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Article

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STUDIES IN *MESPILUS*, *CRATAEGUS*, AND ×*CRATAEMESPILUS* (ROSACEAE), I. DIFFERENTIATION OF *MESPILUS* AND *CRATAEGUS*, EXPANSION OF ×*CRATAEMESPILUS*, WITH SUPPLEMENTARY OBSERVATIONS ON DIFFERENCES BETWEEN THE *CRATAEGUS* AND *AMELANCHIER* CLADES

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Abstract

The paper argues the position for retaining a monotypic *Mespilus*, i.e., in the sense of *M. germanica*, the medlar. Recent cladistic papers lend support for *Mespilus* being sister to *Crataegus*, and there is a clear morphological distinction from *Crataegus*, emphasized by adaptation to carnivore frugivory. *Mespilus* secured, the paper then treats each of the known hybrids between *Mespilus* and *Crataegus*, making the new combination *Crataemespilus* ×*canescens* (J.B. Phipps) J.B. Phipps.

Keywords: *Crataemespilus* ×*canescens* (J.B. Phipps) J.B. Phipps comb. nov.; inflorescence position; medlar; *Mespilus* a folk-genus; *Mespilus* distinct from *Crataegus*; Rosaceae; taxonomic history of *Mespilus*

Introduction

The author has a long-standing interest in generic delimitation in the Maloid genera of the Rosaceae (Maleae Small, formerly Maloideae C. Weber, Pyrinae Dumort.), as shown particularly in a series of papers with K. Robertson, J. Rohrer, and P.G. Smith (Phipps *et al.* 1990, 1991; Robertson *at al.* 1991, 1992; Rohrer *at al.* 1991, 1994) which treated all 28 genera of Maleae as recognised by us. There is also a revisionary treatment of New World *Heteromeles* M.J. Roemer and *Photinia* Lindley (Phipps 1992). The number of genera in Maleae is variable, primarily as to the preferred treatment of *Sorbus* L. *s. l.*, *Malus* Mill. *s. l.*, *Photinia s. l.*, and *Crataegus* L. *s. l.* The first three are polyphyletic (e.g., Li *et al.* 2012) but the last, the subject of this paper, is monophyletic. Here, two closely related genera, *Crataegus* and *Mespilus* L., together with the less closely related *Hesperomeles* Lindley, constitute the *Crataegus* clade which is sister to the *Amelanchier* Medik. clade, though with very different morphology. The differences between the two clades are particularly noticeable in characters of the carpel whether in flower or fruit (Robertson *et al.* 1991; Rohrer *et al.* 1991, 1994). Maloids are characterized by their animal-dispersed fruit in which a soft, attractive and digestible hypanthium invests the carpels and in which hard elements are excreted undigested by frugivores. In the *Crataegus* group of genera the hard elements are bony carpellary walls (containing flake-like seed) while in the *Amelanchier* group it is the seed alone that is hard. The two fruit types may be differentiated as pome and ‘pseudoberry’. Other significant differences include the predominantly thorny nature of the *Crataegus* clade versus the thornless *Amelanchier* clade. A further interesting feature of some of the *Amelanchier* clade lies in sylleptic growth of the inflorescence which Lo *et al.* (2007) considered a differentiator and which is discussed below. Both clades have their greatest diversity in the New World and are presumed to have originated there.

Notably, all the molecular papers cited here show *Mespilus* as sister to *Crataegus*. However, that by Lo *et al.* (2007) is the only paper to argue that *Mespilus* should be sunk in *Crataegus*, which, accordingly, is carried out by Dickinson and Lo in the paper just cited, together with the nomenclatural changes needed to support this position. As such, the Lo *et al.* (op. cit.) paper will be given particular attention, see below. Lo *et al.* hold that the differences between *Mespilus* and *Crataegus* are few and insignificant while I intend to show that there are ample differences between the two genera.

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The present paper is also triggered by the awkward treatment under *Mespilus* of *M. canescens* J.B. Phipps in the *Flora of North America* vol. 9, Rosaceae (Phipps 2015), a taxon demonstrated by Lo *et al.* (2007) to be a *Mespilus*-*Crataegus* hybrid. The *Flora of North America* treatment in 2015 could not be helped if a *Crataegus* assignment was to be avoided due to the lack of a name for *M. canescens* in the nothogenus ×Crataemespilus E.G. Camus. This is remedied here. The present paper thus commences by a review of the relevant molecular work, especially Lo *et al.* (op. cit.), followed by a detailed elaboration of the morphological identity of medlar not only as distinct from hawthorns as a whole, but also specifically from *Crataegus brachyacantha* Sargent & Engelmann, a postulated basal taxon in the clade. It concludes with a review of the nothogenus ×*Crataemespilus*.

Mespilus distinct from *Crataegus*?

Molecular studies

Firstly, I consider evidence from the cladistic literature. Some of this covers Maleae as a whole, while other papers deal only with the *Crataegus* clade plus necessary outgroups. All molecular papers seen resolve *Mespilus* as closely related to a monophyletic *Crataegus*, e.g., Verbylaité *et al.* (2006: Fig. 1), Campbell *et al.* (2007: Fig. 6), Potter *et al.* (2007), Lo *et al.* (2009), Lo & Donoghue (2012), and Li *et al.* (2012). All the papers except Lo *et al.* (2007) accept *Mespilus* as a monotypic genus sister to *Crataegus.*

FIGURE 1. *Mespilus germanica.* Fruiting branches of wild type. Note fruit about 15 mm diam. with wide hypanthial openings. Cult., Kew. (photo K.R. Robertson).

Thus it is the paper by Lo *et al.* (2007) that is of particular interest here. It specifically posed the question '*Mespilus* and *Crataegus*, one genus or two?', and returned the answer 'one'. Then, to enable fusion of the genera, and rather than make a huge number of new combinations under *Mespilus*, *Crataegus* was proposed for conservation (Talent *et al.* 2008). Brummitt (2011) recorded the passing of this proposal by the *Nomenclature Committee for Vascular Plants* (report no. 62), which was approved by the International Botanical Congress in Melbourne (McNeill *et al.* 2012). Results similar to Lo *et al.* (2007) are reported by Lo *et al.* (2009) but in the latter paper attention is directed to the phylogeography of *Crataegus* and the hybrid origin of the *C. phenopyrum-spathulata-marshallii* group of species.

Importantly, the conclusions reached by Lo *et al.* (2007) were dependent on their including for the first time *Crataegus brachyacantha*. This taxonomically rather isolated species is a large, black-fruited hawthorn of the southern United States with narrow unlobed leaves and was shown to be on the most basal branch of *Crataegus s. str*. By contrast, *Mespilus germanica* is a large, brown-fruited plant also with narrow leaves, native to the Pontic (Black Sea) area. The many other *Crataegus* species constitute a mix with narrow, unlobed leaves and those with pinnately (usually shallowly) lobed leaves; red is the most common fruit color while a minority are yellowish or blackish. Lo *et al.* (2007) also included in their analysis the then putative nothospecies *M. canescens*, a rare Arkansas endemic, in which they had a special interest.

FIGURE 2. *Mespilus germanica.* Wild type in flower, diam. ca. 30 mm. Note some petals notched, long sepals, 28–30 stamens, red anthers. Cult., Kew.

Lo *et al.* (2007) used both nuclear (ITS and LEAFY) and chloroplast data. These three data sets were analyzed independently and together, using both maximum parsimony and maximum likelihood. My focus here is on the relationship of *Crataegus brachyacantha*, *Mespilus germanica* and *M canescens* in various analyses as set out in their Figs. 1–4; Fig. 5 presents the results without *M. canescens*. In every analysis (i.e., both separate and combined data) that includes *M. canescens* the critical three taxa *C. brachyacantha*, *M. germanica* and *M. canescens* consistently formed a triad (their Figs. 1–4). The order of clustering in this triad varies, the first fusion being always involving *M. canescens* and either *C. brachyacantha* or *M. germanica*, different orders of fusion occurring in the combined nuclear maximum parsimony and the chloroplast maximum parsimony analyses (their Figs. 2 and 3). There are also notable discrepancies between analyses in the order of clustering of some other taxon groups. In this respect it is informative to compare their Figs. 4 (containing *M. canescens*) and 5 (absent *M. canescens*). Figure 4 compares the maximum likelihood tree for the combined nuclear results (Fig. 4a) with that for the chloroplast results (Fig. 4b). In both these trees the *Mespilus*-*C. brachyacantha* triad was sister to *C.* sect. *Crataegus* (mainly red-fruited, +/- deeply pinnately-lobed leaves). Also in both, this larger group was sister to the remainder of *Crataegus*. However, when nuclear and chloroplast data were combined and *M. canescens* omitted from the analysis (their Fig. 5), the sister grouping to the *M. germanica* and *C. brachyacantha* pair was the entire remainder of *Crataegus*, not just *C.* sect. *Crataegus*. As well, in Lo *et al.*'s Fig. 5a (max. parsimony) *M. germanica* was shown to be sister to *C. brachyacantha*, while the same paper's Fig 5b (max. likelihood) showed *M. germanica* sister to all *Crataegus.* The authors concluded that "after removing conflicts due to hybridization or other factors, the analyses of the combined nuclear and chloroplast data (Lo *et al.,* Fig. 5) suggest that *C. brachyacantha* is sister to the remaining *Crataegus* species, rather than to *M. germanica*". Nevertheless, the authors proceeded with the steps required to combine *Mespilus* and *Crataegus* under the latter genus. Why was this?

FIGURE 3. *Mespilus germanica.* Fruit of cv. Nottingham. Note proportionately broad leaves, very large fruit (ca. 35 mm diam.), wide-spaced, very long sepals. Arrowed are: (a) style projecting through disc tissue; (b) undulating surface of disc tissue covering pyrenes; (c) split in side of fruit caused by inadequate allometric growth. Cult., Ailsa Craig, Ontario.

Lo *et al.*'s (2007) primary reason for uniting the two genera is clearly their perception that there are so few morphological characteristics that convincingly differentiate *Mespilus* from *Crataegus*, effectively, only the covered pyrenes of *Mespilus* lacked by *Crataegus*, which they clarify by reference to Medikus and Lindley. This distinction is undoubtedly correct, as far as it goes. Lo *et al.* further note that attempts to distinguish the two genera on other characteristics have often failed because "character states supposed to be diagnostic of *Mespilus* occur in species of *Crataegus*". This is also certainly true, as articulated in my companion paper (Phipps 2016) and illustrates the confusion of many botanists on the issue. Finally, Lo *et al.* (2007) state in support of their position: "…because the number of morphological differences between the *Mespilus*-*Crataegus* clade and *Amelanchie*r is considerably greater than those distinguishing *Mespilus* and *Crataegus* from each other, it seems more reasonable to sink the smaller genus in the larger...". Such a statement, besides being not logically compelling, is partly based on incorrect premises. This feeds into the discussion, below, of inflorescence differences among the relevant genera and clades. As a result, Lo *et al.* have unnecessarily presented new and unfamiliar names to the botanical public.

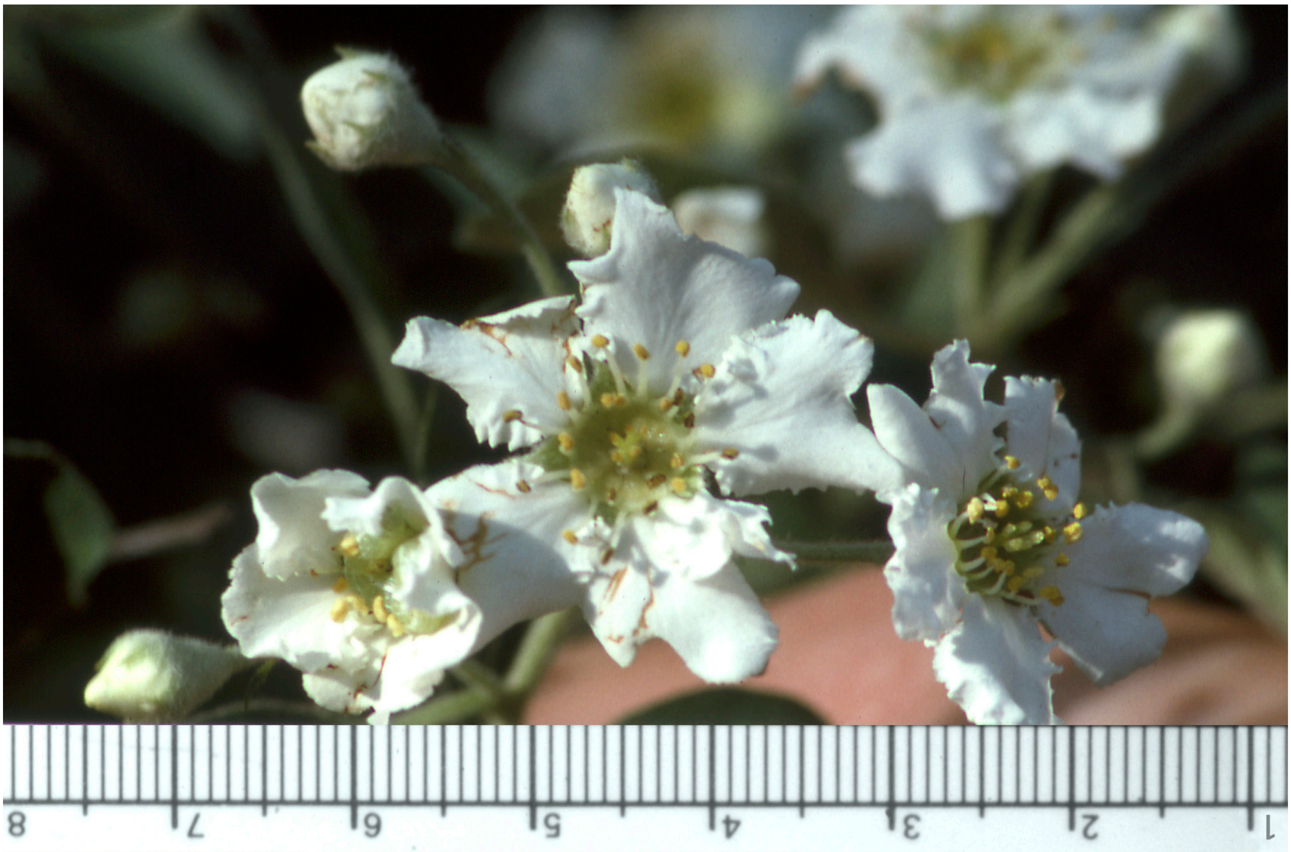

FIGURE 4. *Crataemespilus ×canescens* flowers. Note large size (ca. 25 mm diam.), ca. 20 stamens, yellow anthers, notched petals. Arkansas.

FIGURE 5. *Crataegus brachyacantha* infructescence showing blackish fruit with small hypanthial opening. Texas. (photo R.W. Lance).

Of the other cited authors who maintained *Mespilus*, two also used *Crataegus brachyacantha.* The first, another paper by the senior author (Lo *et al.* 2012), but on the entire tribe Maleae (there subtribe Pyrinae), also using both chloroplast and nuclear DNA evidence, though excluding the nothospecies *Mespilus canescens*, made *Mespilus* sister to *Crataegus*. Interestingly, in this paper the authors showed no inclination to resuscitate the rarely used combination *C. germanica* (L.) K. Koch, but rather stuck with the familiar *M. germanica*. A very similar result was produced by Li *et al.* (2012), also on the entire tribe Maleae (again, as subtribe Pyrinae). Here, the authors did use both *C. brachyacantha* and *M. canescens*, though the analysis was based on only ITS nuclear ribosomal DNA data. In this paper, Li *et al.* found *Mespilus* to be weakly supported, a result which actually strengthens the case for retaining *Mespilus*, in view of the fact that the presence of the nothospecies *M. canescens* may be expected to dilute the support for *Mespilus*. Consequently, had the authors not used *M. canescens*, *M. germanica* should have been more strongly supported.

Tree topologies are affected by choice of taxa, and the inclusion for the first time of *Crataegus brachyacantha* by Lo *et al.* (2007) was very significant in this respect. Not only was a species from the black-fruited group, in which these authors already had a special interest, included for the first time, but this species was a taxon with a narrow, lobeless leaf type, now established as being plesiomorphic in the *Crataegus* clade. Thus, one also eagerly awaits investigations which include the taxonomically isolated red/yellow-fruited Chinese species *C. scabrifolia* (Franchet) Rehder which has a narrow, lobeless leaf type, and which may well alter the basal topology again.

Thus, because *Mespilus* is always concluded to be sister to *Crataegus* in the cladistics literature, and because my view, discussed below, is that there is ample difference between the genera, I regard the case for merging *Mespilus* and *Crataegus* as at best optional or even unnecessary.

FIGURE 6. *Crataegus brachyacantha* inflorescences showing numerous small flowers on type A inflorescence. Texas.

Evidence from intergeneric hybrids in Maleae, especially ×Crataemespilus

I feel that too much can be made of the frequency of intergeneric hybrids in the Maleae as an argument for uniting genera. It is worth noting that although hybrids between many pairs of Maloidean genera are known (Robertson *et al.* 1991), except for those involving *Sorbus* most are very rare in nature else only known in botanic gardens as human creations. Also, except for those alloploid species derived from crosses of *Sorbus* with *Aria* (Persoon) Host, *Chamaemespilus* Medicus, and *Torminaria* M. Roemer, nearly all are highly sterile. Notably, in the case of *Mespilus*-*Crataegus*, western Eurasian wild examples of the nothogenus ×*Crataemespilus* are nearly unknown, even where both genera are common elements of the native flora. The naturally occurring Arkansas endemic *Mespilus canescens* is also nearly sterile (see discussion under the nothospecies) and only known from one population. One may additionally note the complete absence of natural intergeneric crosses in Maleae between certain pairs of common, sympatric, speciose genera, especially *Malus* with *Pyrus* L., or either with *Crataegus*, as well as between such sister-genera as *Cormus* Spach and *Sorbus*, which underscores the contention made at the beginning of the paragraph.

FIGURE 7. *Crataegus brachyacantha*. Note short shoot bearing fruit. Louisiana.

Mespilus and Crataegus distinguished morphologically

Mespilus is distinguished from all species of *Crataegus* by a number of characters. The presence of several consistent differences is the more notable in view of the considerable variation existing within the large genus *Crataegus*. Nevertheless, the basic morphology of the two genera is broadly similar, the fruit of both, for instance, being a kind of polypyrenous pome (erroneously, and impossibly, called a polypyrenous drupe by some).

FIGURE 8. *Amelanchier arborea.* Herbarium specimen in flower. Note sylleptic growth (at a), and types A and B inflorescence origin, arrowed (respectively at c2 and b). Ontario.

Mespilus s. str., i.e., monotypic, is a large, sometimes thorny, shrub with simple, finely serrate to entire leaves, usually uniflorous inflorescences, large hairy, eglandular bracteoles rather like those of certain other Maloideae outside the *Mespilus-Crataegus* clade (e.g., *Amelanchier*), large, perigynous, hawthorn-like flowers, and large brown fruit in which tissues of the disc completely cover the pyrenes, and through which style remnants penetrate (Figs. 1, 2, 3). The flesh of the fruit of *M. germanica* is also particularly rich in stone cells (Rohrer *et al.* 1991).

Crataegus is a large genus of shrubby or subarboreal habit, usually thorny, with entire to deeply pinnatifid leaves, distinctly marginally toothed in most, usually multiflorous inflorescences that are both monopodial and domed, with usually much smaller flowers and fewer stamens than *Mespilus*, smallish fruit (5–15 mm, except cvs.), most often reddish in color, though many are blackish and some yellow to orange; hypanthium in fruit nearly closed; pyrene tips exposed.

Formal descriptions of *Mespilus and Crataegus* and key to genera are given under 'Taxonomy', below.

Fruit differences

It is in the fruit of *Mespilus* that the most distinctive characters are found. In fact, the brownish fruit of *M. germanica* has been shown to be specifically adapted to mammalian carnivore dispersal (Herrera 1989). This fits well the notion of genus as an adaptive suite and has parallels in other brown-fruited Maloidean genera such as *Pyrus*, *Torminalis*, and *Cormus*, as Herrera (op. cit.) points out. This relationship is also evident in an UPGMA phenogram of an 18 fruit-character Manhattan distance of 173 species of Maloideae (Rohrer *at al.* 1991: Fig. 35). The distinctive features of *Mespilus* fruit are mirrored in the characteristic flavor of medlar fruit when made into a delicious conserve by specialist firms (Phipps *et al.* 2003), or as eaten fresh but sightly decayed ('bletted'), which is quite different from similar mayhaw (*Crataegus* ser. *Aestivales*) or tejocote (*C. mexicana*) products. Note also the very large, foliaceous, unlobed, +/- entire fruiting sepals that are erect to connivent and distant in *Mespilus* (Fig. 8).

Flowering differences

In flower, *Mespilus* differs from *Crataegus* both in petal form and bracteole type. The petals of *M. germanica* are usually notched (Fig. 2) as they are also in its hybrid *M. canescens* (Fig. 4). With regard to the bracteole distinction from *Crataegus*, *Mespilus* has large, densely abaxially hairy and eglandular bracteoles. No *Crataegus* shares this ensemble, one which can, however, be found in *Amelanchier*. Most *Crataegus* have smaller, abaxially glabrous and gland-margined bracteoles while those with larger bracteoles are almost always conspicuously gland-margined, an exception being *C. viridis* L. (*C.* sect. *Coccineae*, *C.* ser. *Virides*), which is also glabrous. Those that are significantly abaxially hairy are restricted to *C.* sect. *Crataegus* (many), *C.* sect. *Sanguineae* ser. *Nigrae* (most), *C.* sect. *Coccineae* ser. *Molles* s.l. (general), and the apparently closely related series *C.* ser. *Triflorae*, *Bracteatae*, and *Parvifoliae*, but all the above have bracteoles that are strongly gland-bordered. There remains only *C. brachyacantha*, which has small, eglandular bracteoles in which the pubescence is very sparse. These differences were not considered by Lo *et al.* (2007).

Resting bud differences

The resting buds of medlar and hawthorns are basically similar though conical, dull and gray-brown in *Mespilus* as opposed to +/- globular, shiny and reddish in *Crataegus*. Resting bud differences were not considered by Lo *et al.* (2007).

Other evidence

Folk-taxonomy always distinguishes *Mespilus* from *Crataegus*, as reviewed in detail in a companion paper (Phipps 2016). Thus, the distinctive folk names of *Mespilus*, as well as its cultural significance as reviewed by Baird & Thieret (1989), represent additional reasons for retaining *Mespilus*. Further, the academic taxonomy traced since Linnaeus (Phipps 2016) demonstrates a consistent preference for two genera, though often with an inadequate understanding of their differences.

Molecular analyses routinely indicate a *Mespilus-Crataegus* clade, and all researchers but Lo *et al.* (2007, 2009), who favor its union with *Crataegus*, maintain *Mespilus*. Lo *et al.* (2007) was significant for including *C. brachyacantha* (which comes from a basal branch) and *M. canescens* for the first time. Natural hybrids between *Crataegus* and *Mespilus* are very rare and more or less sterile—in the Maloidean context not a strong argument for generic fusion. The fundamental differences between *M. germanica* and *Crataegus* are largely in the fruit but there are also lesser differences in the flowers, bracteoles and dormant buds, though not in inflorescence position. I regard the suite of fruit characters as central, especially in view of Herrera's demonstration of adaptation to carnivore frugivory. In my view the differences found between *Mespilus and Crataegus* are more than ample for the continued recognition of *Mespilus* as a distinct genus.

However, as will be demonstrated in a companion paper (Phipps 2016) it is the inadequate or even quite wrong understandings of these differences that has sometimes lead to the idea that the differences are slight, and as such, might justify combining these genera. Thus, Lo *et al.*'s (2007) arguments that significant character overlap can be found between these two genera carry little weight; indeed character overlap is to be expected between related genera. Similarly, their view that there is little actual difference between *Mespilus* and *Crataegus* must be rebuffed as the distinctions between *Mespilus* and *Crataegus* are evident and sufficient. Finally, the close contact of rural people with plants that impact their lives, and that has lead them always to distinguish medlar from hawthorn, makes an interesting validation of the thesis presented here, and is discussed in the companion paper (Phipps 2016).

Comparisons with *Crataegus brachyacantha* and the *Amelanchier* clade

Crataegus brachyacantha

Because *Crataegus brachyacantha* is the *Crataegus* species branching off closest to *Mespilus germanica* (e.g., Lo *et al.* 2007, 2012; Li *et al.* 2012), it is instructive to compare these two species directly. *Crataegus brachyacantha* and *M. germanica* are not particularly similar, beyond characteristics common to the clade. Rather, large differences exist beyond those that distinguish the genera. For example, *C. brachyacantha* has fruits which are quite small and have a very small hypanthial opening (Fig. 5) and are black (in common with a considerable minority of *Crataegus*), has multiflowered, small-flowered inflorescences (Fig. 6) with the typical proleptic *Crataegus* type A2 inflorescence placement (Fig. 7), sepals much shorter than petals—almost universal in *Crataegus*, 20 stamens—one of the two common values in *Crataegus*, and numerous other details. Nevertheless, it does share with *Mespilus germanica* petals that discolor with age (in *M. germanica* to pale fawn, in *C. brachyacantha* to quite a bright orange-yellow, though the phytochemistry of this is unknown), and abaxially hairy, eglandular bracteoles (though these are much smaller and much less hairy in *C. brachyacantha*), and very short thorns, mostly characteristics that are rare or uncommon in *Crataegus*, as well as narrow, unlobed leaves, found in many *Crataegus*. Thus, *Crataegus brachyacantha* is, for the most part, already a 'typical' *Crataegus* with substantial morphological divergence from *M. germanica*. It is therefore evident that at least one of these two, presumably *M. germanica*, differs greatly from their common ancestor.

The distributions of *Crataegus brachyacantha* and *Mespilus germanica* are somewhat similar, though on different continents. *Mespilus germanica* as a minor fruit is now widely but sparsely naturalized in the southern half of Europe but its native range is from extreme southeast Europe to northern Iran according to Browicz (1968), with northern limits near Yalta, Crimea, at 44° N, and a southern limit at high altitude in Iraqi Kurdistan at ca. 37° N, an area with a predominantly Mediterranean (winter max. precipitation) climatic type. Its greatest wild concentration appears to be across much of northern Turkey and the Caucasus (Browicz 1968) where the summer precipitation is stronger. The lowest branch on the phylogenetic tree of *Crataegus*, *C. brachyacantha*, is known only as a wild plant and occurs in Louisiana, U.S.A. and adjacent states at ca. 29° N–34° N with an isolated and apparently extinct record in Georgia (Phipps 1998). This area has a more humid warm temperate climate lacking seasonal precipitation. Both taxa thus occur in regions with mild to moderate winters well to the south of the northern limit of *Crataegus*, much of the later radiation of which involved adaptation to colder climates.

Time of divergence of Mespilus-Crataegus and similarities to Amelanchier

With their considerable differences and somewhat southern locations separated by a large oceanic barrier, the *Mespilus-Crataegus* divergence must have been long ago, whether it was early Oligocene, e.g., Lo *et al.* (2012), perhaps via a North Atlantic route, or trans-Beringian in a later warm episode. Since molecular studies by Campbell *et al.* (2007), Potter *et al.* (2007), Lo & Donoghue (2012), Li *et al.* (2012) all unite *Mespilus-Crataegus* with the *Amelanchier* clade it is likely that their common origin is in the New World as believed by Lo *et al.* (2009). Lo *et al.* (2009) left the location of common origin ambiguous but considered it to result in a North Atlantic vicariance. If so, the *Mespilus* ancestor, as an early disperser to the Old World, has apparently left only one extant descendent there, *M. germanica.* The deep relationship to the *Amelanchier* clade is supported by *Mespilus* bracteoles (very large, eglandular, abaxially hairy) being similar to those of many *Amelanchier* species and by both these genera having two locations of origin of the annual reproductive shoot (lateral to extension shoots and at the tips of woody short shoots), as noted above.

FIGURE 9. *Amelanchier laevis.* Flowering herbarium specimen. Note type A1 inflorescence origin, with short shoots, arrowed. Ontario.

Inflorescence type and position

The Maloid inflorescence is of a monopodial and monotelic construction, usually branched to at least the second order, with 1 to several hundred flowers. Anthesis is normally in spring and the inflorescence is usually terminal on a relatively few-leaved fertile shoot of the season, the uppermost leaf or two of which are sometimes bracteal. *Mespilus* differs from *Crataegus* by having 1 to few flowers per inflorescence vs. 1 to ca. 50.

The location of origin of the flowering shoot varies in the *Crataegus* and *Amelanchier* clades. The origin may often be subterminal on a woody shoot, itself commonly a short shoot. I will provisionally call this fertile shoot position (i.e., terminal or subterminal on woody short shoots) 'type A'. However, it is interesting to note that the flowering shoot may instead be borne lateral to the extension shoot, which position I will provisionally call 'type B'. The type A situation is seen in *Amelanchier arborea* (Michaux f.) Fernald (Fig. 8c) and also in all the inflorescences in *A. laevis* Wiegand (Fig. 9) while the type B situation may be clearly seen in the same specimen of *A. arborea* (Fig. 8b). Similarly, in wild-sourced *Mespilus germanica* specimens cultivated at Copenhagen and Kew, both type A (Fig. 10) and type B (Fig. 11) fertile shoot origins may be observed. With regard to *Crataegus*, by far the predominant situation is type A, with the leafy flowering shoot arising subterminally from a woody short shoot, as illustrated in *C. brachyacantha* (Fig. 7). In *Crataegus*, the type B origin was first noticed by Phipps *et al.* (2006) in the widespread though only locally occurring southeast United States species *C. triflora* Chapman of *C.* ser. *Triflorae* (Fig. 12). It is believed that this was the first explicit record of the different origins of the fertile short shoot in Maleae. The type B situation has since been recognized in the apparently extinct *C. austromontana* Beadle of the same series, and to a limited extent in *C. harbisonii* Beadle of the related *C.* ser. *Bracteatae* (Phipps *et al.* 2006), perhaps itself a hybrid of *C.* ser. *Triflorae*. It can also occur in the Chinese species *C. cuneata* and may also occasionally be seen in *C. uniflora* (*C.* ser. *Parvifoliae*), the only *Crataegus*, like *M. germanica*, with sepals longer than petals. Thus, neither inflorescence type nor position of origin of the fertile shoot separates *Mespilus* from *Crataegus.* On the other hand, inflorescences arising from woody short shoots (type A) in *Amelanchier* may be separated from those of *Mespilus* and *Crataegus* by being borne on terminal (type A1) or subterminal (type A2) buds in *Amelanchier* and from subterminal buds only in *Mespilus* and *Crataegus* (type A2).

Lo *et al.* (2007) correctly pointed out that the *Amelanchier* and *Crataegus* clades differ by much more than do the sister genera *Mespilus and Crataegus*. In emphasizing this fairly deep separation they draw attention to the presence of sylleptic growth of vegetative shoots from the fertile shoots of *Amelanchier* (see a, Fig. 8), a feature not observed in the *Crataegus* clade, nor indeed, in most of the Maleae. However, the situation appears to be more complicated than this as sylleptic branching has so far not been detected in *Peraphyllum* or *Malacomeles*, the other two members of the *Amelanchier* clade and thus that clade cannot be defined by this. In fact, it is worth asking whether sylleptic growth in *Amelanchier* is not merely reflective of the elongated, racemose inflorescence form common in *Amelanchier*, and apparently unique in Maleae, which allows space for such sylleptic growth to take place. Indeed, even though it is quite common in the genus, sylleptic branching from reproductive shoots in *Amelanchier* clearly does not occur below all inflorescences. Likewise, the corollary which Lo *et al.* (2007) note, a proleptic fertile shoot arising from a subterminal dormant bud, generating a sympodial short shoot system, does not appear to be universal in *Mespilus-Crataegus*, though it is by far the most common.

With regard to the *Malacomeles* and *Peraphyllum* subclade of the *Amelanchier* clade, perennial short shoots, if any, are extremely short and in *Malacomeles nervosa* (Decaisne) G.N. Jones, the fertile shoot bearing an inflorescence may on occasion arise from a leaf axil as is evident in *Phipps 5889* (UWO!) from Comitán, Chiapas, Mexico, collected in October (1985). Neither do *Malacomeles* and *Peraphyllum* show any sign of sylleptic branching from the leafy part of the shoot below the inflorescence as mentioned above. It thus seems that use of the feature of sylleptic vs. proleptic branching to separate the two subclades does not work.

The complicated issues of inflorescence position and sylleptic branching in the inflorescence aside, Lo *et al.* (2007) detail many differences between the *Amelanchier* and *Crataegus* subclades. I regard the most powerful of these as the carpellary differences in flower, and the hard elements in fruit. In the *Amelanchier* subclade the seed is the hard part that is not digested by the frugivore and which is excreted; in the *Mespilus-Crataegus* subclade, it is the carpellary wall that is hardened. Thus two very different fruit types are created—a pseudoberry and a pyrenous pome.

Taxonomy

Key to Mespilus and Crataegus

1. Fruit large (15–40 (–70!) mm), brown, with abundant grit cells; hypanthium open from abt. 50% to 90% width of fruit, exposing the mature, undulating, firm hypanthial disc, but not the pyrene tips, unless damaged; sepals in fruit, firm, long, bases distant;

bracteoles abaxially hairy, eglandular, 6–15 mm, some persistent and +/- scarious; petals notched; resting buds conical, dark grey-brown, +/- dull .... ***Mespilus***

- Fruit smaller (5–15 mm, except cultivars), +/- brightly colored, commonly red or blackish (more rarely yellow to orange), grit cells few to plentiful; hypanthium open from abt. 10% or less to ca. 30% width of fruit, mature hypanthial disc reduced to a remnant ring, pyrenes sometimes exposed apically but more usually hidden within the hypanthium by stamen and style remnants; sepals in fruit firm to erose, short to long, bases flared so as to be +/- contiguous (rarely circumscissile); bracteoles abaxially hairy or glabrous, not both abaxially hairy and eglandular, glandular or not, 2–12 mm, usually caducous or deciduous, occasionally persistent, usually membranous, at most herbaceous, never +/- scarious; petals entire; resting buds usually +/- globular (subconical in some sect. *Crataegus*), deep red or reddish brown, shiny .... ***Crataegus***


HERBARIUM OF THE UNIVERSITY OF WESTERN ONTARIO (UWO)
PLANTS OF SCANDINAVIA
Western

Name: *Mespilus germanica* L.
Locality and Notes: Denmark, Sjaelland, Hoersholm. Arboretum.

4 m tall; vigorous tree; fruit brown. Arb. no. 1983.0507.

Collector and Number: J. B. Phipps 9327 with K.I. Christensen
Date: 03 October 2006
UWO Number: 52803

Department of Biology
London, Ontario, N6A 5B7
Canada

FIGURE 10. *Mespilus germanica.* Fruiting herbarium specimen; wild type. Note type B origin infructescences, arrowed. Cult., Kew.

Formal descriptions of Mespilus and Crataegus

Mespilus L. (1753: 478). (Figs. 1–3, 10, 11, 17, 18)

Type: *Mespilus germanica* L. (syn. *Crataegus germanica* (L.) Kuntze).

HERBARIUM OF THE DEPARTMENT OF
PLANT SCIENCES
UNIVERSITY OF WESTERN ONTARIO (U.W.O.)

HERBARIUM OF THE ILLINOIS NATURAL HISTORY SURVEY
CULTIVATED PLANTS OF THE ROYAL BOTANIC GARDEN, KEW
RICHMOND, SURREY, ENGLAND

Mespilus germanica L.

Locality Coordinates: 434
Accession Number: 114-35-11405
Notes:

K. R. Robertson 3952 SEP 18 85

Funding provided by the National Science Foundation

FIGURE 11. *Mespilus germanica.* Fruiting herbarium specimen; wild type. Note type A infructescence origin, with short shoots, arrowed. Cult., Kew.

Shrub or small tree, 3–6 (–8) m. Bark of trunk grayish or gray-brown (Fig. 17), when older flaking and revealing orange-brown fresh bark; on younger stems (1–2 cm diam.) grayish, often with horizontal lenticels (Fig. 18). Twigs unarmed or armed with straight, blackish, determinate thorns 1–2 cm; woody short shoots present in some forms, absent in others; current growth canescent. Winter buds 3–6 mm, conical, 8–12-scaled, scales imbricate, dark gray-brown or dull brownish-red. Leaves simple, entire or with minute teeth, particularly distally, 3–12 cm, narrow-obovate or elliptic to +/- oval, pubescent, multi-veined, venation camptodromous. Inflorescences 1(–2)-flowered, with about

2–5 leaves below the flower(s), subterminal on woody short shoots (type A2—Fig. 11) or borne terminally or directly lateral to extension shoots (type B—Fig. 10); few-bracteolate, bracteoles 5–15 mm long, very narrow, acuminate, +/- membranous to coriaceous, caducous to persistent, abaxially hairy, eglandular. Flowers 25–35 mm diam.; hypanthium densely canescent; disc canescent centrally, disc saucer-shaped with opening for styles; sepals narrow, acuminate, 10–30% longer than petals, margins sometimes with a few, very narrow, +/- long, teeth; petals +/- circular, very short clawed, somewhat cupped, white, often notched apically; stamens ca. 25–35, anthers red (cream); styles 5, adnate to ventral side of carpel for most of length and projecting through central opening in disc; carpels 5, connate, adnate to hypanthium and disc, ovules 2, collateral. Fruit +/- spherical to somewhat turbinate, 12–15 mm (wild types), 25–40 mm or more (cultigens), brown, glabrous or pubescent, punctate; hypanthial opening very wide, 60–90% width of fruit; flesh of hypanthium firm at first, whitish, acid, later becoming brown, mushy, fragrant, +/- sweet; sepals green, distant, much enlarged since flower, narrow, erect to connivent; tissue of disc confluent, covering pyrenes, surface smooth but uneven (Fig. 8); styles erose to present, projecting through disc tissue; pyrenes 5, large, hidden within hypanthial enclosure below tissues of disc, hard, dorsally grooved, sides somewhat irregular. x = 17 (2n = 34).

FIGURE 12. *Crataegus triflora* flower. Note large stamen no. (ca. 35), first report of this (photo 12.iv.1999), flower diam. ca. 27 mm. Alabama.

One species, southeastern Europe and southwestern Asia.

It is also notable that the Linnaean type of *Mespilus germanica*, of which there is a good image on the website 'Linnaean plant names and their typifications', shows the flowering shoots to be of type A origin.

Crataegus L. (1753: 475).

Type: *Crataegus oxyacantha* L., nom. rejic. (= *C. rhipidophylla* Gandoger).

Shrubs or small trees, 0.5–8 (–12) m. Bark of trunk commonly grayish or gray-brown, when older flaking and revealing orange-brown fresh bark, alternatively deeply corrugated and dark, more rarely smooth and finely exfoliating or smooth and with horizontal lenticels; on younger stems (1–2 cm diam.) usually pale to dark gray, seldom with horizontal lenticels. Twigs usually armed with straight to curved, dark when young, determinate thorns, 1–6 (–11) cm, or rarely +/- unarmed; else twigs tipped with indeterminate thorns; woody short shoots present; current growth glabrous to tomentose. Winter buds 2–4 mm, usually spherical, sometimes subconical, 6–10-scaled, scales imbricate, usually dark shiny reddish. Leaves simple, entire to deeply pinnatifid margins usually with numerous small, even teeth, 1–8 (–10) cm, suborbiculate to narrow-lanceolate, widest part variably positioned, glabrous to variably pubescent, 1–10-veined per side, venation commonly craspedodromous, sometimes camptodromous. Inflorescences 1–50-flowered shallowly domed monopodial panicles (or in few-flowered forms reduced to racemes or uniflory), with about 2–8 leaves below the flower(s), sometimes with leafy bracts subtending proximal branches; usually subterminal on short shoots (type A2) or borne terminally or laterally direct on extension shoots (type B); bracteoles few to numerous 2–15 mm long, linear to narrow-ovate, usually acute, +/- membranous to subherbaceous, caducous to persistent, abaxially hairy or glabrous, commonly gland-margined. Flowers: 8–25 mm diam., perigynous; hypanthium +/- obconic, constricted around disc, disc saucer-shaped except for style opening; sepals 5, free, distinct, triangular, usually much shorter than petals, margins entire to serrate or sometimes laciniate, the teeth gland-tipped; petals 5, 3–12 mm, free, white (except pink to red in mutants), usually suborbiculate, barely clawed, +/- entire margined; stamens 5-ca. 20 (usually ca. 10 or ca. 20, in *Crataegus triflora* 30–45), anthers white to cream or anthocyanic (pink to red or purplish); carpels 1–5, free but laterally touching, adnate to hypanthium, styles 1–5, lateral and adnate to ventral side of carpel for most of length, free, exserted from hypanthial opening, ovules 2, superposed. Pomes: subspheric to ellipsoid or pyriform, 6–15 (–20) mm diam. (–25 mm or somewhat larger in some cultivars), red to yellow or purplish to black at maturity, glabrous to tomentose, sometimes punctate; flesh often becoming soft, often insipid, sometimes sweet and pleasant to eat; hypanthial opening present (tissues of disc absent), 10–35% width of fruit; sepals often persistent, sometimes erose or circumscissile, appressed to erect, bases usually nearly touching; shriveled filaments and dried styles often persisting though may be erose; pyrenes 1–5, within hypanthial enclosure though tips sometimes visible, very hard, dorsally grooved, sides smooth or pitted. x = 17 (2n = 34, 51, 68, usually).

FIGURE 13. ×*Crataemespilus* collage. *Crataemespilus* ×*gillotii* 1–3 (lhs); *C.* ×*grandiflora* 4–9 (rhs). Note deeper leaf lobing in *C.* ×*gillotii*, deeper stipule lobing in *C.* ×*grandiflora* (from Beck 1914).

Ca. 250 species, north temperate regions; a few introduced in southern hemisphere temperate regions and tropical Andes.

FIGURE 14. *Crataemespilus* ×*grandiflora* trunk showing exfoliating bark; freshly exposed bark bright orange-brown. Cult., Kew. (photo K.R. Robertson).

HERBARIUM OF THE UNIVERSITY OF WESTERN ONTARIO (UWO)

PLANTS OF THE UNITED KINGDOM

Name: xCRATAEMESPILUS grandiflora E.G. Camus

Locality and Notes:
Collected as xCrataemespilus grandiflora E.G. Camus
Royal Botanic Gardens, Kew, Richmond, Surrey. 0°18'W 51°28'N.
Alt. approx. 30' a.s.l. Kew #000-73.19136. Young 4 m
bush in 345. Flowers white, anthers pink; almost scentless.

Collector & Number: J.B. Phipps #5640
Date: 21 May 1985

UWO Number:

Department of Plant Sciences
Biological & Geological Building
London, Canada N6A 5B7

FIGURE 15. *Crataemespilus ×grandiflora* flowering herbarium specimen. Note short shoots, arrowed. Cult., Kew.

×*Crataemespilus* Camus (1899: 326). (Figs. 4, 13–16, 19–24)

Type: *Crataemespilus* ×*grandiflora* (Smith) E.G. Camus (= *Mespilus grandiflora* Smith).

It is difficult to characterize nothogenera and no real attempt will be made to do so. Suffice it to say that all three nothospecies have obvious similarities to *Mespilus germanica* and two also show similarities to particular *Crataegus* species. Figure 13 illustrates a collage of the European taxa taken from Beck in Reichenbach (1914).

FIGURE 16. *Crataemespilus* ×*grandiflora* immature fruits. Note leaves proportionately broader than wild-type *Mespilus germanica*, smaller hypanthial openings, fr. diam. ca. 15 mm. Cult.. Kew. (photo K.R. Robertson).

×*Crataemespilus* was erected by E.G. Camus in 1899 to accommodate a presumed intergeneric hybrid originating in European horticulture that had first been described as a *Mespilus*, even though it was already firmly believed to be an intergeneric hybrid. Byatt *et al.* (1977) concurred with Smith's 'very unambiguous statement concerning the parentage' that *C. laevigata* (Poir.) DC. was one parent, particularly on the basis of leaf shape. In 1914 Beck added to ×*Crataemespilus* the very rare, naturally occurring, presumed nothospecies *C.* ×*gillotii*, proposing the parentage *C. monogyna* × *M. germanica*, this interpretation being accepted by Byatt *et al.* (1977) as reasonable. Gillot (1876) had already published the latter nothotaxon under the invalid name *C. oxyacantha-germanica* and held it to have the same origin. We may now recognize three nothospecies in ×*Crataemespilus*, the third, added in this paper, being based on *Mespilus canescens*. For those who wish, the three nothospecies of ×*Crataemespilus* may be placed in two nothosections, as set out in Lo *et al.* (2007), and the authors of *Crataegus* nothosect. ×*Phippsara* T.A. Dickinson & E.Y.Y. Lo are thanked for their generous comments.

Attempts to substitute the prior name +*Crataegomespilus* Simon-Louis ex Bellair (1899: 482) should be rebuffed. Not only is the name invalid under the Code, but this strange organism is an unstable chimaera produced by grafting, in which tissues of the *Crataegus* and *Mespilus* are intermixed, giving at first an appearance of hybridity. As plants of this so-called 'graft-hybrid' age there tends to develop a segregation of tissue such that pure branches of *Mespilus* or *Crataegus* may be seen. Older bushes sometimes revert fully, at least as far as macroscopic observation is concerned, to either *Mespilus* or *Crataegus*. In my view, such plants (there are few other examples), in which the two genomes are haphazardly and unstably arranged cannot be equated with normal taxa.

FIGURE 17. *Mespilus germanica*, wild type, trunk of mature tree. Cult., Kew. (photo K.R. Robertson).

Crataemespilus ×*grandiflora* is well known in cultivation and its variability apparently encompasses the narrow range of the variability of *C. gillottii*. Consequently, these two European hybrids cannot at this stage be convincingly separated in a key although the characters used by Beck will be used in an attempt to do so. Note that the very low level of sexual fertility of all three nothospecies of ×*Crataemespilus* underscores the width of these hybrids and further supports the recognition of *Mespilus* as distinct from *Crataegus* in line with the earlier general discussion of intergeneric hybrids in the Maloideae.

Key to nothospecies of ×*Crataemespilus*

1. Bushes with fasciculate stems; leaves grayish-canescent; inflorescences 2–6-flowered, racemose; petals notched; anthers pale

yellow; fruit 8–12 mm, bright red; Arkansas, USA .... 3. ***C.*** **×*canescens***

- Bushes with 1 to several stems, latter divergent; leaves shiny green at maturity; inflorescences uniflorous to 2–4-flowered, cymose-paniculate; petals entire or sometimes slightly notched; anthers pink; fruit 12–15 mm, golden ripening to burgundy; western Europe .... 2.

2. Stipules entire; leaves completely lacking lobes or sometimes with slight bulges .... 1. ***C.*** **×*grandiflora***

- Stipules serrate; some leaves distinctly lobed ....2. ***C.*** **×*gillotii***

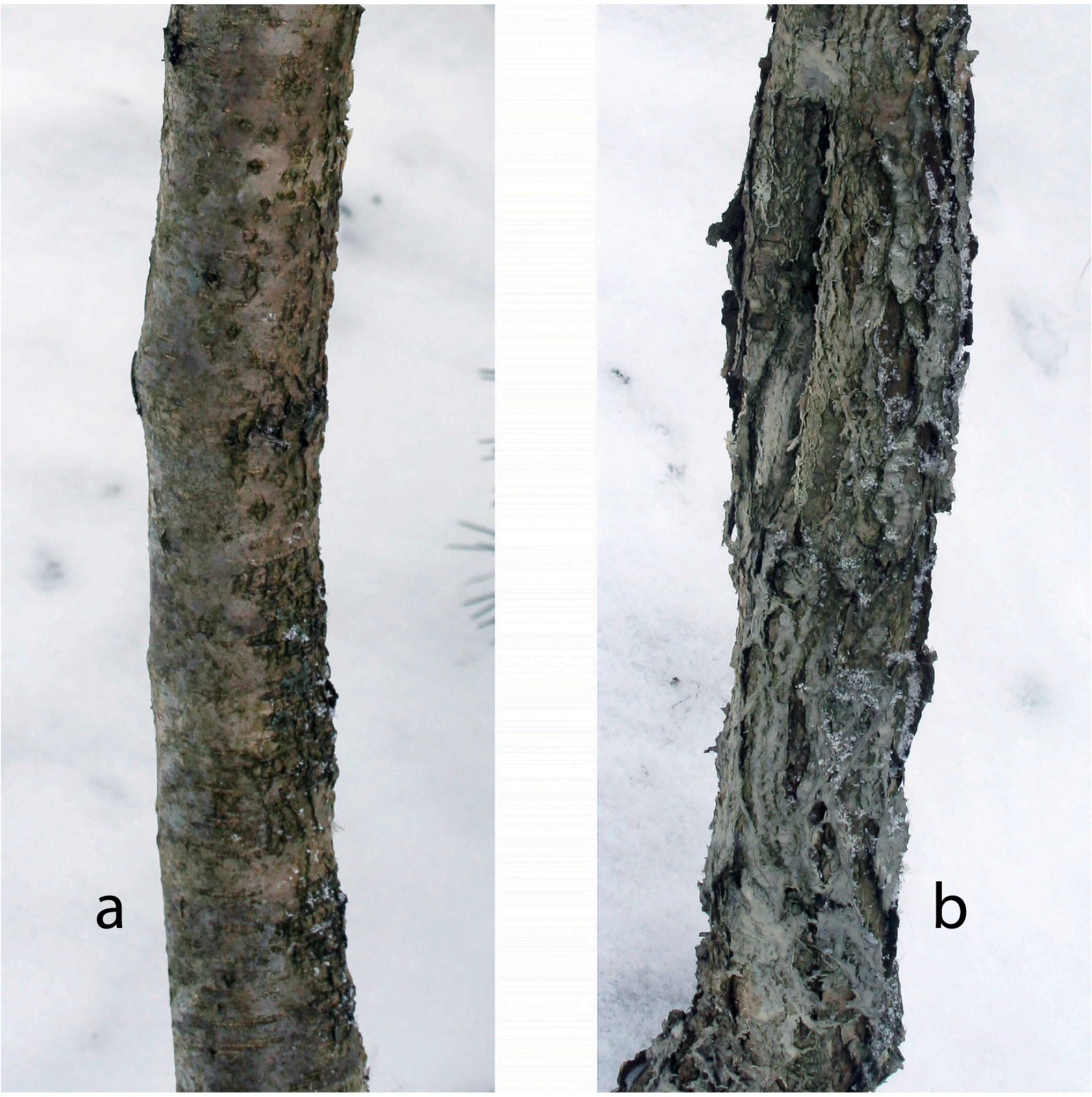

FIGURE 18. *Mespilus germanica* cv. Nottingham, trunk of young tree ca. 20 yrs. old. Note younger part of trunk (25a) with smooth, pale gray bark with some large horizontal lenticels low down, bark on older part (25b) breaking into rectangular strips. Cult., Ailsa Craig, Ontario.

1. ***Crataemespilus*** **×*grandiflora*** (Smith) Camus (1899: 326). *Mespilus grandiflora* Smith (1805: 33). *Mespilus smithii* Candolle (1825: 633), nom. illeg. superfl. *Crataegus smithii* Chalon (1868: 174), nom. inval. (Figs. 13 (4–9), 14–16)

= *Mespilus lobata* Poiret (1816: 71). *Crataegus lobata* (Poiret) Bosc (1821: 223).

Bush or small tree, 2–5 m; trunks 1 to few. Reproductive short shoots present; twigs sometimes with a few short thorns, young growth pubescent. Leaves 3–6 cm, commonly broad elliptic, sometime obovate, then shallowly 1-lobed per side, lobes rounded to subacute, margins +/- serrate, glabrous, or pubescent abaxially, venation semi-camptodromous, midvein pubescent adaxially and abaxially. Inflorescences subterminal from short shoots (type A2; Fig. 15), 1–3 (–5)-flowered; bracteoles few, 3–12 mm, narrow-ovate (shorter) to linear (longer), scarious, fawn, caducous, glabrous, eglandular. Flowers (flat) 22 mm diam. in *K.R. Robertson 3519* (UWO!) and 30 mm diam. in *KRR 3319* (UWO!); hypanthium dense-pubescent, disc dense-villous centrally, peripherally glabrous; sepals triangular, ca. 35% petal length, margins glandular serrate; petals cupped, sometimes slightly notched, white (pale fawn when dried); stamens ca. 23–25, anthers pink; styles 2–3. Fruit +/- spheric, ca. 12–15 mm, glabrous, golden ripening to burgundy; hypanthial opening wide (ca. 50%); sepals very narrow, margins entire, +/- erect to wide-spreading; pyrenes 2–3, tips exposed.

FIGURE 19. *Crataemespilus* ×*canescens* habit. Note fasciculate trunks. AR.

Crataemespilus ×*grandiflora* is regarded by Byatt *et al.* (1977), primarily on the basis of Smith's (1805) unequivocal statement, as having the origin *Crataegus laevigata* Poir. × *Mespilus germanica* L. It is intermediate between its two parents. There are no certain wild records but it is quite widely cultivated as an ornamental, for which purpose it is excellent. Mature small trees of this nothospecies line suburban roads such as in Harborne, Birmingham, UK, for instance. It may be found in many of the more prominent arboreta and is also offered for sale commercially on a small scale. Plants are normally propagated by grafting rather than attempting to recreate the plant by controlled pollination.

Plants of *Crataemespilus* ×*grandiflora* are seed sterile and pollen was ca. 4.5% sound (Byatt *et al.* 1977).

2. ***Crataemespilus* ×*gillotii*** Beck (1914: 30, t. 107). *Crataegus gillotii* (Beck) T.A. Dickinson & E.Y.Y. Lo in Lo *et al.* (2007: 609). *Crataegus oxyacantha-germanica* Gillot (1876: 14–25), nom. inval. (Fig. 13, 1–3)

Description as *Crataemespilus* ×*grandiflora* except for key characters. In the small sample involved the leaves range from entire-margined (relatively few) to deeply lobed, the stipules are serrate, and the styles 2, as may be seen in Fig. 13 (1–3) taken from Beck (1914).

Crataemespilus ×*gillotii* is intermediate between *Mespilus germanica* and *Crataegus monogyna* and the differences from *Crataemespilus* ×*grandiflora* are few. This nothotaxon rests on material from its type location, Autun, Saône-et Loire, France, where it was found in a hedge. It is seldom, if ever, cultivated.

Crataemespilus ×*gillotii* was first recognized by Gillot (1876) under the name *Crataegus oxyacantha-germanica.* Gillot's lengthy and detailed paper carefully distinguishes the hybrid from its parents and although he called one parent *C. oxyacantha* he recognized two elements within it—*C. monogyna* and '*C. digyna*' (now *C. laevigata* (Poir.) DC.)—and pointed out that the depth of leaf lobing of the hybrid suggested *C. monogyna* was the actual parent. Beck (1914) later honoured Gillot in his specific epithet. Byatt *et al.* (1977) confirmed the parentage *M. germanica* × *C. monogyna.*

FIGURE 20. *Crataemespilus* ×*canescens* trunk showing loosely exfoliating bark; freshly exposed olive-green. Arkansas.

3. ***Crataemespilus* ×*canescens*** (J.B Phipps) J.B. Phipps, **comb. nov.** *Mespilus canescens* Phipps (1990: 26–32). *Crataegus canescens* (J.B. Phipps) T.A. Dickinson & E.Y.Y. Lo in Lo *et al.* (2007: 609). (Figs. 4, 19–24)

Holotype: U.S.A. Arkansas: Prairie Co., 2 mi S of Slovak, 15 Apr. 1970, *J.E. Stern s.n.* (UARK!).
Stern's Medlar.

Bush, 2–5 m, stems slender, fasciculate; bark exfoliating in irregular strips, various pale colors. Reproductive short shoots sometimes present; twigs sometimes with a few straight thorns 2–4 cm, young growth canescent. Leaves 2–4 cm, narrowly elliptic to narrowly obovate, margins finely serrate distally, entire proximally, venation camptodromous, veins 5–7 per side, canescent. Inflorescences racemes (larger sub-paniculate) borne either terminating woody short shoots (type A), or lateral to and terminal on extension shoots (type B), 2–6-flowered; bracteoles several, 5–15 mm, very narrow, acuminate, margins sometimes with very narrow, long teeth, firm, green, persistent, hairy, with several very large, ellipsoid marginal glands. Flowers 18–20 mm; hypanthium canescent; disc saucer-shaped, bristly around style bases; sepals triangular, 25–30% petal length, margins entire, abaxially canescent; petals cupped, notched, white (fawn when dried); stamens ca. 20, anthers pale yellow; styles 5. Fruit +/- spheric, 8–12 mm, glabrescent, usually with residual indumentum least at ends, bright to deep red; hypanthial opening ca. 30–50% width of fruit; hairy residual disc tissue sometimes present; sepal remnants usually present; pyrenes 5, tips usually exposed.

FIGURE 21. *Crataemespilus ×canescens* inflorescence in bud. Note leafy bracts; long, narrow, green, herbaceous bracteoles, arrowed. Arkansas.

The small red fruit is hawthorn-like and usually solitary (Fig. 24). It produces pyrenes but few seeds. Stern's Medlar has excellent ornamental characteristics as summarized in Phipps (1990) and Phipps *et al.* (2003) and is already produced commercially on a small scale for ornamental horticulture. Lo *et al.* (2007) showed that *Crataemespilus ×canescens* was a hybrid of *Mespilus germanica* (cultivated or escaped) and *C. brachyacantha* (wild), presumably originating at or close to where it is found today in Arkansas. Intriguingly, they also averred that there was an additional, red-fruited, *Crataegus* ancestor for ×*C. canescens* but did not suggest what it might be, a matter that will be discussed in a future paper.

Conclusions

A review of molecular analyses showed that researchers consistently found a *Mespilus-Crataegus* clade with the *Amelanchier* clade as the nearest outgroup. *Mespilus* was sister to the whole of *Crataegus* in all these papers. *Crataegus brachyacantha* was shown by the three molecular studies that used it to be the first species among those analyzed to split from the *Crataegus* tree. In the two papers where *Crataemespilus ×canescens* was also used, the nothospecies always nested with *C. brachyacantha* and *M. germanica.* Probably also for this reason, though not explicitly, plus the fact that they regarded *Mespilus* as insufficiently different from *Crataegus* in morphology, Lo *et al.* (2007) believed that *Mespilus* should be united with *Crataegus*. This was then facilitated by Talent *et al.* (2008) who proposed the conservation of *Crataegus*. My view is that this was an unnecessary move as I hold that ample difference exists between *Mespilus* and *Crataegus*.

FIGURE 22. *Crataemespilus ×canescens* inflorescences. Note pendulous axis, upcurving of pedicels. Arkansas.

HERBARIUM OF THE UNIVERSITY OF WESTERN ONTARIO (UWO)

PLANTS OF ARKANSAS

Name: Mespilus canescens Phipps

Locality and Notes: Prairie Co., near Slovak. Konecny Grove Natural Area. 91°35'W, 34°37'N; alt. 222' a.s.l. 6 m multi-stemmed bush with white flowers. Anthers light yellow. Scent: Filipendula-like, but fainter.
About 8 cuttings collected for S.F.A. Sheet 1 of 2.

Collector & Number: J. B. Phipps 6373 & R. O'Kennon

Date: 1 May 1989

FIGURE 23. *Crataemespilus ×canescens* flowering herbarium specimen; a = leafy bract; b = bracteole; c = main axis; d = example of type B inflorescence origin.

Most of the remainder of this paper has comprised a detailed comparison between *Mespilus* and *Crataegus* in which their differences are articulated in detail. Emphasis has been placed on fruit characters, ecological adaption, the extreme rarity of natural hybrids and inability to produce fertile hybrids. In addition, the primary features distinguishing *Mespilus* from *Crataegus*—their distinctive fruit structure and color with its ecological significance, together with petal shape, bracteole type and form of resting bud are shown to be distinctive in *Mespilus*. Thus, the morphological distinction of *Mespilus* from *Crataegus* seems more than adequate for retaining *Mespilus* as a genus. This is particularly so in view of Herrera's finding that the trait of carnivore frugivory is held in common with other brown-fruited Maloids such as *Cormus*, *Torminalis* and *Pyrus*. Each of these brown-fruited genera represents an example of the genus as an adaptive suite and it is particularly interesting that the relationship *Mespilus-Crataegus* so closely parallels that of *Cormus-Sorbus*.

FIGURE 24. *Crataemespilus ×canescens* fruit. Note relatively small size (ca. 10 mm diam.), red color. Arkansas.

On the other hand, the existence of a few nothospecies between *Mespilus* and *Crataegus* with high degrees of sterility (quite common in the Maloids) is considered a weak argument for uniting sister taxa with such strong differences and deep separation. A review of the nothospecies of ×*Crataemespilus* is therefore provided to consolidate this position and *Mespilus canescens* is transferred there to ×*Crataemespilus* as *C. ×canescens.* An intriguing question about the ancestry of *Crataemespilus ×canescens* is flagged for further exploration.

A subsidiary analysis of inflorescence type and position of origin, as well as sylleptic vs. proleptic branching, the latter touted as significant by Lo *et al.* (2007) fails to find consistent differences in these respects between either *Crataegus* and *Mespilus* or between the *Crataegus* and *Amelanchier* clades.

A companion paper (Phipps 2016) shows that folk-taxonomy always distinguishes *Mespilus* from *Crataegus* and speaks to the cultural value of retaining *Mespilus*, while academic taxonomy has usually observed the distinction. Baird & Thieret (1989) also emphasize the cultural distinctness of medlar.

Thus, a monotypic *Mespilus* is accepted here.

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