8-1985

Anatomy and systematics of Penthorum L.

Melanie Lynn Haskins

Recommended Citation

Haskins, Melanie Lynn, "Anatomy and systematics of Penthorum L." (1985). *Master's Theses.* Paper 493.

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 intervascular 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.

ANATOMY AND SYSTEMATICS OF <u>PENTHORUM</u> L.

BY

MELANIE LYNN HASKINS

APPROVED:

W. John Haydon

COMMITTEE CHAIRMAN

William S. Woolcott

Wilton R. Tenney

R D Decker

COMMITTEE MEMBERS

EXAMINING FACULTY:

W. R. West Jr.

ANATOMY AND SYSTEMATICS OF PENTHORUM L.

By

MELANIE LYNN HASKINS

B.S., Roanoke College, 1982

A Thesis
Submitted to the Graduate Faculty
of the University of Richmond
in Candidacy
for the degree of
MASTER OF SCIENCE
in
Biology

August, 1985
Richmond, Virginia

Werth. His unfailing enthusiasm for research has been a constant boon to me throughout this project.

My most heartfelt thanks go to my advisor, Dr. W. John Hayden. His inspiration, patience, counsel, and energy have been invaluable to my research and I am grateful for the encouragement he has offered in pursuit of my career.

Finally, I am most grateful to my family for their continuous faith and support of my endeavors as a graduate student.

PREFACE

The genus *Penthorum* L. consists of two species, the occidental *P. sedoides* L., which ranges from Maine and Quebec south through Florida and west to Minnesota, Oklahoma and Texas (Spongberg, 1972) and the oriental *P. chinense* Pursh, which inhabits far eastern Russia, China, Korea and Japan (Borisova, 1939). Two other species, *P. intermedium* Turcz. and *P. humile* Rgl. & Maack, have been named but are probably best interpreted as minor variants of *P. chinense* (Engler, 1930; Borisova, 1939; Spongberg, 1972). Within its geographical distribution, plants of *Penthorum*, commonly known as the ditch stonecrop, occur in poorly drained areas, ditches, marshes, swamps and floodplains. *Penthorum sedoides* is occasional in the mountains of eastern North America, but more common in other provinces, especially the coastal plain (Radford, Ahles and Bell, 1968; Spongberg, 1972). The plants are often characterized by substantial insect damage to the leaves, and are easily recognized by their unusual star-shaped greenish and nearly naked five-merous flowers. *Penthorum* well deserves its name, which is derived from the Greek words *pente* (five) and *horos* (mark).

Penthorum is a perennial, rhizomatous, semiaquatic herb which produces erect leafy stems to 1 m tall. The plant spreads by creeping rhizomes often found submerged or slightly so. Stem bases are terete, glabrous and decumbent, giving rise to erect stems which are angled, slightly pubescent and often widely branched above. The leaves are non-succulent, alternate, simple, lanceolate or elliptic, and bright green and shining with occasional small abaxial trichomes. Leaves have narrowed cuneate subpetiolar bases, acute to acuminate leaf apices and unevenly serrate margins. Leaf venation is pinnate.

The inflorescences of Penthorum are found on two to several terminal or axillary branches as spiked to scorpioid cymes. Axes of the cymes are stipitate-glandular. The flowers are perfect, greenish and short-stalked. The calyx consists of five to seven ovate, marginally toothed lobes which are partially united into a shallow floral cup, which persists in fruit. The corolla is lacking or rarely present and consisting of lanceolate, slightly clawed, short petals, isomerous with the sepals. Ten stamens are inserted on the floral cup, five opposite the sepals and five alternate with them; filaments taper only slightly to basifixed, oblong, longitudinally dehiscent anthers. The gynoecium is composed of five to seven carpels, which are fused basally and are adnate to the floral cup below the placental position. The short styles are erect at anthesis and curve outwardly in fruit. Ovules are located on a pendulous placenta adaxially attached to the carpel wall above the syncarpous region. At maturity the reddish capsules dehisce circumscissilely above the fused portion of the gynoecium to release many small, elliptic, tuberculate, rust-colored seeds (Rydberg, 1905; Spongberg, 1972; Godfrey and Wooten, 1981). Vegetative growth and flowering occur throughout the summer, mainly in the months of July and August, continuing until frost. Rhizome initiation near the end of the growing season is thought to be triggered by shortening day length (Spongberg, 1972).

The two species of _Penthorum_ are very similar, but _P. chinense_ has narrower leaves, more robust styles and fewer flowers per inflorescence than _P. sedoides_. The chromosome count of _P. sedoides_ is 2n=18, while that of _P. chinense_ is 2n=16 (Spongberg, 1972).

This genus has a long taxonomic history; nevertheless, its familial status remains unsettled. _Penthorum_ is considered transitional between the stonecrop or orpine family, Crassulaceae, and the saxifrage family, Saxifragaceae. The family Crassulaceae consists of approximately 25 genera and 900 species found most commonly in dry temperate regions of the world. Members of this family include the familiar genera _Sedum_ L., _Kalanchoë_ Adanson, and _Crassula_ L., frequently used as ornamentals in rock gardens (Cronquist, 1981). The Saxifragaceae is a much larger and more diverse family of 70 or 80 genera of herbs, shrubs, small trees and woody vines, one-third of which exist in North America. Some representatives of this family are the genera Philadelphus L. (Mock Orange), Hydrangea L., Saxifraga L., and Ribes L. (Gooseberry, Currants), often used as ornamentals in yards and gardens (Benson, 1979). The two families are classified in the order Saxifragales (Takhtajan, 1980) or in the order Rosales (Engler, 1930; Cronquist, 1981). Penthorum resembles both families morphologically in some characteristics. For example, like the Crassulaceae, flowers of Penthorum have as many carpels as sepals and also bear an overall resemblance to some crassulaceous flowers. On the other hand, like the Saxifragaceae, the genus is nonsucculent, the flowers are slightly perigynous with partially connate carpels, and the carpels lack the nectariferous appendages present in Crassulaceae (Cronquist, 1981).

The familial position of Penthorum has been a subject of interest to botanists for over 150 years. In 1830 DeCandolle placed it in the tribe "Crassulaceae Anomalae" along with Diamorpha Nutt., a genus that has a shallow floral cup and syncarpous gynoecium (Spongberg, 1972). Torrey and Gray (1840) assigned it to the crassulaceous tribe Diamorpheae, but in 1871 Baillon removed Penthorum to a tribe of the Saxifragaceae. Prior to van Tieghem (1898), nearly all botanists had considered Penthorum a member of

Crassulaceae; however, impressed with several anatomical and morphological differences between *Penthorum* and Crassulaceae, van Tieghem (1898) proposed the family Penthoraceae on the basis of stem, leaf, root and reproductive structures. He based this new family on the lacunose cortex and formation of fibrous "pericyclic" bundles outside the phloem in the roots, the apetalous flowers and the mode of fruit dehiscence. In 1930 Engler made *Penthorum* the basis of a subfamily of Saxifragaceae, and the current *A. Engler's Syllabus der Pflanzenfamilien* (Schulz-Menz, 1964) still maintains it as such. In more recent systems, the familial position is still ambiguous. Benson (1979), Takhtajan (1980) and Cronquist (1981) all believe it fits best in the Saxifragaceae, Hutchinson (1973) and Borisova (1971) place it in the Crassulaceae and Airy-Shaw (1973) and Stern (1974a) place it in its own family, Penthoraceae.

Studies in several subdisciplines of systematics have been undertaken by researchers hoping to discern the relationships of *Penthorum*. Flavonoid analyses of the ditch stonecrop have suggested only very slight chemical affinity with Saxifragaceae (Jay, 1970; Soltis and Bohm, 1982). One cytological study reported equal chromosome numbers for *Penthorum* and *Diamorpha cymosa*, suggesting inclusion in the Crassulaceae (Baldwin and Speese, 1940). Palynological studies have revealed conflicting results; some authors believe *Penthorum* is intermediate between the two families (Agababian, 1961; Hideux and Ferguson, 1976) or more like Saxifragaceae (Wakabayashi, 1970). Serological comparisons of seed proteins of *Penthorum* to those of Saxifragaceae and Crassulaceae have yielded inconclusive results (Grund and Jensen, 1981).

Coupled with characteristics of floral morphology and evidence from the systematic subdisciplines mentioned above, anatomical features are extremely useful in discerning evolutionary and taxonomic relationships (Bailey, 1944). Anatomical characteristics have been used for over a century for systematic purposes, both for identification of specimens and establishment of phylogenetic relationships among plants at and above the specific level (Radford et al., 1974). Indeed, Bailey (1951) and Metcalfe (1954) asserted that anatomical information alone could be used to construct a phenetic classification of the dicotyledons.

Of these anatomical features, certainly the one most demonstrative of evolutionary trends is secondary xylem. The idea that vessel elements have evolved from tracheids is well established, and their evolutionary transformation is measurable in several dimensions. For example, vessels that resemble tracheids in being very long and possessing highly oblique end walls, small diameters, and long scalariform perforation plates with many bars are recognized as primitive. Phylogenetic trends for wood rays, fibers and axial parenchyma have also been determined with substantial certainty (Dickison, 1975; Stern, 1978b; Metcalfe and Chalk, 1983). Moreover, anatomical characters tend to remain typical of taxonomic groups at the generic level and above (Metcalfe and Chalk, 1950). The combination of numerous well-accepted phylogenetic trends and generic constancy renders anatomical data extremely valuable in making systematic comparisons.

Very little anatomical data exist for the two species of _Penthorum_ other than dated qualitative descriptions by Solereder (1908) and van Tieghem (1898). Although its habit is herbaceous, _Penthorum_ tends to accrue considerable secondary xylem tissue. On this basis, a thorough qualitative and quantitative anatomical investigation of both species was undertaken to augment existing knowledge of the histology of _Penthorum_ and to attempt to resolve the familial status by comparison with corresponding characters in Saxifragaceae and Crassulaceae.

Another goal of this study is to employ modern phylogenetic principles in assessing the relationships of _Penthorum_ with Crassulaceae and Saxifragaceae. Of prime importance is the distinction between shared primitive characters (symplesiomorphies) and shared derived characters (synapomorphies); only the latter are judged to be significant in indicating a common phylogeny for a given pair of organisms (Wiley, 1981). Phylogeny can be defined as the sequential change in characteristics which occur in the genetic lineage of an organism and its descendants. During phylogeny, then, the only significant, or even detectable, event is the transformation of certain characters from their original condition (primitive or plesiomorphic character state) to some changed condition (advanced, derived or apomorphic character state). Thus, the patterns of synapomorphies observed in taxa comprising a monophyletic group are the direct results of the events which occurred during their phylogeny, whereas the symplesiomorphies merely indicate which characters were static or remained unchanged during phylogeny. In reconstruction of a phylogeny, then, symplesiomorphies provide no insight into what may have transpired. Only synapomorphies provide clues to the actual events that occurred in a given phylogenetic lineage. Reconstruction of phylogenies using synapomorphies must, however, be tempered with the knowledge that reversals and parallelisms are possible and tend to obscure true monophyletic groups or suggest monophyly for groups which really are not monophyletic.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

The genus *Penthorum* L. (ditch stonecrop) consists of two species: *P. sedoides* L. native to the eastern half of the United States and *P. chinense* (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 Crassulaceae, *Penthorum* has as many carpels as sepals. On the other hand, like Saxifragaceae, the genus is nonsucculent, the flowers are slightly perigynous with partially fused carpels, and the carpels lack nectar glands present in Crassulaceae (Spongberg, 1972; Cronquist, 1981).

The unresolved familial position of *Penthorum* has been of interest for over 150 years. *Penthorum* has been considered as a member of Crassulaceae (DeCandolle, 1830; Torrey and Gray, 1840; Hutchinson, 1973), as a member of Saxifragaceae (Baillon, 1871; Engler, 1930; Takhtajan, 1980; Cronquist, 1981) or as 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), palynology (Hideux and Ferguson, 1976), cytology (Baldwin and Speese, 1951), chemistry (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 roots, young stems, nodes, leaves and especially secondary xylem tissues of *Penthorum* in order to make comparisons with corresponding features typical of Crassulaceae and Saxifragaceae and to attempt to elucidate the familial status of *Penthorum*.

MATERIALS AND METHODS

Anatomical 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 are 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 µm 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 stained with a 1 percent solution of toluidine blue and mounted in Hoyer's solution to demonstrate vascularization.

Leaves were cleared by treatment with 2.5--5 percent 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 µm 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 decriptions of secondary tissues are in agreement with those suggested by the Committee on Nomenclature of the International Association 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: 10 measurements per specimen of stomatal length and width, vessel wall thickness, intervascular pit diameter, fiber-tracheid diameter, fiber-tracheid wall thickness, fiber-tracheid pit border diameter, 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 diameter, vessel element length, and fiber-tracheid length. Pore frequency and distribution are based on counts of 10 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 Appendix 2.

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 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. 3); cuticle up to 2 µm thick. Collenchyma beneath epidermis mostly angular, sometimes lacunar, in discontinuous patches of two to four layers. Cortex aerenchymatous, but cells near cortex boundaries compact; cortical bundles absent; cortex cells becoming sclerified with age (Fig. 19). Primary vasculature resembling an ectophloic siphonostele (Fig.5), even in young stems. Phloem sieve plates compound with two to many sieve areas; perivascular thick-walled fibers sparse, becoming 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 common (Fig. 4).

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; druses present. Petiolar vasculature a simple arc-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. Leaf margin serrate. Teeth rosoid, glandular, compound, 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, approximately 130 µm 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 in P. sedoides; course uniformly curved, sometimes abruptly curved in 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, in P. sedoides arising at right angles admedially and acute angles exmedially, in P. chinense ranging from acute to obtuse admedially and mostly acute exmedially. 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 foraminate, principle vein central, direct; accessory veins present, connivent (Fig. 7).

Upper and lower epidermides uniseriate (Fig. 9, 10); cuticle slightly differentiated; darkly stained deposits common except around midrib. Epidermal cells infrequently slightly papillate (Fig. 10), thin-walled, anticlinal walls straight or sinuous (Fig. 14), circular to elliptic in cross-section, larger in upper epidermis than in lower epidermis (Fig. 10). Stomates on both surfaces, more frequent abaxially, anomocytic (Fig. 14); guard cell pairs circular to elliptic, 23--31 (18--35) µm long, 16--23 (15--27) µm 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 cells circular, or rectangular and procumbent. Primary vein a simple arc surrounded by large parenchyma cells, 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 percent solitary, 8--17 percent radial multiples, 26--41 percent clusters; pores per mm^2 very numerous, 455--717; pore area 0.21--0.34 mm^2 per mm^2 cross-sectional area of wood. Pore outlines angular (Fig. 17, 18); wall thickness 1--2 (0.75--2) µm; tangential diameter extremely to very small, 21--30 (12--37) µm. Perforation plates scalariform, varying in position from terminal to subterminal; bars many, 18--34 (9--57) per plate, often branched (Fig. 22,23); end walls inclined 76--84 (60--88) degrees from the horizontal. Intervascular pits circular, alternate to scattered; diameter very small, 2--3 (1.5--4) µm (Fig. 21). Vessel element length medium, 477--764 (280--1270) µm, ligulate or ligules absent, 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--1300) µm; lumen diameter greater than wall thickness (Fig. 17); wall thickness 2--3 (1--4) µm; tangential diameter 15--22 (10--27) µm; vertical diameter of pit borders 2--3 (1.5--3) µm; 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 mm; 26--61 percent uniseriate, 39--74 percent multiseriate. Uniseriate ray width extremely fine, 7--12 (2--17) µm; height extremely to very low, 416--914 (160--1940) µm or 6--10 (2--25) cells. Multiseriate ray width extremely to moderately fine, 14--26 (9--47) µm or 2 (2--4) cells; height very low to low, 584--1126 (220--2820) µm or 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 thus may possess 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 serial sections of vigorously growing stems is suggested to confirm the fundamentally eustelic structure for stems of Penthorum.

Previous anatomical investigations of Penthorum performed 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 here showed only slight lignification of the endodermis, variation in the number of xylem arms, and no pith. In keeping with the tradition of their day, van Tieghem and Solereder described a strongly differentiated endodermis and a three to four layer pericycle from the primary stem of Penthorum; these structures probably correspond with the inner, nonin *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 μm in *P. sedoides* and 663--911 μm 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, 1978a; 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. Similarly, 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 often hypothesized as slightly more primitive than Saxifragaceae by virtue of its free carpels (Hutchinson, 1973). The two families resemble members of the Rosaceae. Crassulaceae may be distinguished by its succulence, exstipulate leaves, and nectariferous carpel glands (Lawrence, 1951). Saxifragaceae may be distinguished from Rosaceae by its usually exstipulate, sometimes opposite leaves, fewer carpels and stamens, and copious endosperm (Spongberg, 1972).

Crassulaceae is well-defined morphologically and taxonomically. Considered by botanists as comprising a natural assemblage, Crassulaceae is characterized by a number of adaptations to xeric environments: a thick waxy leaf covering, an abundance of foliar water storage tissue, hydathodes, well developed parenchyma in the 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 of which are herbaceous and the other 10 being basically woody. Many modern systems split the family, in which the herbaceous members embody one family, Saxifragaceae, and the woody members are separated into other families. For the purpose of comparisons with *Penthorum*, the 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 1. Other than the obvious succulence of Crassulaceae and the different stomatal type, anatomical features of the primary plant body are equivocal concerning the relationships of *Penthorum*. On the basis of these features alone, *Penthorum* could fit comfortably within 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, many such crassulaceous plants possess anomalous structure consisting of a variety of peculiar vascular tissue arrangements: a ring of fibers external to primary vessels; a ring of fibers with long parenchyma cells; rings of fibers, vessels and parenchyma arranged in concentric circles; or bundles separated by rays (Solereder, 1908; Metcalfe and Chalk, 1950, 1979, 1983). Other advanced anatomical characteristics of Crassulaceae include multi-trace nodes, anisocytic stomata, simple perforation plates, and libriform fibers. In contrast to its relatively primitive floral structure, Crassulaceae is typified by numerous specialized anatomical features not shared with Penthorum. The ditch stonecrop would be misplaced in Crassulaceae.

As mentioned above, many features of the secondary xylem of Penthorum are also commonly encountered in the woody "saxifrages." On a purely phenetic basis, then, Penthorum could easily be accomodated 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.

Two aspects of the morphology of *Penthorum* seem to provide possible, but conflicting synapomorphies, one with Crassulaceae, the other with Saxifragaceae. With further study these features may provide additional insights. The first of these features concerns the remarkable circinately coiled inflorescence branches of *Penthorum*. It is unclear whether these "scorpioid cymes" of numerous authors should be considered autapomorphous or whether they are homologous with the various modified cymes of Crassulaceae. The other feature concerns the gynoecium, which consists of a whorl of five to seven basally fused carpels, and has long been compared to similar structures in Saxifragaceae and may reasonably be hypothesized as synapomorphous with Saxifragaceae. Fusion of the carpels is only partial, however, in *Penthorum*, and it must also be observed that certain Crassulaceae also possess basally fused carpels. Further, it has not been widely recognized, that the gynoecium of *Penthorum* is similar, at least in gross morphology, to that of *Trochodendron aralioides* Sieb. & Zucc. (Hamamelidae, Trochodendraceae) differing chiefly in the manner of dehiscence (loculicidal in *Trochodendron*, circumscissile in *Penthorum*). *Trochodendron* is well known for its combination of primitive features including vesselless wood and scarcely sealed and weakly connate carpels (Cronquist, 1968). Placentation and the divergence of fruiting stigmas seem similar in both genera. Although evidence for a close relationship with *Trochodendron* would be most unexpected, a thorough study of floral anatomy of *Penthorum*, *Trochodendron*, and multicarpellate Saxifragaceae *sensu lato* would be of interest.

The anatomical perspective provided by the present study is consistent with widely held opinions that *Penthorum* is intermediate between Crassulaceae and Saxifragaceae.

Penthorum simply possesses too few synapomorphies with either Crassulaceae or Saxifragaceae to place it with confidence in either of these families. Most distinctive anatomical and morphological features of *Penthorum* are either unambiguously primitive, very common adaptations to an aquatic environment, or of uncertain status as to their primitive or derived nature. The genus is probably best interpreted as a relictual element little changed from its divergence from the ancestral stem of Rosidae. As such, classification in van Tieghem's Penthoraceae seems preferable to inclusion in either Crassulaceae or Saxifragaceae.

LITERATURE CITED

Agababian, V. S. 1961. Materials toward the palyno-systematic study of the family Saxifragaceae s.l. (In Russian). Izv. Biol. Nauki. 14(2): 45-61.

Airy-Shaw, H. K. 1973. Willis' dictionary of the flowering plants and ferns, 7th ed. University 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.

______. 1951. The use and the abuse of anatomical data in the study of phylogeny and classification. Phytomorphology 1: 67-69.

______. 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. Histoire des Plantes. 3: 323-464.

Baldwin, J. T., Jr. and B. M. Speese. 1951. Penthorum: its chromosomes. Rhodora 53: 89-91.

Beck, C. B., R. Schmid, and G. W. Rothwell. 1982. Stelar morphology and the primary vascular system of seed plants. Bot. Rev. 48: 691-815.

Benson, L. 1979. Plant classification, 2nd ed. D. C. Heath Co., Lexington, Massachusetts.

Borisova, A. G. 1939. Crassulaceae. In V. L. Komarov [ed.], Flora of the U.S.S.R., Vol. 9, pp. 8-105, [Translated by Israel Program for Scientific Translations, Jerusalem, 1971].

Candolle, A. P. de. 1830. Penthorum. Prodromus sytematis naturalis regni vegetabilis... 3: 414.

Carlquist, S. 1975. Ecological strategies of xylem evolution. University of 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. 1968. The evolution and classification of flowering plants. Houghton Mifflin, Boston.

_____. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York.

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.

Godfrey, R. K. and J. W. Wooten. 1981. Aquatic and wetland plants of southeastern United States: dicotyledons. The University of Georgia Press, Athens.

Grund, C. and U. Jensen. 1981. Systematic relationships of the Saxifragales revealed by serological characteristics of seed proteins. Plant 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., Vol. 1, pp. 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.

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 biochemie 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.

Lawrence, G. H. M. 1951. Taxonomy of vascular plants. The Macmillan Company, New York.

Mauritzon, J. 1933. Studien über die embryologie der familien Crassulaceae und Saxifragaceae. Håkan Ohlssons Buchdruckerei, Lund.

Metcalfe, C. R. 1954. An anatomist's views on angiosperm classification. Kew Bull. 9: 427-440.

_____, and L. Chalk. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford.

_____, and L. Chalk. 1979. Anatomy of the dicotyledons, Vol 1: Systematic anatomy of leaf and stem, with a brief history of the subject. Clarendon Press, Oxford.

_____, and L. Chalk. 1983. Anatomy of the dicotyledons, 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. Veg. 39: 329-341.

Radford, A. E., H. E. Ahles and C. R. Bell. 1968. Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill.

_____, W. C. Dickison, J. R. Massey, and C. R. Bell. 1974. Vascular plant systematics. Harper and Row, New York.

Rocén, T. 1928. Beitrag zur Embryologie der Crassulaceen. Svensk. Bot. Tidskr. 22: 368-376.

Rydberg, P. A. 1905. Penthoraceae. North Amer. Flora 22: 75.

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. Gebrüder Borntraeger, Berlin-Nikolassee.

Solereder, H. 1908. Systematic anatomy of the dicotyledons. [Translated by L. A. Boodle and F. E. Fritsch; revised by D. H. Scott]. Clarendon Press, Oxford.

Soltis, D. E. and B. A. Bohm. 1982. Flavonoids of *Penthorum sedoides*. Biochem. Syst. Ecol. 10: 221-223.

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. Bull. 1978: 33-39.

_____, E. M. Sweitzer, and R. E. Phipps. 1970. Comparative anatomy and systematics of woody Saxifragaceae: *Ribes*. *In* N. K. Robson, *et al*., eds., New research in plant anatomy. J. Linn. Soc., Bot. 63. Supplement 1. 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, Phillippines.

Thorne, R. F. 1976. A phylogenetic classification of the Angiospermae. Evol. Biol. 9: 35-104.

Tieghem, P. van. 1898. Sur le genre Penthore considéré comme type d'une famille nouvelle les Penthoracées. J. Bot. (Morot). 12: 150-154.

Torrey, J. and A. Gray. 1840. A flora of North America, New York.

Wakabayashi, M. 1970. On the affinity in Saxifragaceae *s. lato* with special reference to the pollen morphology. Acta Phytotax. Geobot. 24: 128-145.

Wiley, E. D. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley & Sons, New York.

Table 1. Anatomical comparisons of *Penthorum*, Crassulaceae, and

Character	Crassulaceae*	Penthorum
Primary Stem		
Stele	continuous cylinder; eustele	continuous cylinder
Node**	3:3 or 1:1	1:1
Petiole	arc of bundles, median one often larger	continuous arc
Leaf blade		
Stomate type	anisocytic	anomocytic
Hydathodes	present	present
Wood		
Vessels		
Perforation plates	simple	scalariform
Intervascular pits		
Type	simple	bordered
Arrangement	***	alternate to scattered
Imperforate elements	absent, or libriform fibers	fiber-tracheids
Rays	rarely developed	uniseriate and multiseriate homocellular erect
Axial xylem	abundant (often dominant)	absent

---

*References used in compilation of this chart include: Cronquist
Solereder (1908); Spongberg (1972; 1978); Stern (1974b; 1978a);

**The first number of this notation refers to number of leaf traces,
unilacunar node.

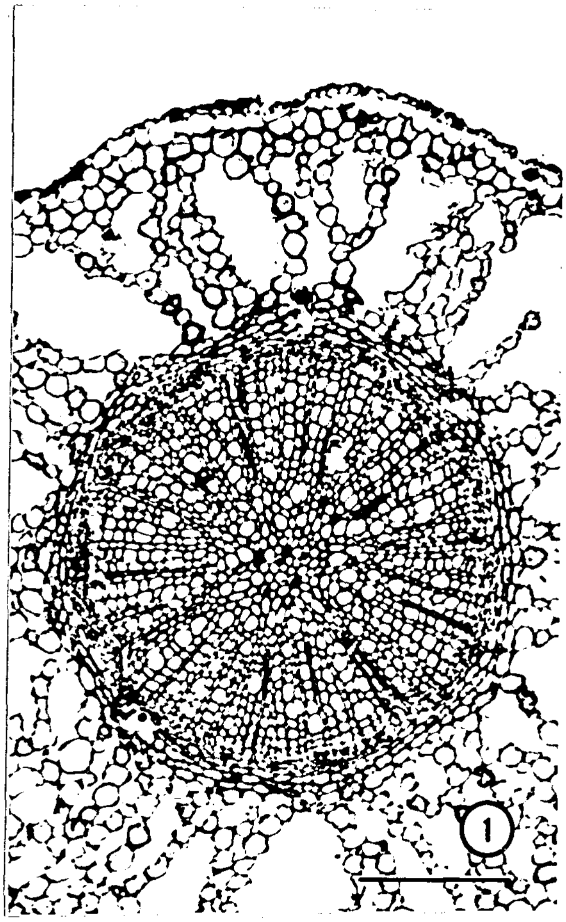
***Data not available

Saxifragaceae

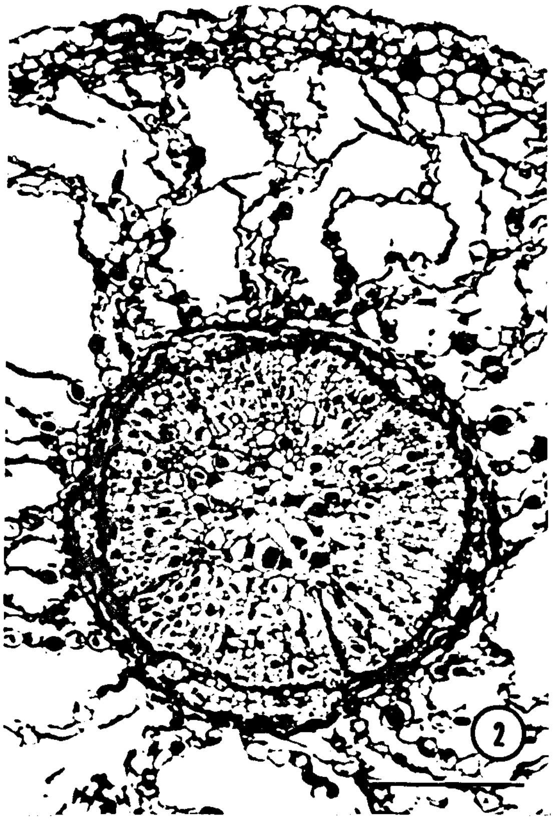
Woody Saxifrages*	Herbaceous Saxifrages*
continuous cylinder; eustele	eustele, continuous cylinder
3:3 (3:3 to 7:7 in *Hydrangea*; 1:1 in *Escallonia*)	3:3 (1:1 in *Parnassia*)
1 to many bundles	1-3 concentric bundles
anomocytic	anomocytic
present	present
scalariform (simple)	simple
simple or bordered	***
scalariform or opposite; alternate to transitional	***
fiber-tracheids (septate or non-septate) or tracheids; vasicentric tracheids	***
uniseriate, homocellular erect and multiseriate heterocellular	***
absent or diffuse apotracheal or scanty abaxial paratracheal	***

(1981); Jensen (1968); Metcalfe and Chalk (1950; 1979); Moreau (1976)
Stern, Sweitzer, and Phipps (1970); and Styer and Stern (1979a; 1979b)
the second to leaf gaps. Therefore, 3:1 is a three-trace

Fig. 1, 2. Roots of *Penthorum*. **1.** *Penthorum sedoides*, *Hayden 952*, cross-section. **2.** *Penthorum chinense*, *Tobe 81*, cross-section. Note greater abundance of dark deposits in comparison with *P. sedoides*. Bars = 200 µm.

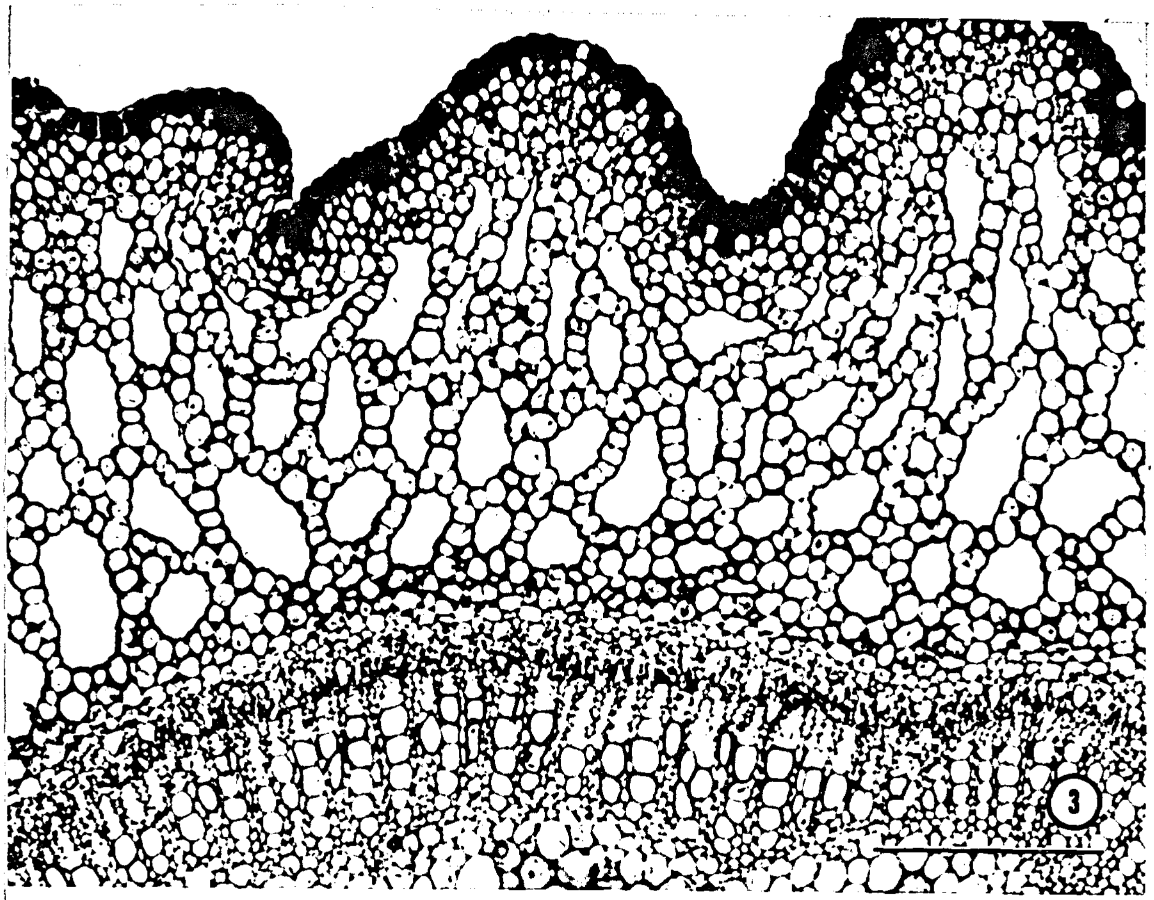


①



②

Fig. 3, 4. Young stems of *Penthorum*. Note aerenchymatous cortex. **3.** *Penthorum chinense*, *Shi* *s.n.*, cross-section. **4.** *Penthorum sedoides*, *Hayden* *798*, cross-section. Bars = 200 µm.


③

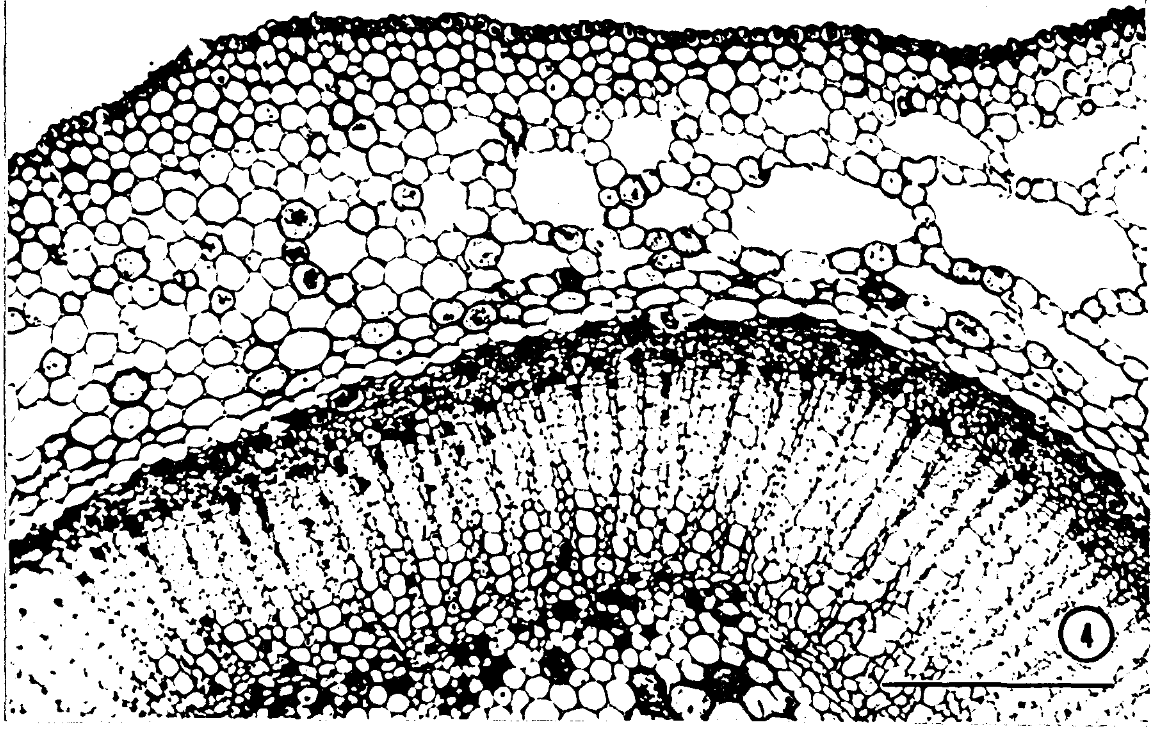
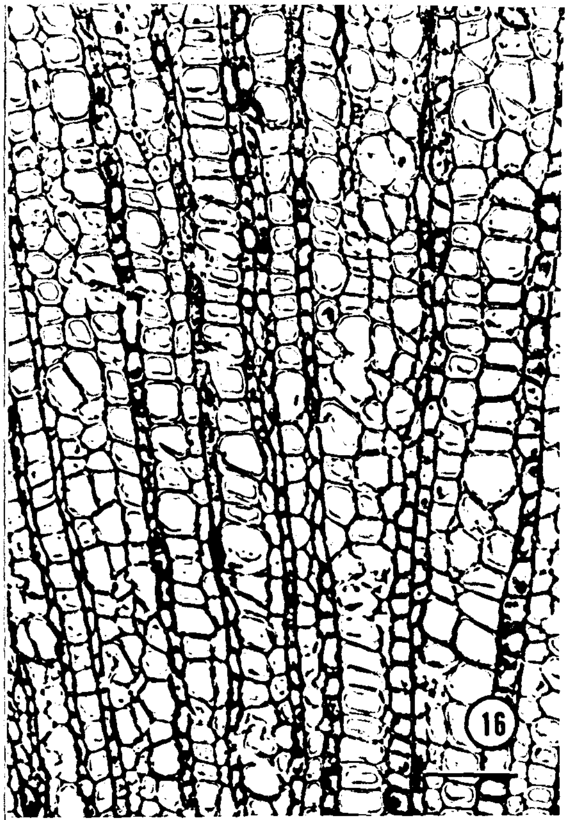
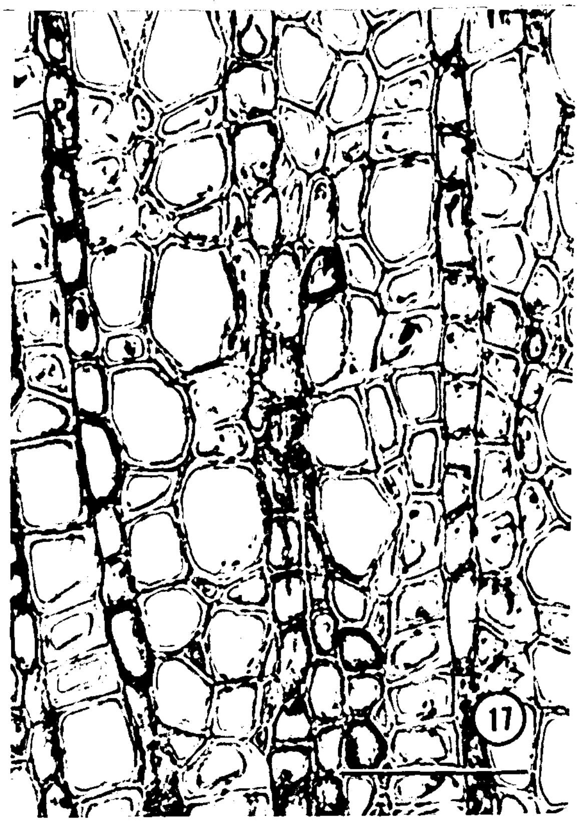

④

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 µm. Bars for Fig. 7-10 = 50 µm.

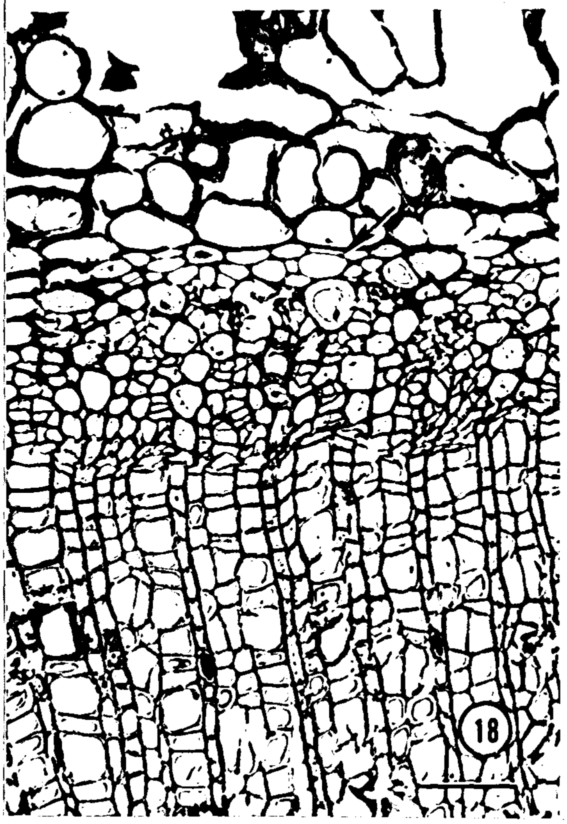
Fig. 16-19. Old stems and secondary tissues. **16, 17.** Penthorum chinense, Shi s.n., cross-sections of wood. **18.** Penthorum sedoides, Hayden 958, cross-section of stem showing wood, cambial zone, secondary phloem, and cortex. Arrow indicates phloem fiber. **19.** Penthorum sedoides, Hayden 798,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



16



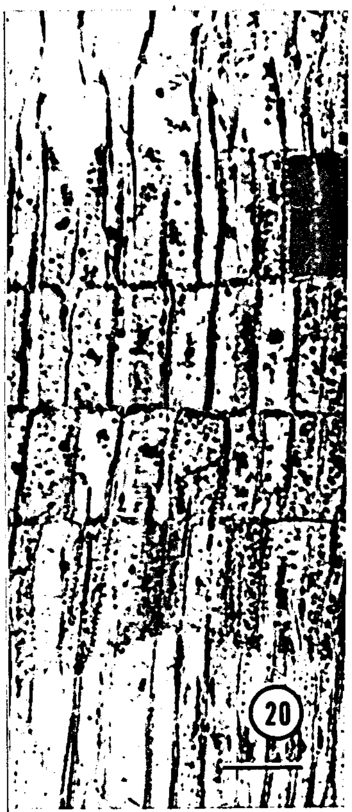
17

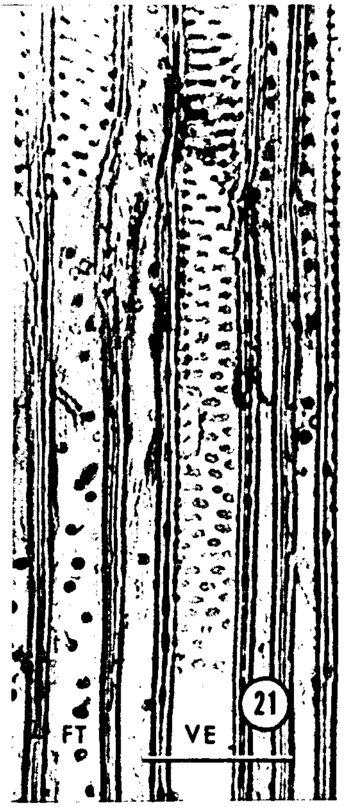


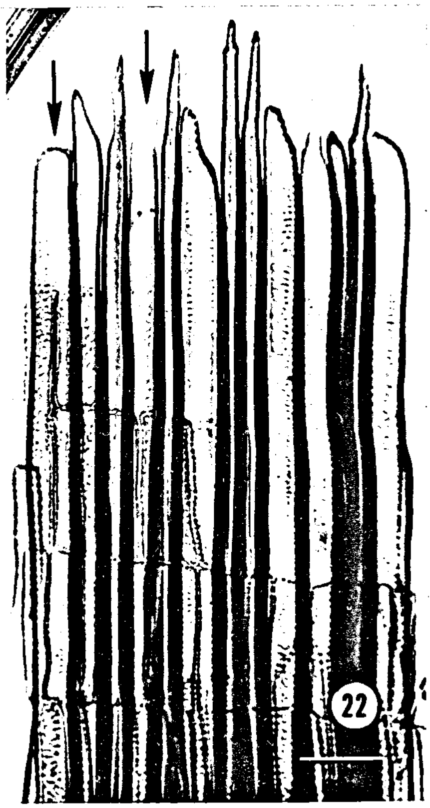
18

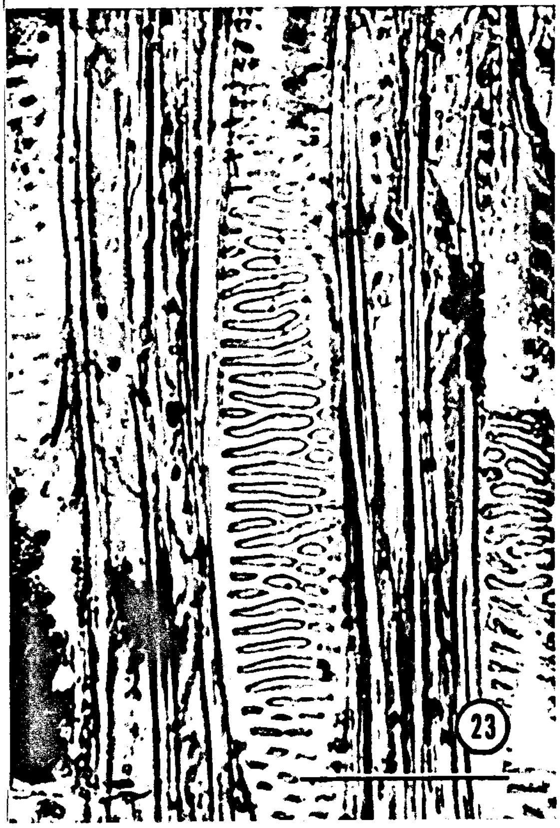
19

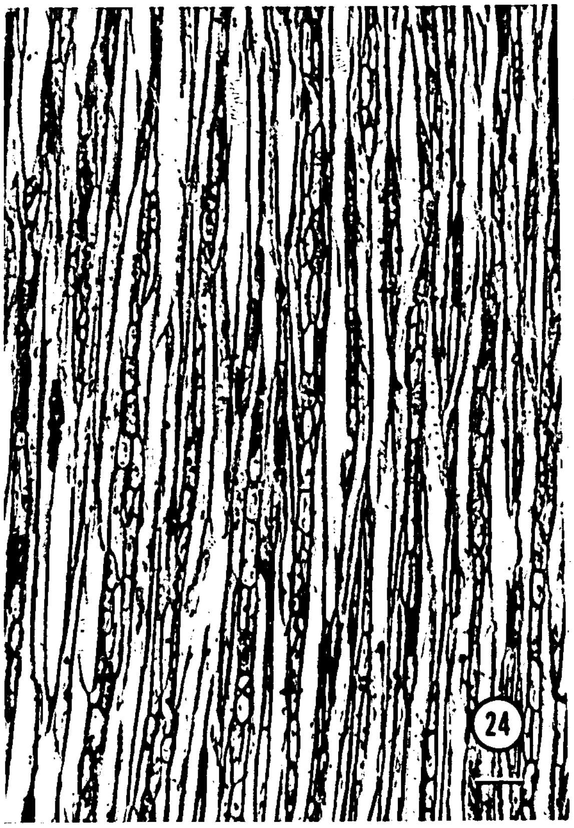
Fig. 20-24. Wood of Penthorum. **20.** Penthorum sedoides, Hayden 958, radial section, showing homocellular erect ray cells. **21.** Penthorum chinense, Shi s.n., radial section showing fiber-tracheid pits and intervessel pits. FT = fiber-tracheid. VE = vessel element. **22.** Penthorum sedoides, Hayden 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. Bars = 40 μm.


20


FT
VE
21


22


23


24

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 Holmgren, Keuken, and Schofield, 1981, *Index Herbariorum*, 7th ed., Dr. W. Junk, The Hague.

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.

UNITED STATES, 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).

Appendix 2. Average values of anatomical characteristics of *Penthorum*

Characteristic	*Penthorum chinense* specimens*			
	1	2	3	4
Pore distribution				
% Solitary	49	49	46	50
% Radial multiples	11	17	13	12
% Clusters	40	34	41	38
Pores/mm^2	620	455	717	577
Pore area, mm^2/mm^2	0.34	0.28	0.25	0.26
Vessel elements				
Pore diameter, µm	26	28	21	24
Bars/perforation plate	29	31	21	32
Length, µm	633	764	514	749
End wall angle, degrees	80	79	76	84
Fiber-tracheids length, µm	801	911	663	834
Rays				
Frequency				
% Uniseriate	61	37	26	53
% Multiseriate	39	63	74	47
Rays/mm transect	18	19	18	19
Uniseriates				
Width, µm	8	9	10	11
Height, µm	767	503	462	914
Height, no. of cells	10	6	8	10
Multiseriates				
Width, µm	17	19	21	21
Width, no. of cells	2	2	2	2
Height, µm	1126	1072	899	1059
Height, no. of cells	15	14	16	12

**Penthorum chinense*: 1 = Wang 1130; 2 = Xiong 0001; 3 = Shi s.n.; 7 = Hayden 952; 8 = Hayden 958; 9 = Haskins 76; 10 = Hayden 798;

**Data unavailable

chinense and *P. sedoides*

		Penthorum sedoides specimens*				
5	6	7	8	9	10	11
51	**	59	48	51	51	60
8	**	8	15	13	13	14
41	**	33	37	36	36	26
624	**	572	594	594	584	676
0.22	**	0.21	0.24	0.31	0.23	0.25
21	30	22	23	26	22	22
31	27	31	34	18	19	23
688	755	608	554	477	597	610
82	82	83	81	81	77	80
792	851	640	623	563	702	639
54	37	31	51	57	34	29
46	63	69	49	43	66	71
20	19	24	19	20	18	16
12	8	7	9	7	12	9
662	**	534	742	730	500	416
7	**	7	9	10	6	6
18	21	16	21	14	26	20
2	2	2	2	2	2	2
984	**	822	851	946	962	584
11	**	12	11	13	13	11

4 = *Tobe* *80*; 5 = *Tobe* *81*; 6 = *Wakabayashi* *s.n.* *Penthorum* *sedoides*:
11 = *Hayden* *1004*.