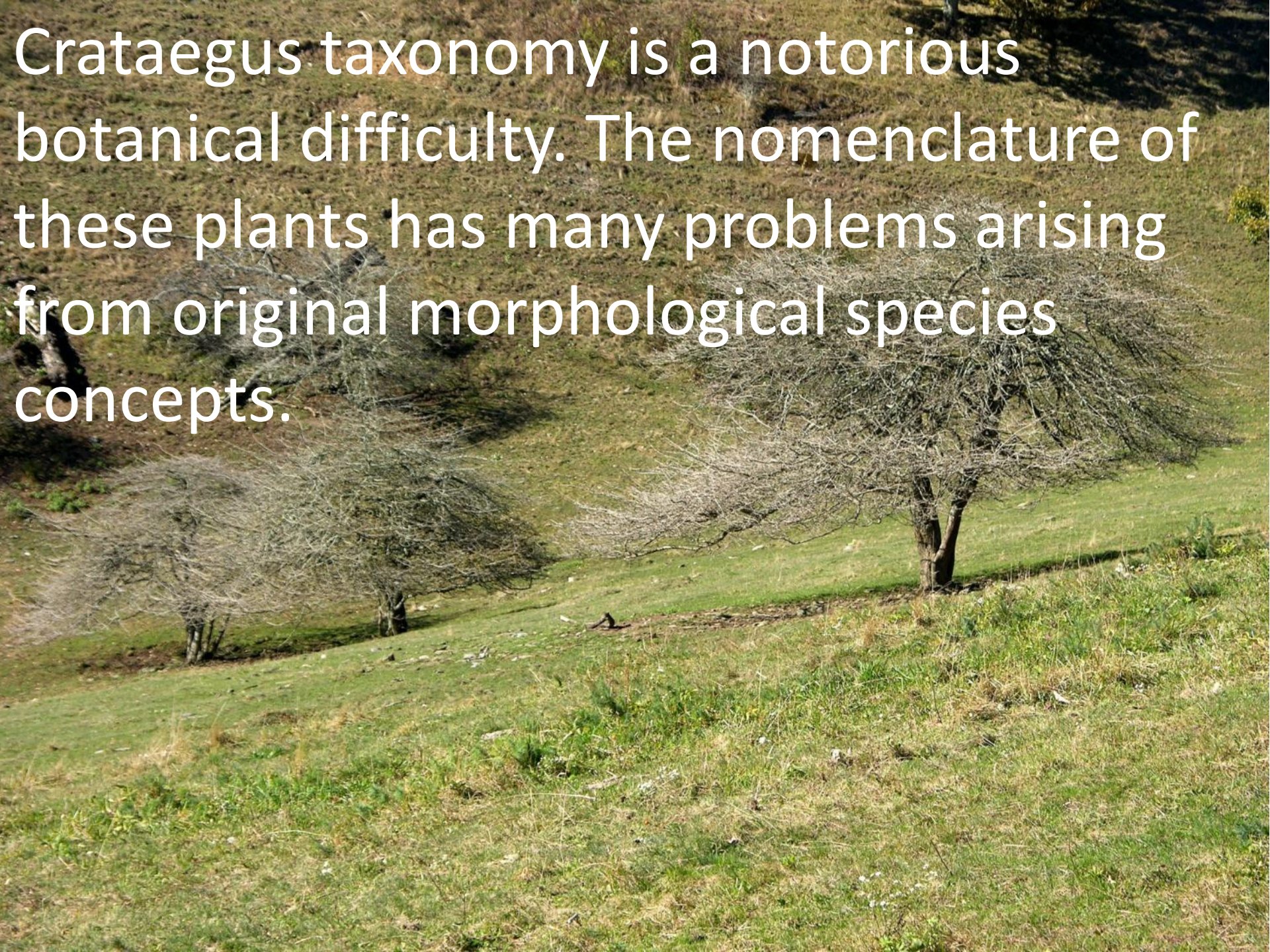


Crataegus systematics
and the classification of
North American species

Ron Lance

Crataegus Study Day
October 8, 2017

Crataegus taxonomy is a notorious botanical difficulty. The nomenclature of these plants has many problems arising from original morphological species concepts.



Species concepts as initiated with Linnaeus were distinguished by their morphological variation: *Taxonomic species*



C. viridis L.

In time, recognition of diversity in plant reproduction and genetics has rendered other species concepts, including:

Evolutionary species: part of a lineage evolving separately from others and with its own unique evolutionary tendencies.

Ecological species: a set of organisms adapted to a particular set of resources or nich

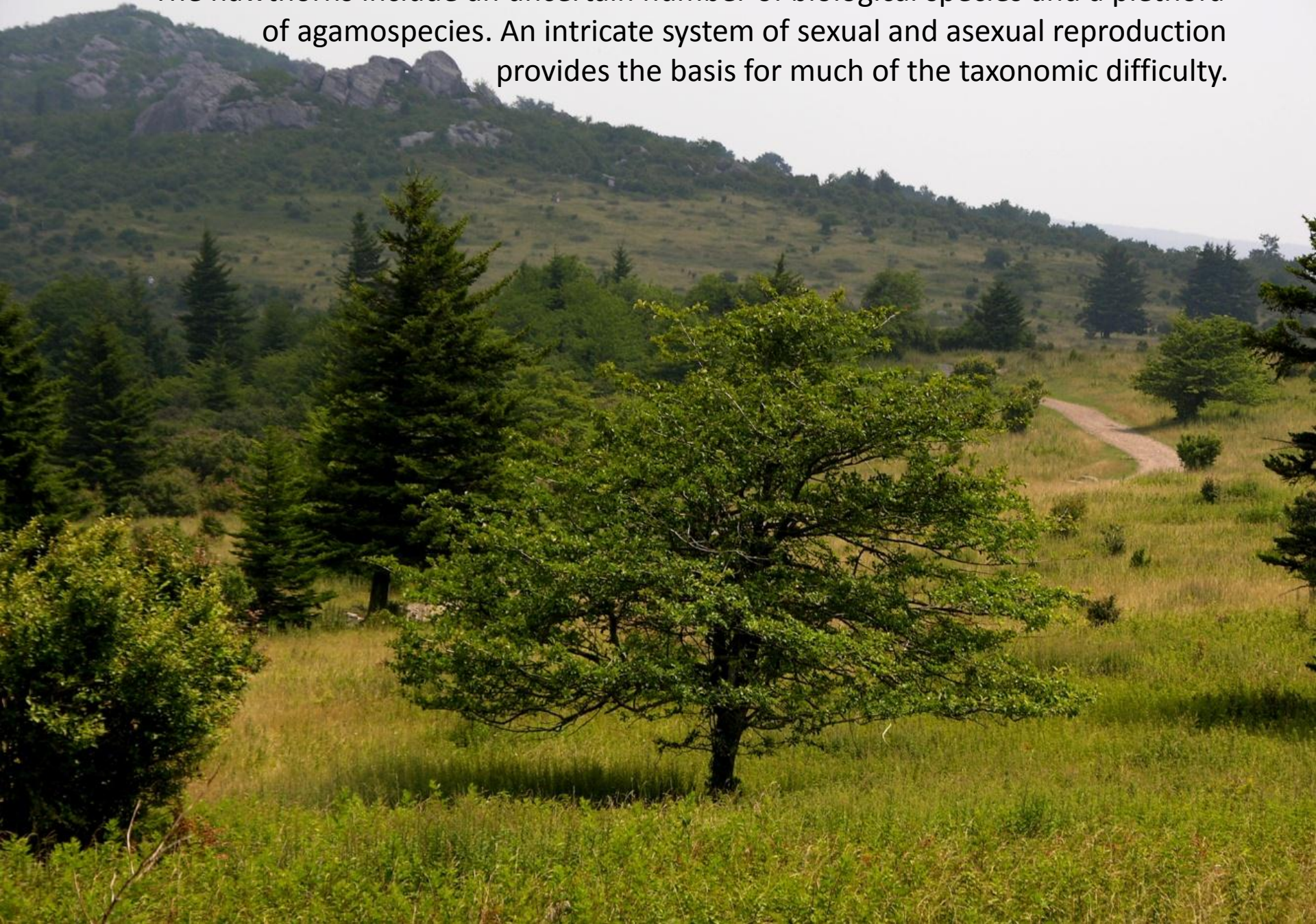
Biological species: groups of sexually interbreeding natural populations reproductively isolated from other groups and which promote gene flow within, and constrain gene flow between, species.

Microspecies: a small, localized population differentiated from related forms.

Compilospecies: acquires genes from other species by hybridization.

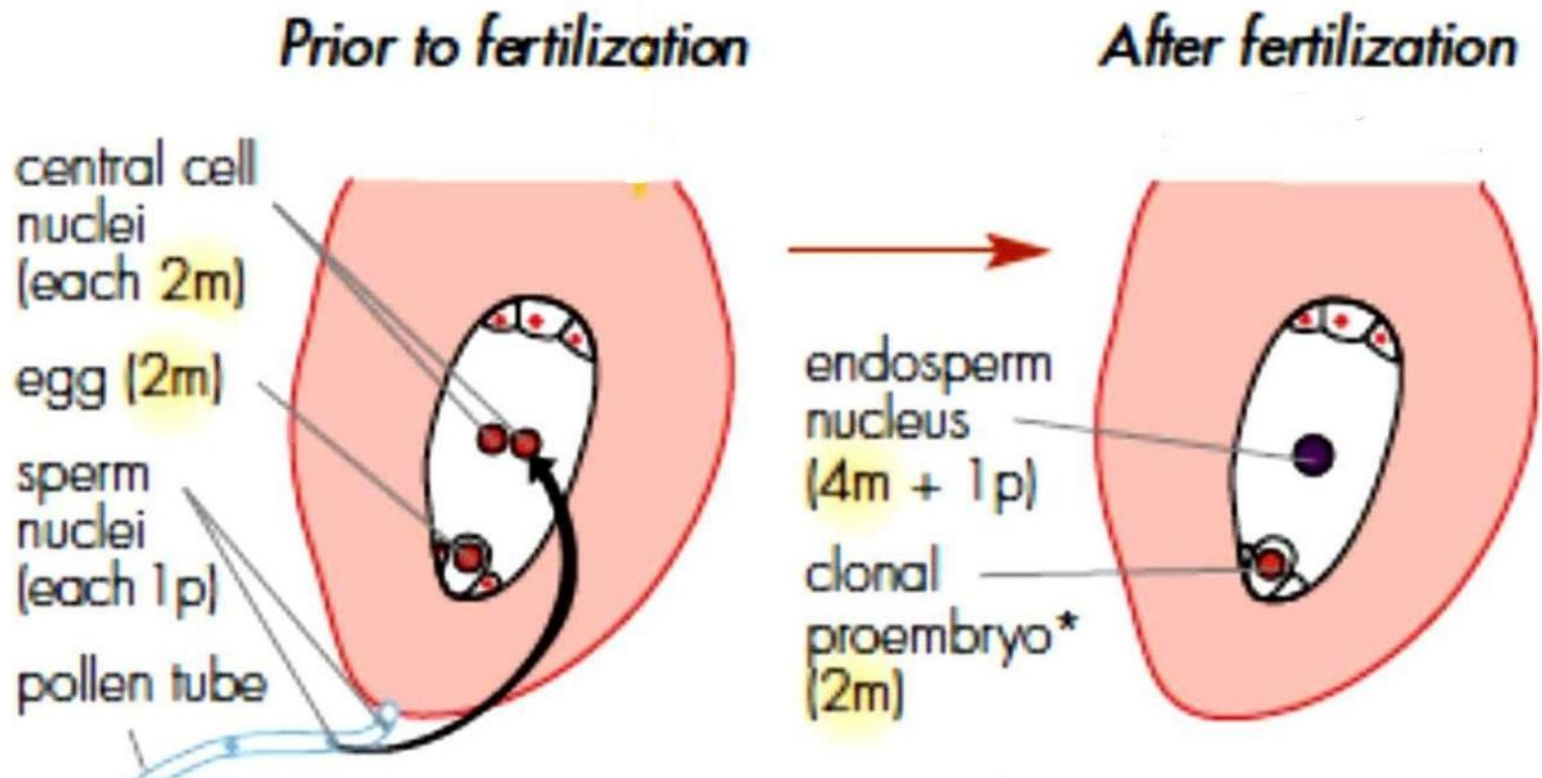
Agamospecies: asexually reproducing biotypes regarded as equivalent to a species.

The hawthorns include an uncertain number of biological species and a plethora of agamospecies. An intricate system of sexual and asexual reproduction provides the basis for much of the taxonomic difficulty.



Apomixis and Agamospermy: asexual reproduction in which seeds are produced from unfertilized ovules; these originating from egg nuclei without mitotic division (parthenogenesis). No gamete exchange occurs in the embryo, although pollination may be needed for embryo promotion and endosperm development (pseudogamous apomixis). Clonal offspring are produced, having no male inheritance.

CLONAL (ASEXUAL) REPRODUCTION



Agamic complexes: Apomictic taxa which are said to use “too little sex” to perpetuate, yet display morphological distinctiveness in local populations.



C. harbisonii

Crataegus are also sexual breeders, particularly the diploid species. Both reduced and unreduced gametes may be formed in the same taxa.

C. monogyna



Some *Crataegus* taxa include both diploids and polyploids
Triploids and tetraploids are most numerous in North America.
Apomixis is strongly linked with polyploidy, but not restricted to such.



C. aprica

Diploids are usually sexual outbreeders, suspected of being self-incompatible.
Triploids are obligate apomicts, usually pollen-sterile.
Tetraploids are facultative apomicts and self-compatible.

Reticulate *Crataegus* reproductive capabilities have thus complicated the systematics of the genus.



C. mollis- diploid (partly)



C. lanuginosa- triploid



C. holmesiana- tetraploid

Many entities of divergent genotypes and of possible hybrid origin have been named. Such recognizable entities may persist for many generations through **agamosperry**. These may have been derived from one or more known or unknown (or extinct) sexual ancestors. Upholding some type of species recognition for these taxa is preferable to dismissal since there may be identifiable values ecologically, biologically or economically.





In North America, 9 species and 2 varieties were known in 1753. The number of accepted species hovered between 10-20 during 1857-1899, but with about 175 names having been published. Between 1899-1922, the tally of names jumped to over 1100. Most were described by 3 workers: C.D. Beadle (147), W. W. Ashe (216), and C. S. Sargent (754).

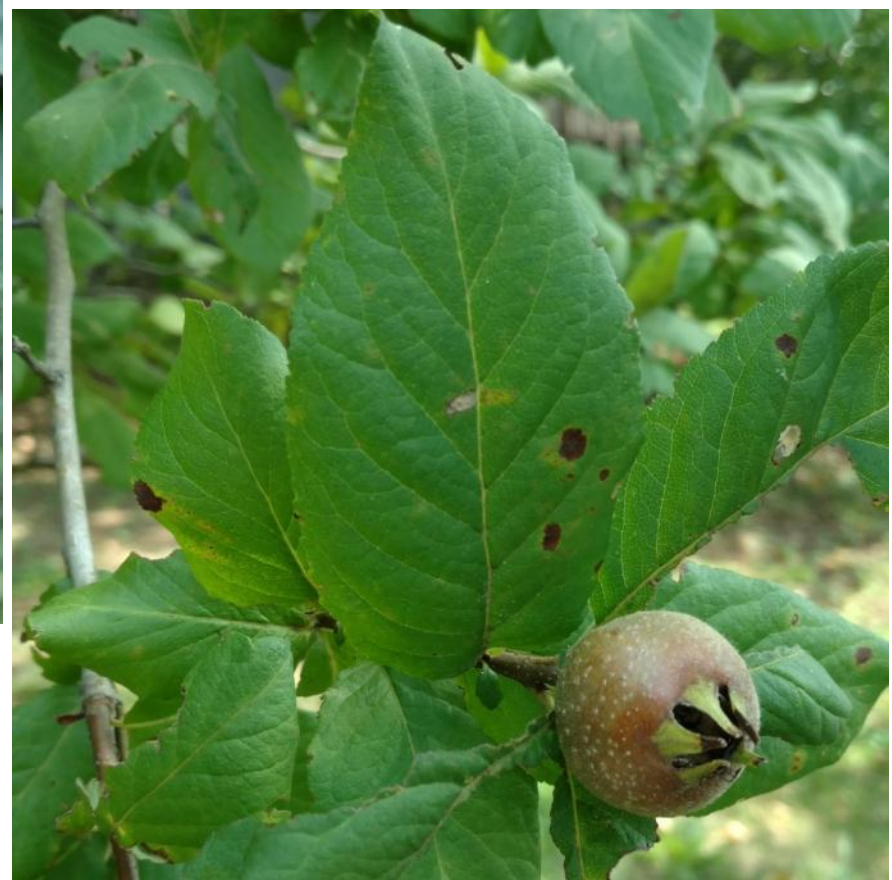


Crataegus classification:

Family **Rosaceae**

Subfamily **Maloideae** (now **Amygdaloideae**)

Tribe **Maleae**



Genus *Crataegus* is sister to *Mespilus*

By molecular evidence, *Amelanchier* is sister to *Crataegus-Mespilus*, but *Amelanchier* is different morphologically.

El-Gazzar in 1980 established the subgenus *Crataegus* (European) and subgenus *Americanae* (North American), but several morphological characters used to define these groups are not consistent. For example, the presence of major veins running to sinuses of short-shoot leaves in European affiliates is also seen in American *marshallii*, *spathulata*, *phaenopyrum*.



C. phaenopyrum



C. marshallii



C. spathulata

Additionally, primary veins running to sinuses of extension shoot leaves may be seen in American *brachyacantha* and some taxa in series **Virides** and **Lacrimatae**.

Parsley hawthorn (*C. marshallii*) of the southeastern U.S. shows closest morphological affinity to European and Asian species.

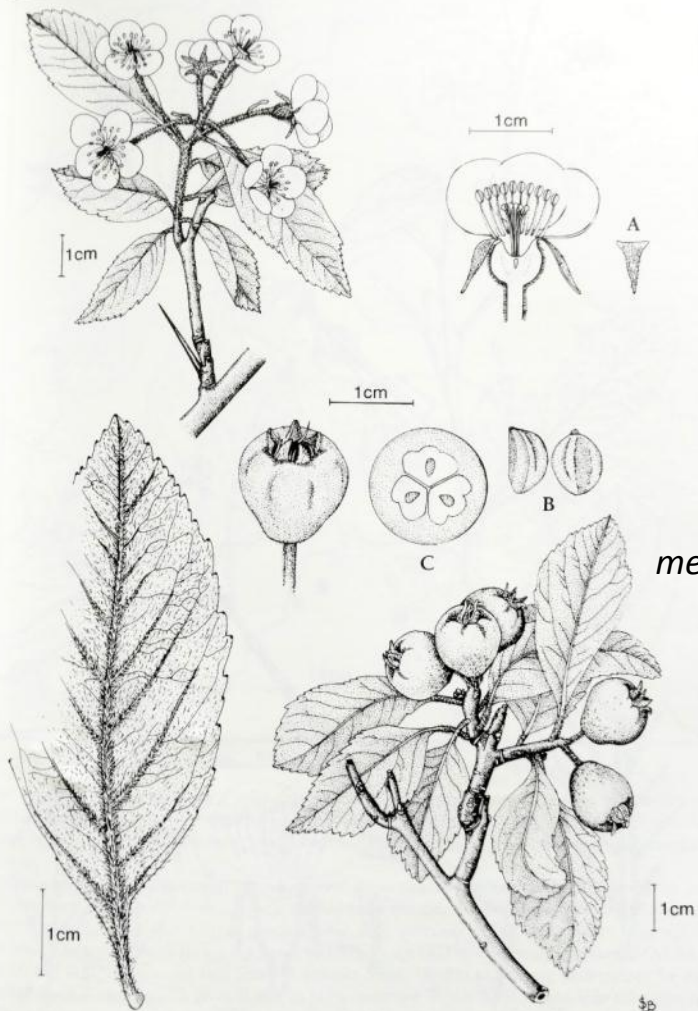
Crataegus marshallii



Crataegus ambigua



C. mexicana is most similar to the Yunnan species *scabrifolia*; these may indicate a primitive basal stock of warm-temperate origin, and may have migrated in the early Tertiary or Miocene westerly and southward.



mexicana

scabrifolia

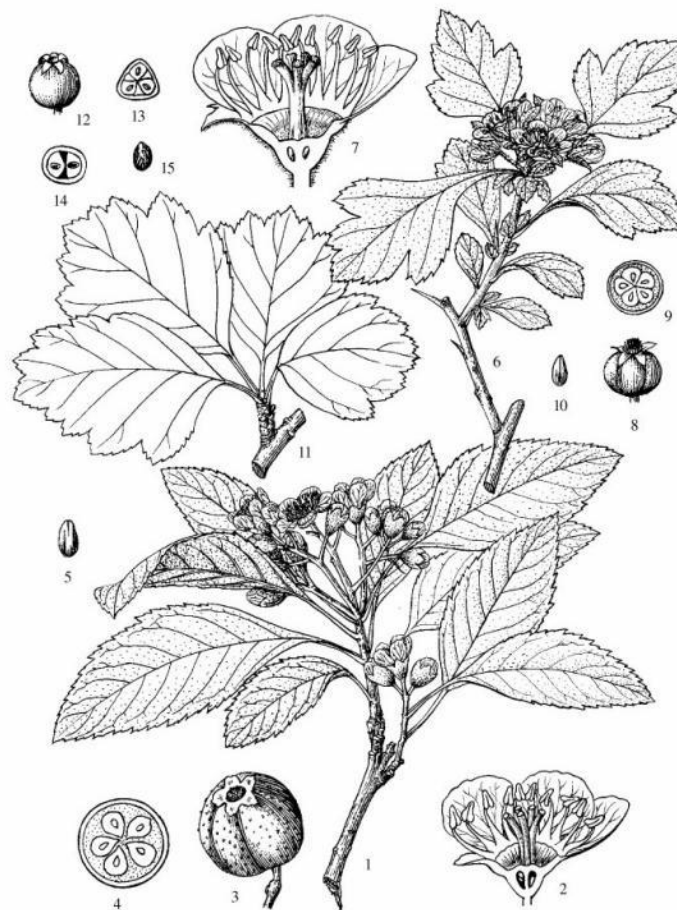
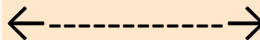


Figure 50. 1-5. *Crataegus scabrifolia* (Franchet) Rehder, 云南山楂 yun nan shan zha. —1. Flowering branch. —2. Flower longitudinal section showing stamens, pistil and longitudinal section of ovary. —3. Fruit. —4. Fruit cross section. —5. Seed. 6-10. *C. cuneata* Siebold & Zuccarini var. *cuneata*, 野山楂 (原变种) ye shan zha (yuan bian zhong). —6. Flowering branch. —7. Flower longitudinal section showing stamens, pistil and longitudinal section of ovary. —8. Fruit. —9. Fruit cross section. —10. Seed. 11-15. *C. wilsonii* Sargent, 少毛山楂 shao mao shan zha. —11. Sterile branch. —12. Fruit. —13, 14. Fruit cross sections. —15. Seed. (FOC 113, 114; FRPS 36: 193, pl. 25. 1974. —吴彰桦 Wu Zhanghua; redrawn by 蔡淑琴 Cai Shuqin).

FIG. 15. *Crataegus mexicana* Moc. & Sesse.: fruiting specimen and parts from Wifford 86-151 (UWO); inflorescence and flower parts from Phipps 5520 & Robertson (UWO). A = calyx lobe, adaxial surface; B = pyrenes; C = fruit, cross-section.

Today, most Eurasian *Crataegus* are possibly derived from Chinese stock. Evidence suggests *Crataegus* is an old genus of possibly early Tertiary age, spreading once or twice into the Americas with two major diversifications and likely late Tertiary extinctions. Except for the supposed relictual taxa, no other North American species appear closely related to Asian/European taxa.



tanacetifolia



pinnatifida



laevigata



wilsonii

Nearly all Eurasian species and North American diploids have 20 stamens.



C. laevigata



C. punctata

North American species are unusual in commonly having stamen counts of 5, 10, 15.
Lower stamen numbers than 20 may result from a loss of stamen whorls.



Crataegus subgenus Americanae:

tools with which to sort out eastern North American hawthorns

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Crataegus

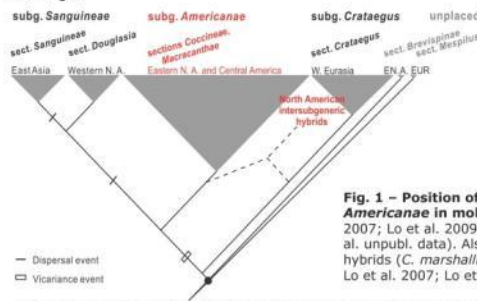


Fig. 1 – Position of Crataegus subgenus Americanae in molecular phylogenies (Lo et al. 2007; Lo et al. 2009a; cf. Zarrei et al. 2015; Liston et al. unpubl. data). Also shown, putative intersubgeneric hybrids (*C. marshallii*, *C. phaenopyrum*, *C. spathulata*; Lo et al. 2007; Lo et al. 2009).

The **infrageneric classification of Crataegus** (Loudon 1838; Schneider 1906; Palmer 1925; Palmer 1946; Phipps 2015) has been largely stable, and most groups recognized (subgenera, sections, series) represent groupings of species that are readily distinguished by features of the leaves, thorns, flowers, and fruits. Moreover, many of these groupings have found support from molecular data (Fig. 1). **Crataegus subgenus Americanae** El-Gazzar is now understood to comprise most of the hawthorns found in eastern North America. These represent almost exclusively just two sections of the genus, *Coccinea* Loudon and *Macracantha* Loudon (Phipps 2015). Almost nothing is known about the cladistic structure within the subgenus, because too few species and individuals have been studied to date. Here we point out the resources that are available, and suggest how they might be used to remedy this situation.

- **Recent treatments of North American hawthorns** make it possible to identify most individuals, if well-prepared specimens of both flowering and fruiting branches are available. Such pigeonholing of collections can make it possible to focus on groups for which there is a plausible, testable null hypothesis of descent from a common ancestor. Phipps' (2015) treatment of the genus in volume nine of *Flora of North America* (Fig. 2) enables most individuals to be identified to section and series, if not always to species. Images of type specimens of many of the taxa in *FNA* are increasingly available on line. Students in the southeastern United States have the additional advantage of a copiously illustrated field guide to the genus (Lance 2014). Both of these resources base their conclusions not only on morphological variation but also on data, where available, on the frequency of hybridization, gametophytic apomixis, and polyploidy in *Crataegus*.
- **Flow cytometry** has made it possible to determine not only the ploidy level of an individual, but also the breeding system by which its seeds are produced (Talent and Dickinson 2005, 2007). Surveys carried out to date suggest that diploids are to be found only among individuals with approximately 20 stamens per flower, whereas those with 10 or fewer stamens have proven to be predominantly tetraploid. Triploids have been found among both morphotypes. These differences are vital to understanding patterns of variation and potential reproductive success because diploids exhibit gametophytic self-incompatibility that breaks down in tetraploids (Dickinson and Phipps 1986; Dickinson et al. 1996).
- **Data from microsatellites** have been used successfully to study population structure and genetic variability in western North American hawthorns. Lo et al. (2009b) distinguished between allo- and autopolyploids, and were able to demonstrate isolation by distance in diploids, but not in closely related tetraploids. Microsatellite data (Lo et al. 2010) have also confirmed inferences about population structure, breeding system, and the taxon concepts applied to hawthorns by earlier workers (Dickinson and Phipps 1985, 1986).
- **Data from sequencing a few to many nuclear and plastid loci** have been essential. Morphological data are unsatisfactory for cladistic analyses of hawthorns (Christensen 1992; Dickinson and Love 1997; Phipps 1999) because they provide few characters with well-defined, discrete states. Sequence data using several well-chosen plastid loci (Lo and Donoghue 2012) have provided reasonably well supported trees (Zarrei et al. 2015) with topologies that are seen in analyses of NGS data (Liston et al. unpubl. data). Analyses of cloned ITS2 sequences have documented the occurrence of hybridization (Zarrei et al. 2014).



Fig. 4a – Crataegus phaenopyrum.
Photo © R. W. Lance



Fig. 2 – Illustration of Crataegus brachycantha (*C. sect. Brevispinae*) by Marjorie Leggett for *Flora North America* vol. 9 (Phipps 2015), in memory of Jane M. Bowles © *Flora North America*.

To date, insights concerning evolution in North American *Crataegus* have been achieved mainly in western North America where the hawthorn flora is less complicated. We suggest, however, that in eastern North America the tools now available can yield important insights into hawthorn systematics and evolution.

- **Do morphologically distinctive groups like C. series Apricae and Lacrimatae** each include diploids? Can a "diploids first" approach provide a robust phylogeny for *C. subg. Americanae*?
- **Are the eastern North American species C. phaenopyrum, C. spathulata, and C. marshallii (fig. 4a-c)** really paleohybrids between western Eurasian subgenus *Crataegus* and North American species?
- **What, if any, morphological variation in Crataegus is adaptive?** Variation in relative allocation of resources to dispersal as opposed to establishment appears to contribute to the relatively wide geographic ranges of allotetraploids (Coughlan et al. 2014).
- **What are the population-genetic consequences of frequent apomixis?** What species concepts are appropriate for use with hawthorns?
- **Finally, what do hawthorns and other Maleae contribute** to the discussion of the relationship between gametophytic apomixis, polyploidy, and diversification?

We gratefully acknowledge financial support from the Natural Sciences and Engineering Research Council of Canada and the Royal Ontario Museum.



Fig. 4b, 4c – Crataegus spathulata and Crataegus marshallii.
Photos © R. W. Lance

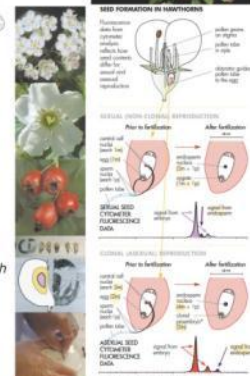


Fig. 3 – Using flow cytometry to determine the breeding system in hawthorns. Illustration from a popular publication (Dickinson and Talent 2007) with artwork by Tara Winterhalt (ROM) and Nadia Talent. Photo credits (top to bottom) T. A. Dickinson, N. Talent, R. Presgrave © ROM, T. A. Dickinson, N. Talent.

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Genetic evaluations for North American *Crataegus* has included flow cytometry as one way of quantifying nuclear DNA in embryo and endosperm; this has revealed ploidy levels of many species but database is very incomplete.

In North America, 6 sections are divided into 32 series. Some species may act as a connecting link between series.

Phipps (2014) established series **Anomalae**, which consists wholly of prospective hybrids involving series **Macracanthae**.

About 240 taxa are generally accepted for North America.

Crataegus asperifolia



In Europe, Knud Christensen (1992) revised *Crataegus* in the Old World to consist of Section **Crataegus** and Nothosection **Crataeguineae**.
He listed 26 species and 16 nothospecies among 5 series, 3 subseries and 5 nothoserries.

18 species are listed for China in *Flora of China*

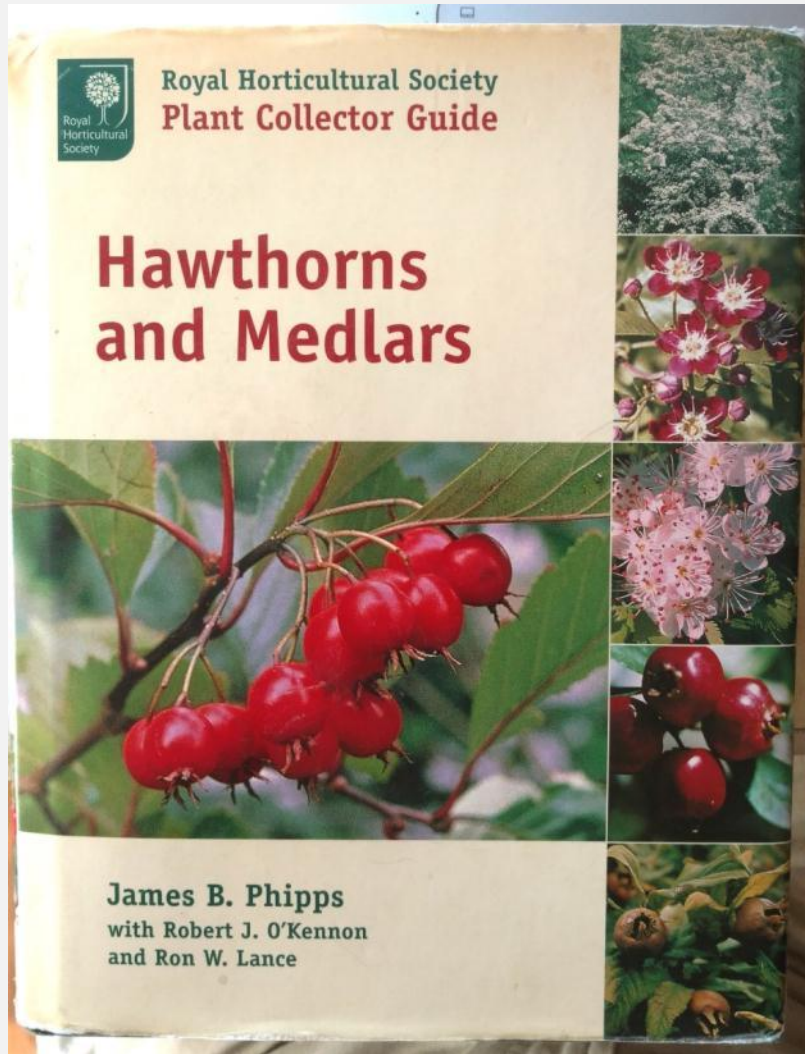
Phipps, et al (1990) listed 14 sections in *Crataegus*; 262 species worldwide, in 35 series.
By 2003, Phipps listed 40 series worldwide



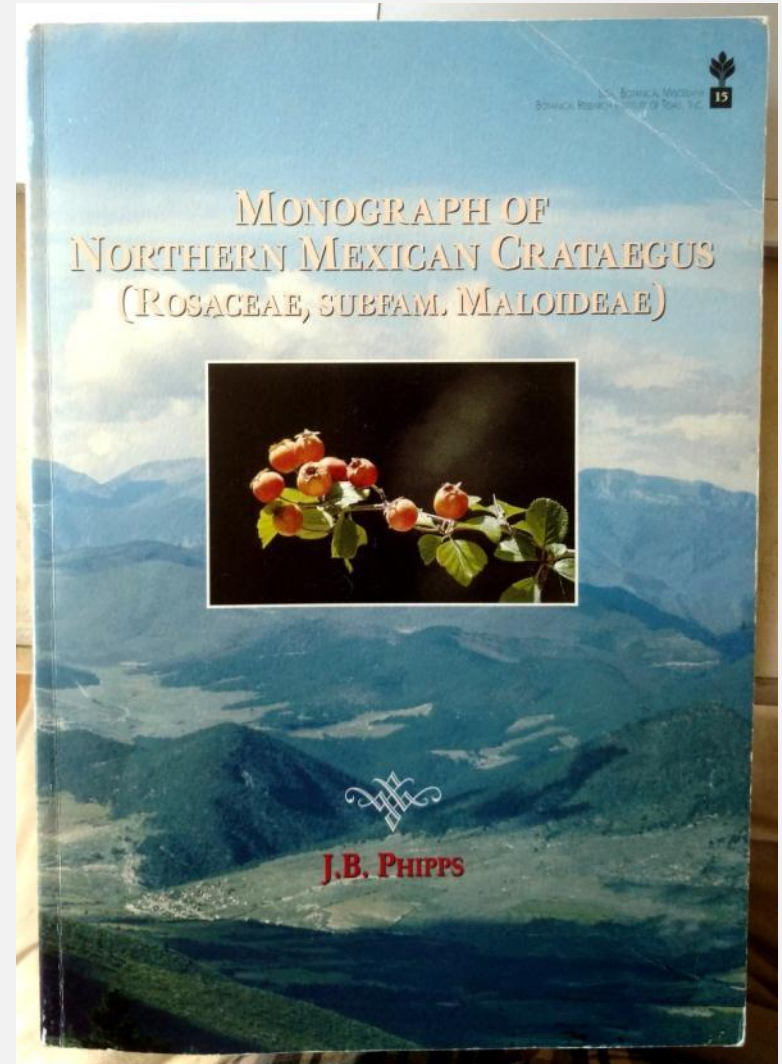
Approximately 300 recognizable *Crataegus* taxa worldwide is a modern general consensus.

Two texts by J.B. Phipps

2003, Timber Press



1997, Sida, Bot Res Inst Tex



Crataegus Sectional and Serial Classifications since 1990

Phipps 1990 (world)
14 Sections; 34 Series;
265 species

Sect Crataegus
 Ser Crataegus
 Ser Pentagynae
 Ser Azaroli
 Ser Pinnatifidae
 Ser Nigrae
 Ser Sanguineae
 Ser Apiifoliae
Sect Mexicanae
 Ser Mexicanae
 Ser Henryanae
Sect Hupehensis
 Ser Hupehensis
Sect Cuneatae
 Ser Cuneatae
Sect Cordatae
 Ser Cordatae
Sect Microcarpae
 Ser Microcarpae
Sect Brevispinae
 Ser Brevispinae
Sect Douglasii
 Ser Douglasii
Sect Virides
 Ser Virides
Sect Lacrimatae
 Ser Lacrimatae
Sect Aestivales
 Ser Aestivales
Sect Crus-galli
 Ser Crus-galli
Sect Parvifoliae
 Ser Parvifoliae
Sect Coccineae
 Ser Coccineae
 Ser Molles
 Ser Bracteatae
 Ser Triflorae
 Ser Tenuifoliae
 Ser Rotundifoliae
 Ser Intricatae
 Ser Pulcherrimae
 Ser Brainerdianae
 Ser Macracanthaceae
 Ser Silvicolae
 Ser Suborbiculatae
 Ser Pruinosaes
 Ser Dilatatae

Phipps 2003 (world)
no Sections shown; 40 Series;
140 species

Ser Crataegus
Ser Pentagynae
Ser Pinnatifidae
Ser Nigrae
Ser Sanguineae
Ser Apiifoliae
Ser Mexicanae
Ser Henryanae
Ser Hupehenses
Ser Tanacetifoliae
Ser Orientales
Ser Cuneata
Ser Cordatae
Ser Microcarpae
Ser Brevispinae
Ser Douglasianae
Ser Cerrones
Ser Purpureofructi
Ser Greggianae
Ser Baroussaneae
Ser Macracanthae
Ser Brainerdianae
Ser Molles
Ser Coccineae
Ser Tenuifoliae
Ser Silvicolae
Ser Pruinosaes
Ser Dilatatae
Ser Pulcherrimae
Ser Intricatae
Ser Rotundifoliae
Ser Lacrimatae
Ser Flavae
Ser Triflorae
Ser Parvifoliae
Ser Virides
Ser Aestivales
Ser Crus-galli
Ser Punctatae
Ser Madrenses

Phipps 2014 (US, Canada)
6 Sections; 31 Series (*34 for world,
if 3 added from Christensen, 1992*)
230 species

Sect Crataegus
 Ser Crataegus
 Ser Apiifoliae
 Ser Cordatae
 Ser Microcarpae
Sect Brevispinae
 Ser Brevispinae
Sect Douglasiae
 Ser Purpureofructus
 Ser Cerrones
 Ser Douglasianae
Sect Sanguineae
 Ser Altaicae
Sect Macracanthae
 Ser Macracanthae
 Ser Anomalae
Sect Coccineae (20 Series)
 Ser Virides
 Ser Crus-galli
 Ser Punctatae
 Ser Aestivales
 Ser Madrensis
 Ser Greggianae
 Ser Molles
 Ser Coccineae
 Ser Tenuifoliae
 Ser Populneae
 Ser Pruinosaes
 Ser Coccinioides
 Ser Pulcherrimae
 Ser Intricatae
 Ser Rotundifoliae
 Ser Parvifoliae
 Ser Bracteatae
 Ser Triflorae
 Ser Apricae
 Ser Lacrimatae

Christensen 1992 (Old World)
1 Section, 5 Series, 3 Subseries,
5 Nothoserries; 26 sp, 16 hybrids

Sect Crataegus
 Ser Crataegus
 Subser Crataegus
 Subser Erianthae
 Subser Dzhairenses
 Nothoser Tanacetitales
 Nothoser Crataegifoliae
 Nothoser Orientagynae
 Nothoser Orientaegus
 Nothoser Crataegynae
 Ser Apiifoliae
 Ser Tanacetifoliae
 Ser Orientales
 Ser Pentagynae

200 Significant *Crataegus* taxa in North America*

<i>aemula</i>	(se US)	<i>georgiana</i>	(se US)	<i>pennsylvanica</i>	(e US, e Can)
<i>aestivalis</i>	(se US)	<i>gilva</i>	(se US)	x <i>peariensis</i>	(n-cen US)
<i>alabamensis</i>	(se US)	<i>glabriuscula</i>	(s-cen US)	x <i>persimilis</i>	(ne US, e Can)
<i>allegheensis</i>	(se US)	<i>gracilior</i>	(Mex)	<i>pexa</i>	(se US)
<i>aprica</i>	(se US)	<i>grandifolia</i>	(Mex)	<i>phaenopyrum</i>	(e US)
<i>aquacervensis</i>	(cen Can)	<i>greggiana</i>	(Tex, n Mex)	<i>phippisii</i>	(nw US, w Can)
<i>ashei</i>	(se US)	<i>harbisonii</i>	(se US)	<i>pinetorum</i>	(se US)
x <i>atrurubens</i>	(cen US)	x <i>harveyana</i>	(cen US)	<i>populnea</i>	(ne US, e Can)
<i>atrovirens</i>	(w Can)	<i>halmesiana</i>	(ne US, e Can)	<i>prona</i>	(ne US, e Can)
<i>ourescens</i>	(Mex)	<i>ignava</i>	(se US)	<i>pruinosa</i>	(e US, e Can)
<i>austromontana</i>	(se US)	x <i>incaedua</i>	(cen US)	<i>pulcherrima</i>	(se US)
<i>baroussana</i>	(Mex)	<i>incilis</i>	(se US)	<i>punctata</i>	(e US, e Can)
<i>beata</i>	(n US, e Can)	<i>integra</i>	(se US)	<i>purpurella</i>	(cen Can)
<i>berberifolia</i>	(se US)	<i>intricata</i>	(e US, e Can)	<i>pyracanthifolia</i>	(se US)
x <i>bicknellii</i>	(ne US)	<i>invicta</i>	(se US)	<i>quaesita</i>	(se US)
<i>biltmoreana</i>	(e US)	<i>iracunda</i>	(se US)	<i>reverchonii</i>	(s-cen US)
<i>boyntonii</i>	(se US)	<i>irrasa</i>	(ne US, e Can)	<i>rivularis</i>	(w US)
<i>brachyacantha</i>	(se US)	<i>jesupii</i>	(n US, e Can)	<i>rivuloadamensis</i>	(w Can)
<i>brainerdii</i>	(ne US, e Can)	<i>johnstonii</i>	(Mex)	<i>rivulopugnensis</i>	(w Can)
<i>brazoria</i>	(Tex)	<i>jonesiae</i>	(e Can)	<i>rosei</i>	(Mex)
<i>brittonii</i>	(se US)	x <i>kelloggii</i>	(cen US)	<i>rubella</i>	(se US)
<i>buckleyi</i>	(se US)	<i>lacrimata</i>	(se US)	<i>rubribacteolata</i>	(w Can)
<i>calpodendron</i>	(e US)	<i>laevigata</i>	(naturalized)	x <i>rufula</i>	(se US)
<i>castlegarensis</i>	(w US, w Can)	<i>lanata</i>	(se US)	<i>rugosa</i>	(e US)
<i>chrysocarpa</i>	(n US, s Can)	<i>lancei</i>	(se US)	<i>saligna</i>	(w US)
<i>coccinea</i>	(e US, e Can)	<i>lanuginosa</i>	(cen US)	<i>sargentii</i>	(se US)
<i>coccinioides</i>	(cen, ne US, e Can)	<i>lassa</i>	(se US)	<i>scabrifa</i>	(ne US, e Can)
<i>cognata</i>	(ne US, e Can)	<i>laurentiana</i>	(n-cen US, e Can)	<i>schuettei</i>	(e US, e Can)
x <i>coleae</i>	(n US)	<i>leonensis</i>	(se US)	<i>segnis</i>	(se US)
x <i>collicola</i>	(e US)	<i>lepida</i>	(se US)	<i>sentata</i>	(se US)
<i>collina</i>	(cen, se US)	x <i>lettermannii</i>	(cen US)	<i>serraticissima</i>	(Mex)
<i>colonica</i>	(se US)	<i>levis</i>	(ne US)	<i>sheila-phippisae</i>	(w Can)
<i>communis</i>	(se US)	x <i>lucorum</i>	(cen US, e Can)	<i>sheridana</i>	(n-cen US, Can)
<i>compacta</i>	(ne US, e Can)	<i>lumaria</i>	(ne US, e Can)	<i>shuswapensis</i>	(w Can)
<i>condigna</i> [= <i>ravenellii</i>]	(se US)	<i>macracantha</i>	(n, w US, s Can)	x <i>sicca</i>	(cen US)
<i>craytonii</i>	(se US)	<i>macrocarpa</i>	(e US, e Can)	<i>sororia</i>	(se US)
<i>crocea</i> [= <i>recurva</i>]	(se US)	<i>magniflora</i>	(ne US, e Can)	<i>spatulata</i>	(se US)
<i>crus-galli</i>	(e US, e Can)	<i>magnifolia</i>	(cen US)	<i>spes-aestatum</i>	(cen US)
<i>cupressocollina</i>	(cen Can, nw US)	<i>margarettae</i>	(e US, e Can)	<i>stolonifera</i>	(ne US, e Can)
<i>cuprina</i>	(Mex)	<i>marshallii</i>	(se US)	<i>straminea</i>	(se US)
x <i>dallasiana</i>	(Tex)	<i>mendosa</i>	(se US)	<i>submolliis</i>	(ne US, e Can)
<i>delawarensis</i>	(ne US)	<i>meridiana</i>	(se US)	<i>suborbiculata</i>	(ne US, e Can)
<i>dispar</i>	(se US)	<i>meridionalis</i>	(se US)	<i>succulenta</i>	(e US, e Can)
x <i>disperma</i>	(ne US)	<i>mexicana</i>	(Mex)	<i>sulfurea</i>	(Mex)
x <i>dispersa</i>	(cen US)	<i>minor</i>	(s-cen US)	<i>tecta</i>	(se US)
<i>dodgei</i>	(cen-ne US, e Can)	<i>mira</i>	(se US)	<i>teres</i>	(se US)
<i>douglasii</i>	(w US, Can)	<i>mohrii</i>	(se US)	<i>texana</i>	(s-cen US)
<i>dumetosa</i>	(cen US)	<i>molliis</i>	(e US)	<i>tracyi</i>	(Tex, n Mex)
<i>egens</i>	(se US)	<i>monogyne</i>	(naturalized)	<i>triflora</i>	(se US)
<i>egregia</i>	(se US)	<i>munda</i>	(se US)	<i>turnerorum</i>	(Tex)
<i>enderbyensis</i>	(w Can)	<i>nananixonii</i>	(Tex)	<i>uniflora</i>	(e US, Mex)
<i>engelmannii</i>	(s-cen US)	<i>neobushii</i>	(se US)	<i>ursopedensis</i>	(nw US, w Can)
<i>erythropoda</i>	(w US)	x <i>nitida</i>	(cen US)	x <i>vailiae</i>	(se US)
<i>exilis</i>	(se US)	x <i>noelensis</i>	(cen US)	<i>venusta</i>	(se US)
<i>extraria</i>	(se US)	x <i>notha</i>	(se US)	x <i>verruculosa</i>	(cen US)
x <i>fecunda</i>	(cen US)	x <i>nuda</i>	(cen US)	<i>viburnifolia</i>	(Tex.)
<i>flabellata</i>	(ne US, e Can)	<i>oaksiana</i>	(ne US)	<i>virella</i>	(e US)
<i>flava</i>	(se US)	<i>okanaganensis</i>	(nw US, w Can)	<i>viridis</i>	(cen, se US)
<i>florens</i>	(se US)	<i>okennonii</i>	(nw US, w Can)	<i>visenda</i>	(se US)
<i>floridana</i>	(se US)	<i>opaca</i>	(se US)	<i>wattiana</i>	(naturalized)
<i>florifera</i>	(e Can)	<i>opima</i>	(se US)	<i>williamsii</i>	(nw US)
<i>fluviatilis</i>	(ne US, e Can)	<i>orbicularis</i>	(w Can)	<i>wootoniana</i>	(sw US)
<i>formosa</i>	(ne US, e Can)	<i>oreophila</i>	(se US)		
<i>fortunata</i>	(e US)	<i>ouachitensis</i>	(s-cen US)		
x <i>fretalis</i>	(ne US)	<i>padifolia</i>	(s-cen US)		
<i>frugiferans</i>	(se US)	<i>pagensis</i>	(cen US)		
<i>furtiva</i>	(se US)	<i>pollens</i>	(se US)		
<i>gattereri</i>	(e US)	<i>palmeri</i>	(s-cen US)		
<i>gaylussacia</i>	(w US, w Can)	<i>parvula</i>	(e US)		

* An additional 40 varietal taxa are treated by J.B. Phipps (2014, Flora of North America)

Additional 50 North American taxa treated by J.B. Phipps
 In Flora of North America (2014) and in
 Monograph of Mexican Crataegus (1997):

annosa (se US)
atrita (se US)
baroussana var. *jamensis* (Mex)
chrysocarpa var. *blanchardii* (ne US, e Can)
chrysocarpa var. *faxonii* (ne US, e Can)
chrysocarpa var. *phaeniceoides* (ne US, e Can)
chrysocarpa var. *pipei* (nw US, w Can)
chrysocarpa var. *praecox* (ne US)
chrysocarpa var. *subrotundifolia* (ne US, s Can)
chrysocarpa var. *vernonensis* (w Can)
chrysocarpa var. *vigintistamina* (ne US, e Can)
coccinea var. *fulleriana* (n-cen US, e Can)
coccinea var. *pringlei* (ne US, e Can)
collina var. *hirtiflora* (s-cen US)
collina var. *sordida* (cen US)
collina var. *succincta* (cen US)
grandifolia var. *potosina* (Mex)
greggiana var. *pepo* (Mex)
x latebrosa (s-cen US)
margarettae var. *angustifolia* (n-cen US, e Can)
margarettae var. *brownii* (cen US)
margarettae var. *meiophylla* (n-cen US)
mollis var. *incisifolia* (cen US)
nelsonii (Mexico)
okanaganensis var. *wellsii* (w US, w Can)
padifolia var. *incarnata* (cen US)
pruinosa var. *dissona* (c, ne US, e Can)
roribacca (se US)
rosei var. *amoena* (Mex)
rosei var. *mahindae* (Mex)
rosei subsp. *parryana* (Mex)
scabrida var. *asperifolia* (ne US, e Can)
scabrida var. *cyclophylla* (ne US, e Can)
scabrida var. *egglestonii* (n-cen US, e Can)
schuettei var. *cuneata* (n-cen US)
schuettei var. *ferrissii* (n-cen US)
schuettei var. *gigantea* (n-cen US)
sheila-hippsiae var. *saskatchewanensis* (cen Can)
x sicca nothovar. *glabrifolia* (cen US)
succulenta var. *gemmosa* (n-cen US)
succulenta var. *michiganensis* (n-cen US, e Can)
succulenta var. *neofluvialis* (cen, e US)
succulenta var. *pisifera* (ne US)
texana var. *dasyphylla* (s-cen US)
tracyi var. *coahuilensis* (Mex)
tracyi var. *madrensis* (Mex)
viridis var. *lanceolata* (se US)
viridis var. *nitens* (cen US)
viridis var. *ovata* (s-cen US)
viridis var. *velutina* (s-cen US)

Additional 17 taxa treated in R.W. Lance (2014):

x brachyphylla (s-cen US)
calpodendron var. *mollicula* (cen US)
calpodendron var. *globosa* (cen US)
calpodendron var. *hispidula* (cen US)
calpodendron var. *microcarpa* (se US)
coccinioides var. *dilatata* (ne US)
crus-galli var. *capillata* (ne US)
crus-galli var. *regalis* (cen, se US)
x danielsii (cen US)
dodgei var. *flavida* (ne US)
intricata var. *horseyi* (n-cen US)
x kellermanii (n-cen US)
reverchonii var. *stevensiana* (Tex)
rigens (se US)
x simulata (cen US)
succulenta var. *pertomentosa* (cen US)
x whittakeri (n-cen US)

Total taxa: 267

Significant *Crataegus* taxa in Europe/Asia:

54 species, 22 nothospecies *

<i>altaica</i>	(cen. Asia)	x <i>aberrans</i>	(Russia)
<i>ambigua</i>	(s. Russia-Turkey)	x <i>albanica</i>	(Greece)
<i>aurantia</i>	(n. China)	x <i>armena</i>	(Armenia)
<i>azarolus</i>	(Mediterr.-Iran)	x <i>bornmuelleri</i>	(Anatolia)
<i>caucasica</i>	(Caucasus)	x <i>browicziana</i>	(Anatolia)
<i>chlorosarca</i>	(ne. Asia)	x <i>chersonensis</i>	(Crimea)
<i>chungtienensis</i>	(sw. China)	x <i>dsungarica</i>	(cen. Asia)
<i>clarkii</i>	(w. Himalayas)	x <i>grignonensis</i>	(cult., France)
<i>cuneata</i>	(se. China, Japan)	x <i>hafniensis</i>	(cult., Denmark)
<i>dahurica</i>	(e. Siberia-Japan)	x <i>killinica</i>	(s. Greece)
<i>dzhairensis</i>	(Usbekistan)	x <i>kyrtostyla</i>	(cen. Europe-Crimea, Baltic)
<i>heldreichii</i>	(Greece-Albania)	x <i>lavellei</i>	(cult., France)
<i>heterophylla</i>	(England, France)	x <i>lambertiana</i>	(Hungary)
<i>heterophylloides</i>	(Asian Turkey)	x <i>macrocarpa</i>	(cen. Europe)
<i>hissarica</i>	(cen. Asia)	x <i>media</i>	(England-Baltic-Italy)
<i>hupehensis</i>	(China)	x <i>peloponnesiaca</i>	(s. Greece)
<i>isfarjamensis</i>	(Pamirs, Tajikistan)	x <i>pseudoazarolus</i>	(Turkmenistan)
<i>jozana</i>	(ne. Asia)	x <i>rubrinervis</i>	(Romania, Turkey)
<i>kansuensis</i>	(China)	x <i>sinaica</i>	(Mediterr.)
<i>karadaghensis</i>	(Crimea)	x <i>tianschanica</i>	(cen. Asia)
<i>kurdistanica</i>	(Iraq-Afghanistan)	x <i>yosgatica</i>	(Turkey)
<i>laevigata</i>	(w., cen. Europe)	x <i>zangezura</i>	(Iran, Caucasia)
<i>longipes</i>	(e. Turkey, Syria)		
<i>maximowiczii</i>	(ne. Asia)		
<i>meyeri</i>	(Ukraine-Iran)		
<i>microphylla</i>	(Turkey-Iran)		
<i>monogyna</i>	(w. Europe-n. Africa)		
<i>necopinnata</i>	(e. Asia)		
<i>nevadensis</i>	(Spain, Morocco)		
<i>nigra</i>	(cen. Europe)		
<i>oresbia</i>	(nw. Yunnan)		
<i>orientalis</i>	(Mediterr.-Turkey)		
<i>pallasii</i>	(Armenia)		
<i>pamiroalaica</i>	(Pamirs, Tajikistan)		
<i>pentagyna</i>	(se. Europe-sw. Asia)		
<i>pinnatifida</i>	(China, Japan, e. Russia)		
<i>pseudoheterophylla</i>	(Turkey-Iran)		
<i>pycnoloba</i>	(Greece)		
<i>remotilobata</i>	(cen. Asia)		
<i>rhipidophylla</i>	(Baltic-France-Turkey)		
<i>russanovii</i>	(Baltic)		
<i>sakranensis</i>	(n. Iraq)		
<i>sanguinea</i>	(Russia-n. China)		
<i>scabrifolia</i>	(se. China)		
<i>shandongensis</i>	(Shandong, e. China)		
<i>shensiensis</i>	(Shanxi, n. China)		
<i>songarica</i>	(Iran-India-nw. China)		
<i>sphaenophylla</i>	(Crimea)		
<i>tanacetifolia</i>	(n. Turkey)		
<i>tangchungchangii</i>	(Guizhou, sw. China)		
<i>theodori</i>	(Turkmenistan)		
<i>trilobata</i>	(Kirgizistan)		
<i>wattiana</i>	(se. Iran)		
<i>wilsonii</i>	(sw. China)		

*compiled from Christensen (1992), Phipps (1990, 2003), Flora of China (1994)

THE END

