

effects of Poison Ivy (*Rhus toxicodendron*) and Poison Dogwood (*Rhus vernix*). If bracelets and necklaces are worn for prolonged periods, symptoms of poisoning will begin to appear, redness of the skin being in evidence in susceptible people, in about two days. Undoubtedly the season of the year will have a direct influence on the degree of toxicity, and if in hot weather lacquer-damascene of comparatively recent origin is worn against the skin by one who is extraordinarily sensitive to *Rhus* poisoning, well marked symptoms of dermatitis may develop rapidly and cause serious trouble. The necklace which caused the most severe case of *Rhus* dermatitis on the S. S. Columbus (cf. Pl. 29) is in large part made of gold, the lacquered parts being of comparatively negligible area. Furthermore only the metallic part of the necklace was worn in direct contact with the skin, yet the symptoms of poisoning encircled the neck of the wearer.

SUMMARY

The cases of *Rhus* dermatitis or lacquer poisoning caused by wearing or handling Japanese damascene are attributable to lacquer, the prepared latex of *Rhus verniciflua* Stokes, dyed black. The Japanese product in which lacquer is used should be called lacquer-damascene to avoid confusion and to warn those who are susceptible to *Rhus* or lacquer poisoning.

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EXPLANATION OF PLATE 27

The bracelet at the top of the plate has one of the designs (executed on a metal tablet) removed to show the method of construction. (Bot. Mus. Harvard U. no. 4485.) The cigarette case is lacquered where black is shown. (Bot. Mus. Harvard U. no. 4486.) The necklace is reproduced from the one which caused the first case of *Rhus* dermatitis on the S. S. Columbus. (Bot. Mus. Harvard U. no. 4463.)

THE ORIGIN AND RELATIONSHIPS OF THE POMOIDEAE

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Plate 28

CYTOLOGICAL studies of the more polymorphic genera of the Rosaceae have shown the probable origin and relationship of many species. The larger genera such as *Rosa*, *Rubus*, and *Prunus* each contain a number of species with the same basic chromosome number, and a large series of polyploids. The Pomoideae on the other

hand consists of genera which are usually diploid, with a few tetraploids and triploids.

The basic chromosome number is 7 for the larger genera of the Rosoideae and 8 for the Prunoideae, but is 17 for all of the genera in the Pomoideae. Nebel (1929) and Darlington and Moffett (1930) have suggested that the Pomoideae are aneuploids derived from a 7 chromosome ancestor by chromosome duplication. Nebel suggests that the present *Malus* species are halved pentaploids derived from an ancestor with 35 somatic chromosomes. Darlington and Moffett also believe that the basic chromosome number of *Malus* is 7, but that the present forms are secondary polyploids with a basic number of 7 pairs of chromosomes, of which 4 are represented twice and 3 are represented three times. These authors go even further and suggest that the morphological characteristics of the Pomoideae are due to the establishment of a secondary basic chromosome number. These conclusions are based on the fact that the more important genera of the Rosoideae have 7 chromosomes as the basic number and that in species of *Malus* quadrivalents and sexivalents are found at the first meiotic divisions. Such an unbalanced secondary number of chromosomes must be considered remarkable in view of the fact that all of the species and varieties in the Pomoideae are orthoploid, with chromosome numbers of 17 or multiples of 17.

The present investigation was made in order to obtain chromosome counts of most of the genera of the Pomoideae. In view of the theory that this sub-family originated from a 7 chromosome form, a further survey of chromosome numbers was made in other genera of the Rosaceae. Most of the chromosome counts were obtained from acetocarmine smears of pollen mother cells. Mr. Dermen has made the counts of the *Prunus* species and most of the Spiraeoideae recorded, while Mrs. Sax is responsible for the counts in the *Amelanchier* species. The taxonomic grouping is based on Rehder's Manual (1926).

The chromosome numbers of representative genera are given in the following table. Counts obtained by previous investigators are indicated. In genera with polyploid species only the basic and highest polyploid numbers are given.

CHROMOSOME NUMBERS IN THE ROSACEAE

Sub-family	Genus	Chromosome No.	Native habitat
Spiraeoideae	<i>Physocarpus</i>	9	N. Am., Asia
	<i>Spiraea</i>	8 +	N. Am., Asia
	<i>Pentactina</i>	9	Korea
	<i>Sibiraea</i>	9	Eu., Asia
	<i>Exochorda</i>	8	Asia

Pomoideae	<i>Cotoneaster</i>	17-34	Eu., Afr., Asia
	<i>Mespilus</i>	17	Eu.
	<i>Crataegus</i>	16-32 L. ¹	
		17-34	N. Am., Eu., Asia
	<i>Sorbus</i>	17	N. Am., Eu., Asia
	<i>Aronia</i>	17	N. Am.
	<i>Photinia</i>	17	Asia
	<i>Eriobotrya</i>	17 M.	Asia
	<i>Chaenomeles</i>	17 K. M.	Asia
	<i>Cydonia</i>	17 R. K.	Asia
	<i>Malus</i>	17-34 ² R. K. N. D.	N. Am., Eu., Asia
	<i>Pyrus</i>	17- ² R. K.	Eu., Asia
	<i>Amelanchier</i>	17-34	N. Am., Eu., Asia
Rosoideae	<i>Neviusia</i>	8	N. Am.
	<i>Rhodotypus</i>	8	Asia
	<i>Rubus</i>	7-28 L. C.	N. Hemisphere
	<i>Potentilla</i>	7-14 Ti. S.	N. Hemisphere
	<i>Rosa</i>	7-28 T. B. H. E.	N. Hemisphere
Prunoideae	<i>Fragaria</i>	7-28 L. I.	Am., Eu.
	<i>Maddenia</i>	16	Asia
	<i>Prunus</i>	8-88 ² K. O. D. Me.	N. Hemisphere
	<i>Prinsepia</i>	16	Asia
	<i>Osmaronia</i>	6 K.	N. Am.

¹ L.—Longley, M.—Morinaga, K.—Kobel, R.—Rybin, N.—Nebel, D.—Darlington, T.—Tackholm, B.—Blackburn and Harrison, H.—Hurst, E.—Erlanson, I.—Ichijima, Me.—Meurman, C.—Crane, Ti.—Tischler, S.—Shimotomai.

² Triploids also found especially among the cultivated varieties of *Malus* and *Pyrus*.

The chromosome counts in the Spiraeoideae were obtained from the following species:—*Physocarpus monogynus*, *P. intermedius*, *P. stellatus*, and *P. capitatus*; *Spiraea pubescens* and the hybrid *S. oxyodon*; *Pentactina rupicola*; *Sibiraea laevigata*; and *Exochorda Giralddii Wilsonii*.

Most of these genera contain few species and *Pentactina* is monotypic. There are about 80 species of *Spiraea*, however, and a considerable number of species hybrids. This genus undoubtedly contains some polyploid species although exact counts of the higher chromosome numbers could not be obtained. The basic numbers for this sub-family are 8 and 9.

In the Rosoideae chromosome counts were obtained for the following species:—*Neviusia alabamensis*, *Rhodotypus scandens*, *Potentilla fruticosa* (7) and *P. tridentata* (14). *Neviusia* and *Rhodotypus* are monotypic genera. *Potentilla* is a large genus with more than 300 species of which only a few are woody. Both the woody and herbaceous species of *Potentilla* have 7 pairs of chromosomes as the basic number (Tischler 1929, Shimotomai 1929) instead of 8 as earlier investigators reported. The haploid chromosome number is 8 for the two monotypic genera, but is 7 for the polymorphic and polyploid genera *Rubus*, *Rosa*, *Potentilla* and *Fragaria*.

In the subfamily Prunoideae, chromosome counts have been obtained for *Maddenia hypoxantha*, and *Prinsepia uniflora*. According to Kobel the monotypic genus *Osmaronia* has only six pairs of chromosomes. The large genus *Prunus* has eight chromosomes as the basic number. Chromosome counts of the following species have also been made. Species with eight pairs of chromosomes include *Prunus incana*, *P. avium*, *P. serrulata sachalinensis*, *P. incisa serrata*, *P. subhirtella*, *P. glandulosa*, *P. pennsylvanica*, *P. allegheniensis*, *P. pumila susquehanae*, *P. angustifolia*, *P. americana*, *P. japonica Nakaii*, *P. orthosepala*, *P. hortulana*, *P. Munsoniana*, *P. maritima*, and *P. lanata*. Two species were found to be tetraploids; *Prunus Padus* and *P. virginiana*. Previous investigators have found diploids, triploids, tetraploids, hexaploids and aneuploids in the genus *Prunus* (Kobel 1927, Okabe 1928, Darlington 1928-30) and in one species Meurman (1929) found about 88 pairs of chromosomes. The two genera *Maddenia* and *Prinsepia* are apparently tetraploids but *Osmaronia* does not seem to have the typical basic number of 8.

CHROMOSOME NUMBERS IN THE POMOIDEAE

All of the genera of the Pomoideae have 17 pairs of chromosomes or polyploids with a basic number of 17. In some genera, especially *Cotoneaster* and *Crataegus*, it was difficult to obtain clear division figures with the acetocarmine technique. In some cases there appeared to be only 16 pairs of chromosomes in *Crataegus* as Longley (1924) has reported. In most genera there is more or less association between the chromosomes at the first meiotic division, as previous investigators have found, so that it is often difficult to determine the exact number of bivalent chromosomes. The following chromosome counts were determined from acetocarmine smears of pollen mother cells.

Cotoneaster moupinensis and *C. salicifolia* are diploids with 17 pairs of chromosomes while *C. horizontalis* is a tetraploid. The 17 bivalent chromosomes of *C. moupinensis* at diakinesis are shown in figure 4. The chromosomes of the tetraploid species are shown in figure 3. Other species were also found to have more than 17 pairs of chromosomes although exact counts were not obtained. It seems probable that a relatively large proportion of the *Cotoneaster* species are polyploids.

Mespilus germanica has 17 pairs of chromosomes and not 16 pairs as reported by Meyer (1915). The meiotic chromosomes at 1 M are shown in figure 2.

Only a few species of *Crataegus* were examined because this genus was thoroughly studied by Longley (1924). Longley reports that 16 is the basic chromosome number in *Crataegus* and he finds numerous triploid and a few tetraploid species. The great variation in morphological characters in this genus is attributed to hybridization between species.

In several species of *Crataegus* the acetocarmine preparation showed only 16 pairs of chromosomes but other species undoubtedly have 17 chromosomes as the basic number. The 16 groups of chromosomes in the hybrid *C. Lavalleyi* are shown in figure 1. In *C. Deweyana* there are clearly 17 pairs of chromosomes at late diakinesis (figure 8). In this species, as well as most other species in the Pomoideae, there is a tendency for bivalents to be associated in groups of two or even three. At the first metaphase *C. lawrencensis* appears to have 17 or 18 pairs of chromosomes (figure 7), but at the telophase of the division there are about 33 chromosomes at one pole (figure 6) and 32 at the other, with one lagging chromosome still at the metaphase plate. The chromosomes in this pollen mother cell were especially clear. It is possible that *Crataegus* is a transitional genus with both 16 and 17 chromosome forms, and that such species as *C. lawrencensis* with apparently 32 bivalents and 2 univalents could produce segregates with either 16 or 17 chromosomes as the basic number. The association of chromosomes into tetravalents is the result of duplication of the primary basic number of chromosomes.

In the *Sorbus* species there is much less tendency for the bivalents to form a secondary association and exact chromosome counts were easily made. *Sorbus Aucuparia*, *S. americana*, *S. discolor*, *S. alnifolia*, and *S. Aria* are all diploids with 17 pairs of chromosomes. The meiotic chromosomes of *S. aucuparia* and *S. alnifolia* are shown in figures 5 and 12.

The closely related genus *Aronia* also has 17 pairs of chromosomes. Two of the three species were studied and both *A. melanocarpa* and *A. arbutifolia* were found to be diploids (figure 11).

Only one species of *Photinia* was available for study in the Arnold Arboretum. It was found to be diploid with 17 pairs of chromosomes which are shown in figure 10.

The chromosome number of *Eriobotrya* was determined from root tip counts from seedlings grown in the greenhouse. The somatic chromosome number is 34 which is in accord with the count obtained by Morinaga (1929) for the same species, *E. japonica*.

The 17 chromosomes of *Chaenomeles sinensis* are shown in figure 9. This count agrees with the number previously reported by Mor-

inaga (1929). Rybin (1926) and Kobel (1927) also find 17 pairs of chromosomes in the closely related genus *Cydonia*.

Rybin (1926) found 34 somatic chromosomes in several species of *Pyrus* and Kobel (1927) found 17 bivalents in certain species and varieties, but a variable number of chromosomes in many of the cultivated forms. It is probable that these forms with irregular chromosome behavior are triploids with 51 somatic chromosomes.

The genus *Malus* has been investigated by a number of cytologists (Rybin 1926, Kobel 1927, Nebel 1929, and Darlington and Moffett 1930). Most of the species are diploids with 17 pairs of chromosomes, but several tetraploid species have also been described. In two cases triploids were found but other forms of the same species were found to be diploid. Triploid species could not reproduce themselves by sexual reproduction and would be expected to occur only occasionally. Among the cultivated varieties of apples, however, triploid forms are frequently found, and although they are partially sterile, enough flowers develop to produce a commercial crop of fruit. About 75 horticultural varieties of apples have been investigated and of these about one-third are triploids. No tetraploid horticultural varieties have been described.

Counts of somatic chromosomes were obtained from root tips of seedlings several years ago, but since so many species have been studied recently, it was considered unnecessary to carry this phase of the work further. The following species were found to be diploid: *Malus baccata*, *M. prunifolia*, *M. micromalus*, and *M. brevipes*. *Malus angustifolia*, *M. coronaria*, and *M. glaucescens* are tetraploids. In general these results are in accord with those of previous investigators. *Malus adstringens*, *M. Scheideckeri*, *M. Soulandi*, *M. robusta*, *M. zumi*, and *M. Dawsoniana*, are all recognized as species hybrids by Rehder (1926) and all of them are diploids and have 34 somatic chromosomes. It is possible, of course, that chromosome counts from seedlings do not indicate the chromosome number of a parental tree because a triploid might produce a diploid seedling, but the fertility of the parental trees and the uniformity in chromosome counts in the seedlings indicated that the counts obtained from seedlings also represent the parental chromosome numbers in these species.

All of the pure species of *Amelanchier* which have been studied are diploids, but two natural species hybrids are tetraploids. The diploid species are *Amelanchier asiatica*, *A. humilis*, *A. stolonifera*, *A. sanguinea* and *A. oblongifolia*. The chromosomes of *A. oblongifolia* are shown in figure 16. In *Amelanchier*, as in *Sorbus*, there is little tendency for the bivalents to form secondary associations.

The tetraploid hybrid *A. grandiflora* is a cross between *A. canadensis* and *laevis*, while *A. spicata* is a cross between *A. oblongifolia* and *stolonifera* (?) according to Rehder. In these tetraploids the chromosomes usually pair as bivalents at meiosis.

GENERIC HYBRIDS IN THE POMOIDEAE

A relatively large number of natural generic hybrids have been found in the Pomoideae. Among the hybrids recognized by Rehder are *Crataegomespilus* (*Crataegus* $\times$ *Mespilus*), *Sorbaronia* (*Sorbus* $\times$ *Aronia*), *Sorbopyrus* (*Pyrus* $\times$ *Sorbus*), *Amelasorbus* (*Amelanchier* $\times$ *Sorbus*), and *Pyronia* (*Pyrus* $\times$ *Cydonia*).

Representatives of three of these generic hybrids are growing in the Arnold Arboretum and the chromosome behavior of two of the hybrids has already been described (Sax 1927).

Two types of *Crataegomespilus* have been studied. *Crataegomespilus Dardari* is a graft hybrid which developed from the graft union of *Mespilus germanica* on *Crataegus monogyna*. Meyer's (1915) study of this graft hybrid shows that the outer layers of tissue are those of *Mespilus* although the fruit shape is like that of *Crataegus*. It is probable that the gametes are derived from *Mespilus* tissue. The number of chromosomes at the first reduction division is 17 as shown in figure 15 and are probably from *Mespilus* cells.

The generic hybrid *Crataegomespilus grandiflora* is supposed to be a cross between *Crataegus Oxyacantha* and *Mespilus germanica*. *Mespilus germanica* is a diploid species and according to Longley *C. Oxyacantha* is also a diploid form, but the F_1 hybrid seems to have more than 17 pairs of chromosomes. There are 17 groups of chromosomes at the first metaphase shown in figure 14, but at late diakinesis (figure 13) there are about 17 bivalents and 6 univalents. It is possible that there are only 34 somatic chromosomes in this hybrid and that there is incomplete pairing of chromosomes, but the presence of so many apparently bivalent chromosomes makes it seem more probable that one of the parental gametes was diploid. About 75 per cent of the pollen is obviously sterile.

Sorbaronia Dippelii is a cross between *Sorbus Aria* and *Aronia melanocarpa*. Both of these parental species are diploids. In the F_1 hybrid there is apparently complete compatibility of the two sets of chromosomes and 17 chromosomes are found at the first meiotic division of the pollen mother cells (figure 21). Several other generic hybrids between *Sorbus* and *Aronia* are also described by Rehder (1926). Prof. J. G. Jack has found several such hybrids and Mr. F. Hyland has recently found a hybrid between *S. Aucuparia*

and *A. floribunda* growing near Orono, Maine. These hybrids all seem to be completely fertile and set fruit abundantly.

A hybrid between *Sorbus* and *Pyrus* is known as *Sorbopyrus auricularis* and is supposed to be a cross between *P. communis* and *S. Aria*. The variety *bulbiformis* is a seedling of *S. auricularis* and is more like *Pyrus* than the F_1 hybrid. A cytological examination of the pollen mother cells of this variety shows that there are 34 chromosomes at metaphase of which about half are univalents (figure 18). The first meiotic division is somewhat irregular but usually the bivalents seem to pass to the poles first and most of the univalents lag behind. A typical division figure is shown in figures 17-19 where there are 17 chromosomes at one pole, 19 at the other and about 14 lagging univalents.

The variety *bulbiformis* evidently has two sets of *Pyrus* chromosomes and one set of *Sorbus* chromosomes, and probably originated by the union of a diploid F_1 egg cell with a haploid *Pyrus* male gamete. The fact that the chromosomes in the triploid segregate, and do not form trivalent chromosomes does not necessarily mean that the *Pyrus* and *Sorbus* chromosomes are incompatible, but since the F_1 hybrid is relatively sterile this interpretation is probably correct. The parental genera must be closely related, however, since the two sets of chromosomes function normally in somatic development.

Pyronia Veitchii is a hybrid between *Cydonia oblonga* and *Pyrus communis*. The F_1 plant sets fruit but no seeds are formed. Apparently these genera are closely related but pairing between the two sets of chromosomes does not occur.

Another generic hybrid discovered by Prof. Jack is *Amelasorbus Jackii*, which is a cross between *Amelanchier florida* and *Sorbus sitchensis*. Plants of this hybrid in the Arboretum are not large enough to produce flowers so that nothing is known about its cytological behavior. It sets seed freely in its native habitat which would indicate that the two parental sets of chromosomes are compatible with each other, although it is possible that it is a tetraploid, as are the *Amelanchier* species hybrids. If so, the F_1 might be fertile even if the parental chromosomes did not pair with each other.

SPECIES FORMATION IN THE ROSACEAE

Cytological and genetic studies in several genera of the Rosaceae have shown the relationship and origin of many species. A brief survey of this work will be presented here as a basis for the discussion of the origin and relationships of the genera of the Pomoideae.

The polymorphic genus *Rosa* has been found to contain an extensive series of polyploid types with diploid, triploid, tetraploid, pentaploid, hexaploid, and octoploid forms. (Tackholm 1922, Blackburn and Harrison 1921, Hurst 1927 and Erlanson 1929.) More than 1000 species and forms of *Rosa* have been examined and these include all of the sections of the genus distributed over the northern hemisphere. Of these forms studied 377 are diploids with 7 pairs of chromosomes, while over 600 are polyploids. A few aneuploid forms have been found by Tackholm and Erlanson, but practically all of the species have a chromosome number of 7 or a multiple of 7.

According to Hurst there are five fundamental diploid types, each with a different set of 7 chromosomes. These five fundamental diploid sets of chromosomes have been identified by genetic and cytological tests. The chromosomes of one set will not pair with those of another set, and each set is responsible for certain morphological differences. The species containing set AA is represented by *R. sempervirens*, BB by *R. sericea*, CC by *R. rugosa*, DD by *R. carolina* and EE by *R. macrophylla*. A duplication of the same set of chromosomes results in what Hurst calls duplicational polyploid varieties which have the same characteristics as their basic species. Differential polyploids, however, contain two or more different sets of chromosomes, such as AABB, and are distinct species. Twenty-six regular polyploid species are possible of which 18 have been identified. Irregular polyploids are those containing at least one set of bivalent chromosomes and from one to four sets of univalents. Of the 180 different possible combinations which would result in irregular polyploid species, only 25 have been identified in the wild state. According to Hurst there are 211 possible species of *Rosa*, if the 180 irregular polyploids are included, of which about 50 have been identified. Some taxonomists have recognized nearly 5000 species of *Rosa* although Rehder states that there are only one to two hundred good species.

The irregular polyploids are best represented by the species of the Caninae section. These species have 7 bivalents and either 14, 21 or, in a few species, 28 univalents. Tackholm found that the reduction was irregular in these forms. The bivalents divide normally but the univalents lag behind and are irregularly distributed in the first and second meiotic divisions of the pollen mother cells. Micronuclei are often formed, pollen sterility is high, and the few functional pollen grains have 7 chromosomes derived from the division of the bivalents. In the reduction division of the megaspore mother cells, however, 7 chromosomes from the bivalents

and all of the univalents pass to one pole. From this cell the female gamete is formed with 21, 28 or 35 chromosomes. It may be fertilized with a 7 chromosome male gamete and reproduce the parental type, or due to apomictical reproduction the parental type is reproduced asexually. Thus these types of unbalanced polyploids of undoubted hybrid origin breed true due to the peculiar chromosome distribution and apomixis.

The cytological and genetic work on *Rosa* clearly indicates that most of the numerous species and forms of the genus have originated from a few basic types by hybridity and polyploidy or by hybridity followed by apomixis.

The genus *Rubus* also contains a series of polyploid forms. Longley (1924) has found diploid, triploid, tetraploid, pentaploid, hexaploid, and octoploid species in this genus. Crane and Darlington (1927) have presented cytological and genetic evidence which seems to show that there are at least three different basic sets of 7 chromosomes each, in this genus. The genetic evidence seems to show that the chromosomes of two different basic septets may also pair with each other (Crane and Darlington). Apparently in this genus chromosome differentiation is not complete so that pairing occurs between different sets of chromosomes. According to Crane and Darlington unreduced egg cells frequently function in *Rubus* hybrids and apogamy also occurs. According to Longley there are about 10 bivalents at the first meiotic division of triploids and about 17 in pentaploids which would indicate that there is pairing between non-homologous chromosomes.

Fragaria is another polyploid genus containing diploid, tetraploid, hexaploid and octoploid species (Longley 1926, Ichijima 1926). The tetraploid form has not been found in natural species, but was obtained from a cross between two 7 chromosome species followed by somatic doubling in F_1 (Ichijima). Ichijima found that *Duchesnea indica* has 42 gametic chromosomes and since it can be crossed with *Fragaria* it is possibly a dodecaploid form of *Fragaria*.

The chromosomes of all 7 chromosome species seem to be compatible and pair in species hybrids. In crosses between 7×28 chromosome species there are 7 bivalent and about 21 univalents at meiosis in the F_1 which would indicate that there are at least three and possibly four different sets of 7 chromosomes each (Ichijima 1926).

Yarnell (1929) found that Ichijima's tetraploid bred true. When back crossed with one of the 7 chromosome parents a triploid was produced. In this triploid 7 bivalents and 7 univalents were occasionally found at the first meiotic division of the pollen mother

cells but usually there were 10 bivalents and 1 univalent. At the second reduction division 10 or 11 chromosomes were most frequent at metaphase. The triploid plants were partially fertile. In *Fragaria*, as in *Rubus*, there is evidently pairing of the non-homologous chromosomes.

The genus *Prunus* contains diploid, triploid, tetraploid, hexaploid and aneuploid species (Kobel 1927, Okabe 1928, Darlington 1928, 1930), and in one species Meurman (1929) has found a remarkable case of polyploidy where the basic somatic chromosome number is reduplicated eleven times. The basic somatic chromosome number is 8, and many species, even those belonging to different subgenera, seem to have similar sets of chromosomes so that chromosome pairing occurs in many species hybrids. Darlington (1930) finds chromosome pairing in a series of hybrids: *P. domestica* (6n) $\times$ *P. cerasifera* (2n), *P. triflora* (2n) $\times$ *P. cerasifera* (2n), *P. triflora* (2n) $\times$ *P. Persica* (2n) and *P. Persica* (2n) $\times$ *P. Amygdalus* (2n). *Prunus Persica* (Peach) and *P. Amygdalus* (Almond) belong to the subgenus *Amygdalus* while the species of Plums belong to the subgenus *Prunophora*. In the cross between *P. domestica* and *P. cerasifera* the F_1 behaves like a tetraploid which indicates that there are at least two similar sets of chromosomes in the hexaploid parent. In the cross between the Peach and the Almond some chromosomes frequently fail to pair, but fruit production is not seriously impaired. Rehder (1926) also describes a number of hybrids between species of different subgenera. The hybrid *P. dasycarpa* is probably a cross between *P. Armeniaca* (Apricot) and *P. cerasifera* (Plum) and rarely sets fruit. Only in one case is there any record of a cross between cherry and plum species. *Prunus pumila* (Sand Cherry) $\times$ *P. cerasifera* (Plum) produced a hybrid which sets fruit. In general the first two subgenera of this genus seem to be genetically similar in many cases, although it is improbable that all crosses between species of these two groups would produce fertile hybrids. Subgenera 4 and 5, *Padus* and *Laurocerasus*, are somewhat similar, but are probably well differentiated from the other groups. Thus in the genus *Prunus* there are at least several different basic sets of chromosomes and in addition there is some evidence that chromosome differentiation is now in progress.

Okabe finds that the flowering Cherries are triploids which accounts for their sterility. The Sweet Cherries (*P. avium*) are usually aneuploid with from 17 to 19 somatic chromosomes (Darlington 1928). The occurrence of autosyndesis and secondary chromosome association in hybrids and species of *Prunus* indicate

that polyploidy in this genus is often due to duplication of a single basic set of chromosomes. Species differentiation seems to be due largely to differences in basic sets of chromosomes.

The larger genera of Rosaceae have many similar characteristics in chromosome behavior. They all contain a series of polyploid species which may be caused by a duplication of the same basic set of chromosomes, or may be due to the combination of different basic sets of chromosomes. Most of the species are orthoploid and aneuploid forms are rarely found in nature. Species formation is due to genetic differentiation of basic sets of chromosomes so that the chromosomes often fail to pair in species hybrids, and to hybridization of distinct species followed by polyploidy. The production of diploid gametes is relatively frequent in this family and apogamy often permits the reproduction of unbalanced polyploid types which could not be maintained by sexual reproduction.

The chromosomes in autopolyploid species usually form bivalents instead of tetravalents at the first meiotic division due to the lack of sufficient chiasmata to bind more than two chromosomes together. In *Rubus*, *Fragaria* and *Crataegus* non-homologous chromosomes seem to pair in triploids although it seems improbable that there is an intimate association of chromatids in such an association of chromosomes. The association of non-homologous chromosomes does suggest, however, that chromosome pairing is not always a reliable indication of genetic homology.

THE ORIGIN AND RELATIONSHIPS OF THE GENERA OF POMOIDEAE

The genera of Pomoideae form a distinct and closely related group. All of the genera investigated have 17 pairs of chromosomes as the basic number. This subfamily is undoubtedly of Asiatic origin since all but three of the 18 genera enumerated by Rehder are represented by Asiatic species. The monotypic genus *Mespilus* is found in south-eastern Europe and Persia, while the monotypic genus *Peraphyllum* and the genus *Aronia* are natives of North America. *Mespilus*, however, is very closely related to *Crataegus*; *Aronia* is simply a form of *Sorbus* as indicated by genetic and cytological relationships; and *Peraphyllum* may be only an aberrant type of *Amelanchier*. Twelve of the genera of Pomoideae are not found in America while 7 are found only in Asia.

We may conclude then that the Pomoideae originated in Asia and that before the migration of the various species over the northern hemisphere, a period of perhaps millions of years, this group of plants had 17 chromosomes as the basic number. It would be most remarkable if each genus developed the same unbalanced polyploid number independently.

The chromosome behavior of any genus of this subfamily should, therefore, indicate the chromosome relationships of the entire group. According to Nebel the genus *Malus* is a halved pentaploid with 7 as the basic chromosome number. There is little evidence for this conclusion except that there is a tendency for the meiotic chromosomes to form secondary associations. Darlington and Moffett believe that *Malus* has developed from a 7 chromosome type, of which four chromosomes are represented twice and 3 chromosomes represented three times, or in other words, the present *Malus* species are of the gametic constitution of $2n + 3$.

The evidence presented by Darlington and Moffett to support this theory is very weak. Multiple association of chromosomes occurs at the first meiotic division so that in extreme cases four quadrivalents and three sexivalents are seen in polar views instead of 17 bivalents. This clumping of chromosomes, especially in sectioned material, may have little significance, however, and in side views of the metaphase of the first meiotic division no such general association of bivalents is shown. In the eight figures of "diploids" shown on page 136 (Darlington and Moffett 1930) there is usually only one quadrivalent shown in each figure and in only one case is there any indication of a sexivalent group of chromosomes. In triploid apple varieties these investigators find bivalents and trivalents most frequently but also a few quadrivalents, and only one group of 9 chromosomes. As Darlington has shown earlier, the larger multiple associations might not be expected to occur frequently because of limitations in chiasma formation.

The chromosome numbers in seedlings from triploids is also presented to support the theory that *Malus* is a secondary polyploid with 7 chromosomes as the basic number. The progeny from a triploid pollinated with a diploid should have from 34 to 51 somatic chromosomes. Darlington and Moffett find that in 13 seedlings the lowest somatic count is 38 and the highest 47. Three seedlings have 40 somatic chromosomes and four have 41. The authors conclude that since the greatest chromosome frequency is 41 there is a tendency for the chromosomes to form segregates with the secondary diploid number 34, plus the primary haploid number 7. But it could equally well be argued that the basic number is 8. However, a frequency distribution of this type based on only 13 individuals shows nothing except that gametes with intermediate chromosome number are functional, and is of no significance in determining the basic chromosome number.

The work of Crane and Lawrence (1930) shows that the progeny of triploid Apple varieties are usually weak, presumably due to

their aneuploid condition. If the basic chromosome number of *Malus* is 7 and the basic sets are not sufficiently differentiated to prevent occasional pairing, as Darlington and Moffett believe, then one might expect new polyploid forms with 41 or 48 chromosomes to function as well as triploids, but such types have never been found.

If secondary chromosome association in the Pomoideae indicates polyploidy, it would seem much more probable that 8 is the original basic number and that the present genera are tetraploids plus one bivalent, as Tischler (1929) has assumed. Such an association of chromosomes would account for the occasional quadrivalents and sexivalents observed by Darlington and Moffett. It would also account for the 16 and 24 bivalent types of *Crataegus* found by Longley, although the 24 chromosomes in triploids may be due to pairing of non-homologous chromosomes as occurs in *Rubus* and *Fragaria*. Species and varieties which have an additional pair of chromosome are found in many genera whereas diploids or tetraploids plus several bivalents are rare in natural species. For instance most of the genera of Ericaceae have a chromosome number of 12 or a multiple of 12 (Hagerup 1928) but several genera, including the polymorphic genus *Rhododendron*, have 13 chromosomes as the basic number. The fact that one genus has 6 haploid chromosomes and another 18 would suggest that 6 is the primary basic chromosome number for this family and that *Rhododendron* is really a tetraploid plus one bivalent. It would seem improbable, however, that *Rhododendron* has been differentiated from other genera of Ericaceae simply by tetraploidy plus a bivalent chromosome. Darlington and Moffett suggest, however, that the establishment of the secondary basic chromosome number as described in *Malus* may be responsible for the differentiation of the Pomoideae from the other Rosaceae. The chromosome numbers in other Rosaceae do not support this suggestion. The aneuploid types of *Fragaria*, *Rosa*, and *Prunus*, are all very similar to the orthoploid species.

Many of the genera of Pomoideae are closely related and the subfamily as a whole includes a distinct group of genera. The fact that intergeneric hybrids can be made between *Pyrus* and *Sorbus*, *Cydonia* and *Pyrus*, *Amelanchier* and *Sorbus*, and between *Aronia* and *Sorbus* indicates that these genera are closely related. In fact *Aronia* must be considered simply as a form of *Sorbus* since crosses between these two genera produce fertile hybrids in which there is complete compatibility between parental chromosomes. It is possible that such genera as *Aronia* and *Mespilus* are now in the process of differentiation and that ultimately they might become genetically

distinct from their closely related forms so that chromosome pairing could not occur in intergeneric hybrids.

Many of the genera have never been crossed with each other although in many cases there has been ample opportunity for such hybrids to occur. There are no known hybrids between *Malus* and *Pyrus* although these genera are morphologically very similar.

In the larger genera of Pomoideae there are a few triploid or tetraploid species. In *Malus* there is good evidence that triploids and tetraploids are autopolyploids. The fact that about a third of the cultivated Apples are triploids and that no tetraploid varieties have been found indicates that chromosome duplication is caused by the occasional production of a diploid gamete. Similar evidence of autopolyploidy is also found in *Crataegus* and *Pyrus*. In *Amelanchier* the only known tetraploids are natural species hybrids, but it seems improbable that there are two different basic sets of chromosomes in these closely related parental species.

Polyploidy seems to have played a minor part in genus and species differentiation in the Pomoideae, although it is possible that the present diploid forms are polyploids with a basic chromosome number of 8. The genetic similarity of so many genera, and the morphological similarity of genetically differentiated genera, would indicate, however, that not more than one basic set of chromosomes was involved in the origin of the present genera. It seems probable that the genera of *Pomoideae* all originated by genetic changes in the basic set of 17 chromosomes and that various degrees of chromosome differentiation now exist in the different genera.

Within the genera further changes have occurred, but in many or perhaps in most cases they are not great enough to prevent chromosome pairing in species hybrids. The species of *Malus*, *Crataegus*, *Sorbus*, and *Amelanchier* hybridize rather freely in nature and many more species hybrids could undoubtedly be made. It is probable, however, that certain species in the larger genera are completely differentiated from each other. With the exception of *Crataegus* most of the genera of Pomoideae contain relatively few species.

According to Sargent (1922) there are more than 1000 species of *Crataegus*. In most cases species differentiation is based on minor morphological differences. Palmer (1925) in his introduction to the "Synopsis of North American *Crataegi*" states that "in these tables the color of the anthers, number of stamens, glabrous or pubescent character of corymbs at flowering time and general shape of the leaves were adopted for most groups, in the order named. . . . The taxonomic value of characters varies in different

groups, but generally there appears to be considerable variability even within the species in such particulars as the size of the flowers, the number in the corymbs and the compactness or laxity of the latter. The shape of the leaves is even less stable and dependable, many types often being found on a single branch. . . . The fruit is often one of the best guides to group distinctions, but there is quite too much variation in such particulars as shape, size and color for them to be depended upon rigidly as specific criteria. . . . Even the presence or absence of pubescence on the corymbs, often one of the best specific distinctions, cannot always be relied upon." The number of stamens and color of anthers are considered one of the most definite criteria for distinguishing species, but stamen number is also variable and anther color is often correlated with the color of the fruit.

Seedlings of the more ornamental types have been grown in considerable numbers at Rochester Park and at the Arnold Arboretum. My colleague, Mr. E. J. Palmer, informs me that in most cases the species of *Crataegus* breed true from seed, even to the most minute characters. Many species have a wide geographic range while others are of very local geographic distribution.

Longley has investigated about 80 species of *Crataegus* and found that about three-fourths of these species are triploids. Standish (1916) found that pollen sterility was prevalent in about 80 per cent of the species studied and in many cases pollen sterility was complete. It seems probable then that about 75 per cent of the *Crataegi* are triploids and form partially or completely sterile pollen. In view of the prevalence of triploids and pollen sterility in this genus it is remarkable that almost all species of *Crataegus* produce fruits abundantly. And still more remarkable some of these triploid forms with partially sterile pollen are known to breed true from seed. The only explanation of these phenomena seems to be that the triploid species are apogamous, or that seeds develop, from unreduced egg cells, so that the progeny receive the maternal set of somatic chromosomes and would of course breed true.

This explanation of seed production in the triploid *Crataegi* will account for the numerous species found in this genus. It is quite probable that there are at least several distinct types of *Crataegi* whose chromosomes are completely differentiated, but for the most part the different forms have similar basic sets of chromosomes. Variations caused by mutation and by hybridization between similar types which differed in such characters as size and color of fruit, pubescent or glabrous corymbs, color and number of anthers and leaf shape would produce many different types of segregates

differing only in these minor characters. The occasional production of diploid gametes, which seems to be characteristic of many genera of the Rosaceae, would frequently result in the production of triploids. These triploids seem to have developed a type of apogamous reproduction so that they breed true for both morphological characters and chromosome number. The older triploid types would be expected to have as great a geographic range as the diploids but the more recent ones would have only a local range.

Triploids could also be derived from homozygous diploids and from crosses between diploids and tetraploids. The production of triploid forms from diploid species will cause chromosome irregularity and pollen sterility, so that these phenomena are not necessarily associated with hybridity. Chromosome irregularity can also be caused by genetic factors, grafting, X-rays, segmental interchange between non-homologous chromosomes, and to some extent by environmental conditions.

There is also some evidence for apogamy in the genus *Malus* (Kobel 1927). Mr. W.H. Judd of the Arnold Arboretum tells me that some of the *Malus* species breed true from seed. In the Arboretum a number of species are grouped together and in many cases a species is represented by a single tree. In view of the fact that all horticultural varieties of *Malus* are cross pollinated, it is remarkable that any of the species grown in the Arboretum should breed true, unless they develop seed by apogamy or from unreduced egg cells. Certainly the cultivated varieties do not breed true from seed. In connection with some breeding experiments a number of flowers of *Malus theifera* were emasculated while the anthers were green and before the buds opened. The stigmas were also cut off at the same time and yet most of the fruits developed to maturity and seeds were obtained. Thus there are several lines of evidence that some species of *Malus* are apogamous or parthenogenetic, but further work should be done with both *Crataegus* and *Malus*.

In view of the close relationships of many genera of the Pomoideae and the frequency of fertile species hybrids in most genera the validity of the taxonomic grouping must be questioned. Of course the differentiation of species limits is a matter of personal opinion as best indicated perhaps by the recognition of about 5000 species of *Rosa* by some taxonomists as compared with 100 to 200 recognized by Rehder.

There should be a specific genetic test to determine species relationships. The use of the term species as used by most taxonomists seems to be almost as indefinite as it was in Darwin's time. From the standpoint of genetics and cytology a species might be defined as

a group of individuals of common descent which possess genetically similar sets of chromosomes. Such a definition will have to be modified at times in view of occasional genetic factors which may inhibit hybridization and affect the fertility of hybrids even in varietal crosses, but it is fundamentally sound. Of course such a test of genetics and cytological relationships can be applied only to a limited extent, but it should provide a more precise and natural system of classification for many groups of plants.

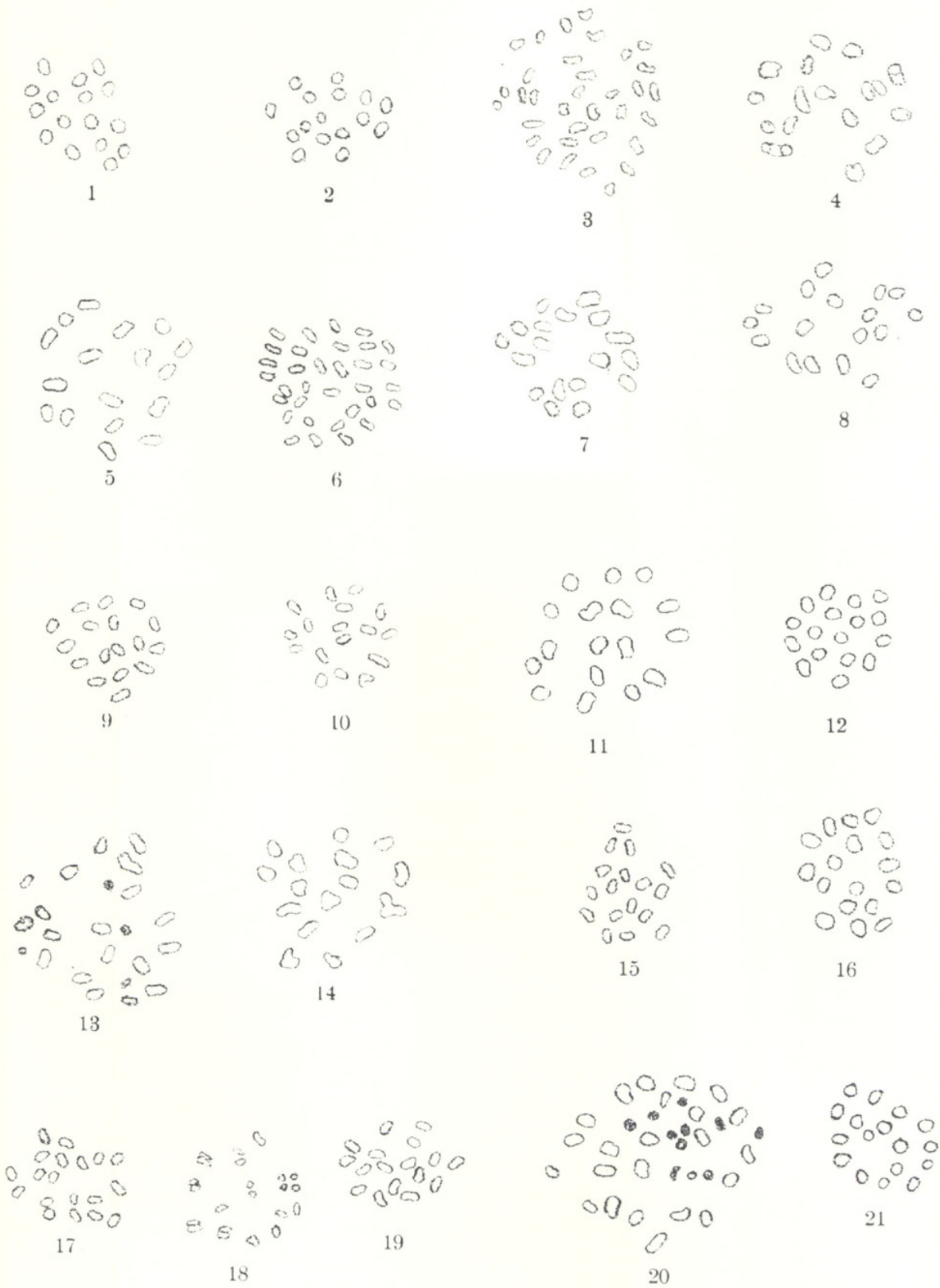
According to the genetic system of classification perhaps all of the Pomoideae could be classed as one genus and most of the present genera could be regarded as genetic species. In some cases two different genera, such as *Sorbus* and *Aronia*, should be combined in one genetic species. In the larger genera it is quite probable that there are a number of good genetic species so that the number of genetic species would exceed the present number of genera. This reversion to the older system of classification of the Pomoideae seems to be more in accord with genetic relationships than the present system, although a considerable amount of work must be done to determine the relationships of all of the genera and species.

SUMMARY.

In the Rosaceae the basic chromosome number is 8 and 9 for the Spiraeoideae, 7 and 8 for the Rosoideae, 8 for the Prunoideae, but is 17 for the Pomoideae. In the Rosoideae and Prunoideae, and probably in the Spiraeoideae, the larger genera include a series of polyploid species. In several genera which have been extensively studied it has been shown that species differentiation is caused by genetic differentiation of basic sets of chromosomes and by hybridization associated with polyploidy.

In the Pomoideae a few of the larger genera contain many triploids and a few tetraploids, but these forms are probably autopolyploids. The genera of Pomoideae have apparently had a common origin and have developed by genetic differentiation within the basic set of 17 chromosomes.

Many of the genera of Pomoideae are very closely related. *Sorbus* and *Aronia* have similar sets of chromosomes which pair in F_1 hybrids. Generic hybrids are also known to occur between *Crataegus* and *Mespilus*, *Sorbus* and *Amelanchier*, *Sorbus* and *Pyrus*, and *Pyrus* and *Cydonia*. Other genera are morphologically very similar although no generic hybrids are known to exist. The species in the larger genera are often closely related and natural species hybrids are commonly found.



ORIGIN OF POMOIDEAE

On a genetic and cytological basis of classification all of the present genera of the Pomoideae might be classed as genetic species under one genus. In at least one case two genera should be combined in one species.

Most of the numerous species of *Crataegi* are triploids and are fruitful and breed true apparently due to apogamy or parthenogenesis. Most of these triploid forms are probably the result of polyploidy within a genetic species and should be classed as varieties which breed true by asexual reproduction.

There is some evidence of secondary chromosome association at meiosis which may indicate that the present diploid genera are polyploids with an original basic chromosome number of 7 or 8.

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DESCRIPTION OF PLATE 28

From acetocarmine preparations of pollen mother cells.

- Figure 1. *Crataegus Lavalleyi*. First metaphase.
2. *Mespilus germanica*. First metaphase.
3. *Cotoneaster horizontalis*. Second metaphase.
4. *Cotoneaster moupinensis*. Diakinesis.
5. *Sorbus Aucuparia*. First metaphase.
6. *Crataegus lawrencensis*. Telophase.
7. *Crataegus lawrencensis*. First metaphase.
8. *Crataegus Deweyana*. Late diakinesis.
9. *Chaenomeles sinensis*. Second metaphase.
10. *Photinia villosa*. Second metaphase.
11. *Aronia melanocarpa*. First metaphase.
12. *Sorbus alnifolia*. First metaphase.
13. *Crataegomespilus grandiflora*. Late diakinesis.
14. *Crataegomespilus grandiflora*. First metaphase.
15. *Crataegomespilus Dardari*. First metaphase.
16. *Amelanchier oblongifolia*. First metaphase.
17-19. *Sorbopyrus auricularis bulbiformis*. Telophase.
20. *Sorbopyrus auricularis bulbiformis*. First metaphase.
21. *Sorbaronia Dippelii*. First telophase.

The bivalents have divided and are shown at each pole in figures 17 and 19, while the lagging univalents are shown in figure 18.

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