

STUDIES IN THE RANUNCULACEAE OF THE SOUTHEASTERN UNITED STATES

II. THALICTRUM L.^{1, 2}

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While completing a treatment of the Ranunculaceae for the forthcoming *Vascular Flora of the Southeastern United States*, certain nomenclatural and taxonomic decisions had to be made which call for additional clarification. This treatment of *Thalictrum* is conservative in that I follow a species concept allowing for considerable intraspecific population variability. Unless populations show discrete geographic patterns correlated with morphological discontinuities, I see no compelling reason to describe subspecies, varieties, etc. Furthermore, unless breeding studies suggest intraspecific relationships, I prefer to recognize morphologically defined species. The aim throughout is to provide a rationale for certain taxonomic and nomenclatural conclusions, plus a key to the species and their distribution within the southeastern United States.

As a genus, *Thalictrum* can be distinguished from other Ranunculaceae by its alternate, ternately compound or decompound leaves, actinomorphic apetalous bisexual or unisexual flowers with numerous well-developed stamen filaments and non-plumose achenes crowded on small receptacles. Although 120 species of *Thalictrum* have been described for the world (Buchheim, 1964), I am recognizing only 14 species within the southeastern United States, an area bounded by and including Louisiana, Arkansas, Kentucky, West Virginia, Maryland, and Delaware.

¹Based on a manuscript and notes compiled for the forthcoming *Vascular Flora of the Southeastern United States*. In general, the format follows Radford et al. (1967). Any suggestions relating to this treatment should be sent to me so that necessary corrections and additions can be made before the *Vascular Flora* is in press.

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Table I.

Chromosome Numbers of the Species of *Thalictrum*
in the Southeastern United States

Species	Chromosome Number	Reference
<i>T. arkansanum</i>	—	
<i>T. clavatum</i>	$n = 7$	Jensen (1944)
<i>T. cooleyi</i>	—	
<i>T. coriaceum</i>	$2n = 70$	Gregory (1941)
	$n = 70$	Jensen (1944)
<i>T. dasycarpum</i>	$2n = \text{ca. } 100$	Zhukova (1961), cited in Cave (1962) Zhukova (1967), cited in Ornduff (1969)
<i>T. debile</i>	—	
<i>T. dioicum</i>	$n = 14$	Jensen (1944)
	$2n = 42$	Kuhn (1928), cited in Gregory (1941)
	$2n = 42$	Zhukova (1967), cited in Ornduff (1969)
<i>T. macrostylum</i>	—	
<i>T. mirabile</i>	--	
<i>T. pubescens</i> (= <i>T. polygamum</i>)	$n = 42$	Jensen (1942)
	$2n = 84$	Löve & Löve (1966), cited in Ornduff (1968)
	$2n = 154$	Gregory (1941)
<i>T. revolutum</i>	$2n = \text{ca. } 133$	Gregory (1941)
<i>T. subrotundum</i>	—	
<i>T. steeleanum</i>	--	
<i>T. thalictroides</i>	$2n = 14$	Gregory (1941)
(= <i>T. anemonoides</i> ,	$2n = 14$	Sorokin (1929)
<i>Anemonella</i>	$2n = 42$	Kuhn (1928), cited
<i>thalictroides</i>)		in Gregory (1944)

Even though *Thalictrum* has been treated by Lecoyer (1885), Trelease (1886), Gray (1895), Davis (1900), and most recently by Boivin (1944), the species in eastern North America still need a thorough study from a modern biosystematics standpoint. This is especially the case for the *T. debile* complex, *T. pubescens*, *T. dasycarpum*, *T. coriaceum*, and the *T. macrostylum* complex. Although Kaplan and Mulcahy (1971) studied pollination and floral sexuality in selected species, I know of no recent population-based biosystematic studies of any species of *Thalictrum* in eastern North America. Furthermore, chromosome counts for seven species are needed, and several other species (*T. revolutum*, *T. pubescens*, *T. dasycarpum*) should be reassessed (Table I).

KEY TO SPECIES

1. Inflorescence umbelliform; plants usually less than 2(-3) dm tall. 1. *T. thalictroides*.
1. Inflorescence paniculate; plants usually more than 2 dm tall.
 2. Flowers perfect; sepals 5; fruits long-stipitate, flat, with a minute stigma.
 3. Dorsal margin of mature fruits concave, up to twice the stipe in length; filaments usually more than 3 mm long. 2. *T. clavatum*.
 3. Dorsal margin of mature fruits straight, about equalling the stipe in length; filaments usually less than 3 mm long. 3. *T. mirabile*.
 2. Flowers imperfect, rarely perfect; sepals 4(-6); fruits sessile or short-stipitate, plump, tipped by a long stigmatose style.
 4. Leaflets 3 (or more)-lobed apically, the lobes often crenate; filaments colored, filiform; plants dioecious, rarely polygamous.

5. Achenes sessile; upper cauline leaves often long-petioled; plants flowering in early spring.
6. Plants erect, usually over 3 dm tall; roots fibrous; largest leaflets over 15 mm wide. 4. *T. dioicum*.
6. Plants lax, usually less than 3 dm tall; roots tuberous; largest leaflets less than 15 mm wide.
7. Mature fruits elliptic-lanceolate, 0.7-1.2 mm broad; sepals usually 1-2 mm long. 5. *T. debile*.
7. Mature fruits ellipsoid, 1.5-2 mm broad; sepals usually 1-3 mm long. ... 6. *T. arkansanum*.
5. Achenes stipitate, the stipes wing-angled; upper cauline leaves sessile or subsessile; plants normally flowering in early summer.
8. Plants caudiciferous, but not rhizomatous; terminal leaflets mostly longer than wide; anthers 2-3.5 mm long. ... 7. *T. coriaceum*.
8. Plants rhizomatous; terminal leaflets mostly shorter than wide; anthers 3.2-5 mm long. 8. *T. steeleanum*.
4. Leaflets entire or 3-lobed apically, the lobes entire (rarely crenate); filaments usually white, often more or less clavate; plants usually polygamous or polygamodioecious.
9. Leaflets usually stipitate-glandular beneath (or occasionally muricate or whitened papillose, rarely pubescent otherwise), coriaceous with strongly revolute margins; achenes more or less sessile, often stipitate-glandular; anthers 1.8-2.8 mm long. ... 9. *T. revolutum*.
9. Leaflets glabrous or pubescent beneath, their texture and margins various; achenes short-stipitate to sessile, glabrous to pubescent; anthers either 0.5-1.5 or 1.5-3.5 mm long.

10. Leaflets narrowly lanceolate to oblanceolate, 5-10 times longer than wide.
..... 10. *T. cooleyi*.
10. Leaflets suborbicular to obovate, usually less than 2 times longer than wide.
11. Leaflets usually entire or occasionally 3-lobed apically, glabrous beneath, the largest usually less than 15 mm wide; sepals 1-2 mm long.
12. Plants rigid, erect; leaves usually coriaceous, greyish to brownish or yellowish green, usually prominently reticulate beneath; filaments rigid, usually distinctly clavate.
..... 11. *T. macrostylum*.
12. Plants lax, reclining; leaves usually thin, membranous, greenish, not prominently reticulate beneath; filaments flexuous, scarcely clavate.
..... 12. *T. subrotundum*.
11. Leaflets 3-lobed apically, usually pubescent beneath, the largest 15-40 mm or more wide; sepals 2-5 mm long.
13. Stigmas about $\frac{1}{2}$ length of the achene body; filaments rigid, ascending, strongly clavate; anthers usually less than 1.5 mm long. ... 13. *T. pubescens*.
13. Stigmas nearly as long as the achene body; filaments flexuous, filiform, scarcely dilated distally; anthers 1.5-3.5 mm long.
..... 14. *T. dasycarpum*.

1. ***T. thalictroides*** (L.) Eames and Boivin, Rue Anemone.

Woods, banks, and thickets; chiefly mts. and pied. Ark., Fla., Ga. pied., Ky. pied., Md., N. C., S. C., Tenn., Va., W. Va. [All except Tex.] *Anemonella thalictroides* (L.) Spach — Fernald (1950), Gleason and Cronquist (1963); *Syndesmon thalictroides* (L.) Hoffmegg. — Small (1933).

No other species of the Ranunculaceae in our flora has been placed among as many genera as the common Rue Anemone. Linnaeus (Sp. Pl. 1: 542. 1753) initially described it as an *Anemone*, but on cytological and morphological grounds its affinities are clearly elsewhere (Gregory, 1941; Boivin, 1957b; Tamura, 1968). Michaux (Fl. Bor.-Am. 1: 322. 1803) treated the species as a member of *Thalictrum* (as *T. anemonoides*), and later Hoffmannsegg (Flora 15: Pt. 2, Intell. n. 4, p. 34. 1832) placed it in his new genus *Syndesmon*, a *nomen nudum* taken up later by Britton (1891) and others. Eventually Spach (Hist. Nat. Vég. 2: 339. 1839) erected the genus *Anemonella* which was accepted by Gray (1886) and subsequently adopted in various regional manuals (e.g., Fernald, 1950; Gleason and Cronquist, 1963).

The taxonomic question therefore is whether the Rue Anemone is sufficiently distinctive to warrant its separation from *Thalictrum* as Gray (1886) and others maintained. Boivin (1957b) reviewed this problem and concluded on the basis of its tuberous roots, compound leaves, sepal, stamen, carpel and fruit characteristics, the Rue Anemone should be classified in *Thalictrum* section *Physocarpum* DC. Moreover, as Eames (quoted in Boivin, 1957b) pointed out, the involucre leaves are not truly opposite or whorled — they are “merely approximate by telescoping,” and the multiple carpellary traces in Rue Anemone and *Thalictrum* are unlike all other genera in the Ranunculaceae. Furthermore, other species of *Thalictrum* within section *Physocarpum* have subopposite leaves and compact corymbiform inflorescences (Boivin, 1957b).

In short, Rue Anemone appears to be an end reduction in an evolutionary lineage featuring alternate leaves and

a non-leafy inflorescence (Boivin, 1957b). I concur with Boivin that Rue Anemone does not have sufficiently distinctive characteristics to warrant its separation as a monotypic genus (*Anemonella*), a conclusion also reached by Buchheim (1964), Tamura (1968), Radford (1968), and others.

2. **T. clavatum** DC., Mountain Meadowrue.

Rich moist woods, cliffs, seepage slopes, and mountain streams; mts. and pied. Ga. mts., Ky., N. C., S. C., Tenn., Va. pied., W. Va.

3. **T. mirabile** Small

Moist sandstone bluffs, sinks and rocky crevices, rare. Ala. cp., Ky. mts. and IP, Tenn. IP.

This species is scarcely separable from *Thalictrum clavatum*. Apparently it is more delicate and lax with longer stipes and straight dorsal achene margins. Population studies are needed to assess the comparative differences between this species and *T. clavatum*.

4. **T. dioicum** L. Early Meadowrue.

Rich rocky woods, ravines, and alluvial terraces; chiefly mts. and pied. Ala., Ga. mts., Ky., N. C., S. C., Tenn., Va., W. Va. [Mo., Ill., Ind., Ohio, Pa., N. J.].

5. **T. debile** Buckley

Rich, rocky limestone woods; all prov. Ala., Ga. mts. [Tex.].

6. **T. arkansanum** Boivin

Low grounds and upland woods, rare. Ark. cp.

This species is scarcely separable from *Thalictrum debile*. It is retained as a species pending comparative studies of these two species plus *T. texanum* from central Texas.

7. **T. coriaceum** (Britton) Small

Rich rocky woods; chiefly mts. and pied. Ky. mts., Md. pied., N. C., Tenn. mts., Va., W. Va. Incl. *T. caulophylloides* Small — Small (1933).

Small (1933) characterized *Thalictrum caulophylloides* on the basis of its longer anthers and sepals and more ellipsoid achenes. I am following Boivin (1944) in regarding *T. caulophylloides* as conspecific with *T. coriaceum*, although population studies may show regional morphological differences worthy of taxonomic distinction.

8. ***T. steeleanum*** Boivin

Moist alluvial thickets, rare; chiefly cp. and pied. Md., Va., W. Va. [Pa.].

This species needs additional study. Apparently it is closely related to *Thalictrum coriaceum*, but *T. steeleanum* differs from this species by its rhizomatous habit, longer anthers and achenes, and the terminal leaflets usually shorter than wide. *T. steeleanum* is usually found in moist alluvial thickets whereas *T. coriaceum* generally grows in rich woods.

9. ***T. revolutum*** DC.

Dry open woods, brushy banks, thickets, and barrens; all prov. S. E. except La. [Mo., Ill., Ind., Ohio, Pa., N. J.].

The outstanding characteristic of this species is the stipitate-glandular pubescence usually investing both the abaxial surfaces of the leaflets as well as the achenes. No other species of *Thalictrum* in eastern North America has this character. However, occasional specimens lack the stipitate-glandular pubescence, the leaflets then being merely muricate or whitened-papillose beneath. Sometimes such forms (forma *glabra* Pennell, 1931) occasionally have been mistaken for other species (Table II). Usually the petioles and leaf abaxial surfaces of the glabrous forms tend to be glaucous which aids in distinguishing this form of *T. revolutum* from *T. pubescens* and *T. dasycarpum* which usually have puberulent petiolules and leaflets. Anther, sepal, and leaflet size also aid in distinguishing glabrous forms of *T. revolutum* from *T. macrostylum* (Table II). In studying plants belonging to these species (Table II), special care should be given in assessing overall leaflet

Table II. Comparison of Species in the *T. revolutum* — *T. pubescens* Complex.¹

Character	<i>T. revolutum</i>	<i>T. macrostylum</i>	<i>T. pubescens</i>	<i>T. dasycarpum</i>
Leaflets:				
width of largest (mm)	5-40	3-17	15-45	15-45
pubescence	Stipitate-glandular (or muricate to whitish papillose) beneath	Glabrous beneath	± Puberulent with soft trichomes	Minutely puberulent (or glabrous?)
color	Greyish to brownish green	Greyish to brownish green	Usually dark green	Usually dark green
texture	Coriaceous	± Coriaceous to membranous	Membranous to coriaceous	Membranous to firm
margin	Strongly revolute	± Revolute	Revolute to flat	Revolute to flat
Petiolules	Usually glabrous and glaucous	Usually glabrous and glaucous	Usually puberulent	Usually puberulent
Sepal length (mm)	3-4	1-2	2-3.5	3-5
Anther length (mm)	1.5-2.8	0.5-1.2	1.0-1.5	1.5-3.5
Filaments	Slightly clavate, flexuous	Clavate, rigid	Prominently slenderly clavate	± Filiform, flexuous
Stigma length (mm)	2.0-3.5	0.6-1.7	0.5-2.0	2-5
<i>n</i> =	ca. 67	—	42, 77	ca. 50
Habitat	Dry open woods, brushy banks, thickets, and barrens	Rich wooded slopes, bluffs, meadows, and limestone sinks	Rich woods, low thickets, swamps, wet meadows, and stream banks	Damp thickets, swamps, and wet meadows
Range in southeastern United States	Throughout	All prov., Va. to S.C., Ala. mts., Miss.	Chiefly pied. and mts., Md. to Ga., Ky., Tenn. and W. Va.	Cp. and mts., Ark. to La.

¹Based in part on Boivin (1944).

size, color, texture and pubescence, and anther and style length.

10. **T. cooleyi** Ahles

Savannahs, very rare. N.C. cp.

This interesting species, recently described by Ahles (1959), has relatively long, narrow leaflets. Further field work is needed to establish the overall variability of this species.

11. **T. macrostylum** Small & Heller

Rich wooded slopes, bluffs, meadows, and limestone sinks; all prov. Ala. mts., Miss., N.C., S.C., Va. cp.

Characteristically *Thalictrum macrostylum* has small brownish-green coriaceous to membranous glabrous leaflets with generally entire and inrolled margins which amply distinguish this species although glabrous forms of *T. revolutum* may be confused with it. However, such forms of *T. revolutum* usually have larger leaflets, longer anthers, stigmas and sepals, and the filaments tend to be different (Table II).

12. **T. subrotundum** Boivin

Low woods, rare; cp. and pied. Ala., Fla., Ga., S.C.

This species is poorly understood and more field work is needed to establish clearly its identity from *Thalictrum macrostylum*. In general *T. subrotundum* tends to be more lax and taller and its leaves greener and more membranous (Table III). Pending further analysis I am retaining *T. subrotundum* as a species although it may well be a local geographic subspecies of *T. macrostylum*.

13. **T. pubescens** Pursh

Rich woods, low thickets, swamps, wet meadows, and stream banks; chiefly mts. and pied. Ga., Ky. IP, Md., N.C., Tenn., Va., W. Va. [Ind., Ohio, Pa., N.J.]. *T. polygamum* Muhl. — Small (1933), Fernald (1950), Gleason and Cronquist (1963), Radford et al. (1968); incl. *T. perelegans* Green — Small (1933).

No species of *Thalictrum* in our flora has been subject to as much nomenclatural or taxonomic confusion as *T. pubescens*. First, the name appearing in most current manuals is *T. polygamum* Muhl., but this is a *nomen nudum*, Muhlenberg having merely listed it in his *Index Florae Lancastriensis* published in 1793. Later, Sprengel (Syst. Veg. 2: 671. 1825) validated Muhlenberg's name, but by this time, Pursh (1814) had already validly published *T. pubescens*.

Boivin (1957a), in reviewing the nomenclature of this species, recognized the priority of *Thalictrum pubescens*, but recommended that *T. polygamum* Muhl. ex Sprengel be

Table III. Comparison of *T. macrostylum* and *T. subrotundum*.¹

Character	<i>T. macrostylum</i>	<i>T. subrotundum</i>
Height (m)	Up to 1	1-2
Habit	Erect	Lax, ± reclining on adjacent vegetation
Leaflets:		
color	Greyish or brownish green	Green
texture	± Coriaceous	Thin, membranous
margin	Entire to apically 3-lobed	Usually entire
venation	Prominently reticulate beneath	Scarcely reticulate beneath
Filaments	Rigid, distinctly clavate	Weak, scarcely clavate
Stigma length (mm)	ca. 1	1-2
Habitat	Rich wooded slopes, bluffs, meadows, and limestone sinks	Low woods
Range	All prov., Va. to S.C., Ala. mts., Miss.	Cp. and pied., S.C. to Fla. and Ala.

¹Based in part on Boivin (1944).

conserved in the interest of nomenclatural stability. Despite Boivin's persuasive argument, the present International Code of Botanical Nomenclature (Art. 14) forbids such practice and consequently the earliest correct name (*T. pubescens*) must be used.

Second, *Thalictrum pubescens* is a widespread highly variable species. Its variability is borne out in the work of E. L. Greene who around 1910 described at least thirteen species which according to Boivin (1944) are all taxonomic synonyms referable to *T. pubescens* (= *T. polygamum*).

Table IV. Comparison of *T. pubescens* and *T. dasycarpum*.¹

Character	<i>T. pubescens</i>	<i>T. dasycarpum</i>
Inflorescence	± Rounded	± Pointed, pyramidal
Flowers	Usually bisexual	Unisexual
Sepals	Elliptic, rounded	± Lanceolate, acute
Filaments	Clavate, ascending	Filiform, flexuous
Anther length (mm)	0.8-1.5	1.5-3.5
Achenes	Short stipitate	Obtuse at ± sessile base
Stigmas:		
length (mm)	0.5-2.0 (ca. ½ length of achene body)	2-5 (ca. equal to length of achene body)
shape	Sharply curved (like a fiddlehead), with densely matted hairs 0.1 mm long	± Straight, with short hairs 0.05 mm long
Habitat	Rich woods, low thickets, swamps, wet meadows, and stream banks	Damp thickets, swamps, and wet meadows
Range in south-eastern U.S.	Chiefly pied. and mts., Md. to Ga., Ky., Tenn., and W. Va.	Cp. and mts., Ark. to La.

¹Based in part on Boivin (1944).

In *Gray's Manual*, Fernald (1950) recognized three varieties (two occurring outside of the southeastern United States), but Gleason and Cronquist (1963) included only the species. *Thalictrum pubescens* certainly needs study on a population basis throughout its range, but pending such research I prefer to regard it as a single polymorphic species.

Frequently *Thalictrum pubescens* is confused with *T. dasycarpum* and both these species can be confused with *T. coriaceum* and *T. steeleanum*, although with adequate material the distinctions can usually be made (see Tables IV, V).

Table V. Comparison of the *T. coriaceum* Complex with the *T. pubescens* Complex.¹

Character	<i>T. coriaceum</i> and <i>T. steeleanum</i>	<i>T. pubescens</i> and <i>T. dasycarpum</i>
Leaflets:		
lobe number	3	0-3
lobe margin	Crenate	Entire
pubescence	Usually glabrous beneath	± Puberulent beneath
Stipes:		
length (mm)	0.5-3.0	0-1
cross-section	± Wing-angled	± Terete
Filaments	Filiform, colored	± Clavate, white
Anther length (mm)	2-4 (in <i>T. coriaceum</i>) 3.5-4.4 (in <i>T. steeleanum</i>)	0.8-1.5 (in <i>T. polygamum</i>); 1.5-3.5 (in <i>T. dasycarpum</i> , an infrequent species)

¹Based in part on Boivin (1944).

14. ***T. dasycarpum*** Fischer & Avé-Lall., Purple Meadowrue.

Damp thickets, swamps, and wet meadows; cp. and mts. Ark., La., Miss. [Tex., Okla., Mo., Ill., Ind., Ohio, Pa.].

Thalictrum dasycarpum is apparently closely related to *T. pubescens*, although mature specimens can usually be

distinguished (Table IV). Nevertheless, *T. dasycarpum* is a similarly variable species in need of further study. Between 1909 and 1912 Greene described at least six species which according to Boivin (1944) are all taxonomic synonyms of *T. dasycarpum*. More recently, Rydberg (1931) described plants from Texas and Kansas (*T. hypoglaucum*) which he stated were similar to *T. dasycarpum* but differed by having glabrous leaves and smaller, glabrous achenes. Although Boivin (1944) later reduced *T. hypoglaucum* to a variety under *T. dasycarpum*, the taxonomic status and relationship of this taxon remains in doubt. For example, glabrous forms of both *T. revolutum* and *T. dasycarpum* ("var. *hypoglaucum*") are difficult to distinguish (see Steyermark, 1963, p. 675), and further study is needed to clarify the taxonomic relationship.

Pending further work, I am regarding *Thalictrum dasycarpum* as a polymorphic species occurring chiefly in the central to northwestern United States and adjacent Canada, but which is infrequent within the southeastern United States.

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