

2-1987

# Anatomy and Affinities of Penthorum

Melanie Lynn Haskins

W. John Hayden

*University of Richmond*, [jhayden@richmond.edu](mailto:jhayden@richmond.edu)Follow this and additional works at: <http://scholarship.richmond.edu/biology-faculty-publications>Part of the [Botany Commons](#), [Other Plant Sciences Commons](#), and the [Plant Biology Commons](#)

## Recommended Citation

Haskins, Melanie Lynn, and W. John Hayden. "Anatomy and Affinities of Penthorum." *American Journal of Botany* 74, no. 2 (February 1987): 164-77.

This Article is brought to you for free and open access by the Biology at UR Scholarship Repository. It has been accepted for inclusion in Biology Faculty Publications by an authorized administrator of UR Scholarship Repository. For more information, please contact [scholarshiprepository@richmond.edu](mailto:scholarshiprepository@richmond.edu).

## ANATOMY AND AFFINITIES OF PENTHORUM<sup>1</sup>

MELANIE L. HASKINS AND W. JOHN HAYDEN

Department of Biology, University of Richmond, Richmond, Virginia 23173

### ABSTRACT

The genus *Penthorum* L. consists of two species of perennial herbs, *P. sedoides* of eastern North America and *P. chinense* of eastern Asia. *Penthorum* has long been considered intermediate between Crassulaceae and Saxifragaceae. An anatomical study of both species was undertaken to contribute to a better understanding of the relationships of these plants. Prominent anatomical features of *Penthorum* include: an aerenchymatous cortex and closely-spaced collateral vascular bundles of stems; one-trace unilacunar nodes; brochidodromous venation, rosoid teeth bearing hydathodes, and anomocytic stomata of leaves; angular vessel elements with many-barred scalariform perforation plates and alternate to scattered intervacular pits; thin-walled non-septate fiber-tracheids; abundant homocellular erect uniseriate and biseriate rays; and absence of axial xylem parenchyma. In general, *Penthorum* possesses neither the morphological nor the anatomical synapomorphies which define Crassulaceae, and features shared with Saxifragaceae are largely symplesiomorphous. Thus *Penthorum* is probably best classified in the monogeneric Penthoraceae.

THE GENUS *Penthorum* L. (ditch stonecrop) consists of two species: *P. sedoides* L. native to the eastern half of the U.S. and *P. chinense* Pursh (including *P. intermedium* Turcz. and *P. humile* Rgl. & Maack) native to far eastern Russia, China, Korea and Japan. These plants are perennial rhizomatous herbs that are similar in some morphological characteristics to both Saxifragaceae and Crassulaceae. Like genera of the Crassulaceae, *Penthorum* has as many carpels as sepals. On the other hand, like Saxifragaceae, the plants are nonsucculent, the flowers are slightly perigynous with partially fused carpels, and the carpels lack the nectar glands present in Crassulaceae (Spongberg, 1972; Cronquist, 1981).

The familial position of *Penthorum* has been of interest for over 150 years. *Penthorum* has been considered a member of Crassulaceae (de Candolle, 1830; Torrey and Gray, 1840; Hutchinson, 1973), Saxifragaceae (Baillon, 1871; Engler, 1930; Takhtajan, 1980; Cronquist, 1981), or the type of its own monogeneric family, Penthoraceae (van Tieghem, 1898; Airy-Shaw, 1973; Stern, 1974a). Systematic studies comparing characteristics of embryology (Rocén, 1928; Mauritzon, 1933), palynol-

ogy (Agababian, 1961; Wakabayashi, 1970; Hideux and Ferguson, 1976), cytology (Baldwin, 1940; Baldwin and Speese, 1951), chemistry (Jay, 1970; Soltis and Bohm, 1982) and seed protein serology (Grund and Jensen, 1981) of *Penthorum* to those of Crassulaceae and Saxifragaceae have revealed conflicting or inconclusive results.

A search of the literature has shown only brief qualitative anatomical descriptions of *Penthorum* by van Tieghem (1898) and Solereder (1908). The objective of the present work is to investigate thoroughly quantitative and qualitative histological features of vegetative tissues of *Penthorum* in order to assess its relationships with Crassulaceae and Saxifragaceae.

**MATERIALS AND METHODS**—Specimens of both species of *Penthorum* were gathered from various localities in Virginia, China and Japan. Collection data for all specimens studied appear in Appendix 1.

Histological procedures used follow standard techniques outlined in Johansen (1940). All tissues including roots, young stems, nodes, leaves and woody stem bases were preserved in formalin-acetic acid-alcohol prior to embedding in paraffin. Sections were made at 10  $\mu$ m thickness with a rotary microtome, stained with Heidenhain's iron-alum haematoxylin and safranin, dehydrated, and mounted on slides with Permount.

Petioles were examined at three points: the base adjoining the stem, the midpoint, and the base of the blade. Semipermanent sections were obtained by the freehand method and were

<sup>1</sup> Received for publication 30 December 1985; revision accepted 8 July 1986.

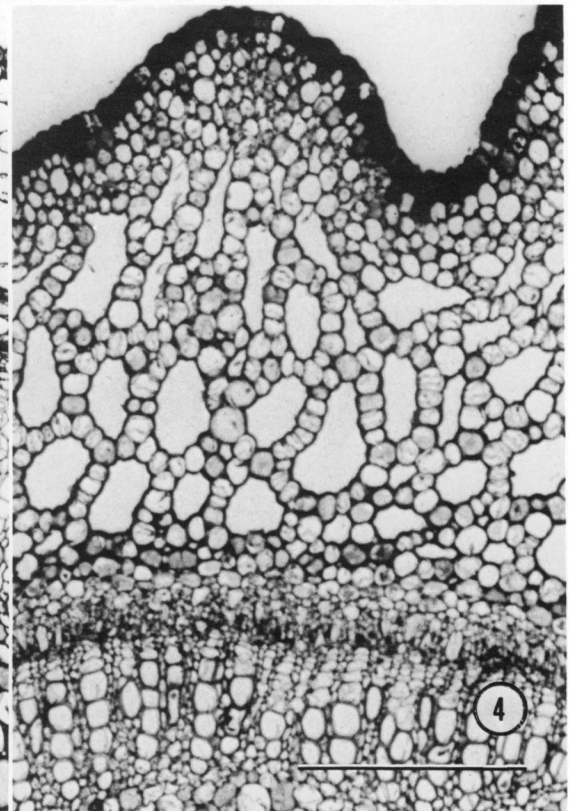
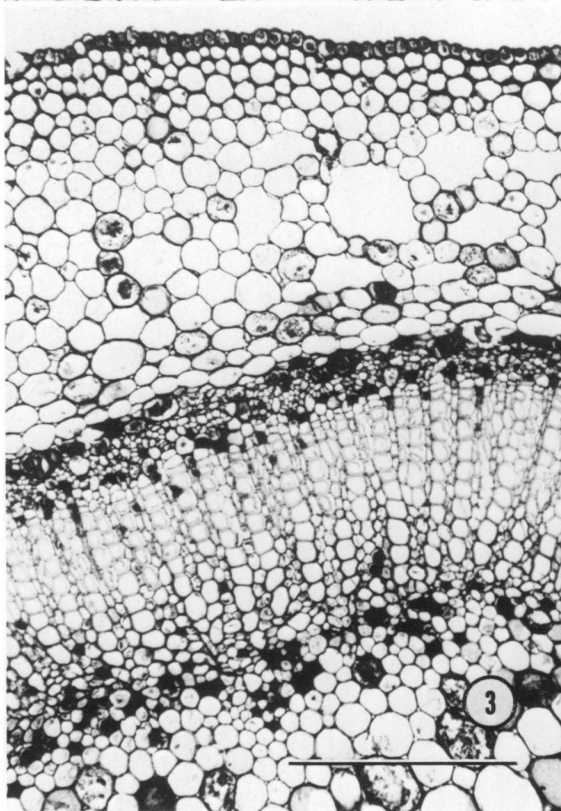
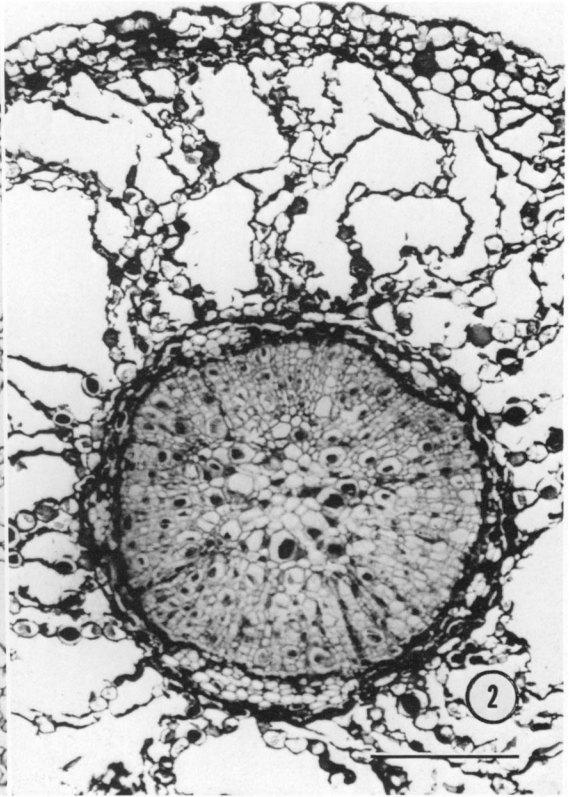
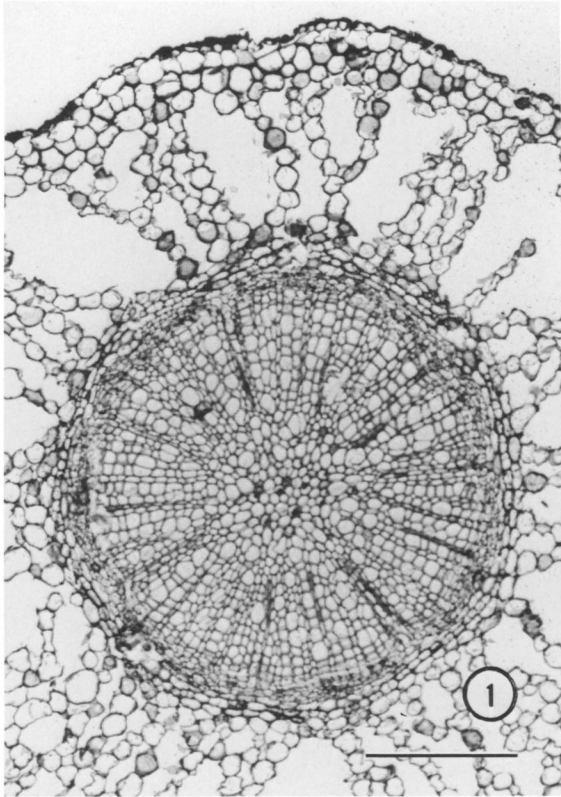
We are indebted to Li Zhengli and Wang Jinwu of Peking University, He Shan-an and Y. N. Xiong of the Nanjing Botanical Garden, M. Wakabayashi of Tokyo Univ., Hiroshi Tobe of Chiba Univ., and Kuo Chun-Yen and Shi Guoliang of the South China Institute of Botany for providing specimens of *Penthorum chinense*. Research was supported by Univ. of Richmond Graduate School and the Natl. Science Foundation Grant BSR: 84-07594.

TABLE 1. Average values of anatomical characteristics of *Penthorum chinense* and *P. sedoides*

Characteristic	<i>Penthorum chinense</i> specimens <sup>a</sup>						<i>Penthorum sedoides</i> specimens <sup>a</sup>				
	1	2	3	4	5	6	7	8	9	10	11
<b>Pore distribution</b>											
% Solitary	49	49	46	50	51	— <sup>b</sup>	59	48	51	51	60
% Radial multiples	11	17	13	12	8	— <sup>b</sup>	8	15	13	13	14
% Clusters	40	34	41	38	41	— <sup>b</sup>	33	37	36	36	26
Pores/mm <sup>2</sup>	620	455	717	577	624	— <sup>b</sup>	572	594	594	584	676
Pore area, mm <sup>2</sup> /mm <sup>2</sup>	0.34	0.28	0.25	0.26	0.22	— <sup>b</sup>	0.21	0.24	0.31	0.23	0.25
<b>Vessel elements</b>											
Pore diam, $\mu$ m	26	28	21	24	21	30	22	23	26	22	22
Bars/perforation plate	29	31	21	32	31	27	31	34	18	19	23
Length, $\mu$ m	633	764	514	749	688	755	608	554	477	597	610
End wall angle, degrees	80	79	76	84	82	82	83	81	81	77	80
Fiber-tracheids length, $\mu$ m	801	911	663	834	792	851	640	623	563	702	639
<b>Rays</b>											
Frequency											
% Uniseriate	61	37	26	53	54	37	31	51	57	34	29
% Multiseriate	39	63	74	47	46	63	69	49	43	66	71
Rays/mm transect	18	19	18	19	20	19	24	19	20	18	16
Uniseriates											
Width, $\mu$ m	8	9	10	11	12	8	7	9	7	12	9
Ht, $\mu$ m	767	503	462	914	662	— <sup>b</sup>	534	742	730	500	416
Ht, no. of cells	10	6	8	10	7	— <sup>b</sup>	7	9	10	6	6
Multiseriates											
Width, $\mu$ m	17	19	21	21	18	21	16	21	14	26	20
Width, no. of cells	2	2	2	2	2	2	2	2	2	2	2
Ht, $\mu$ m	1,126	1,072	899	1,059	984	— <sup>b</sup>	822	851	946	962	584
Ht, no. of cells	15	14	16	12	11	— <sup>b</sup>	12	11	13	13	11

<sup>a</sup> *Penthorum chinense*: 1 = Wang 1130; 2 = Xiong 0001; 3 = Shi s.n.; 4 = Tobe 80; 5 = Tobe 81; 6 = Wakabayashi s.n. *Penthorum sedoides*: 7 = Hayden 952; 8 = Hayden 958; 9 = Haskins 76; 10 = Hayden 798; 11 = Hayden 1004.

<sup>b</sup> Data unavailable due to unsatisfactory sections.



stained with a 1% solution of toluidine blue to demonstrate vascularization and mounted in Hoyer's solution.

Leaves were cleared by treatment with 2.5–5% NaOH followed by Stockwell's solution (Schmid, 1977), with water washes after each treatment. Cleared leaves were stained in safranin, dehydrated, and mounted in Permount. Foliar trichomes were examined from leaf clearings and herbarium specimens. Transverse, radial and tangential sections of woody stem bases were successfully obtained at a thickness of 10  $\mu\text{m}$  from paraffin-embedded material and were stained in the manner previously described. Wood macerations were prepared with Jeffrey's fluid, washed, stained with safranin, dehydrated, and mounted.

Terms used in description of leaf architecture follow those set forth by Hickey (1979); terms used in descriptions of secondary tissues are in agreement with those suggested by the Committee on Nomenclature of the Internatl. Assoc. of Wood Anatomists (1957). Size classes of secondary tissue features follow those designated by Tamolang et al. (1963). Quantitative data in the descriptions are based on: ten measurements per specimen of stomatal length and width, vessel wall thickness, intervascular pit diam, fiber-tracheid diam, fiber-tracheid wall thickness, fiber-tracheid pit border diam, and ray frequency; 20 measurements per specimen of ray width and ray height; 30 measurements per specimen of vessel end-wall angles and number of bars per perforation plate; and 50 measurements per specimen of pore diam, vessel element length, and fiber-tracheid length. Pore frequency and distribution are based on counts of ten fields per specimen. Quantitative and qualitative descriptions refer to both *P. chinense* and *P. sedoides*, as the two were very similar anatomically. For measurements reported, numbers outside of parentheses represent the range of means for all specimens studied; numbers in parentheses represent the range of all observations for a given characteristic. Quantitative data for each specimen are tabulated in Table 1.

**RESULTS—Root (Fig. 1, 2)—**Epidermis uniseriate, becoming cutinized or exfoliating with age; cells irregular, containing granular or,

occasionally, amorphous deposits. Cortex consisting of an outer exodermis of vacuolate cells, mostly one to two cells deep, and a broad inner aerenchymatous region. Endodermis frequently with dark deposits (Fig. 2), remaining unsclerified or only slightly sclerified with age. Phloem alternating with arms of xylem in primary growth, forming a cylinder in secondary growth; phloem fibers present in older roots in positions corresponding to the location of primary phloem, forming groups of one to 37 cells, the groups occasionally coalescent. Primary xylem pentarch to polyarch; secondary xylem resembling that of stem. Pith absent.

*Primary stem (Fig. 3, 4, 5)—*Epidermis uniseriate; cells circular to squarish in cross section with dark deposits (Fig. 4); cuticle up to 2  $\mu\text{m}$  thick. Collenchyma beneath epidermis mostly angular, sometimes lacunar, in discontinuous patches of two to four cell layers. Cortex aerenchymatous, but cells near inner and outer cortex boundaries compact; cortical bundles absent; cortex cells becoming sclerified with age (Fig. 19); druses common. Primary vasculature a pseudo-siphonostele (Fig. 5). Phloem sieve plates compound with two to many sieve areas; perivascular fibers thick-walled, sparse, but more abundant in stems with secondary growth (Fig. 18, 19), dark deposits common. Primary medullary rays absent. Early protoxylem elements separated by two to three parenchyma cells. Pith circular; pith cells becoming sclerified with age, circular with small intercellular spaces, darkly stained deposits and druses common (Fig. 3).

*Node and petiole—*Nodes one-trace unilacunar (Fig. 15). Leaf trace a continuous collateral arc of xylem and phloem; cells with dark deposits occasionally present within and near the leaf trace. Petiolar vasculature a simple arch-shaped collateral vascular bundle, remaining unchanged through proximal, medial and distal regions (Fig. 6).

*Leaf blade (Fig. 7–14)—*Leaves simple, lanceolate (*P. chinense*, Fig. 11) or elliptic to narrowly elliptic (*P. sedoides*, Fig. 12). Blade apex acute; base cuneate and short petiolate; margin serrate. Teeth rosoid, glandular, compound,

←

Fig. 1–4. Roots and young stems of *Penthorum*. Note aerenchymatous cortices. 1. *Penthorum sedoides*, Hayden 952, cross-section of root. 2. *Penthorum chinense*, Tobe 81, cross-section of root. Note greater abundance of dark deposits in comparison with *P. sedoides*. 3. *Penthorum sedoides*, Hayden 798, cross-section of young stem. 4. *Penthorum chinense*, Shi s.n., cross-section of young stem. Bar = 200  $\mu\text{m}$ .

irregularly spaced; apical angle acute, apical side straight to concave, basal side convex (especially in *P. chinense*), or, occasionally, both sides acuminate, sinuses angular (Fig. 7). Hydathodes commonly associated with teeth apices (Fig. 9). Trichomes present in *P. sedoides* only (Fig. 10), distributed evenly on abaxial surfaces, commonly attached to veins, approx. 130  $\mu\text{m}$  long, scale-like, simple, multicellular, three- to four-seriate, glandular, apices often slightly swollen and darkly colored, bases clear. Venation pinnate, brochidodromous (Fig. 11, 12). Primary vein stout to massive (*P. chinense*) or moderate (*P. sedoides*); course straight. Secondary veins moderate in thickness; angle of divergence moderately acute, occasionally wide basally (*P. sedoides*); course uniformly curved, sometimes abruptly curved (*P. chinense*), joining superadjacent secondaries at right to obtuse angles throughout (*P. chinense*) or at acute angles basally and at right to obtuse angles apically (*P. sedoides*); often enclosed by secondary arches. Simple intersecondary veins present, some originating from the primary, others percurrent between secondary veins. Tertiary veins random reticulate, arising at right angles admedially and acute angles exmedially (*P. sedoides*), or ranging from acute to obtuse admedially and mostly acute exmedially (*P. chinense*). Quaternary veins randomly oriented. Marginal ultimate venation looped. Veinlets simple to twice branched (Fig. 13). Areoles imperfect, random, irregular, small to medium (Fig. 13). Teeth clear glandular; apex forminate; principle vein central, direct; accessory veins present, connivent (Fig. 7). Both epidermides uniseriate (Fig. 9, 10); cuticle thin. Epidermal cells larger in upper epidermis than in lower epidermis (Fig. 10), circular to elliptic in cross section, thin-walled, anticlinal walls straight or sinuous (Fig. 14), outer periclinal walls infrequently slightly papillate; darkly stained deposits common except near the primary vein. Stomates on both surfaces, more frequent abaxially, anomocytic (Fig. 14); guard cell pairs circular to elliptic, 23–31 (18–35)  $\mu\text{m}$  long, 16–23 (15–27)  $\mu\text{m}$  wide, length to width ratio 1.4:1; guard cells reniform; adjacent cells occasionally project over inner periclinal walls of guard cells.

Mesophyll bifacial (Fig. 9, 10); palisade layer uniseriate; spongy layer four to six cells thick. Primary vein a simple arc of xylem and phloem surrounded by large parenchyma cells, and collenchyma near epidermis (Fig. 8). Higher order veins without pronounced bundle sheaths or extensions.

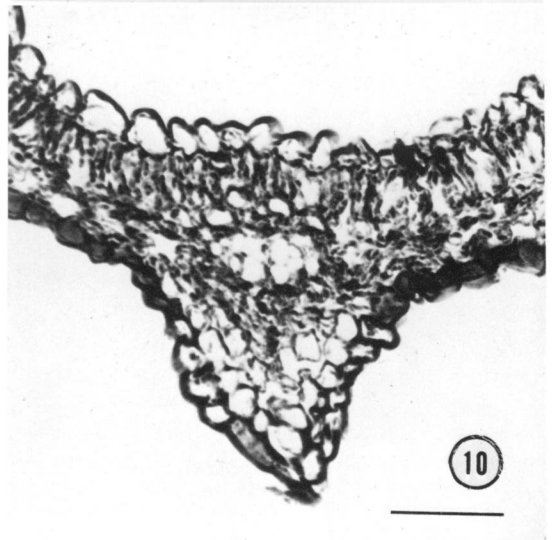
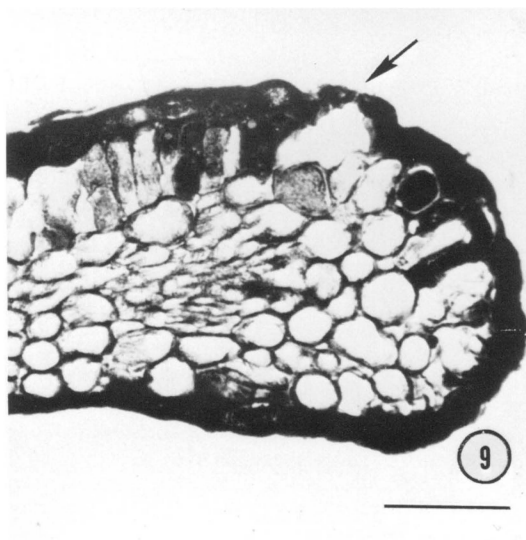
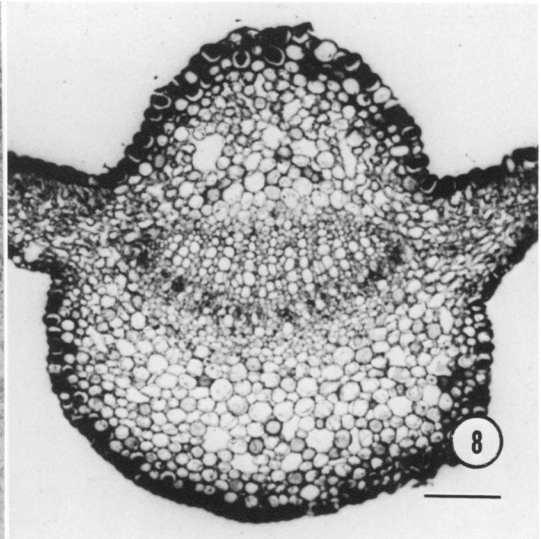
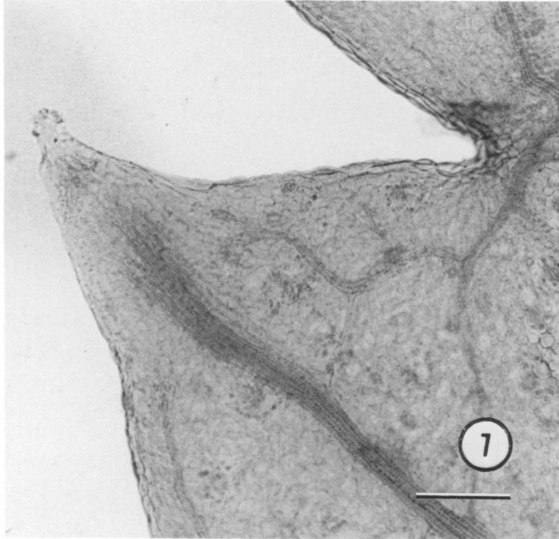
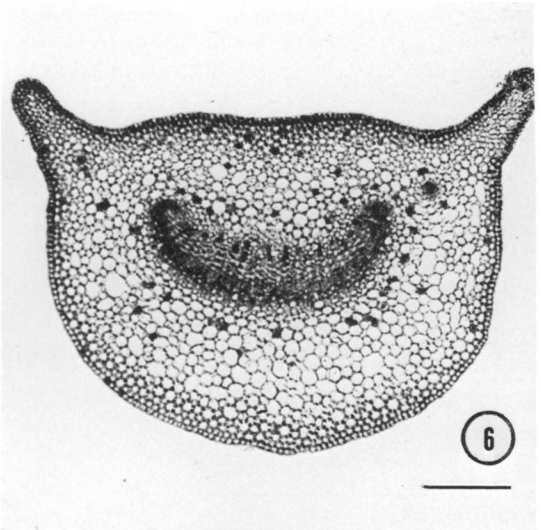
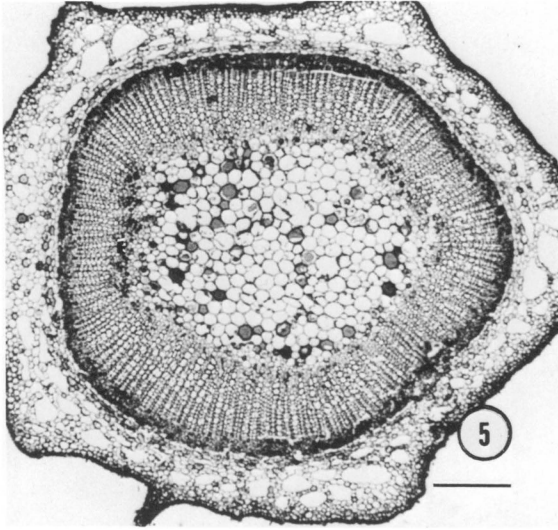
*Wood* (Fig. 16–24)—Growth rings absent, stems annual. Pores evenly distributed (Fig. 16); pore groups 46–60% solitary, 8–17% radial multiples, 26–41% clusters; pores per  $\text{mm}^2$  very numerous, 455–717; pore area 0.21–0.34  $\text{mm}^2$  per  $\text{mm}^2$  cross-sectional area of wood. Pore outlines angular (Fig. 17, 18); wall thickness 1–2 (0.75–2)  $\mu\text{m}$ ; tangential diam extremely to very small, 21–30 (12–37)  $\mu\text{m}$ . Perforation plates scalariform, varying in position from terminal to subterminal; bars many, 18–34 (9–57) per plate, sometimes branched (Fig. 22, 23); end walls inclined 76–84 (60–88) degrees from the horizontal. Intervascular pits circular, alternate to scattered; diam very small, 2–3 (1.5–4)  $\mu\text{m}$  (Fig. 21). Vessel element length medium, 477–764 (280–1,270)  $\mu\text{m}$ ; ligules present or absent. Vessels infrequently occluded with darkly stained deposits; spiral thickenings absent.

Imperforate elements fiber-tracheids and vascular tracheids, (Fig. 22) intergrading with each other, especially in early formed secondary xylem. Fiber-tracheids non-septate; length short to medium, 563–911 (310–1,300)  $\mu\text{m}$ ; lumen diam greater than wall thickness (Fig. 17); wall thickness 2–3 (1–4)  $\mu\text{m}$ ; tangential diam 15–22 (10–27)  $\mu\text{m}$ ; vertical diam of pit borders 2–3 (1.5–3)  $\mu\text{m}$ ; pit shape circular (Fig. 21), inner aperture included within or slightly extended beyond pit border; granular deposits occasional; spiral thickening absent.

Rays homocellular, mostly uniseriate or biseriate (Fig. 24), consisting of erect cells only (Fig. 20), very numerous (Fig. 16, 24), 16–24 (12–29) per  $\text{mm}$ ; 26–61% uniseriate, 39–74% multiseriate. Uniseriate ray width extremely fine, 7–12 (2–17)  $\mu\text{m}$ ; ht extremely to very low, 416–914 (160–1,940)  $\mu\text{m}$  or 6–10 (2–25) cells. Multiseriate ray width extremely to moderately fine, 14–26 (9–47)  $\mu\text{m}$  or 2 (2–4) cells; ht very low to low, 584–1,126 (220–2,820)  $\mu\text{m}$  or

Fig. 5–10. Young stem and leaves of *Penthorum*. 5. *Penthorum sedoides*, Hayden 798, cross-section of young stem showing nearly continuous vascular cylinder. 6. *Penthorum sedoides*, Hayden 798, cross-section of distal end of petiole. 7. *Penthorum sedoides*, Hayden 798, Marginal tooth from leaf clearing. 8. *Penthorum chinense*, Shi s.n., primary vein from cross-section of leaf. 9. *Penthorum chinense*, Tobe 81, hydathode from leaf cross-section. Note stomate at arrow. 10. *Penthorum sedoides*, Haskins 76, abaxial scale-like trichome from cross-section of leaf. Bars for Fig. 5, 6 = 250  $\mu\text{m}$ . Bars for Fig. 7–10 = 50  $\mu\text{m}$ .





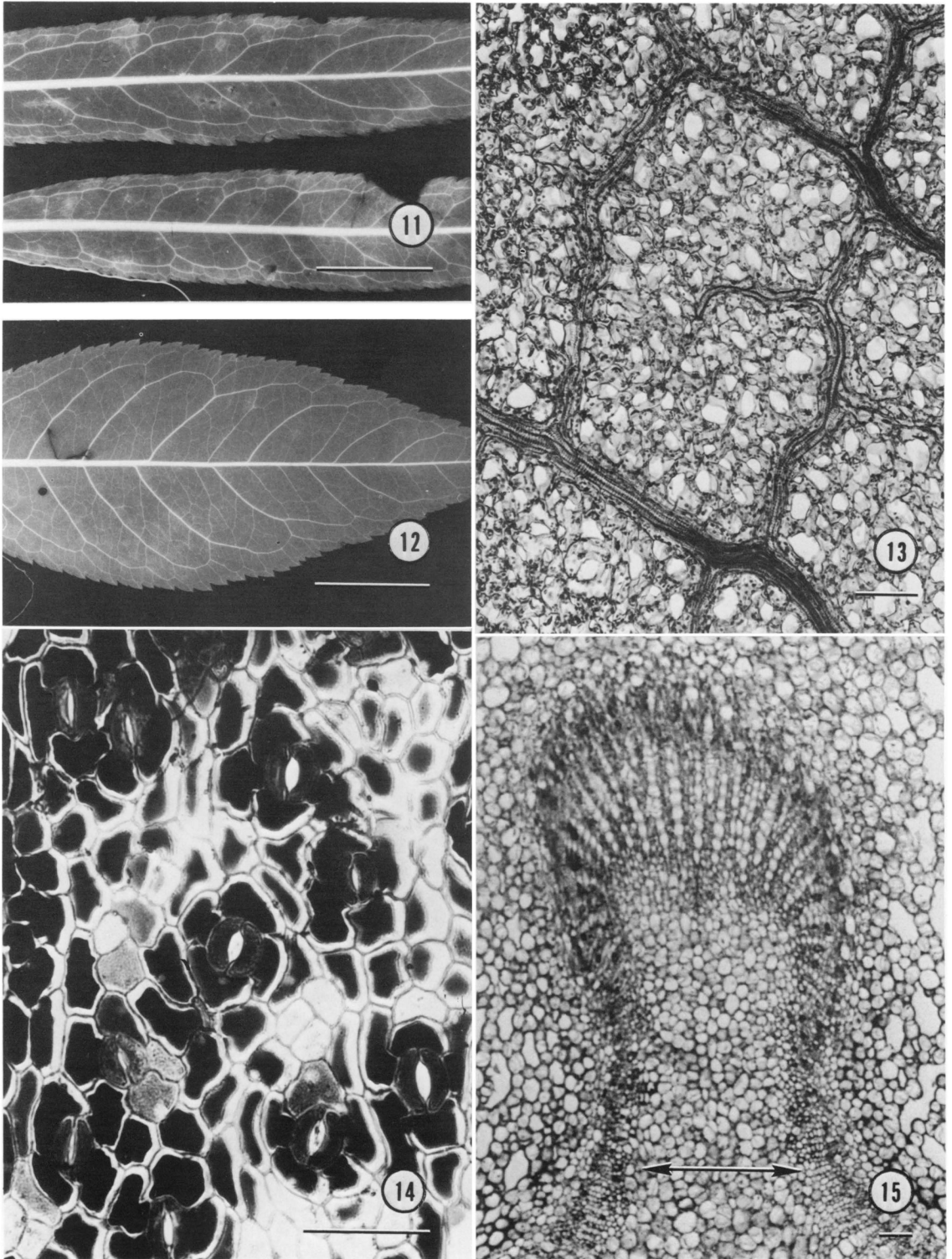


Fig. 11–15. Leaves and node of *Penthorum*. 11. *Penthorum chinense*, Tobe 81, leaf clearings. 12. *Penthorum sedoides*, Hayden 798, leaf clearing. 13. *Penthorum sedoides*, Hayden 798, veinlets and areoles from leaf paradermal section. 14. *Penthorum chinense*, Tobe 81, abaxial epidermis with anomocytic stomata from leaf paradermal section. 15. *Penthorum chinense*, Shi s.n., portion of one-trace unilacunar node from stem cross-section. Double-headed arrows indicate leaf gap. Bars for Fig. 11, 12 = 10 mm. Bars for Fig. 13–15 = 50  $\mu$ m.



11–16 (2–36) cells. Darkly stained deposits frequent (Fig. 20). Vessel to ray pitting circular to elliptic, irregularly scattered.

Axial xylem parenchyma absent.

**DISCUSSION**—Although stems of *Penthorum* exhibit a nearly continuous cylinder of vascular tissue, sections from very young growing stems suggest that separate bundles may be present originally in this plant. *Penthorum* is thus described as possessing a “pseudo-siphonostele” (Beck, Schmid and Rothwell, 1982), in which the early formed secondary xylem has obscured the distinctness of protoxylem strands. A complete ontogenetic study of vigorously growing stems is suggested to confirm the fundamentally eustelic structure for stems of *Penthorum*.

Previous anatomical investigations of *Penthorum* by van Tieghem (1898) and Solereder (1908) generally concur with the results presented above. A few differences are noteworthy, however. Van Tieghem reported an endodermis with lignified cell walls, a pentarch arrangement of primary xylem, and a pith that becomes sclerified with age in the roots. Specimens examined in the present study showed only slight lignification of the endodermis, variation in the number of xylem arms, and no pith. Consistent with early stelar theory, van Tieghem and Solereder described a strongly differentiated endodermis and a three to four layer pericycle from the primary stem of *Penthorum*; these reported structures probably correspond with the inner, non-aerenchymatous regions of the cortex. Van Tieghem reported leaves of *Penthorum* as lacking hairs; both van Tieghem and Solereder failed to mention the presence of stomata on both leaf surfaces of *Penthorum*. Solereder characterized the wood fibers of *Penthorum* as thick-walled; however, fibers observed here possess lumina wider than the cell walls and are thus classified as thin-walled (Tamolang et al., 1963). *Penthorum* was not specifically mentioned in Metcalfe and Chalk (1950).

Overall, anatomical features of *Penthorum chinense* and *P. sedoides* are similar. Nevertheless, some differences between the two species were detected. In comparison with *P. sedoides*, cells of *P. chinense* tend more frequently to possess dark deposits, especially in the cortex and epidermis of the root, in the epidermis of young stems, and in ray cells and vessel elements of secondary xylem. As observed above, only *P. sedoides* exhibited scale-like foliar trichomes.

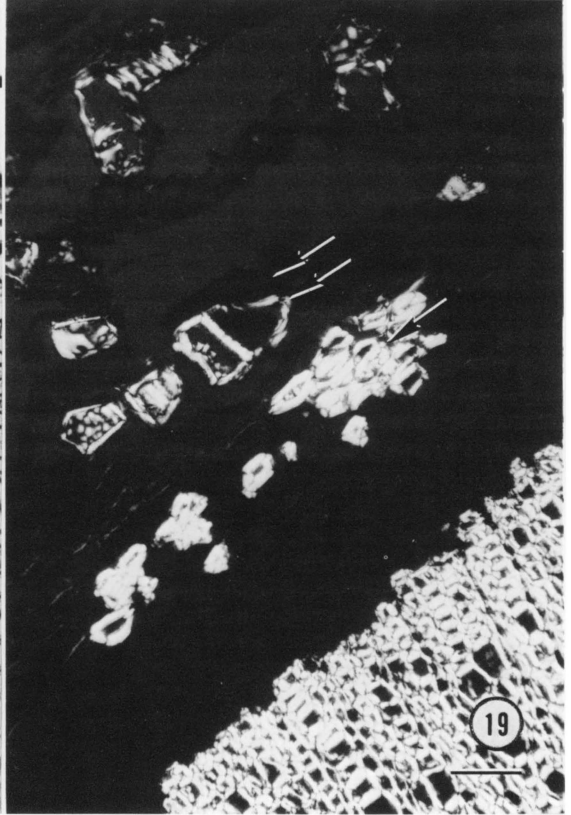
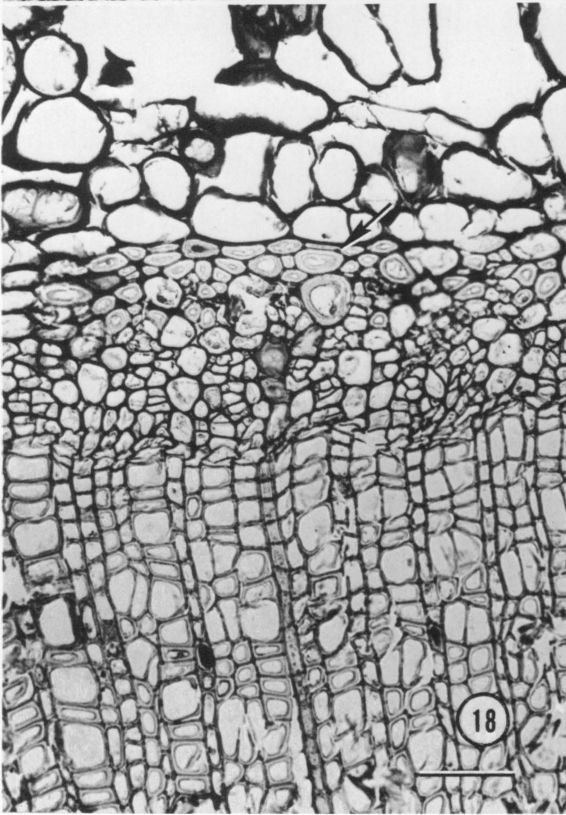
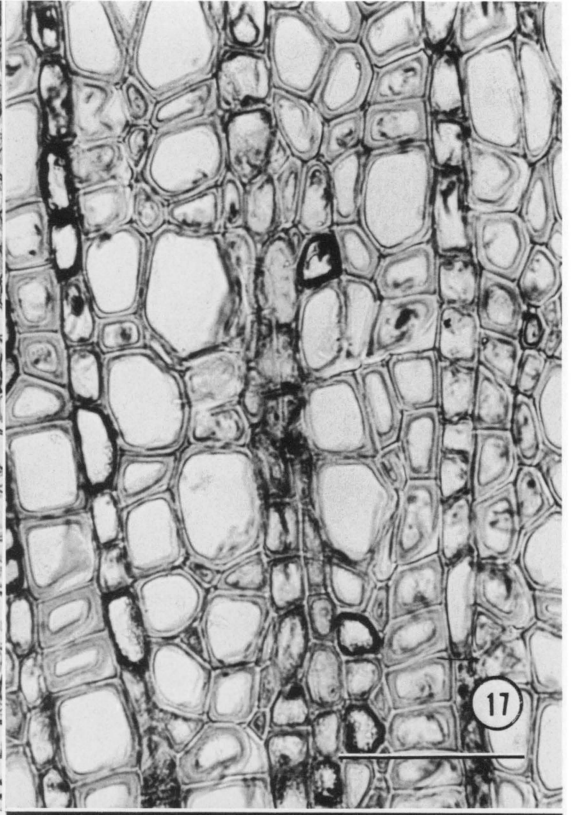
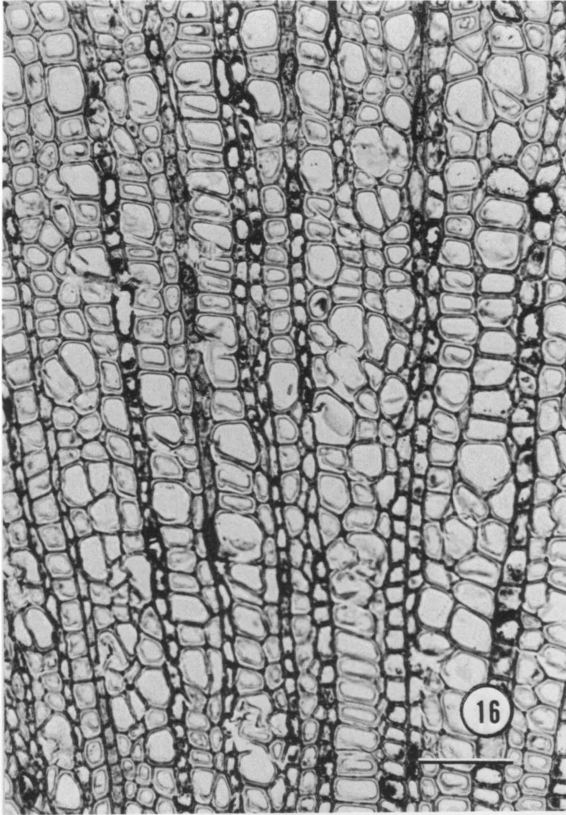
Differences in leaf architecture between *P. chinense* and *P. sedoides*, i.e., size of primary vein and origin and course of secondary veins

and tertiary veins, are probably related to lamina width. For example, in the longer, narrower blades of *P. chinense*, secondary veins diverge at more acute angles from the primary vein, form more flattened loops, and join super-adjacent secondaries at more obtuse angles than in the broader leaves of *P. sedoides*. Similarly, the greater variability of tertiary vein origin in *P. chinense* than in *P. sedoides* may also be related to lamina width.

Except for length of fiber-tracheids, which tended to be somewhat longer in *P. chinense* than in *P. sedoides*, secondary xylem features were consistent throughout the specimens examined. The ranges of mean fiber length per specimen, 563–702  $\mu\text{m}$  in *P. sedoides* and 663–911  $\mu\text{m}$  in *P. chinense*, do, however, show sufficient overlap that this character alone could not serve to distinguish woods of these species.

The angularity of vessel walls and, especially, the scalariform perforation plates with averages of up to 35 bars per plate are features indicative of primitive vessel morphology (Bailey, 1944, 1957; Dickison, 1975; Stern, 1978b; Metcalfe and Chalk, 1983). Such primitive vessel elements are relatively uncommon and, thus, of considerable interest. In Carlquist's (1975) list of woody dicotyledonous families with scalariform perforation plates, only 31 families possess exclusively long plates (i.e., over 20 bars), and many of these are monogeneric families. Moreover, the vast majority of herbaceous dicots have simple perforations. *Penthorum* is consistent with many taxa bearing scalariform perforation plates in that it is restricted to highly mesic or hydric environments. Carlquist (1975) has hypothesized that taxa with such primitive vessels are relicts restricted to habitats imposing minimal selection for efficiency of water conduction. Other primitive features of *Penthorum* include: fiber-tracheids, very numerous homocellular uniseriate rays of erect cells only, and multiseriate rays with long uniseriate wings.

Within either the Saxifragales (Takhtajan, 1980) or the Rosales (Schulz-Menz, 1964; Thorne, 1976; Cronquist, 1981), Crassulaceae and Saxifragaceae generally are considered closely related, with Crassulaceae hypothesized as the more primitive of the two, at least florally, by virtue of its free carpels (Hutchinson, 1973). Crassulaceae is well-defined morphologically and taxonomically and is widely considered to comprise a natural assemblage. Crassulaceae is characterized by a number of adaptations to xeric environments: thick waxy cuticle, abundant foliar water storage tissue, parenchymatous stem, and crassulacean acid metabolism (Spongberg, 1978). Saxifragaceae,



on the other hand, is a much larger, diverse family fraught with taxonomic controversy. In the traditional Englerian classification system (Engler, 1930; Schulz-Menz, 1964), Saxifragaceae comprises 17 subfamilies; seven subfamilies are herbaceous and ten are woody. Many modern systems split the family, with herbaceous members comprising Saxifragaceae sensu stricto, and woody members separated into several other families. For the purpose of comparisons with *Penthorum* in the following discussion, herbaceous and woody "saxifrages" will be considered separately, with the latter equivalent to Hydrangeaceae and Grossulariaceae of Cronquist (1981).

Salient anatomical features of *Penthorum* and those of its putative relatives, to the extent that they are known from the literature, are presented in Table 2. Other than the obvious succulence and anisocytic stomata of Crassulaceae, anatomical features of the primary plant body are equivocal concerning the relationships of *Penthorum*. On the basis of these features alone, *Penthorum* is reasonably consistent with either Crassulaceae or Saxifragaceae sensu lato. On the other hand, secondary xylem features clearly show a great deal of similarity with woody "saxifrages" and a number of important differences with Crassulaceae.

Crassulaceous plants that achieve thickened stems do not do so by the development of extensive cambial activity and the ordinary arrangement of secondary tissues. Rather, stem parenchyma tissue often divides generally and contributes substantially to lateral growth. Further, old stems of many crassulaceous plants possess a variety of anomalous structures (Solereder, 1908; Metcalfe and Chalk, 1950, 1979, 1983); these growth patterns are reasonably interpreted as evolutionarily advanced characters within the family. Other advanced anatomical characteristics of Crassulaceae include multi-trace nodes, anisocytic stomata, simple perforation plates, and libriform fibers. Thus, in contrast to its relatively primitive floral structure, Crassulaceae is typified by numerous specialized anatomical features that are not shared with *Penthorum*. *Penthorum* would be misplaced in Crassulaceae.

As mentioned above, many features of the secondary xylem of *Penthorum* are also com-

monly encountered in the woody "saxifrages." On a purely phenetic basis, then, *Penthorum* could easily be accommodated within Saxifragaceae sensu lato. However, it should be noted that the anatomical features shared with the woody "saxifrages" are, without exception, primitive character states according to the well-accepted concepts of secondary xylem evolution (Bailey, 1944, 1957; Dickison, 1975; Stern, 1978b; Metcalfe and Chalk, 1950, 1983). According to the principles of phylogenetic systematics, however, shared primitive character states, or symplesiomorphies, are not useful in indicating relationships (Wiley, 1981). In essence, the presence of primitive xylem features in *Penthorum* and Saxifragaceae merely show that these taxa have shared no evolutionary advancements of xylem during their phylogeny. Indeed, without any shared advanced characters, or synapomorphies, there is no real evidence that they share any significant common phylogeny.

In a larger sense, the perspective given by phylogenetic systematics readily explains the nature of past taxonomic controversy concerning *Penthorum*. The morphological feature most often cited as evidence for relationship with Crassulaceae, i.e., carpels isomerous with the perianth, is certainly plesiomorphous. Similarly, absence of succulence is symplesiomorphous with Saxifragaceae sensu lato, and the five or more carpels of *Penthorum* and certain "saxifrages" are probably plesiomorphous relative to the typical bicarpellate condition of many Saxifragaceae sensu lato. The weakness of symplesiomorphies has probably been the factor most responsible for the divergence of opinion in classifying *Penthorum* in both families, or characterizing it as a "transitional" element.

Evidence from other disciplines is also equivocal. Rocén (1928) found that embryogenesis in *P. sedoides* is similar to that of *Sedum acre* L. and several other Crassulaceae. Yet in another embryological study, Mauritzon (1933) placed *Penthorum* in Saxifragoideae, since it resembles this group in the construction of the nucellus and division of the endosperm chamber. On the basis of pollen features, Agabian (1961) found *Penthorum* intermediate between Crassulaceae and Saxifragaceae, while

←

Fig. 16–19. Old stems and secondary tissues. 16, 17. *Penthorum chinense*, Shi s.n., cross-sections of wood. 18. *Penthorum sedoides*, Hayden 958, cross-section of stem showing wood, cambial zone, secondary phloem, and cortex. Arrow indicates phloem fiber. 19. *Penthorum sedoides*, Hayden 798, cross-section of stem showing wood, cambial zone, secondary phloem, and cortex, photographed with crossed polarizing filters. Double arrows indicate sclerified cortex cells, single arrow indicates phloem fibers. Bar = 50  $\mu$ m.

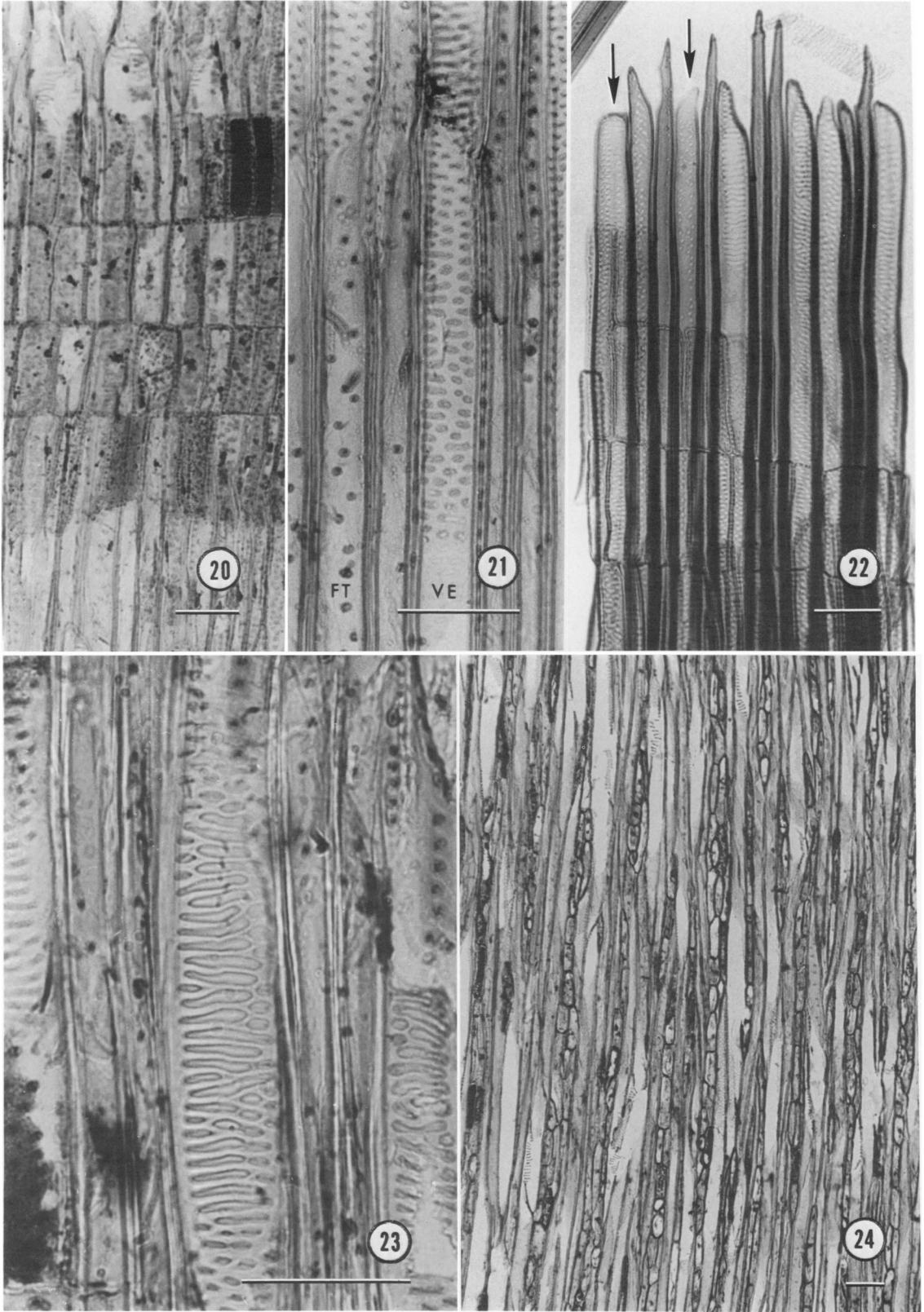


TABLE 2. *Anatomical comparisons of Penthorum, Crassulaceae, and Saxifragaceae*

Character	Crassulaceae <sup>a</sup>	<i>Penthorum</i>	Woody saxifragae <sup>a</sup>	Herbaceous saxifragae <sup>a</sup>
<b>Primary stem</b>				
Stele	continuous cylinder; discrete bundles	continuous cylinder	continuous cylinder; discrete bundles	continuous cylinder; discrete bundles
Node <sup>b</sup>	3:3 or 1:1	1:1	3:3 (3:3 to 7:7 in <i>Hydrangea</i> ; 1:1 in <i>Escallonia</i> )	3:3 (1:1 in <i>Parnassia</i> )
Petiole	1 to several collateral bundles	1 continuous collateral arc	1 to many collateral bundles	1 to many concentric or collateral bundles
<b>Leaf blade</b>				
Stomate type	anisocytic	anomocytic	anomocytic	anomocytic
Hydathodes	present	present	present	present
<b>Wood</b>				
Perforation plates	simple	scalariform	scalariform (simple)	simple
<b>Intervascular pits</b>				
Type	simple	bordered	simple or bordered	— <sup>c</sup>
Arrangement	— <sup>c</sup>	alternate to scattered	scalariform or opposite; alternate to transitional	— <sup>c</sup>
Imperforate elements	absent, or libriform fibers	fiber-tracheids	fiber-tracheids (septate or non-septate) or tracheids; vasicentric tracheids	fiber-tracheids
Rays	rarely developed	uniseriate and multiseriate homocellular erect	uniseriate, homocellular erect and multiseriate heterocellular	— <sup>c</sup>
Axial xylem parenchyma	abundant (often dominant)	absent	absent or diffuse apotracheal or scanty abaxial paratracheal	— <sup>c</sup>

<sup>a</sup> References used in compilation of this chart include: Cronquist (1981); Jensen (1968); Metcalfe and Chalk (1950, 1979); Moreau (1976); Solereder (1908); Spongberg (1972, 1978); Stern (1974b, 1978a); Stern, Sweitzer and Phipps (1970); and Styer and Stern (1979a, b).

<sup>b</sup> The first number of this notation refers to number of leaf traces, the second to leaf gaps. Therefore, 3:1 is a three-trace unilacunar node.

<sup>c</sup> Data not available.

Wakabayashi (1970) found no positive evidence to link it to Crassulaceae. More recently, Hideux and Ferguson (1976) found *Penthorum* similar to many species of *Sedum* L. of Crassulaceae and *Abrophyllum* Hook f. and *Cuttsia* F. Muell. of Grossulariaceae (or Escalloniaceae); in all these genera thinning of the end-exine and endoaperture are continuous and form an H shape. Overall, however, *Pentho-*

*rum* was judged by Hideux and Ferguson (1976) to be intermediate between Crassulaceae and Saxifragaceae sensu stricto. Although Baldwin (1940) suggested *P. sedoides* belonged in Crassulaceae because it shared the same base chromosome number as *Diamorpha cymosa* (Nuttall) Britton, the numbers of *P. sedoides* ( $N = 9$ ) and *P. chinense* ( $N = 8$ ) fall within the ranges of both Crassulaceae ( $N = 4-22+$ ) and Saxi-

←

Fig. 20–24. Wood of *Penthorum*. 20. *Penthorum sedoides*, Hayden 958, radial section, showing homocellular erect ray cells. 21. *Penthorum chinense*, Shi s.n., radial section showing fiber-tracheid pits and intervessel pits. FT = fiber-tracheid. VE = vessel element. 22. *Penthorum sedoides*, Hayden 958, showing fiber-tracheids, ray cells, vascular tracheids, and vessel elements from macerated wood. Arrows indicate vascular tracheids. 23. *Penthorum chinense*, Tobe 81, radial section showing scalariform perforation plate. 24. *Penthorum chinense*, Shi s.n., tangential section. Bar = 40  $\mu$ m.



fragaceae ( $N = 6-15$ , 17) as summarized by Cronquist (1981). Jay (1970) found phenols of *Penthorum* to differ from those of Crassulaceae but to resemble those of *Bergenia* Moench and *Peltoboykinia* (Engl.) Hara of Saxifragaceae, especially in the shared presence of ellagic acid. Soltis and Bohm (1982), however, could make no positive statements concerning affinities of *Penthorum*, since it contains numerous complex compounds which may be gallo catechin/gallic acid derivatives or as yet unidentified compounds unlike anything found in Saxifragaceae. Moreover, *Penthorum* lacks myricetin, flavones, flavonol glycoside gallates, extra hydroxylation at position 6 of flavonols, and O-methylation present in some saxifrages. A seed protein serology study (Grund and Jensen, 1981) revealed very little antigen-antiserum reactivity with a *Sedum* reference system and some reactivity with a *Saxifraga* system. However, in at least one test, seeds of *Hamamelis* L. showed a greater degree of serological correspondence to *Saxifraga* than did *Penthorum*. Citing inadequate amounts of seed material with which to work, Grund and Jensen (1981) declined to place *Penthorum* in either Crassulaceae or Saxifragaceae.

It is probably premature to attempt assignment of evolutionary polarities to the pertinent character states of embryology, pollen, cytology, and chemistry of *Penthorum*, Crassulaceae, and Saxifragaceae discussed in the preceding paragraph. Further, since evidence from gross morphology and these ancillary disciplines shows no clear overall phenetic resemblance to either Saxifragaceae or Crassulaceae, and since Crassulaceae is clearly defined by anatomical synapomorphies not shared with *Penthorum*, two options for classification remain. *Penthorum* could be classified in a monogeneric subfamily of Saxifragaceae, as it has been treated by Engler (1930), Spongberg (1972), Thorne (1976), Benson (1979) and Takhtajan (1980). It is not clear, however, that such an assignment can be defended cladistically by convincing synapomorphies between *Penthorum* and other Saxifragaceae. As discussed above, most distinctive anatomical and morphological features of *Penthorum* are either unambiguously primitive or of uncertain status as to their primitive or derived nature. From a cladistic perspective, the genus is probably best interpreted as a relictual element little changed from the ancestral stem of Rosidae. As such, classification in van Tieghem's Penthoraceae seems preferable to inclusion in either Crassulaceae or Saxifragaceae. Diagnostic characters of the family Penthoraceae would thus include its herbaceous habit, scalariform

perforation plates, and five to seven carpels which are half inferior at anthesis, wholly superior at maturity, and dehisce as individual pyxides.

#### LITERATURE CITED

- AGABABIAN, V. S. 1961. Materials toward the palyno-systematic study of the family Saxifragaceae s. 1. (In Russian.) *Izv. Biol. Nauki.* 14(2): 45-61.
- AIRY-SHAW, H. K. 1973. Willis' dictionary of the flowering plants and ferns, 8th ed. Univ. Press, Cambridge, England.
- BAILEY, I. W. 1944. The development of vessels in angiosperms and its significance in morphological research. *Amer. J. Bot.* 31: 421-428.
- . 1957. The potentialities and limitations of wood anatomy in the study of the phylogeny and classification of angiosperms. *J. Arnold Arbor.* 38: 243-254.
- BAILLON, H. 1871. Saxifragacées. *Hist. Pl.* 3: 325-464.
- BALDWIN, J. T., JR. 1940. Cytophyletic analysis of certain annual and biennial Crassulaceae. *Madroño* 5: 184-192.
- , AND B. M. SPEESE. 1951. *Penthorum*: its chromosomes. *Rhodora* 53: 89-91.
- BECK, C. B., R. SCHMID, AND G. W. ROTHWELL. 1982. Stellar morphology and the primary vascular system of seed plants. *Bot. Rev.* 48: 691-815.
- BENSON, L. 1979. *Plant classification*, 2nd ed. D. C. Heath and Company, Lexington, MA.
- CARLQUIST, S. 1975. Ecological strategies of xylem evolution. Univ. California Press, Berkeley.
- COMMITTEE ON NOMENCLATURE, INTERNATIONAL ASSOCIATION OF WOOD ANATOMISTS. 1957. International glossary of terms used in wood anatomy. *Trop. Woods* 107: 1-36.
- CRONQUIST, A. 1981. *An integrated system of classification of flowering plants*. Columbia Univ. Press, New York.
- DE CANDOLLE, A. P. 1830. *Penthorum*. *Prodromus systematis naturalis regni vegetabilis*. 3: 414.
- DICKISON, W. C. 1975. The bases of angiosperm phylogeny: vegetative anatomy. *Ann. Missouri Bot. Gard.* 62: 590-620.
- ENGLER, A. 1930. Saxifragaceae. In A. Engler and K. Prantl [eds.], *Die natürlichen Pflanzenfamilien*, 2nd ed. 18a: 74-226. Wilhelm Englemann, Leipzig.
- GRUND, C., AND U. JENSEN. 1981. Systematic relationships of the Saxifragales revealed by serological characteristics of seed proteins. *Pl. Syst. Evol.* 137: 1-22.
- HICKEY, L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. In C. R. Metcalfe and L. Chalk [eds.], *Anatomy of the dicotyledons*, 2nd ed. 1: 25-39. Clarendon Press, Oxford.
- HIDEUX, M. J., AND I. K. FERGUSON. 1976. The stereostructure of the exine and its evolutionary significance in Saxifragaceae sensu lato. In I. K. Ferguson and J. Muller [eds.], *The evolutionary significance of the exine*, pp. 327-377. Academic Press, London.
- HOLMGREN, P. K., W. KEUKEN, AND E. K. SCHOFIELD. 1981. *Index Herbariorum*, 7th ed. Dr. W. Junk, B.V., The Hague.
- HUTCHINSON, J. 1973. *The families of flowering plants*, 3rd ed. Clarendon Press, Oxford.
- JAY, M. 1970. Quelques problèmes taxonomiques et phylogénétiques des Saxifragacées vus à la lumière de la biochimie flavonique. *Bull. Mus. Hist. Nat. (Paris) Ser. 2.* 42: 754-775.



- JENSEN, L. C. W. 1968. Primary stem vascular patterns in three subfamilies of the Crassulaceae. *Amer. J. Bot.* 55: 553–563.
- JOHANSEN, D. A. 1940. *Plant microtechnique*. McGraw-Hill, New York.
- MAURITZON, J. 1933. Studien über die Embryologie der Familien Crassulaceae und Saxifragaceae. Håkan Ohlssons Buchdruckerei, Lund.
- METCALFE, C. R., AND L. CHALK. 1950. *Anatomy of the dicotyledons*. Vol. I, II. Clarendon Press, Oxford.
- , AND ———. 1979. *Anatomy of the dicotyledons*, 2nd ed., Vol. 1: Systematic anatomy of leaf and stem, with a brief history of the subject. Clarendon Press, Oxford.
- , AND ———. 1983. *Anatomy of the dicotyledons*, 2nd ed., Vol. 2: Wood structure and conclusion of the general introduction. Clarendon Press, Oxford.
- MOREAU, F. 1976. Types stomatiques et trichome foliaire des Saxifragoïdées (Saxifragacées). *Rev. Cytol. Biol. Vég.* 39: 329–341.
- ROCÉN, T. 1928. Beitrag zur Embryologie der Crassulaceen. *Svensk. Bot. Tidskr.* 22: 368–376.
- SCHMID, R. 1977. Stockwell's bleach, an effective remover of tannin from plant tissues. *Bot. Jahrb. Syst.* 98: 278–287.
- SCHULZ-MENZ, G. K. 1964. Rosales. In H. Melchior [ed.], *A. Engler's Syllabus der Pflanzenfamilien*, Bd. 2, pp. 193–242. Gebrüder Borntraeger, Berlin-Nikolassee.
- SOLEREDER, H. 1908. Systematic anatomy of the dicotyledons. [Transl., L. A. Boodle and F. E. Fritsch; revd., D. H. Scott.] Clarendon Press, Oxford.
- SOLTIS, D. E., AND B. A. BOHM. 1982. Flavonoids of *Penthorum sedoides*. *Biochem. Syst. Ecol.* 10: 221–224.
- SPONGBERG, S. A. 1972. The genera of Saxifragaceae in the southeastern United States. *J. Arnold Arbor.* 53: 409–498.
- . 1978. The genera of Crassulaceae in the southeastern United States. *J. Arnold Arbor.* 59: 197–248.
- STERN, W. L. 1974a. Saxifragales. *Encyclopedia Britannica*, 15th ed. 16: 291–302.
- . 1974b. Comparative anatomy and systematics of woody Saxifragaceae: *Escallonia*. *J. Linn. Soc., Bot.* 68: 1–20.
- . 1978a. Comparative anatomy and systematics of woody Saxifragaceae: *Hydrangea*. *J. Linn. Soc., Bot.* 76: 83–113.
- . 1978b. A retrospective view of comparative anatomy, phylogeny, and plant taxonomy. *Int. Assoc. Wood Anat. News Bull.* 2, 3: 33–39.
- , E. M. SWEITZER, AND R. E. PHIPPS. 1970. Comparative anatomy and systematics of woody Saxifragaceae: *Ribes*. In N. K. B. Robson et al. [eds.], *New research in plant anatomy*. *J. Linn. Soc., Bot.* 63. Supplement 1, pp. 215–237. Academic Press, London.
- STYER, C. H., AND W. L. STERN. 1979a. Comparative anatomy and systematics of woody Saxifragaceae: *Philadelphus*. *J. Linn. Soc., Bot.* 79: 267–289.
- AND ———. 1979b. Comparative anatomy and systematics of woody Saxifragaceae: *Deutzia*. *J. Linn. Soc., Bot.* 79: 291–319.
- TAKHTAJAN, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev.* 46: 225–359.
- TAMOLANG, F. N., R. R. VALBUENA, J. A. MENIADO, AND B. C. DE VELA. 1963. Standards and procedures for descriptions of dicotyledonous woods. *Forest Products Research Institute, Bull.* 2. College, Laguna, Philippines.
- THORNE, R. F. 1976. A phylogenetic classification of the Angiospermae. *Evol. Biol.* 9: 35–104.
- TORREY, J., AND A. GRAY. 1840. *A flora of North America*, Vol. I. Wiley and Putnam, New York.
- VAN TIEGHEM, P. 1898. Sur le genre *Penthoraceae* considéré comme type d'une famille nouvelle les *Penthoracées*. *J. Bot. (Morot)* 12: 150–154.
- WAKABAYASHI, M. 1970. On the affinity in Saxifragaceae s. lato with special reference to the pollen morphology. (In Japanese; English summary.) *Acta Phytotax. Geobot.* 24: 128–145.
- WILEY, E. O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. John Wiley and Sons, New York.

## APPENDIX 1

The following list comprises collection information for each specimen examined. Entries include locality, collector, collection number and location of herbarium voucher. Abbreviations of herbaria are in accordance with *Index Herbariorum*.

*Penthorum chinense* Pursh—PEOPLE'S REPUBLIC OF CHINA: Beijing (Peking), *Wang 1130* (Herbarium, Dept. of Biology, Peking University); Jiangsu Prov., Nanjing, *Xiong 0001* (URV); Kwangtung Prov., Mt. Ding Hu Shan, *Shi s.n.* (IBSC). JAPAN: Chiba Pref., Chosei-gun, Torami, *Tobe 80*, *Tobe 81* (TI); Kanagawa Pref., Honshu, Yokosuka, *Wakabayashi s.n.* (MAK).

*Penthorum sedoides* L.—U.S., VIRGINIA: Chesterfield Co., Pocahontas State Park, *Hayden 952*, *Hayden 958* (URV); Goochland Co., Beaverdam Cr., *Hayden 798*, *Hayden 1004* (URV); Montgomery Co., Pandapis Pond, *Haskins 76* (URV).