The zonal geranium, *Pelargonium X hortorum* Bailey, probably originated from hybridization of natural species of the subgenus *Ciconium* (Sweet) Harvey of the genus *Pelargonium* l’Her. ex Ait. (11, 25). Although *P. zonale* was introduced into Europe from South Africa in 1609, it was not until 1814 that other *Pelargonium* species reached Europe. Since interspecific hybridization is readily accomplished under greenhouse conditions, the plant breeders of the time soon produced a number of forms different from the wild species (10, 11). *Pelargonium* breeding has, therefore, been carried out for over 150 years and, as few records have been kept until quite recently, the problem of species classification and determining the phylogeny of the cultigens is difficult (28).

### Origin

Although only 2 species, *P. zonale* (L.) L’Her. ex Ait. and *P. inquinans* (L.) L’Her. ex Ait. were once considered to be the ancestors of *P. X hortorum* Bailey, 5 other species belonging to the subgenus *Ciconium* namely, *P. scandens* Ehrh., *P. hybridum* (L.) L’Her. ex Ait., *P. frutetorum* Dyer, *P. stenopetalum* Ehrh., and *P. acutatum* L., also may have contributed to the cultigen (11).

Clifford (11) noted that, traditionally, the origin of *P. X hortorum* was *P. inquinans* × *P. zonale* with *P. zonale* making the greater contribution. However, he noted that *P. inquinans* is more horticulturally desirable than *P. zonale* and may in fact be the major contributor to *P. X hortorum*. The latter hypothesis is substantiated in part by chromatographic studies of the secondary biochemical constituents from crude alcoholic leaf extracts in which the chromatogram of one cultivar ‘Penny Irene’ was identical to that of *P. inquinans* and those of 5 other cultivars had biochemical profiles similar to that of *P. inquinans*. However, the biochemical profiles of *P. zonale* and *P. inquinans* were highly similar, differing only in one compound found in *P. inquinans* and absent in *P. zonale* (20). Chow and Harney (10), in crossability studies of *P. X hortorum* cv. Mme. Buchner and *P. zonale*, *P. inquinans*, *P. scandens*, and *P. stenopetalum*, noted that the highest fertilities were between *P. X hortorum* and *P. inquinans*. In a subsequent study, cross-fertility was high in the *P. zonale* × *P. inquinans* cross but not in the reciprocal (21). Furthermore, the hybrid seedlings of *P. zonale* × *P. inquinans* were highly self-fertile whereas those of *P. inquinans* × *P. zonale* were not. There would, nevertheless, have been enough successful crosses to have permitted the extensive use of these two species in the development of *P. X hortorum*.

The chromatographic studies further indicated that *P. inquinans*, *P. zonale*, *P. hybridum*, *P. frutetorum*, and *P. scandens* had 7 compounds in common with the 14 *P. X hortorum* cultivars analyzed (20). But 2 compounds specific for *P. hybridum* and another specific for *P. stenopetalum* were not found in the leaves of any of the cultivars analyzed. These 2 species may not have contributed to the cultigen or conversely, they may have been selected against or may eventually be found in other cultivars not analyzed. *Pelargonium hybridum* has several morphological characteristics which are advantageous to a horticultural plant and which resemble those of *P. X hortorum*. Considering morphological characters as well as biochemical markers therefore, the logical conclusion is that *P. hybridum* may have contributed to *P. X hortorum* in spite of the lack of *P. hybridum* specific compounds in the cultigen. By the same criteria, horticulturally undesirable characteristics in *P. stenopetalum* would have mitigated against its continued use in a breeding program. Chow and Harney (10) found the low fertility of the cross *P. X hortorum* × *P. stenopetalum* to be due to inefficiency in fertilization and low seed set. The reciprocal cross was unsuccessful. The species *P. stenopetalum* is self-incompatible, and was found unsuccessful as a female parent and relatively successful as a male parent in interspecific crosses (21). Clifford (11) was probably correct in doubting the contribution of *P. stenopetalum* to *P. X hortorum*.

It seems possible from the chromatographic data to state that *P. scandens*, about which Clifford (11) also had doubts, has indeed contributed to the development of *P. X hortorum* (20). One *P. scandens* specific compound was found in 5 cultivars, and although another one was not found in any of the cultivars this could indicate that it was selected against during the development of the cultigen or that a wider sampling of cultivars might indicate its presence. A male-sterile clone of *P. scandens* was used and therefore offspring were obtained in only one direction (10, 21). A consideration of the success of *P. scandens* × *P. X hortorum* crosses alone would suggest that *P. scandens* has had a very minor role in the development of *P. X hortorum* but...
this cannot be proven until reciprocal crosses are made. Fertility was low in P. scandens crosses with P. zonale, P. inquinans and P. stenopetalum; however seed was obtained more easily by selfing hybrids of P. scandens x P. zonale and P. scandens x P. inquinans than from crossing the parental species.

Although a compound specific for P. acetosum was found in chromatograms of one cultivar, the contribution of this species to the development of P. X hororum remains questionable due to lack of data and its undesirable horticultural characteristics (20). The presence of a compound specific for P. frutetorum in 5 cultivars of P. X hororum would indicate that P. frutetorum has probably contributed to the development of the cultiven. Unfortunately P. hybridum, P. acetosum, and P. frutetorum have not yet been used in crossability studies with P. X hororum or the other putative ancestors of the cultiven. Such studies might give some further indication of their contributions to the development of P. X hororum. Contrary to the general belief of hybrid ancestry for P. X hororum (10, 11, 25), Badr and Horn (2) suggested that only one species was involved in the origin of the cultivars they studied. This idea was based on the finding of unusually high frequencies of multivalents in pollen mother cells of tetraploid cultivars. They claim further confirmation of the autotetraploidy of P. zonale cultivars from genetic studies of a number of characters in tetrploids (3).

For example, the segregation patterns of flower color and floret doubleness were characteristic of autotetraploidy.

Cytology

Four basic chromosome numbers, x = 8, 9, 10, and 11 occur among the natural species of Pelargonium (15, 18). The species from which P. X hororum was developed are diploid with a basic chromosome number of 9 and all belong to the section Ciconium (11). With the exception of Pelargonium cultivars propagated commercially from seed, the majority of the older cultivars in North America and Europe tend to be diploid and the more recent ones to be tetraploid (2, 24). Breeding is apparently first at the diploid level with horticulturists later unknowingly selecting tetraploid cultivars (10). Badr and Horn (2) reported that the first polyploid Pelargonium cultivars appeared in France around 1880 and were described by Daunthenay in 1897. Clifford (11), Philippi (31) and Badr and Horn (2) noted that tetraploid cultivars cannot be crossed with diploids. However there have been reports of parthenogenetically formed seeds developing after crosses between parents with different ploidy levels (4).

Badr and Horn (2) have published a preliminary idiogram of the chromosomes of P. zonale cv. White in which the basic genome includes 3 short, 3 medium long and 3 long chromosomes, all showing submedian to subterminal centromeres. The chromosomes are small, being from 2 to 4 μ in length. One of the longest chromosomes has a secondary constriction in its long arm. In contrast, Daker (14) has found the satellite to be at the end of the short arm of one of the long chromosomes.

Daker (15) reported several instances of aneuploidy among cultivars on P. X hororum. An interesting example was found in ‘Madame Salleron’, a cultivar which does not flower, in which somatic cells showed the loss of one chromosome (2n = 17). Two plants from separate sources showed the same deficiency.

The cultivar ‘Kleine Liebling’ is a true haploid with only 9 somatic chromosomes (14, 16). It is thought to have arisen by parthenogenesis from an earlier cultivar; the seedling would subsequently have been selected because of its miniature characteristics and propagation vegetatively. Although haploids can be fertile by doubling their chromosomes with colchicine, such efforts failed to produce fertile diploid plants of ‘Kleine Liebling’. The diploid branches did root and produce flowering plants which proved to be somewhat larger in size but they were as sterile as the haploid.

A detailed cytological study of ‘Kleine Liebling’ was undertaken by Daker (13, 14, 16). The shoot system was haploid but the roots were found to be haploid, mixed haploid-diploid or diploid and each of the 3 types of root occurred on a single cutting. Analysis of microsporogenesis of haploid ‘Klein Liebling’ indicated the formation of a small number of bivalents which appeared to be genuine chiasmate formations. Furthermore, trivalents were found in the colchicine-induced haploid and the associations observed in the haploid closely resembled the bivalents found in the diploid. These chromosomal associations in meiotic cells of haploid and diploid plants are indicative of interchromosomal homology within the genome. Daker (14) stresses the characteristic “tail” of the anaphase univalents in both haploid and diploid plants. He believed this to be a continuation of the effect observed at diakinesis where one end of the chromosome tends to be less contracted. The differential contraction of the chromosomes observed at diakinesis in ‘Kleine Liebling’ seems to be a characteristic of the genus as evidenced by similar occurrences in diakinesis of P. zonale, P. scandens, P. inquinans, and a number of diploid cultivars of P. X hororum (P.M. Harney and J. J. Enghardt, unpublished data).

In haploid plants, as in diploids produced from them, only a small proportion of the pollen mother cells progressed through a second division resulting in normal quartet formation. Most showed a premature cleavage of the cytoplasm at the binucleate stage. This abnormal meiosis is believed by Daker (14) to be due to accumulation of deleterious recessive genes which adversely affect meiosis. Different accessions of ‘Kleine Liebling’ varied in meiotic behavior. It would be expected that, because of the chromosome homology in the colchicine-induced diploid, chromosomal pairing at meiosis should have been normal but in fact it was very similar to that in the haploid, with a large proportion of univalents and pseudobivalents or non-chiasmate bivalents. This reinforced the suggestion that non-synapsis of the chromosomes in the cultivar, whether haploid or diploid, is due to genes rather than lack of chromosomal homology. Such genes could accumulate through lack of selective pressures over a long period of vegetative propagation.

Badr and Horn (2) investigated, in a number of diploid and tetraploid cultivars of commercial importance in Germany, whether univalents and rod bivalents were present in all diploid cultivars. There were significant differences between the frequency of univalents, rod bivalents, and chiasmata between cultivars. In 2 cultivars irregularities such as lagging chromosomes at anaphase I and telophase I were seen. There also seemed to be differences in the number of pollen mother cells per anther, with fewer found in cultivars having semidouble florets than in cultivars having single florets. Chromosomal configurations typical of autotetraploids were noted at meiosis in tetraploid cultivars. Univalents, bivalents, and multivalents occurred regularly, with significantly higher frequencies between cultivars as were the frequencies of chiasmata. In addition to rod and ring bivalents, 4 different types of trivalents and 8 types of quadrivalents were found. Among the multivalents chains of 3, rings of 4, chains of 4 and Y-shaped tri- and quadravalents were most common. Between 35% and 54% of the chromosomes occurred as multivalents and between 36% and 53% as bivalents with the latter almost exclusively rod-like. Because of this chromosomal behavior at diakinesis, chromosomal distribution later on in meiosis was abnormal in all tetraploids analyzed. Lagging chromosomes were noted at anaphase I and telophase II with some anaphase cells having different numbers of chromosomes. Chromosome bridges were also noted in anaphase.

Badr and Horn (2) found a significant correlation between the number of
univalents and the ability of the pollen of tetraploid cultivars to fertilize. Similarly there were relationships between the frequency of quadrivalents and that of chiasmata. Such relationships were not found in diploid cultivars.

Tokumura (40), in a study of 2 cultivars of Pelargonium \(2n = 22\), the male-sterile 'Prince Rupert' and the male-fertile 'Lemon Crispum', noted that meiosis was apparently normal in both. Eleven bivalents were normally formed at metaphase I. Many of the bivalents were rod bivalents with a few ring bivalents. Each bivalent disjoined regularly at anaphase I and 11 chromosomes were usually arranged on each of the metaphase II plates. There was no meiotic difference between the male sterile and the male fertile cultivar. Furthermore meiosis was normal in most hybrids obtained from them.

Studies are in progress at the University of Guelph on the meiotic behavior of a number of species believed to have contributed to \(P. \times \text{hortorum}\), interspecific hybrids, and certain diploid cultivars of \(P. \times \text{hortorum}\). Although these are not yet completed certain interesting facts have been ascertained. As reported by Badr and Horn (2) for cultivars, relatively high frequencies of univalents and rod bivalents were found in the species \(P. \text{zonale}\), \(P. \text{inquinans}\), and \(P. \text{scandens}\). There does not appear to be any appreciable difference between meiotic configurations of \(P. \text{scandens}\) which is male sterile and the other species which are not. Nearly one-third of the chromosomes were present at anaphase and pseudo-bivalents, that is chromosomes in close association but without any indication of chiasmata. Pseudobivalents may be due to asynapsis or desynapsis of homologous chromosomes. Univalents occur when chromosomes do not pair and rod bivalents arise when chiasmata are formed in one arm of the chromosome and are, therefore, the result of incomplete synapsis of homologous chromosomes. Badr and Horn (2) believe this lack of normal chromosomal pairing is due to structural heterozygosity or asynaptic genes. The theory of structural heterozygosity is supported by the presence of anaphase bridges and the difference in the description of the satellite chromosomes by Badr and Horn (2) and Daker (14). Seed produced cultivars were found by Badr and Horn (2) to have abnormal synapsis of chromosomes during meiosis which they attribute to genes rather than structural chromosomal differences as passage through the gametophyte usually acts as a sieve for chromosome mutations.

Both Badr and Horn (2) and Daker (14) have reported that the abnormal synapsis patterns noted in their plants were followed by further meiotic abnor-

mality leading to a high degree of pollen sterility. Studies at the University of Guelph indicated that, although chromosomes are very loosely paired, later stages of meiosis appeared normal with little evidence of anaphase bridges, and telophase I and II configuration contain the correct number of chromosomes. This is reflected in pollen staminate of 99.3% in \(P. \text{zonale}\) and 98.4% in \(P. \text{inquinans}\) (10). The data on \(P. \text{scandens}\), which produces no pollen, is not yet complete and there is, therefore, no real evidence on the effect of meiosis on the later disintegration of the developing pollen grain in this species.

**Genetics**

The distinctive feature of the genus *Pelargonium* is the spur, which takes the form of a small tube running from the uppermost sepal along the flower stem and adnate to it. Sometimes this nectar-bearing tube is very long and extends nearly the whole length of the individual flower stalk, but in a few cases it is very shallow (11). Ballard (5) reported the presence of a spur to be correlated with floret singleness. Chow and Harney (10) found no spur in the cultivar Mme. Buchner which has semi-double florets whereas the species \(P. \text{zonale}\), \(P. \text{inquinans}\), \(P. \text{scandens}\) and \(P. \text{stenopectalum}\), all of which have single florets, had a spur. They found that in every cross involving \(P. \times \text{hortorum}\) cv. Mme. Buchner the plants segregated into those having a spur and those lacking a spur.

*Pelargonium* florets are of three general types: single, having 5 petals; semidoubles having 6 to 15 petals; and doubles with more than 15 petals. The florets of the parental species are single with the first semidouble cultivar having been observed in France by Victor Le-moine in 1864 (31). Although Ballard (5) had observed the correlation between floret type and spur presence, he did not interpret the results in terms of an inheritance pattern. Emsweller et al. (19) stated that floret singleness was dominant to doublesness and Barnhart (6) reported that self-pollination of singles produced only single flowered progeny whereas semi-doubles produced single, semidouble and double-flowered progeny. More recently, Craig (12) showed that floret type was controlled by one gene acting without dominance and that expression of the double character was affected by modifiers and environmental effects. Nugent and Snyder (29), using parental material different from Craig's (12) concluded that the inheritance of floret doublesness was due to one major gene \(D\) and 3 recessive modifier genes. The modifiers, which acted only in the presence of the dominant \(D\) allele, controlled the number of petals found in the various non-single phenotypes.

Although Badr and Horn (3) used different symbols and European cultivars they arrived at essentially the same conclusions as Craig (12) regarding the inheritance of flower color and floret doublesness in diploid geraniums. The incompletely dominant allele \(s\) for floret doublesness showed dose proportionality in its effect in tetraploid cultivars. Because no exceptional phenotypes which might have been ascribed to double reduction were observed, the \(s\) locus was believed to be located close to the centromere. They found seasonal modification in the number of petals and suggested that since the number of sepal is apparently governed by the same gene, and remained quite constant, this character was a more reliable index for the classification of floret doublesness than the petal number.

Craig (12) determined that 3 independent genes, \(p\), \(sa\), and \(v\) govern 7 flower colors in inbred lines of \(P. \times \text{hortorum}\) cultivars. When all 3 genes were dominant, the phenotype was red with the phenotypic expression of homozygous recessive \(sa\) and dominant \(P\), and homozygous recessive \(p\) with dominant or recessive \(sa\) producing pink flowers. The variegated character is expressed as a wedge of white at the base of pigmented petals. Plants which are heterozygous or homozygous dominant for the \(v\) gene have non-variegated petals, except pink flowers in which they are variegated regardless of genotype. In addition, the presence of color is probably governed by another gene \(w\), so that flowers having the genotype \(ww\) are white whereas \(WW\) or \(Ww\) genotypes would be colored with the actual color being determined by the other genes. The intensity of color is determined by the gene \(d\) which, in the homozygous recessive condition, acts as a dilutor of the base pigment.

The gene \(v\) has a pleiotropic effect in that it not only governs the variegated character of the petals but also influences stigma color and leaf zonation. Flowers having the \(vv\) genotype have colorless stigmas as do white flowers due to \(ww\) being epistatic to \(v\) or \(V\). Whether a leaf is zoned or not is determined by the gene \(z\); zoned leaves being \(zz\) and zoneless leaves being \(z\). Gene \(v\) governs the color of the zone, with \(vv\) producing a green zone and \(V\) a red zone. However \(z\) is epistatic to \(v\) so that the anthocyanin does not appear in the absence of a zone except under unfavorable environmental or nutritional conditions (12).

Nugent and Snyder (29) reported on a character in geranium flowers called “center color” which may be the same as the variegated character of Craig (12). They concluded that this phenotype was conditioned by one gene \(c\) with the dominant condition producing a solid colored flower whereas the homozygous recessive resulted in a
white area in the center of the flower.

Badr and Horn (3) have suggested that their flower color locus $Aa$ was identical to Craig's $Pp$ and their $Bb$ to his $S_{asa}$. However, they did not observe the pleiotropic action of $Vv$ on leaf zonation as reported by Craig (12). Chromatographic analyses showed that two genetic loci $Cc$ and $Bb$ controlled the glycoside structure of 2 anthocyanidins with the gene $Cc$ influencing color intensity as did the dose of dominant $B$ alleles in tetraploids. They did not, however, identify the anthocyanidins. Genetic analyses of tetraploids indicated further that, because of the incidence of double reduction in such plants, the $A$ and $B$ loci were likely located distant from the centromere.

Nugent and Snyder (29) concluded that plant height was monogenically controlled by the gene $d/w$ with dwarf being dominant to tall. This dominance of dwarf over tall had previously been reported by Chittenden (9). However, Henault and Craig (23) reported plant habit was due to a major gene $dw$ acting without dominance. They found F$_1$ hybrids to be intermediate in height between tall and dwarf inbreds. The F$_2$ generation segregated into tall, semi-dwarf, and dwarf plants. Craig (12) noted that Henault suggested the possible involvement of modifier genes since height classes other than the 3 basic phenotypes were observed among other breeding lines.

One of the most detailed genetic studies in Pelargonium has been that of Tilney-Bassett (34, 35, 36, 37, 38, 39) on plastid inheritance. Bauer (7) had found that, on selfing, white margined cultivars of Pelargonium produced white offspring, green cultivars produced green offspring and reciprocal crosses between them produced varying proportions of green, variegated and white progeny. He also noted that F$_1$ seedlings from reciprocal crosses were neither of one uniform type, nor of 2 or more types segregating in a Mendelian ratio; instead their proportions varied with the direction of the cross. Baur (7) therefore concluded that plastid inheritance was not Mendelian and proposed a hypothesis on the genetic continuity of plastids with a non-Mendelian, biparental pattern of inheritance and segregation from mixed cells during embryo development. Among others, Tilney-Bassett (35, 36, 37) confirmed Baur's (7) findings but found an unexpected discrepancy between observed and expected results. Although reciprocal crosses between cultivars containing normal green and mutant white plastids in their germ cells gave rise to a mixture of green, variegated and white seedlings, reciprocal crosses did not yield reciprocal results. Green seedlings tended to predominate when the male parent was likewise green. White seedlings were rare, often absent, but occasionally were quite frequent. Variegated seedlings were sometimes more frequent, sometimes less frequent than green seedlings and sometimes, like the white, were altogether absent.

Tilney-Bassett (38) has suggested that any interpretation of the varying proportions of green, variegated and white embryos following different crosses must consider possible control by the nuclear and the plastid genotype and must also relate the behavior of the plastids with the sequence of cell division during embryogenesis. He has proposed that, after fertilization, the zygote divides into a 2-celled embryo consisting of a basal and a terminal cell with the former developing into the suspensor. A group of 8 cells is formed from the next 3 divisions of the terminal cell. The basal quadrant nearest the suspensor divides first and becomes the root and the hypocotyl and the upper quadrant into the cotyledons and shoot. The fertilization of a green plastid egg by a white plastid sperm, for example, would form a zygote containing both green and white plastids. These must sort out at the first division to produce a terminal cell having only green or white plastids as most of the progeny of white x green and green x white crosses are non-variegated. Chimaeras, which would be the logical result of the division of a mixed terminal cell are found however. It should be noted that the performance of a parent in one cross is no guarantee of a similar performance in subsequent ones. Although Tilney-Bassett (38) has suggested 4 models to explain these phenomena he favors one which is based on the assumption that within a given zygote each kind of plastid has a specific probability of replicating first and consequently inhibiting the replication of the other, giving rise to a pure-celled embryo. He suggests that the control of this synchrony would operate through the varying interactions between different nuclei and different plastids. His crossing results support this suggestion with the female nucleus and color of the plastids apparently being particularly important. The mother cell of such plants, Meiosis in pollen mother cells of such plants. Meiosis in pollen mother cells of the one diploid cultivar examined was normal. With generous pollination there should have been enough viable pollen grains germinating, even in tetraploids, to penetrate the pistil and fertilize the ovules and produce more seeds than were in fact obtained. In tetraploids, sterility also resulted from either lack of germination of the pollen grains or to the swelling of the tip of the pollen tubes of those pollen grains which did germinate. Such swollen pollen tubes stopped growing in the style before reaching the ovule. Self-sterility in the diploid cultivar Meteor was due to few pollen tubes penetrating the whole length of the style, to embryos aborting in the first 3 or 4 days of their development and to death of the embryos as much as 5 to 13 days after fertilization. Philipp (31) also noted frequent embryo abortion in tetraploid plants.

The clone of P. scandens in the University of Guelph collection was male sterile; the anthers shrivelled, did not dehisce and produced no pollen (21). Hybrids of P. scandens and P. stenopetalum, P. inquinans and P. zonale showed varying degrees of male sterility, ranging from complete indehiscence of the anthers, to dehiscence of some anthers in a floret, to dehiscence or non-dehiscence depending on environmental conditions.

Incompatibility

Members of the genus Pelargonium have a sporophytic system of incompatibility and trinucleate pollen grains (8). Such pollen grains do not normally germinate on an incompatible stigma. Harney and Chow (20) found P. stenopetalum to be self-incompatible, whereas the varying degrees of seed set following self-pollination of P. zonale and P. inquinans suggested that these might be pseudo self-incompatible, a condition found in cultivated plants in which there has been a partial breakdown of the self-incompatibility mechanisms due to selection for self-compatibility during domestication (32). As the accessions used in this study were obtained from botanical garden collections and commercial sources they have undergone some domestication. In addition to being self-incompatible, cultivars of cultivated P. zonale, some of which were unsuccessful in interspecific crosses as a pistillate parent although it was partially successful as the staminate parent (20).

Male sterility

Philippi (31) has reported a high frequency of sterile pollen grains in cultivars of P. zonale. This was particularly true of pollen grains from tetraploid plants which he ascribed to the abnormal meiosis noted in the pollen mother cells of such plants. Meiosis in pollen mother cells from the one diploid cultivar examined was normal. With generous pollination there should have been enough viable pollen grains germinating, even in tetraploids, to penetrate the pistil and fertilize the ovules and produce more seeds than were in fact obtained. In tetraploids, sterility also resulted from either lack of germination of the pollen grains or to the swelling of the tip of the pollen tubes of those pollen grains which did germinate. Such swollen pollen tubes stopped growing in the style before reaching the ovule. Self-sterility in the diploid cultivar Meteor was due to few pollen tubes penetrating the whole length of the style, to embryos aborting in the first 3 or 4 days of their development and to death of the embryos as much as 5 to 13 days after fertilization. Philipp (31) also noted frequent embryo abortion in tetraploid plants.

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Male sterility was present in some of the hybrids of all of the crosses made between *P. × hortorum* cv. Mme. Buchner and 4 of its putative ancestral species, *P. zonale*, *P. inquinans*, *P. scandens*, and *P. stenopetalum* (10). With one exception, all plants having some doubling were partially male sterile, consisting of florets containing functional and nonfunctional anthers.

Meyer (27) and Clifford (11) noted that petaloidy occurred at the expense of stamens. Double flowers contain extra petals many of which bear anthers which may or may not be functional. Doubling may also involve the total transformation of the entire sexual apparatus into full scale petals resulting in sterile flowers. It may also involve the flattening of the filaments into petals, but some of the anthers bear functional pollen. In the semi-double florets of *P. × hortorum* and of hybrids of the cultivar and the ancestral species, extra petals were present, some non-functional. It would appear, therefore, that while partial sterility was associated with floret doubling in the hybrids in which it occurred, it was not entirely due to petaloidy.

Harney and Kung (22) conducted a detailed study of anther development in partially male sterile plants of the tetraploid cultivar Jacqueline. This male sterility was characterized by shrunk brown anthers which did not produce any pollen. It was not complete male sterility in that one or more of the 6 to 11 anthers in a floret would produce pollen. There was no apparent difference in the development of functional and non-functional anthers until the microspores began breaking away from their quartet formation. In sterile anthers the tapetum remained in position on the anther wall and, although it eventually disintegrated, the breakdown was slower than in normal anthers and was not accompanied by movement toward the microspores and their growth and maturation. This prolonged adherence of the tapetum may indicate that it is not serving its presumed function in nutrition of the developing microspores and may be the reason for the premature degeneration of the latter. In sterile anthers, the endothecium had degenerated to a thin and heavily stained line of tissue and the anthers did not dehisce. In the normal anthers of *Pelargonium*, prior to dehiscence, the partition of cells between each sporangium in a lobe had gradually grown thinner and eventually disappeared resulting in one large cavity per lobe which contained the maturing microspores. In abnormal anthers this partition had gradually thickened until, at anthesis, it was several cells in thickness and the outer wall of the microsporangium had collapsed and the microspores were empty and shrunken. Craig (12) has reported that Cohen found male sterility of *P. × hortorum* is due to two different recessive genes, *ms1* and *ms2*. Sixteen different lines of single petalled, diploid plants were analyzed and found to be either male sterile or to contain male steriles in their selfed progeny. Although the male sterility of some lines was determined by the recessives *ms1* and *ms2*, others were not and Dale and Rogers (17) suggested that other genes may also be involved which control male sterility and so may interactions with the environment. Cohen, cited by Craig (12), showed temperature to be partially responsible for the male sterile condition in the lines he investigated.

Embryo sac and embryo development

*Pelargonium* species have a compound inflorescence consisting of a number of florets each of which has a single style with a five-lobed stigma. The flowers are protandrous, with the anthers maturing as long as 3 days before the stigma becomes receptive (31). The ovary, with axile placentation, consists of 5 carpels each of which contains 2 superposed ovules to give a total of 10 ovules per floret. Only one of these superposed ovules normally develops into a seed (41). Tilney-Bassett (37) has determined that in *P. zonale* some unfertilized ovules appeared structurally normal and capable of being fertilized whereas others were abnormal, had no embryo sac and, therefore, could not be fertilized. He also noted that, of the two superposed ovules per carpel, the upper one was preferentially fertilized. There did appear, however, to be genetic control of this preferential fertilization, as 3.5% of the developing ovules were found in the lower position in 'Paul Crampel' compared to 20.6% in 'Flowers of Spring'. In *P. × hortorum* cv. Purple Heart, 92% of the developing ovules were found in the upper position and only 8% in the lower position (41). Philippi (31) has shown that although the embryo sac and egg apparatus developed normally in both upper and lower ovules in diploid and tetraploid cultivars of *P. zonale*, only one ovule, usually the upper one, developed into a seed. He also found that in older unfertilized flowers the lower ovule would be dried up while the upper one was still turgid.

Philippi (31) observed that the embryo sac development in *P. zonale* and compared his observations with those of Schurhoff (33). Both found the embryo sac to consist of a single ovule which possesses eight nuclei and the nucellus, to be strongly bent. Whereas Schurhoff (33) observed that the antipodals degenerated quickly, Philippi (31) found them still present in fertilized ovules. He could not confirm Schurhoff's (33) observations that the polar nuclei lay directly alongside the synergids assuming the same position as the egg cell, although he did find it in the vicinity of the egg apparatus but distinctly separated from it.

Adams (1) stated that ovules in the family Geraniaceae are campylotropous and having observed only 4 nuclei, namely the egg apparatus and one polar nucleus in *P. × hortorum* suggested that *Pelargonium* possesses the monosporic 4-nucleate Oenothera type of embryo sac.

A detailed study of megasporogenesis and megagametogenesis in *P. × hortorum* cv. Purple Heart by Tsai, Harney, and Peterson (41) clarified a number of the ambiguities mentioned above. The superposed ovules are bitemic and crassinucellar and the upper ovule of each pair is campylotropous while the lower one is anatropous. A single archesporial cell functions directly as the megaspore mother cell. Meiotic division of the megaspore mother cell results in the formation of a linear tetrad of megaspores of which the chalazal megaspore is functional. Embryo sac development is of the Polygonum type. Rapid degeneration of the 3 antipodals occurs soon after their formation, followed by the fusion of the 2 polar nuclei. As noted by Philippi (31) the polar nucleus was in the vicinity of the egg apparatus but distinctly separated from it; it did not assume the same position as the egg cell as stated by Schurhoff (33).

Philippi (31) compared normal embryonic development following the selfing of the diploid 'Meteor' and the death during development of the embryos of the cross 'Meteor' x 'Volkskanzler'. 'Meteor' was diploid and 'Volkskanzler' was tetraploid; theoretically, the embryo was triploid and the endosperm tetraploid and no viable seeds were produced.

In selfed 'Meteor' flowers in which embryo development was normal fertilization occurred between 7 and 17 hours after pollination. Twenty-four hours after pollination the endosperm had already divided several times with 4 to 8 endosperm nuclei being present but the zygote had not yet divided. After 2 days the embryo consisted of 6 to 8 cells whereas 15 to 20 endosperm nuclei were present. In 3 days the interior of the embryo sac was a gigantic vacuole with 80 or so endosperm nuclei around the outer edge of the embryo sac and around the embryo itself. The embryo, at this stage, consisted of a head of about 20 cells and a suspensor of 7 to 8 cells. Four days after fertilization the endosperm was still not cellular. At 6 days the embryo was made up of 100—200 cells and the...
endosperm was cellular and multilayered around the suspensor but still nuclear and one-layered at the chalazal end of the embryo. The cellular development of the endosperm observed by Philippi (31) was in disagreement with Schurhoff (33) who noted that usually no cell walls were laid down in the endosperm of *P. zonale*. At 10 days the embryo had developed from a heart-shaped structure to being distinctly bilobed and the suspensor cells had undergone a longitudinal cleftage and the suspensor was 2 or 3 cell layers thick with the endosperm becoming increasingly cellular. There were also giant endosperm nuclei formed by the fusion of several small nuclei and containing 20 to 25 nucleoli. After 12 days is more than 1 mm long and had reached the curve of the embryo sac. The endosperm was still nuclear at the chalazal end but became cellular and multilayered near the embryo. After 14 days the endosperm was almost completely cellular but had remained one-layered in the chalazal part of the embryo sac and little of the nucellus remained. At 14 days the embryo was 1.9 mm long and growing very rapidly so that at the end of 18 days it completely filled the sac at which time the endosperm began to degenerate. At the 18 day stage the primordium of the first 2 foliage leaves could be distinguished in the plumule palisade and spongy tissue in the cotyledons. The seed coat was still colorless and transparent so that the plumule palisade and spongy tissue 2 foliage leaves could be distinguished in

Future studies on the meiotic behavior of chromosomes in species and diploid and tetraploid cultivars of *P. × hortorum* should contribute to fundamental knowledge of chromosomal behavior as well as to a better understanding of the genus. In addition, the gene pool of the geranium could be greatly increased and enhanced if intersubgeneric reproductive barriers could be eliminated or circumvented. So far little has been done in this regard.

**Conclusion**

It is evident from the foregoing that, although there have been a number of studies on the origin, cytology, genetics, cyto genetics and reproductive morphology of the geranium many aspects remain to be investigated. The ancestry of the cultigen, for example, is still not known with certainty. The suggestion of Badr and Horn (2) that it arose from one species because of the apparent autotetraploidy of *P. × hortorum* requires further investigation in view of information from other workers (10, 11, 25).

**Literature Cited**


