

Journal of the Torrey Botanical Society 132(2), 2005, pp. 173–186

## Wood, bark, and pith anatomy in *Pittocaulon* (~*Senecio*, Asteraceae): Water storage and systematics<sup>1</sup>

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OLSON, M. E. (Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito s/n, C.U., Copilco, Coyoacán A. P. 70-367, C. P. 04510, México, D. F., México). Wood, bark, and pith anatomy in *Pittocaulon* (~*Senecio*, Asteraceae): water storage and systematics. J. Torrey Bot. Soc. 132: 173–186. 2005.—Anatomy of wood and bark are described for all five species of *Pittocaulon*, the stems of which consist of a very thick, water storing pith surrounded by a thin-walled cylinder of xylem which is in turn surrounded by a thick, water-storing parenchymatous bark with a wide cortex. The samples examined came from a wide range of water availability, but showed only slight or no differentiation in vessel diameter or other characteristics that commonly track water availability closely. These observations are offered as supporting the hypothesis that the xylem of water-storing plants exists in a selective environment that is in many ways more similar to that of mesic plants than to that of sympatric conventional woody plants. It is hypothesized that the Young's modulus of the small amount of wood present is high, and that the parenchymatous cortex, which has collenchyma beneath the periderm in all species, contributes significantly to the support of the stems. The strata of the chambered pith in *Pittocaulon* may expand and contract with varying amounts of stored water. *Pittocaulon praecox* and *P. velatum* share a lack of sclerified elements in the bark and fusiform cell nuclei. Fibers and druses in the bark may be synapomorphies of the *P. bombycophole* + *P. filare* + *P. hintonii* clade.

Key words: adaptation, anatomy, Asteraceae, ecological wood anatomy, Mexico, *Pittocaulon*, *Senecio*, systematic wood anatomy.

The sensitivity with which wood anatomy reflects environmental conditions is such that two fields of science are built upon these responses. Ecological wood anatomy uses differences in wood structure between sites, and usually between species, to identify structure-function correspondences (Carlquist 1975, Lens et al. 2004). The field of dendrochronology examines even finer changes, with seasonal climate variations producing structural differences within the same individual. In most woody plants, vessel diameter is strongly and positively correlated with moisture availability, both within and between species (Hacke and Sperry 2004; note that it is actually the vessel wall thickness/ diameter ratio that is associated with water availability). An ex-

ception may be water-storing plants, whose vessels have been suggested to be buffered from the effects of external conditions within what can be thought of as an internally mesic environment (Carlquist 1975, Carlquist and Hoekman 1985). The genus *Pittocaulon* (~*Senecio*, Asteraceae) offers an opportunity to test this idea, because the five species of this group vary little in habit (Fig. 1) but occupy a variety of habitats in tropical Mexico, from moist to very dry. In all species, the stems consist of thick water-storing bark and pith, with a relatively thin xylem cylinder. *Pittocaulon* species bear small clusters of leaves in the rainy season and are leafless during the drought the rest of the year.

If plants that store water have an internally mesic environment, and more or less factoring out habit correlations, strong differences would not be expected in vessel dimensions between sites varying in moisture availability between or within species. Low vessel grouping would also be expected to be associated with an internally mesic environment, if vessel grouping represents an adaptation to conditions in which embolism due to water stress is likely (Carlquist 1984). Likewise, one would predict a failure of vessel or libriform fiber wall thickness to be negatively correlated with moisture availability because low xylem water tensions are avoided (Hacke and Sperry 2001). Vessel pit aperture dimensions would also be expected both to vary little

<sup>1</sup> Field and lab work were supported by National Geographic Society Committee for Research and Exploration Grant 7400-03, the Dirección General de Asuntos del Personal Académico/Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica, UNAM, the Instituto de Biología, UNAM, the Idea Wild Foundation, and the Research Grants Program of the Cactus and Succulent Society of America.

<sup>2</sup> Special thanks to Julieta Rosell and José Luis Vilaseñor. I am grateful for the assistance of Ivalú Cacho, Sherwin Carlquist, Jocelyn Durán, Calixto León, Alison Miller, and Ed Schneider. Dedicated to the memory of Camilla V.

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Received for publication July 7, 2004, and in revised form September 9, 2004.



FIG. 1. Habit of *Pittocaulon*. All species have thick stems that branch, following flowering, well above the base. Variation among species is chiefly in the number of branches produced from the base of the plant. A. *Pittocaulon velatum* ssp. *velatum* (910) leafing out at the beginning of the rainy season on a rocky cliff face. B. *Pittocaulon velatum* ssp. *tzimolensis* at the locality 944 in full leaf in mid-rainy season, with stems extending from a vertical cliff face. C. *Pittocaulon praecox* (1020) leafless in the dry season growing atop a basalt boulder.

across species and to be large relative to other plants that experience higher water tensions. This expectation is based on the observation that pits are often the site of drought-induced embolism and that small pit apertures weaken the vessel wall less and appear to be correlated with higher capacity to resist low xylem pressures (Sperry and Hacke 2004). I also test the assumption that, if water availability is not strongly affecting xylem characteristics, then plant size might be, by comparing the amount of xylem accumulated with vessel diameter across samples (cf. Gartner 1995).

The stem construction in *Pittocaulon* is almost unheard of in the temperate zone, and is mostly restricted to dry tropical areas. Dry tropical taxa have been neglected in anatomical studies relative to temperate and wet tropical plants, and therefore many stem structural plans, including that of *Pittocaulon*, remain to be documented anatomically. Additionally, anatomical study provides the foundation for ongoing biomechanical studies of *P. praecox* (Cav.) H. Rob. & Brettell. Study of how *Pittocaulon* stems support themselves with such thick, heavy bark and pith and with such a thin-walled cylinder of xylem promises to reveal a heretofore-undocumented plant biomechanical syndrome.

A special effort was made to examine distinctive features of the pith. First, the pith is notably larger in the lower parts of a stem than near the apex. Pith of woody plants is usually encased within a rigid xylem cylinder; once the xylem cylinder forms, the pith is not free to enlarge. I show that delayed fusion of fascicular areas permits this marked pith expansion. In addition, I suggest that the highly chambered pith of *Pittocaulon* represents a mechanism for accommodating varying quantities of water stored between wet and dry seasons.

Finally, anatomical similarities within the group are largely congruent with current hypotheses of relationships and are noted here. *Pittocaulon* is a segregate genus from *Senecio* Sect. *Terminales* and is probably a clade nested within *Senecio* s. l. All five species are found in Mexico, with one also occurring in Guatemala. All of the species are found in tropical dry habitats, often on rocky outcrops or steep cliffs. *Pittocau-*

*lon praecox* (Fig. 1C) is the most widely distributed member of the group, and is a conspicuous element of the lava flow vegetation in the Valley of Mexico. Occurring near such a large population center, it is the species that has been most-studied morphologically (e.g., Reiche 1921, Carlquist 1962, Ishiware and Baqueiro 2000). It is found in many parts of the central Mexican highlands from Zacatecas to Oaxaca. *Pittocaulon velatum* (Greenm.) H. Rob. & Brettell ssp. *velatum* (Fig. 1A) is also widely distributed in central Mexico, and occurs in dry, rocky areas from Nayarit to Oaxaca. The rest of the taxa are more restricted. *Pittocaulon velatum* ssp. *tzimolensis* (T. M. Barkley) B. L. Clark (Fig. 1B) is highly disjunct from *P. velatum* ssp. *velatum*, being found on rock outcrops and canyon walls in seasonally moist habitats in Chiapas and southeastern Oaxaca, with a limited number of localities in Guatemala. *Pittocaulon filare* (McVaugh) H. Rob. & Brettell was known until recently only from a single locality in Colima state but has recently been found in Jalisco; *P. hintonii* H. Rob. & Brettell is known only from two localities in Michoacán state, each locality corresponding to a distinct subspecies. One, *P. hintonii* ssp. *hintonii*, is included here. *Pittocaulon bombycophole* (Bullock) H. Rob. & Brettell (Fig. 1D) is restricted to Michoacán and Guerrero and a small part of México state. *Pittocaulon bombycophole* often grows on bare rock, as do other *Pittocaulon* species, but it also has more of a tendency than the others to occur as an understory element in open dry tropical forest. *Pittocaulon praecox* and *P. velatum* ssp. *velatum* are species of the highlands, usually being found above 1500 m, with the other taxa being lowland species usually found below this elevation.

**Materials and Methods.** Material was collected in the field and fixed in 70% aqueous ethanol. Sites were assigned a "moisture rank" by estimating moisture availability based on soil, slope, and type and extent of vegetation cover. Deeper soils, gentler slopes, and taller and denser vegetation were presumed to reflect higher water availability. Localities and their moisture ranks are listed in App. 1. Numbers in the text

←

This species branches abundantly from the base. D. *Pittocaulon bombycophole* (1008) in flower in the dry season; this species only forms abundant branches from the base with age. Figs. 1A, B, D, scale bar = 40 cm; Fig. 1C, scale bar = 75 cm.

following the species names correspond to collection numbers in App. I; vouchers are deposited at MEXU. The amount of xylem accumulated can be described in most woody plants by citing the stem diameter minus bark. However, the stem of *Pittocaulon* presents a very different situation, bearing a tube of xylem separating the very wide pith and bark. Therefore, the amount of xylem accumulated is represented by the distance from the outer limit of the pith to the cambium, and is referred to here as "xylem cylinder wall thickness", analogous to measuring the thickness of the wall of a pipe.

Samples that included both xylem and bark or xylem and pith were softened in 10% ethylenediamine, dehydrated, embedded in paraffin, cut with a rotary microtome (method of Carlquist 1982) at 13  $\mu\text{m}$ , and stained in safranin-fast green. Most samples that included only xylem were sectioned on a sliding microtome at 15–40  $\mu\text{m}$  and stained in safranin. Macerations were prepared using Jeffrey's solution (Ruzin 1999) and stained with safranin. Hand sections of some samples were stained with  $\text{KI}_3$  to check for the presence of starch. Measurements of vessel element and libriform fiber length, and libriform fiber diameter were measured from macerations. Quantitative data are based on 25 measurements using an ocular micrometer. Terminology follows Carlquist (2001).

T-tests were performed on vessel diameter between the samples of species of which more than one sample was available. A one-way ANOVA was performed to test for significant differences in vessel diameter between samples for which a moisture rank was available. To achieve equality of variances, one variable was inverse-transformed. Spearman rank correlations were conducted to search for correlations between moisture rank and vessel diameter, libriform fiber diameter, vessel-axial parenchyma pit height and width, and libriform fiber wall thickness. For comparison with moisture ranks, the weather station closest to each collection locality that was assigned a moisture rank was identified using the ERIC II database (IMTA 1995). Information from this database was used to calculate average annual rainfall values for each of these weather stations. The relationship between annual rainfall and average vessel diameter was described using standard Pearson correlation. Tests employed Statistica 6 (Statsoft Inc., Tulsa, OK). *Pittocaulon velatum* ssp. *tzimolensis* was excluded from the analysis because the only sample available was from a young seedling.

**Results.** Quantitative data are presented in Table 1. Crystal types in libriform fibers and ray cells and cell types showing storying are summarized in Table 2. Growth rings are faint, usually with smaller, more polygonal libriform fibers and ray cells in latewood (Fig. 2A, 2B). Sometimes a band of earlywood paratracheal axial parenchyma is formed (e.g. Fig. 2A). Most vessel elements are short and wide, with more or less perpendicular perforation plates. Grouping tends to be very low, but when present is chiefly found in radial pairs. Vessels usually show restriction patterns, rarely being in contact with rays (Fig. 2A, B). Perforation plates are almost always simple with distinct borders, and occasionally have Y-shaped or square projections of wall material in the perforation (Fig. 2C) or threadlike extensions of wall material, apparently of symmetrical disposition, resembling a partially-formed scalariform perforation plate (Fig. 2D). Lateral wall pits have distinct borders. Vessel-axial parenchyma pitting varies from alternate to pseudoscalariform. When alternate, the pit cavities may be strongly polygonal with oval apertures, but when pseudoscalariform, the border closely follows the aperture shape. Vessel-vessel pits have a similar range of arrangements, but individual pits tend to be smaller. Tyloses were not observed, but a deposit that often stained in safranin was common in vessels and adjacent axial parenchyma cells. This deposit appeared to have the form of globules of a semi-solid that fissured upon dehydration, and was sufficiently abundant to obscure vessel features in some cases.

Imperforate tracheary elements are present in the form of non-septate libriform fibers. Nuclei were observed in fibers of all species. Nuclei were compact and lozenge-shaped in all species but *P. praecox* and both subspecies of *P. velatum*, in which the nuclei are narrowly fusiform. Pits appear to be slightly larger on the radial faces of fibers than the tangential faces. So-called carbonized resin deposits were observed between some of the cells of most species. Tiny, elongate rhomboidal crystals or small druses were sparse in the libriform fibers of *P. flare*, *P. bombycophole*, and both subspecies of *P. velatum*. None were observed in the remaining samples.

Vasicentric axial parenchyma is present in all species, normally in a sheath a single cell thick surrounding vessels, but in some cases, the sheath may be 2–3 cells thick or incomplete. These cells are almost always divided into short

Table 1. Quantitative features of *Pittocaulon* xylem. Features marked “—” were not measured. Measurements are means with coefficient of variation in parentheses. Measurements in  $\mu\text{m}$  unless specified. CWT = xylem cylinder wall thickness (mm); VD = vessel diameter; VWT = vessel wall thickness; VL = vessel element length; V/G = vessels per group; VMM = vessel density (vessels/square mm); VPW = vessel-parenchyma pit aperture width; VPH = vessel-parenchyma pit aperture height; FL = libriform fiber length; FD = libriform fiber diameter; FW = libriform fiber wall thickness; C/S VP = cells per strand of vasicentric axial parenchyma; MRH = multiseriate ray height; RW = ray width in number of cells. Species abbreviations are as follows: *bom* = *P. bombycophole*; *fil* = *P. filare*; *hin* = *P. hintonii*; *prae* = *P. praecox*; *tzi* = *P. velatum* spp. *tzimolensis*; *vel* = *P. velatum* ssp. *velatum*; RI = root interior; RP = root periphery; NP = near pith.

	CWT	VD	VWT	VL	V/G	VMM	VPW
<i>bom</i> 903	9.9	51.7 (30)	3.5 (29)	220.9 (21)	1.3 (42)	11.6 (19)	8.5 (56)
<i>bom</i> 985	16.6	59.8 (20)	3.2 (25)	—	1.5 (54)	8.5 (19)	7.1 (47)
<i>fil</i> 897	5.0	52.9 (23)	2.8 (26)	189.9 (15)	1.5 (48)	11.1 (15)	7.3 (33)
<i>fil</i> 897 RP	—	52.7 (16)	—	311.1 (15)	—	—	—
<i>hin</i> 878	12.5	67.3 (21)	2.8 (30)	217.1 (20)	1.2 (42)	9.9 (15)	10.7 (50)
<i>prae</i> RI	—	61.3 (25)	2.7 (25)	—	1.9 (50)	21.9 (29)	—
<i>prae</i> RP	—	53.6 (24)	3.5 (37)	244.6 (11)	1.2 (32)	12.4 (25)	5.9 (53)
<i>prae</i> 1020	12.0	63.8 (29)	3.0 (38)	262.0 (17)	1.4 (41)	12.5 (39)	4.9 (19)
<i>prae</i> 1020 NP	—	59.0 (20)	2.5 (40)	—	1.8 (58)	16.3 (18)	—
<i>prae</i> 1021	12.1	59.9 (22)	3.4 (27)	263.0 (14)	1.3 (42)	7.5 (26)	7.2 (61)
<i>tzi</i> 944	1.0	38.5 (29)	—	219.0 (18)	2.1 (74)	—	—
<i>vel</i> 910	1.9	61.2 (25)	4.5 (22)	202.7 (17)	1.4 (49)	7.6 (30)	7.5 (34)
<i>vel</i> 978	22.5	59.8 (15)	3.9 (30)	229.0 (19)	1.5 (40)	13.8 (16)	6.5 (33)
	VPH	FL	FD	FW	C/S VP	MRH	RW
<i>bom</i> 903	2.5 (47)	594.1 (18)	39.9 (16)	1.4 (29)	2.1 (16)	1766.6 (71)	4.5 (15)
<i>bom</i> 985	2.4 (38)	574.0 (15)	47.7 (22)	1.9 (29)	1.9 (28)	2116.3 (49)	5.6 (16)
<i>fil</i> 897	3.6 (12)	421.5 (20)	42.3 (25)	1.8 (30)	1.9 (21)	1021.2 (51)	5.4 (18)
<i>fil</i> 897 RP	—	445.2 (18)	44.1 (20)	—	—	1218.1 (77)	3.6 (20)
<i>hin</i> 878	4.0 (37)	433.9 (25)	35.5 (15)	1.5 (25)	1.9 (32)	817.0 (40)	4.2 (18)
<i>prae</i> RI	—	—	—	1.7 (29)	—	—	—
<i>prae</i> RP	1.0 (21)	529.0 (15)	35.1 (23)	1.9 (21)	2.0 (25)	931.8 (36)	3.2 (18)
<i>prae</i> 1020	2.3 (23)	547.0 (18)	31.3 (27)	2.8 (25)	1.9 (26)	1273.4 (46)	4.9 (16)
<i>prae</i> 1020 NP	—	—	—	2.4 (24)	—	—	—
<i>prae</i> 1021	1.3 (21)	502.4 (22)	39.0 (23)	3.9 (22)	2.0 (26)	1009.0 (53)	4.4 (24)
<i>tzi</i> 944	—	463.9 (20)	30.4 (18)	—	—	—	—
<i>vel</i> 910	1.4 (15)	468.3 (27)	28.8 (22)	1.6 (33)	2.0 (26)	850.3 (57)	4.4 (24)
<i>vel</i> 978	1.3 (21)	499.0 (22)	35.0 (22)	2.0 (23)	2.0 (14)	1308.3 (37)	7.5 (28)

Table 2. Crystals and storying in *Pittocaulon* xylem. Species abbreviations as for Table 1. Cell type abbreviations are: LF = libriform fiber; VP = vasicentric axial parenchyma; VE = vessel elements; PAP = paratracheal axial parenchyma. Scorings are as follows: “—” = not observed; “t” = tiny; “r” = rare; “e” = elongate; “1/c” = small, usually one per cell; “o” = occasional; “d” = distinctly; “+” = smaller rays; n/a = cell type not present.

	LF: druses	LF: rhomboidal crystals	Rays: druses	Rays: rhomboidal crystals	Storying: LF	Storying: rays	Storying: VP	Storying: VE	Storying: PAP
<i>bom</i> 903	—	t, e	1/c	—	o	+	—	—	n/a
<i>bom</i> 985	—	—	1/c	r, t	o	+	—	—	n/a
<i>fil</i> 897	t	t	1/c	e	d	+	—	—	n/a
<i>fil</i> 897 RP	r	—	—	—	d	—	d	—	n/a
<i>hin</i> 878	—	—	1/c	r, te	d	+	—	—	n/a
<i>prae</i> RI	—	—	—	—	d	—	—	—	n/a
<i>prae</i> RP	—	—	—	—	d	+	d	d	d
<i>prae</i> 1020	—	—	—	—	o	+	d	—	n/a
<i>prae</i> 1020 NP	—	—	—	—	—	—	—	—	n/a
<i>prae</i> 1021	—	—	—	—	—	—	—	—	n/a
<i>tzi</i> 944	—	—	—	—	—	—	—	—	n/a
<i>vel</i> 910	r	t, e	o, t	—	d	+	d	—	d
<i>vel</i> 978	—	—	o, t	—	d	+	d	d	n/a

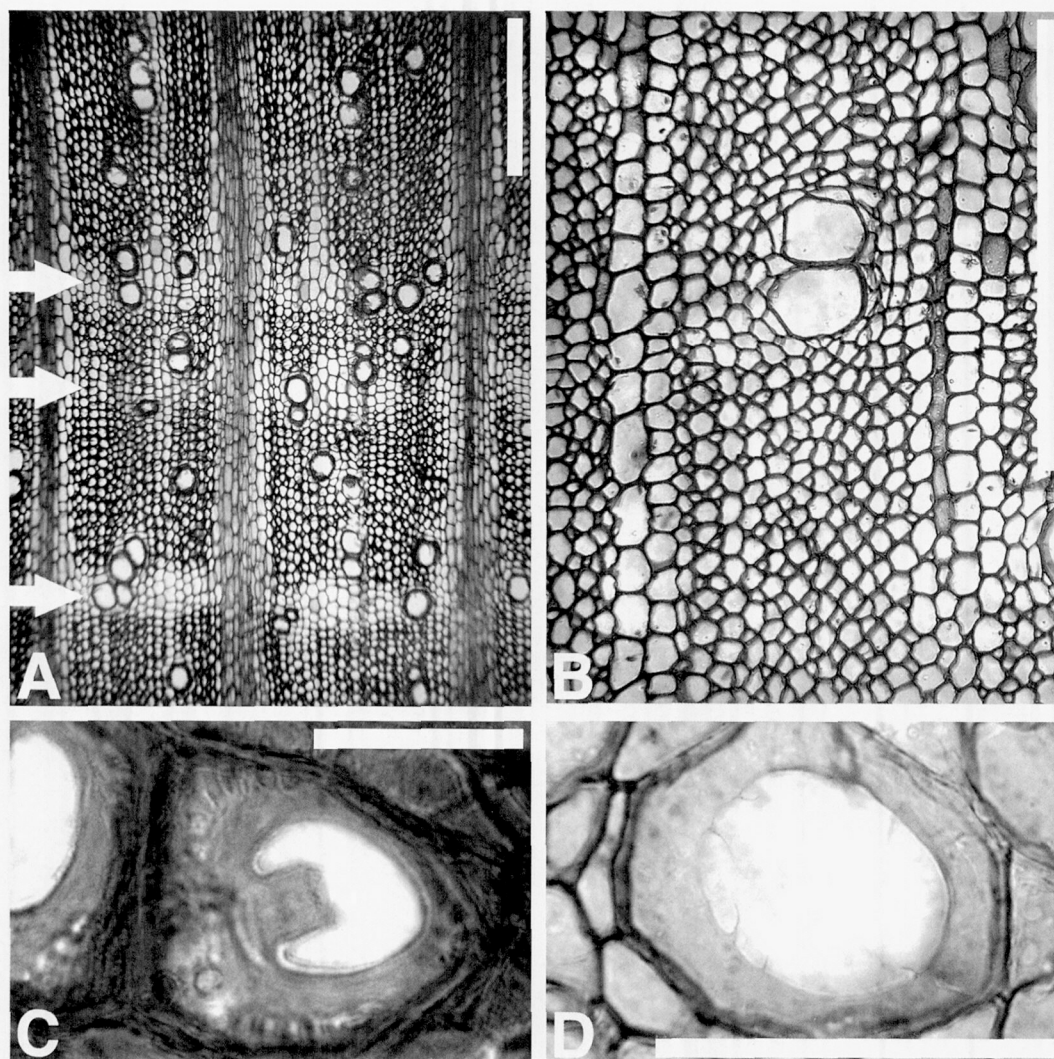


FIG. 2. Xylem of *Pittocaulon*, stem transections. A. *Pittocaulon velatum* ssp. *velatum* (978) showing portions of four growth rings, including three bands of paratracheal axial parenchyma, and vessel restriction patterns, with vessels only very rarely touching rays. Vessels are rarely grouped. B. *Pittocaulon hintonii* (878), showing large vessels not in contact with rays. A growth ring ends just below the vessel pair at center. C. *Pittocaulon bombycophole* (985) showing a common perforation plate variant, in which a square or Y-shaped tongue of wall material projects into the perforation. D. *Pittocaulon filare* (897) perforation plate with filiform extensions into the perforation, an uncommon variant. Figs. 2A, B, scale bar = 500  $\mu$ m; Fig. 2C, scale bar = 50  $\mu$ m; Fig. 2D, scale bar = 100  $\mu$ m.

strands. In *P. velatum* ssp. *velatum* and *P. prae-cox*, bands of paratracheal axial parenchyma may be present in earlywood (Figs. 2A, 3D). These cells are only occasionally divided into strands (Fig. 3D) but have distinctly thinner walls than adjacent libriform fibers and larger pits that resemble those of adjacent vasicentric axial parenchyma cells.

Ray histology in all species, from the largest to the smallest, consists of basically square cells

(Fig. 3E) with upright flanking cells. Almost all rays are multiseriate, from the pith outward. Uniseriate rays are very short, sometimes just one cell tall (Fig. 3B), and are very rare. As might be expected from the woody herb habit of *Pittocaulon*, the rays are very similar to Paedomorphic Type II (Carlquist 2001). The rays of *P. bombycophole*, *P. filare*, and *P. hintonii* usually have a single small druse per cell (Fig. 3F), and occasionally have tiny elongate rhomboidal



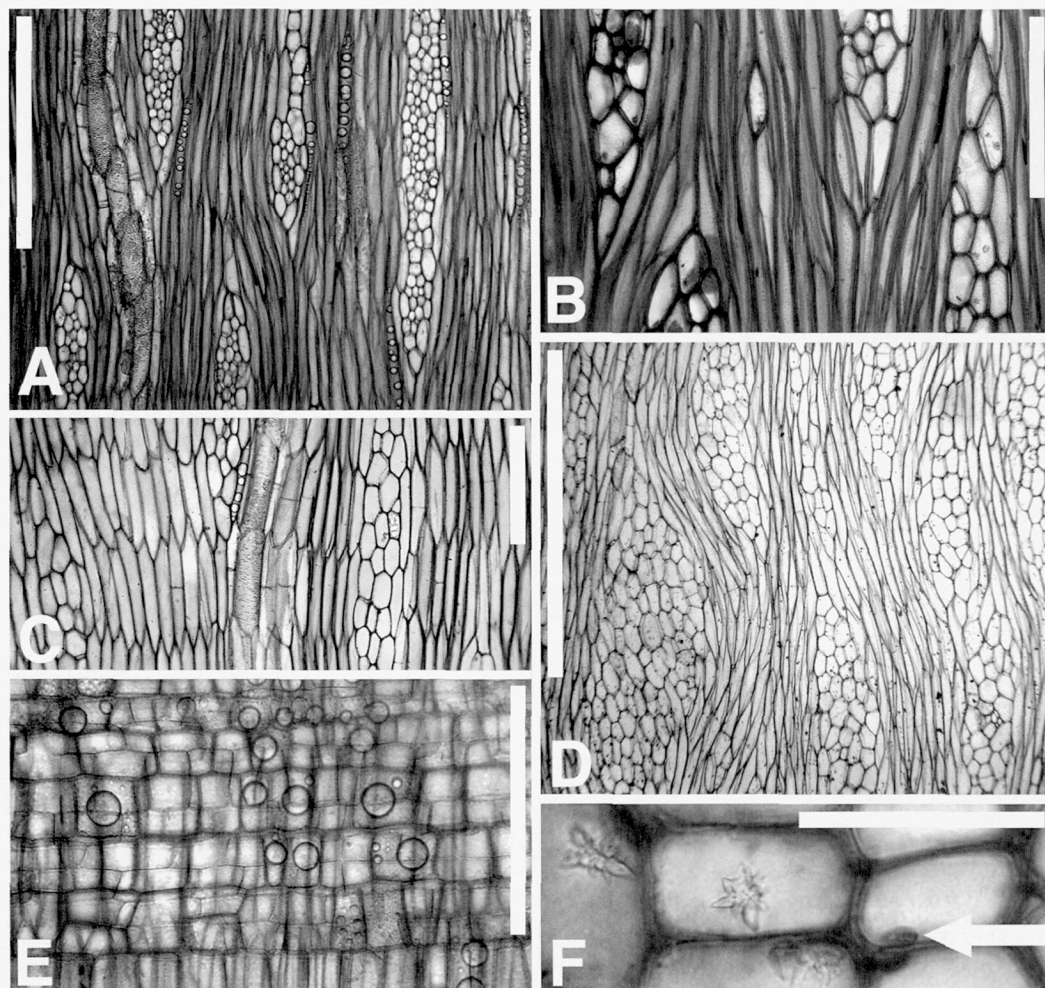


FIG. 3. Xylem of *Pittocaulon*; stem unless specified. A. *Pittocaulon velatum* ssp. *velatum* (910), tangential section, showing storying of libriform fibers and the smaller rays. Vasicentric axial parenchyma surrounds the vessel at left, and clear globules occasionally fill libriform fibers, as at right center. B. *Pittocaulon bombycophole* (985), tangential section showing druses in the cells of the ray at right, nuclei in the cells of the ray at left. A single-celled ray is to the left of upper center. C. *Pittocaulon praecox*, root tangential section showing storied axial parenchyma that is mostly undivided into strands (a strand of two cells is at lower left center). Vasicentric parenchyma is adjacent to the vessel at center. D. *Pittocaulon filare* (897), tangential section showing wide, short rays and convoluted vascular regions. A compound ray is at lower left. E. *Pittocaulon velatum* ssp. *velatum* (910) radial section showing mostly square or upright cells. F. *Pittocaulon hintonii* (878), transection showing druses in ray cells and nuclei in libriform fibers (arrow). Fig. 3A, scale bar = 500  $\mu$ m; Figs. 3B, C, E, scale bar = 250  $\mu$ m; Fig. 3D, scale bar = 1 mm; Fig. 3F, scale bar = 50  $\mu$ m.

crystals, whereas in those of *P. praecox* and *P. velatum* they are rare or absent. Small compound rays resulting from the fusion of three or four rays were occasionally observed (Fig. 3D).

Transparent spheres were commonly observed in ray (Fig. 3E) and axial parenchyma cells (Fig. 3C) and libriform fibers (Fig. 3A). These bodies lack a central hilum and did not stain in safranin or with KI<sub>3</sub>, indicating that they are not starch.

Storying (Table 2) was always observed in vasicentric axial parenchyma (Fig. 3C), and at least part of each section exhibited storying of libriform fibers (Fig. 3A). When present, paratracheal axial parenchyma was invariably storied (Fig. 3C). Storying in rays is likely mostly obscured by confluence of rays in vertical series, so rays were only vaguely storied at best. Adjacent vessels were only observed occasionally

because of the narrowness of vascular regions, but when vessels were adjacent, they had storied elements.

**MECHANISM OF PITH ENLARGEMENT.** From the tip of the stem toward the base, the stem markedly thickens at the two-year mark (Fig. 4A). Concomitant with this increase in external dimensions is an increase in the pith diameter. Fascicular areas are separate near the stem apices (Fig. 4B) and remain so for about two years. After two years, a continuous xylem cylinder is produced. Pith dimensions are enlarged in the interim not by cell division, but by marked enlargement of the parenchyma cells of the pith and interfascicular regions. For example, mean pith cell dimensions in the young portion of a stem of *P. praecox* was 3.2  $\mu\text{m}$ ; dimensions in the enlarged portion of the same stem was 12  $\mu\text{m}$ . Some bands of parenchyma within the fascicular areas also show evidence of enlargement in large stems (Fig. 4C).

**BARK.** In all species, bark at all ages contains narrow wedges of relatively intact phloem, a thick cortex, generally with evidence of many radial divisions, and a periderm of varying thickness (Figs. 5A, B). The main differences between species are the differing proportions of sclerified elements. *Pittocaulon praecox* and both subspecies of *P. velatum* lack sclereids of any kind in their bark (Fig. 5B), whereas *P. hintonii* and *P. filare* have moderately thick-walled brachysclereids in the cortex, and thick-walled fibers in the outer phloem. *Pittocaulon bombycophole* has fibers throughout the phloem and even sporadically in the phloem rays (Fig. 5A). Thin-walled brachysclereids are common in the cortical parenchyma in this species. Druses are common in the phloem rays and cortical parenchyma in *P. bombycophole* and *P. filare*, whereas druses are apparently restricted to the phloem rays in *P. hintonii*. Druses are absent from the bark of *P. praecox* and both subspecies of *P. velatum*. Small cambia with associated strands of phloem and sometimes xylem were occasionally observed in the cortical parenchyma of stems of all ages of *P. praecox* (Fig. 5B). The outermost 10–20 layers of cortical parenchyma in stems of all ages consist of collenchyma cells (Figs. 5A, B) with relatively thin walls that may be slightly lignified in older stems. The walls are usually more or less evenly thickened, but in some cases the tangential walls are slightly thicker than the radial walls.

**VARIATION OF VESSEL FEATURES WITH WATER AVAILABILITY.** Within-species t-tests revealed no significant differences between the means of any of the samples of the species for which more than one sample was available. Likewise, the ANOVA of vessel diameter indicated no significant differences between any of the samples. The only significant correlation found between moisture rank and the anatomical characters examined was vessel diameter (Spearman  $r = 0.83$ ; Fig. 6A). In contrast, the correlation between average annual precipitation and vessel diameter was negligible ( $r = 0.26$ ; Fig. 6B). Note that the ordering of localities from moist to dry did not always correspond between moisture ranks and climate station data (Table 3). Correlation between xylem cylinder wall thickness and vessel diameter was not significant.

**Discussion.** The vessels of two plants of different life form and phenology growing in the same place may experience very different selective environments. The chief means of managing water flow of an evergreen desert shrub are the vessel characteristics. Such a plant would almost certainly have narrow, thick-walled vessels with small pits, and it would not be surprising to find vasicentric tracheids. In great contrast, the chief means of water management of a succulent growing next to the same shrub are metabolic and phenological, with transpiration, likely at night, occurring virtually only when water is abundant and thus highly negative xylem pressures are not needed. Succulents thereby pass long dry periods with tissues replete with water while conventionally woody plants in the same site suffer highly negative xylem pressures. Therefore, the conditions that the vessels of a succulent experience are those of abundant moisture, and this inference is supported by the characteristics of the vessels of succulents: they are generally wide, thin-walled, and with gaping pit apertures (Carlquist 1975). None of these characteristics would contribute to mechanical reinforcement and are consistent with the idea that the vessels of succulents never are subjected to highly negative xylem pressures.

The marked succulence that characterizes the stems of *Pittocaulon* does appear to buffer xylem features from external conditions to a remarkable degree relative to what is commonly observed in conventional woody plants across a similar range of habitats. Figure 6 illustrates this point graphically, showing a striking lack of variation in vessel element diameter, libriform fiber



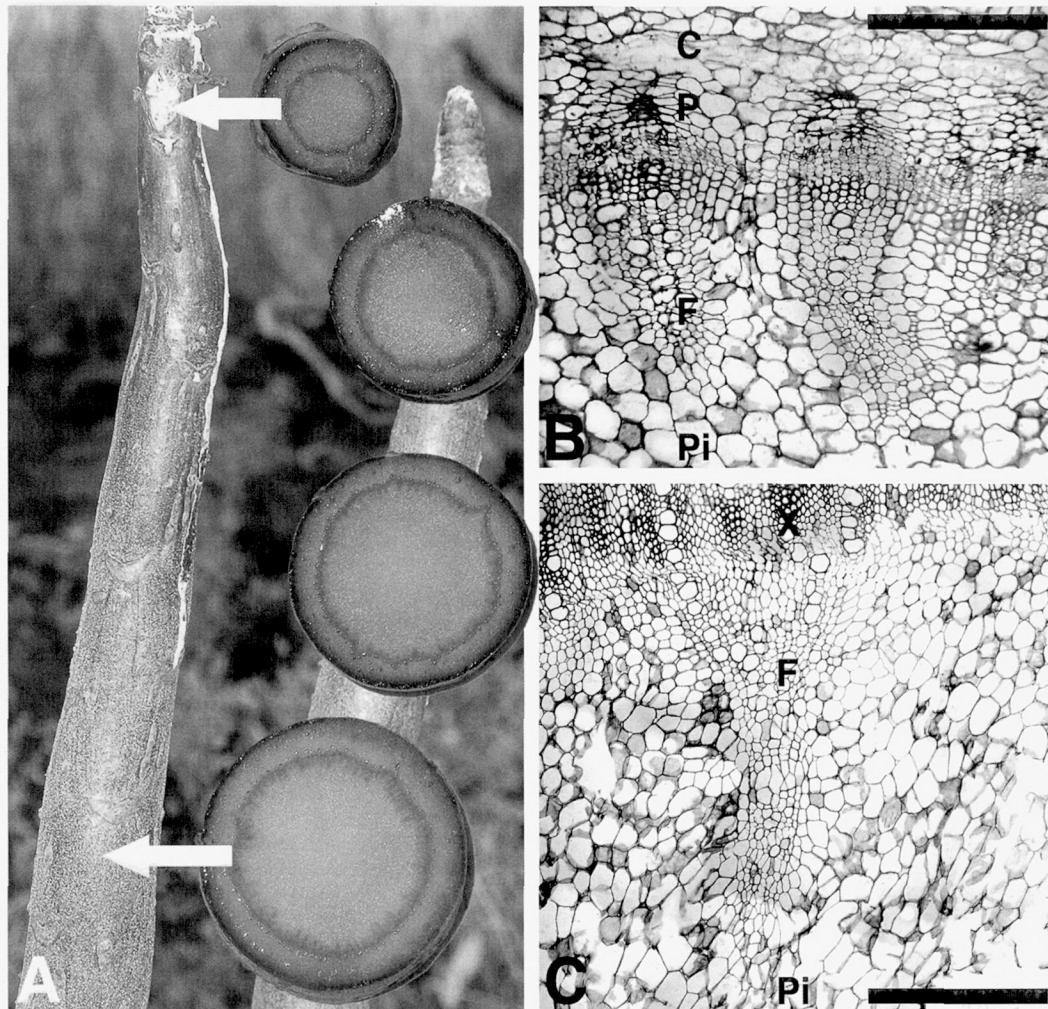


FIG. 4. Mechanism of pith enlargement in *Pittocaulon* (all images *P. praecox* 1020). A. Upper stem at left with sections of stem at right to show that pith becomes progressively larger with age. Two years of growth are shown. The upper arrow indicates the position of the section in Fig. 4B, the lower arrow that of Fig. 4C. B. Young stem, showing separate fascicular areas (F) and small pith (Pi) and interfascicular parenchyma cells. Small patches of phloem (P) are opposite the fascicular areas, and the cortex (C) is at top. C. Fascicular area (F) in an older stem. Distance from other fascicular areas is greatly increased by the enlarged pith (Pi) and interfascicular parenchyma cells, and there is some enlargement of axial parenchyma cells within the fascicular area. Note also the continuous xylem cylinder (X) at top and intact primary xylem. Fig. 4A, Upper stem section 1 cm in diameter; Figs. 4B, C, scale bars = 500  $\mu$ m.

diameter, vessel element wall thickness, and libriform fiber wall thickness across a broad range of water availability. The ANOVA was conducted using vessel diameter because these cells typically are the most sensitive to differences in water availability, yet no significant differences were found. I interpret this lack of variation to be consistent with the notion of an internally mesic environment in the succulent stems of *Pittocaulon*. All other factors being equal, a uniform internally mesic environment across the

genus would lead one to expect no significant differences within and between all taxa across all sites.

Given the diversity of habitats of *Pittocaulon*, these anatomical similarities in quantitative features that are highly sensitive to moisture availability in conventional woody plants is striking. The collection localities are remarkably different edaphically, from the open, bare lava of the *P. praecox* locality at 2300 m to the open forest on deep soil of *P. bombycophole* 985 at 1200 m, to

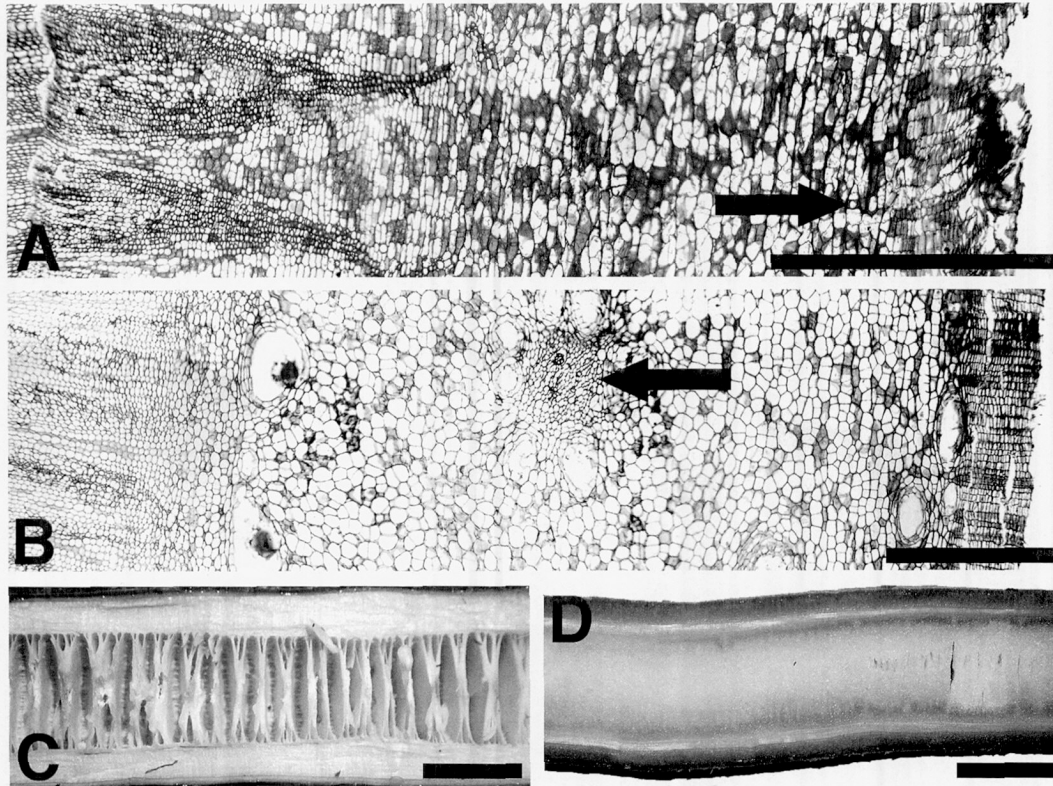


FIG. 5. Bark and pith features of *Pittocaulon*. A. *Pittocaulon bombycophole* (985) bark transection, with xylem at left and phellem at right, showing phloem with abundant fibers and a thick cortex with occasional sclereids (three are indicated by the arrow). B. *Pittocaulon praecox* (1020) with part of the phloem at left, phellem at right, showing lack of fibers and sclereids. Gum ducts are common in both the inner and outer cortical parenchyma. Arrow indicates a patch of phloem surrounded by gum ducts. C. *Pittocaulon hintonii* (878) stem split at the end of the dry season showing separated strata of pith parenchyma depleted of water. Fascicular areas can be seen as small axial ridges (cf. Fig. 4C). D. *Pittocaulon praecox* (1020) showing pith in rainy season. Pith strata are replete with water and almost entirely in contact with one another (clearly separated strata can still be seen at right). Figs. 5A, B, scale bars = 2mm; Figs. 5C, D, scale bars = 1 cm.

the shady limestone outcrop of *P. filare* below 500 m, to the limestone outcrop in tall, seasonally moist dry forest of *P. hintonii*. Despite these great differences in water regime and temperature, *P. hintonii* is very close in vessel dimensions to *P. praecox* and *P. velatum*, both from much drier highland situations.

Though the differences between samples are not significant, vessel diameter is slightly positively correlated with moisture rank, suggesting that the buffering of vessel features from the external environment is not complete. That the sample from the moistest locale should have wider vessels than the samples from drier locales suggests that succulence in *Pittocaulon* is not entirely sufficient to buffer them from low xylem pressures and allow them to maintain vessels of dimensions similar to those of *P. hintonii*. It might be thought that plant size could be in-

voled to explain the differences in vessel size, because the sample of *P. hintonii* had a large xylem cylinder wall thickness. It is a common observation that vessel diameter increases with stem thickness (Carlquist 1975, Gartner 1995). However, this factor cannot account for all of the differences, because various samples had a xylem cylinder of much greater wall thickness but narrower vessel elements (Table 1), and no correlation was found between these features. The "internally mesic environment" of *Pittocaulon* thus appears sufficient to buffer the vessels from a wide range of external conditions, but not from all extremes. It seems possible that it is the presence of leaves with few adaptations for resisting drought that might be responsible for this slight tracking of moisture availability by the vessels of *Pittocaulon*. A similar study within a group of leafless succulents might find

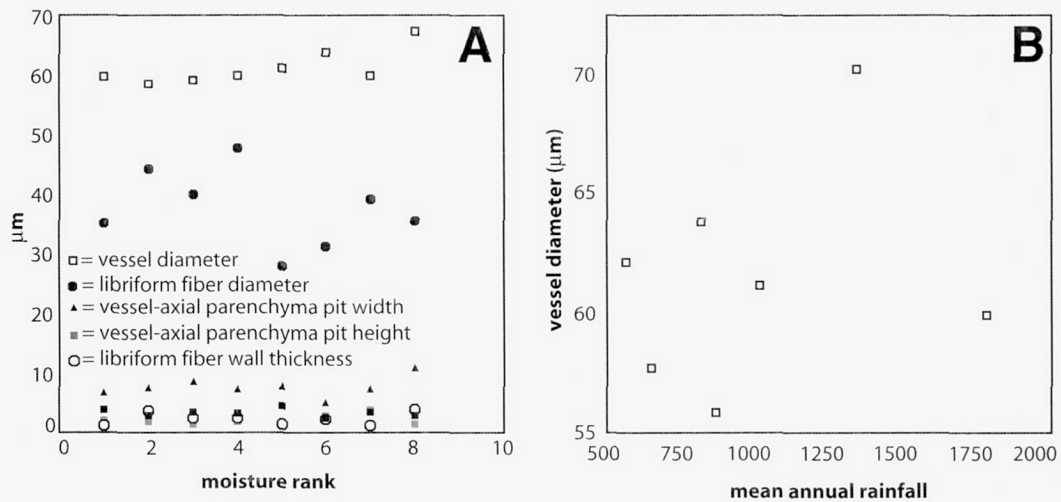


FIG. 6. Measurements of xylem features vs. water availability to show lack of strong correlation with moisture availability, a pattern congruent with the idea of an "internally mesic" environment in water-storing plants. A. Anatomical characteristics vs. water availability as estimated from soil depth and texture, exposure, type and extent of vegetation cover ("moisture rank"). B. Vessel diameter vs. average annual rainfall from weather station data.

an even more complete isolation of the vessels from external conditions.

All other characteristics examined (vessel wall thickness, libriform fiber wall thickness, and libriform fiber diameter) showed no significant correlations with moisture rank. Not only were no significant correlations encountered, but non-significant trends are not even suggested by the data (Fig. 6A). These results suggest that natural selection in these cells is not strongly driven by the need to resist highly negative xylem pressures, as would certainly be the case for a nonsucculent growing in the same habitats as *Pittocaulon*. For example, Barradas et al. (2004) show that *Pittocaulon praecox* at the same locality of 1020 and 1021 had leaf water potentials that were never as negative as those of the sympatric *Buddleja cordata* HBK, and *Dodonaea viscosa* Jacq., both evergreen conventional

woody plants; a similar pattern is to be expected across the range of *Pittocaulon*. Vessel grouping in *Pittocaulon* is in all cases lower than that found in Asteraceae as a whole (3.62 vessels/group, Carlquist 1966). This finding is consistent with the idea that *Pittocaulon* does not experience highly negative xylem pressures, and thus is at little risk for drought-induced embolism.

The evaluation of water availability by moisture ranks reflected anatomy to a much greater extent than did weather station data. This effect was likely observed for two reasons. First, moisture ranking takes into account local and microsite information. The closest weather stations were often 10 km or more from the collection locality, with different situations relative to mountains, exposures, and elevations. As a result, the estimated relative moisture availability (moisture rank) between sites and precipitation records from the nearest weather station were often in disagreement (Table 3). For example, the wettest locality as assessed by moisture rank was the second-wettest as inferred from weather station data. Second, not even a weather station at the exact collection locality can distinguish between microsites, such as at the *P. praecox* locality, where one sample was growing atop a bare lava boulder and the other was collected at the bottom of a deep, shady crevice in the lava, shaded by tall trees. These factors are likely responsible for the significant correlation between vessel diameter and moisture rank and the lack

Table 3. Moisture rank vs. average annual precipitation.

Collection	Moisture rank	Mean ppt/yr (mm)
<i>P. velatum</i> ssp. <i>velatum</i> 978	1	589
<i>P. filare</i> 897	2	906
<i>P. bombycophole</i> 903	3	677
<i>P. bombycophole</i> 985	4	1821
<i>P. velatum</i> ssp. <i>velatum</i> 910	5	1050
<i>P. praecox</i> 1021	6	853
<i>P. praecox</i> 1021	7	853
<i>P. hintonii</i> 878	8	1386

of correlation with precipitation as assessed by weather station data.

**SYSTEMATICS.** Stem anatomy is very similar across the genus. There are particularly strong anatomical similarities between both subspecies of *P. velatum* and *P. praecox*, from the absence of druses, fibers, and brachysclereids in the bark, to the markedly fusiform shape of the nuclei in fibers and ray cells. Clark's (1996) 50% majority-rule consensus tree of an analysis of the fifteen species in *Senecio* Sect. *Terminales* shows *P. bombycophole* sister to a clade composed of *P. filare* and *P. hintonii*. *Pittocaulon praecox* is sister to this clade, and *P. velatum* is in turn sister to the rest of the genus. Clark's morphological analysis may be considered preliminary, and analysis with molecular characters may recover a different arrangement. For example, there are no anatomical characters to suggest that the *P. praecox* and *P. velatum* group should be paraphyletic, and it would not be surprising to find that these species form a clade. The presence of phloem fibers and druses probably are synapomorphic of the *P. bombycophole* + *P. filare* + *P. hintonii* clade. No matter what phylogenetic hypothesis of *Pittocaulon* is used, phylogenetic inertia is low in *Pittocaulon* with respect to vessel element dimensions. That is, more closely related species do not resemble each other more than distantly related ones. For example, *P. hintonii* differs markedly from its putative sister taxon *P. filare*. It therefore seems unlikely that taking into account the phylogeny of *Pittocaulon* in the statistical analysis of quantitative characters would lead to finding stronger differences between species than the analysis used here, which considers the species as independent of one another.

**WATER STORAGE AND MECHANICAL CONSIDERATIONS.** Both the ontogeny of the pith and its construction show strategies for maximizing water storage. The pith enlargement mechanism described here results in a pith of maximal dimensions, and one that exceeds what could be produced with a xylem cylinder that is complete around the stem from its inception. The observation that the strata of the chambered pith of *Pittocaulon* separate in the dry season and apparently regain turgidity and even fill to the point of giving the appearance of a solid pith in the wet season (Figs. 5C, D) suggest a mechanism for accommodating varying quantities of stored water. The construction of many columnar cacti, with rods of xylem arranged in a cyl-

inder between a thick pith and cortex, permits expansion and contraction of the pith with varying amounts of stored water (Gibson and Nobel, 1986). Such expansion and contraction is impossible in segments of *Pittocaulon* stems over two years old, because of the rigid xylem cylinder. *Villaseñoria* and *Telanthophora*, close relatives of *Pittocaulon* from moister parts of Mexico and Central America, have solid piths (Clark 1996), as does *Pachyramnus* (~*Eupatorium*), an Asteroid composite with a habit similar to that of *Pittocaulon*.

The proportion of a given *Pittocaulon* stem in transection that is occupied by xylem is very slight (Fig. 5A), and what is present is surrounded by thick bark and thus not optimally placed to resist compression and tension when the stem is bent (cf. Vogel 2003). Vulnerability to bending due to self-loading would seem to be great in *Pittocaulon* because the large amounts of water in pith and cortex must be extremely heavy relative the amount of xylem present. Several species have phloem fibers, but in all species the cortex is well over half of the area of the bark. The bark in *P. praecox* and *P. velatum* lacks fibers entirely and is mostly parenchyma. Such bark construction makes an abundant volume available for water storage but would not seem optimal for mechanical support. However, all the species have several layers of collenchyma immediately below the periderm. This construction is reminiscent of that described by Niklas et al. (2003), who show that cortical parenchyma with peripheral collenchyma makes significant contributions to resisting bending in some species of small cereoid cacti. The second moment of area of the bark in *Pittocaulon* probably exceeds that of the wood in most stems and thus, despite a relative paucity of tissue with high elastic moduli, may contribute significantly to the support of the thick, heavy stem. If the xylem contributes a significant amount of support in the stems of *Pittocaulon*, then the very small amount of it present suggests that the wood Young's modulus should be relatively high.

**Conclusions.** Water-storing plants are extremely common in dry tropical habitats. Extremely dry or seasonally cold areas seem to lack such plants, but the moderate temperatures and regular, if sometimes low, rainfall of the dry tropics apparently is ideal for water storage in woody plants. The stems of *Pittocaulon* consist of thick water-storing bark and pith with a thin xylem cylinder. Succulence appears to obviate

the majority of water availability-related variation that is commonly observed in woody plants, such as higher vessel wall thickness/diameter ratios and thicker libriform fiber walls in drier habitats. The lack of response to water availability in these characters in *Pittocaulon* is strongly supportive of the idea that water storage in combination with a phenology that reduces water use in dry periods creates a selective environment in the xylem that involves xylem water tensions that are much less negative than those of conventionally woody dryland plants (cf. Barradas et al. 2004). The stems of *Pittocaulon* show numerous features that allow a large amount of water to be stored within a cylindrical trunk. Over the first two years of growth, the pith enlarges substantially, greatly increasing the volume available for water storage. The pith appears to have a mechanism that allows it accommodate varying amounts of water despite being encased within the rigid cylinder of xylem.

The stem construction of *Pittocaulon* in some respects resembles some columnar cacti, and is a response to similar conditions under which most columnar cacti live: warm, dry tropical conditions. Also like some columnar cacti, an important factor in the support of the heavy stems of *Pittocaulon* is probably the complex of tissues in the peripheral cortex, including non-lignified parenchyma and collenchyma. Unlike columnar cacti, the stems of *Pittocaulon* do not have ribs, and do have conventional periderms instead of long-lived epidermal tissues. Thus, the anatomy of *Pittocaulon* represents yet another example of a stem construction unique to the dry tropics.

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## Appendix 1.

Collection localities, habitats, and moisture rankings.

Taxon	Collector and #	Locality	Habitat and moisture ranking
<i>Pittocaulon bombycophole</i>	Olson and Cacho 903	México: Michoacán: ca. 1 km al N de la estación de microondas en la carretera Mex 37 Playa Azul-Nueva Italia. 18°25'19.9"N 102°06'41.9"W, 900 m.	Steep hillside of decomposing granite with dense tropical dry forest; 3
<i>Pittocaulon bombycophole</i>	Olson and Cacho 984	México: Guerrero: Slopes of Cerro el Jumil near microwave tower NNE of Iguala. 18°24'02.02.7"N 99°29'3.4"W, 1193 m.	Low dry tropical forest
<i>Pittocaulon bombycophole</i>	Olson and Cacho 985	México: Guerrero: Tiuribe microwave station N of Iguala. 18°25'36.9"N 99°38'33.8"W 1171 m.	Open, disturbed tropical dry forest; 4
<i>Pittocaulon bombycophole</i>	Olson and Cacho 1008	México: Guerrero: Between Buenavista and Coaxacatlan. 18°29'45.2"N 99°27'22.8"W 1728 m.	Open scrub on rocky hillside
<i>Pittocaulon filare</i>	Olson, Cacho, and Miller 897	México: Colima: About 5 km S of the intersection to Los Asmoles on the non-toll highway Colima-Manzanillo. 19°04'05"N, 103°46'34"W, 464 m.	On very steep ~W-facing slope with decomposed limestone; 2
<i>Pittocaulon hintonii</i>	Olson and Cacho 878	México: Michoacán: Mpio de Coalcomán: Rancho La Parota. 18°42'39.9"N 103°18'53.1"W, 1230 m.	In shallow soil on highly dissected limestone; 8
<i>Pittocaulon praecox (sun)</i>	Olson and Durán 1020	México: Distrito Federal: Pedregal de San Ángel. 19°19'14.3"N 99°11'40.6"W, 2316 m	Atop basalt boulder, open exposure; 6
<i>Pittocaulon praecox (shade)</i>	Olson and Durán 1021	México: Distrito Federal: Pedregal de San Ángel. 19°19'14.3"N 99°11'40.6"W, 2316 m	In deep crack in lava flow in the shade of tall trees; 7
<i>Pittocaulon praecox (root)</i>	Rosell 2	México: Distrito Federal: Pedregal de San Ángel. 19°19'14.3"N 99°11'40.6"W, 2316 m	On lava flow in dry scrub
<i>Pittocaulon velatum ssp. tzimolensis</i>	Olson, Cacho, and Miller 944	México: Chiapas: Cañon El Sumidero, Mirador La Coyota. 16°42'N 103°18'W, 1230 m	Young seedling growing on lip of enormous limestone canyon
<i>Pittocaulon velatum ssp. velatum</i>	Olson, Cacho, and Miller 910	México: Jalisco: Mex Hwy 15 between Morelia and Ciudad Hidalgo, 46 km W of Mil Cumbres. 19°39'41.8"N 100°55'20.5"W, 2235 m.	Steep rocky hillside with some deep pockets of dark soil; 5
<i>Pittocaulon velatum ssp. velatum</i>	Olson and Cacho 978	México: Oaxaca: Municipio de Santiago Cacaloxtotec. Between Huajuapán and Tamazulapán on Mex Hwy 190, 5 km from La Reforma toward Tamazulapán. 17°42'54.0"N 97°39'23.6"W, 2089 m.	Open, low dry tropical forest on rocky hillside; 1