

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



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