By polyploidy is meant an increase in the number of sets of chromosomes in a plant or animal. The bodies of animals and of the higher plants normally contain two sets of chromosomes, one derived from each parent. In ordinary sexual reproduction this number is reduced to one half in the maturation of the germ cells, and the diploid or \(2x\) number is restored in the process of fertilization by the union of two germ cells whose nuclei are each carrying the haploid or \(x\) number. But the comparative study of chromosomes shows that there are many instances in plants and animals where additional sets of chromosomes have been acquired by the organism, thus giving rise to species, genera, or individuals which are triploid (3\(x\)), tetraploid (4\(x\)), pentaploid (5\(x\)), hexaploid (6\(x\)), or even decaploid (10\(x\)) in their chromosome outfit. These conditions of polyploidy have a number of interesting consequences and evolutionary bearings which it is the purpose of this article to discuss.

It may first be pointed out that polyploidy may arise naturally or under experimental conditions. Boveri (1905) showed many years ago that if the division of a sea-urchin's egg which is undergoing its first cleavage be suspended at the right moment by shaking, so that the chromosomes have split but the daughter halves have not separated too far, a single nucleus with twice the usual number of chromosomes will result, and this tetraploid condition may persist in later cleavages. Similarly F. R. Lillie (1906) was able, by treating

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the egg of the annelid worm Chaetopterus with a solution of potassium chloride, to induce many successive divisions of the chromosomes but without any accompanying nuclear or cell division. There was a periodic formation and division of the chromosomes as in normal cleavage; but in the absence of a spindle the formation of separate nuclei or cells did not take place, a ciliated trochophore-like larva with usually a single huge nucleus being the result. The chromosomes in this nucleus were too numerous to be accurately counted but, judging from the rate of development of a normal larva, this structure corresponded to the 64-cell stage. Since the $x$ number of chromosomes is 9, the number of chromosomes present would be $9 \times 64 = 576$, and the nucleus was found to contain roughly this number, i.e. $64x$. The chromosomes were, moreover, arranged more or less definitely in 9 groups, the members of each group being descended from a different chromosome.

Again, it has been found by Holt (1917) that in the cells of the intestine of the mosquito Culex, there is a tendency for the sets of chromosomes to multiply until, instead of the usual three pairs there may be as many as 72, or $24x$. This occurs during metamorphosis in the cells of the pupal intestine. The chromosomes of each cell appear to pass through several successive longitudinal divisions, giving rise to numbers which are multiples of three. They are oftenest 12, 24, 48 (the 6 series), but are frequently 9, 18, 36, and even 72 (the 9 series). The latter series must arise by splitting of only one (maternal or paternal) set of 3, followed by all the chromosomes splitting simultaneously in later divisions. In some individuals only the 9 series is found. The above multiples are the only ones which occur, with the exception of one cell observed containing 42 chromosomes. Records of single tetraploid cells or groups of cells are not uncommon in the literature of animal cytology (see, for example, Hoy, 1916, and Metz, 1916). Some of the cells surrounding the ovary in insects, or cells from the fat body, are often found to be tetraploid.

A somewhat different type of increase in chromosome number has been observed by Nachtsheim (1913) in the honey
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bee. The egg and sperm are found to contain 8 chromosomes. These fall apart into 16 in the egg, so that the parthenogenetic eggs, which produce drones, contain at first 16 chromosomes, but during embryo development these increase to 32 and 64. A similar increase in number, apparently through fragmentation, takes place in the development of fertilised eggs which produce females.

Probably in a majority of cases, whether produced experimentally or naturally, increase in chromosome number is accompanied by increase in the size of the nuclei and cells. It is well known that Boveri (1905) first pointed out this relation in experiments on sea-urchin eggs. It was afterwards found, however (Gates, 1909, in *E. gigas*), that in tetraploid forms there is not merely a doubling in volume of the nuclei and cells in all the tissues. Thus in the stigma cells of *E. gigas* the volume was three times that of the corresponding cells in the diploid parent *E. Lamarckiana*, and in the anther epidermis the respective volumes averaged nearly 4 : 1, while, on the other hand, in pollen mother cells the relative sizes were 1.5 : 1. In the case of the polyploid cells of Culex, Boveri’s law breaks down entirely, as does also the Kernplasma ratio of Hertwig. The multiplication of the chromosomes does not lead here to the formation of larger cells. There appears to be an accelerated growth and division of the chromosome threads, but not of the cytoplasm, and Holt suggests that this is a phenomenon of increased metabolism of the older epithelial cells just before they break down to furnish a supply of growth material for the cells of the adult gut. Something of a similar kind is found in the tapetal cells of the anthers of flowering plants; but here the number of *nuclei* increases by mitosis, while the number of chromosomes in each nucleus usually remains diploid. The difference will be due to the absence of spindle fibres from these cells of the mosquito.

How commonly polyploidy may occur as a normal condition in somatic tissues is unknown. Tetraploid or higher polyploid nuclei have been produced in growing root tips by the use of chloral hydrate and other substances, particularly in the experiments of Némec (1910) and Sakamura (1920). Such
polyploid nuclei tend to disappear later, probably because they divide more slowly than the smaller diploid nuclei and cells. In any case they have no chance of ever affecting the lineage of cells which constitute the germ plasm.

In other cases, however, the doubling occurs directly in the line of the germ cells, and then it constitutes a germinal change. The reduction of the chromosomes from the diploid to the haploid number normally occurs in the pollen mother cells. Rare instances have been observed, however (Gates, 1915, p. 216), in which a diploid pollen grain was being formed. Similarly, giant spermatozoa are known to occur in a number of animals and in man. In some cases at least these are known to have the diploid number of chromosomes (Hartman, 1913).

Tetraploidy as a germinal change has also occurred under controlled conditions in several plants and animals. The first case discovered was that of *E*nothera gigas referred to above, which arose as a mutation in the cultures of De Vries, and was afterwards shown (see Gates, 1909) to have larger cells and nuclei containing 28 ( = 4x) chromosomes (Lutz, 1907). It is stouter in all its parts, with broader leaves, its pollen grains have four lobes instead of three, and it develops more slowly than the parent *E*. Lamarckiana. It is an organism built as it were, of larger bricks, but with alterations also in the shape of the "bricks" in some tissues.

Similar parallel tetraploid giant mutations have since been found to occur in several other species of *E*nothera (see Gates, 1921, p. 44). The gigas mutation from the wild species *E*. stenomeres was investigated by Tupper and Bartlett (1916). This will be referred to later.

In all cases of true polyploidy the increase in chromosome number is by a longitudinal fission of the chromosomes.* This is essentially an act of reproduction on the part of the chromosome, and is to be distinguished sharply from a transverse fission. This distinction is of fundamental significance in relation to the structure of the chromosome. Transverse

* Or by the fusion of nuclei with a polyploid aggregate of chromosomes. That the endosperm of Angiosperms is usually triploid arising from the union of three haploid nuclei, has of course long been known. Numerous cases of polyploidy probably arising through crossing will be discussed later.
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segmentation of chromosomes occurring in somatic cells may be looked upon as a more or less temporary fragmentation; but such segmentations may be of phyletic value if they occur in the line of the germ cells. This has apparently occurred, for example, in Yucca (Liliaceae), in which there are 5 pairs of long chromosomes and 42 to 46 short ones (Bonnet, 1911). Such Liliaceous genera as Lilium have 12 pairs of long chromosomes and no short ones. It would therefore appear that the numerous short chromosomes of Yucca may have been derived from the segmentation of 7 of the long pairs in certain other genera. Similarly in Albuca (Muller, 1912) there are 54 chromosomes, including 9 long pairs and 18 small ones. Precisely how this “phylogenetic transverse segmentation” takes place we do not know, but it implies some definite change in the organisation of the nucleus. That the converse process of end-to-end fusion of two chromosomes to form one may occur, is indicated in the genus Drosophila, where in different species \(2x = 12, 10, \text{or } 8\) (Metz, 1916). Since the usual number in other Muscidae appears to be 12 (Harvey, 1920), it seems that in such species as D. melanogaster, which has 4 pairs, the 2 long pairs have been formed by permanent end-to-end union of 4 short pairs. It is significant that these long chromosomes are broadly V-shaped and are conspicuously thin at the apex of the V, which would be the point of union. The significance of this interpretation is enhanced by the fact that in a certain strain of Drosophila (Lilian Morgan, 1922) which has arisen, the two X-chromosomes of the females have united end-to-end and behave at reduction as a single body.

That the end-to-end coalescence occurs between different chromosomes in different species is indicated by a comparison of D. Willistoni with D. melanogaster. Lancefield and Metz (1922) have studied 28 sex-linked characters in the former species, certain of which such as “yellow” and “scute,” are probably parallel to similar mutations in D. melanogaster. Now in the latter species the crossing over percentages indicate that these two factors are located near the end of the X- (rod) chromosome, while in D. Willistoni they are located near the middle of one of the long V’s which contains...
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the sex factor in this species. The indications are that the X-chromosome of *melanogaster* corresponds to one arm of the X-containing V in *Willistoni*. Hence it appears that in these two species the end-to-end fusion has been between different pairs, i.e., between two autosomes in *melanogaster* and between X and an autosome in *Willistoni*. Various other fusions of a more temporary character have been discussed elsewhere (Gates and Rees, 1921, p. 389).

Returning to the subject of the increase in chromosomes by longitudinal fission, a well-known case was studied by Guignard, Miss Sargant, Mottier, and Strasburger (1908). In the embryo sac of Lilium, in the telophase of the first (reduction) division the nucleus at the chalazal end of the sac begins to enlarge, the difference in the size of the nuclei becoming more conspicuous in the prophase of the next mitosis. The number of chromosomes in the nuclei at the antipodal end of the sac increases from 12 to 20 to 24 and even 32. This was believed to happen through a prophase split in the chromosomes, which was regarded as precocious. But it is now known that the chromosomes normally undergo their fission in the prophase of mitosis, at least in some forms. One must therefore suppose that in the Lilium sac the split is followed by the immediate separation of the halves and a subsequent second split of certain chromosomes, perhaps as late as the metaphase.

Similarly, in the embryo sac of *Tulipa Gesneriana*, Ernst (1901) found that the lower nucleus of the binucleate sac became larger, and Strasburger (1908) observed the same increase in chromosomes as occurs in Lilium. In both cases this increase in growth and multiplication of the chromosomes was interpreted as the result of greater nutrition at the antipodal end of the sac.

In *Myricaria Germanica* Frisendahl (1912) describes a different condition in the embryo sac. The four nuclei when formed are at first of equal size, and have the normal haploid number (12) of chromosomes. Then as a large central vacuole develops in the sac the two lower nuclei grow in size, and when they appear in prophase they are seen to contain a largely increased number (40 to 70) of chromatin bodies. This
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increase has not been produced by longitudinal fission; but the individual chromosomes are much shorter than normal and the increase in number seems to have occurred through fragmentation, or rather through the smaller chromatin units failing to join end-to-end to form 12 long aggregate chromosomes.

Polyploidy in the somatic tissues of plants, especially in growing root tips, has been induced by many agencies, particularly by rise of temperature, wounding, and the action of such substances as chloral hydrate and quinine sulphate. In this connection the work of Němec (1910) and Sakamura (1920) has been most extensive. Such changes of course have no chance of becoming germinal, and the tetraploid nuclei gradually disappear in later growth. Their disappearance is probably not accomplished by reduction divisions, but they appear to be gradually eliminated by their slower growth and division compared with surrounding diploid cells. That tetraploid (syndiploid) nuclei may also occur in roots under normal conditions is shown by an observation of Stomps (1910), who found in the root tip of Spinacia oleracea certain larger cells with 24 (= 4x) chromosomes. Strasburger and others have made similar observations in the roots of Pisum sativum, etc., and it is probable that occasional tetraploid cells are by no means uncommon in root tips and other somatic cells.

Of greater interest than these somatic occurrences are changes in the chromosome sets which take place in the line of the germ cells and are therefore of direct phylogenetic importance. We may mention first the experiments of the Marchals (1909, 1911). By wounding the sporophyte of various mosses they were able to obtain the development of a protonema (gametophyte) directly from the base of the sporangium and having 2x chromosomes. These gave rise to plants with sex organs in which in monoeccious mosses, fertilisation took place, thus producing a 4x sporophyte. These bore 2x spores and so a tetraploid race was established. These tetraploids were scarcely altered in the size of their vegetative organs, but their sex organs were larger and had proportionally larger cells and nuclei, the increase in volume
being near to 2 : 1. Such races were obtained in *Barbula muralis*, *Funaria hygrometrica*, *Bryum capillare* (x = 10), *B. caespiticium*, *Amblystegium serpens* (x = 12), and *Mnium hornum* (x = 6). In some mosses a 4x gametophyte was obtained by again wounding the sporogonium of the tetraploid forms, but in *Amblystegium serpens* and *Barbula muralis* only a weak non-viable protonema was obtained in this way. In all cases but one the polyploid condition was merely accompanied by a somewhat stouter size, but in *Phascum cuspidatum* the aposporously produced tetraploid form showed a profound alteration in its specific characters and was looked upon as a mutation. In the tetraploid *Amblystegium serpens* the chromosomes at the time of sporogenesis were grouped in fours, which were known as bigemini.

In a subsequent further study of *Amblystegium*, Ém. Marchal (1912) found that while in *A. serpens* and *A. irriguum* x = 12, in *A. riparium* the gametophyte number was 24. Hence this moss is already tetraploid, and it is significant that a further doubling of its chromosome number could not be obtained by wounding.

Recently a similar experimental study of the regeneration of fragments of the unripe sporogonia has been made by Schweizer (1923) in the moss *Splachnum sphericum*. This moss is strongly dioecious, but the wounded sporogonium produces a diploid protonema which is homothallic, bearing both antheridial and archegonial shoots. These 2x gametophytes (x = 8) have in general larger nuclei, cells, and organs than the normal haploid. The chloroplasts are also larger in some cases, but they show much variation. Certain monstrous diploid forms were also produced. By transferring a drop of water containing spermatozoids to the archegonia, Schweizer was able to cross-fertilise the different types. He thus obtained 3x sporophytes by crosses between an x female gametophyte and a 2x male gametophyte, or vice versa, and 4x sporophytes by crosses between 2x gametophytes. He also found that 4x sporophytes could be regenerated and form 4x gametophytes bearing normally formed antheridia. It is evident that wounding in nature is a method by which polyploidy could arise in mosses.
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A well-known case of experimental tetraploidy is found in the work of Winkler (1916) with Solanum. In his chimera experiments Winkler, using *S. lycopersicum* (tomato) and *S. nigrum* (nightshade) adopted the method of cutting off the stem of one form and cross-grafting it upon the other. After the graft had "taken" the stem was severed so as to cut across the grafted surfaces. Adventitious shoots then grew up, some of which were periclinal chimeras, in which the inner layers of tissue belonged to one parent and the outer to the other. In normal *S. lycopersicum* the chromosome number is $2x = 24$, while in *S. nigrum* $2x = 72$. Various periclinal chimeras were described under the names of *Koelreuterianum*, *Gaertnerianum*, *tubingense*, etc. In his later studies of these chimeras tetraploid forms were recognised as occurring amongst them. Thus *Koelreuterianum*, which has the epidermis of *S. nigrum* and the inner tissues of *S. lycopersicum*, appeared also in a giant form which was larger and stronger with broader leaves. The cells of the inner tissues had usually 48 chromosomes, which is the tetraploid number for the tomato. By making further cuttings from the chimera, *S. lycopersicum gigas* was obtained without an epidermal layer from *S. nigrum*. It flowered and set seed. By similar methods giant forms of *S. nigrum* were obtained. The method was also tried of grafting the tomato or nightshade upon itself to obtain tetraploid forms through nuclear fusions at the cut surfaces. The precise method of origin of the $4x$ condition in the tetraploid *Koelreuterianum* is not very clear, but it might be supposed that it arose from suspended mitoses resulting from the wounding incidental to the severing of the stem at the graft. It might also arise, as Winkler suggests, from the division of tetraploid cells already present in the stem. It is difficult to understand how tetraploidy could arise in the chimeras through fusion of nuclei along the cut surfaces of scion and stalk. Such fusions would be expected to give rise to nuclei with $24 + 72 = 96$ chromosomes if between scion and stalk. Winkler, however, strongly inclines to the view that the tetraploid condition arises through nuclear fusions in the wounded tissues, and not by a doubling of the chromosomes. In this view he is in agreement with Němec. The chief
difficulty with this view would appear to be that it necessitates the passage of nuclei through cell walls in the wounded tissues. But Winkler points out (p. 498) that the pressures incidental to inserting the graft might easily rupture the delicate walls of the cambium, and so lead to migration and fusion of nuclei. He finally, however, leaves the question open as to whether these tetraploid grafts arose from fusion of nuclei or from splitting of chromosomes.

In *S. lycopersicum gigas* the chromosome number was usually 48, but occasionally 50 to 52. In *S. nigrum gigas* the pollen mother cells had regularly 72 chromosomes, the somatic number being 144 (= 12x). A point of much interest in this work is that the chromosome number has been doubled in somatic cells, either by fusion of nuclei or splitting of chromosomes, and that the double number persists until it is halved as usual in the reduction divisions. It is hoped by self-pollination to obtain a tetraploid race from seed. Comparison of the diploid and tetraploid forms shows that the latter have larger cells throughout (as in *E. netherig gigas*), but also as in *E. gigas* the pollen grains have four instead of three germ pores, being approximately quadrangular instead of triangular in shape. Moreover, the chloroplasts and leucoplasts are larger. Evidently these differences all follow from the larger size of the nuclei. In *E. stenomeres* mutant gigas which is exactly parallel to the gigas from *Lamarchiana* in every way, Tupper and Bartlett (1916) have shown that a comparison of the wood structure of the tetraploid with the diploid form brings out some interesting differences. In the tetraploid mutant none of the tall medullary rays (up to 139 cells high) which are present in the diploid, were found. In macerated wood it was found that the vessels of the giant were 50 per cent. longer and 59 per cent. greater in diameter, thus giving relative volumes of nearly 4:1. The tracheids showed an increase of 50 per cent. in length, and the same in mean width, the relative volumes being, therefore, as 3:1. In the medullary ray cells there was an average increase of 78 per cent. in width, 35 per cent. in radial, and 55 per cent. in vertical dimensions, thus giving a change in shape of the cells similar to that found in other tissues (Gates,
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The increase in volume of the ray cells was about 274 per cent.

It has been shown by Mrs Arber (1920) and others that binucleate cells are not uncommon in many plants, particularly near the growing points and in the pith. Binucleate pollen mother cells have also been observed (Gates and Rees, 1921). If such nuclei afterwards fused a tetraploid nucleus would result, and it is probable that tetraploid somatic cells not infrequently arise in this way. Probably the binucleate condition usually arises through an inhibition of wall formation following mitosis. Winkler (1916, p. 477) describes polyploid cells in various tissues of the tomato, especially in the pith, endodermis, and collenchyma of the stem. Large cells are found in the pith with 48 to 52 chromosomes, hence tetraploid, with sometimes a few additional, owing to the split of certain chromosomes. A collenchyma cell from *S. Koelreuterianum* is figured with 102 chromosomes (= 8x + 6). Such hyper-octoploid cells arise from the fusion of tetraploid nuclei. The highest number of chromosomes found probably arose through a repetition of the same process, a collenchyma cell of the tomato having 198 chromosomes, or 16x + 6. In several other cells the number was 195. In *S. lycopersicum gigas*, where the normal somatic number of chromosomes is 48, cells not infrequently occur with 100 to 106 chromosomes, or 8x + .

It is unknown at the present time how widespread polyploidy in somatic tissues may be. Winkler (p. 490) makes the suggestion that certain tissues may regularly become polyploid (as we have seen to be the case in the wall cells of the pupal intestine of the mosquito during metamorphosis). He also suggests that since the cells of the endodermis are always conspicuously larger, with larger starch grains than the other tissues, they may be polyploid. This is a point which should be investigated.

Increase in chromosome number by fragmentation is well known in the somatic tissues of animals, but is a totally different phenomenon from polyploidy. There is the classical case of chromatin diminution and fragmentation in the somatic cells of Ascaris. Or to cite a recent case, Hance (1917) finds that in the pig the somatic chromosome number ranges from 163
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40 to 58, while the spermatogonial \((2x)\) number is 40. Hance (1918) has described a similar fragmentation in the somatic cells of \(\textit{C}\text{enothera scintillans}\), but as in our experience (Gates and Thomas, 1914) a critical examination shows that the "fragments" of a chromosome in \(\textit{C}. \textit{lata}\) always remain in alignment, and connected by very delicate threads, we are not disposed to look upon this as true fragmentation. It is rather the development of a clear area in the length of a chromosome.

Turning now to the phylogenetic aspects of polyploidy, we may first consider the numerous cases now known of wide variation in chromosome number within a genus. The numbers are fixed for each species, and they usually run in multiples of some number which is fundamental for the genus. The more striking cases have been brought together in the table on page 165. The considerable number of additional genera in which only \(2x\) and \(4x\) species are at present known, are not included here.

In examining this table a number of interesting features appear. The fundamental or haploid number of each genus is given in the first column. This basal number is 9 in six genera, 8 in three, 12 in three, 7 in two, 13 in one, and 17 in one. It will be seen that the range of chromosome number in some genera is remarkable. In \(\textit{Erigeron}\) four species are known to be diploid, two are triploid, \(\textit{E. annuus}\) having 27 chromosomes and \(\textit{E. macranthus}\), 26. The latter species has probably come from a line of descent in which the odd chromosome has been lost. One species, \(\textit{E. unalaschkensis}\), is tetraploid, and two species, \(\textit{E. linifolius}\) and \(\textit{E. bonariensis}\), are hexaploid. Thus in \(\textit{Erigeron}\) we have species with \(2x\), \(3x\), \(4x\), and \(6x\) chromosomes; in \(\textit{Rosa}\), species with \(2x\), \(3x\), \(4x\), \(5x\), \(6x\), and \(8x\); in \(\textit{Taraxacum}\), \(2x\), \(3x\), and \(5x\); in \(\textit{Hieracium}\), \(2x\), \(3x\), and \(4x\) as well as other numbers; in \(\textit{Chrisanthemum}\), \(2x\), \(4x\), \(6x\), \(8x\), and \(10x\); in \(\textit{Rumex}\), \(2x\), \(3x\), \(4x\), \(6x\), \(8x\), \(10x\); in cultivated banana varieties, \(2x\), \(3x\), \(4x\), \(6x\); in wheat and oat species, \(2x\), \(4x\), \(6x\); in \(\textit{Wikstroemia}, \textit{Solanum}\) and \(\textit{Siphylea}\), \(2x\) and \(6x\); in \(\textit{Eupatorium}\) and \(\textit{Daphne}\), \(2x\) and \(3x\); in \(\textit{Acer}\), \(2x\), \(4x\), and higher numbers approximating \(6x\) and \(8x\).
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The conditions in the maples are interesting and unexpected. The fundamental haploid number is 13. Thus in *Acer saccharum* and *A. platanoides* the somatic number is 26, but in the latter species only 11 heterotypic chromosomes were found, apparently owing to a temporary fusion of four pairs to form two. *A. pseudo-platanus*, *A. saccharinum*, and *A. carpinifolium* are tetraploid, having 52 chromosomes. In the root-tips of *A. saccharinum* cells were occasionally found having approximately twice this number. In *A. rubrum* the numbers are highest of all and do not appear to fit into the maple series. Mottier (1914) found $x = 36$ in this species, and Taylor (1920) finds the same number in certain individuals. But in other plants the somatic count is very much higher, indicating that they are tetraploid ($x = 72$) while still others may be triploid hybrids ($2x = 108$). As these numbers are very high and difficult to count it is too early to affirm with certainty that the numbers in *A. rubrum* are not higher members of the polyploid maple series. That some species of a genus depart from the regular series for the genus is shown by such cases as Eupatorium, in which in certain species $x = 10$, while other species belong to the 17 series. To discuss the origin of the numerous cases of this kind would take us too far afield. Thus in Lactuca the numbers in different species are known to be 5, 8, 9, 11-12, and 24. Again in Carex, where Heilborn (1922) has found species with $x$ numbers 9, 15, 16, 19, 26, 27, 28, 31, 32, 34, 35, 36, 38, 40, 41, and 42, no polyploid species are known. Some such cases were referred to elsewhere (Gates, 1915). We wish here to confine ourselves to the origin and significance of polyploidy.

The above table is sufficient to show that polyploidy is a widespread phenomenon in plants, and when chromosome counts are more numerous this list will no doubt be greatly extended. Useful lists of chromosome numbers already known are given by Tischler (1922) for plants, and by Harvey (1916, 1920) for animals. It appears that in animals tetraploidy, or species with $4x$ chromosomes, are by no means common, while the higher degrees of polyploidy are rare. But the conditions in animals will be discussed later. In plants, certain
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species of *Chrysanthemum* and *Rumex* have reached the 10x condition, while 8x species are also recorded in the same genera. In the family of Rosaceae, the fundamental number is 7 in Rosa, but in several other genera it is 8 or a multiple of 8. Thus in Prunus $x = 8$, in Potentilla $x = 8$ or 16, i.e., several species are tetraploid. In the known Crataegus species $x = 16$, while in Alchemilla in some species $x = 16$ and in others (mostly apogamous) $x = 32$ (see Gates, 1915, p. 197). The latter species are therefore octoploid if we consider 8 the primitive chromosome number in the family. With further knowledge there is no doubt that the chromosome numbers will furnish interesting evidence regarding the phylogeny and relationships of families, genera, and species of plants. To take one other example, from the Compositae, in the Anthemideae (several genera) the chromosome numbers are multiples of 9, while in the Heliantheae they are multiples of 8. This implies that in some way a rearrangement of the nuclear organisation from a 9 to an 8 basis, took place in the origin of these tribes, and that no equally fundamental change in the organisation of the nuclei has occurred in their subsequent evolution.

Regarding the origin of polyploid conditions, we may first consider tetraploidy. It is a fortunate circumstance that giant tetraploid mutations are known to have arisen several times in different species of *Centenothera* under controlled conditions. Triploid mutants (*semigigas*) with 21 chromosomes have also arisen from several sources. The facts concerning these forms are recorded elsewhere (Gates, 1915). Since the investigation of these cases in *Centenothera*, similar 3x and 4x mutations have been discovered in *Datura* (Blakeslee, 1920) and 3x mutations in *Drosophila* (Bridges, 1921). The precise manner of origin of the triploid and tetraploid mutations in *Centenothera* was much discussed, and cannot even yet be regarded as settled. Without discussing the subject afresh here it may be pointed out that among the various possible methods by which a plant species might double its chromosomes, two general methods have been regarded as most likely: (1) a split of the chromosomes in the fertilised egg and their subsequent failure to separate owing to a suspended mitosis; (2) the union
of two germ cells both of which have the diploid number of chromosomes. The triploid condition might arise from the union of a diploid with a haploid gamete, or from both male nuclei fusing with the egg, a condition described by Némec in Gagea lutea. Ishikawa (1918) also figures an actual case in which two male nuclei are fusing with the egg nucleus in Cbanothera. This would give rise to a triploid mutant. He also figures a case in which three male nuclei are present in the embryo sac, probably owing to the entrance of two pollen tubes. There is, then, positive evidence that triploid mutations can arise through a triple fusion of haploid gamete nuclei. Whether they also may arise from the union of a diploid male cell and a haploid egg is uncertain. Probably this form of triploidy will occur most frequently when two pollen tubes enter the same embryo sac. That diploid pollen grains occasionally occur is practically demonstrated, but it would appear that they are rarely, if ever, functional. On the other hand, there is evidence that a diploid egg cannot be fertilised. Thus in Alamosco texana (Pace, 1913), which is apogamous, the embryo sac develops without a reduction division, but the pollen develops normally and forms pollen tubes which enter the embryo sac. One of the male nuclei fuses with the two polar nuclei to form the endosperm, but the other disintegrates while the diploid egg develops without fertilisation. A male nucleus actually enters the cytoplasm of the egg and even lies alongside the egg nucleus, while the nuclear membrane of the latter breaks down and the chromosomes are formed preparatory to the first division of the egg. But no fusion occurs. Clearly the diploid egg is incapable of fertilisation. Since the haploid chromosome number is 12, the endosperm nucleus must have $5x = 60$ chromosomes.

There are therefore difficulties in supposing that tetraploidy arises through the union of two diploid germ cells. Let us examine the possibilities regarding a split in the chromosomes. It was originally suggested (Gates, 1909) that the most likely method of origin of Cbanothera gigas was through a suspended mitosis in the fertilised egg, the arrest of division taking place after the chromosomes had split. This view was supported
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by Strasburger and opposed by De Vries. The subsequent discovery of triploid mutants which may have arisen from a union between a diploid pollen grain and a haploid egg, does not settle the matter of the origin of *gigas* as was at first supposed. That a doubling of the chromosome number can arise through a split in the chromosomes has been shown by a variety of experimental results. In addition to the cases already mentioned, Loeb has found that in some at least of the artificially parthenogenetic frogs produced by prickling the haploid egg with a needle the diploid chromosome number is restored, presumably through a split in the chromosomes. There is a high mortality in the early development of such eggs, and it may be that only those in which an early doubling has occurred are able to complete their development. That a haploid organism is capable of complete development has been shown, however, in several cases. Baltzer (1922) obtained a haploid salamander (*Triton taeniatus*) by cutting into two parts with a fine hair an egg which had been entered by several sperm. The portion of the egg which contained only a sperm nucleus developed merogonically into a haploid individual with smaller nuclei. Similar haploid parthenogenetic amphibian larvae were obtained by the Hertwigs by treating the eggs with radium. In plants, Blakeslee and others (1922) have recently described a haploid mutant in *Datura stramonium* which may have resulted from the application of cold. In the pollen formation of this haploid plant the twelve chromosomes usually separate or undergo a sort of reduction, but the only functional pollen grains are those in which there has been no reduction division.

It is evident from the above results that a haploid number may be restored to the diploid through a longitudinal split in the chromosomes, but that this does not always occur. It appears equally probable that such a split in the chromosomes of the fertilised egg may on occasion produce a tetraploid form from a diploid, and that any condition which interrupted the first division of the fertilised egg would have this effect. It should be possible to test this hypothesis by subjecting plants in which tetraploid mutations occur to a sudden drop in...
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Temperature at about the time when the first division of the fertilised egg is taking place. In the higher animals, and especially mammals, where the body temperature is internally controlled, tetraploidy when it occurs must be produced by some other stimulus. But we have already seen that tetraploidy in animals appears to be relatively infrequent.

It has long been recognised that there is a relation between higher chromosome number and apogamy, but this relation is by no means an absolute one. Thus in *Erythraea gigas* there is no indication of a tendency to apogamy, and the same is true of the tetraploid form of *Primula sinensis* (Gregory, 1914). Thus a single doubling is not necessarily accompanied by apogamy, but with a second doubling apogamy probably nearly always supervenes. At least one species of *Alchemilla* with 64 chromosomes (= 8x) is said, however, to be normally fertilised. On the other hand, apogamy occurs in *Chara crinita* (2x = 24) and *Marsilia Drummondii* (2x = 32) without any increase in chromosome number compared with ordinary sexual species of these genera. Again, the triploid species in *Erigeron*, *Hieracium*, *Taraxacum*, *Eupatorium*, and *Rosa* reproduce apogamously. Were it not so they could not remain true as "species," because of the irregular redistributions of their chromosomes which always occur in the meiotic divisions of the pollen. As it is, the pollen development does not enter into their life cycle.

In the genus *Daphne*, Osawa (1913) has shown that four species are diploid and reproduce normally, while in a fifth species, *D. odora*, he states that the number of chromosomes "appears to be probably 28." In this species both the pollen and the embryo sacs degenerate, so the plant is sterile. It is probably a triploid species with 27 chromosomes, as Holmgren (1919) suggests. The latter author also suggests that *D. odora*, as well as all other triploid species, arose through crossing between a diploid and a tetraploid species. Apart from the fact that no tetraploid forms are at present known in *Daphne*, *Taraxacum*, or *Eupatorium*, the origin of triploid species can be at least equally well accounted for as mutations from the diploid forms. Such mutations are known
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and have been investigated in Conothera,* and more recently in Datura and Drosophila.

Osawa (1916) has found a somewhat similar condition in garden races of mulberry. The various races studied are supposed to have been derived from Morus bombycis, M. alba, M. indica, and M. multicaulis?. In thirty-two such races the somatic chromosome number was found to be 28, including a very large pair. In ten other (triploid) races the chromosome number was 42 (=3x), including three very large chromosomes. No tetraploid form was found. The races were all sterile, but propagated vegetatively. They would appear to have arisen as triploid mutants.

The possible relation of hybridisation to the origin of polyploid species will be discussed later. Here it may be pointed out that, so far as triploid forms are concerned, none of the triploid mutations which have occurred in cultures are known to show any tendency to apogamous reproduction, while as already pointed out, triploid species must reproduce apogamously in order to remain true to type. The triploid mulberry races, which are sterile, should afford interesting evidence on the origin of this condition. In all cases careful comparisons of the characters, as well as measurements of nuclei, cells and chromosomes, should be made, in order to throw light on this question.

We may next consider the genera in which 2x, 4x, and 6x species or varieties occur. The most interesting of these are probably wheat, oats, and bananas. Through the work especially of Sakamura (1918), Sax (1921), and Percival (1923) we now know the chromosome numbers in a large number of wheats, as follows:—

- Einkorn wheat (diploid).
  * T. monococcum, x = 7.

- Emmer wheats (tetraploid).
  * T. dicoccum, x = 14.
  * T. durum.
  * T. durum.
  * T. durum.
  * T. polonicum.

- Vulgar* wheats (hexaploid).
  * T. vulgare, x = 21.
  * T. compactum.
  * T. spelta.

* Triploid mutations are known (Gates, 1921, p. 44) from OE. Lamarckiana, OE. biennis, and OE. grandiflora. There is no suggestion of apogamy in any of them. Whether the apogamous triploid species known in other genera have originated in any other way will depend largely on the evidence derived from a comparison of their characters. So far as at present known both apogamy and interspecific sterility appear to arise only in nature.

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In addition to these numbers, which have been shown to be correct by the work of Sax, the following numbers have been determined by Percival for forms which he believes are involved in the ancestry of the hexaploid wheats:—*Triticum (Ægilops) cylindrica*, *x* = 7, *A. ovata*, *x* = 14, *A. ventricosa*, *x* = 14.

The forms within each group are fertile with each other, but crosses between groups give rise to sterile hybrids. Percival (1921) has shown that all three groups can be traced back to prehistoric times. Tetraploidy and hexaploidy are therefore very ancient conditions in wheat. It appears that the primitive Einkorn was one of the main wheats grown in Europe in Neolithic times, while Emmer wheat was prehistoric in Europe and was grown in Egypt as early as 5400 B.C. It was supplanted by Durum and Vulgare wheats during the Græco-Roman period. Varieties of the economically more valuable Vulgare wheat are known to have been prehistoric in Europe, but they only became the chief cultivated varieties in relatively recent times. One must therefore assume that the 4* and 6* conditions arose very early, perhaps in the wild condition, and that the members of each group have either differentiated since or have not had a common origin.

*Ægilops ovata* and *A. cylindrica* are said to show many of the same differences which distinguish Vulgare from Emmer wheats. Percival therefore concludes that the Vulgare group arose from an early hybrid between the Emmer group and *Ægilops*. Sax (1922) finds that the cells of the wheats increase in size along with the chromosome number. Thus the pollen grains in the 2*, 4*, and 6* forms have relative volumes of 72, 94, and 114 respectively, showing that they are truly polyploid. Sax also shows that in hybrids between diploid and tetraploid wheats there are in the first meiotic division 7 bivalent and 7 single chromosomes. Further, in crosses between 4* and 6* wheats the F₁ hybrids similarly form 14 bivalent and 7 single chromosomes. This means that, as usually happens in crosses between a diploid and a tetraploid plant species (for example the classical case of Drosera investigated by Rosenberg, and the polyploid roses recently investigated by Blackburn and Harrison (1921) and Täckholm.
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(1922), 7 of the 14 chromosomes from the tetraploid parent have mated with 7 from the diploid parent, leaving 7 without mates. Sax points out that this differential mating of chromosomes should not occur if the tetraploidy had arisen simply through a duplication of the original set of chromosomes. It is possible to assume that differentiation of the sets has occurred in the long interval since tetraploidy or even hexaploidy arose, but the various chromosome pairings in wheats and roses will probably afford valuable evidence of the origin of the forms in which they occur.

Another fact which bears on the origin of polyploidy in wheats and which can only be touched upon here, is the frequent occurrence of two or three factors for the same character. This was first investigated by Nilsson-Ehle (1909, 1911) in wheat crosses in which black or white glumes and red or white grain colour were studied. Ratios of $15:1$ and $63:1$ as well as $3:1$ were obtained, indicating the presence of two or three factors for these characters in some families. The Howards (1912) obtained similar ratios with wheat in India, with results often remarkably close to the ratios expected. This condition could be explained by assuming that the mutations for black glumes or red had occurred before the subsequent duplication of the chromosome series. It must be pointed out, however, that Oenothera rubraclaya, which at first behaved as a simple Mendelian dominant, afterwards gave in crosses $15:1$ as well as $3:1$ ratios, in plants derived from $3:1$ families, although the chromosome number remained diploid. This is probably explained by the same mutation having occurred in a second chromosome. (See Gates, 1915a.)

Sax makes the statement that in Oenothera, Primula, and Datura, where tetraploidy has occurred in cultures, the chromosomes of a tetrascopic set assort at random. This conclusion appears to be a mistaken one. For example, in Oenothera gigas a dwarf mutant has occurred which behaves as a simple Mendelian recessive. This could only happen, on present views of Mendelian behaviour, if the chromosomes of gigas only mated in pairs. In many of the Oenotheras both diploid and tetraploid, the pairing of chromosomes is so loose that it is difficult to say in how far it actually occurs. In triploid
forms of mulberry, however, which are probably mutants in origin, Osawa (1916) finds that 14 bivalent and 14 univalent chromosomes occur in the reduction division. But these conditions of chromosome pairing in various hybrids are too complicated to discuss here. There seems, however, no reason to suppose that the polyploidy in wheats has been different in its origin from that in these forms.

The conditions in oats appear to be precisely the same as in wheat, while in cultivated banana varieties, where the chromosome numbers are $2x$, $3x$, $4x$, $6x$, there is complete seed sterility so that they can only reproduce vegetatively. Hence if the polyploid bananas arose as hybrids they must have lost their sexuality since that time. In any case the seedless condition seems to follow on after apogamy.

The relations between apogamy, polyploidy, and hybridisation have been much discussed especially by Winge (1917), Ernst (1918), Holmgren (1919), Winkler (1920), and Täckholm (1922). The first two writers endeavoured to explain all cases of polyploidy as resulting from crossing, while Winkler strongly opposes this view. Winge, for instance, suggests that tetraploidy arises through the failure of the chromosomes in a hybrid between two diploid species to pair with each other, all the chromosomes dividing instead to produce mates with which they form a pair. While this is possible, there is really no evidence that it ever occurs, and it does not help matters if we make the unnecessary assumption that \textit{C}Enothera Lamarckiana is such a hybrid in which this form of doubling occasionally occurs to produce \textit{C}E. gigas. Various writers have pointed out that in \textit{Chara crinita} and \textit{Marsilia Drummondii} at least this hypothesis will not hold together, since these species are apogamous while remaining diploid. Probably the best evidence favouring Winge's view of the origin of tetraploidy is to be found in the chromosome behaviour of the hybrids between \textit{Pygæra curtula} ($x = 29$) and \textit{P. anachoreta} ($x = 30$) investigated by Federley (1913). He found that in the meiotic divisions of spermatogenesis and oögenesis the chromosomes derived from the two parents do not pair but remain single and divide, the final number in the germ cells thus being the sum of those in the two
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parents. In such back crosses as \( P. \text{anachoreta} \times \text{curtula} \) \( \times \text{anachoreta} \) homologous chromosomes pair. Thus we have in synapsis 30 bivalent \( \text{anachoreta} \) chromosomes and 29 univalent \( \text{curtula} \) chromosomes. If apogamy developed in such a hybrid, we should have the condition found in some of the roses.

On the other hand, it does appear probable that crossing of species has been involved in at least some of the higher ranges of polyploidy, as in the roses. Sax (1922) has studied the chromosome behaviour in crosses between \( 4x \) and \( 6x \) wheats. He obtains a pentaploid hybrid \( (2x = 35) \) in which homologous chromosomes pair, giving 14 bivalent and 7 univalent chromosomes as in some of the pentaploid roses. But in the latter the reproduction is apogamic, while in artificial hybrids this appears never to be the case. In the wheats it would be an attractive hypothesis to suppose that hexaploidy arose from crosses between diploid and tetraploid forms, producing a triploid form in which a split in the chromosomes gave each of the \( 3x \) chromosomes a mate. Of course it is known that hybrids between the \( 2x \) and \( 4x \) species are now sterile, but it might be supposed that such crosses continued to take place accidentally, and that finally such a doubling as we have suggested produced a hexaploid form which was fertile and could give rise to a new race. If that were really the origin of the Vulgare wheats it ought to be possible to produce the result again by cold or other stimuli applied to the fertilised egg in a cross made between a diploid and a tetraploid form.

In this connection it may be pointed out that Haberlandt (1921) has succeeded in inducing the egg in the embryo sac of \( \text{E} \text{nothera Lamarckiana} \) to undergo one division parthenogenetically by squeezing the ovary of the flower. He attributes the development to the stimulus of “wound hormones” produced by the rupture of some of the cells, and believes that with care in experimentation the haploid embryos would develop further. By sticking a fine steel or glass needle into the ovary he caused the development of adventive \( (2x) \) embryos from the nucellus. Some of these were probably capable of developing into functional seeds. This suggests that under
certain conditions a spontaneous condition of apogamy might arise. The results are in some respects comparable with the well-known cases of artificial parthenogenesis in animal eggs.

As regards their chromosome pairing, the roses fall into six groups: (1) $7_{II} + 7_{I} (= 3x)$; (2) $7_{II} + 14_{I} (= 4x)$; (3) $7_{II} + 21_{I} (= 5x)$; (4) $7_{II} + 28_{I} (= 6x)$; (5) $14_{II} + 7_{I} (= 5x)$; (6) $14_{II} + 14_{I} (= 6x)$. Hence there are two kinds of pentaploid roses, one with 7 bivalent and the other with 14 bivalent chromosomes, and the same is true of the hexaploid forms. This implies a difference in origin.

While the hybridisation hypothesis of polyploidy is a very attractive one, there are certain cases to which it cannot apply. Its applicability to cases of triploid and tetraploid species is at least doubtful, until we know more as to how the apogamous condition arises in nature. The origin of the triploid condition in Óenothera is sufficiently explained by dispermy, but these forms show no signs of apogamy as do the triploid species Eupatorium glandulosum and Erigeron annuus. On the other hand E. bonariensis, which is hexaploid, reproduces sexually, so one must suppose that the doubling of the triploid chromosome number has restored the sexuality which was lost. But (Holmgren, 1919) these two species of Erigeron have the same size of nuclei, while the chromosomes of E. bonariensis are about half as large as in E. annuus. As far as can be judged from Holmgren's figures and description, the chromosomes are of equal length in both species but of about half the width in E. bonariensis. This condition differs, therefore, from the known cases of experimental tetraploidy. This serves to emphasise the fact that each case of polyploidy needs to be investigated for itself, with reference to all the conditions of size relations of chromosomes, nuclei, and cells, as well as the external characters and manner of reproduction of the related species in the genus. Again, in comparing E. eriocephalus ($2x = 18$) with E. unalaschkensis ($2x = 36$) Holmgren (l.c., pp. 14, 32) finds that, while the nuclei of the latter are somewhat larger they are probably not twice the volume, and the species itself is by no means a giant, but is one of the smallest and most delicate of the Swedish

\* $II =$ bivalent; $I =$ univalent.

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species in the group in which it is placed. These facts serve to show the complexity of chromosome studies in their bearing on problems of systematic botany and phylogeny. But that they have an important bearing on such problems is already clear.

That a mere doubling in the number of chromosome bodies may take place in various ways, is also shown by the case of Primula Kewensis. This well-known form is a hybrid between P. verticillata and P. floribunda, both of which have $2x = 18$ chromosomes. P. Kewensis originally had the same number, but various forms with 36 chromosomes have since been obtained by making this cross. As the careful measurements of Farmer and Digby (1914) have shown, however, the increase in size of the nuclei in the 36-chromosome form is only in the ratio $5:4$, while the total volume of the chromosomes has remained the same. The authors, no doubt correctly, interpret this case as a transverse fission of the chromosomes, the resulting increased surface of the 36 bodies leading to some increase in the volume of the nucleus. Hence the change involved here is of quite a different nature from that in either Enothera gigas or Erigeron unalaschkenis. There is no clue as to why it should take place with such regularity, but one may surmise that the exigencies of a new metabolism in the hybrid may have some part in bringing it about.

Turning now to conditions in animals, it may first be pointed out that, so far as chromosome counts have been made, polyploidy appears to be much less frequent in animals than in plants. Whereas in the evolution of many genera of plants there appear to have been successive multiplications of the number of chromosomes, in animals other types of chromosome change seem to have been more frequent, and the higher degrees of polyploidy very rare. The varieties univalens and bivalens with $2x$ and $4x$ chromosomes respectively have long been known in Ascaris megalcephala, Helix pomatia, Echinus microtuberculatus, and Artemia salina. In the first three, no particular significance seems to attach to the bivalent or tetraploid condition. Examination of the chromosome lists compiled by Harvey (1916, 1920) shows a number of cases in which one species or genus is tetraploid compared with
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another, but nearly all of them require investigation from the point of view of the relative sizes of their chromosomes and nuclei. In the genus Rana the numbers $2x = 12, 16, 24,$ and $26$ have been recorded, and in the Urodela the same numbers $12, 16, 24$ are found. In a few genera, such as Cyclops, wide and irregular variation in number occurs. The basal or type $(x)$ numbers seem to agree very well with those of plants. Thus they appear to be for Crustacea 8, for Hemiptera 7, Orthoptera 12, Coleoptera 10, Diptera 6, Lepidoptera 31.

The most interesting case of tetraploidy in animals, to which we may briefly refer, is that of the phyllopod Crustacean *Artemia salina*. Artom (1921, 1922), who has published a number of papers on the subject, finds that there are two forms of this species. One, sexually reproducing and with the sexes in equal numbers, has 42 chromosomes; the other is parthenogenetic, males are absent, and there are 84 chromosomes in the nuclei. The tetraploid race has larger nuclei and is spoken of as macropyrenic, while the diploid race is micropyrenic. As the name indicates, the species lives in salt lakes, and as there is no other species of Artemia occupying this habitat with which it might cross, Artom points out that the tetraploid condition cannot be a result of hybridisation, as is so frequently assumed in plants. His hypothesis is that tetraploidy has arisen through an egg forming but not emitting its polar body, the nucleus of the latter afterwards uniting with the egg nucleus. In order to account for the doubling in this way it is necessary to assume that the first meiotic division is not a reduction division.

Artom (1921b) has examined Artemia from various parts of the world and finds micropyrenic (presumably diploid) races in Cagliari, Cadiz, Cairo, Cyprus, Damascus, Lake Utah, the island of Saint José and the Gulf of California. He finds macropyrenic races in Capodistria, Margherita di Savoia, and from localities in Sicily, Germany, Hungary, France, Algeria, and Morocco. A fact that requires explanation is the presence apparently of only the diploid or the tetraploid form in each locality.

From the facts summarised here it will be seen that the phenomena of polyploidy in plants and animals are of wide
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biological interest. They occur much more commonly in plants, and it is certain that all cases of tetraploidy do not arise in the same way. Evidence concerning the manner of origin of this condition can be obtained by comparative measurements of chromosomes, nuclei, cells, and individuals in tetraploid and related diploid species. The relation of polyploidy to apogamous reproduction is an interesting one, but at present no case is known in which either apogamy or complete inter-varietal sterility has arisen in cultivation. In such plants as the bananas and pineapples apogamy has been followed by parthenocarpy or the failure to produce seeds. Polyploidy has occurred in many of our cultivated plants, either before or since they were taken into cultivation. This includes wheat, oats, and perhaps other cereals, sugar cane, bananas, pineapples, dahlias, and other plants. It is possible in all these cases that man has been responsible for the selection of polyploid forms when they appeared (through mutation or in some cases through crossing) on account of their larger size. But it is certain that the same evolutionary tendency to polyploidy has occurred in many genera of wild plants, for example in roses, maples, docks, and chrysanthemums. They emphasise the dictum of biology that the fundamental unit of structure in organisms is the cell.

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