CRATAEGUS (MALOIDEAE, ROSACEAE) OF THE SOUTHEASTERN UNITED STATES, I. INTRODUCTION AND SERIES AESTIVALES

J. B. Phipps[1]

This paper is the first of a series completely revising *Crataegus* for the southeastern United States. The taxonomic history of North American *Crataegus* is outlined, and modern evidence (polyploidy, apomixis, hybridization) for the taxonomic complexity in the genus in North America is summarized. *Crataegus* is described in detail, and its relationship to the other genera of tribe Crataegeae of subfam. Maloideae is discussed. Twenty-one series of *Crataegus* are commonly accepted for the southeastern United States. The revisionary treatment opens with ser. *Aestivales,* a very distinctive group of plants of early anthesis, early fruiting, unusual (seasonally flooded) habitat, and umbellate inflorescences. Two common, almost completely allopatric, polar species and an intermediate, putatively hybrid species are included.

I am preparing the treatment of *Crataegus* L. for *The Vascular Flora of the Southeastern United States.* Since the format of the flora is highly condensed, this series of papers details the revisions underlying that account. Since 1982 I have undertaken fieldwork in all the southeastern states to become familiar with variation in natural populations. The need for a revision, which will be detailed later, has led to the assembly at the University of Western Ontario of nearly all the extant herbarium material of *Crataegus* for the southeastern United States. I have taken advantage of this situation to map (for the first time, in many instances) all the species studied. Discrimination between some taxa—and within several species-groups—has always been difficult, so a morphometric approach to resolving these problems has been incorporated where appropriate. Because typification in this genus in the southeastern United States has generally not been carefully undertaken hitherto, I have given this critical attention wherever appropriate.

Crataegus is a large (about 60 species), ecologically and economically important genus in the southeastern United States, defined here as the area treated by *The Vascular Flora of the Southeastern United States* (Radford *et al.*, 1980)—i.e., east of the Mississippi as far north as Kentucky, West Virginia, Maryland, and Delaware, and also west of the Mississippi to Louisiana and Arkansas. The majority of United States *Crataegus* species (at least, as broadly defined) occur in this region due to the paucity of species in the west of the country and to the fact that most northeastern North American series of *Crataegus* have representatives in the Appalachian area. Of the distinct and reasonably

[1]Department of Plant Sciences, University of Western Ontario, London, Ontario N6A 5B7, Canada.

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common United States and Canadian species, only *C. erythropoda* Ashe (series uncertain; Colorado), *C. douglasii* Lindley sensu lato (ser. *Douglasianae* (Rehder ex Schneider) Rehder; Pacific northwest to Upper Great Lakes area), *C. saligna* Greene (best serial affiliation uncertain; Colorado), and *C. chrysocarpa* Ashe (ser. *Rotundifoliae* (Eggl. ex Eggl.) Rehder; wide-ranging northern) do not occur within the study area. The other moderately distinct taxa not found in the southeastern flora include *C. columbiana* Howell (ser. *Rotundifoliae*; Pacific northwest), members of the series *Brainerdianae* and *Suborbiculatae,* and some Texan endemics like *C. tracyi* Ashe. This revision will therefore be one of the most comprehensive for this genus in North America.

TAXONOMIC PROBLEMS

Some perspective on the taxonomic problems inherent in the genus may be gained from a brief historical overview. Prior to 1895 only some 20 species were recognized from the United States and Canada, many described from plants grown in European botanical gardens. But Ashe, Beadle, and Sargent, between about 1898 and 1912, described some 1500 "species" of North American hawthorn. Brown (1910) provided an interesting discussion of this situation, analyzing the species concepts and the views on hybridization of the cited authors and others. While a good number of names have been placed in synonymy, the proper disposition of many remains uncertain due to lack of study, poor quality of the type material (or, in the case of many Ashe names, its absence), the necessity to lectotypify (mainly ignored until very recently), or simply the intrinsic taxonomic problems of any particular group of *Crataegus.* Consequently, numerous nomenclatural problems exist (see, for example, Phipps, 1988a, 1988b). The number of species to accept is therefore very arguable, and modern limits lie between the 100 or so of Palmer (1952) and the 20 of Gleason and Cronquist (1963). Palmer (e.g., 1946, 1950, 1952, 1956) and Kruschke (1965), both following the tradition of Eggleston (e.g., 1908), attempted to maintain "moderate" species concepts, although Gleason and Cronquist's approach represents an unabashed attempt to reduce the number of entities to a "manageable" level. In the latter case, a substantial number of well-known species were summarily, and without evidence, dismissed as hybrids. The problem remains, therefore, how to treat this complex genus optimally.

In my view (see Phipps & Muniyamma, 1980) a "moderate" approach is generally most useful in *Crataegus.* This is liable to result in 35 to 50 broadly circumscribed species for the Southeast and an as-yet-unknown number of taxa of lower rank or narrower definition. However, as will become clear later, many of the "microspecies" of earlier authors do appear to represent real entities and cannot automatically and cavalierly be disregarded. The "*Crataegus* problem" (Eggleston, 1910; Palmer, 1932; Camp, 1942) requires acknowledging the existence of a multitude of microspecies arising due to apomixis and hybridization, compounded by polyploidy (Phipps, 1983). Some microspecies of earlier workers survive rigorous numerical analysis (e.g., Sinnott & Phipps, 1983), while others do not and their names are clearly synonyms. However, some species (e.g., *C. punctata* Jacq.) are known to be sexual diploids (Muniyamma & Phipps, 1985) and present no problems.

The Source of Taxonomic Complexity

Generally, a large number of taxonomic synonyms indicates a genuine taxonomic problem. Although some of the synonyms may be due to simple carelessness (redescribing exactly the same entity), this is not always the case. Components of a large and continuous spectrum of variation might, for instance, provisionally warrant new species names. In *Crataegus,* however, the most serious problem arises from discontinuous variation within the limits often accepted for a broad species concept. *Crataegus* has been shown to be apomictic and polyploid in North America and introgressive in Europe (Byatt, 1975, 1976; Christensen, 1982, 1984). Many names given therefore represent major components of geographic variation, while others correspond to fixed hybrids (common or sporadic); some are part of a mosaic of often locally distinguishable apomictic clones. Nowhere is this more clear than in the *C. crus-galli* complex, where a substantial number of reasonably distinct forms can often be found at any one site (e.g., northern Louisiana). Yet for taxonomic recognition of such entities, they must be both globally and locally distinct. Evaluating whether a form is sufficiently and universally distinct is the essence of the *Crataegus* problem.

The Need for a Revision

Chapman (1860) recognized 11 species of *Crataegus* from the southeastern United States, but Beadle (1903) raised this number to 185 in Small's *Flora of the Southeastern United States.* By 1919, 300 species had been described, yet most of these names did not make their way into subsequent floras. Tidestrom (1933), for instance, recognized only 33 species, while Radford, Ahles, and Bell (1964) offered the very conservative approach of only 13 species for two states. Strausbaugh and Core (1953), however, treated 25 species for West Virginia. Correll and Johnston (1970) listed 33 species for Texas (all but the nine endemic or western ones occurring in the Southeast), while Vines (1960; key contributed by E. J. Palmer) gave 69 species for the southwest. Other works (e.g., Clark, 1971) also list the taxa of *Crataegus* that occur in a particular state or area.

All the above works are to some extent defective. Chapman's, of course, is out of date. Beadle's useful treatment contains too many microspecies for a modern flora; Tidestrom's is too succinct and is taxonomically obsolete in some cases; and those of Clark and of Radford and colleagues contain identifiable taxonomic errors. Palmer, the mid-twentieth-century author in the best position to treat southeastern *Crataegus,* unfortunately did not do so comprehensively. Portions of his northeastern treatments are nevertheless pertinent to the southeast, but his contribution to Vines was merely a key. In 1925 he produced a nomenclator, indicating type localities for each species and arranging all species by series. This valuable work is not, however, a revision, since virtually no decisions were made at the species level. In his later works

(1950, 1952, 1956) he moved to moderate species concepts, but unfortunately none of these papers constitutes a complete revision, questions of typification being almost entirely neglected and those of synonymy restricted to a list for the northeastern area (1946). Kruschke's (1965) valuable work can also be partly extrapolated to the southeast, but he did not deal systematically with the species complexes of that area, and his paper does not contain keys or species descriptions, although there are numerous valuable nomenclatural notes. There is, therefore, strong need for a modern revision.

RELATIONSHIP TO OTHER GENERA

Crataegus is a natural genus belonging to the tribe Crataegeae Koehne. It is quite closely related to *Mespilus* L., *Hesperomeles* Lindley, and *Pyracantha* M. Roemer and forms both a graft chimaera and a hybrid with *Mespilus* (Byatt & Ferguson, 1977). *Crataegus* is more distant from *Osteomeles* Lindley, *Cotoneaster* Medikus, *Chamaemeles* Lindley, and *Dichotomanthes* Kurz, if indeed the last-named belongs here. Differences among these genera are shown in TABLE 1 and the key to genera.

KEY TO THE GENERA OF TRIBE CRATAEGEAE

1. Leaves pinnate; inflorescences open, dome-shaped panicles; petals narrow. .... *Osteomeles.*
1. Leaves entire, although sometimes deeply lobed; neither inflorescences nor petals as above.
   2. Carpels, styles, and pyrenes 1.
      3. Pomes with pyrene ⅓–⅖ extruded. .... *Dichotomanthes.*
      3. Pomes completely enclosing pyrene, although hypanthial rim perhaps not fully closed.
         4. Inflorescences elongate panicles of flowers < 10 mm in diameter; plant unarmed; pomes cream-yellow. .... *Chamaemeles.*
         4. Inflorescences flat-topped to somewhat convex corymbs or panicles; flowers generally > 10 mm in diameter; plant thorny; pomes red to black (rarely yellow). .... *Crataegus,* pro parte.
   2. Carpels, styles, and pyrenes 2 to 5.
      5. Leaves entire, although maybe slightly wavy; stems unarmed.
         6. Inflorescences uniflorous; stamens 30 to 40; pomes 25–45 mm in diameter, brown, with wide hypanthial opening; sepals foliaceous. .... *Mespilus.*
         6. Inflorescences usually with up to 50 flowers, although uniflorous in several species; stamens 20; pomes < 15 mm in diameter, red or black, hypanthial opening closed; sepals not foliaceous. .... *Cotoneaster.*
      5. Leaves usually serrate or crenate, also sometimes ± deeply lobed; stems usually thorny.
         7. Plant deciduous; resting buds ± globular; leaves thin or less often coriaceous, often lobed, usually serrate; petals white or very rarely pink; hypanthium open in fruit, although not necessarily widely so; pyrenes 2-seeded. .... *Crataegus,* pro parte.
         7. Plant evergreen; resting buds ± conical; leaves ± coriaceous at maturity, the margin variable, sometimes entire; petals cream-white to pink; hypanthium closed in fruit; pyrenes 1- or 2-seeded.
            8. Usually densely gnarled shrub; leaves variously crenate or dentate to few-lobed; pomes red or purple; petals white or pink; pyrenes 1-seeded; Costa Rica to Bolivia. .... *Hesperomeles.*

8. Stiff and erect or more laxly branched shrub; leaves ± entire to finely and regularly crenate or serrate, never lobed; pomes orange to red; petals cream-white; pyrenes 2-seeded; Old World. .... *Pyracantha.*

REVISION OF SOUTHEASTERN UNITED STATES CRATAEGUS

Crataegus L. Sp. Pl. **1:** 475. 1753; Gen. Pl. 213. 1754. TYPE SPECIES:[2] *C. laevigata* (Poiret) DC. (= *C. oxyacantha* L., *pro parte*).

Small trees or shrubs, deciduous (or with leaves persistent through part of winter in some southern taxa), nearly always thorny; branching patterns varied—erect, tabulate, drooping, or irregular, ultimate twigs usually fairly straight but sometimes zigzag at inflexions where thorns occur; thorns 1.5–9 cm long, variously sharp-tipped short shoots, simple shoots of determinate growth, or branched thorns on trunk, if simple then straight to recurved, fine to stout, and usually blackish to reddish-brown when ca. 2 years old; resting buds small, globose, often reddish, showing 6 to 8 bud-scales. Leaves alternate, petiolate (occasionally ± subsessile); petiole occasionally alate; blade generally elliptic or broad-elliptic to ovate or deltoid, sometimes obovate, 2–6(–8) by 0.5–5 cm, shallowly lobed (then with veins only to lobe tips) or deeply so (then with veins to both sinuses and lobe tips), or unlobed, the margin usually serrate (occasionally crenate), the lateral veins 4 to 8, generally increasing in number with narrower leaf types, the surfaces glabrous or pubescent, eglandular or with conspicuous sessile or very short-stalked, black or reddish glands along margin and petiole. Inflorescences paniculate-corymbose or very rarely ± umbellate or uniflorous, (1- to) 6- to 20- (to 50-)flowered, sessile or borne on short, leafy shoots of current season (these always borne on perennial spur shoots), glabrous to very pubescent, bracteolate, sometimes glandular-sticky, flowering in single flush in spring (occasional autumnal flowering known near Gulf Coast). Flowers 5-merous, perigynous; hypanthial bowl ± salverform; calyx lobes triangular, small, entire to pectinate, glandular to eglandular; petals borne on hypanthial rim, usually ± circular in outline with short claw (rarely broadly elliptic), 4–15 mm long, concave, spreading in open bowl at full anthesis; stamens borne on hypanthial rim, generally in approximate multiples of 5 (5 to 8, 9 to 12, 17 to 21), filaments up to length of petals, anthers white, cream, pink, red, or purplish; pistils in center of hypanthial bowl, the styles 1 to 5, corresponding to number of carpels, the ovules 2 per carpel. Fruit a pome, oblate-spheroidal to ellipsoid or pyriform, 5–20 mm long in wild forms to 35 mm long in cultivars, red or reddish (more rarely black, purplish, orange, yellow, or light yellow flushed pink), with filament bases and/or calyx remnants often persistent on hypanthial rim; hypanthial cup in fruit fleshy, floury, succulent and juicy, or dryish, the hypanthial opening almost closed to wide open (3–6 mm) and exposing the pyrenes; pyrenes 1 to 5, corresponding in number to styles, usually grooved dorsally and sometimes erose laterally.

Crataegus comprises about 150 species, approximately 90 North American (ca. 50 in the area of this flora) and 60 Eurasian. The exact number is non-

[2]The question of the type species of *Crataegus* has been discussed by Dandy (1946) and Byatt (1974).

TABLE 1. **Comparison of the genera of tribe Crataegeae.**

Genus	Character				
	DISTRIBUTION; NO. OF SPECIES	HABIT	THORNS	LEAVES	RESTING BUDS
Chamaemeles	Madeira; 1	Evergreen small shrub	Lacking	Medium-sized, simple, ± entire	Small, ± conical, dark, short-pubescent
Cotoneaster	Eurasia; 100 to 200	Evergreen or deciduous small to large shrub	Lacking	Small to large, unlobed, entire	Often larger than those of other genera, ± conical, usually red or brown, densely pubescent
Crataegus	North-Temperate; 150	Deciduous small shrub to small tree	Usually simple thorns, but sometimes thorn-tipped short shoots	Small to large, unlobed to deeply lobed, nearly always serrate	Small, ± globular, deep red, ± glabrous
Dichotomanthes	China; 1	Deciduous medium-sized shrub	Lacking	Medium-sized, unlobed, entire	Small, round, light brown, densely crisped-pubescent
Hesperomeles	Central and South America; 5 to 10	Evergreen shrub or small tree	Short shoots, sometimes thorn tipped	Small, shallowly lobed or not, entire to denticulate or coarsely crenate-serrate	Small, ± conical-pointed, plum red, crinkly-rufous-pubescent
Mespilus	Europe, western Asia; 1	Deciduous large shrub	Short shoots, often thorn tipped	Large, simple, ± entire	Small, narrow-globose to conical, plum red, glabrous, bud scales marginally ciliate
Osteomeles	Eastern Asia to Polynesia (Hawaii); 3	Winter-green small to medium-sized shrub	Lacking	Large, pinnate, entire	Small, conical, brown, ± pubescent
Pyracantha	Eurasia; 9	Evergreen medium-sized shrub, often with arching branches	Short shoots, often thorn tipped	Small, unlobed, serrate	Small, ± conical, color variable, glabrous or pubescent, bud scales marginally ciliate

TABLE 1 (*continued*).

Genus	Character					
	INFLORESCENCES	PETALS	STAMEN NO.	POMES	PY-RENE NO.	OVULES PER CARPEL
Chamaemeles	Elongate panicles	Small, round, red and white	20	Small, closed, cream-yellow	1	?
Cotoneaster	Uniflorous, corymbs, or ± flat-topped panicles	Small, ± round, white or reddish	20	Small, closed, red or black	2 to 5	2
Crataegus	Uniflorous, corymbs, or ± flat-topped panicles	Small to medium-sized, ± round, white	5 to 12 or 17 to 21	Small to medium, slightly open, yellow, red, or black	1 to 5	2
Dichotomanthes	± Flat-topped panicles	Small, round, white	20	Small, brownish; nutlet 35% exposed	1	2
Hesperomeles	Corymbs	Small, round, white or pink	20	Small, closed, red or darker	5	1
Mespilus	Uniflorous	Large, round, white	30 to 40	Medium, open, brown	5	2
Osteomeles	Panicles	Small, narrow-elliptic to obovate, white	20	Small, closed, red to black	5	1
Pyracantha	Flat-topped panicles	Small, ± round, white	20	Small, closed, red	5	2

definable due to inconsistent application of species concepts. The breeding system ranges from sexual amphimixis through obligate apomixis, and both introgression and hybridization occur. The base chromosome number (x) is 17, with diploids, triploids, and tetraploids known (Moffett, 1931; Darlington & Wylie, 1955; Gladkova, 1966; Muniyamma & Phipps, 1979a).

Crataegus is common through much of the southeast, although least so in Kentucky, Tennessee (Ulf-Hansen, 1985), Virginia, and North Carolina; it is completely absent from the southern part of Florida. The species range from extreme heliophiles and xeromorphs (e.g., ser. *Flavae,* as conventionally understood) to those with some shade tolerance (sers. *Apiifoliae, Brevispinae, Virides*). Species of some series (for instance, *Aestivales* and *Virides*) flourish in wet ground. However, hawthorns are most common in mesic open woodland (predominantly oak and oak-pine) and open successional sites, including pastures, fence lines, roadsides, and erosion slopes. Most species are strongly browse resistant due to thorniness.

Hawthorns are mass flowering in spring and are open pollinated, mainly by a variety of Hymenoptera and Diptera (Power, 1980). The species exhibit strong phenological rank-order of flowering (Smith, Phipps, & Dickinson, 1980), and the times of flowering of Ontario taxa can be predicted with some accuracy on the basis of summated heat units after an appropriate (specific to species and locality) starting date. Sexual species are self-incompatible, while facultative apomicts are mostly pseudogamous and self-compatible (Dickinson & Phipps, 1986). Apomixis is mainly aposporous (Muniyamma & Phipps, 1979b, 1984).

The fruits ripen in the fall and are dispersed by birds (large and medium-sized passerines and game birds). However, they often persist through the fall and into the winter, or at least until very cold weather. Additionally, the fruits are eaten off the tree by ungulates and off the ground by rodents and ungulates, which are also agents of dispersal (Hoover, 1961). Virtually nothing is known about the relative effectiveness of different dispersing agents.

Infrageneric Groupings

El-Gazzar (1980) divided *Crataegus* into two subgenera—*Crataegus* and *Americanae* El-Gazzar—on inadequate criteria because these subgenera are not fully allopatric nor do they have different base chromosome numbers (Phipps, 1983). Subgenus *Crataegus,* which comprises species often lacking simple thorns and having generally smallish, deeply lobed leaves with veins to the sinuses, is probably a valid grouping, if restricted to sects. *Crataegus* (= *Oxyacanthae*) (western Eurasia) and *Azaroli* (western Eurasia and North Africa) and also perhaps ser. *Apiifoliae* (North America). However, El-Gazzar's subg. *Americanae* is a mélange of quite varied taxa, mainly eastern Asiatic and North American, and may well eventually be broken down into several natural units (see Phipps, 1983; Phipps *et al.,* in prep.).

The most commonly employed infrageneric ranks in *Crataegus*—series and sections—have generally been used alone to provide a direct split of the genus (see, for example, Loudon, 1838; Schneider, 1906; Rehder, 1940; Palmer, 1952;

Rusanov, 1965); therefore, choice of rank does not reflect hierarchy. I utilize series in this work due to the obviously narrow circumscriptions being adopted. More hierarchy is given in Phipps and colleagues (in prep.).

For the 90 or so North American species, some 25 series are generally accepted (Phipps, 1983), all but three of which (*Brainerdianae, Douglasianae,* and *Mexicanae*) are represented in the Southeast. Each series represents a natural group of small taxonomic size and little internal diversity. By contrast, diversity among the North American series of *Crataegus* is substantial. Also, while some series (e.g., *Aestivales, Brevispinae, Microcarpae*) are quite discrete, others (e.g., *Pulcherrimae* and *Virides*) are obscurely differentiated (see Phipps, 1988a), while yet others (e.g., *Crus-galli* and *Punctatae*) intergrade through rare putative hybrids (Wells, 1985). However, the frequency of individuals intermediate between series is generally low, and thus the series can still be construed as representing natural units. Some series (e.g., *Brainerdianae, Dilatatae,* and possibly *Pulcherrimae*), however, themselves appear to be of interserial hybrid origin (Phipps, 1984).

Crataegus sers. *Aestivales, Apiifoliae, Bracteatae, Brevispinae, Coccineae, Cordatae, Crus-galli, Flavae, Intricatae, Macracanthae, Microcarpae, Molles, Oxyacanthae, Pruinosae, Pulcherrimae, Punctatae, Rotundifoliae, Silvicolae, Tenuifoliae, Triflorae,* and *Virides* are generally recognized as occurring in the southeastern United States and will be treated in an order reflecting convenience of work. Note that at this stage this list represents the conventional serial names and circumscriptions developed by Palmer (1952, and *in* Vines, 1960) and Kruschke (1965). In some cases the authorities cited, the names, or the circumscription of the series may have to be changed.

Species Concepts, Synonymy, Typification Practices, and Hybrids

Within-series taxonomy, except for the actual or presumed sexual species, is often extremely difficult, and it is here where the many taxonomic problems reside. In the southeastern United States typical examples of very difficult situations are to be found in sers. *Crus-galli, Flavae* (sensu American authors), *Intricatae,* and probably *Parvifoliae* and *Virides.* In the revision for *The Vascular Flora of the Southeastern United States,* I plan to treat apomictic species complexes as coordinate with sexual species, i.e., to give them a binomial. Apomictic microspecies, where worthy of continued recognition, will be given varietal rank. The wide variety of intermediate forms, however, together with numerous distinctive but rare types, will complicate the picture. Many of the known named forms will undoubtedly prove to be hybrids. However, I do not believe that systematics is served by the bold, but mere, assertion of hybrid origin. Hybrids (or presumed hybrids) of a persistent, distinct nature will be recognized at the species rank. A brief discussion pertinent to each case will give the reasons for the taxonomic decision made or the nomenclatural options presented.

As indicated above, about 300 species of *Crataegus* have been described from the southeastern states (Palmer, 1925), and my preferred disposition will be indicated for as many of these names as possible. Many will presumably disappear in synonymy. However, at this point it is not possible to estimate what proportion of the remaining 1200 or so names proposed for North American *Crataegus* have application in the Southeast. The enormous synonymy of specific names created by the descriptions of Ashe, Beadle, Sargent, and (to a lesser extent) Murrill can probably not be completely clarified even in this revision. While the synonymy should be better documented than hitherto, it will still not be complete.

Because many species have not been explicitly typified so far, extensive lectotypification will likely be required. There will also be some situations with especially difficult problems of typifying the oldest name (e.g., in sers. *Crus-galli* and *Flavae,* especially if the type is European—but see Phipps, 1988a, 1988b). The potential neotypification of a number of Ashe names has already been alluded to. Nevertheless, so many names exist in the literature that taxonomic novelties, except for rank changes, are expected to be very few.

The ability of *Crataegus* to hybridize, even with species in other maloid genera, is well known (summarized in Phipps, 1984). There are numerous horticultural hybrids reported, and a large number of taxa, some of which occur in our area, have been suspected to be of hybrid origin (Gleason & Cronquist, 1963; Phipps, 1983). There are also many binomials referring to evanescent, apparently hybrid taxa. Actual or presumed, permanent or evanescent hybrids will receive an appropriate comment.

Series I. AESTIVALES (Sarg. ex Schneider) Rehder, Man. Cult. Trees, ed. 2. 366. 1940.

Sect. *Aestivales* Sarg. ex Schneider, Ill. Handb. Laubholzk. **1:** 794. 1906. TYPE SPECIES: *C. aestivalis* (Walter) Torrey & A. Gray.
Aestivales Sarg. Silva (Suppl.) **13:** 35. 1902, *in clavem,* without rank.

Shrubs to 8 m tall, occasionally more; mature bark fibrous; branchlets gray; thorns few to fairly numerous, short (1–2 cm), stout, straight. Leaves not appearing before flowers and often entirely after anthesis, elliptic to broad-elliptic, unlobed or slightly (wavy-)lobed, entire to finely serrate, glossy or matte, ± glabrous to conspicuously rufous-tomentose. Inflorescences umbellate, ± sessile, few-flowered, glabrous to rufous-pubescent. Flowers medium to large (12–28 mm in diameter); calyx lobes ± triangular, ± entire to slightly glandular-serrate; petals white to pale pink; stamens 20, the anthers small or large, usually reddish; styles 5. Fruit 0.8–1.5 cm in diameter, red, succulent, ripening very early (May in south); pyrenes 5, dorsally ribbed.

Three species, one probably deriving from introgression between the other two; Coastal Plain of south-central Texas to North Carolina, south to central Florida, and north through Louisiana to extreme southern Arkansas. Essentially restricted to seasonally inundated sites: sinks, potholes, drainage ditches, low-lying woodlands.

Breeding system unknown, although variation patterns of *Crataegus opaca* and *C. aestivalis* suggest amphimixis with some apomixis. If *C. rufula* is an

TABLE 2. **Characters used in the numerical taxonomic study of Crataegus ser. Aestivales.**

CHARACTER NUMBER	CHARACTER	SCORING
	Branch	
*1.	Tomentum on twigs of current season	None (0) to dense (5)
2.	Length of thorn	In mm
	Leaf size	
*†3.	Length of lamina	In mm
4.	Length of petiole	In mm
5.	Maximum breadth of lamina	In mm
	Leaf shape	
6.	Length/breadth quotient	
*7.	Location of widest part	In tenths from base of blade
*†8.	Tip	Obtuse (0) through acute (3)
*†9.	Lobes	Mean no. per side
*10.	Leaf incision index	Largest lobe (%)
	Leaf margin	
*†11.	Serrations greater than 1 mm deep	Absent (0) or present (1)
12.	Teeth blunt, through sharp	0–1
13.	Percent (from tip) with teeth still at frequent intervals	0–100
14.	Glands	Absent (0) or present (1)
	Leaf venation	
*†15.	Mean no. per side	
*†16.	Mean angle from midrib	In degrees
	Leaf tomentum	
*17.	On upper surface	Absent (0) through dense (5)
*18.	On lower surface between veins	Absent (0) through dense (5)
*19.	On lower surface on mid-vein	Absent (0) through dense (5)

*Included in 12-character set.
†Included in six-character set.

introgressant, this supports these assumptions. Chromosome number: not counted (probably includes diploids in at least *C. opaca* and *C. aestivalis*).

Series *Aestivales* is among the most distinct of all series of American hawthorns due to its anthesis before leaf expansion, inflorescence form, early fruiting, and habitat. *Crataegus rufula* is quite variable, strikingly so in flower size, and may well be in part apomictic. This would suggest that at least some individuals of *C. opaca* or *C. aestivalis* are also apomictic. The almost perfect allopatry of the last two species, with just slight overlap in southern Alabama, is not easy to explain except by separate southeastern and southwestern Pleistocene refugia, in which case the eastern limits of *C. opaca* and western limits of *C. aestivalis* may still be mobile. Series *Aestivales* is very distinct from other North American *Crataegus* series, and its nearest relatives are unclear. Interserial hybrids are not suspected unless *C. fruticosa* Sarg. (to be treated in a later

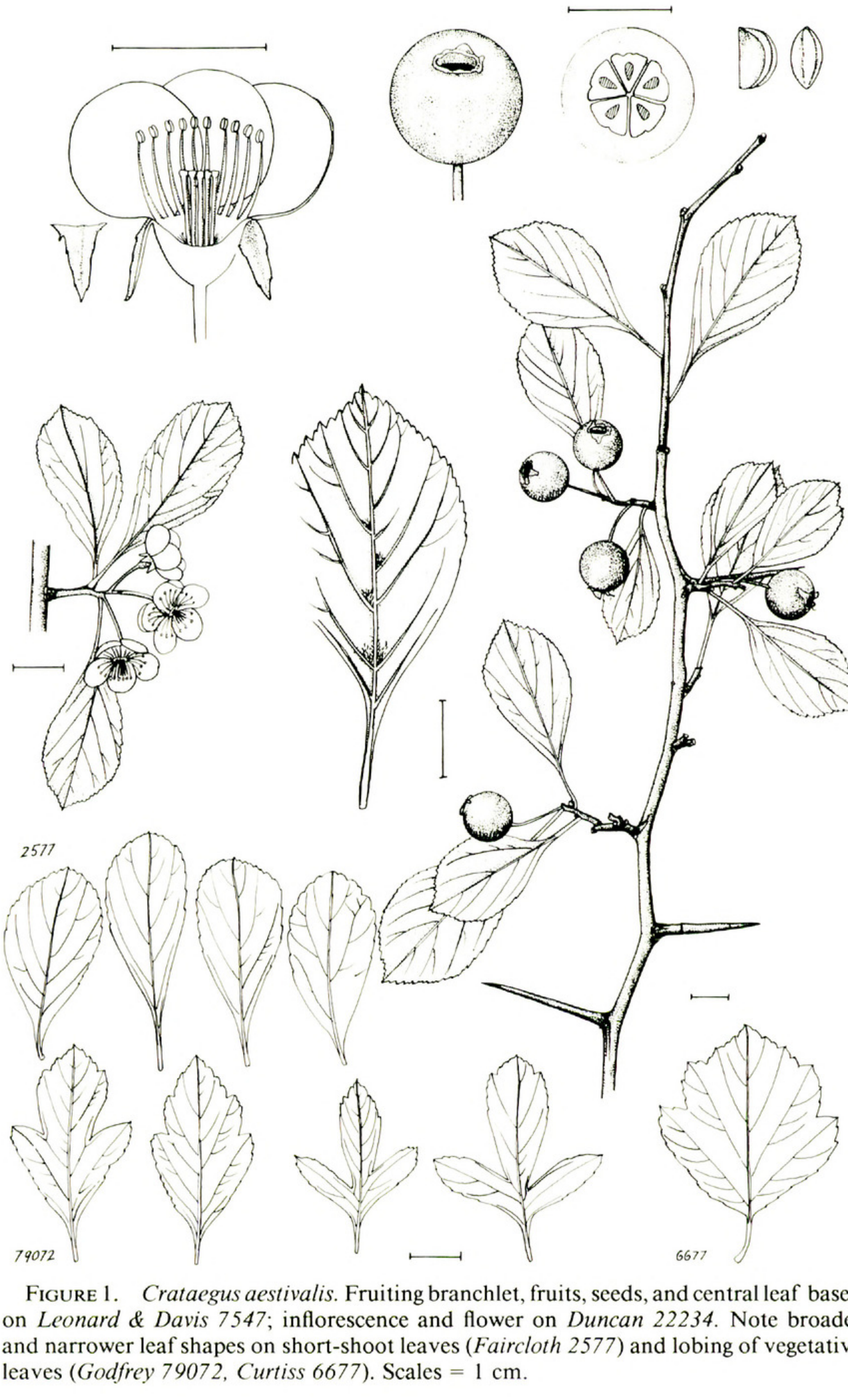


FIGURE 1. *Crataegus aestivalis.* Fruiting branchlet, fruits, seeds, and central leaf based on *Leonard & Davis 7547*; inflorescence and flower on *Duncan 22234.* Note broader and narrower leaf shapes on short-shoot leaves (*Faircloth 2577*) and lobing of vegetative leaves (*Godfrey 79072, Curtiss 6677*). Scales = 1 cm.

FIGURE 2. *Crataegus opaca,* based on *Rylander 111.* Note tomentose undersurfaces of leaves in enlargements. Scales = 1 cm.

installment) belongs here. Except for the *C. rufula* situation, the two more common species are highly distinct. Therefore, to examine this problem series *Aestivales* was subjected to a small-scale numerical taxonomic study.

NUMERICAL TAXONOMIC STUDY

Forty-five OTUs were initially studied, 22 of "pure" *Crataegus aestivalis,* 13 of "pure" *C. opaca,* and ten from the *C. rufula* complex. Original OTU 25 was rejected as anomalous, and thus the numbering on the diagrams is 1–24 and 26–45. Herbarium specimens were selected from the entire geographic range of the three species. Nineteen characters were scored from vegetative (mostly foliar) characters (see TABLE 2). As can be seen from the illustrations, there is substantial difference between the foliage of *Crataegus aestivalis* (FIGURE 1) and that of *C. opaca* (FIGURES 2, 3), and these two species were considered the polar ones in the hybrid index run; *C. rufula* (FIGURE 4) is intermediate. Flower characters were not used in this analysis because, prior to the numerical taxonomic study, even approximate species assignations could not be made with flowering material. Fruiting characters were likewise not used since no taxonomically meaningful variation could be identified.

This data matrix was subjected to single-link and minimum-variance clustering on the Euclidean distance matrix, principal-components analysis, and character ranking based on variance ratios (Jancey, 1979). A minimum spanning tree was also produced. These results (see FIGURES 5–8) clearly indicate the division *aestivalis*/(*opaca* + *rufula*). The character-ranking algorithm (TABLE 3) demonstrates that characters 19 and 18, in that order, best differentiate *Crataegus aestivalis* from the other two, while—as in the R-PCA—characters 11, 12, and 1 are also important. Inspection of the raw data bears out these interpretations. The Wells Hybrid Index (FIGURE 9) clearly shows the intermediacy of *rufula* OTUs. As in other analyses of the 44-OTU data set, however, *C. opaca* and *C. rufula* are slightly mixed. The Wells Hybrid Index was rerun on a reduced, 12-character matrix, derived by rejecting low-ranking characters determined from R-PCA and variance-ratio tests (see TABLE 3), to obtain better discrimination (see FIGURE 10). However, the results are similar: in both Wells Hybrid indices, all the *rufula* OTUs lie within the inner semicircle, indicating intermediacy of all characters combined.

The *Crataegus opaca* and *C. rufula* data matrix was then reanalyzed using the six characters (19, 18, 12, 1, 11, and 9) that best discriminated between them on the character-ranking algorithm. In the new results there is still some overlap between what had initially been considered C. *rufula* and C. *opaca.* Nevertheless, a somewhat better separation of these two species was thereby achieved (FIGURES 11–13). On the basis of this separation, it was possible to infer (from matched flowering and mature foliage material) that the inflorescence of *C. rufula* is always rufous-tomentose. By contrast, those of both *C. opaca* and *C. aestivalis* are glabrous to subglabrous. In general, the foliage of *C. rufula* is broader than that of *C. opaca* and sometimes lacks the sinuate margins typical of the latter species; it also has fewer lateral nerves, which branch at a wider angle (more like those of *C. aestivalis*). However, *C. aestivalis*

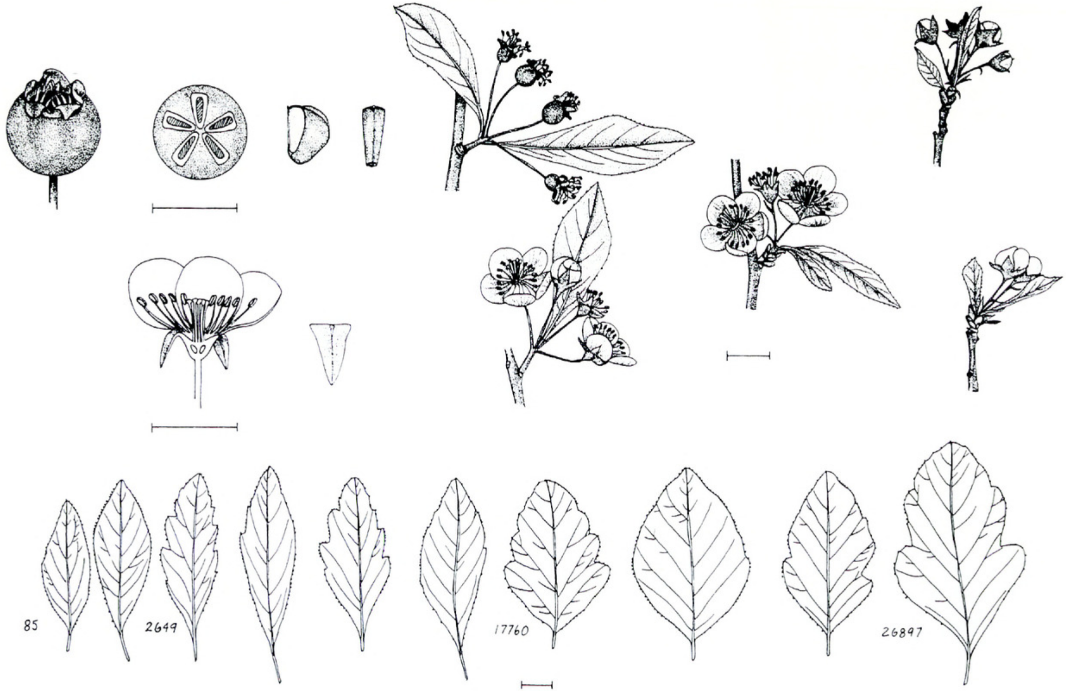


FIGURE 3. *Crataegus opaca*: fruits (*Holmes 2649*), inflorescences and flower (*Allen 6422*), and leaves (*Small 85, Holmes 2649, Thieret 17760* and *26897*). Scales = 1 cm; sepal × 2.

FIGURE 4. *Crataegus rufula,* based on *Harbison 19.* Scale lines = 1 cm.

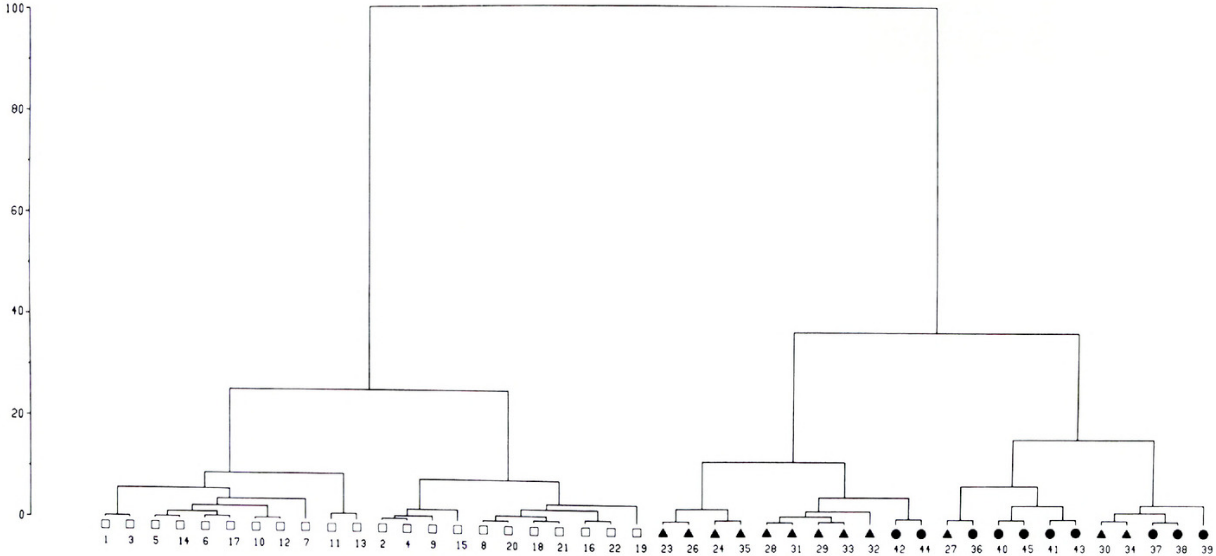


FIGURE 5. Sum of squares agglomeration of Euclidean distance of 44 OTUs of *Crataegus* ser. *Aestivales*: squares = *C. aestivalis,* triangles = *C. opaca,* circles = *C. rufula.* Note clear division into *C. aestivalis* and remainder.

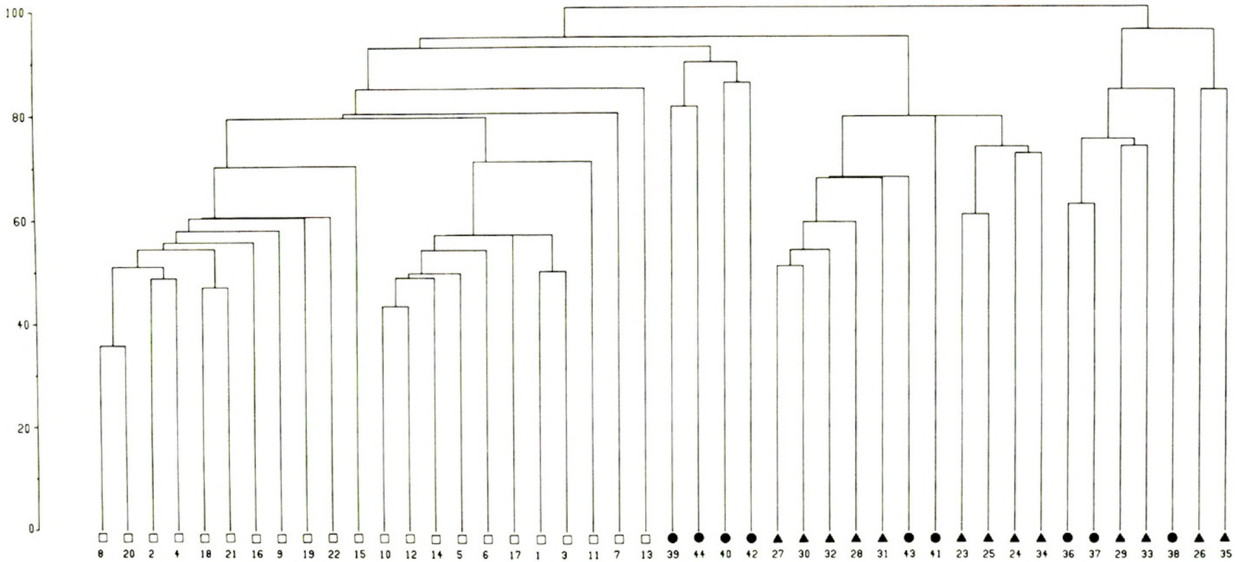


FIGURE 6. Single-link clustering of Euclidean distance of 44 OTUs of *Crataegus* ser. *Aestivales* (symbols as in FIGURE 5).

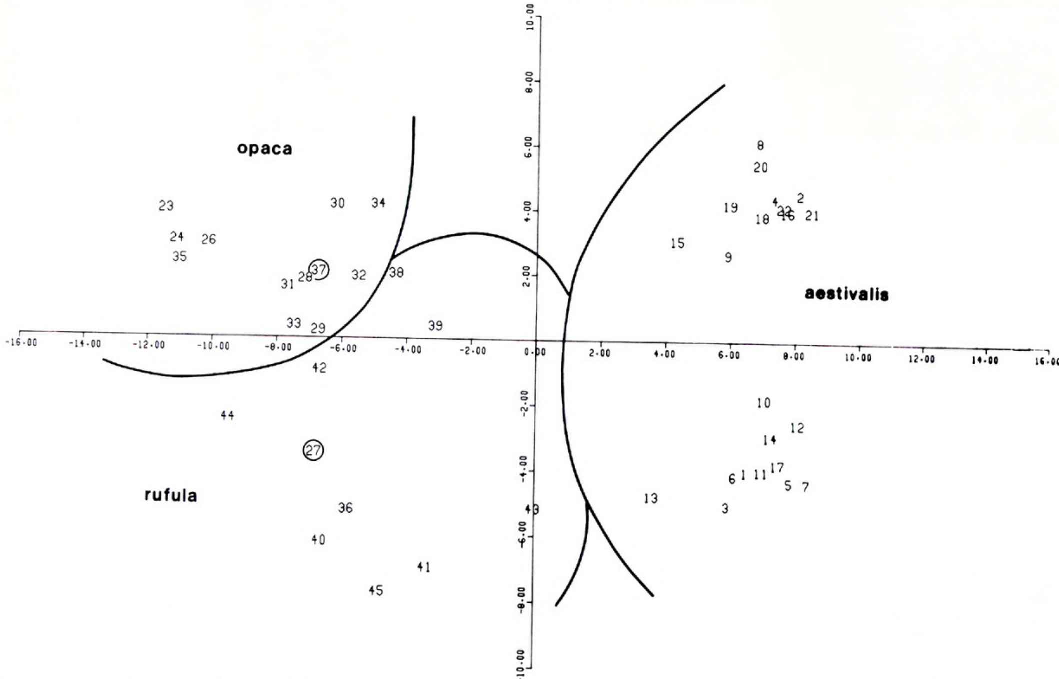


FIGURE 7. Principal-components analysis of 44 OTUs of *Crataegus* ser. *Aestivales*: nos. 1–22 = *C. aestivalis*, 22–35 = *C. opaca*, 36–45 = *C. rufula* (OTU no. 25 not used). Note partial intermediacy of *C. rufula* OTUs.

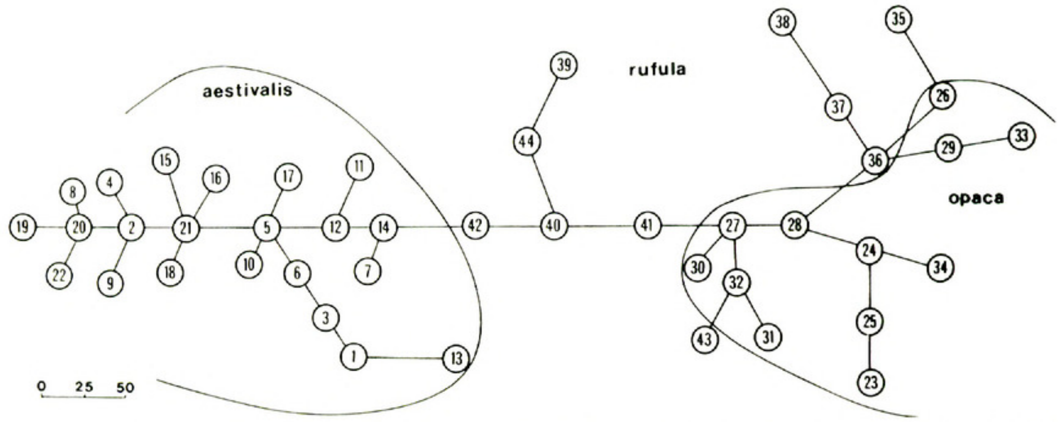


FIGURE 8. Minimum spanning tree of 44 OTUs of *Crataegus* ser. *Aestivales* (scaled to distance units computed by single-link data used for FIGURE 6).

and *C. opaca* are far too different to be treated as a single species in spite of the linkage represented by *C. rufula*. Note also that OTU 43, prior to this study identified as an *aestivalis-rufula* intermediate, sometimes shows up close to the *C. opaca* grouping (see, for example, FIGURE 8).

The intermediacy in foliar characteristics and geographic range, together with local abundance, suggest the hypothesis that *Crataegus rufula* is a variable, relatively new species of hybrid origin. This hypothesis may best be tested with detailed biosystematic studies by workers with easy access to living populations. *Crataegus rufula* is most conveniently treated as a separate species, even though it varies considerably in leaf shape (albeit tending to the broader shape of *C. opaca*), somewhat in foliar tomentum, and greatly in flower size.

KEY TO SERIES AESTIVALES

1. Leaves of short shoots 3–5 cm long, broadly elliptic-obovate, distally clearly serrate or crenate, the margin usually eglandular (glands occasionally present on teeth), unlobed, the surface usually glossy, ± glabrous except for tufts of usually whitish hairs in axils of mid-vein and lateral veins below. .... 1. *C. aestivalis.*
1. Leaves of short shoots 5–7 cm long, variable in shape, the margin gland-dotted, not regularly and finely serrate-crenate but often sinuous, the surface usually matte, rufous-tomentose below.
   2. Leaves of short shoots elliptic to broad-elliptic, ± sinuate-lobed, lateral veins 5 to 9 (or 10); pedicel ± glabrous. .... 2. *C. opaca.*
   2. Leaves of short shoots long-obovate to broad-elliptic, rarely ± crenate, lateral veins 3 to 5; pedicel ± rufulous-tomentose. .... 3. *C. rufula.*

1. **Crataegus aestivalis** (Walter) Torrey & A. Gray, Fl. N. Amer. **1:** 468. 1838. FIGURE 1.

Mespilus aestivalis Walter, Fl. Carol. 148. 1788. Type not seen.
Crataegus cerasoides Sarg. Trees & Shrubs **2:** 237. 1913. TYPE: Florida, Volusia Co., near Seville, *Curtiss 6842* (holotype, A).
C. luculenta Sarg. Trees & Shrubs **1:** 11. *pl. VI.* 1902. TYPE: Florida, Flagler Co., Haw Creek, *Curtiss 6679* (holotype, A; isotype, DOV).

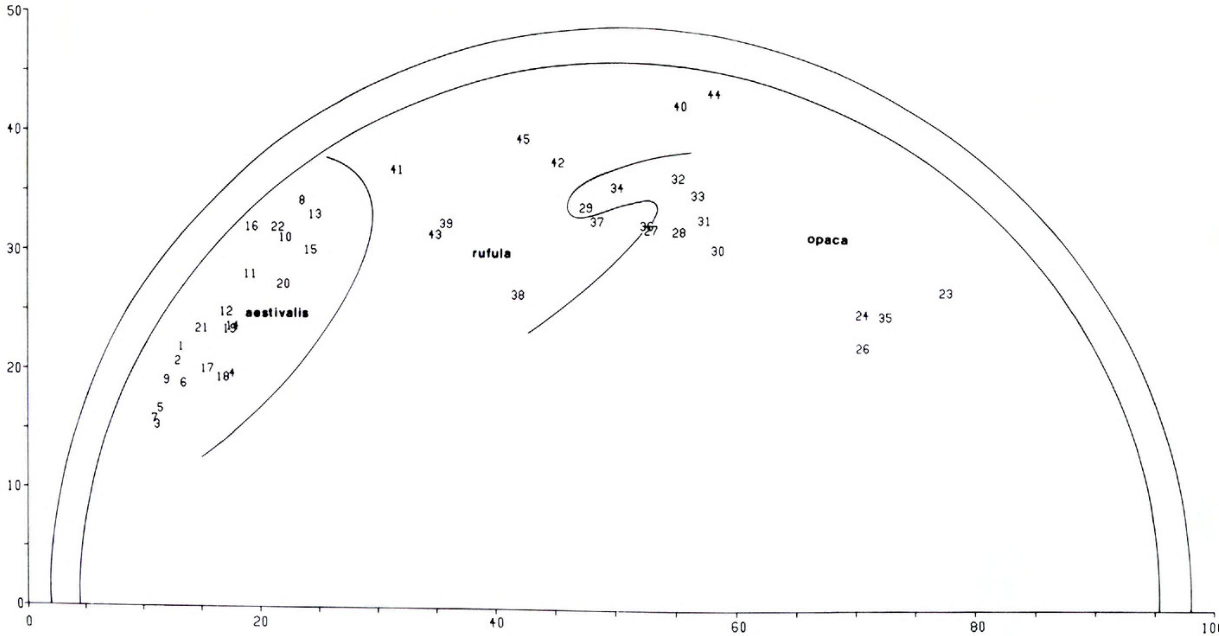


FIGURE 9. Wells Hybrid Index run on 44 *Crataegus* ser. *Aestivales* OTUs with putative hybrid *C. rufula*. Results clearly show intermediacy of *C. rufula*.

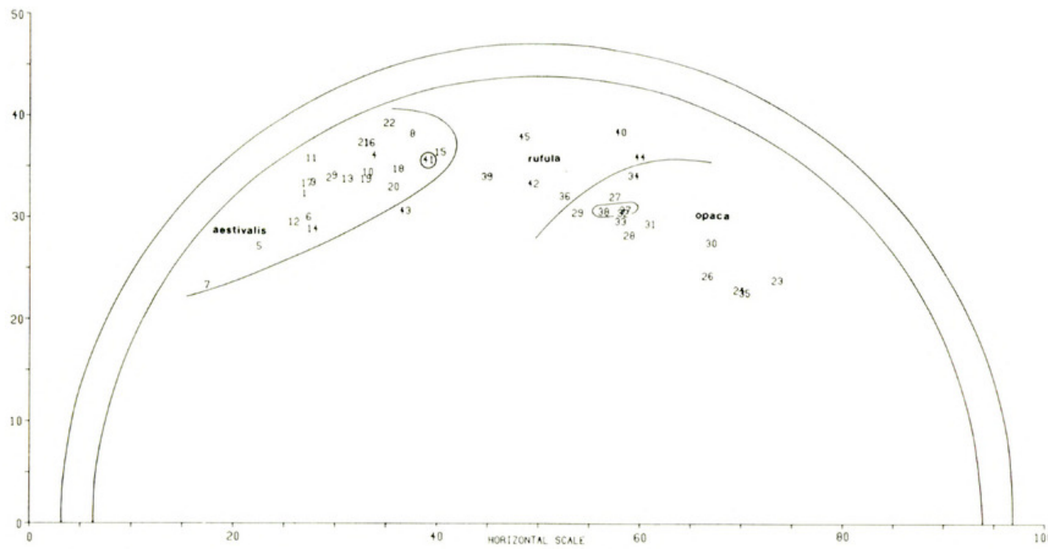


FIGURE 10. Wells Hybrid Index run on 44-OTU, 12-character set. Note results similar to 44-OTU, 19-character set (FIGURE 9).

C. maloides Sarg. Trees & Shrubs **1:** 9. *pl. V.* 1902. TYPE: Florida, Volusia Co., Haw Creek, *Curtiss 6777* (holotype, A).
C. lucida Elliott(?), Sketch Bot. S. Carolina **1:** 548. 1821. Type not seen.
C. elliptica Pursh(?), Fl. Amer. Sept. **1:** 337. 1814. Type not seen.

Shrub to small tree 3–12 m tall; branches gray (those of current season dark brown in late summer), glabrous; thorns less abundant on older shoots, 2–4 cm long when full grown, stout at base, ± straight, transforming ± readily into short shoots; elongating shoots with small, broadly circinate, glandular-margined stipules. Leaves appearing at or after anthesis; petiole 3–8 mm long, alate distally; blade elliptic to oblanceolate or narrowly so, 3–5 by 1.5–2 cm, sometimes much larger on elongating shoots (then sometimes few-lobed, sometimes deeply, even almost tripartite), finely serrate to crenate mainly in distal half,

TABLE 3. **Relative importance of 19 characters used in Crataegus ser. Aestivales study based on percentage of total variance accounted for by each character (R-PCA) and on variance ratio (C. aestivalis vs. others).**

CHARACTER NO.	PERCENT OF TOTAL VARIANCE	VARIANCE RATIO	CHARACTER NO.	PERCENT OF TOTAL VARIANCE	VARIANCE RATIO
1	10.0	196	11	13.9	267
2	2.5	71	12	12.1	238
3	2.2	82	13	3.1	53
4	2.0	71	14	0.7	8
5	2.7	113	15	4.2	101
6	0.7	50	16	1.5	102
7	5.0	58	17	5.5	134
8	5.6	142	18	12.0	755
9	3.8	167	19	10.1	1840
10	2.4	32			

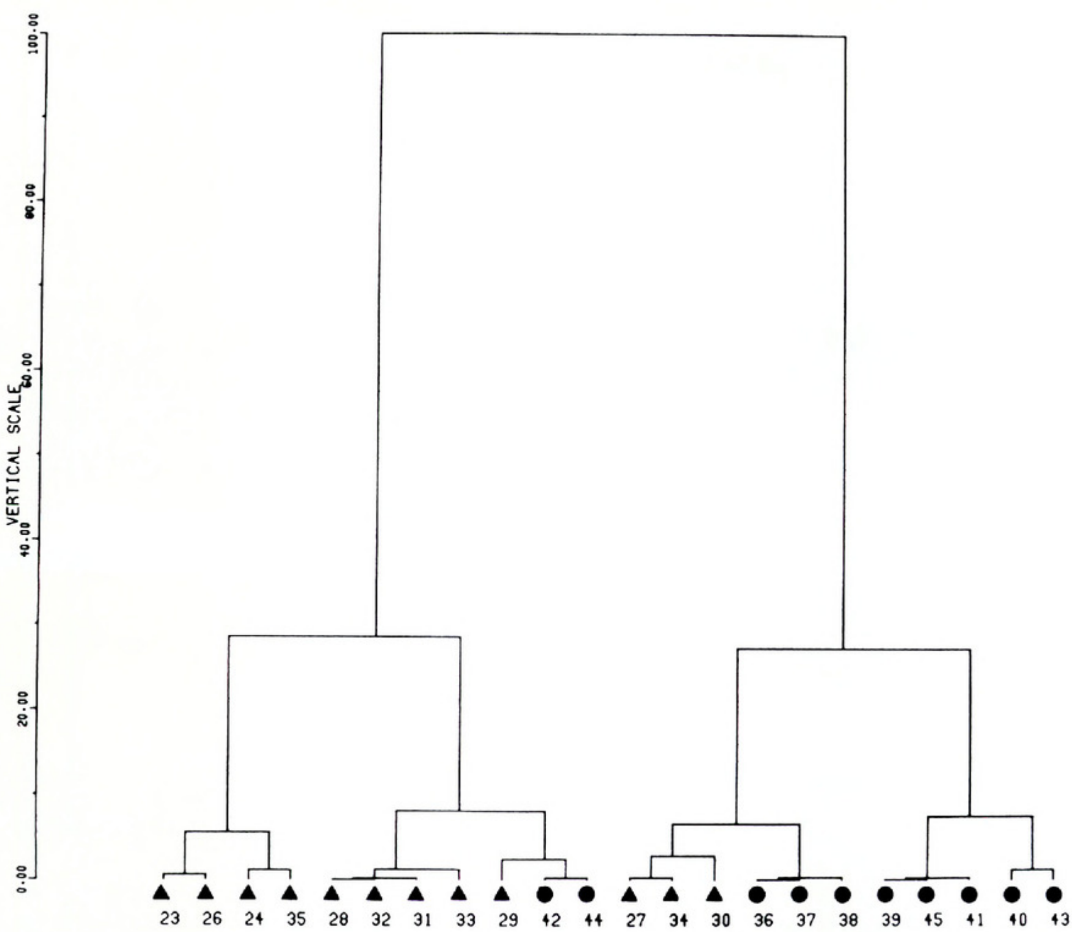


FIGURE 11. Sum of squares agglomeration of Euclidean distance of 22 *Crataegus* ser. *Aestivales* OTUs, 6 characters (symbols as in FIGURE 5).

tips of teeth sometimes with small black glands, coriaceous, the upper surface ± dark green, somewhat shiny, scabrous to glabrous, the lower surface glabrous but with tufts of gray (sometimes somewhat rufous) hair in axils of lateral veins and sometimes also along mid-vein. Umbels 2- to 4-flowered, glandular-bracteolate; pedicels glabrous to sparsely long-pilose; anthesis February–March (later northward). Flowers 1.2–1.5 cm in diameter; hypanthia glabrous; calyx lobes ± entire, glabrous; stamens 20, anthers pink(?); styles 4 or 5. Fruit red, fleshy, edible, ripening as early as May in southern part of range and as late as July in North Carolina; pyrenes 4 or 5.

EASTERN MAYHAW.

Common in northern Florida and southern Georgia, continuing up Coastal Plain to about New Bern, North Carolina (see MAP 1). Scarce in northern portion of range. Almost confined to seasonally inundated depressions, including ditches, sink holes, and riversides with fluctuating water levels. Chromosome number and breeding system unknown—possibly a polyploid facultative apomict. See Sargent (1902, *pls. V, VI*), for good illustrations of *Crataegus aestivalis* (as *C. maloides* and *C. luculenta*).

REPRESENTATIVE SPECIMENS EXAMINED. **Alabama.** HOUSTON CO.: 9.8 mi SE of Gordon, *McDaniel 8501* (IBE). **Georgia.** BURKE CO.: in natural pond 7.3 mi W of Waynesboro,

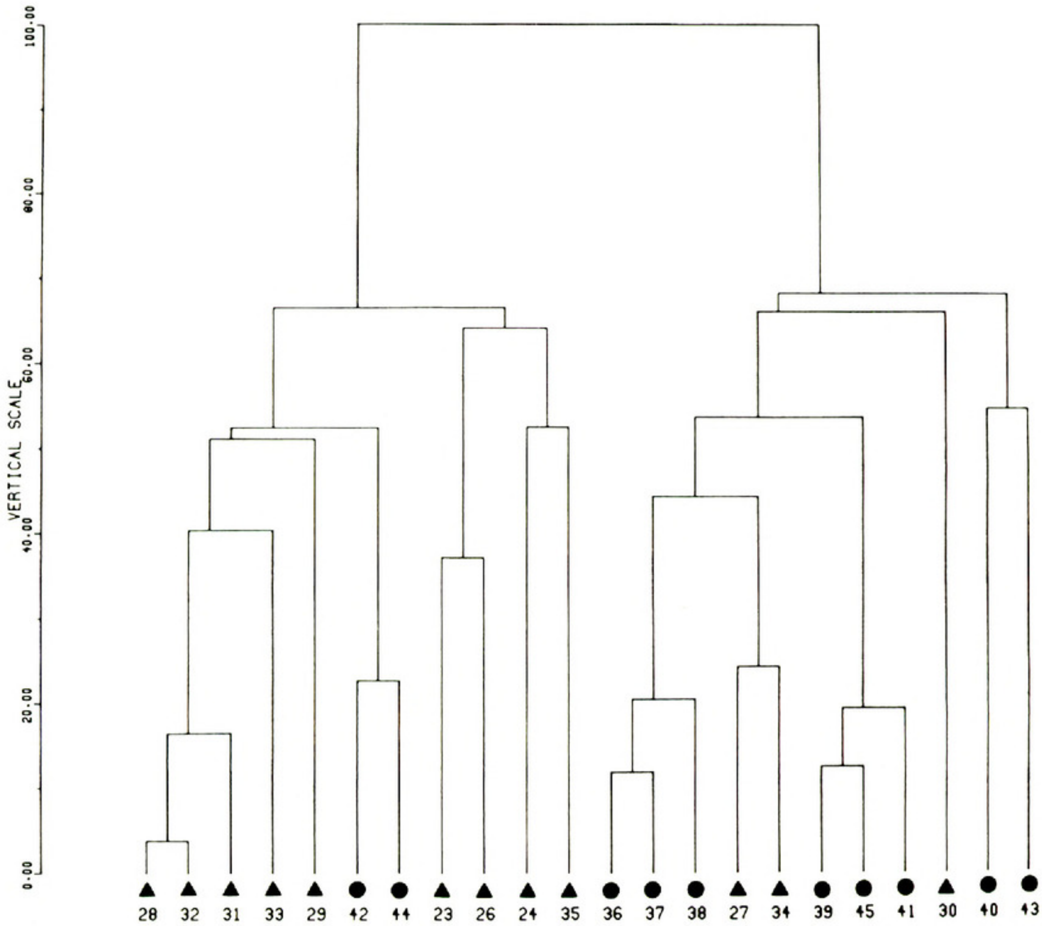


FIGURE 12. Single-link clustering of Euclidean distance of 22 *Crataegus* ser. *Aestivales* OTUs, 6 characters (symbols as in FIGURE 5).

W. H. Duncan 22234 (GA, LAF). CHARLTON CO.: Traders Hill, swamp, *Harbison 13963* (TENN); near Folkston, *J. H. Miller 2* (GA); on limestone shelf at edge of Satilla R. in NE part of county, *W. H. Duncan 23298* (GA); on banks of St. Mary's R. just E of St. George, *W. H. Duncan 2066* (GA). TATTNALL CO.: low swampy soil near river, 11 mi, 29 degrees SW of Glennville, *Padgett 262* (GA); THOMAS CO.: ephemeral pond at bottom of slope of pineland, Wade Tract of Tall Timbers, Inc., between Thomasville and Metcalf by Georgia Rte. 122, *Godfrey 80608* (UWO), *80609* (UWO), *80610* (UWO); W side of Georgia Rte. 122, ca. 5 km S of U.S. 319, *J. B. Phipps 5218* (UWO). WARE CO.: low slough area on S side of Satilla R., N of Georgia Power Substation off U.S. hwy. 82, *Faircloth 8164* (GA). **South Carolina.** HORRY CO.: wooded bank of Waccamaw R. at Red Bluff, *C. R. Bell 7738* (USF). **North Carolina.** PENDER CO.: along E channel of Northeast Cape Fear R., ca. 2.5 river mi downstream from Stag Park, *S. W. Leonard & R. J. Davies 7547* (VDB). **Florida.** ALACHUA CO.: near Gainesville, *Murrill s.n.,* 10.iii.1940 (GA, no. *23158*). COLUMBIA CO.: Rice R., *Murrill s.n.,* 9.iii.1940 (FLAS, no. *34598*). FLAGLER CO.: Middle Haw Creek, W of Bunnell, by Florida Rte. 100, *Godfrey 78724* (IBE). GADSDEN CO.: W bank of Ochlocknee R., SE of Havana, *R. J. Wilmont s.n.,* 21.v.1940 (FLAS, no. *35187*). JACKSON CO.: W side of Florida Rte. 271, 16.6 mi N of Sneads (from jct. of U.S. Rte. 90), *Godfrey 80333* (UWO). LEON CO.: W end of Lake Iamonia, *Griscom 21579* (GH); ca. 2 mi S of Talquin Dam, locally common in backwater slough of Ochlocknee R., *McDaniel 7478* (IBE). LIBERTY CO.: *Canby s.n.,* iii.1890 (DOV, no. *4715*). VOLUSIA CO.: low woods bordering Haw Creek, *A. H. Curtiss 6677* (DOV).

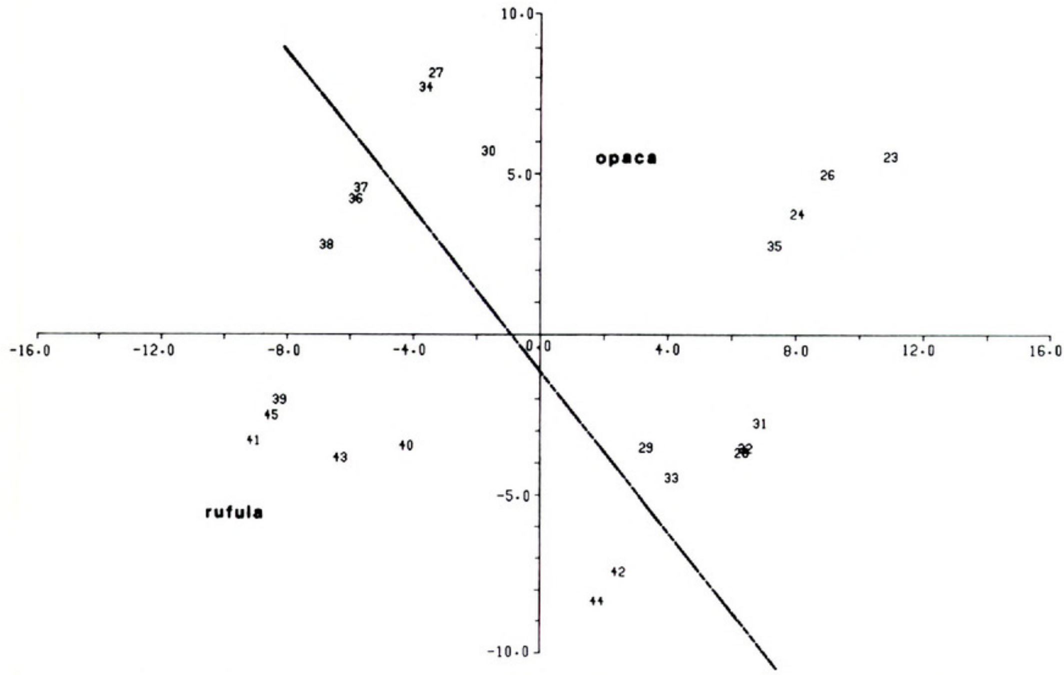
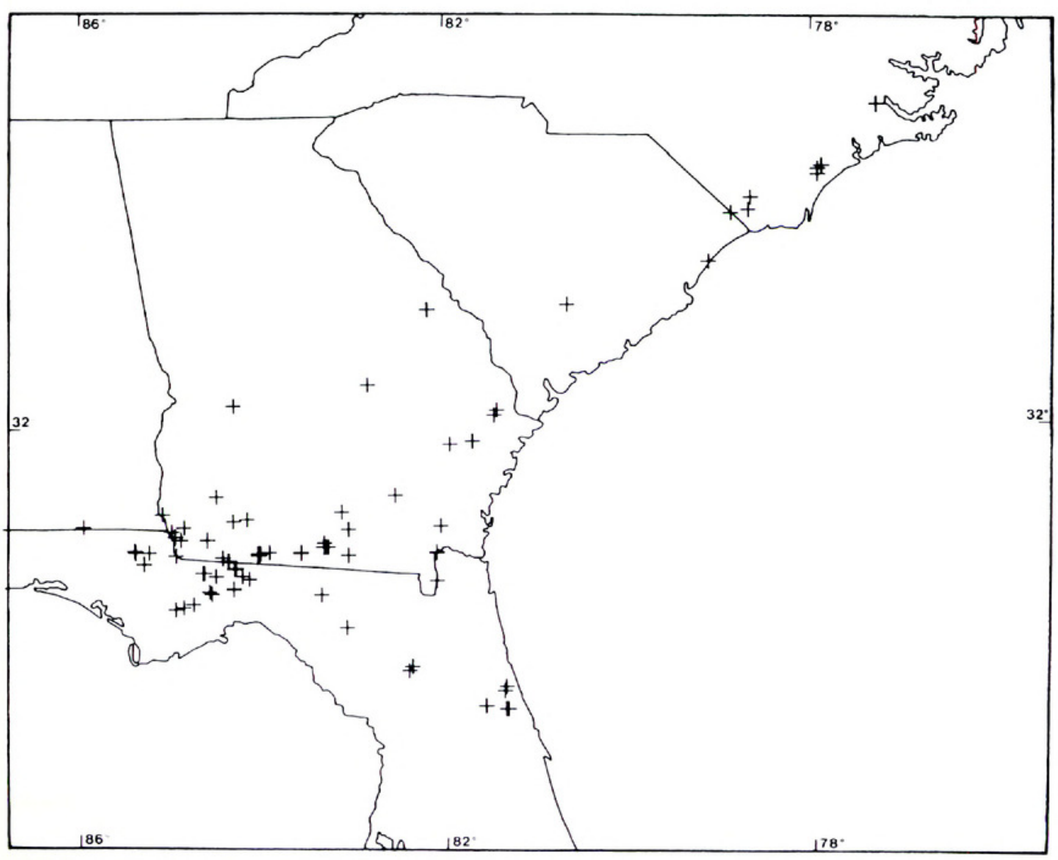


FIGURE 13. PCA of 22 *Crataegus* ser. *Aestivales* OTUs, 6 characters: 23–35 = *C. opaca*, 36–45 = *C. rufula*.



MAP 1. Distribution of *Crataegus aestivalis* based on collated herbarium records.

Torrey and Gray's description of *Crataegus aestivalis*, together with the distribution they ascribed to it, indicates that they included in that species what is now called *C. opaca* Hooker & Arn. Nevertheless, the type location, the original description, and the photograph of a vegetative specimen at BM collected by Walter and possibly *C. aestivalis* (therefore type material) all indicate that the basionym, *Mespilus aestivalis*, must pertain to the plant dealt with here. There is, however, no Walter specimen of *Crataegus aestivalis* in flower or fruit at the British Museum. Likewise, I have been unable to locate Pursh's type of *C. elliptica* (reputedly at BM, OXF) or to access Elliott's material (CHARL) of *C. lucida*. Sargent (1920) thoroughly discussed typification of *C. aestivalis* and presented a convincing argument that these three names represent the same species.

2. **Crataegus opaca** Hooker & Arn. Companion Bot. Mag. **1**: 25. 1835. TYPE: Louisiana, New Orleans, *Drummond 104* (holotype, E[3]). FIGURES 2, 3.

Tree to 8 m or occasionally more; trunk sometimes to 0.3 m in diameter; mature bark flaking; branches medium to dark gray; twigs of current season rufous-tomentose, especially when young; thorns few to moderate in number, 2–4 cm long, stout, straight. Leaves not appearing before flowers and often entirely after anthesis; petiole 4–7 mm long, short rufous-tomentose; blade ± elliptic to lance-elliptic or sometimes broader, 5–7 cm long, gland dotted and unlobed to sinuate lobed at margin (sometimes more deeply and irregularly lobed on vegetative shoots, lobes often broader, margin sometimes obscurely or very shallowly distant-crenate), 5- to 9- (or 10-)nerved, the upper surface scabrate, especially when young, the lower surface rufous-tomentose, especially along veins, occasionally glabrous in old leaves. Umbels 3- to 6-flowered, ± sessile to short stalked, ± glabrous; bracteoles few, oblong-linear, gland-margined, glabrous; anthesis February–March. Flowers 1.25–1.75 cm in diameter; hypanthium glabrous; calyx lobes triangular, 4 mm long, entire to slightly glandular-serrate; petals ca. 7 mm long, white to occasionally pale rose; stamens 20, the anthers 1 mm long, reddish or rose; styles (4 or) 5. Fruit (0.8?–)1.2–1.5 cm in diameter, red, succulent, ripening May–June; pyrenes 4 or 5, shallowly grooved dorsally, with portions of calyx accrescent.

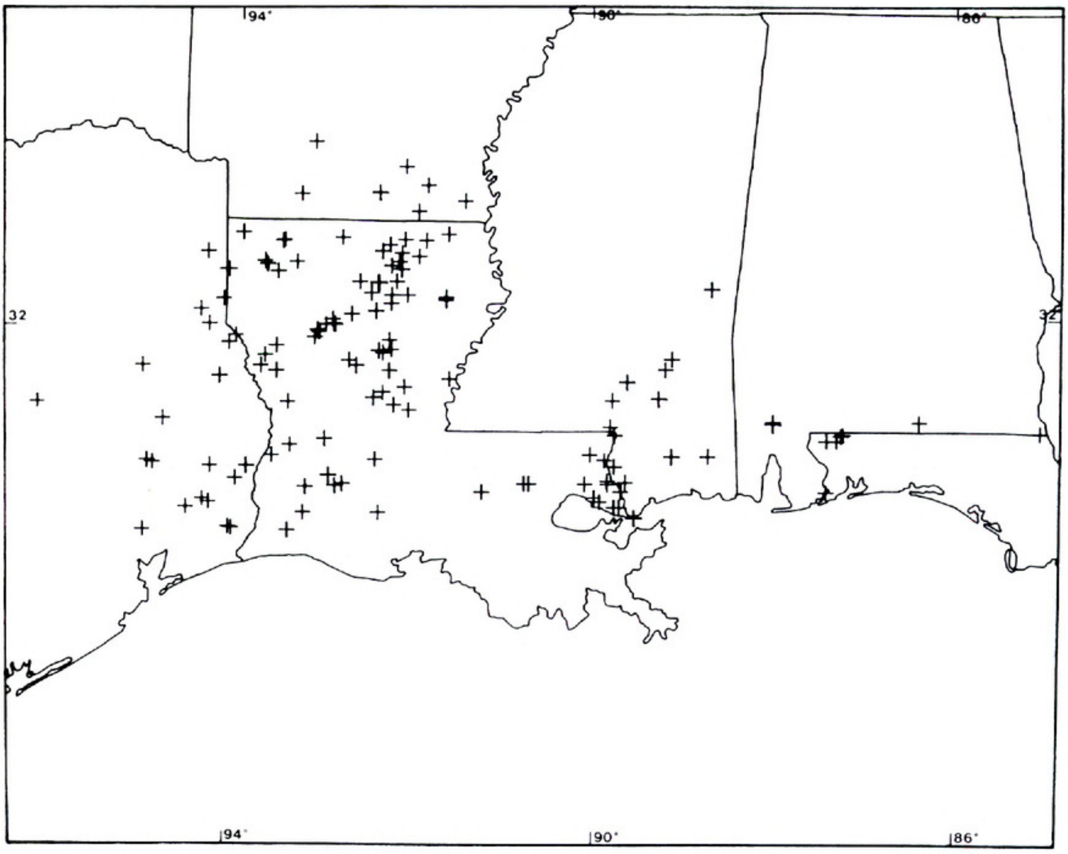
WESTERN MAYHAW.

Eastern Texas to Alabama, most common in Louisiana, apparently rare east of Pearl River (see MAP 2). Chromosome number and breeding system unknown, although possibly a sexual diploid.

Fruit edible and used locally for conserves. Sargent (1890, *pl. CXCII*) illustrated a specimen that is presumably this species under *Crataegus aestivalis*.

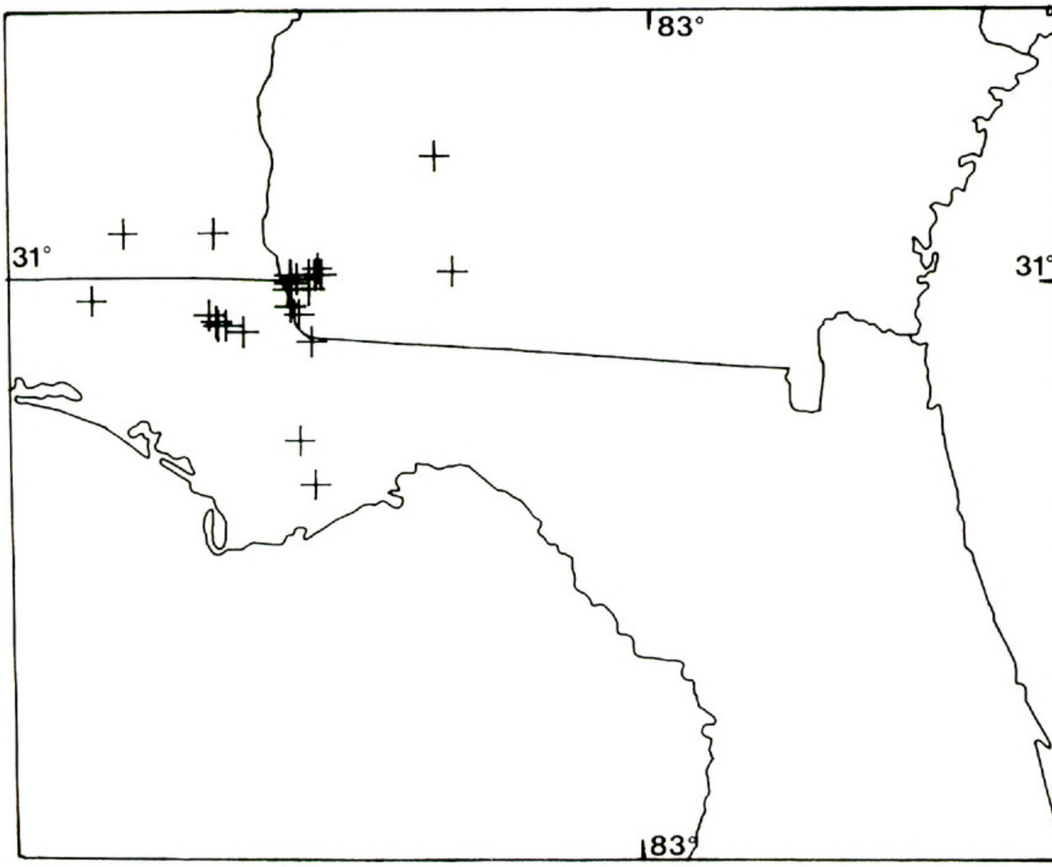
REPRESENTATIVE SPECIMENS EXAMINED. **Texas.** ANGELINA CO.: 2.6 mi SE of Diboll, *Shinners 18200* (SMU). HARRISON CO.: Caddo Lake State Park, W end of park along old abandoned trail, *A. E. Orr 155* (SMU). JASPER CO.: bayou ca. ½ mi E of Neches R., W of Kirbyville, *McVaugh 6834* (SMU). ORANGE CO.: ca. 10 mi E of Beaumont, *C. L. Lundell & A. A. Lundell 10914* (LL, SMU). POLK CO.: in flatwoods ca. 5 mi S of Livingston

[3]The specimen of *Drummond 104* at K is a species of *Prunus*.



MAP 2. Distribution of *Crataegus opaca* based on collated herbarium records.

on Rte. 146, *D. S. Correll 151107* (TEX-LL). TYLER CO.: ca. 1 mi S of Town Bluff, *Whitehouse 22997* (SMU). **Arkansas.** ASHLEY CO.: W of Crossett at Ouachita R. Bridge, water's edge, *D. M. Moore & C. Moore 68141* (UARK). BRADLEY CO.: Johnsonville prairie, 5.9 mi SW of Johnsonville on unnamed county road, *S. Leslie & D. Taylor 94* (UWO). **Louisiana.** ALLEN PARISH: low woods along Barnes Creek, sect. 4, ca. 4 mi SW of Reeve, *Thieret 21896* (DUKE, USLH). BOSSIER PARISH: 3.8–4 mi SE of Benton (by road) from jct. of Louisiana 3 and Bellevue Road, Cypress Black Bayou Reservoir, *Barbour 1109* (LSU). MOREHOUSE PARISH: edge of woods beside Pratt Brake S of Beekman along Louisiana 142, *R. D. Thomas 51378 & P. Pias 734* (NLU); along Morehouse Rd. 2705 just W of Stevenson Fire Tower in Georgia, Pacific Game Management Area, *R. D. Thomas 51380 & P. Pais 736* (NLU). NATCHITOCHES PARISH: Creston, *E. J. Palmer 7024* (NO). OUACHITA PARISH: West Monroe, *Canby et al. 26* (CM, DOV); swampy area beside Louisiana 34 S of Bawcomville, *R. D. Thomas et al. 27538* (NLU); Ark. Road, West Monroe, *Tucker s.n.,* 12.v.1960 (NLU, no. *24968*). ST. TAMMANY PARISH: ca. 2 mi N of Talisheek, *S. Darwin 1320* (IBE, LSU, NO); Honey Is. Swamp, low, wet woods of Carpina, *Sundill 1747* (NO). UNION PARISH: beside Louisiana 2 at DeLoutre Bayou, *Scarbrough s.n.,* 11.v.1969 (NLU, no. *25030*). WASHINGTON PARISH: 5 mi E of Angie, *S. Darwin & Sundill 1255* (NO). WEBSTER PARISH: 2 mi W of Sarepta, *Goldsby s.n.,* 3.v.1971 (NATC, no. *9918*). **Mississippi.** GEORGE CO.: along Red Creek, 5 mi E of Ramsey Springs, *Ray 8119* (USF). JEFFERSON DAVIS CO.: 4 mi NE of Bassfield, *McDaniel 2867* (IBE, UNA). MARION CO.: roadside thicket ca. 7 mi N of Columbia, *M. S. & D. E. Eyles 8319* (DUKE). **Alabama.** COVINGTON CO.: ca. 5 mi N of Florala by U.S. 31, *R. Kral 41875* (VDB). MOBILE CO.: Mount Vernon, *C. Mohr s.n.,* 15.iv (UNA).



MAP 3. Distribution of *Crataegus rufula* based on collated herbarium records.

3. **Crataegus rufula** Sarg. J. Arnold Arbor. **2:** 251. 1920. LECTOTYPE (here designated): Florida, Jackson Co., Cottondale, *Harbison 19* (A). FIGURE 4.

Shrub to small tree 3–5 m tall, variably thorny; thorns 1–3(–5) cm long, stout at base, tapering, straight. Leaves petiolate; blade elliptic to ovate, 2.5–4.5 cm long, those on rapidly elongating shoots larger, usually proportionately broader than those on short shoots, and sinuate lobed, short-shoot leaves sometimes sinuate lobed, all entire, or barely serrate or crenate in distal ⅓ or ½, glandular-margined, densely white- or rufous-tomentose when young, at maturity scabrous above and densely rufous-tomentose below especially on veins; lateral veins 3 to 5. Umbels 2- to 5-flowered, glabrous to rufous-tomentose, including pedicels, hypanthia, and calyx lobes; anthesis February–March. Flowers 1.5–2.75 mm in diameter; petals to 12 mm long; stamens 20, anthers red; styles (4 or) 5. Fruit a pome, 1 cm in diameter, red, juicy; pyrenes 5, dorsally ribbed. RUFOUS MAYHAW.

Mainly restricted to the Florida panhandle, adjacent Georgia, and southeastern Alabama (see MAP 3).

REPRESENTATIVE SPECIMENS EXAMINED. **Georgia.** DOUGHERTY CO.: N of R.R. to Milth's just before leaving pasture, Albany, *J.W.G. E3288* (GA). SEMINOLE CO.: 7 mi SW of Donaldsonville by Georgia Rte. 285, just E of jct. with Georgia Rte. 91, *Godfrey 70500* (UWO); in angle formed by jct. of Georgia Rtes. 92 and 285, 7 mi SW of Donaldsonville, *Godfrey 80341* (UWO), *80342* (UWO), *80343* (UWO), *80344* (UWO), *80440* (UWO); 7 mi SW of Donaldsonville, by Georgia Rte. 91 at jct. with road E to Seminole State Park, *Godfrey 80596* (UWO), *80597* (UWO), *80598* (UWO). **Florida.** JACKSON CO.: ponds in pine barrens near Marianna, *A. H. Curtiss 6745* (DOV); to W side of Florida Rte. 271, 16.6 mi N of Sneads (from jct. of U.S. Rte. 90), *Godfrey 80331* (UWO), *80335* (UWO), *80336* (UWO).

Occurring as it does at the exact interface of *Crataegus aestivalis* (more easterly) and *C. opaca* (more westerly), as well as being intermediate in almost all respects between these two species, *C. rufula* represents a presumed hybrid swarm or its descendents, probably with some elements fixed by apomixis. Although in many characters (e.g., the usually sinuate leaf margin) it is more like *C. opaca,* it lacks the characteristic elongate leaves of the latter species. *Crataegus rufula* also tends to intergrade (e.g., in OTU 43) with *C. aestivalis,* with which it is more sympatric. The frequency of *C. aestivalis*–like intermediates could well be accounted for by the fact that pure *C. aestivalis* is reasonably common right up to the *C. rufula* range, while *C. opaca* is very scarce at the interface. Another possibility is that *C. rufula* constitutes a compilospecies in the sense of Harlan and De Wet (1963). Some, but not all, individuals of *C. rufula* have very large flowers.

Crataegus rufula is locally common and is conveniently treated as a species for the purpose of this flora. Detailed cytological, breeding, and morphometric studies are required to clarify its status.

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