gaskin 1065*, MO). Dry conditions permitted air-drying the samples in the field with the bark left intact. Samples from a single plant of *Hypericopsis* were available for study, the caudex of which was about 6 cm in diameter, with a single taproot 1.5 cm in diameter. The caudex gave rise to branches up to 5 mm in diameter and ca. 40 cm tall. For comparison with these slender branches, twigs of *F. hirsuta* 6 mm in diameter were selected. Roots of *F. hirsuta* were not collected.

Prior to sectioning, the samples were boiled in water and stored in 50% aqueous ethanol. Sections of *Hypericopsis* were made on a sliding microtome and stained either in safranin or a safranin-fast green combination. Bark was embedded in paraffin and sectioned on a rotary microtome. To section the thick, fragile bark intact with the xylem, stems of *Frankenia hirsuta* were softened in ethylenediamine and embedded in paraffin (method of Carlquist, 1982). Macerations were prepared with Jeffrey's solution and stained with safranin. Sliding microtome sections for scanning electron microscope (SEM) observation were air-dried overnight between glass slides and mounted with a conductive carbon cement to aluminum stubs. Paraffin-sectioned samples were mounted on stubs with Haupt's adhesive and cleared in xylene. After air-drying, samples of both treatments were sputter-coated in an Emtech K550 and observed with a Hitachi S-2460N in the SEM facility of the Instituto de Biología of the Universidad Nacional Autónoma de México.

Means are based on 25 measurements unless otherwise indicated. Vessel diameters are diameters of the lumen; diameter of vessels oval in transection is a chord estimated to be the diameter of a circle with the same area as the vessel. Wood terminology follows Carlquist (2001a). Conductive area was calculated from images using standard image analysis software. These calculations include only wider vessels and not vasicentric tracheids or very narrow vessels because of the difficulty of distinguishing these cells consistently from libriform

fibers in transections. In addition to calculation of vessel element length based on sampling of the total vessel element population, length means were also gathered for vessel elements 14.5 μm or narrower to provide a basis for comparison with vasicentric tracheids, which almost never exceed this diameter.

RESULTS

Wood in both species examined is made up mostly of thick-walled libriform fibers and vessel elements with simple, non-bordered perforation plates. Perforation plate angle ranges from 90° to nearly parallel with the element axis, especially in the narrowest cells, a high proportion of which are fibriform. Vestures were not noted with light or electron microscopy. Imperforate tracheary elements are present in the form of vasicentric tracheids and libriform fibers. Libriform fibers are non-septate and have simple pits. Vasicentric tracheids may form complete sheaths around vessels but often do not. Macerations are essential for distinguishing vasicentric tracheids from narrow vessel elements, because this is impossible to do dependably in sections. Axial parenchyma is not a regular feature of the material examined, but is found occasionally at the margins of growth rings. When present, at least part of each mass of axial parenchyma is always found contacting vessels and may thus be considered paratracheal. These cells are fusiform and usually not divided into strands. Tyloses and reaction wood were not observed. Storying was not common in the samples examined, but when present involved mostly vessel elements.

***Hypericopsis persica*: root.** — Slightly larger, more numerous vessels characterize earlywood (note dense band of large vessels traversing Fig. 2A just above center; vessels are smaller and less common just above this band), with bands of axial parenchyma occasionally terminating a ring (Fig. 2B shows this phenomenon in the stem). Normal and fibriform vessel elements are present in approximately equal quantities. Mean vessel diameter is 18.4 μm; mean vessel element length is 81 μm (N = 50). The mean length of vessel elements 14.5 μm or less in diameter is 73.7 μm. Vessels are usually solitary, with a mean of 1.4 vessels per group. When grouped they are usually in tangential or diagonal pairs, more rarely in globular groups of up to four vessels. Vessels are rounded in transection, although the rounded lumen may contrast with an angular external surface (Fig. 2B). Vessel density is 230.3 vessels per mm^2 with a conductive area of 0.12 mm^2 of vessel area per mm^2 of transection. Vessel-vessel and vessel-vasicentric tracheid pits are alternate, with narrow oval apertures and round to slightly polygonal cavities. Rarely, the apertures of two adjacent pits may be confluent. Vessel-libriform fiber pits are smaller, with no or only slight borders, and are more sparse. Mean vessel wall thickness is 2.7 μm. Imperforate tracheary elements are present in the form of abundant libriform fibers and the less-common vasicentric tracheids (Figs. 2C, D). Mean libriform fiber length is 226.1 μm; mean libriform fiber diameter is 18 μm. Libriform fiber wall thickness is 2.1 μm. Mean dimensions of vasicentric tracheids are 101.2 μm in length and 12.6 μm in diameter. In addition to the occasional bands of axial parenchyma mentioned above, plates of axial parenchyma that resemble rays in transectional appearance were irregularly encountered (Fig. 2B). These plates, the cells of which were commonly observed to bear druses, always were in contact with the tangential parenchyma bands and were of limited radial extent. These aggregations do not appear to provide a means of regular communication between the interior and periphery of the stem, and true rays are absent.

All the cells of the 10 or so layers of phellem are filled with very dark contents. The 5–7 ranks of phelloderm cells are apparently free of such contents. The periderm is underlain by a layer approximately 20 cells thick of cortical parenchyma, the cells of which are readily distinguished from the phloem parenchyma cells that are interior to them because of the presence of radial divisions in the often tangentially-widened cells of the cortical parenchyma. Fibers are not formed in the secondary phloem, but highly sclerified fibers can be found scattered among the cells of the inner cortical parenchyma. The peridermal cells occasionally bear druses, the cortical and phloem parenchyma much more commonly so (Fig. 2E). In these latter cell types, crystals that are basically rhomboidal or rhomboidal transitional to druses are occasionally found (Fig. 2F).

***Hypericopsis persica*: stem.** — Growth rings are present in the form of slight fluctuations in vessel abundance and vessel and fiber diameter. Some rings are associated with a band of axial parenchyma (Fig. 2B). Normal and fibriform vessel elements are present in approximately equal quantities. Vessel elements average 12.8 μm in diameter. Vessel elements often have a single tail at one end. This tail is often about a quarter of the total cell length, which averages 84.7 μm. The narrowest vessel elements average 70.9 μm in length. Vessel grouping is as described for the root with the exception that large clusters of many small vessels were observed in one stem (this area was not included in vessel density and conductive area calculations). Mean vessel density is 311.2 vessels/mm^2 with a conductive area of 0.08 mm^2 per mm^2 of transection. Lateral wall pitting is as described for the root. Mean vessel wall thickness is 3.1 μm. Vessels are rounded in transection, being generally round to slightly radially oblong. Mean libriform fiber dimensions are 179

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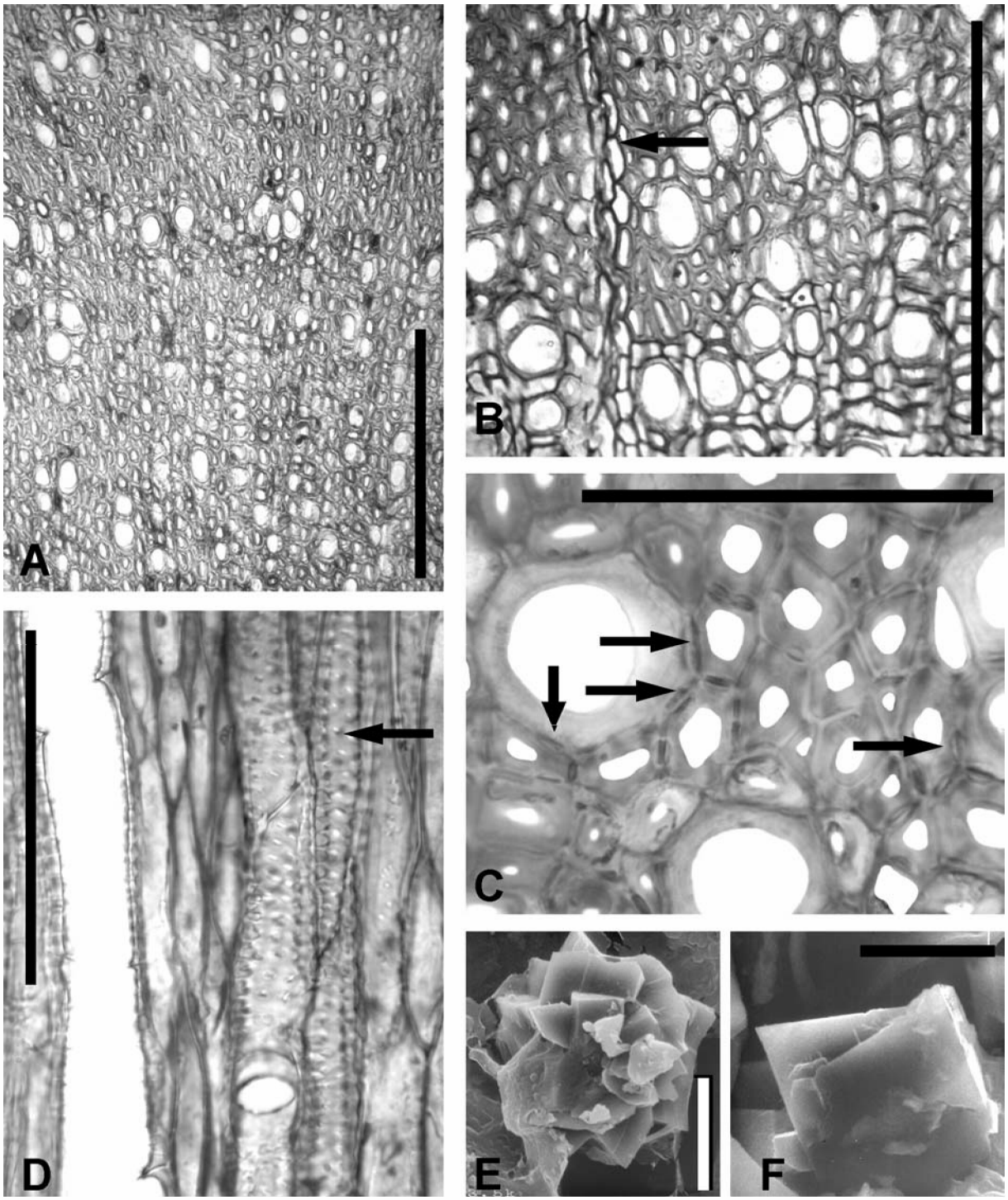

Fig. 2. Wood and bark of *Hypericopsis* (*Frankenia*) *persica*, LM and SEM images. A, root wood transection showing raylessness and faint growth rings, scale bar = 250 µm; B, stem transection showing band of axial parenchyma (thinner-walled cells at bottom) and a ray-like plate of axial parenchyma (arrow), scale bar = 250 µm; C, transection from stem showing vessels, vasicentric tracheids, and libriform fibers (some vessel-vasicentric tracheid pits are indicated by arrows), scale bar = 50 µm; D, root wood, tangential section showing a vessel at left and just to the right of the middle of the image [fusiform axial parenchyma cells are between the vessels; parts of three vasicentric tracheids (one indicated with arrow) are to the right of the right vessel; libriform fibers with minute pits are at right], scale bar = 100 µm; E, SEM image of druse from transection of stem phloem parenchyma, scale bar = 10 µm; F, SEM image of rhomboidal crystal from transection of root cortical parenchyma, scale bar = 5 µm.

μm long, 11.1 μm in diameter, with a mean wall thickness of 1.8 μm. Vasicentric tracheids are broadly fusiform, with mean dimensions of 92.5 μm in length, and 12.9 μm in diameter. As in the root, axial parenchyma is occasionally observed in bands or, more rarely, plates of limited extent (Fig. 2B), and the stem is rayless.

The bark of the stem is similar in qualitative characteristics to that of the root, with the exception that resin-like droplets are common in cortical cells.

***Frankenia hirsuta*: stem. —** Growth rings are faint (Fig. 3A), with most rings being characterized by vessels fluctuating slightly in abundance. Some rings are terminated with a narrow band of axial parenchyma. Fibriform vessel elements made up about 40% of the elements observed. Mean vessel element dimensions are 92.0 μm long and 12.6 μm in diameter. Vessel elements in the smallest diameter classes (<14.5 μm; comparable in diameter to vasicentric tracheids) have a mean length of 84.3 μm. Vessels are generally solitary (Figs. 3A) or in occasional pairs, and average 1.5 vessels per group. Vessels average 375 per mm^2 with a conductive area of 0.08 mm^2 per mm^2 of transectional area. Pitting is usually alternate, and varies from narrowly oval apertures with slight borders to broadly oval apertures with distinct rounded borders. Vessel walls have a mean thickness of 4.7 μm. Irregular convolutions observed in some vessel and fiber walls (Fig. 3B) may be an artifact resulting from the use of ethylenediamine. Pits occur in more or less helical grooves (Fig. 3C, D). Occasionally, in vessels surrounded by parenchyma, pits may be very wide and irregular in arrangement. Vessels are generally rounded in transection, sometimes somewhat radially widened, with external contours being angular at times (Fig. 3B). Libriform fibers are broadly fusiform with intrusive tails moderately differentiated from the main body of the cell. Mean fiber length is 166.1 μm and mean diameter is 14.0 μm with a wall thickness of 2.7 μm. Vasicentric tracheids are found adjacent to vessels (Fig. 3F) and average 106.4 μm in length and 8.7 μm in diameter. Narrow bands of paratracheal axial parenchyma were uncommon in the outer secondary xylem. Rays are absent (Fig. 3E). No crystals were observed in the xylem.

The phellem is composed of 10–20 layers of boxlike cells most of which are filled with dark brown contents. The phelloderm is of 5–6 layers and, like the phellem, lacks crystals. The cortex consists of 20–25 layers of rounded, often tangentially widened cells that lack crystals. In contrast, the cells of the phloem are much smaller and often contain single crystals, usually druses but rhomboidal and transitional crystals were also observed. Elongate sclerenchymatous fibers were common in the cortical parenchyma. A few such fibers appeared in the outermost phloem near the phloem-cortex interface, but never in the innermost phloem.

DISCUSSION

Systematics. — Wood anatomical information is entirely congruent with the notion that *H. persica* belongs in *Frankenia*. Both taxa have basically identical wood with vessel elements bearing minute lateral wall pits in an alternate arrangement, vasicentric tracheids, libriform fibers as the dominant axial elements, small amounts of axial parenchyma, and no rays. More compelling are fine-scale similarities such as the small, narrow sizes of vessel elements, which average 12.7 μm in diameter and 88.4 μm long in the stems examined. Whalen (1987) highlighted the small size of axial elements in *Frankenia*, noting that just 10% of dicots at large (based on Metcalfe & Chalk, 1950) have vessels less than 40 μm in mean diameter, and just 5% have mean vessel element lengths of less than 200 μm. The findings reported here also agree with Surgis (1922; *fide* Metcalfe & Chalk, 1950) in the presence of cortical fibers in *Hypericopsis*. The main difference between the material studied and that reported in the study of Whalen (1987) is that axial parenchyma and storying were more common in the material that she studied, which were generally larger stems than those used here.

Monophyly of the sister families Frankeniaceae and Tamaricaceae has been confirmed by recent molecular phylogeny reconstructions (Gaskin, unpubl.). The main stem anatomical differences between the two families are the large multiseriate rays of Tamaricaceae versus the raylessness of Frankeniaceae, and the lack of vasicentric tracheids in Tamaricaceae. Likewise, Metcalfe & Chalk (1950) report water-storage tracheids in the cortex of young stems of *Tamarix*, but these were not observed in Frankeniaceae. Similarities that can be cited between the two families include similar pitting patterns at vessel-vessel and vessel-ray interfaces and fusiform axial parenchyma cells (Tamaricaceae wood characteristics from Metcalfe & Chalk, 1950 and lists of Carlquist, 2001a).

In a larger phylogenetic context, the material examined here shares the non-bordered perforation plates that may be a synapomorphy of the broadly-defined Caryophyllales + Santalales (Carlquist 2000, 2001b; Caryophyllales as delimited by phylogeny reconstructions of Cuénod & al., 2002, and references therein). Minute lateral wall pits have been reported in Plumbaginaceae and Polygonaceae (Carlquist & Boggs, 1996), which together may form the sister group to the Frankeniaceae + Tamaricaceae clade, so this character may be a synapomorphy of the four-family clade. Plumbaginaceae and Polygonaceae share the presence of silica bodies (Carlquist & Boggs, 1996), but these are apparently absent in the Frankeniaceae + Tamaricaceae clade. Within the four-family clade, raylessness seems

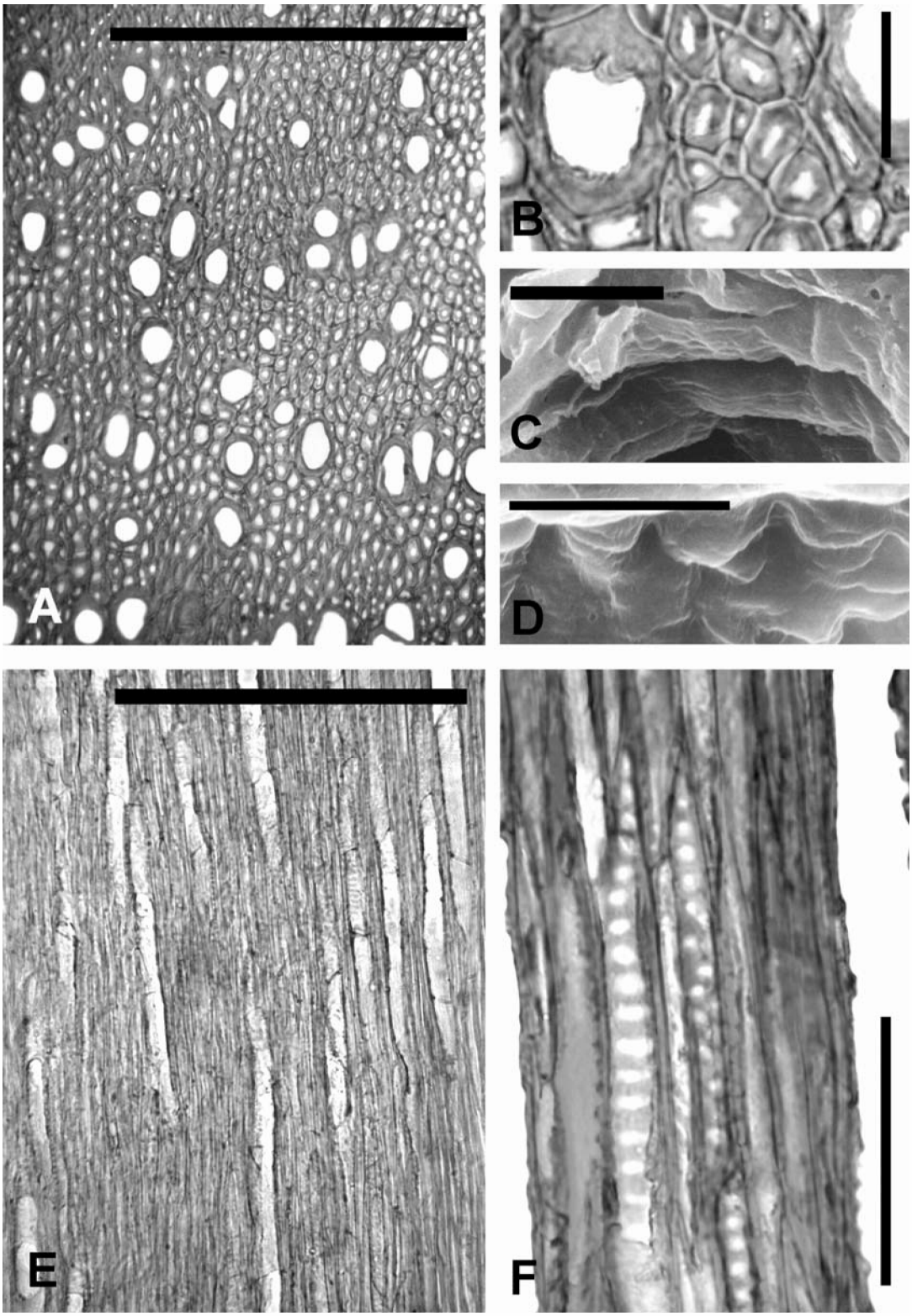

Fig. 3. Stem wood of *Frankenia hirsuta*, LM and SEM images. A, transection showing raylessness and faint growth rings, scale bar = 250 µm; B, transection showing thick-walled fibers and vessel elements, scale bar = 25 µm; C, SEM image of vessel interior from transection, scale bar = 5 µm; D, SEM image of vessel interior from tangential section, scale bar = 10 µm; E, tangential section showing raylessness, scale bar = 300 µm; F, tangential section showing vasicentric tracheids (conspicuously-pitted cells at middle) surrounded by libriform fibers, with vessels at left and right, scale bar = 50 µm.

independently derived in Frankeniaceae and some Plumbaginaceae. In Tamaricaceae and Polygonaceae, rays are multiseriate to uniseriate and do not conform to paedomorphic types that would suggest secondary woodiness. Therefore, their presence in these families seems most likely symplesiomorphic. Fibrifrom vessel elements are reported here in *Frankenia* and have been noted in *Drosophyllum*, *Nepenthes*, and Dioncophyllaceae (Carlquist & Wilson, 1995), which are likely to be part of the sister group to the four-family clade that includes Frankeniaceae. The distribution of these structures may be due to shared ancestry; ecological or habital correlations seem unlikely given the very distinctive habits and habitats of these taxa. Höster & Liese (1966) cite absence of reaction wood in Plumbaginales, Polygonales, Caryophyllales and Tamaricales as conceived by Takhtajan (1959).

Adaptive aspects: anatomical correlations with habit and ecology. — Numerous anatomical correlations with habit and ecology were noted in American *Frankenia* by Whalen (1987), including smaller vessel element length and diameter with smaller internode lengths, which were in turn found to be correlated with habit, with cushion plants having the shortest internodes. Comments here are limited to correlations not addressed in Whalen's study. *Hypericopsis* is not directly comparable in habit to any of the species that Whalen examined, eight of which were small shrubs and three of which were cushion plants. Nevertheless, cell dimensions of the material examined here are within the range of mean dimensions that she encountered among species (14–31 µm vessel diameter, walls included; 64–116 µm vessel element length; 146–306 µm libriform fiber length). That the measurements reported here are toward the small end of this range can be accounted for by the fact that the stems of *Hypericopsis* are short-lived and are best compared with twigs rather than the older axes with more secondary xylem accumulation. Consistent with this notion is the observation that the dimensions of cells in twig wood of *F. hirsuta* are comparable to those reported in *H. persica*. Following a frequently-documented trend, vessel diameter and conductive area in the root of *Hypericopsis* are notably greater than that of the stem of either of the species surveyed.

Thick vessel walls have commonly been cited as a consequence of selection for mechanical strength to resist the highly negative xylem pressures that desert shrubs commonly experience (Carlquist, 1980; Baas & al., 1983). However, the vessel wall alone may be insufficient to resist implosion and stresses are likely propagated to adjacent cells via the middle lamella (Hacke & Sperry, 2001). Hacke & al. (2001) found strong correlations between cavitation resistance and the thicknesses of vessel walls relative to vessel diameter in a variety of dicotyledonous shrubs and trees. The authors suggest that thickness of vessel and fiber walls may be the result of selection for resistance to implosion in the face of extreme negative xylem pressures rather than selection for mechanical strength of stems and roots. Stem features of Frankeniaceae support this hypothesis. Thick vessel and fiber walls and very narrow vessels are conspicuous features of Frankeniaceae, all of which are small-statured plants that would not appear to require exceptional amounts of support tissue. This is even more striking in the relatively short-lived twigs of *Hypericopsis*.

Moreover, the elimination of rays from the stems of Frankeniaceae may be a further factor that eliminates weak vessel contact points that would be vulnerable to implosion. Carlquist (1975) has postulated that raylessness may result from selection for increased mechanical strength in stems of limited duration and xylem accumulation. If, as Hacke & al. (2001) have suggested, selection for high-density woods with thick vessel and fiber walls is not so much the result of selection for stem support as cavitation resistance in some species, then, in some cases, elimination of rays could be the result of similar selection pressure. Stems of *Frankenia* are frequently very long-lived, and do not fit the architectural paradigm embodied in the notion of raylessness increasing mechanical strength in the stems of such genera as *Plantago* and *Aeonium* (Carlquist, 1970, 1975, 2001a). These plants generally have large piths and cortices, with a small amount of very strong xylem, and relatively short-lived stems. Instead, Frankeniaceae have small piths with thick cylinders of xylem, with some species of *Frankenia* employing successive cambia as a means of enervating the stem in the absence of rays (e.g., *F. grandiflora*, Barghoorn, 1941).

Vasicentric tracheids. — The interpretation offered here differs from that of Whalen (1987), who identified these cells as vascular tracheids. These cells are not limited to the last-formed layers of a growth ring, are adjacent to vessels, and thus must be considered vasicentric tracheids (in the sense of Carlquist, 1985).

Vasicentric tracheids are presumably derived from evolutionary modification of vessel elements. If vasicentric tracheids were simply vessel elements so narrow that they were unable to form perforation plates, then one would expect that vasicentric tracheids would be of similar length as normal vessel elements and that vessel elements of comparable diameter to vasicentric tracheids should not occur. However, the vessel elements in the material examined, especially the very narrow vessel elements comparable in diameter to vasicentric tracheids, are much shorter than vasicentric tracheids (e.g., 73.7 µm vs. 101.9 µm in the root of *Hypericopsis*), showing that vasicentric tracheids undergo considerably more intrusive elongation than vessel elements of comparable

diameter. Some vessel elements have perpendicular perforation plates, but many, especially those in the smallest size classes, have perforation plates oriented axially or nearly so. It might be supposed that vessel elements with lateral perforation plates are less constrained in their capacity to elongate intrusively than vessel elements with perpendicular perforation plates, but in the material studied here, no such trend was observed. This observation highlights the ontogenetic distinctness between vasicentric tracheids, which elongate moderately beyond the height of the fusiform cambial initials that gave rise to them, and vessel elements, which elongate scarcely if at all regardless of their diameter and perforation plate orientation. Additionally, there is complete overlap at the lower end of the range of vessel element diameter with vasicentric tracheid diameter, indicating that there is no mechanism requiring a certain minimum cell size for perforation plate formation. Vasicentric tracheids must thus be regarded as cambial products that are markedly distinguished in their ontogeny and function from vessel elements.

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