

**Infrageneric nomenclature adjustments in *Crataegus* L. (Maleae, Rosaceae)****Roman A. Ufimov** ORCID iD 0000-0002-9753-5858

Austrian Research Centre for Forests, Department of Forest Genetics, Seckendorff-Gudent-Weg 8, 1131 Vienna, Austria and Komarov Botanical Institute, Russian Academy of Sciences, Herbarium of Vascular Plants, ul. Prof. Popova 2, 197376 St. Petersburg, Russian Federation  
[roman.ufimov@bfw.gv.at](mailto:roman.ufimov@bfw.gv.at)

and

**Timothy A. Dickinson** ORCID iD 0000-0003-1366-145X

Royal Ontario Museum, Department of Natural History, Green Plant Herbarium, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6 and Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario, Canada M5S 3B2  
[tim.dickinson@utoronto.ca](mailto:tim.dickinson@utoronto.ca)

**ABSTRACT**

Until recently, classification of *Crataegus* (Maleae, Rosaceae) has been mostly based on morphological data. Phenetic and cladistic approaches allowed taxonomists to establish classifications of the genus at the levels of sections and series, but without revealing clear phylogenetic relationships between these infrageneric groups. Molecular studies suggest the existence of major evolutionary lineages, some of which correspond to previously published subgenera (*C. subg. Americanae* and subg. *Sanguineae*). The present paper aims to complete the subgeneric classification of *Crataegus* by raising *C. sect. Mespilus* and *sect. Brevispiniae* to subgenera. Also, in order to depict current knowledge of the phylogenetic relationships within *C. subg. Sanguineae*, a new *C. sect. Salignae* is described. In addition, we provide a new description of *Crataegus* and keys to distinguish it from other related *Maleae* genera, to determine the subgenera and, within *C. subg. Sanguineae*, to determine the sections. In conclusion, we summarize the current classification of *Crataegus*, excluding nothosubgenera and nothosections, in relation to the phylogeography and leaf venation patterns of the genus. Published on-line [www.phytologia.org](http://www.phytologia.org) *Published on-line www.phytologia.org Phytologia 102(3): 177-199. (Sept 21, 2020). ISSN 030319430.*

**KEY WORDS:** *Crataegus Salignae* sect. nov., *Crataegus Brevispiniae* stat. nov., *Crataegus Mespilus* stat. nov., identification, phylogeography

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*Crataegus* L. (Rosaceae Juss., subfam. Amygdaloideae Arn., tribe Maleae Small) is a well-defined genus including over 200 species (Phipps, 2015) that mainly occur throughout the temperate zone of the Northern Hemisphere in high light intensity habitats with hydrological regimes permitting the growth of woody trees. Some species are cultivated as ornamentals, or for their fruit. The flowers, fruit, and foliage are also the sources of natural health products (Edwards et al., 2012). *Crataegus* taxonomy is considered complicated and has attracted the attention of researchers seeking to provide a solid basis for its classification. J. C. Loudon (1838) proposed the first infrageneric divisions for the genus. He noted how the number of “sorts” of hawthorns had more than doubled since the turn of the century and explicitly chose to throw them “...into natural groups, according to the majority of their points of resemblance...,” rather than preparing a technical key to sections; this was supplied instead as an appendix by the horticulturalist George Gordon (Loudon, 1838). Loudon’s natural classification of *Crataegus* into 14 sections (as now understood) provided the basis for subsequent workers to deal with the rapid increase in the number of hawthorn species described through the first half of the twentieth century.

By the end of 1980s, the number of groups/sections/series had been nearly doubled. Most of the treatments employed a hierarchy with just a single level between genus and species, either sections (Schneider, 1906; Palmer, 1925; Cinovskis, 1971) or series (Rehder, 1940; Palmer, 1952; Kruschke, 1965; Rusanov, 1965). The first multilevel infrageneric classification of the whole genus was published by J. B. Phipps (1983), who grouped series into sections. At that time the division of the genus into two subgenera (*C. subg. Crataegus* and *Americanae* El Gazzar) by El-Gazzar (1980) was, besides being recognized as being based in part on faulty data, a nomenclatural act of little immediate significance. Rather, classification of *Crataegus* at the level of sections and series was well established as a means of organizing the morphological diversity seen within the genus (Christensen, 1992; Lance, 2014; Phipps, 2015). However, while phenetic and cladistic analyses of *Crataegus* morphological data corroborated the existence of groups, the latter failed to demonstrate definitive phylogenetic relationships (Phipps, 1983; Christensen, 1992; Dickinson and Love, 1997; Phipps, 1999).

Since then, molecular phylogenies have demonstrated greater success in elucidating cladistic relationships between sections. Molecular studies (Lo et al., 2007; Lo et al., 2009a; Lo et al., 2009b; Zarrei et al., 2014; Zarrei et al., 2015) revealed the main lines of evolution in the genus, which, it turned out, corresponded partially to the distinctions recognized by El-Gazzar (1980). Lo et al. (2009a) analyzed a sufficiently wide sample of species to be able to delineate clades corresponding not only to El-Gazzar's subgenera but also to the one subsequently described as *C. subg. Sanguineae* Ufimov (Ufimov, 2013). We have completed the subgeneric classification of *Crataegus* by raising two further sections to subgenera. In addition, in recognition of the cladistic relationships within *C. subg. Sanguineae* (Zarrei et al., 2015) we describe one further section of the genus.

## OBJECTIVES

We provide a comprehensive subgeneric classification for the genus *Crataegus* in order to facilitate communication and help focus research attention on the most challenging taxonomic problems, such as relationships within *C. subg. Americanae* and *Crataegus*. In addition, we also describe *C. sect. Salignae* T.A.Dickinson & Ufimov sect. nov. in order to accommodate *C. ser. Cerrones* J.B.Phipps in a way that reflects its position within *C. subg. Sanguineae*, namely as sister group to *C. sect. Douglasianae* Rehder ex C.K. Schneid.<sup>1</sup> and sect. *Sanguineae* Zabel ex C.K.Schneid. Finally, we interpret this classification in light of the phylogeny on which it is based, using data from leaf venation that may be relevant to the future interpretation of fossils, and the (limited) fossil data that are currently available.

## MATERIALS AND METHODS

We illustrate the phylogenetic relationships between the infrageneric groups that we discuss using a result from an earlier work (Fig. 1; Lo and Donoghue, 2012) and data from a recent study (Fig. 2; Liston et al. in prep.; used with permission) in which whole plastome DNA alignments were obtained from 14 diploid *Crataegus* accessions and aligned to the *Malus ×domestica* 'Golden Delicious' plastome sequence (Velasco et al., 2010). Relationships between these accessions were summarized as a maximum likelihood tree (RAxML; Stamatakis, 2014), rooted using the apple reference plastome. This tree was then collapsed to show just the relationships between five subgenera (and the three sections in *C. subg. Sanguineae*; Table 1) that are of interest here, using the function **makeCollapsedTree** in the R package TREESPACE (Jombart et al., 2017). We project this tree onto a north polar projection of a

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<sup>1</sup> According to Art. 21.2 and Art. 32.1 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018) the sectional name *Douglasii* was not validly published by Loudon (1838: 823) as it is a noun in the genitive singular. The articles mentioned do not allow simple correction, so the earliest valid publication of a section containing *C. douglasii* is that of C. K. Schneider (1906: 775), and his name is the correct one that we use here.

tectonic plate reconstruction for 37 Ma produced using the ODSN Plate Tectonic Reconstruction Service (Hay et al., 1999; <https://www.odsn.de/odsn/services/paleomap/paleomap.html>) in order to show informally the present-day biogeographic relationships between the terminals. 37 Ma was chosen as the approximate time of diversification of the ‘Crataegus’ clade at Eocene-Oligocene boundary (Lo and Donoghue, 2012).

Although the main purpose of this paper is to publish new names needed to complete the infrageneric classification of *Crataegus*, we also wish to document leaf venation, a little-studied aspect of morphological variation across the subgenera, and one that is critical for identification of fossil leaf material. Leaves from specimens in the Green Plant Herbarium of the Royal Ontario Museum (TRT; Table 1) were imaged with x-rays on Kodak Industrex M100 x-ray film using a Hewlett Packard Faxitron Model K43805 (Ross, 2008) and digitized from the x-ray negative using a Hasselblad H5D-200c MS or similar camera. The original x-ray film images are negatives, with veins in white against a bluish background. “Positive” images (venation dark, against a light background) were produced using the “negative” functions of image processing software for the Macintosh™ computer (ToyViewer v5.5, Ogihara, 2014; all other images reproduced here were produced using Adobe PhotoShop™ and Pixelmator Pro™). Access to an online taxonomic database of these and additional downloadable *Crataegus* leaf venation images (Dickinson et al., 2020) is made possible by MorphoBank (O’Leary and Kaufman, 2011, 2012).

We also refer to our own field observations and the field photographs of others, as well as to published illustrations, in order to incorporate additional morphological data, notably concerning the proleptic or sylleptic growth of lateral short shoots in the ‘*Amelanchier*+*Crataegus*’ clade (clade A in Fig. 1). Sylleptic and proleptic growth are understood as they are described by Hallé et al. (1978, p. 42 ff.).

## RESULTS

The genera of the Maleae together with the genus *Gillenia* Moench form a clade (Fig. 1; Potter et al., 2007; Lo and Donoghue, 2012) that can be referred to as supertribe Pyrodae C.S.Campb., R.C.Evans, D.R.Morgan & T.A.Dickinson. Within the Pyrodae fruit type is heterogeneous, the four basal genera having dry dehiscent fruits, while the remainder of this clade (subtribe Malinae Reveal) has fleshy fruits developing from flowers that are epigynous (perigynous in *Dichotomanthes* Kurz; Rohrer et al., 1994). Within the Malinae, composite fruit walls (lignified endocarp, fleshy epicarp, as in *Prunus* L.) occur repeatedly, so as to make up tribe Crataegeae Koehne (Kalkman, 2004; Kalkman excludes *Dichotomanthes* from the Crataegeae on the grounds that its fruit is an achene partially enclosed by an accrescent hypanthium). However, the Crataegeae (named genera with black dots, Fig. 1) is clearly not monophyletic as the component genera are distributed in each of Malinae clades A, B, and C (Fig. 1) as well as in the two genera found in trichotomies (*Pyracantha* M.Roem., *Osteomeles* Lindl.; Fig. 1). The remaining genera (not listed in Fig. 1) in clades A<sup>2</sup>, B<sup>3</sup>, and C<sup>4</sup> have berry-like fruits (the *Cydonia* group and tribe Maleae in Kalkman, 2004).

All the subgenera of *Crataegus* are monophyletic (Fig. 2; Liston et al., in prep.). *Crataegus* subg. *Brevispiniae* (Beadle) Ufimov & T.A.Dickinson and *Mespilus* (L.) Ufimov & T.A.Dickinson are monotypic; *C.* subg. *Americanae* and *Sanguineae* were each represented by multiple accessions in the original analysis by Liston et al. (in prep.). *Crataegus* subg. *Crataegus* has been shown to be

<sup>2</sup> *Amelanchier* Medik., *Malacomeles* (Decne.) Decne., *Peraphyllum* Nutt.

<sup>3</sup> *Aria* (Pers.) Host, *Aronia* Medik., *Chaenomeles* Lindl., *Cydonia* Mill., *Docynia* Decne., *Docyniopsis* Koidz., *Eriolobus* (DC.) M.Roem., *Malus* Mill., *Pourthiaea* Decne., *Pseudocydonia* (C.K.Schneid.) C.K.Schneid.

<sup>4</sup> *Cormus* Spach, *Eriobotrya* Lindl., *Heteromeles* M.Roem., *Micromeles* Decne., *Photinia* Lindl., *Pyrus* L., *Rhaphiolepis* Lindl., *Sorbus* L. s. str.

monophyletic elsewhere (Lo et al., 2010; Lo and Donoghue, 2012). *Crataegus* ser. *Cerrones* has been shown to be monophyletic and sister to one or both of *C.* sect. *Douglasianae* and *Sanguineae* (Lo et al., 2010; Zarrei et al., 2014), and so warrants placement in *C.* subg. *Sanguineae* in its own section, *C.* sect. *Salignae*. The subgenera we recognize can also be seen to differ to some extent in their patterns of secondary venation (Fig. 3). The festooned semicraspedodromous secondary venation of *C.* subg. *Brevispinae* (*C. brachyacantha*; Fig. 3a) is also seen in *Hesperomeles* Lindl. (online image, Kelly, 2008), the sister genus of *Crataegus* (Li et al., 2012; Liu et al., 2020). *Crataegus* subg. *Mespilus* appears to be unique in its reticulodromous secondary venation (*C. germanica*; Fig. 3b). The remainder of the genus exhibits mostly craspedodromous or semicraspedodromous secondary venation (Fig. 3c–j; Dickinson et al., 2020). Sylleptic development of short shoot vegetative increments occurs not only in *Amelanchier* (Fig. 8a, Phipps 2016a) but apparently also in *Malacomeles* (Velazco-Macias, 2014) and *Peraphyllum* (Boone, 2002–onwards; Campbell, 2015), in that these latter images appear to show two coeval shoots developing, one reproductive and more advanced, and the other vegetative.

### TAXONOMY

We provide a new description for *Crataegus* in the currently accepted circumscription as well as descriptions of the new subgenera and section. We also provide keys to distinguish *Crataegus* from some other genera in Maleae, a key to determine subgenera, and a key to determine sections in *C.* subg. *Sanguineae*.

***Crataegus* L., Sp. Pl., 1: 475. 1753, nom. cons.** (Talent et al., 2008; Brummit, 2011; Barrie, 2011).

= *Mespilus* L., Sp. pl., 1: 478. 1753.

= *Oxyacantha* Medik., Phil. Bot., 1: 150. 1789.

= *Azarolus* sensu M.Roem., Fam. nat. syn. monogr. 3: 132. 1847, non *Lazarolus* Medik., Phil. Bot., 1: 134. 1789.

= *Halmia* Medik. ex M.Roem., Fam. nat. syn. monogr. 3: 134. 1847.

= *Anthomeles* M.Roem., Fam. nat. syn. monogr. 3: 140. 1847.

= *Phaenopyrum* M.Roem., Fam. nat. syn. monogr. 3: 152. 1847. ≡ *Gymnomeles* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn, 1859: 111. 1860, nom. illeg. ≡ *Phalacros* Wenz., Linnaea, 38, 1: 164. 1874, nom. illeg.

= *Polyomeles* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn, 1859: 111. 1860.

= *Symphymeles* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn, 1859: 111. 1860.

Type (lectotype, designated by W. W. Eggleston in Britton and Brown, 1913: 294): *C. oxyacantha* L. nom. utique rej. (Lambinon, 1981; Brummitt, 1986; Voss, 1987) (= *C. rhipidophylla* Gand.).

Shrubs and polycormic or monocormic trees up to 10–15 m tall. Resting buds subglobose or ovoid, sometimes subconical, rarely conical, indumentum more or less the same as on the twigs. Twigs of the current year epruinose, rarely pruinose, glabrous or more or less pubescent to densely tomentose, lanate or villous. Young twigs (of the previous years) variable in color from grey, brown and reddish to yellow and orange. Mature bark greyish or brownish, sometimes more or less orange, platelike, exfoliating in small, angular scales. Aphyllous thorns present at least on some shoots, variable in length (1–10 cm), curvature, stoutness and color. Spine-tipped, leafy short shoots (leafy thorns, as in *Pyracantha*, Fig. 26 in Phipps, 1983) present or absent. Branched thorns may be present on mature trunks. Long (extension) shoots present, sterile short shoots present or not. Leaves deciduous, sometimes winter-persistent, alternate, in spiral phyllotaxy, simple, separated by internodes 2–3 cm long on long shoots, more or less crowded on short shoots (internodes often < 0.5 cm), glabrous or pubescent, microphylls, notophylls, or mesophylls (for the explanation of terms see Ellis et al., 2009); stipules caducous or persistent, free, falcate, margins entire to finely serrate, glandular or eglandular; petioles present, sometimes glandular; leaf blades often more variable in shape on long shoots than on short shoots, unlobed or more or less lobed to deeply incised, more or less narrowly to broadly ovate, elliptic, or obovate, margins entire, serrate, crenate, or dentate, teeth sometimes gland-tipped; secondary venation reticulodromous or weakly brochidodromous,

craspedodromous or semi-craspedodromous, in some cases approaching camptodromous. Inflorescence terminal (on few-leaved short flowering shoots, which arise from the resting buds on short, long, or flowering shoots of previous year), 1–50-flowered, sympodial, corymbose, umbellate, or flowers solitary; bracts sometimes present, leafy; bracteoles caducous or persistent, symmetric or falcate/stipuliform, with entire or glandular-serrate/dentate margin; pedicels present, pedicels and peduncles glabrous or pubescent, their indumentum similar to that of the twigs. Hypanthium more or less obconic, constricted apically, glabrous or pubescent, its indumentum usually similar to that of the inflorescence, but can be quite different. Indumentum of young twigs, leaves, inflorescence, and hypanthium tends to change over time and can disappear when fruits are mature. Inner surface of the free portion of the hypanthium nectar-secreting. Perianth and androecium epigynous, inserted on the rim and inner portion of the free portion of the hypanthium; ovary inferior; sepals 5, triangular, entire or more or less glandular-serrate/dentate, usually persistent, rarely caducous (e.g. *C. phaenopyrum* (L.f.) Medik.), usually shorter than the petals; petals 5, white, rarely pale cream or pinkish, more or less orbicular or elliptic, base barely clawed, apex rounded or notched; stamens 5–45, usually shorter than petals, anthers variable in color from white, cream, and pink to reddish, or purple; carpels 1–5 (–6), adnate to hypanthium and more or less fully connate; styles 1–5 (–6), free or more or less connate/touching, usually persistent, attached to pyrenes apically or more or less laterally, exerted or emerging through hypanthial disc; ovules 2 per locule, superposed, with an obturator at the bases of the two funiculi. Both ovules are fertile, but only the micropyle of the lower one is adjacent the obturator, so that only very exceptionally (<< 0.1%) is the upper ovule fertilized and also develops into a seed. Mature fruits ellipsoidal, orbicular, or pyriform polypyrinous drupes, up to 4 cm in diameter, varying in color from brown, greenish, yellow and orange, to red, bluish/purplish, and black, glabrous or pubescent; grit cells absent to abundant; hypanthial opening narrow to broad, mature hypanthial disc well developed, undulating and firm or reduced to a remnant disc, pyrene apices covered by its tissue or not so, and exposed; carpels woody; pyrenes 1–5 (–6), with one seed each, dorsally grooved, plane or more or less pitted/eroded/excavated/sulcate on ventral/radial surfaces, hypostyle glabrous or pubescent.

**Key to genera in Rosaceae tribe Maleae with fruits drupaceous or drupe-like** (*Crataegus*, *Chamaemeles*, *Dichotomanthes*, *Hesperomeles*, *Osteomeles*, *Cotoneaster*, *Pyracantha*) **and, within the ‘Amelanchier+Crataegus’ clade (Fig. 1, clade A), the other genera lacking such fruits** (*Amelanchier*, *Peraphyllum*, *Malacomeles*). Clade attributions (A–C) refer to the phylogeny based on plastid loci (Fig. 1 here; left side of Fig. 1 in Lo and Donoghue, 2012).

1. Flowers perigynous. Ovary superior, unicarpellate, free from hypanthium, but hypanthium persistent and fleshy at maturity. Fruit an achene but appearing functionally drupaceous because of the accrescent hypanthium. 2 collateral ovules per locule, 1 seed per achene. Thorns absent. China.  
..... ***Dichotomanthes* (clade B)**
- Flowers epigynous. Ovary inferior (hypanthial), 1–5 (–6)-carpellate. Fruit fleshy. Thorns present on at least some shoots or absent. ....2
2. Leaves compound, pinnate, leaflets entire. Ovary inferior, 1–5-carpellate, 1 ovule per locule. Fruit drupaceous. China and Pacific islands. .... ***Osteomeles* (in a trichotomy with clades B and C)**
- Leaves simple crenate, serrate, dentate, or entire, lobed or unlobed. ....3
3. Lateral inflorescence-bearing short shoots develop sylleptically. Fruits baccate, endocarp not lignified. Ovary inferior or semi-inferior, carpels 1–5 with additional false partitions, thus fruit 4–10-loculed. ....4
- Lateral inflorescence-bearing short shoots may develop proleptically. Fruits drupaceous, seeds contained within thick-walled, lignified endocarps (pyrenes) that are themselves enclosed in a more or less fleshy pericarp. ....6
4. Leaves drought-deciduous or persistent. Thorns absent. Texas, Mexico, Central America.  
..... ***Malacomeles* (clade A)**
- Leaves winter-deciduous. ....5

5. Leaves faintly and scarcely serrate, subentire or entire. Leaf blades more or less narrowly elliptic to oblanceolate or linear. Inflorescence reduced, few-flowered. Carpels 2–3. Mature fruits yellow-orange. Western USA. .... ***Peraphyllum* (clade A)**  
 — Leaves serrate or dentate, sometimes doubly, often only in the distal 1/2 or 1/3, rarely almost entire. Leaf blades elliptic, oval, ovate, obovate, more or less oblong, or orbiculate. Inflorescence usually 5–15-flowered, rarely number of flowers is less than 5. Carpels 2–5. Mature fruits pinkish or brownish to bluish, purple or black. Eurasia, north Africa, North America. .... ***Amelanchier* (clade A)**
6. Ovary unicarpellate, with 2 collateral ovules, 1 seed per pyrene (achene). Mature fruits white. Madeira. .... ***Chamaemeles* (clade B per Li et al., 2012)**  
 — Carpels (1–) 2–5. Mature fruits orange or red to black. .... 7
7. Leaves entire. Carpels not connate, basal 2/3 adnate. 2 collateral ovules per locule, 1 seed per pyrene. Thorns absent. Eurasia. .... ***Cotoneaster* (clade C)**  
 — At least some leaves more or less crenate-dentate or serrate, rarely subentire. Thorns present. .... 8
8. Ovules usually 1 per locule, rarely 2, if 2 then superposed, 1 seed per pyrene. Central and South America. .... ***Hesperomeles* (clade A per Li et al., 2012; Liu et al., 2020)**  
 — Ovules usually 2 per locule. .... 9
9. Leaves deciduous, sometimes winter-persistent. Carpels mostly connate and adnate. Ovules superposed, pyrenes typically single-seeded. North America, Eurasia. .... ***Crataegus* (clade A)**  
 — Evergreen. Carpels half adnate and not connate. Ovules collateral. Eurasia. .... ***Pyracantha* (unresolved; in a trichotomy with clade A and the clade comprising *Osteomeles* and clades B and C)**

***Crataegus* subg. *Mespilus* (L.) Ufimov & T.A.Dickinson, stat. nov.**

Basionym: *Mespilus* L., Sp. pl. 1: 478. 1753. ≡ *Crataegus* sect. *Mespilus* T.A.Dickinson & E.Y.Y.Lo in E.Y.Y.Lo, Stefanović et T.A.Dickinson, Syst. Bot., 32, 3: 609. 2007.

Type: *M. germanica* L. (lectotype, designated by M. L. Green in Hitchcock and Green, 1929: 158).

Single species *C. germanica*. This species appears to be sister to the rest of the genus, or to all of the genus except for *C. brachyacantha* (Lo et al., 2007), or to all of the genus except for *C.* subg. *Crataegus* (Liu et al., 2019; Liu et al., 2020; Liston et al., in prep.).

***Crataegus* subg. *Brevispinae* (Beadle) Ufimov & T.A.Dickinson, stat. nov.**

Basionym: *Crataegus* [unranked] *Brevispinae* Beadle in Small, Fl. S.E. U.S.: 532. 1903.

≡ *Crataegus* sect. *Brevispinae* (Beadle) C.K.Schneid., Ill. Handb. Laubholz., 1: 791. 1906.

≡ *Crataegus* ser. *Brevispinae* (Beadle) Rehder, Man. Cult. Trees, ed. 2: 366. 1940.

Type: *C. brachyacantha* Sarg. & Engelm.

Single species *C. brachyacantha*. This species appears to be sister to the rest of the genus, or to all of the genus except for *C. germanica* (Lo et al., 2007), or to all of the genus except for *C.* subg. *Crataegus* (Liston et al., in prep.).

**Key to subgenera in *Crataegus***

1. Leafy thorns present. Aphyllous thorns less than 15 mm long. Stipules usually persistent, rarely caducous (*C. germanica*), eglandular or inconspicuously glandular. Leaf margins serrate, crenate or entire. .... 2  
 — Leafy thorns absent. Aphyllous thorns usually more than 15 mm long, often more than 20 mm long. Rarely thorns can bear buds and reduced, caducous leaves. Stipules caducous or persistent, if persistent then conspicuously glandular-serrate. Leaf margins serrate; secondary venation craspedodromous or semicraspedodromous; teeth with principal veins. .... 4
2. Leaf blades of short and flowering shoots more or less lobed, sometimes only shallowly to almost unlobed (e.g. *C. laevigata* (Poir.) DC. Fig. 3d, *C. cuneata* Siebold & Zucc.), very rarely unlobed (e.g. *C. scabrifolia* (Franch.) Rehder), margin more or less serrate and never entire; teeth usually with a principal vein (Fig. 3c, d). Leaf blades of long shoots usually more or less lobed, very rarely unlobed. Each lobe with a secondary vein conspicuously reaching its apex; other secondary veins often reach

apices of teeth, especially in the distal 1/3 of lamina; single secondary veins leading to nadirs of sinuses present (secondary venation craspedodromous or semicraspedodromous; Fig. 3c, d). Mature fruits varying in color from yellow to red, purple, and black. Pyrenes sulcate or plane on ventral/radial surfaces.

.....**subg. *Crataegus***  
 — Leaf blades of short and flowering shoots unlobed with finely crenate-serrate, serrate or entire margins, their secondary veins not conspicuously reaching the apices of teeth, but rather forming nodes just below the sinuses between them. Leaf blades of long shoots unlobed or more or less lobed; if lobed, secondary veins reaching the tips of lobes and teeth sometimes present, single secondary vein leading to nadirs of sinuses sometimes present. Mature fruits brown or bluish/purplish black. Pyrenes plane on ventral/radial surfaces. ....3

3. Aphyllous thorns recurved. Resting buds subglobose or ovoid. Stipules more or less persistent, especially on long shoots. Leaves glossy; leaf blades of flowering and short shoots up to 3 cm long. Teeth of leaves of flowering and short sterile shoots present, lacking a principal vein (Fig. 3a); secondary venation festooned semicraspedodromous. Inflorescence multi-flowered. Sepals considerably shorter than petals. Post-mature petals more or less orange. Stamens 20. Mature fruits up to 15 mm in diameter, bluish or purplish black, hypanthial opening narrow (10–30% of width of fruit); pyrenes not covered by tissue of hypanthial disc. ....**subg. *Brevispinae***

— Aphyllous thorns straight. Resting buds conic. Stipules caducous. Leaves not glossy, abaxially pilose; leaf blades up to 12 cm long. Teeth of leaves of flowering and short sterile shoots absent (Fig. 3b), or present with a small principal vein; secondary venation reticulodromous. Inflorescence 1–2-flowered. Sepals are equal or longer than petals. Post-mature petals pale brown. Stamens 20–40. Mature fruits up to 40 mm in diameter, brown, hypanthial opening wide (50–90% of width of fruit); pyrenes covered by tissue of hypanthial disc unless fruit cracks. ....**subg. *Mespilus***

4. Considerable proportion of stipules persistent, especially on long shoots. Stipuliform, falcate bracteoles present. Leaves lobed to varying extents; secondary veins of leaves of flowering and short sterile shoots leading to sinus nadirs present (Fig. 3h) or not (Fig. 3e–g, i, j). Pyrenes strongly pitted on ventral/radial surfaces. ....**subg. *Sanguineae*** (sect. *Sanguineae*)

— Stipules usually caducous, but sometimes persistent on long shoots. Stipuliform, falcate bracteoles absent. Secondary veins of leaves of flowering and short sterile shoots leading to sinus nadirs absent. Pyrenes plane, eroded or pitted on ventral/radial surfaces. ....5

5. Mature fruits black, purplish black or purple. ... **subg. *Sanguineae*** (sect. *Douglasianae*, sect. *Salignae*)

— Mature fruits usually red, sometimes yellow, orange, pinkish or green. ....**subg. *Americanae***

### ***Crataegus* sect. *Salignae* T.A.Dickinson & Ufimov, sect. nov.**

Type: *Crataegus saligna* Greene

Shrubs or small trees up to 5 m tall; thorns 15–30 (40) mm long, more or less straight, slender, 1.5–3.5 mm in diameter at the base; young shoots of the current year glabrous or sparsely pubescent, mature shoots of the previous year vary from reddish brown to red purple, older branches gray or copper-colored. Leaf blades of flowering and short shoots (notophylls-) microphylls, vary from lanceolate and oblanceolate to more or less elliptic or rhombic-elliptic, 20–60 mm long and (10)15–40 mm wide, glabrous at maturity, unlobed (Fig. 3j) or sparsely lobed, sinuses shallow. Inflorescence 5–10(15)-flowered. Pedicels, peduncles and hypanthia glabrous. Sepals entire, 1.0–1.5 mm long, stamens 20, anthers cream, and styles 4–5 (*C. saligna*), or sepals more or less glandular-serrate, 3.5–4.0 mm long, stamens 10, anthers pink, and styles 3–5 (*C. erythropoda* Ashe, *C. rivularis* Nutt. ex Torr. & A.Gray). Fruit purple to black (diameters of dry fruits in mm: *C. saligna*, 5–6.5; *C. rivularis*, 6.5–8.5; *C. erythropoda*, 7.5–8.5).

*Crataegus* sect. *Salignae* is distinguished by its fruit color from the red-, orange-, and yellow-fruited members of *C.* sect. *Sanguineae* (*C.* ser. *Sanguineae* (Zabel ex C.K.Schneid.) Rehder and ser. *Altaicae* J.B.Phipps; not *C.* ser. *Nigrae* (Loudon) Russanov). It differs from black-fruited *C.* ser. *Nigrae* and *C.* sect. *Douglasianae* in thorn diameter, leaf shape, and geographic distribution.

### Key to sections in *Crataegus* subg. *Sanguineae*

1. Stipules usually persistent. Inflorescence with falcate bracteoles at the base of lower branches. Mature fruits vary in color from yellow, orange, and red to purple or black. Pyrenes strongly pitted on ventral/radial surfaces. Plants native to Eurasia. ....**sect. *Sanguineae***  
 — Stipules usually caducous, but sometimes persistent on long shoots. Inflorescence without bracteoles at the base of lower branches. Mature fruits purple, purplish black or black. Pyrenes more or less plane, shallowly pitted or excavated on ventral/radial surfaces. Plants native to North America. ....2
2. Thorns slender. Subterminal leaf blades of flowering shoots usually more than 2 times as long as wide. Rocky Mountains and southwestern United States. ....**sect. *Salignae***  
 — Thorns stout, conic. Subterminal leaf blades of flowering shoots usually less than 1.5 times as long as wide. Pacific Northwest and disjunct in the Upper Great Lakes Basin. ....**sect. *Douglasianae***

Though E. L. Greene (1896) initially noted a probable affinity to *C. rivularis*, *C. saligna* was considered closely related to *C. brachyacantha* by E. J. Palmer (1925) and included in sect. *Brevispinae*, which was accepted by Phipps et al. (1990). Although field observations and a cladistic analysis (of morphological data) led Phipps (1999) to observe that *C. saligna* is allied to *C. rivularis* and *C. erythropoda*, he refrained from concluding that the North American black-fruited *Crataegus* species are monophyletic because of the limited sample of red-fruited out-group species in the analysis. At the same time, however, *C. erythropoda* was the sole and type species of ser. *Cerrones* (Phipps, 1998: 1872) when first published. Subsequently, however, Phipps et al. (2003) included *C. rivularis* in ser. *Cerrones*. Analyses of microsatellite (Dickinson et al., 2008) and a combination of nuclear and plastid loci sequence data (Lo et al., 2009a) led to enlarging ser. *Cerrones* further by adding *C. saligna*, the series thus comprising all three black-fruited species found in the southern Rocky Mountains (Colorado, Idaho, New Mexico, Utah, Wyoming) and adjacent states (Arizona, Nevada; Dickinson et al., 2008). This concept of the series was then used in Flora of North America (Phipps, 2015).

*Crataegus* sect. *Salignae* includes only one series — ser. *Cerrones* — and forms a clade within *C.* subg. *Sanguineae* sister to members of *C.* sect. *Douglasianae* and *Sanguineae* in phylogenetic analyses of DNA sequence variation in ITS2 (Zarrei et al., 2014), cpDNA loci (Fig. 2; Zarrei et al., 2015; Liston et al., in prep.), and 245 single-copy nuclear loci (Liston et al., in prep.). The section appears to be an agamic complex, in which *C. saligna* is the diploid taxon, and *C. rivularis* and *C. erythropoda* are apomictic allotetraploids whose pollen parents are tetraploid members of red-fruited *C.* subg. *Americanae* (thorns long, calyces abundantly toothed, 10 stamens per flower). The allotetraploids are thus morphologically intermediate in some respects between *C. saligna* and their *C.* subg. *Americanae* parents (Table 2 in Liston et al., in prep.). Nevertheless, all three species demonstrate high morphological affinity (in thorn length and diameter, color of mature twigs and fruits, shape of leaves) that can be easily observed in the field. We do not support the idea of separating *C. rivularis* and *C. erythropoda* from *C. saligna* into nothotaxa of any rank, although we cannot exclude such possibility in future work. Therefore, in order to maintain nomenclatural stability, we chose to describe a new section with an orthospecies *C. saligna* as the type rather than publish a name at new rank.

## DISCUSSION

Potter et al. (2007) inferred a North American origin for the Rosaceae as a whole but pointed out the need for detailed studies of the phylogeny and phylogeography of the different tribes of the family. The predominantly Holarctic distributions of large genera in the Maleae (and not just *Crataegus*, Fig. 2) makes it clear that the history of these genera involves one or both of the Bering Land Bridge (BLB) and the North Atlantic Land Bridge (NALB; terminology as in Graham, 2018). Graham uses the large, cosmopolitan non-Rosaceous genus *Ilex* L. as an exemplar of a group for which some data are equivocal, but nevertheless support migration across the BLB and from North America into South America, aided in part by its fleshy red fruits and concomitant bird and mammal dispersal much as is known to occur in



hawthorns (reviewed in Dickinson, 1985). Comparisons can also be made with other fleshy fruited genera like *Toxicodendron* Mill. (Jiang et al., 2019) and *Viburnum* L. (Landis et al., 2020). We envision roles for land bridges for hawthorns, rather than (extreme) long distance dispersal (LDD), because simulations (Nathan, 2006) and observational studies (on *Prunus*; Jordano, 2017) suggest that short to medium distance (up to 10s of km) dispersal events will be much more frequent than ones that are 10 to 100 times longer. Short to medium distance dispersal events also seem more likely to deposit seeds within habitats permitting offspring to germinate and establish. Moreover, given the gametophytic self-incompatibility found in the Maleae diploids (Dickinson et al., 2007), successful spread must have depended on multiple dispersals to any given patch of suitable habitat, in order for newly established individuals to be able to reproduce successfully.

Recent molecular phylogenies of similarly fleshy-fruited *Amelanchier* (Burgess et al., 2015), *Malus* (Nikiforova et al., 2013), and *Sorbus* s. str. (Li et al., 2017) each show sister-group relationships across the BLB. The *Amelanchier* results suggest a North American origin of the genus followed by expansion of two sister clades, one in western North America (clade A; Burgess et al., 2015) and the other, crossing the BLB, into Eurasia (clade O; Burgess et al., 2015). The earliest (Eocene) divergence in *Malus* is between North American *M.* sect. *Chloromeles* (Decne.) Rehder and the rest of the genus, all of which occurs in Eurasia (Nikiforova et al., 2013). Nikiforova et al. also corroborate earlier indications of the uniqueness in North America of *M. fusca* (Raf.) C.K.Schneid. (Dickson et al., 1991; Routson et al., 2012). This Pacific Northwest crabapple, in Asian *M.* sect. *Sorbomalus* Zabel, evidently crossed the BLB from west to east (Nikiforova et al., 2013), probably no earlier than the late Miocene and possibly much more recently (Williams, 1982; Routson et al., 2012). *Sorbus* s. str. diversified in Eurasia, but each of two early diverging clades (*S.* sect. *Sorbus* and *Commixtae* McAll.) contain North American species whose ancestors could have crossed the BLB from west to east as early as the Oligocene or Miocene (Li et al., 2017). Li et al. did not include North American members of *S.* sect. *Tianshanicae* (Kom. ex T.T.Yu) McAll. (*S. occidentalis* (S.Watson) Greene, *S. sitchensis* M.Roem.) in their sample, but if affiliation of these species with *S.* sect. *Tianshanicae* (McAllister, 2005) is confirmed, then this group too is one in which a later crossing of the BLB occurred (late Miocene at earliest; Li et al., 2017).

*Crataegus* (Fig. 2) appears to resemble its sister genera, *Amelanchier* and Central and South American *Hesperomeles*, in their strong (or exclusive) association with the New World (cf. Evans, 1999). Unlike these other genera, however, the early diversification of *Crataegus* appears to have taken place across the NALB beginning in the Eocene or possibly earlier (Lo et al., 2009a; Lo and Donoghue, 2012; Wen et al., 2016). Ancestors of *C.* subg. *Crataegus* persisted on the east side of the Atlantic but became extinct in North America apart from their modern, apparently hybrid derivatives, *C. marshallii* Eggl., *C. spathulata* Michx., and *C. phaenopyrum* (L.f.) Medik. (Lo et al., 2009a; Phipps, 2015). Extinction of *C.* subg. *Crataegus* in North America is suggested by its absence at present, and the occurrence of fossil leaves resembling those of *C.* subg. *Crataegus* in the late Eocene Florissant Beds of Colorado (e.g. *C. copeana* MacGinitie; MacGinitie, 1953; iDigPaleo, ongoing). In contrast, the ancestors of *C.* subg. *Brevispinae* persisted on the west side of the Atlantic and became extinct in Eurasia if they were ever present there. *Crataegus* subg. *Americanae* and *Sanguineae*, however, likely arose on the west side of the NALB. Difficulties in resolving which of the earliest arising groups (*C.* subg. *Crataegus*, *Brevispinae*, and *Mespilus*; Fig. 2) is sister to the rest of the genus could be explained by their rapid radiation, with the single species of the latter two subgenera being all that remains from their precursors, on either side of the expanding Atlantic and extinct elsewhere. Long distance dispersal could also explain the presence of the hybrid derivatives of *C.* sect. *Crataegus* in North America but, as noted above, such events seem less likely than either the shorter distance dispersals underlying migrations across land bridges, or a combination of vicariance and extinction events (but we note the evidence for LDD from species with bipolar distributions; Popp et al., 2011; Villaverde et al., 2017). Vicariance related to the disappearance of the NALB and asymmetric extinctions appear to us as better explanations of the geographic relationships of *C.* subg. *Brevispinae* and *Mespilus*. Understanding this history will require

better resolution of the early branching in the phylogeny, and more data from fossils that would provide location and time control.

Fossil wood (*Maloidoxylon* Grambast-Fessard) resembling that of *Amelanchier* and *Crataegus* is known from the Eocene and Miocene of Colorado (Wheeler and Matten, 1977; Wheeler and Manchester, 2002), as well as from the Miocene of Patagonia (Pujana, 2009) and Europe (InsideWood, 2004–onwards; Wheeler, 2011). Fossil leaves attributed to *Crataegus* are known from not only as early as the Eocene of North America (MacGinitie, 1953; Dillhoff et al., 2005; DeVore and Pigg, 2007) but also, from the Oligocene on, in Europe (Paleobiology Database, <http://fossilworks.org>). Paleogeographic reconstructions in Sanmartin et al. (2001) and Graham (2018) suggest that the NALB was available into the Oligocene so that migration from North America into Eurasia from the west, followed by vicariant diversification on each continent as the North Atlantic widened, seems plausible.

Because leaves are so abundant in the fossil record, it is important for paleobotanists to appreciate the range of leaf morphologies present within just the genus *Crataegus*. The soft x-ray leaf images (Ross, 2008 in Dickinson et al., 2020) in Fig. 3 are a selection from those deposited and freely accessible online (Dickinson et al., 2020). This collection of images augments *Crataegus* leaf images available in the Cleared Leaf Image Database (Das et al., 2014) and elsewhere (e.g. the University of California Museum of Paleontology Cleared Leaf Collection, <https://ucmp.berkeley.edu/collections/paleobotany-collection/ucmp-cleared-leaf-collection/>), and provides greater detail and more comprehensive taxonomic coverage of the genus than is available elsewhere. It is important to note, however, that the resolution obtained in x-ray images is limited by the size and resolution of the x-ray images. The images are the same size as the leaves themselves, so that resolution is a function here of the grain size of the x-ray film and then, of the resolution of the digital camera that captures the image from the x-ray negative. Digital x-ray imaging is available commercially or can be accomplished using synchrotron (x-) radiation (Blonder et al., 2012). Alternatively, magnified, high resolution digital images of leaf venation can be obtained using the lenses and sensor of a digital camera and chemically cleared and stained leaves (Buechler, 2010; Das et al., 2014; Zhu and Manchester, 2020; Blonder, undated). However, this approach is much more labor intensive, and effectively represents destructive sampling when leaves are obtained from herbarium specimens (cf. Wing, 1992; Dickinson et al., in prep.).

## CONCLUSIONS

Whereas there is no debate on *C. brachyacantha* being *Crataegus*, *C. germanica* is often and arguably treated outside of *Crataegus* as the only species of *Mespilus* (Phipps, 2016a, b). Even though one can always find morphological characters to distinguish these two genera, their close relationship is evident from both recent molecular studies (Lo et al., 2007; Zarrei et al., 2015; Liston et al., in prep.) and morphological affinity. Moreover, synapomorphies such as proleptic lateral shoots, presence of thorns, two superposed ovules with only one being fertilized, absence of false locules, and woody endocarp, make them very distinct from the ‘*Amelanchier*’ clade, which appears to be sister to the ‘*Crataegus+Hesperomeles*’ clade (Li et al., 2012; Lo and Donoghue, 2012; Liu et al., 2019; Liu et al., 2020). Given the impossibility of finding objective measures of dissimilarity that can be applied universally to discriminate taxonomic ranks and the fact that there is always some arbitrariness in distinguishing such ranks especially at and above the genus level (Stevens, 1997), we believe that accepting *Mespilus* and *Crataegus* as a single genus can only lead to a better understanding of their evolution. A concept of *Crataegus* that embraces *Mespilus* promotes taxonomic stability (Talent et al., 2008; Kurtto et al., 2013) and fosters research programs focused on understanding evolution in all the descendants of a common ancestor.

The current classification of *Crataegus* includes five subgenera corresponding to main lineages discovered by molecular studies (Table 1), each of which, apart from *C.* subg. *Crataegus*, has a largely

stable array of sections and series. Sections in *C.* subg. *Crataegus*, however, are somewhat debatable since no study to date has used sufficient accessions to represent all the putative sections or series in the subgenus. *Crataegus* sect. *Crataegus* sensu K. I. Christensen (1992) seems to be monophyletic and morphologically consistent, whereas *C. pinnatifida* Bunge is most likely sister to it (either included or separated to sect. *Pinnatifidae* Zabel ex C.K.Schneid.). The few molecular data available for *C.* sect. *Cuneatae* Rehder ex C.K.Schneid. and *Hupehenses* J.B.Phipps suggest they should be placed in *C.* subg. *Crataegus*, but these data fail to suggest what the relationship between *C. cuneata* and *C. hupehensis* Sarg. and *C.* sect. *Crataegus* is. Finally, there are almost no molecular data for *C. scabrifolia* (Franch.) Rehder (*C.* sect. *Henryanae* Sarg.). Those that are available (Du et al., 2019) are suspect because the illustration for their material may suggest inaccurate identification of studied species. Li et al. (2017) included vouchered *C. scabrifolia* as the sole *Crataegus* species among the outgroup taxa in their study of the phylogeny of *Sorbus* s. l., but none of their sequence data are from loci shared with other phylogenetic studies of *Crataegus* to date. Including *C. scabrifolia* in *C.* subg. *Crataegus* has been based up to now entirely on morphological evidence (e.g. occasional presence of leafy thorns, short aphyllous thorns, and more or less persistent stipules on long shoots) and has ignored the unlobed leaves found in this species.

The system we present does not include hybrids between species belonging to different subgenera (or sections). Nothosubgenera have not yet been described. At the sectional level, only *C. nothosect. Crataeguineae* K.I.Chr., *Coccitaegus* K.I.Chr. & T.A.Dickinson, *Crataeglasia* K.I.Chr. & T.A.Dickinson, *Phippsara* T.A.Dickinson & E.Y.Y.Lo, and *Crataemespilus* (Camus) T.A.Dickinson & E.Y.Y.Lo are known. Distant hybrids and hybrids with ambiguous parentage in *Crataegus* are to be the main focus of further studies, so some additional sections are very likely to get status of nothosections, and a number of new ones might need to be described. In addition, *C. marshallii*, *C. phaenopyrum*, and *C. spathulata* need to be confirmed as paleohybrids between some species of *C.* subg. *Americanae* and *Sanguineae* and members of an extinct lineage close to *C.* subg. *Crataegus* (as was suggested by Lo et al., 2009a). Considering that many allotetraploids have yet to be discovered (especially in *C.* subg. *Americanae*), we refrain from providing a comprehensive classification of *Crataegus* with respect to nothotaxa.

#### ACKNOWLEDGEMENTS

We thank Torsten Eriksson (Bergen) for the extremely useful suggestions in his review of our paper. An anonymous reviewer also made helpful comments of an earlier version. Roberto Pujara (Buenos Aires) and Elisabeth Wheeler each kindly provided us with literature not otherwise readily available to us. Roman Ufimov thanks Alexey Grebenjuk (Komarov Botanical Institute of Russian Academy of Sciences, St. Petersburg, Russia), Alexander Sennikov (University of Helsinki, Helsinki, Finland; Komarov Botanical Institute of Russian Academy of Sciences, St. Petersburg, Russia), and Irina Sokolova (Komarov Botanical Institute of Russian Academy of Sciences, St. Petersburg, Russia) for discussion of nomenclatural issues in *Crataegus*. At the Royal Ontario Museum (ROM) Timothy Dickinson thanks Cary Gilmour for introducing him to x-ray imaging and Patricia Ross for preparing the radiographs of ROM specimens; also, Brian Boyle and Wanda Dobrowlanski of the ROM Ivey Imaging Center for supplying digital images of the x-ray films. Taylor Harding skillfully curated the x-ray images and Nicola Woods facilitated their ROM copyright clearance. We are indebted to the Robarts Library of the University of Toronto, and Sian Meikle and Nancy Fong, for making possible the online availability of the TRT *Crataegus* specimen images.

The work by Roman Ufimov was funded by Austrian Science Fund (project no. P 31512) and the institutional research project of the Komarov Botanical Institute, Russian Academy of Sciences, "Vascular plants of Eurasia: systematics, flora and plant resources" (no. AAAA-A19-119031290052-1). That of Timothy Dickinson has been generously supported by the Natural Sciences and Engineering Research Council of Canada (Discovery Grant A3430); at the ROM, by the Future Fund, the Department of Museum Volunteers, and the Governors of the Royal Ontario Museum, and the Royal Ontario Museum

Curatorial Association; and at the University of Toronto, by the Department of Ecology and Evolutionary Biology (and its predecessor Botany Department).

#### LITERATURE CITED

- Barrie, F. R. 2011. Report of the General Committee: 11. *Taxon*, 60: 1211–1214. <https://doi.org/10.1002/tax.604026>
- Blonder, B. Undated. How to make leaf skeletons. Tucson AZ, University of Arizona. [http://www.u.arizona.edu/~bblonder/leaves/The\\_secrets\\_of\\_leaves/Making\\_skeletons.html](http://www.u.arizona.edu/~bblonder/leaves/The_secrets_of_leaves/Making_skeletons.html) (accessed 16-October-2014).
- Blonder, B., F. D. Carlo, J. Moore, M. Rivers, and B. J. Enquist. 2012. X-ray imaging of leaf venation networks. *New Phytologist*, 196: 1274–1282. <https://doi.org/10.1111/j.1469-8137.2012.04355.x>
- Boone, J. 2002–onwards. Wild Crab Apple (*Peraphyllum ramosissimum*). Birdandhike.com [https://www.birdandhike.com/Veg/Species/Shrubs/Peraph\\_ram/\\_Per\\_ram.htm](https://www.birdandhike.com/Veg/Species/Shrubs/Peraph_ram/_Per_ram.htm) (accessed 23-April-2020).
- Britton, N. L., and A. Brown. 1913. An illustrated flora of the northern United States, Canada and the British possessions, ed. 2. Vol. 2. Charles Scribner's Sons, New York, [i]–iv + 735 pp.
- Brummitt, R. K. 1986. Report of the Committee for Spermatophyta: 30. *Taxon*, 35: 556–563. <https://doi.org/10.2307/1221918>
- Brummitt, R. K. 2011. Report of the Nomenclature Committee for Vascular Plants: 62. *Taxon*, 60: 226–232. <https://doi.org/10.1002/tax.601024>
- Buechler, W. K. 2010. Alternative Leaf Clearing and Mounting Procedures (update of 2004 original). Walter Buechler, Boise ID, 29 pp.
- Burgess, M. B., K. R. Cushman, E. T. Doucette, C. T. Frye, and C. S. Campbell. 2015. Understanding diploid diversity: A first step in unraveling polyploid, apomictic complexity in *Amelanchier*. *American Journal of Botany*, 102: 2041–2057. <https://doi.org/10.3732/ajb.1500330>
- Campbell, C. S. 2015. *Peraphyllum*. In: Flora of North America Editorial Committee (eds.), Flora of North America North of Mexico. Vol. 9. Oxford University Press, New York and Oxford, p 662.
- Campbell, C. S., R. C. Evans, D. R. Morgan, T. A. Dickinson, and M. P. Arsenault. 2007. Phylogeny of subtribe Pyrinae (formerly the Maloideae, Rosaceae): limited resolution of a complex evolutionary history. *Plant Systematics and Evolution*, 266: 119–145. <https://doi.org/10.1007/s00606-007-0545-y>
- Christensen, K. I. 1992. Revision of *Crataegus* sect. *Crataegus* and nothosect. *Crataeguinae* (Rosaceae—Maloideae) in the Old World. *Systematic Botany Monographs*, 35: 1–199.
- Cinovskis, R. 1971. *Crataegi Baltici*. Zinātne, Riga, 388 pp. (In Russian.)
- Das, A., A. Bucksch, C. A. Price, and J. S. Weitz. 2014. ClearedLeavesDB: an online database of cleared plant leaf images. *Plant Methods*, 10: 8. <https://doi.org/10.1186/1746-4811-10-8>
- DeVore, M. L., and K. B. Pigg. 2007. A brief review of the fossil history of the family Rosaceae with a focus on the Eocene Okanogan Highlands of eastern Washington State, USA, and British Columbia, Canada. *Plant Systematics and Evolution*, 266: 45–57. <https://doi.org/10.1007/s00606-007-0540-3>
- Dickinson, T. A. 1985. The biology of Canadian weeds. 68. *Crataegus crus-galli* sensu lato. *Canadian Journal of Plant Science*, 65: 641–654. <https://doi.org/10.4141/cjps85-087>

- Dickinson, T. A., P. Haripersaud, X. Q. Yan, J. Hwang, S. Han, N. Talent, and M. Zarrei (in prep.) Polyploidy, niche shifts, hybridization, and geographic parthenogenesis in Rocky Mountain black-fruited hawthorns (*Crataegus* L., Rosaceae).
- Dickinson, T. A., E. Y. Y. Lo, and N. Talent. 2007. Polyploidy, reproductive biology, and Rosaceae: understanding evolution and making classifications. *Plant Systematics and Evolution*, 266: 59–78. <https://doi.org/10.1007/s00606-007-0541-2>
- Dickinson, T. A., E. Y. Y. Lo, N. Talent, and R. M. Love. 2008. Black-fruited hawthorns of western North America — one or more agamic complexes? *Botany-Botanique*, 86(8): 846–865. <https://doi.org/10.1139/b08-072>
- Dickinson, T. A., and R. M. Love. 1997. [North American black-fruited hawthorns: III.] What is Douglas hawthorn? *In*: T. Kaye, A. Liston, R. M. Love, D. L. Luoma, R. J. Meinke, and M. V. Wilson (eds.). *Conservation and Management of Oregon's Native Flora*. Native Plant Society of Oregon, Corvallis OR, p. 162–171.
- Dickinson, T. A., R. A. Ufimov, and T. Harding. 2020. Infrageneric nomenclature in *Crataegus* — Leaf venation correlates. MorphoBank. <http://morphobank.org/permalink/?P1390>; <http://dx.doi.org/10.7934/P3190>
- Dickson, E. E., S. Kresovich, and N. F. Weeden. 1991. Isozymes in North American *Malus* (Rosaceae): Hybridization and species differentiation. *Systematic Botany*, 16: 363–375. <https://doi.org/10.2307/2419286>
- Dillhoff, R. M., E. B. Leopold, and S. R. Manchester. 2005. The McAbee flora of British Columbia and its relation to the Early–Middle Eocene Okanagan Highlands flora of the Pacific Northwest. *Canadian Journal of Earth Sciences*, 42: 151–166. <https://doi.org/10.1139/e04-084>
- Du, X., X. Zhang, H. Bu, T. Zhang, Y. Lao, and W. Dong. 2019. Molecular Analysis of Evolution and Origins of Cultivated Hawthorn (*Crataegus* spp.) and Related Species in China. *Frontiers in Plant Science*, 10: 1–12. <https://doi.org/10.3389/fpls.2019.00443>
- Edwards, J. E., P. N. Brown, N. Talent, T. A. Dickinson, and P. R. Shipley. 2012. A review of the chemistry of the genus *Crataegus*. *Phytochemistry*, 79: 5–26. <https://doi.org/10.1016/j.phytochem.2012.04.006>
- El-Gazzar, A. 1980. The taxonomic significance of leaf morphology in *Crataegus* (Rosaceae) *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 101(4): 457–469.
- Ellis, B., D. C. Daly, L. J. Hickey, K. R. Johnson, J. D. Mitchell, P. Wilf, and S. L. Wing. 2009. *Manual of Leaf Architecture*. Comstock Publishing Associates (Cornell University Press) in association with The New York Botanical Garden Press, Ithaca NY, 65 pp.
- Evans, R. C. 1999. Molecular, morphological, and ontogenetic evaluation of relationships and evolution in the Rosaceae. [Doctoral dissertation, University of Toronto, Department of Botany].
- Evans, R. C., and T. A. Dickinson. 2005. Floral ontogeny and Morphology in *Gillenia* (“Spiraeoideae”) and Subfamily Maloideae C. Weber (Rosaceae). *International Journal of Plant Sciences*, 166: 427–447. <https://doi.org/10.1086/428631>
- Graham, A. 2018. *Land bridges: ancient environments, plant migrations, and New World connections*. The University of Chicago Press, Chicago, 288 pp.
- Greene, E. L. 1896. New or noteworthy species, XVII. *Pittonia*, 3(15): 91–116.
- Hallé, F., R. A. A. Oldemann, and P. B. Tomlinson. 1978. *Tropical trees and forests — an architectural analysis*. Springer-Verlag, Berlin, 444 pp. <https://doi.org/10.1007/978-3-642-81190-6>

- Hay, W. W., R. M. DeConto, C. N. Wold, K. M. Wilson, S. Voigt, M. Schulz, A. R. Wold, W.-C. Dullo, A. B. Ronov, A. N. Balukhovskiy, and E. Söding. 1999. Alternative global Cretaceous paleogeography. *In*: E. Barrera and C. C. Johnson (eds.). *Evolution of the Cretaceous Ocean-Climate System*, Geological Society of America, Special Paper 332, pp. 1–47. <https://doi.org/10.1130/0-8137-2332-9.1>
- Hitchcock, A. S., and M. L. Green. 1929. Standard-species of Linnean genera of Phanerogamae (1753–54). *In*: International Botanical Congress, Cambridge (England) 1930. Nomenclature. Proposals by British Botanists. Wyman, and Sons, London, pp. 110–199.
- iDigPaleo. ongoing. Florissant Fossil Beds <https://www.idigpaleo.org/Detail/objects/4367> (accessed 9-May-2020).
- InsideWood. 2004–onwards. Published on the Internet <http://insidewood.lib.ncsu.edu/search> (accessed 10-May-2020).
- Jiang, Y., M. Gao, Y. Meng, J. Wen, X. J. Ge, and Z. L. Nie. 2019. The importance of the North Atlantic land bridges and eastern Asia in the post-Boreotropical biogeography of the Northern Hemisphere as revealed from the poison ivy genus (*Toxicodendron*, Anacardiaceae). *Molecular Phylogenetics and Evolution*, 139: 106561. <https://doi.org/10.1016/j.ympev.2019.106561>
- Jombart, T., M. Kendall, J. Almagro-Garcia, and C. Colijn. 2017. TREESPACE: Statistical exploration of landscapes of phylogenetic trees. *Molecular Ecology Resources*, 17: 1385–1392. <https://doi.org/10.1111/1755-0998.12676>
- Jordano, P. 2017. What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of Ecology*, 105: 75–84. <https://doi.org/10.1111/1365-2745.12690>
- Kalkman, C. 2004. Rosaceae. *In*: K. Kubitzki (ed.). *Flowering plants — Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales*. Springer, Berlin, p. 343–386.
- Kelly, L. M. 2008. Rosaceae: *Hesperomeles heterophylla*. [http://www.plantsystematics.org/users/lkelly/8\\_16\\_08\\_1/08\\_upload\\_2/hesp\\_hetero\\_margin.jpg](http://www.plantsystematics.org/users/lkelly/8_16_08_1/08_upload_2/hesp_hetero_margin.jpg) (accessed 28-July-2019).
- Kruschke, E. P. 1965. Contributions to the taxonomy of *Crataegus*. *Publications in botany, Milwaukee Public Museum*, 3: 1–273.
- Kurtto, A., A. Sennikov, and R. Lampinen. 2013. *Atlas Flora Europaeae. Distribution of Vascular Plants in Europe*. 16. Rosaceae (*Cydonia* to *Prunus*, excl. *Sorbus*). The Committee for Mapping the Flora of Europe, and Societas Biologica Fennica Vanamo, Helsinki, 168 pp.
- Lambinon, J. 1981. (592) Proposition de rejet *Crataegus oxyacantha* L., *Sp. Pl.*, ed. 1: 477. 1753 (Malaceae). *Taxon*, 30, 1: 362.
- Lance, R. W. 2014. *Haws: A Guide to Hawthorns of the Southeastern United States*. Published by the author, Mills River NC, 811 pp.
- Landis, M. J., D. A. R. Eaton, W. L. Clement, B. Park, E. L. Spriggs, P. W. Sweeney, E. J. Edwards, and M. J. Donoghue. 2020. Joint phylogenetic estimation of geographic movements and biome shifts during the global diversification of *Viburnum*. *Systematic Biology*, syaa027. <https://doi.org/10.1093/sysbio/syaa027>
- Li, M., T. Ohi-Toma, Y.-D. Gao, B. Xu, Z.-M. Zhu, W.-B. Ju, and X.-F. Gao. 2017. Molecular phylogenetics and historical biogeography of *Sorbus sensu stricto* (Rosaceae). *Molecular Phylogenetics and Evolution*, 111: 76–86. <https://doi.org/10.1016/j.ympev.2017.03.018>
- Li, Q.-Y., W. Guo, W.-B. Liao, J. A. Macklin, and J.-H. Li. 2012. Generic limits of Pyrinae: Insights from nuclear ribosomal DNA sequences. *Botanical Studies*, 53: 151–164.

- Liston, A., K. A. Weitemier, L. Letelier, J. Podani, Y. Zong, L. Lieu, and T. A. Dickinson (in prep.) Phylogeny of *Crataegus* (Rosaceae) based on 257 nuclear loci and chloroplast genomes: evaluating the impact of hybridization.
- Liu, B.-B., C. S. Campbell, D.-Y. Hong, and J. Wen. 2020. Phylogenetic relationships and chloroplast capture in the *Amelanchier-Malacomeles-Peraphyllum* clade (Maleae, Rosaceae): evidence from chloroplast genome and nuclear ribosomal DNA data using genome skimming. *Molecular Phylogenetics and Evolution*, 147: 106784. <https://doi.org/10.1016/j.ympev.2020.106784>
- Liu, B.-B., D.-Y. Hong, S.-L. Zhou, C. Xu, W.-P. Dong, G. Johnson, and J. Wen. 2019. Phylogenomic analyses of the *Photinia* complex support the recognition of a new genus *Phippsiomeles* and the resurrection of a redefined *Stranvaesia* in Maleae (Rosaceae). *Journal of Systematics and Evolution*, 57: 678–694. <https://doi.org/10.1111/jse.12542>
- Lo, E. Y. Y., and M. J. Donoghue. 2012. Expanded phylogenetic and dating analyses of the apples and their relatives (Pyreae, Rosaceae). *Molecular Phylogenetics and Evolution*, 63(2): 230–243. <https://doi.org/10.1016/j.ympev.2011.10.005>
- Lo, E. Y. Y., S. Stefanović, and T. A. Dickinson. 2007. Molecular reappraisal of relationships between *Crataegus* and *Mespilus* (Rosaceae, Pyreae) — two genera or one? *Systematic Botany*, 32 (3): 596–616. <https://doi.org/10.1600/036364407782250562>
- Lo, E. Y. Y., S. Stefanović, and T. A. Dickinson. 2009b. Population genetic structure of diploid sexual and polyploid apomictic hawthorns (*Crataegus*; Rosaceae) in the Pacific Northwest. *Molecular Ecology*, 18: 1145–1160. <https://doi.org/10.1111/j.1365-294X.2009.04091.x>
- Lo, E. Y. Y., S. Stefanović, and T. A. Dickinson. 2010. Reconstructing reticulation history in a phylogenetic framework and the potential of allopatric speciation driven by polyploidy in an agamic complex in *Crataegus* (Rosaceae). *Evolution*, 64: 3593–3608. <https://doi.org/10.1111/j.1558-5646.2010.01063.x>
- Lo, E. Y. Y., S. Stefanovic, K. I. Christensen, and T. A. Dickinson. 2009a. Evidence for genetic association between East Asian and western North American *Crataegus* L. (Rosaceae) and rapid divergence of the eastern North American lineages based on multiple DNA sequences. *Molecular Phylogenetics and Evolution*, 51(2): 157–168. <https://doi.org/10.1016/j.ympev.2009.01.018>
- Loudon, J. C. 1838. *Arboretum et fruticetum britannicum*. Vol. 2. Longman, Orme, Brown, Green, and Longmans, London, [i]–x + 495–1256 pp.
- MacGinitie, H. D. 1953. *Fossil Plants of the Florissant Beds of Colorado*. Contributions to paleontology (Carnegie Institution of Washington); Carnegie Institution of Washington publication, 599, iii+198 pp.
- McAllister, H. A. 2005. *The genus Sorbus — mountain ash and other rowans*. Royal Botanic Gardens, Kew, 252 pp.
- Nathan, R. 2006. Long-Distance Dispersal of Plants. *Science*, 313: 786–788. <https://doi.org/10.1126/science.1124975>
- Nikiforova, S. V., D. Cavalieri, R. Velasco, and V. Goremykin. 2013. Phylogenetic Analysis of 47 Chloroplast Genomes Clarifies the Contribution of Wild Species to the Domesticated Apple Maternal Line. *Molecular Biology and Evolution*, 30: 1751–1760. <https://doi.org/10.1093/molbev/mst092>
- O’Leary, M. A., and S. G. Kaufman. 2011. MorphoBank: phylophenomics in the ‘cloud’. *Cladistics*, 27: 1–9.

- O'Leary, M. A., and S. G. Kaufman. 2012. MorphoBank 3.0: Web application for morphological phylogenetics and taxonomy. <http://www.morphobank.org>. (accessed 28-July-2020).
- Ogihara, T. 2017. ToyViewer 5.5. [http://www7a.biglobe.ne.jp/~ogihara/en/Mac\\_OS\\_X.html](http://www7a.biglobe.ne.jp/~ogihara/en/Mac_OS_X.html) (accessed 17-Oct-2015).
- Palmer, E. J. 1925. Synopsis of North American Crataegi. *Journal of the Arnold Arboretum*, 6(1–2): 5–128.
- Palmer, E. J. 1952. *Crataegus* L. In: H. A. Gleason. The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. Vol. 2. Lancaster Press, Lancaster PA, pp. 338–375.
- Phipps, J. B. 1983. [Studies in *Crataegus* (Rosaceae: Maloideae) VI.] Biogeographic, taxonomic and cladistic relationships between East Asiatic and North American *Crataegus*. *Annals of the Missouri Botanical Garden*, 70(4): 667–700. <https://doi.org/10.2307/2398984>
- Phipps, J. B. 1998. Introduction to the red-fruited hawthorns (*Crataegus*, Rosaceae) of western North America. *Canadian Journal of Botany*, 76(11): 1863–1899. <https://doi.org/10.1139/b98-148>
- Phipps, J. B. 1999. The relationships of the American black-fruited hawthorns *Crataegus erythropoda*, *C. rivularis*, *C. saligna* and *C. brachyacantha* to ser. *Douglasianae* (Rosaceae). *Sida*, 18(3): 647–660.
- Phipps, J. B. 2015. *Crataegus*. In: Flora of North America Editorial Committee (eds.), Flora of North America North of Mexico. Vol. 9. Oxford University Press, New York and Oxford, pp. 491–643.
- Phipps, J. B. 2016a. Studies in *Mespilus*, *Crataegus*, and  $\times$ *Crataemespilus* (Rosaceae), I. Differentiation of *Mespilus*, *Crataegus*, and  $\times$ *Crataemespilus*, with supplementary observations on differences between the *Crataegus* and *Amelanchier* clades. *Phytotaxa*, 257(3): 201–229. <https://doi.org/10.11646/phytotaxa.257.3.1>
- Phipps, J. B. 2016b. Studies in *Mespilus*, *Crataegus*, and  $\times$ *Crataemespilus* (Rosaceae), II. The academic and folk taxonomy of the medlar, *Mespilus germanica*, and hawthorns, *Crataegus* (Rosaceae). *Phytotaxa*, 260(1): 25–35. <https://doi.org/10.11646/phytotaxa.260.1.3>
- Phipps, J. B., R. J. O'Kennon, and R. W. Lance. 2003. Hawthorns and medlars. Timber Press, Portland OR, 139 pp.
- Phipps, J. B., K. R. Robertson, P. G. Smith, and J. R. Rohrer. 1990. A checklist of the subfamily Maloideae (Rosaceae). *Canadian Journal of Botany*, 68(10): 2209–2269. <https://doi.org/10.1139/b90-288>
- Popp M., Mirré V., and Brochmann C. 2011. A single Mid-Pleistocene long-distance dispersal by a bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*). *Proceedings of the National Academy of Sciences*, 108: 6520. <https://doi.org/10.1073/pnas.1012249108>
- Potter, D., T. Eriksson, R. C. Evans, S. Oh, J. E. E. Smedmark, D. R. Morgan, M. Kerr, K. R. Robertson, M. Arsenault, T. A. Dickinson, and C. S. Campbell. 2007. Phylogeny and classification of Rosaceae. *Plant Systematics and Evolution*, 266: 5–43. <https://doi.org/10.1007/s00606-007-0539-9>
- Pujana, R. R. 2009. Fossil woods from the Oligocene of southwestern Patagonia (Río Leona Formation). Rosaceae and Nothofagaceae. AMEGHINIANA (Review Asociación Paleontológica Argentina), 46 (4): 621–636.
- Rehder, A. 1940. *Crataegus* L. In: Manual of cultivated trees and shrubs hardy in North America, ed. 2. The Macmillan Company, New York, pp. 359–372.
- Rohrer J. R., K. R. Robertson, and J. B. Phipps. 1994. Floral morphology of Maloideae (Rosaceae) and its systematic relevance. *American Journal of Botany*, 81: 574–581.



- Ross, P. D. 2008. X-raying Botanical Specimens Using the Faxitron. Royal Ontario Museum, Toronto, 11 pp.
- Routson, K. J., G. M. Volk, C. M. Richards, S. E. Smith, G. P. Nabhan, and V. W. d. Echeverria. 2012. Genetic Variation and Distribution of Pacific Crabapple. *Journal of the American Society for Horticultural Science*, 137: 325–332. <https://doi.org/10.21273/JASHS.137.5.325>
- Rusanov, F. N. 1965. Introdutsyronayie boiaryshniki botanicheskogo sada AN UzSSR. *In: Dendrologiia Uzbekistana*. Vol. 1. Izd-vo ‘Nauka’ Uzbekskoy SSR, Tashkent, pp. 8–254. (In Russian.)
- Sanmartín, I., H. Enghoff, and F. Ronquist. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, 73: 345–390. <https://doi.org/10.1006/bj1.2001.0542>
- Schneider, C. K. 1906. *Illustriertes Handbuch der Laubholzkunde*. Vol. 1. G. Fischer, Jena, [a]–d + [i]–iii + 810 pp.
- Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Stevens, P. F. 1997. How to interpret botanical classifications—suggestions from history. *Bioscience*, 47: 243–250. <https://doi.org/10.2307/1313078>
- Talent, N. 2006. Gametophytic apomixis, hybridization, and polyploidy in *Crataegus* (Rosaceae). [Doctoral dissertation, University of Toronto, Department of Botany].
- Talent, N. and T. A. Dickinson. 2005. Polyploidy in *Crataegus* and *Mespilus* (Rosaceae, Maloideae): evolutionary inferences from flow cytometry of nuclear DNA amounts. *Canadian Journal of Botany*, 83: 1268–1304. <https://doi.org/10.1139/b05-088>
- Talent, N., J. E. Eckenwalder, E. Y. Y. Lo, K. I. Christensen, and T. A. Dickinson. 2008. (1847) Proposal to conserve the name *Crataegus* against *Mespilus* (Rosaceae). *Taxon*, 57: 1007–1008. <https://doi.org/10.1002/tax.573042>
- Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, W.-H. Kusber, D.-Z. Li, K. Marhold, T. W. May, J. McNeill, A. M. Monro, J. Prado, M. J. Price, and G. F. Smit. (eds.) 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Koeltz Botanical Books, Glashütten, 254 p. <https://doi.org/10.12705/Code.2018>
- Ufimov, R. A. 2013. Notes on the genus *Crataegus* L. (Rosaceae). *Novosti sistematiki vysshikh rastenii*, 44: 113–125. (In Russian.)
- Velasco, R., A. Zharkikh, J. Affourtit, A. Dhingra, A. Cestaro, A. Kalyanaraman, P. Fontana, S. K. Bhatnagar, M. Troggio, D. Pruss, S. Salvi, M. Pindo, P. Baldi, S. Castelletti, M. Cavaiuolo, G. Coppola, F. Costa, V. Cova, A. Dal Ri, V. Goremykin, M. Komjanc, S. Longhi, P. Magnago, G. Malacarne, M. Malnoy, D. Micheletti, M. Moretto, M. Perazzolli, A. Si-Ammour, S. Vezzulli, E. Zini, G. Eldredge, L. M. Fitzgerald, N. Gutin, J. Lanchbury, T. Macalma, J. T. Mitchell, J. Reid, B. Wardell, C. Kodira, Z. Chen, B. Desany, F. Niazi, M. Palmer, T. Koepke, D. Jiwan, S. Schaeffer, V. Krishnan, C. Wu, V. T. Chu, S. T. King, J. Vick, Q. Tao, A. Mraz, A. Stormo, K. Stormo, R. Bogden, D. Ederle, A. Stella, A. Vecchietti, M. M. Kater, S. Masiero, P. Lasserre, Y. Lespinasse, A. C. Allan, V. Bus, D. Chagne, R. N. Crowhurst, A. P. Gleave, E. Lavezzo, J. A. Fawcett, S. Proost, P. Rouze, L. Sterck, S. Toppo, B. Lazzari, R. P. Hellens, C.-E. Durel, A. Gutin, R. E. Bumgarner, S. E. Gardiner, M. Skolnick, M. Egholm, Y. Van de Peer, F. Salamini, and R. Viola. 2010. The genome of the domesticated apple (*Malus ×domestica* Borkh.). *Nature Genetics*, 42: 833–839. <https://doi.org/10.1038/ng.654>

- Velazco-Macias, C. G. 2014. Tlaxistle, *Malacomeles denticulata*. Naturalista. <http://conabio.inaturalist.org/photos/760100> (accessed 23-April-2020.)
- Villaverde, T., M. Escudero, S. Martín-Bravo, P. Jiménez-Mejías, I. Sanmartín, P. Vargas, and M. Luceño. 2017. Bipolar distributions in vascular plants: A review. *American Journal of Botany*, 104: 1680–1694. <https://doi.org/10.3732/ajb.1700159>
- Voss, E. G. 1987. General Committee Report 1986. *Taxon*, 36: 429–429. <https://doi.org/10.2307/1221438>
- Wen, J., Z.-L. Nie, and S. M. Ickert-Bond. 2016. Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. *Journal of Systematics and Evolution*, 54: 469–490. <https://doi.org/10.1111/jse.12222>
- Wheeler, E. A. 2011. InsideWood — a web resource for hardwood anatomy. *IAWA Journal*, 32: 199–211.
- Wheeler, E. A., and S. R. Manchester. 2002. Woods of the Eocene Nut Beds flora, Clarno Formation, Oregon, USA. *International Association of Wood Anatomists Journal*, 3: 1–188.
- Wheeler, E. F., and L. C. Matten. 1977. Fossil wood from an Upper Miocene locality in northeastern Colorado. *Botanical Gazette*, 138: 112–118. <https://doi.org/10.1086/336904>
- Williams, A. H. 1982. Chemical evidence from the flavonoids relevant to the classification of *Malus* species. *Botanical Journal of the Linnean Society*, 84: 31–39. <https://doi.org/10.1111/j.1095-8339.1982.tb00358.x>
- Wing, S. L. 1992. High-Resolution Leaf X-Radiography in Systematics and Paleobotany. *American Journal of Botany*, 79: 1320–1324. <https://doi.org/10.2307/2445060>
- Zarrei, M., N. Talent, M. Kuzmina, J. Lee, J. Lund, P. R. Shipley, S. Stefanovic, and T. A. Dickinson. 2015. DNA barcodes from four loci provide poor resolution of taxonomic groups in the genus *Crataegus*. *AoB Plants*, 7: plv045. <https://doi.org/10.1093/aobpla/plv045>
- Zarrei, M., S. Stefanovic, and T. A. Dickinson. 2014. Reticulate evolution in North American black-fruited hawthorns (*Crataegus* section *Douglasia*; Rosaceae): evidence from nuclear ITS2 and plastid sequences. *Annals of Botany*, 114(2): 253–269. <https://doi.org/10.1093/aob/mcu116>
- Zhu, H., and S. R. Manchester. 2020. Red and Silver Maples in the Neogene of Western North America: Fossil Leaves and Samaras of *Acer* Section *Rubra*. *International Journal of Plant Sciences*, 181(5): 542–556. <https://doi.org/10.1086/707106>

Table 1. Current subgeneric and sectional classification of *Crataegus* (excluding *C. marshallii*, *C. spathulata*, *C. phaenopyrum*, and other intersubgeneric and intersectional hybrids). Includes information for vouchers of hawthorn individuals used here as sources of leaves for x-rays shown in Fig. 3. Ploidy level and other data as per the publications shown. Localities are all in Canada or the U.S.A. Voucher specimens are deposited in the Green Plant Herbarium of the Royal Ontario Museum (TRT). TRT accession numbers are linked to online specimen images (<https://crataegus.library.utoronto.ca/TRTnnnnnnnnn.JPG>); M numbers are the online MorphoBank media numbers (<http://morphobank.org/permalink/?P1390>; <http://dx.doi.org/10.7934/P3190>). Sections marked with (\*) are provisional with very little or no molecular evidence known.

	TRT Accession and MorphoBank numbers (Dickinson et al., 2020)	2n (x=17); stamen number	Collector and number	Publication	Locality
<b><i>Crataegus</i> L.</b>					
<b>subg. <i>Mespilus</i> (L.) Ufimov and T.A.Dickinson</b>					
<b>sect. <i>Mespilus</i> (L.) T.A.Dickinson and E.Y.Y.Lo</b>					
<i>C. germanica</i> (L.) Kuntze	TRT00026644 M584768	2x A <sub>30</sub>	Hess, W., and M. Linden 6220V93	(Evans and Dickinson, 2005; Talent & Dickinson, 2005)	Illinois, DuPage Co. Morton Arboretum (665-80). Cultivated from seed from wild in Tauria, Crimean, State Nikita Bot. Gard., Jalta, Tauria, Ukraine
<b>subg. <i>Brevispiniae</i> (Beadle) Ufimov and T.A.Dickinson</b>					
<b>sect. <i>Brevispiniae</i> Beadle ex C.K.Schneid.</b>					
<i>C. brachyacantha</i> Sarg. & Engelm.	TRT00000025 M584760	2–3x A <sub>20</sub>	Reid, C. 5202	(Talent & Dickinson, 2005)	Louisiana, Ouachita Parish. Ouachita WMA, ca. 7.5 miles SE of Monroe
<b>subg. <i>Crataegus</i></b>					
<b>sect. <i>Crataegus</i></b>					
<i>C. laciniata</i> Ucria sensu K.I.Chr.	TRT00002426 M584673	2x A <sub>20</sub>	Dickinson, T. A. s.n.	(Talent & Dickinson, 2005)	Massachusetts, Suffolk Co. Cultivated, Arnold Arboretum (AA238-71A)
<i>C. laevigata</i> (Poir.) DC.	TRT00002174 M584601	2x A <sub>20</sub>	Zika, P. 18472, with A. L. Jacobson and L. Falb	(Talent & Dickinson, 2005)	Washington, San Juan Co. Bird sown in thickets, T36N R2W S19, San Juan Islands, Crane Island, E end
<b>sect. <i>Pinnatifidae</i> Zabel ex C.K.Schneid.*</b>					
<b>sect. <i>Cuneatae</i> Rehder ex C.K.Schneid.*</b>					
<b>sect. <i>Hupehenses</i> J.B.Phipps*</b>					
<b>sect. <i>Henryanae</i> (Sarg.) J.B.Phipps*</b>					
<b>subg. <i>Americanae</i> El Gazzar</b>					
<b>sect. <i>Coccineae</i> Loudon</b>					
<i>C. opaca</i> Hook. & Arn.	TRT00002042 M584679	2x A <sub>20</sub>	Dickinson, T. A. 2003-33, with N. Talent and S. Nguyen	(Talent & Dickinson, 2005; Zarrei et al., 2015)	Louisiana, Sabine Parish. Cultivated

<i>C. triflora</i> Chapm.	TRT00021431 M584762	2x A <sub>30</sub>	Dickinson, T. A. 2003-22, with N. Talent, S. Nguyen and R. Lance	(Talent & Dickinson, 2005)	Alabama, Autauga Co. Jones Bluff, SSW of Peace
<b>sect. <i>Macracanthae</i> Loudon</b>					
<i>C. calpodendron</i> (Ehrh.) Medik.	TRT00002039 M584551	2x A <sub>20</sub>	Dickinson, T. A., N. Talent NT166 and E. Garrett	(Talent & Dickinson, 2005)	Ontario, Middlesex Co. Mosa Tp., Conc. Rd. VII-VIII, E of Mosa Side Rd. 8
<b>subg. <i>Sanguineae</i> Ufimov</b>					
<b>sect. <i>Salignae</i> T.A.Dickinson &amp; Ufimov</b>					
<i>C. saligna</i> Greene	TRT00001047 M584583	2x + A <sub>20</sub>	Dickinson, T. A. 2004-05	(Talent & Dickinson, 2005; Zarrei et al., 2015)	Utah, Duchesne Co. River Road, 4 miles N of Duchesne
<b>sect. <i>Douglasianae</i> (Rehder) C.K.Schneid.</b>					
<i>C. suksdorfii</i> (Sarg.) Kruschke	TRT00001805 M584618	2x A <sub>20</sub>	Zika, P. F. 18485	(Talent, 2006; Zarrei et al., 2015)	Washington, Clark Co. ca. 1.5 air miles NNW of Ridgefield
<b>sect. <i>Sanguineae</i> Zabel ex C.K.Schneid.</b>					
<i>C. wattiana</i> Hemsl. & Lace	TRT00001881 M584549	4x A <sub>20</sub>	Dickinson, T. A. s.n., and R. C. Evans	(Talent & Dickinson, 2005)	Québec; Cultivated, Jardin Botanique de Montréal, Arboretum (1280-50); det. K.I. Christensen 2011

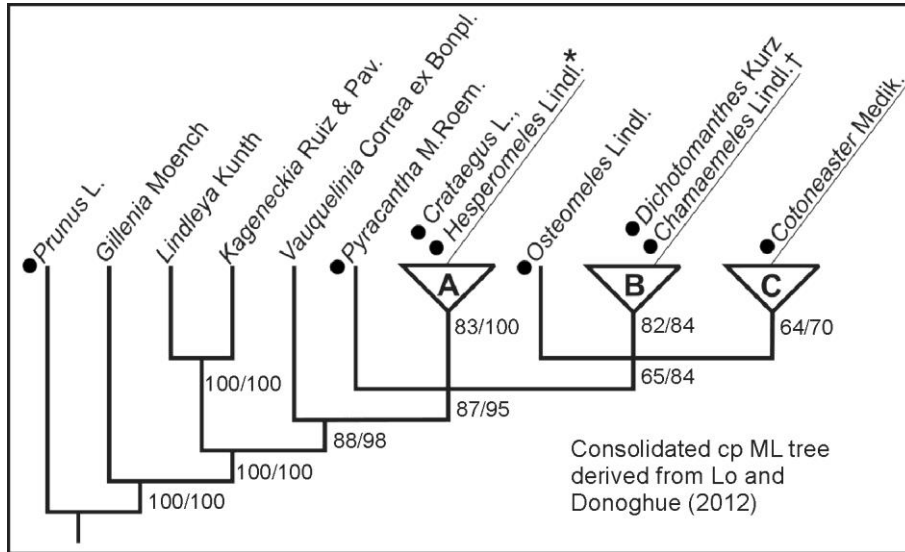
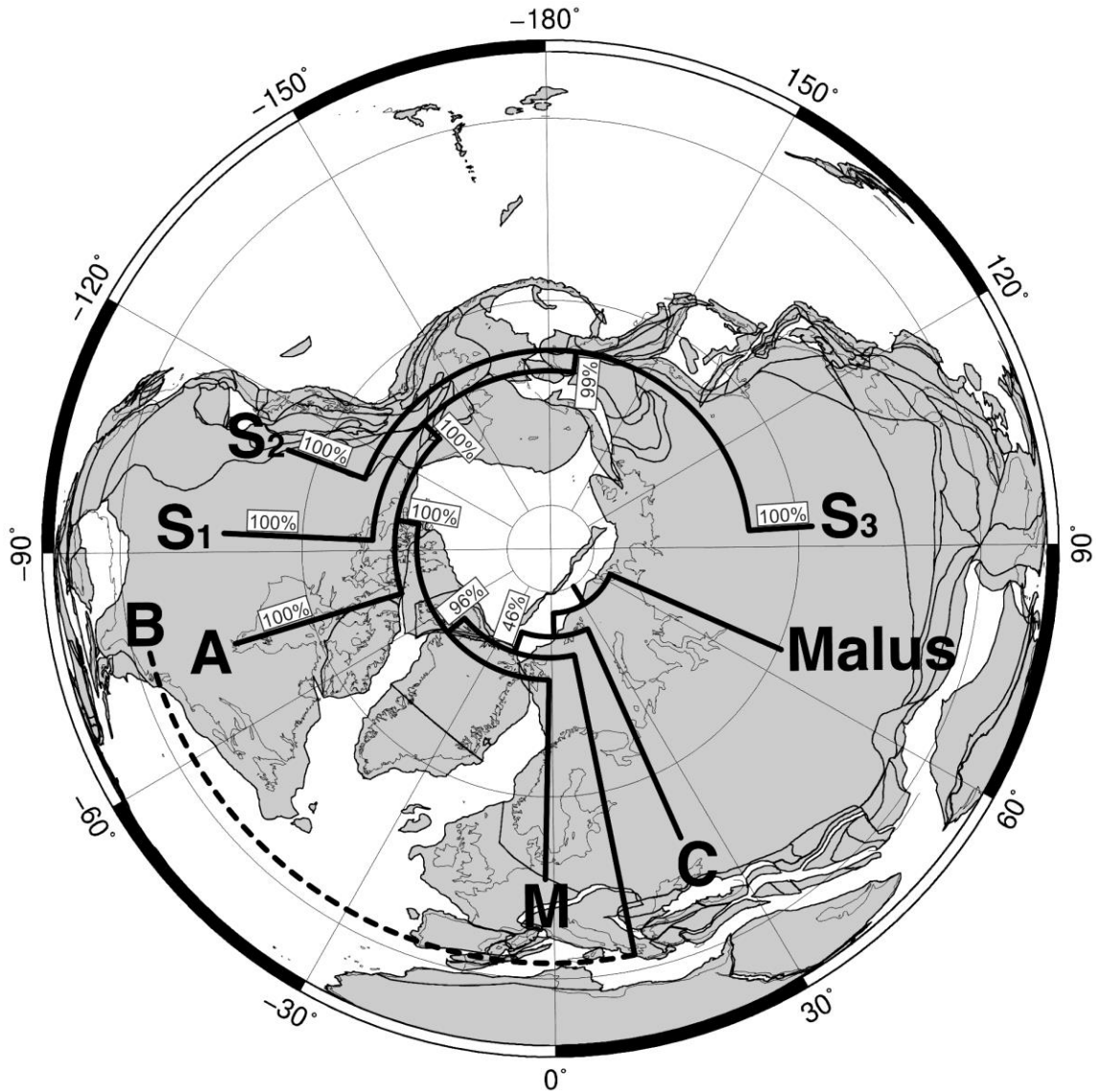
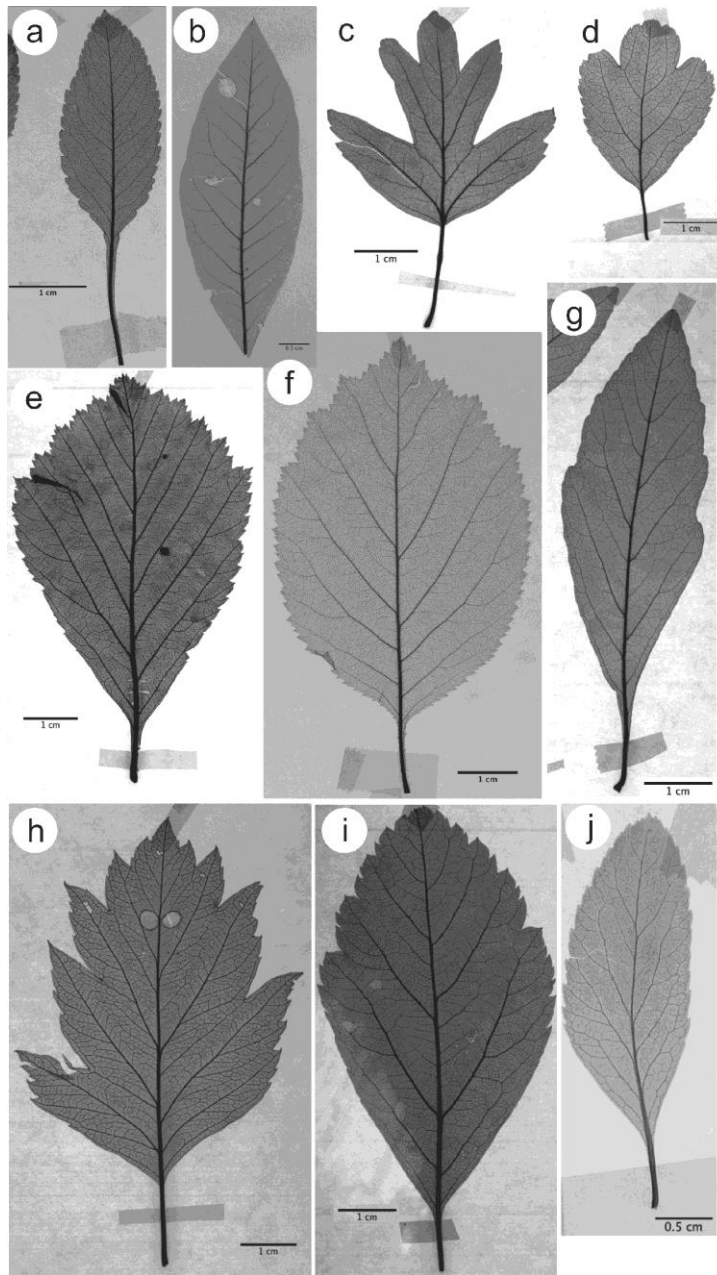


Figure 1. Simplification of the major clades in Rosaceae tribe Maleae (A, B, C; see text for included genera) based on a maximum likelihood tree for 11 plastome loci (coding and non-coding), rooted using species of *Prunus* (left half of figure 1 in Lo and Donoghue, 2012). Branch support indicated by bootstrap (left #) and posterior probability (right #) at nodes. Genera with drupaceous fruits (tribe Crataegeae) indicated by black dots; *Chamaemeles* (dagger) placed on the basis of the results in Li et al. (2012). *Hesperomeles* (asterisk) placed on the basis of the results in Liu et al. (2020).



37 Ma Reconstruction

Figure 2. North polar projection of a tectonic plate reconstruction for 37 Ma produced using the service at [www.ods.de](http://www.ods.de) (Hay et al., 1999). Superimposed on the map is the RAxML tree for *Crataegus* subgenera: C, *C. subg. Crataegus*; A, *C. subg. Americanae*; S, *C. subg. Sanguineae*; B (dashed line), *C. subg. Brevispinae*; and M, *C. subg. Mespilus*. Sections in *C. subg. Sanguineae* are labeled S<sub>1</sub>, *C. sect. Salignae*, S<sub>2</sub>, *C. sect. Douglasiana*, and S<sub>3</sub>, *C. sect. Sanguinea*. The RAxML tree was inferred from a complete plastome alignment for a sample of 14 diploid accessions representing all of the infrageneric groups shown here (Table 1; Liston et al., in prep.), rooted using the apple plastome (Velasco et al., 2010), and collapsed as described in the text to show just the subgenera and the three sections within *C. subg. Sanguineae*. Support values are > 95% for all nodes except the one supporting *C. brachyacantha* (B; 46%). Labels are placed approximately in the center of the geographic distribution of the corresponding group. Branch lengths are arbitrary.



Figures 3. X-ray images of *Crataegus* short shoot leaf venation from taxa in the infrageneric groups discussed here (Table 1). (a) *Crataegus* subg. *Brevispinae*, *C. brachyacantha* (TRT00000025, M584760); (b) *C.* subg. *Mespilus*, *C. germanica* (TRT00026644, M584768); *Crataegus* subg. *Crataegus*, (c) *C. laciniata* (TRT00002426, M584673); (d) *C. laevigata* (TRT00002174, M584601); *Crataegus* subg. *Americanae*, (e) *C. calpodendron* (TRT00002039, M584551), (f) *C. triflora* (TRT00021431, M584762), (g) *C. opaca* (TRT00002042, M584679); *Crataegus* subg. *Sanguineae*, (h) *C. wattiana* (TRT00001881, M584549). (i) diploid *C. suksdorfii* (TRT00001805, M584618); (j) *C.* sect. *Salignae*, *C. saligna* (TRT00001047, M584583). Scale bars either 0.5 cm (b, j) or 1.0 cm in length (all others). Numbers in parentheses are barcode numbers for specimens in the Green Plant Herbarium (TRT) of the Royal Ontario Museum linked to collection data and online images, and the online MorphoBank media numbers. See Table 1 for taxonomy, details of the voucher specimens and images, and details of the MorphoBank project where x-ray images can be accessed.