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Chapter 22

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CHAPTER TWENTY-TWO

Polyploidy: Range and Frequency

Historical Background

The term polyploidy refers to a special arithmetic relationship between the chromosome numbers of related organisms which possess different numbers. The polyploid organism, in the simplest case, has a chromosome number which is twice that of some related form. Or the polyploid condition is some other multiple of the haploid number in a related organism, such as $3x$ or $6x$. Or, finally, the chromosome number of the polyploid is not the average but the sum of the numbers found in two related forms with different lower numbers, as in the series $2n = 10, 12, 22$. All of these cases represent the formation of a higher chromosome number, in the polyploid organism, by the addition of extra whole chromosome sets present in one or more ancestral organisms. In short, polyploidy is the presence of three or more chromosome sets in an organism.

The phenomenon of polyploidy was discovered during the exploratory phase of plant cytogenetics and plant cytotaxonomy in the early years of this century. Winkler (1916), who introduced the term polyploidy, and Winge (1917), who offered a partial explanation, played key roles in the discovery.

Winkler (1916) was studying vegetative grafts and chimeras in *So-*

lanum. Callus tissue develops on the cut surface of the stem and can go on to regenerate a new shoot. Winkler observed that tetraploid plants of *S. nigrum* developed in this way from diploid stocks. This result must have come about through some kind of somatic doubling in the originally diploid tissue.

Winge (1917) compared related species belonging to the same genus in respect to chromosome number. He had some chromosome counts of his own in *Chenopodium* and previously published counts by Tahara (1915) in *Chrysanthemum*. Winge observed a regular arithmetic series in the chromosome numbers. Different species of *Chenopodium* have $2n = 18$ and $2n = 36$. Different species of *Chrysanthemum* have $2n = 18$, 36 , 54 , 72 , and 90 . Thus the chromosome numbers of related species are seen to be multiples of some common basic number.

In order to account for these observations, Winge (1917) proposed the fruitful hypothesis of chromosome number doubling in species hybrids. He suggested that polyploid series develop as a result of the following sequence of events. Interspecific hybridization gives rise to hybrid plants which are sterile owing to failure of chromosome pairing. Doubling of the chromosome number sometimes occurs spontaneously in the hybrid (or hybrid progeny) and converts it into a fertile type. The fertile polyploid plants may then multiply and become a new constant species. Thus two diploid species could give rise by hybridization to a new tetraploid species; hybridization between a diploid and a tetraploid could produce a hexaploid species; and other hybrid combinations could give rise to the higher polyploid types (Winge 1917).

Winge's hypothesis was soon confirmed experimentally by artificial interspecific hybridizations in *Nicotiana*, *Raphanobrassica*, and *Galeopsis* (Clausen and Goodspeed 1925; Karpechenko 1927; Müntzing 1930b, 1932). The classical cases in *Raphanobrassica* and *Galeopsis* were described in chapter 19.

It will be obvious that significant cytogenetic differences exist between the polyploid phenomena dealt with by Winkler and those dealt with by Winge and his followers. On the one hand we have intraspecific nonhybrid polyploidy and, on the other hand, we have polyploidy associated with interspecific hybridization. The first type of polyploidy involves the multiplication of one and the same chromosome set. The second type of polyploidy results from the doubling of the structurally dissimilar chromosome sets in a species hybrid. These distinctions were clarified by the

terminology—autopolyploidy and allopolyploidy—introduced by Kihara and Ono (1926). The term amphiploidy is a convenient synonym of allopolyploidy (Clausen, Keck, and Hiesey 1945).

Scope and Focus

Polyploidy research has expanded enormously since the early investigations, and has produced a voluminous literature. Polyploidy is important in relation to such diverse fields as cytogenetics, physiology, plant breeding, cytotaxonomy, and biogeography. It is obviously impossible to cover the whole subject of polyploidy in all its bearings here.

Good reviews of various aspects of polyploidy in plants are given by Müntzing (1936, 1961, ch. 26), Darlington (1937a, 1973), Clausen, Keck, and Hiesey (1945), Löve and Löve (1949, 1975), Stebbins (1950, 1971), Tischler (1953), Rieger (1963), Gottschalk (1976), and Lewis (1980).

Our central focus in this book is on the evolutionary aspects of polyploidy in higher plants. In order to carry out our objective, we find that we need some, but only some, of the evidence from each of the separate fields concerned with polyploidy. Accordingly, we present selected groups of facts from cytotaxonomy, cytogenetics, and biogeography. The facts to be presented from the various fields are selected on the basis of their relevance to the question before us.

In the immediately following sections of this chapter we will review the evidence which shows that polyploidy has indeed played a very important role in the evolution of higher plants, particularly the angiosperms and pteridophytes. The evidence supporting this conclusion is twofold. A large proportion of the species of higher plants are polyploid. And high ploidy levels are reached in various genera. The next step is to pose the obvious problem. What is the explanation of the observed facts? What are the reasons for the success of the polyploid condition in plant evolution? We will attempt to deal with this question in the following chapters.

Polyploid Series

For purposes of illustration we will list a few well-known examples of polyploidy in the angiosperms. The examples are grouped by type of polyploid series.

The simplest case is that of a genus, section, or species group containing diploids and tetraploids. Classical examples are *Dahlia*, *Gossypium*, and the *Nicotiana tabacum* group.

Several diploid species of *Dahlia* have $2n = 32$, whereas the garden dahlia (*D. variabilis*) is tetraploid with $2n = 64$ (for details and references see Darlington and Wylie 1955). In *Gossypium* the diploid condition is found in numerous wild species and in the Old World cultivated cottons, *G. arboreum* and *G. herbaceum*; while the tetraploid condition occurs in the New World cultivated cottons, chiefly *G. hirsutum* and *G. barbadense*. The chromosome numbers are $2n = 26$ and $2n = 52$, respectively, and the basic number is therefore $x = 13$ (Hutchinson and Stephens 1947). The *Nicotiana tabacum* group ($x = 12$) contains diploid species like *N. glutinosa* and others ($2n = 24$) and the common tobacco, *N. tabacum*, which is tetraploid ($2n = 48$) (Goodspeed 1954).

The next situation is a simple extension of the foregoing one. It is a polyploid series with even multiplies, thus $2x$, $4x$, $6x$, $8x$. The species of *Triticum*, with chromosome numbers of $2n = 14$, 28 , and 42 , exhibit such a series up to the hexaploid level on a basic number of $x = 7$. A longer polyploid series is found in *Chrysanthemum* ($x = 9$), as noted earlier. The $2x$, $4x$, $6x$, $8x$, and $10x$ levels are all represented in this genus along with some still higher numbers (figure 22.1). A still longer series in *Potentilla* ($x = 7$) contains every even multiple from the diploid to the $16x$ level. (See Darlington and Wylie 1955 for data and literature references.)

Polyploid series with both even and odd multiples are illustrated by *Rosa* and *Crepis*. The diploid roses have $2n = 14$. In the *Rosa canina* group there are, in addition, tetraploid, pentaploid, and hexaploid forms with $2n = 28$, 35 , and 42 chromosomes (see Darlington and Wylie 1955). The *Crepis occidentalis* group ($x = 11$) exhibits a longer series consisting of $2x$, $3x$, $4x$, $5x$, $7x$, and $8x$ forms (Babcock and Stebbins 1938). The odd polyploid species in these and other such groups necessarily reproduce by asexual or subsexual methods.

Dibasic polyploids have chromosome numbers which are the sum of two different aneuploid diploid numbers (Darlington 1956b, 1973). An example in *Brassica* consists of *B. oleracea* ($2n = 18$), *B. campestris* ($2n = 20$), and their tetraploid derivative, *B. napus* ($2n = 38$) (U 1935; Clausen, Keck, and Hiesey 1945). Another dibasic polyploid series is seen in a segment of the genus *Clarkia* containing the gametic numbers $n = 8$, 9 , 17 , and 26 . *Clarkia prostrata* ($2n = 6x = 52$) is probably derived

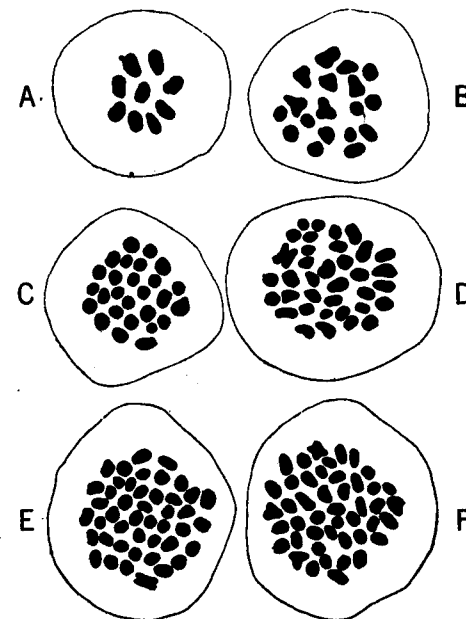


Figure 22.1. Polyploid series in *Chrysanthemum* ($x = 9$). Metaphase I in pollen mother cells. (A) *C. mankinoi* ($2x$, $n = 9$). (B) *C. indicum* ($4x$, $n = 18$). (C) *C. japonense* ($6x$, $n = 27$). (D) *C. ornatum* ($8x$, $n = 36$). (E) *C. yezoensis* ($10x$, $n = 45$). (F) *C. pacificum* ($10x$, $n = 45$). (From Shimotomai, after Müntzing 1961)

from *C. davyi* ($2n = 4x = 34$) and *C. speciosa* ($2n = 2x = 18$); and *C. davyi* ($2n = 34$) in turn is a tetraploid product of two diploid species with $2n = 16$ and $2n = 18$, respectively (Lewis and Lewis 1955).

Polyploids contain much duplication of genetic material in their nuclei and can therefore often tolerate the loss of one or more chromosome pairs. This leads to modified polyploid series ending with what Darlington has called a polyploid drop. A modified series of this type is found in *Hesperis* (Cruciferae), where different species have gametic numbers of $n = 7$, 14 , 13 , and 12 (Darlington 1956b, 1973; Darlington and Wylie 1955).

In the ferns we find polyploid series based on $x = 37$ or $x = 41$ or other high basic numbers. The *Polypodium vulgare* group ($x = 37$), for example, has diploid, tetraploid, and hexaploid forms with $2n = 74$, 148 , and 222 . Another series in *Polystichum* is based on $x = 41$. In such cases it is probable that the basic number inferred from the existing polyploid series is not a truly basic number in the phylogenetic sense. The existing diploid

members are probably old polyploids from an earlier cycle of evolution (Manton 1950).

Similar considerations apply to some relatively high basic numbers in the angiosperms. The tribe Pomoideae of the Rosaceae has a basic number of $x = 17$. The other tribes in the family have basic numbers in the normal diploid range: Rosoideae ($x = 7$), Prunoideae ($x = 8$), and Spiraeoideae ($x = 9$). Darlington therefore suggested that the tribe Pomoideae is a modified tetraploid derivative of more primitive 7-paired members of the Rosaceae (Darlington 1932:224). Stebbins later suggested, on the basis of morphological as well as cytological characteristics, that the Pomoideae ($x = 17$) could well be an allotetraploid product of the Prunoideae ($x = 8$) and the Spiraeoideae ($x = 9$) (Stebbins 1950:361).

The number $x = 13$ in *Gossypium* may be a secondary basic number. The original basic number of this genus might well have been $x = 7$. This number is found in many other genera of Malvaceae. It could have given rise to the 13-paired complements of the existing diploid species of *Gossypium* by doubling and polyploid drop (Tischler 1954).

Systematic Distribution

Polyploidy is widespread in the angiosperms. It is common in the Rosaceae, Rubiaceae, Compositae, Iridaceae, Gramineae, and many other families. It is relatively uncommon but definitely present in other families such as the Caesalpinaceae, Passifloraceae, and Polemoniaceae. In still other families, for instance the Fagaceae and Berberidaceae, the condition exists but is rare.

Stebbins (1950) has called attention to intergeneric differences in the frequency of polyploidy in several angiosperm families. Thus, in the Salicaceae, polyploidy is common in *Salix* but rare in *Populus*. In the Betulaceae, polyploidy is common in *Betula* but relatively uncommon in *Alnus*. The condition is common in *Thalictrum* but rare in *Aquilegia* (Ranunculaceae), and common in *Tulipa* but rare in *Lilium* (Liliaceae) (Stebbins 1950:301).

In the gymnosperms polyploidy is rare and sporadic (Tischler 1953; Khoshoo 1959). Polyploidy is unknown in ginkgo and cycads. Tetraploidy has been reported in *Gnetum* and *Welwitschia* but these reports

are now considered doubtful (Delevoryas 1980). Tetraploidy is common, however, in *Ephedra*.

Among conifers one of the very few authentic natural polyploids is *Sequoia sempervirens* (Taxodiaceae) ($2n = 6x = 66$). The related *Metasequoia* exhibits the diploid condition ($2n = 22$). Another case is *Fitzroya cupressoides* (Cupressaceae) with $2n = 4x = 44$ (Hair 1968). Triploid and tetraploid cultivars are known in *Juniperus* (see chapter 34).

In the pteridophytes, in contrast with the gymnosperms, polyploidy is present almost everywhere and reaches the highest levels known in the plant kingdom. The Polypodiaceae are mostly high polyploids. Polyploidy exists in the two living genera of Psilotales, namely, *Psilotum* and *Tmesipteris*. The species of *Equisetum* are homoploid at a high chromosome number level, $2n = \text{ca. } 216$, so as to indicate ancient polyploidy. In the Lycopodiales, high polyploidy occurs in *Lycopodium* and *Isoetes*, but low diploid numbers ($2n = 18$) persist in *Selaginella*. Good sources of chromosome number data for the pteridophytes are Manton (1950) and Löve et al. (1977).

In the bryophytes polyploidy is fairly common in mosses but uncommon in liverworts. And in the algae polyploidy is well known in the green algae and charophytes, but uncommon in the brown and red algae (Lewis 1980).

Polyploidy is exceedingly rare in the fungus kingdom and animal kingdom. For the fungi see Lewis (1980). The situation in animals is reviewed by Bungenberg (1957), White (1973, 1978), and Lewis (1980).

Probable cases of polyploidy in invertebrates are found in *Lumbricius* and other earthworms (Muldal 1952; Bungenberg 1957). Better known cases occur in arthropods such as *Artemia salina* (Crustacea), *Trichoniscus elizabethae* (Isopoda), *Otiorrhynchus* spp. (Curculionidae, Coleoptera), *Solenobia triquetrella* (Psychidae, Lepidoptera), and *Ochthiphila polystigma* (Chamaemyiidae, Diptera) (Bungenberg 1957; Stalker 1956; Lokki and Saura 1980).

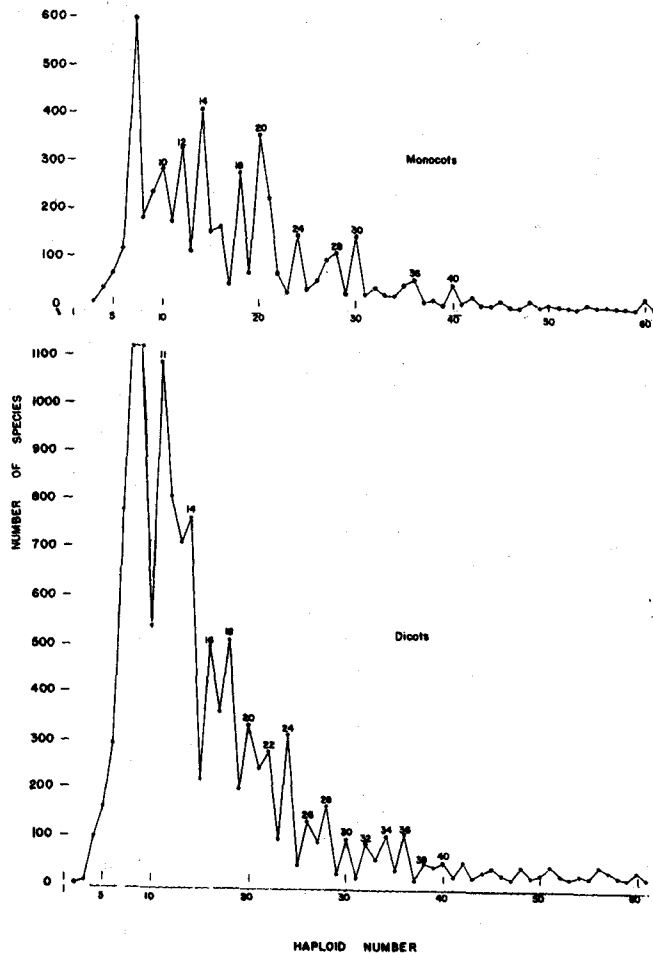
Among vertebrates polyploidy occurs in some fishes (Schultz 1969, 1980). Disagreement exists regarding the polyploid status of certain fish groups such as the Salmonidae (White 1954; Schultz 1969, 1980). A few cases of polyploidy are known in amphibians and lizards, particularly in the lizard genus *Cnemidophoras* (Bogart 1980).

Polyploidy thus occurs sporadically in the animal and fungus kingdoms, but is a characteristic feature of the plant kingdom.

Range in Chromosome Number

Chromosome numbers in the angiosperms range from $2n = 4$ to $2n = \text{ca. } 500$. Both extremes occur in the dicotyledons. The low number is found in *Haplopappus gracilis* ($2n = 4$) and the high one in a species of *Kalanchoe* ($2n = \text{ca. } 500$) (Baldwin 1938; Jackson 1957). Another high polyploid in the dicotyledons is *Buddleia colvilei* with $2n = \text{ca. } 300$ (see Darlington and Wylie 1955). Chromosome numbers in the monocotyledons range from $2n = 6$ to $2n = 226$.

The frequency distribution of angiosperm species with different ga-



metic chromosome numbers is shown in figure 22.2. The graph is based on a sample of 17,138 species listed in the *Chromosome Atlas* (Darlington and Janaki 1945; Darlington and Wylie 1955). This sample was analyzed and tabulated by Dr. Howard Latimer and myself in 1957. It would be possible today to expand the tabulation on the basis of the many new chromosome counts reported since the middle 1950s and compiled in Fedorov (1969) and Moore (1973). However, the sample incorporated in figure 22.2 is a large and representative one, and the table therefore portrays the main statistical features of chromosome numbers in the flowering plants.

The graph shows that there are thousands of angiosperm species with 14 or 15 or more pairs of chromosomes. The higher numbers range in an almost continuous aneuploid series from $n = 14$ to $n = 85$; the series extends on with many gaps to $n = 154$; and then jumps to $n = 250$. The

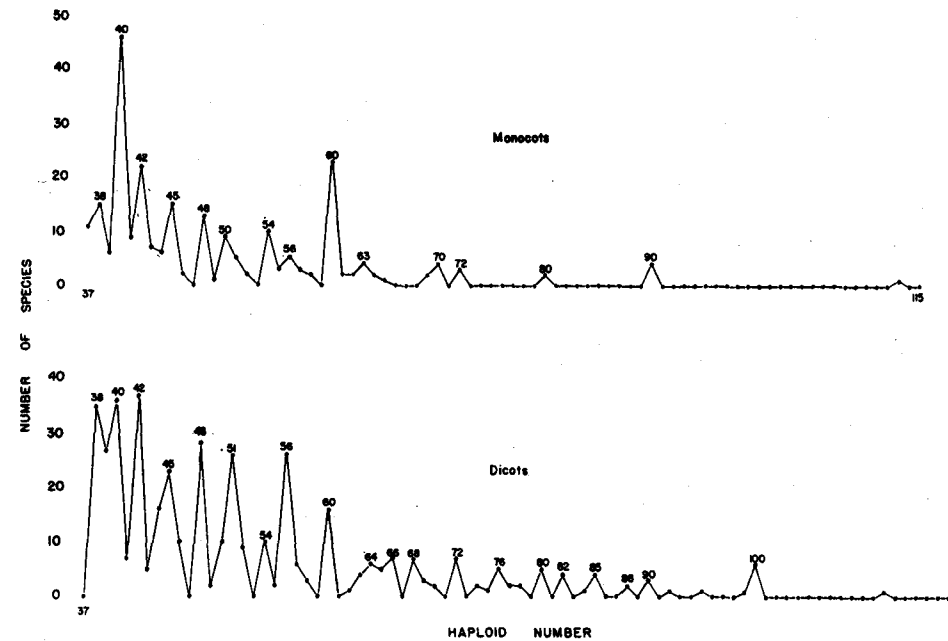


Figure 22.2. Frequency distribution of haploid chromosome numbers in 17,134 species of angiosperms. Left, distribution in range from $n = 2$ to $n = 61$. Right, distribution in range from $n = 37$ to $n = 120$. Four additional species, not shown, have numbers in the range from $n = 132$ to $n = 250$. (From *The Origin of Adaptations*, by Grant, copyright © 1963, Columbia University Press, New York, by permission)

higher polyploid numbers are, as might be expected, represented in fewer species.

The highest chromosome numbers in the plant kingdom are found in the ferns and fern allies (Manton 1950; Löve and Kapoor 1966, 1967; Löve et al. 1977). *Tmesipteris tannensis* has over 400 chromosomes in its somatic complement (Manton 1950). Still higher numbers occur in *Ophioglossum*. The series in this genus starts with $2n = 240$ in 7 species. *Ophioglossum vulgatum* and *O. thermale* have $2n = 480$; *O. azoricum* has $2n = 720$ (figure 22.3); *O. nipponicum* has $2n = 960$; and *O. reticulatum* reaches the highest known chromosome number with $2n = 1260$. (See Löve and Kapoor 1966, 1967, for several new counts and references to earlier counts in *Ophioglossum*.)

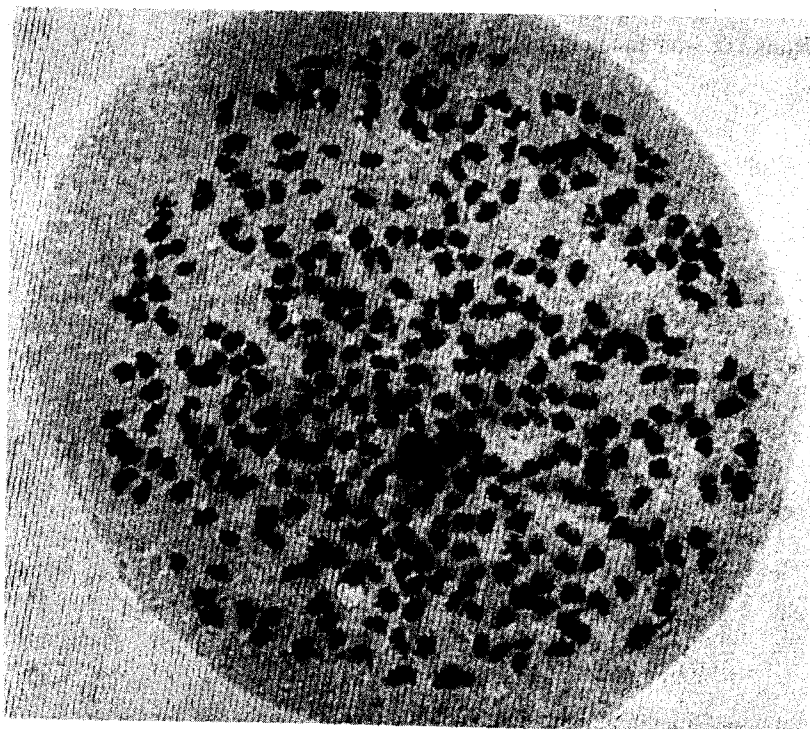


Figure 22.3. A spore mother cell of *Ophioglossum azoricum* with about 360 bivalents. (Löve and Kapoor 1967; photograph by courtesy of Dr. Áskell Löve)

Range in Ploidy Level

When we turn from range in chromosome number to range in ploidy level we frequently encounter uncertainties. Chromosome numbers can be counted. In many plant groups, ploidy levels can be determined accurately by the comparative method. In many other plant groups, however, ploidy level cannot be determined as such, but instead can only be estimated from some basic number which is hypothetical (Darlington 1937a:239; Tischler 1954).

In a genus composed of species with $2n = 14$, 28, 42, and 56 chromosomes, there is no problem in identifying the tetraploids, hexaploids, and octoploids. Uncertainties do arise in a genus containing only the numbers $2n = 28$ and $2n = 56$. The obvious decision, to call the carriers of these numbers diploids and tetraploids, respectively, may be wrong; but the more likely suggestion, that they are tetraploids and octoploids, must remain a matter of hypothesis. Yet the probably correct hypothesis is better than the probably wrong fact, in this situation, as a basis for estimating the level of ploidy or the frequency of polyploids in the plant group.

Manton (1950) found that 13 species of *Equisetum* belonging to two sections of the genus all have $2n = \text{ca. } 216$. We would be misled by the simple facts of observation here if we were to conclude that polyploidy is unknown in *Equisetum*. Actually, all of the species of *Equisetum* seem to be stationed at the same high polyploid level. We cannot hope to know what the basic number is in this isolated and homoploid genus and hence cannot estimate the level of ploidy (Manton 1950).

What levels does polyploidy reach in the angiosperms? Let us begin to deal with this question by citing some angiosperm genera containing high polyploids in which the basic number can be read directly from the cytotoxic record and the upper ploidy level can therefore be determined reliably.

The polyploid series in *Potentilla* ($x = 7$) runs from $2n = 14$ to $2n = 112$. *Potentilla haematochroa* with $2n = 112$ is 16-ploid. In *Chrysanthemum* ($x = 9$) the series contains every even multiple from $2x$ to $10x$. Then, after a break in the series, there are such high numbers as $2n = 160$ and 198. *Chrysanthemum lacustre* with $2n = 198$ would be 22-ploid. One subdivision of *Senecio* with a basic number of $x = 5$ has species at the lower and middle ploidy levels from $2x$ to $16x$. *Senecio roberti-friesii*

in this group has $2n = \text{ca. } 180$ and is thus approximately 36-ploid (Darlington and Wylie 1955, for data and references).

Hair and Beuzenberg (1961) reported a count of $2n = 263\text{--}265$ for *Poa litorosa* in New Zealand. The known primary basic number in *Poa* is $x = 7$. Consequently, *P. litorosa* is 38-ploid with a polyploid drop. This is the highest ploidy level known in the monocotyledons (Hair and Beuzenberg 1961).

Buddleia (Loganiaceae) and *Kalanchoe* (Crassulaceae) are examples of angiosperm genera containing very high chromosome numbers in which the basic number and hence the ploidy level can only be inferred. *Buddleia* includes $2x$, $4x$, and $6x$ species on the base of $x = 19$. *Buddleia colvilei* with $2n = \text{ca. } 300$ is therefore 16-ploid or nearly so. But $x = 19$ in *Buddleia* and related genera probably represents a secondary basic number of old tetraploid derivation. On this basis, *B. colvilei* is not 16-ploid but 32-ploid. In *Kalanchoe* (Crassulaceae) the predominant basic number is $x = 17$. The *Kalanchoe* species with $2n = \text{ca. } 500$ is then approximately 30-ploid with aneuploid deviations. But if, as is likely, $x = 17$ is an old tetraploid number, we would have to double this estimate of ploidy level. *Kalanchoe* apparently reaches the higher level of approximately $60x$ (Darlington and Wylie, 1955, for data and references).

In the ferns and fern allies the actual or known basic numbers are generally high, as noted earlier. Manton (1950) gives the following basic numbers for four genera of Polypodiaceae: *Asplenium* ($x = 36$), *Polypodium* ($x = 37$), *Dryopteris* ($x = 41$), *Polystichum* ($x = 41$). Each of these genera has a polyploid series on its basic number. The *Polypodium vulgare* group ($x = 37$), for example, contains diploids, tetraploids, and hexaploids. The latter have $2n = 222$ chromosomes. But the actual basic numbers almost certainly represent an ancient polyploid condition. What the original or primary basic numbers were in these fern genera is unknown. It is safe to assume, however, that the existing polyploid ferns stand at a rather high level of ploidy (Manton 1950).

Ophioglossum (Ophioglossaceae) presents a polyploid series starting at $2x = 2n = 240$ and ranging through the $4x$, $6x$, and $8x$ levels to over $10x$ in *O. reticulatum* with $2n = 1260$. It has been plausibly suggested that the original or primary basic number in *Ophioglossum* is $x = 15$. On this basis the existing "diploid" species are $16x$, and *O. reticulatum* is 84-ploid (Ninan 1958; Löve and Kapoor 1966).

Levan (1949) studied the viability of various artificially induced poly-

ploid types of *Phleum pratense* ($x = 7$). He found that the timothy plants with $11x = 77$ chromosomes were viable, whereas those with $12x = 84$ had greatly reduced viability. A threshold for viability in this case lies between 77 and 84 chromosomes. Mitosis was disturbed in the $12x$ and $13x$ plants, suggesting that mitotic conditions may be an important factor determining this threshold (Levan 1949).

Similar cytological and physiological difficulties must occur in high polyploids which arise in nature. Yet the levels of polyploidy found in nature far exceed the upper limits that can be reached in experimental cultures. No doubt the high polyploids existing in nature today are a selected sample of ancient lines which have successfully and gradually surmounted the various physiological difficulties.

In the known cases in animals, polyploidy is mostly restricted to low ploidy levels, and only rarely reaches moderately high levels. Thus the polyploids in *Cnemidophorus* and other lizards are triploids. Those in amphibians are mostly triploids and tetraploids; but hexaploidy and octoploidy exist in three known species (Bogart 1980). In weevils (Curculionidae) most of the polyploids are triploids; but there are some $4x$, $5x$, and $6x$ forms. This range of ploidy levels is characteristic of other families of insects which have polyploidy (Lokki and Saura 1980).

Frequency

Our next task is to estimate the proportion of species of higher plants which are polyploid. Accurate estimates are difficult to make for frequency of polyploidy, just as they are for grade of polyploidy, and for the same reason. If we compute the percentage figures from members of cytotaxonomically observable polyploid series, in order to keep on solid ground of factual evidence, we inevitably lose track of many ancient polyploid species, and therefore seriously underestimate the frequency of polyploidy. The only way to guard against this bias is to make certain assumptions concerning original or primary basic numbers.

Among the earlier estimates for the angiosperms are those of Müntzing, Darlington, and Stebbins. Müntzing (1936) and Darlington (1937a, ch. 6) stated in qualitative terms that about half the species of angiosperms are polyploid. Stebbins (1950:300) gave a rough estimate that between 30 and 35% of angiosperm species are polyploid.

Later I approached the problem by combining the known frequency distribution of angiosperm species with diverse chromosome numbers, as shown in figure 22.2, with the plausible and widely accepted assumption that the primary basic numbers for this group are $x = 7, 8$, and/or 9 (Grant 1963:486). The gametic number $n = 14$ then marks a convenient dividing line for statistical purposes. Species with 14 or more chromosome pairs are classified as polyploids, and those with fewer than 14 pairs as diploids.

This method is not free from errors either, owing to the complicating effects of aneuploidy. There are some tetraploid species of angiosperms with $2n = 12, 10$ or even fewer pairs, which are derived from products of aneuploid reduction series. On the other hand, some species with $2n = 14$ or more pairs are diploid products of ascending aneuploidy. We do not know how many species in our sample belong in either category. However, it will be noted that the two sources of error are compensating.

Computations made by the above method give the following conservative estimates of the percentage frequency of polyploid species in the angiosperms (Grant 1963:486):

Dicotyledons	43%
Monocotyledons	58%
Angiosperms	47%

Goldblatt (1980) has recently recalculated the frequency of polyploids in the monocots, using the larger data base in Federov (1969) and Moore (1973), and arrives at a figure of 55% (vs. 58%).

Goldblatt (1980) suggests that my dividing line between $n = 13$ and 14 was set too high, and my estimate of polyploid frequency is consequently too conservative. I had actually figured the percentages for lower cutoff levels in my earlier analysis but had not published the results. If we want to postulate that $n = 13$ or higher is polyploid, then, on the same old data base, the estimated percentage of polyploid species would be:

Dicotyledons	49%
Monocotyledons	60%
Angiosperms	52%

I would hesitate to set the cutoff point any lower than $n = 13$, however, because I suspect that ascending aneuploidy is important up to $n = 12$ and

occurs with substantial frequency at $n = 13, 14$, etc. Perhaps the true percentage frequency of polyploid species in angiosperms lies somewhere between the two sets of figures given above.

In the Coniferales, by contrast, only 1.5% of the species are polyploid, according to Khoshoo, and in the cycads there are no known polyploid species (Khoshoo 1959).

For the pteridophytes we can use Manton's list of chromosome counts as a suitable sample (Manton 1950:302-305). Taxonomic species in this list which contain two or more ploidy levels are counted as two or more species, for our present purposes, and hybrids are not counted. The sample as thus constituted contains 103 species representing all major groups of pteridophytes. Only five of these, among them three species of *Selaginella* with $2n = 18$, are primary diploids. The estimated frequency of polyploids in the pteridophytes is thus 95%.