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Anatomy and Affinities of Penthorum

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ANATOMY AND AFFINITIES OF PENTHORUM

MELANIE L. HASKINS AND W. JOHN HAYDEN

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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, rosid 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 monogenic 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 monogenic family, Penthoraceae (van Tieghem, 1898; Airy-Shaw, 1973; Stern, 1974a). Systematic studies comparing characteristics of embryology (Rocén, 1928; Mauritzon, 1933), palynology (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 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

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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*

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*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.

*a* 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 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 in Permount.

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, intervacular 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 μm 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 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; 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 μm.
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 µm long, scale-like, simple, multicellular, three- to four-seriate, glandular, apices often slightly swollen and darkly colored, bases clear. Vénation 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 foraminate; principle vein central, direct; accessory veins present, convivnet (Fig. 7). Both epidermides uniseriate (Fig. 9, 10); cuticle thin. Epidermal cells larger in upper epidermis than in lower epidermis (Fig. 13). Areoles imperfect, random, irregular, small to medium, 563-911 (310-1,300) µm; lumen diam greater than wall thickness (Fig. 17); wall thickness 2-3 (1-4) µm; tangential diam 15-22 (10-27) µm; vertical diam 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.

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) µm; lumen diam greater than wall thickness (Fig. 17); wall thickness 2-3 (1-4) µm; tangential diam 15-22 (10-27) µm; vertical diam 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% uniseriate, 39-74% multiseriate. Uniseriate ray width extremely fine, 7-12 (2-17) µm; ht extremely to very low, 416-914 (160-1,940) µm or 6-10 (2-25) cells. Multiseriate ray width extremely to moder­ately fine, 14-26 (9-47) µm or 2 (2-4) cells; ht very low to low, 584-1,126 (220-2,820) µm or

**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 mm² very numerous, 455-717; pore area 0.21-0.34 mm² per mm² cross-sectional area of wood. Pore outlines angular (Fig. 17, 18); wall thickness 1-2 (0.75-2) µm; tangential diam 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, 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) µm (Fig. 21). Vessel element length medium, 477-764 (280-1,270) µm; ligules present or absent. Vessels infrequently occluded with darkly stained deposits; spiral thick­enings absent.

**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.

**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. 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 µm.
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 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; Dickinson, 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 monogenic 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 multisierate rays with long uniseriate wings.

Within either the Saxifragales (Takhtajan, 1980) or theRosales (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; Metcalf 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 commonly 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; Metcalf 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 symposiomorphous 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, Agababian (1961) found Penthorum intermediate between Crassulaceae and Saxifragaceae, while
**Table 2. Anatomical comparisons of Penthorum, Crassulaceae, and Saxifragaceae**

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

* 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>a</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 *Cutisia* F. Muell. of Grossulariaceae (or Escalloniaceae); in all these genera thinning of the exine and endoaerture are continuous and form an H shape. Overall, however, *Penthorum* 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 Saxifragaceae.

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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.) Har. 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 lactechin/ 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 0-methylation present in some saxifragas. 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**


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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, Wakahayashi s.n. (MAK).