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Chromosome behaviour and phylogeny of cultivated *Cerasus*

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Introduction

The genus *Cerasus* JUSSIEU (formerly subgenus of the great genus *Prunus* MILLER) contains nearly 130 species, most of them growing in Eastern Asia (EVREINOFF 1956). There are not many cultivated species, some are grown as ornamental trees the others as fruit trees. In the present paper attention will be paid to the latter only. If we do not take into consideration the American species *C. besseyi* BAYLEY and the Chinese *C. tomentosa* THUNBERG and *C. cantabrigiensis* STAPF, then in the European area there remain only three great species commonly known as cherries, i.e. Sweet cherries, Sour cherries and Duke cherries. More detailed attention will be paid to these three species.

The common names are used first intentionally because these species are usually termed in this way in popular pomological books and papers. There is considerable confusion in common pomological names especially in some European languages. English is an exception. Here Sweet cherry denotes the diploid species (2n = 16) *Cerasus avium* (L.) MOENCH (= *Prunus avium* LINNÉ), Sour cherry is the tetraploid (2n = 32) species *C. vulgaris* MILLER (= *Prunus cerasus* L.) and Duke cherry is also a tetraploid species, as now generally accepted, of hybrid origin with the Latin name *C. gondouinii* POITEAU & TURPIN (=*Prunus cerasus dulcacerba* FERKL).The terminological situation is quite clear inside the species *C. avium*. Two main groups, characterized especially by pulp consistency which may be soft or firm, are distinguished taxonomically as well as pomologically. The varietas *duracina* DC. are Bigarreaux, Knorpelkirschen, and var. *juliana* DC. are Guignes, Hearts, Herzkirschen. The two remaining species can be divided systematically and pomologically again into two groups, taking in addition to other signs, the appearance of the fruit as a distinguishing character, especially if their juice is coloured or colourless. In the species *C. vulgaris* the types with dark fruits and deeply coloured sour juice, var. *frutescens* NEILR. (= v. *austera* L.) are known as Griottes, Weichseln, whereas types with light red fruits and colourless or only very slightly coloured juice, var. *caproniana* L. are Montmorencies, Morelles, Amarellen. In *C. gondouinii* dark-fruited types with slightly coloured juice are var. *colorata* FERKL and types with quite colourless juice of a vitreous appearance belong to var. *vitrina* FERKL. Considerable confusion is found especially in the German nomenclature (and also in Slavonic languages). The names Sauerkirschen, Amarellen, Glaskirschen, Süszsaure are used by authors for both types, sometimes some of them even for varieties of the preceding species. Therefore in the subsequent text, including quotations, either Latin names or unambiguous English names will be used.

The chromosome number in the species mentioned was determined many years ago by several authors independently and nearly simultaneously (e.g. DARLINGTON 1927, 1928, KOBEL 1927, OKABE 1928 a.o.). Already in these first papers brief discussion may be found on the possible origin of the tetraploid species. A simple statement of the chromosome number is not sufficient, however, for solving such problems. It is necessary to follow their behaviour during meiosis in detail, where the formation of multivalent configurations and possibly also the occurrence of univalents is of great importance. Chiasma frequency may be judged, too. Thus heterotypic division attracts primary attention of those authors who are concerned with the phylogenetic relations among the species mentioned.

This provides a clear demonstration of how the same observations can be differently interpreted by different authors, sometimes even in an opposite manner, and how the opinion of one author changes in the course of time as a result of wider experimental evidence. This is really instructive for the evaluation of cytological characters in taxonomy, and it is by no means a unique instance. We can see a very similar situation in not too remotely related fruit trees of the subfamily *Pomoideae*, i.e. apples and pears. The occurrence of multivalents or a secondary association of chromosomes may be interpreted very differently from the phylogenetical point of view. According to DARLINGTON & MOFFET (1930) the secondary basic chromosome number $x = 17$ originated by means of aneuploidy acquired by polysomy, whereas SAX (1932) explains the origin of this number (very strange in the family *Rosaceae*) as a result of distant hybridization followed by amphidiploidy. The very recent investigations of UHLÍK (1961) seem rather to confirm SAX's opinion.

The subfamily *Prunoideae* also illustrates the importance of avoiding generalization when considering the origin and phylogenetic relations of related species. The origin of hexaploid cultivated plums (*Prunus domestica* L. sensu lato) as an amphidiploid which arose by crossing the diploid species *Prunus cerasifera* EHRH. with the tetraploid *P. spinosa* L. has been proved experimentally (RYBIN 1936). On the other hand, amphidiploidization of a triploid hybrid between Sweet and Sour cherries did not succeed in producing a new fruit tree species (HUNTER & WALKER 1955). The hexaploid plants obtained after colchicine treatment are not only completely autosterile, but no species pollinating them have been found (HUNTER, written communication). Unfortunately detailed cytological analysis of these hexaploid cherries has not been made hitherto, their somatic chromosome number only has been determined.

For consideration of phylogenetic relations between several species it is important not only to study their own chromosomal behaviour especially during meiosis, but an analysis of meiotic configurations in different hybrid combinations between them is of much greater importance. Therefore most papers dealing with this problem actually contain a cytological analysis of meiosis in artificial as well as spontaneous hybrids between the three species of *Cerasus* mentioned above. They are the papers of the following authors arranged in chronological order: PRYWER 1936, HRUBÝ 1939, RAPTOPOULOS 1941, HRUBÝ 1950, BLASSE 1957, BARG 1958. Their opinions will be mentioned in the discussion. The diploid species *C. avium* is considered least frequently, only one author (HRUBÝ 1950) expresses a suspicion of an ancient hybrid origin of this species, too. The two tetraploid species are considered by some authors as being autotetraploid, by others as allotetraploid; details will be discussed again later. The aim of the present paper is to solve this dilemma by means of a comparison and analysis of our own earlier investigations as well as of those of other authors, and also by a detailed analysis of new hybrid material not investigated hitherto. These are triploid hybrids between the species *C. avium* and *C. vulgaris*, obtained in this direction of cross, i.e. using Sweet cherries as maternal plants.

Material and Methods

It is usually stated that when Sweet and Sour cherries are to be crossed better results are met with if *C. vulgaris* is used as the maternal plant. The possibility of reciprocal crossing is sometimes even denied. Therefore all existing cytological and other investigations have been made in hybrids *C. vulgaris* × *C. avium*. Our experiences are in general quite the reverse, as better results have been obtained after crossing Sweet cherry × Sour cherry. In the years 1950—1955 a total of 16 393 hybrid pollinations in both directions were performed. A total of 9091 pollinations in 128 cultivar combinations were of the type *C. avium* × *C. vulgaris*. 81 combinations (i.e. 63.3 per cent) were successful comprising 6640 flowers, from which 750 ripe fruits were harvested (i.e. 11.3 per cent). This is a very good result indeed in interspecific crossing, as the fruit set within the species *avium* when different compatible cultivars are intercrossed averages 26 (Crane & Lawrence 1938) to 30 (Oldén 1959) per cent. 413 hybrid plants were obtained, i.e. 55.06 per cent (in relation to the number of fruits). 7302 pollinations in 84 cultivar combinations were of the type *C. vulgaris* × *C. avium*. In these crossings only 17 combinations (20. 2 per cent) were successful having 2833 flowers. The number of harvested fruits was 270, i.e. 9.5 per cent. Oldén (1959) gives the fruit set percentage in Sour cherries as from 8 to 44. Our results in distant crosses are therefore again quite satisfactory. 97 seeds germinated which is 35.92 per cent. These relatively poor results in getting living hybrid plants were caused by the fact that during the first two years the stones were sown directly into the soil. As generally known, this gives a very low germinability, not exceeding 25 per cent (cf. Košelenko 1952). Only from 1952 was the operative exstirpation of the embryos and artificial cultivation of young seedlings carried out, giving an increase in the percentage of germinated plants from 11.5 to 66.6 (Hrubý 1954). In the following years many plants died out of the total number of 510. At the present time we have 208 hybrid trees of the combination *avium* × *vulgaris* and 91 trees of *vulgaris* × *avium*. In the former the mortality is five times greater (50.3 per cent against 9.4 per cent); thus crossing *vulgaris* × *avium* is more successful from this point of view. Most trees began to blossom at the age of 5—6 years. The fruit set by free pollination is very low as may be expected in triploids. Further details and a description of other characters of these hybrids will be given later elsewhere.

For cytological investigation ten trees were selected of the combination *avium* × *vulgaris* and one tree of the reciprocal combination. All had plenty of flower buds and were triploid (2n = 24). The one tree *vulgaris* × *avium* was taken for comparison with the results of other authors who have investigated many hybrids of this combination. The following hybrids were investigated:

5229/2	Bigarreau Dönissen × Griotte de Vít
5229/13	Bigarreau Dönissen × Griotte de Vít
5318/2	Bigarreau Hedelfingen × Griotte de Vít
5411/6	Bigarreau Napoleon × Griotte d'Ostheim
5413/2	Bigarreau Noir de Winkler × Griotte d'Ostheim
5421/9	Karešova (Guigne) × Griotte de Büttner
5425/11	Elton Heart × Griotte d'Ostheim
5425/12	Elton Heart × Griotte d'Ostheim
5428/2	Bigarreau Emperor Francis × Griotte de Vít
5442/6	Václavka (September-Cherry) × Griotte d'Ostheim
5511/17	Griotte d'Ostheim × Elton Heart

Reciprocal combination of the same cultivars was selected intentionally. Two trees not quite identical in appearance were also taken intentionally in two cultivar combinations. From trees growing in a planting, branches with flower buds were cut in the first week of March and kept in the laboratory at a temperature of 24 °C for several days. The flower buds were fixed at the time of meiosis. The relation of the course of meiosis to the size of flower buds is not the same in different combinations, as pointed out already by Blasse (1957). The buds were fixed in alcohol-acetic mixture or in Navašin's mixture. Either smears were made and stained with acetic carmine or acetic nigrosin, or objects embedded in paraffin wax were sectioned and the slides stained with Feulgen's nucleal reaction or with Heidenhain's iron hematoxylin. The latter, in particular, gave very good results. In each hybrid combination 130—140 PMC were investigated in detail. Only PMC were observed where the situation was absolutely clear. Attention was focussed on first metaphase configurations. Observations were made by means of the Zeiss-Lumipan microscope, apochromate objective HI 120.

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Results

As expected, in all hybrid combinations investigated, different numbers of trivalents have been found. Their number ranged from one to eight. Both extremes, however, were very rare. Most frequently five or six trivalents were found. Besides trivalents a variable number of bivalents and univalents were present. In the overwhelming majority of cases the number of univalents and bivalents in the cell was the same. It ranged from one to seven. A survey of the situation in all material investigated, is given in Table 1. The heterotypic metaphase configurations are arranged according to the decreasing number of trivalents and correspondingly increased number of both bivalents and univalents.

Table 1

The frequencies of metaphase configurations in the material investigated

Configuration	5318/2 Hedelfingen × Gr. de Vit	5411/6 Big. Napoleon × Gr. d'Ostheim	5421/9 Karešova × Gr. de Büttner	5229/13 Big. Dönissen × Gr. de Vit	5428/2 Emperor Francis × Gr. de Vit	5425/12 Elton Heart × Gr. d'Ostheim	5229/2 Big. Dönissen × Gr. de Vit	5413/2 Big. Winkler × Gr. d'Ostheim	5425/11 Elton Heart × Gr. d'Ostheim	5442/6 Václavka × Gr. d'Ostheim	Total *C. avium* × *C. vulgaris*	5511/17 Gr. d'Ostheim × Elton Heart	Grand total
8^{III}			1	2	1	4	2	2	5	10	27	6	33
$7^{III}1^{II}1^{I}$	7	11	11	14	16	21	27	29	30	36	202	42	244
$6^{III}2^{II}2^{I}$	26	35	32	40	40	51	52	51	43	37	407	49	456
$5^{III}3^{II}3^{I}$	46	46	49	53	47	36	40	29	38	24	408	26	434
$4^{III}4^{II}4^{I}$	36	27	24	27	21	18	19	13	14	16	215	11	226
$3^{III}5^{II}5^{I}$	15	11	12	5	5	6	3	4	3	6	70	1	71
$2^{III}6^{II}6^{I}$	5	5	5	1	2		1	1		1	21		21
$1^{III}7^{II}7^{I}$		1	1		1						3		3
Other										2	2		2
Total	135	136	135	142	133	136	144	129	133	132	1355	135	1490

From this survey it can be seen that the trivalent frequency distribution is very similar in all hybrid combinations. It is always a normal distribution, in single cases, of course, with greater or less asymmetry. There are, however, differences in the mean number of trivalents in the cell. This ranges from 4.70 to 5.80 in combinations *avium* × *vulgaris;* in the reciprocal combination it is 5.98. It is clear at first glance that such an amplitude points to heterogeneity of the material. Testing the significance by means of the t test actually reveals that differences between some combinations are significant or even highly significant, as shown in Table 2. The Mark — means that there is no difference between the mean values, mark + designates a significant difference (at 0.05 probability level), whereas mark +++ shows a highly significant difference (0.01 probability level).

Table 2

Significance of differences between mean numbers of trivalents

4.70	4.92	4.93	5.24	5.25	5.56	5.58	5.71	5.74	5.80
4.70	—	—	+++	+++	+++	+++	+++	+++	+++
	4.92	—	+	+	+++	+++	+++	+++	+++
		4.93	+	+	+++	+++	+++	+++	+++
			5.24	—	+	+++	+++	+++	+++
				5.25	+	+	+++	+++	+++
					5.56	—	—	—	—
						5.58	—	—	—
							5.71	—	—
								5.74	—
									5.80

According to the significance of the differences it is possible to distinguish three groups among the combinations investigated. Inside each group the situation is practically identical, but significant differences occur between groups. This is true not only for the mean number of trivalents in PMC but also for the percentage frequency of trivalents in general. All values mentioned with particular cultivar combinations are given in Table 3.

The combination *C. vulgaris* × *C. avium* (Griotte d'Ostheim × Elton Heart) does not differ from one instance of the reciprocal combination (viz. 5.98 and 5.74), but between it and the second hybrid plant of the reciprocal combination (trivalent mean 5.56) there exists a highly significant difference. These two hybrids themselves (Elton Heart × Griotte d'Ostheim) belong to the same group. But the second couple of identical cultivar combination (Bigarreau Dönissen × Griotte de Vít) reveals a highly significant difference between its members.

These results obtained on numerically adequate material demonstrate quite convincingly that different triploid hybrids between Sweet and Sour cherries, even individual plants of the same cultivar combination, can differ in the mean number of trivalents formed in single PMC as well as in the general frequency percentage of trivalents. The type of distribution remains, however, generally the same in all cases.

Table 3

Mean numbers of trivalents and their percentage frequencies grouped according to significant differences

Combination	Trivalent		Group mean	
	mean in PMC	percentage frequency	in PMC	percentage
Hedelfingen × Gr. de Vít	4.70	41.54	4.85	43.92
Big. Napoleon × Gr. d'Ostheim	4.92	44.39		
Karešova × Gr. de Büttner	4.93	45.82		
Big. Dönissen × Gr. de Vít	5.24	48.68	5.24	48.80
Emperor Francis × Gr. de Vít	5.25	48.92		
Elton Heart × Gr. d'Ostheim	5.56	53.13	5.68	54.99
Big. Dönissen × Gr. de Vít	5.58	53.60		
Big. Winkler × Gr. d'Ostheim	5.71	55.42		
Elton Heart × Gr. d'Ostheim	5.74	55.89		
Václavka × Gr. d'Ostheim	5.80	56.91		
Gr. d'Ostheim × Elton Heart	5.98	60.35		

Discussion

In order to facilitate the utilization of the given results of cytological analysis of triploid hybrids *C. avium* × *C. vulgaris* in elucidation of the phylogenetic relations particularly of the tetraploid species of the genus *Cerasus*, it is necessary to confront and compare them with all material hitherto published, concerning the species as well as different hybrid combinations.

In the species *C. avium* a great regularity of the first meiotic division and formation of eight bivalents was found unanimously by all authors. Only two of them mention the very rare occurrence of univalents (Raptopoulos 1941), their frequency not exceeding 0.25 per cent (Blasse 1957).

Likewise, in one tetraploid species, *C. vulgaris*, the data of all authors are in general agreement. They are summarized in Table 4 where the most important comparable values are given. These values have been calculated by the present author from published data, if they had not been given exactly in the papers. For assessing the validity of these data, the amount of material investigated is of importance, as expressed by the number of cultivars and mainly by the number of PMC observed in each variety.

In addition to data which could be transformed numerically in this table, the results of Barg's investigations should be mentioned. She investigated 22 cultivars in which she found a practically identical situation, two of them were analysed in more detail. She found mostly 16 bivalents, apart from univalents, trivalents and quadrivalents, these last 1—4 in number. It is thus possible for all data available, to note a clear preponderance of bivalents and the formation of a variable number of quadrivalents (4 at most). Moreover Hrubý (1950) found that the frequency distribution of bivalents follows the Poisson series, and that there is no difference between representatives of the two varietal groups, i.e. *frutescens* and *caproniana*.

Table 4

Survey of cytological information in *Cerasus vulgaris*

Author	Number of investigated		Univalents		Bivalents		Trivalents		Quadrivalents	
	cultivars	PMC in each	mean numb.	% freq.	mean numb.	% freq.	mean numb.	% freq.	mean numb.	% freq.
Prywer 1936	4	50	0.51	3.7	10.23	75.2	0.51	3.7	2.37	17.4
Raptopoulos 1941	2	18	1.75	14.2	9.15	65.1	0.59	4.2	2.54	18.2
Hrubý 1950	6	250	1.33	8.1	14.75	89.9	0.13	0.8	0.19	1.2
Blasse 1957	1	36	—	1.6	—	91.3	—	—	—	7.1

In spite of this agreement in cytological characteristics there are two opinions on the origin of this species, on its autopolyploid or allopolyploid state respectively. Most authors consider it as allotetraploid. Already Kobel (1927) expressed the opinion that Sour cherries in general originated by the crossing of two not very distant diploid species and subsequent amphidiploidization of the primary hybrid. Prywer (1936) and Hrubý (1950) are in complete agreement with this theory. Further, Hrubý (1950) considers affinity between genomes of those original ancestors and genomes of other species participating in the origin of the Sweet cherries, as will be discussed thoroughly later. Even though the cytological behaviour points much more to alloploidy, Raptopoulos declares *C. vulgaris* to be an autopolyploid and tries to explain the low frequency of quadrivalents by prolonged selection for increased fertility by sexual propagation, operating by lowering the chiasma frequency. This opinion cannot be either proved nor disproved, but the results of further investigations especially of hybrids do not indicate that it is very probable.

More recent papers (e.g. Evreinoff 1956) consider *C. vulgaris* as a hybridogenous species. It originated most probably by crossing *C. fruticosa* Pallas and *C. avium* (L.) Moench. In order to test this theory experimentally, crosses were made in 1956 at Balsgård in Sweden between *C. fruticosa* and tetraploid Sweet cherry. Similar interspecific crosses were made the following year but instead of tetraploid *C. avium* the diploid cultivar Bigarreau de Schrecken was used (Oldén 1959). Detailed reports on the results of these experiments have not yet been published. It should be noted, however, that in phylogenetic reconstructions the obtaining of primitive original forms cannot be expected if highly specialized contemporary cultivars are used for such synthetic crossing. Possibly the most primitive, really wild growing forms should be sought. Their crossing can result rather in the creation of types resembling the original forms. The work of Mangelsdorf (1958) who obtained an ancestor-like maize by crossing primitive local varieties may be quoted as an example of such successful reconstruction. Therefore, a final solution cannot be expected from the Swedish experiments mentioned above.

An even more complicated situation is met in the second tetraploid species *C. gondouinii*. As in former, Table 5 brings a survey of comparable values obtained by cytological investigation of several authors.

Table 5

Survey of cytological information in *Cerasus gondouinii*

Author	Number of investigated		Univalents		Bivalents		Trivalents		Quadrivalents	
	cultivars	PMC in each	mean numb.	% freq.	mean numb.	% freq.	mean numb.	% freq.	mean numb.	% freq.
Prywer 1936	2	50	0.66	4.8	9.62	71.4	0.66	4.8	2.53	18.9
Hrubý 1939	6	50	0.04	0.4	3.36	37.9	—	—	6.11	61.6
Raptopoulos 1941	6	20	0.55	5.3	3.69	35.6	0.43	4.1	5.69	54.9
Hrubý 1950	6	250	0.27	2.7	3.77	37.3	0.07	0.7	5.99	59.3

From Barg's material only data on a typical representative of the group of "Amarellen" according to her nomenclature, can be utilized. Unfortunately, among 15 listed cultivars there are at least four belonging to var. *caproniana* of the species *C. vulgaris*. The typical one, Doktorkirsche, is, however, a Duke cherry (Glaskirsche) thus really a representative of the species *gondouinii*. A detailed analysis is not given, only the occurrence of a high number of quadrivalents, in some cases even eight. In this Barg's findings are in general agreement with those given in Table 5, except for Prywer's data. As I have already pointed out (Hrubý 1950) there must have been some mistake in her material, as the results actually show a great similarity with *C. vulgaris*. On the other hand, all other investigators conform in the finding of a high number of quadrivalents as a main and typical characteristic of the Duke cherries. The frequencies of these quadrivalents follow the normal distribution as found by Hrubý (1950) in all six cultivars investigated.

The high frequency of quadrivalents is, however, one of the most prominent characteristics of autotetraploids. It is for this reason, and also as a result of further investigations of hybrids between Dukes and both Sour and Sweet cherries, that formerly opinions were expressed that the Dukes are autotetraploid forms originating from the species *C. avium* (DARLINGTON 1928, HRUBÝ 1939). But already KOBEL (1927) considered Duke cherries as hybridogenous types and this opinion was in the course of time, after more detailed investigations, accepted by practically all authors. It is mostly assumed that an unreduced gamete of the species *avium* was fertilized by a normal reduced gamete of the species *vulgaris*. In the origin of types less resembling Sweet cherries, i.e. var. *colorata*, some authors postulate another species in place of *C. avium* as one parent (PRYWER 1936, BLASSE 1957). But cytologically both groups (var. *vitrina* as well as var. *colorata*) behave identically (HRUBÝ 1950) and if we take into consideration the diversity of different wild forms and cultivars of the species *avium*, many of which have been cultivated for centuries, the morphological differentiation of both groups is quite possible, especially if the second supposed parental species is also by no means uniform and can be divided into two distinct variety groups (*frutescens, caproniana*). By combining different representatives of both varietal groups of both parental species a lot of forms can originate — and actually did originate — more or less intermediate or resembling either parental species in general appearance as well as in fruit characters.

Only RAPTOPOULOS (1941) maintains the opinion that *C. gondouinii* is an autotetraploid. According to the number of quadrivalents and high chiasma frequency he believes it to be an autotetraploid form originated by chromosome doubling from *C. avium*. Thus, according to him both, *C. gondouinii* as well as *C. vulgaris*, are autotetraploid species. The former originated, as mentioned, from *avium*, whereas the latter originated by the doubling of chromosomes of an unknown diploid species arisen only by genic differentiation from a diploid ancestor common also to the species *avium*. There may be some reservations against chiasma frequency as a discriminating criterion, as it can change with environmental conditions. RAPTOPOULOS himself found differences in *C. cantabrigiensis* depending on the year and time of fixing the objects. This alone could not disprove any hypothesis, of course. Although in *C. vulgaris* its autotetraploid character cannot yet be directly proved nor denied, there is a reverse situation in *C. gondouinii*. Here two arguments exclude its autoploidy. First, the hybrid origin of at least one Duke cherry cultivar is known exactly. This cultivar, Beauty of the North (Krasa Severa) originated by intentional pollination of a Sour cherry Early of Wladimir with the pollen of a Sweet cherry Guigne Blanche de Winkler, as described exactly by its creator MIČURIN (1907). The Beauty of the North is a typical Duke cherry and behaves cytologically in the same manner as all others investigated (HRUBÝ 1950). The second argument is the existence of autotetraploid Sweet cherries, both spontaneous (DANIELSSON 1947) as well as produced by colchicine treatment (OLDÉN 1954). These plants not only do not have the appearance of Dukes, they fully maintain the character of the species *avium*, but moreover they are highly sterile and the few fruits which are set do not attain the size of fruits in normal diploid cultivars (SANTESSON 1959). Before proceeding to an attempt to elucidate the origin of *C. gondouinii*, let us pay attention to the cytological investigation of artificial hybrids.

Tetraploid hybrids between *C. gondouinii* and *C. vulgaris* were investigated by HRUBÝ (1939) and RAPTOPOULOS (1941). Both these authors by chance carried out investigations in the same cultivar combination, i.e. May Duke × Morello.

There are no essential differences in their findings. This hybrid behaves like the parental species *gondouinii*, i.e. it forms a considerable number of quadrivalents, 5.20—6.61 on an average. Its behaviour again is similar to the situation in autotetraploid organisms. In addition, RAPTOPOULOS investigated the hybrid between the Chinese species *C. cantabrigiensis* (which he considers as allotetraploid) and *C. vulgaris* (cultivar Coe's Carnation). This hybrid which is of little importance for our considerations behaved in correspondence with the situation in both its parents, it formed mostly bivalents (mean number 10.80) and a few quadrivalents (mean per PMC 1.95).

The triploid hybrids Duke × Sweet cherries are characterized by a very high degree of trivalent formation. HRUBÝ (1939) investigated four cultivar combinations and found eight trivalents in one third of all PMC. The mean number was 7.08 and percentage frequency 80.9. RAPTOPOULOS (1941) who studied two hybrid combinations also in this case reached the same general results. He examined 25 PMC in each and gave the following mean numbers: univalents 1.60, bivalents 1.60, trivalents 6.40. Another hybrid investigated by him, *C. cantabrigiensis* × *C. avium*, was quite different; it formed on an average 6 univalents, 6 bivalents and 2 trivalents in one cell. It must be pointed out that hybrids *gondouinii* × *avium* behave again like autotriploid organisms. For this reason RAPTOPOULOS maintained the opinion of an autotetraploid *avium* character of the Duke cherries.

Thus we meet a peculiar situation: A certain species itself behaves as autotetraploid, when crossed with the suspected original diploid species it produces hybrids of an autotriploid behaviour, but after crossing with another tetraploid species it renders hybrids behaving as autotetraploids, too. At the same time its hybrid character is proved experimentally by means of crossing just these two tester species, as well as by its difference from autotetraploid forms of one of them. HRUBÝ (1950) attempted to solve this problem with a working hypothesis of the hybridogenous character of all three participating species, having their genomes composed of three different haplomes more or less alike, thus facilitating greater or lesser conjugability between chromosomes of individual haploid sets.

According to this hypothesis at the time of speciation within the genus *Cerasus* there existed several basic diploid types three of which have participated in the evolution of the species discussed in the present paper. They were types with homozygous genomes: AA the first, BB the second, and CC the third. Two of the haplomes A and B were much more similar, therefore intercrossing of species AA and BB resulted in a fertile hybrid of specific character, having the genotype AB. The genic and morphological affinity of chromosomes made complete pairing at meiosis possible. This type became the original link in the evolutionary chain of the present diploid species *C. avium*. The original basic species of the genome BB also crossed with the third one, having the genotype CC. But haplomes B and C were much more differentiated, thus making possible only limited partial pairing of some chromosomes from each haploid set. This hybrid therefore was practically sterile. But by means of somatic chromosome doubling a fertile amphididiploid species BBCC originated, characterized by potentially complete pairing and the accidental formation of some few quadrivalents. This became the basic type of the tetraploid species *C. vulgaris*. One of its components could have been a type similar to contemporary *C. fruticosa* or its ancestors.

With the above theory the behaviour of *C. gondounii* as well as that of its hybrids can be explained. This species originated by fertilization of an unreduced diploid gamete of *avium* — genotype AB — by a normal gamete of *vulgaris* — genotype BC. Thus a tetraploid hybrid originated having genome ABBC. Its potential genotypic unstability is of less importance as it is continuously propagated vegetatively. If we now suppose that between haplomes A and C a greater genic affinity again exists making possible conjugation of chromosomes from these two haploid sets, then the occurrence of a relatively high percentage of quadrivalents may be expected as well as the formation of numerous trivalents in the products of the back-cross *gondouinii* × *avium.* In this type of back-cross in three quarters of the progeny a very high number of trivalents must be formed. It is not surprising that just these cases were among the few combinations investigated, the more so if such genome combinations facilitating a higher degree of conjugation possess a certain selective advantage in general vitality. In derivatives of the second type of back-crossing, i.e. *gondouinii* × *vulgaris* one half should display a high percentage of quadrivalents whereas the second half of the progeny should have a significantly lower percentage. Unfortunately only one combination has been investigated.

But a proof of the validity of the hypothesis mentioned above can also be obtained by investigation of the chromosome behaviour in triploid hybrids between the species *avium* and *vulgaris.* Since the considerable genic affinity of the respective haplomes and thus the morphological and genic similarity of individual chromosomes makes an exact segregation of complete haploid sets unlikely, it is also impossible to expect exact segregating ratios between types with significantly more multivalent configurations and on the contrary with a low frequency of them. A proof of the above theory would be provided, if individual plants of hybrid combinations differed significantly in forming multivalents, in this case trivalents.

Hitherto only triploid hybrids having *C. vulgaris* as the maternal parent have been investigated. Unfortunately the data of the two authors who carried out these investigations are of such kind that do not allow calculation of standard errors and the testing of the significance of the differences. But according to my own results obtained in reciprocal crosses, which are given in the present paper, I can also evaluate the data of other authors with high accuracy.

Raptopoulos (1941) examined 25 PMC of the hybrid Morello × Mezel. He found the following mean number per cell: univalents 2.92, bivalents 3.28, trivalents 4.84. We are only interested in the last. It can be deduced that this mean number corresponds to a trivalent percentage frequency in the range of 40—45 per cent. Blasse (1957) investigated 412 PMC in 16 seedlings of six cultivar combinations (thus 26 PMC per plant in average). In five combinations Morello (Schattenmorelle) was the maternal plant, only once Kentish Red (Königliche Amarelle). Five different cultivars of Sweet cherries were used as paternal plants. In combinations with Morello he found the trivalent percentage to be 38.7, whereas in the combination with Kentish Red (54 PMC) it was 46.5. Even although the significance of the difference cannot be calculated from these data, it is quite obvious that this difference is significant. In the present paper the results of the author's own investigations are given. In the hybrid Griotte d'Ostheim × Elton Heart in 135 PMC a trivalent percentage frequency of 60.3 was found. Thus, we have at our disposal four comparable values of different hybrid combinations: 38.7, (40—45), 46.5 and 60.3. Results obtained by investigation of the hybrid combinations of reciprocal crosses of *C. avium* × *C. vulgaris*, are listed in Table 3 of the present paper. Individual plants, sometimes even of the same cultivar combination, display between themselves highly significant differences. Thus cytological analysis of triploid hybrids between Sweet and Sour cherries (and reciprocally) is in good agreement with the above hypothesis on the phylogenetic relations of the most important cultivated species of the genus *Cerasus*.

Conclusion

The cytological analysis of the occurrence and frequency of multivalent configurations during the first meiotic division, carried out in species and different hybrid combinations thereof, has shown that all three important cultivated species of the genus *Cerasus* JUSSIEU, i.e. *C. avium* (L.) MOENCH, *C. vulgaris* MILL. and *C. gondouinii* POIT. & TURP. can be considered as hybridogenous. The species *C. avium* is diploid and its genome is formed by two highly alike haplomes AB. The species *C. vulgaris* is amphidiploid with the genome constitution BBCC. The third species *C. gondouinii* originated by fertilization of an unreduced gamete *avium* by a normal reduced gamete *vulgaris*. It is therefore allotetraploid, its genome formula being ABBC. Until another explanation is presented, fitting better all facts hitherto determined, the present explanation may be considered as the most probable.

Summary

The origin of three most important cultivated species of the genus *Cerasus* JUSS. i.e. the Sweet cherries *C. avium* (L.) MOENCH, the Sour cherries *C. vulgaris* MILL. and the Duke cherries *C. gondouinii* POIT. & TURP. is elucidated as a result of the cytological analysis of multivalent first metaphase configurations in these species and their various hybrid combinations.

Cytological evidence hitherto published is reviewed and discussed. Results of the author's own investigation in triploid hybrids between Sweet and Sour cherries are presented.

In view of both previous as well as the present results the earlier hypothesis of the present author is supported as being the most probable explanation of phylogenetic relations of the species mentioned. According to this hypothesis all three species are of hybrid origin, containing in their genotypes two or three different more or less similar haplomes in different assortment.

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