Chapter 25

CHAPTER TWENTY-FIVE

The Polyploid Complex

The same factors which promote the formation of one new tetraploid species from its diploid ancestors often operate to promote the origin of other new tetraploids from other diploids in the same species group. These factors can then lead the tetraploids to produce hexaploids and octoploids. The result of continued polyploidization in different anastomosing lineages is a polyploid complex.

A polyploid complex in one of its simplest possible forms could have the structure shown in figure 25.1. The complex diagrammed here consists of three diploid species, their two possible allotetraploid derivatives, and one allohexaploid. Altogether there are six sibling species, isolated by chromosomal sterility barriers and perhaps by other associated breeding barriers, but sharing much genetic material in common, and therefore overlapping in their range of variation for morphological characters and ecological preferences.

Other possible versions of this simple polyploid complex might include autotetraploids as well as allotetraploids, autoallohexaploids as well as genomic allohexaploids, or allooctoploids as well as hexaploids. Given a larger array of diploid species as foundation stocks, evolution by means of polyploidy can build up a very extensive polyploid complex, containing numerous tetraploid and hexaploid species and reaching the higher ploidy levels in some derivative species.

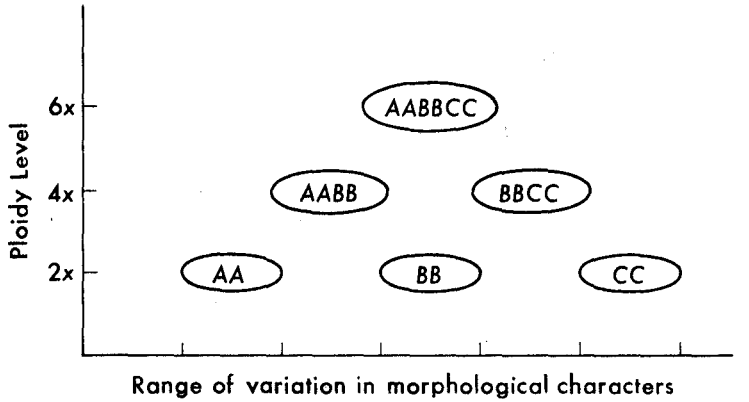

Figure 25.1. Structure of a simple polyploid complex.

Methods of Analysis

A polyploid complex can be identified as such by cytotaxonomic methods of study. The phylogenetic relationships between the constituent sibling species can be worked out by cytogenetic and taxogenetic methods. The phylogenetic analysis of the polyploid complex may be carried out to any degree of completeness. It will be useful for our present purposes to recognize four main stages of analysis.

The first stage is the identification of a polyploid complex as such. We are confronted with a large and taxonomically difficult group of plant species. The evidence of morphology and geographical distribution suggests the existence of sibling species; but their taxonomic boundaries, geographical areas, and genetic nature are unknown. Cytotaxonomic methods are called for. A preliminary series of chromosome counts may reveal a polyploid series within the plant group, giving us our first indication that the group is a polyploid complex.

Extension of the cytotaxonomic studies next enables us to fill in many details and round out the picture. This brings our understanding of the group to the second stage. In the second stage of analysis we may learn that different plants, possessing similar morphological characters and occurring together in the same locality, have different even ploidy numbers.

This information suggests close phylogenetic relationships between the sibling species standing at different ploidy levels. Or we may find a series of forms with different and nonintergrading morphological characters on the same basic ploidy level, and thus revealing the probable foundations of our polyploid complex. As chromosome counts from natural populations accumulate, we can begin to correlate a given condition of ploidy with particular morphological characters, biochemical constituents, or pollen grain or stomatal size. We can extrapolate to some extent from such correlations and predict the taxonomic and geographical boundaries of some of the sibling species. The main outlines of our polyploid complex can now be described on the basis of extensive cytotaxonomic work.

The third stage requires the introduction of experimental methods on a preliminary scale. Crosses are made between some of the sibling species, and the fertility of their hybrids is determined. This third or biosystematic stage of analysis is necessary in order to verify some of the relationships predicted previously on cytotaxonomic evidence. The biosystematic methods enable us to determine a few phylogenetic connections within the polyploid complex.

The fourth stage involves an extension of the experimental taxogenetic methods to all members of the complex. The ancestry of one tetraploid species from its diploid progenitors is worked out by the established methods of artificial hybridization, genome analysis, and resynthesis wherever possible. The same methods are employed to determine the ancestry of the other tetraploid members of the complex. They are used again for the higher polyploids. We can now trace the phylogenetic lines of descent from particular diploid species to particular polyploid species. The postulated phylogeny can be confirmed by cytogenetic analysis of artificial interspecific hybrids between the different polyploid species. The phylogenetic analysis of the polyploid complex is complete.

An analogy with chemical methods of analysis is helpful. We can identify a given unknown compound as a protein by finding that it contains certain constituent elements like nitrogen and sulfur. We can then determine its chemical formula by more refined analytical methods. Its structural formula, showing the bond connections between the elementary components, is revealed by still more detailed and laborious methods. Many kinds of proteins are known as to chemical formula but very few as to their complete structural formula.

So it is with the investigation of a polyploid complex. The identification of a plant group as a polyploid complex (stage 1) is relatively easy. A proper cytotaxonomic analysis (stage 2) is considerably more difficult and requires years of work. The biosystematic analysis (stage 3) is an even more difficult task which can scarcely be carried out by a single worker alone. Needless to say, the complete taxogenetic analysis of a polyploid complex (stage 4) is an enormously laborious and time-consuming project.

Certain common errors of methodology are worth noting. Cytotaxonomists sometimes overestimate the reliability of descriptive cytotaxonomic methods as applied to a polyploid complex and, by the same token, underestimate the importance of the taxogenetic approach. The difference between cytotaxonomic and taxogenetic methods, as regards the amount of time and labor involved, is very great; but the additional effort of the experimental taxogenetic approach is absolutely necessary if the polyploid complex is to be analyzed phylogenetically with any degree of reliability.

Many cytotaxonomists misinterpret their findings by relating them to a taxonomic species concept instead of to a biological or evolutionary species concept. The cytotaxonomist discovers one set of diploids and tetraploids with similar morphologies; he treats them as different "chromosome races" of the same species. A second set of diploids and tetraploids, which are similar inter se but morphologically different from the first set, is treated as another species composed of two "chromosome races." The result is a taxonomic system which often confuses the natural relationships and the fertility relationships. The morphologically different tetraploid types may well be opposite segregates of the same segmental allotetraploid ($A_sA_sA_tA_t$) and, as such, should be recognized as conspecific. The interspecific boundary lines in such cases should be drawn, not through the middle of $A_sA_sA_tA_t$, but between it, taken as a whole, and the diploid species A_sA_s and A_tA_t.

Many plant groups have been identified as polyploid complexes. Quite a few polyploid complexes have reached the stage of thorough cytotaxonomic analysis, and some the stage of preliminary biosystematic analysis. An extensive but incomplete taxogenetic analysis has been carried out in only a small number of polyploid complexes.

In the next two sections we review the main features of some polyploid

complexes which are known cytotaxonomically and biosystematically. Later we consider polyploid complexes in *Triticum-Aegilops*, *Bromus*, and *Gilia* which have had extensive taxogenetic analysis.

Cytotaxonomic Examples

Polyploid complexes in several branches of the genus *Galium* (Rubiaceae) have been analyzed cytotaxonomically by Ehrendorfer and his coworkers. Such polyploid complexes have been described in the *Galium pumilum* group in Europe (Ehrendorfer 1949), the *G. anisophyllum* group in Europe (Ehrendorfer 1964), the *G. incanum* group in Turkey and neighboring areas (Ehrendorfer 1951), and the *G. multiflorum* group in western North America (Ehrendorfer 1961; Dempster and Ehrendorfer 1965).

The *Galium pumilum* group ($x = 11$) in Europe comprises a polyploid series ranging from diploid to octoploid. The diploid member of the complex, *G. austriacum*, occurs as a glacial relict in disjunct areas in the Alps, whereas the polyploids have widespread and continuous distributions (Ehrendorfer 1949).

The polyploid complex in the *G. anisophyllum* group in Europe contains every even ploidy level from $2x$ to $10x$. Here again the diploids occur in a series of scattered glacial refuges in the European mountains. The tetraploids are widespread. And the higher polyploids are scattered, as shown in figure 25.2 (Enrendorfer 1964).

Sanicula crassicaulis and its relatives (Umbelliferae) comprise another polyploid complex on the basic number of $x = 8$ (Bell 1954). The taxonomic species *S. crassicaulis* includes tetraploids, hexaploids, and octoploids, which range widely on the Pacific slope of North America and Chile. The diploid species, *S. laciniata* and *S. hoffmannii* in coastal California, are the probable ancestors of tetraploid *S. crassicaulis*. Another diploid species, *S. bipinnatifida*, is believed on morphological evidence to enter into the ancestry of certain octoploid members of the complex (Bell 1954).

A group of *Asplenium* ferns (Polypodiaceae) in eastern North America form still another polyploid complex on the base of $x = 36$ (Wagner 1954). The diploid species, which possess the extreme morphological characters in this complex, are *A. montanum*, *platyneuron*, and *rhizo-*

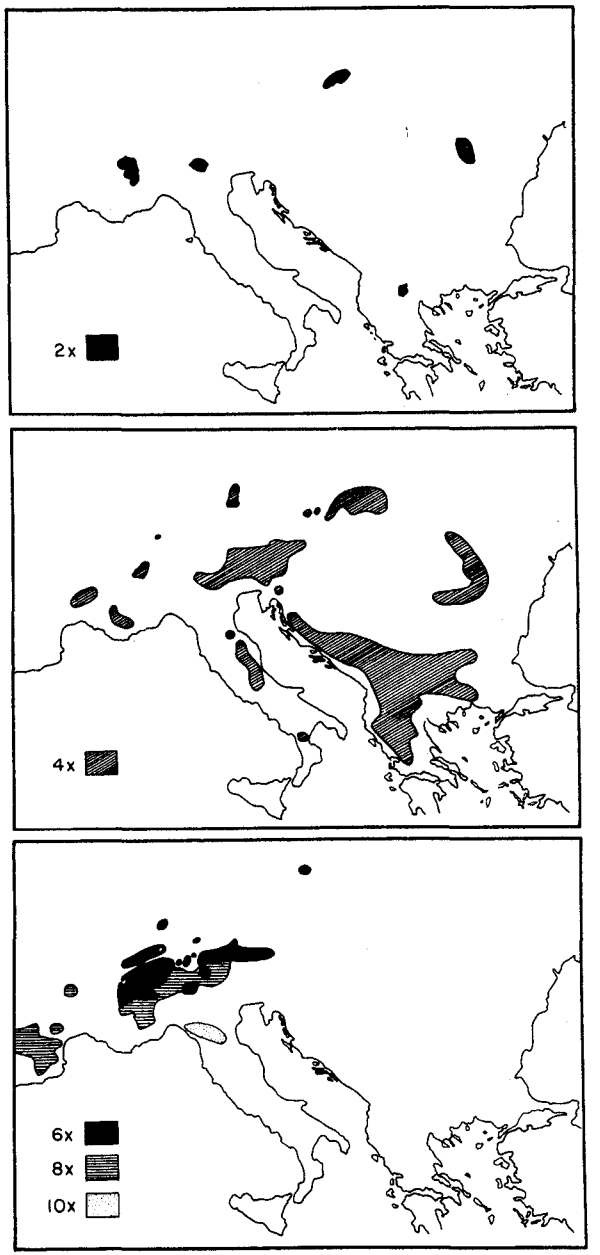

Figure 25.2. Geographical distribution of diploids and polyploids belonging t the *Galium anisophyllum* group. (Redrawn from Ehrendorfer 1964)

phyllum ($2n = 72$). The morphological intermediates are sterile diploid or triploid hybrids in some cases. Other fertile intermediate forms are tetraploids ($2n = 144$). Thus the tetraploid *A. pinnatifidum* is morphologically intermediate between *A. montanum* and *A. rhizophyllum* and is probably an amphiploid derivative of these two diploid species (Wagner 1954).

The relationships in this group of *Asplenium,* as worked out by Wagner (1954) by cytotaxonomic methods, were later checked by chemotaxonomic methods (Smith and Levin 1963). Certain biochemical substances in the various species were assayed by paper chromatography. The natural hybrids and allotetraploids were found to have combinations of the substances present in their putative parental diploids (Smith and Levin 1963). The chemotaxonomic evidence confirmed the phylogeny based on cytotaxonomic evidence.

Other cytotaxonomically studied polyploid complexes are the *Polypodium vulgare* group (Polypodiaceae) in Europe and North America and the *Trillium kamtschaticum* group (Liliaceae) in Japan (Manton 1950, 1951, 1958; Kurabayashi 1958). Among the numerous cytotaxonomically analyzed polyploid complexes in the Gramineae we may mention *Oryzopsis-Stipa* in the northern hemisphere, the circumpolar *Poa alpina* group, and the *Bouteloua curtipendula* group of the North American plains (Johnson 1945; Nygren 1962b; Gould and Kapadia 1964).

Biosystematic Examples

The *Phacelia heterophylla* group consists of outcrossing perennial and biennial herbs which range widely throughout western North America and southern South America. The group is taxonomically difficult because of the existence of many different but intergrading morphological forms. Heckard (1960) has shown that it is a polyploid complex ($x = 11$) consisting of six known diploid species, numerous tetraploids, and some hexaploids.

Artificial hybridizations indicate that crossability and sterility barriers are well-developed between the diploid species. By contrast, the different tetraploid forms mostly cross fairly easily with one another to produce semifertile or fertile hybrids. These differences in degree of internal isolation are correlated with differences in the variation pattern. On the diploid level the taxa are generally separated by morphological discontinuities, whereas those on the tetraploid level are often connected by morphological intergradation (Heckard 1960).

The polyploid members of the *Phacelia heterophylla* group are probably amphiploids derived from different hybrid combinations of the diploid species; this would further explain their morphological intergradation. There is no evidence as yet regarding the ancestry of the various tetraploid and hexaploid forms.

Heckard (1960) has grouped morphologically similar diploid and tetraploid forms together in the same species. The named entities are therefore taxonomic species but not biological or evolutionary species in many cases. The genetic evidence obtained by Heckard is sometimes in disagreement with the morphological evidence, as might be expected. Thus diploid *nemoralis* failed to cross artificially with tetraploid *nemoralis;* but tetraploid *nemoralis* crossed with tetraploid *californica* to produce highly fertile hybrids. The next steps in the analysis of this interesting polyploid complex will be to block out the biological species at the tetraploid and hexaploid levels and to determine their ancestry.

The genus *Clarkia* (Onagraceae) in western North America and temperate South America contains a more extensive polyploid complex (Lewis and Lewis 1955). The diploid species have $2n = 10$, 14, 16, and 18 chromosomes, the ancestral basic number being $x = 7$. These diploid species fall into several distinct species groups which could be and have been recognized as separate genera, such as *Godetia, Eucharidium,* and *Clarkia* sensu stricto. However, the phylogenetic lines, which diverge as branches on the diploid level, fuse in various combinations on the tetraploid and hexaploid levels. These anastomoses provide the rationale for treating the whole assemblage of species as a single genus, *Clarkia* sensu lato (Lewis and Lewis 1955).

The postulated reticulate phylogeny of *Clarkia,* as understood in 1955, is shown diagrammatically in figure 25.3. Much additional evidence has been obtained since 1955 by Lewis and his co-workers. Figure 25.3 shows the probable ancestry of the various polyploid species of *Clarkia* as inferred from the morphological and cytological evidence (Lewis and Lewis 1955).

The *Achillea millefolium* group (Compositae) is a polyploid complex ($x = 9$) which is widespread in the northern hemisphere (Clausen, Keck, and Hiesey 1948; Ehrendorfer 1959). *Achillea millefolium* proper in the Old World and *A. borealis* in the New World are both hexaploid. The

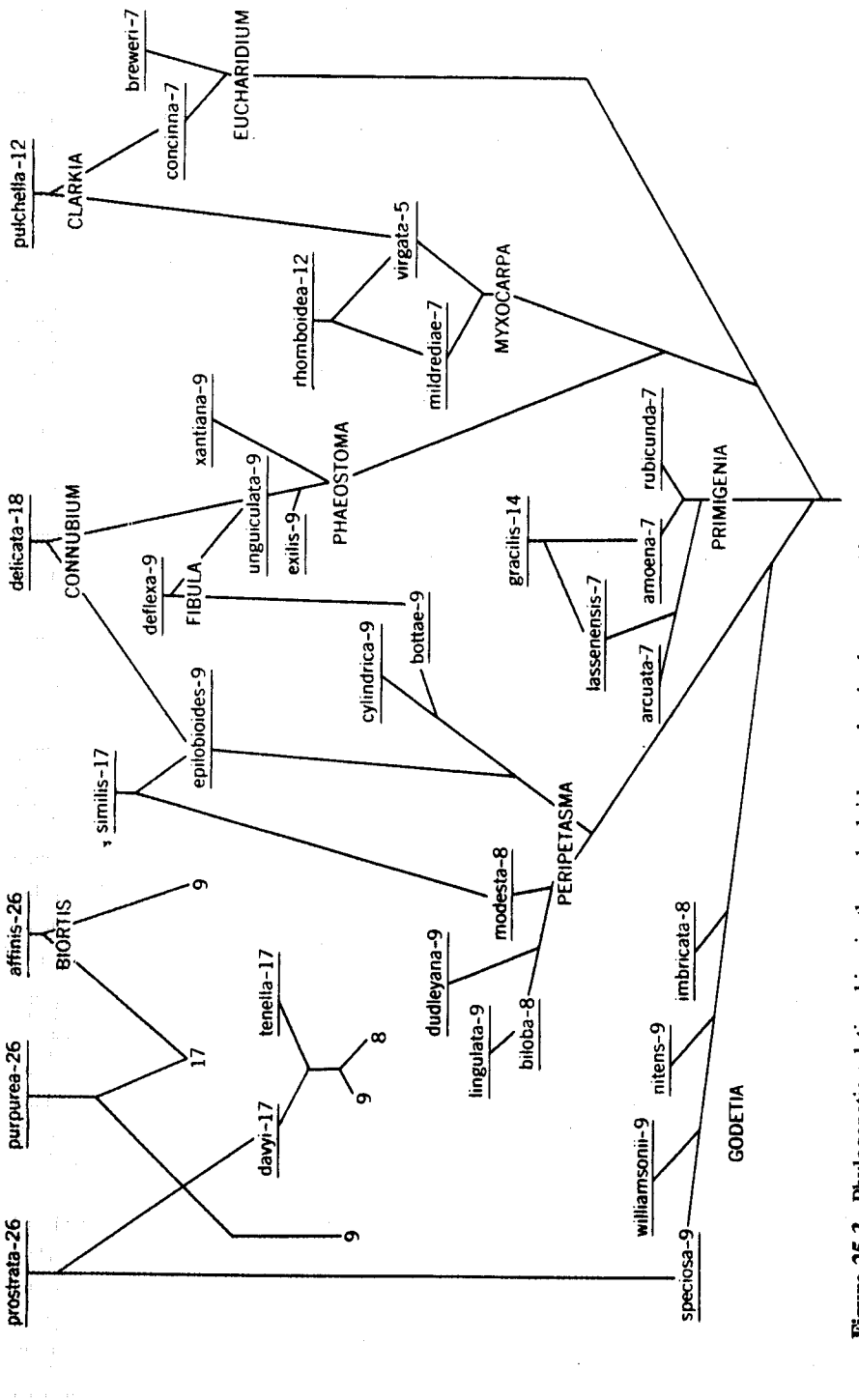

Figure 25.3. Phylogenetic relationships in the polyploid complex in the genus *Clarkia*. The sections of the genus are indicated by capital letters; the species are listed with their normal gametic chromosome numbers. (Lewis and Lewis 1955)

Old World *A. collina* and *A. virescens* and the North American *A. lanulosa* are tetraploid. Two European diploid species are *A. asplenifolia* of moist meadows and *A. setacea* of dry steppes (Clausen, Keck, and Hiesey 1948; Ehrendorfer 1959).

The diploid species *Achillea asplenifolia* and *A. setacea* overlap geographically and, despite strong internal isolating barriers, have undergone natural hybridization to a limited extent. Introgression has taken place on the diploid level from *A. setacea* into *A. asplenifolia* in the Alps. And the tetraploid *A. collina* is an amphiploid derivative of these two diploids. *Achillea collina* then hybridizes with other tetraploid species such as *A. virescens*. Natural hybridization also occurs between the tetraploid and hexaploid species in certain combinations—*A. collina* (4x) × *A. millefolium* (6x) and *A. lanulosa* (4x) × *A. borealis* (6x)—to yield aneuploid progeny which further complicate the variation pattern of the group (Ehrendorfer 1959).

Zohary and Feldman (1962) find a similar situation in the polyploid complex involving *Triticum* and *Aegilops* (Gramineae). Here too, as in *Achillea*, different allotetraploid species with different genomic constitutions hybridize naturally, thus adding to the complexity of an already complex variation pattern in the group (Zohary and Feldman 1962).

The Gilia Inconspicua Complex

The *Gilia inconspicua* group ($x = 9$) is the segment of *Gilia* section *Arachnion* which consists of autogamous annuals. This group is widespread in western North America and recurs in southern South America. There are 23 known species of the complex in North America and 2 known species in South America; and there are good reasons for believing that additional unknown species exist in each area. Of the 23 North American species, 13 are diploid ($2n = 18$) and 10 are tetraploid ($2n = 36$). The tetraploids are amphiploids, and their ancestry has been worked out in most cases.

In chapter 11 we introduced the *Gilia inconspicua* group as an example of a pattern of species relationships which is common in autogamous annual plants. One part of this group containing *G. transmontana* and its relatives was discussed and illustrated also in chapter 4 from the stand-

point of sibling species. Here we consider the group once again as a polyploid complex which has been extensively but incompletely analyzed taxogenetically.

The diploid species fall into five genome groups. Related species belonging to the same genome group usually carry differentiated subgenomes (Grant and Grant 1960).

F_1 hybrids between the tetraploid species have been analyzed cytogenetically in 17 hybrid combinations. Most of these hybrids display a medium degree of chromosome pairing at meiosis. Thus *Gilia malior* × *transmontana* has an average of 9 bivalents, and a range of 7 to 15 II, where 18 II would represent complete pairing. The degree of chromosome pairing in this and similar hybrids suggests that the two tetraploid species involved share one basic genome in common and differ in their other genome (Grant 1964c).

For some pairs of tetraploid species this suggestion has been confirmed and the common diploid genome has been identified by producing the appropriate triploid hybrids and finding the expected *Drosera* type of chromosome pairing. We would expect >9 II + <18 I in triploid hybrids derived from crosses between tetraploid and diploid species belonging to an ancestor-descendant lineage.

Just this type of pairing was in fact observed in triploid hybrids of *Gilia sinuata* (4x) × *G. latiflora* (2x) and *G. modocensis* (4x) × *G. latiflora* (2x) (Grant, 1964c). Therefore the *latiflora* or *T* genome is present in both *G. sinuata* and *G. modocensis*. On morphological and ecological evidence it can be concluded that *G. latiflora* itself, and not some other member of the *T* genome group, was a diploid parent of both *G. sinuata* and *G. modocensis*. These two tetraploid species differ genomically and morphologically as regards their other diploid parent.

Day (1965) made a detailed taxogenetic study of two tetraploid species and their putative diploid parents in the *Gilia transmontana* subgroup. The morphological, ecological, cytological, and cytogenetic evidence pointed to a reticulate derivation of the two tetraploids, *G. transmontana* and *G. malior*, from three diploid species, as shown in figure 25.4. Day then confirmed this phylogeny by artificially resynthesizing *G. transmontana* and *G. malior* from their diploid parents and showing that each artificial amphiploid is interfertile with the corresponding natural tetraploid species (Day 1965).

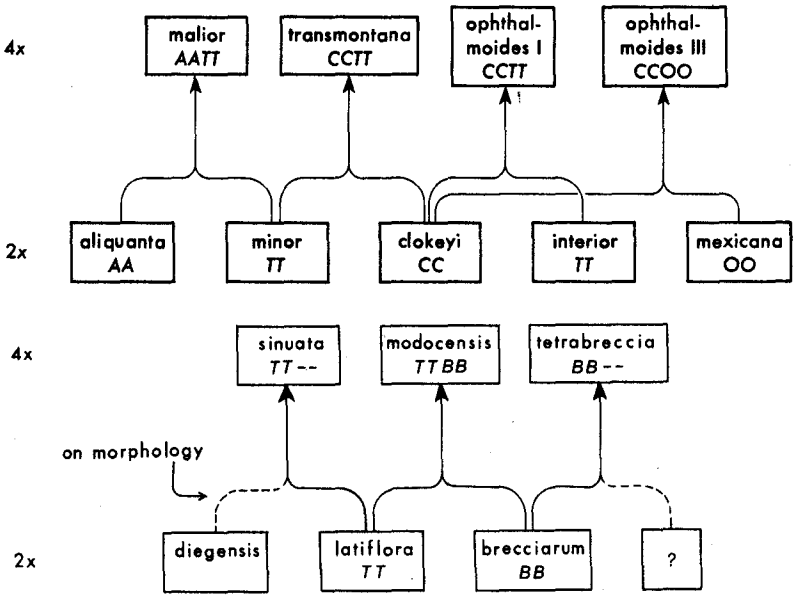

Figure 25.4. Phylogeny of two segments of the polyploid complex in the *Gilia inconspicua* group. (Drawn from data of Grant and Grant 1960; Grant 1964a; Day 1965)

Similar evidence was obtained for the ancestry of the tetraploid species known as *Gilia ophthalmoides* III. This species was believed to be derived from *G. clokeyi* (2x) × *G. mexicana* (2x). Spontaneous tetraploid progeny obtained from this diploid interspecific hybrid turned out to be good *G. ophthalmoides* III, thus confirming the phylogenetic hypothesis (Grant and Grant 1960, and unpublished). Additional evidence points to a partly common, partly different ancestry of a related tetraploid species, *G. ophthalmoides* I.

The reticulate pattern of relationships can be extended to include *G. sinuata, G. modocensis,* and other tetraploid species. The reticulate phylogeny of two segments of this polyploid complex is shown in figure 25.4.

Triticum and Aegilops

The well known polyploid series in wheat is part of a larger polyploid complex involving *Aegilops*. *Triticum* and *Aegilops* are interconnected at the polyploid level. The distinctions between the old generic units, wheat and goatgrass, based on spike and spikelet characters, thus break down. Apparently *Triticum* and *Aegilops* comprise a single genus, and the trend in wheat genetics is to transfer species from *Aegilops* to *Triticum*. The task of taxonomic and nomenclatural reorganization is still unfinished, however, and we have two overlapping sets of genus-species names at the present stage.

Triticum-Aegilops is a group of annual grasses belonging to the subtribe Triticinae of the tribe Hordeae. The basic chromosome number is $x = 7$ in *Triticum-Aegilops* as in the tribe as a whole.

Within *Triticum* in the old narrow sense the taxonomic trend in recent years has been to reduce many of the formerly recognized species to subspecies or cultivars, thus simplifying the taxonomy of the wheats. An outline of the classification of the wheats, based on Feldman (1976), is given in table 25.1.

Table 25.1. Classification and genome constitution of wheats (*Triticum*). (Based on Feldman 1976; distribution notes from Harlan and Zohary 1966, and Zohary et al. 1969)

1. T. monococcum. Einkorn. 2*x*. *AA*.
   - (a) Wild race: T. m. boeoticum.
     Western Asia from Turkey to Iran, and southern Balkans.
   - (b) Cultivated race: T. m. monococcum.
2. T. turgidum. Emmer and durum. 4*x*. *AABB*.
   - (a) Wild race: T. t. dicoccoides.
     Western Asia from Turkey and Israel to Iran.
   - (b) Cultivated race with hulled grains: T. t. dicoccum.
   - (c) Cultivated races with free-threshing grains: T. t. durum, turgidum, polonicum, carthlicum.
3. T. timopheevii. 4*x*. *AAGG*.
   - (a) Wild race: T. t. araraticum.
     Southern Soviet Union in Georgia and Armenia.
   - (b) Cultivated race: T. t. timopheevii.
4. T. aestivum (= T. vulgare). Bread wheat. 6*x*. *AABBDD*.
   - (a) Cultivated races with hulled grains: T. ae. spelta, macha, vavilovii.
   - (b) Cultivated races with free-threshing grains: T. ae. aestivum, compactum, sphaerococcum.

Genome analysis of wheats has been carried out by Kihara (1924, 1954), Sears (1948, 1959), and many others. The *A* genome in polyploid wheat is derived from the diploid species *T. monococcum*. The source of the *B* genome in tetraploid *T. turgidum* is not known; we will return to this question in a moment. The *D* genome in hexaploid *T. aestivum* comes from the diploid species *Aegilops squarrosa* (= *T. tauschii*) which has a wide range in western and south-central Asia.

The *B* genome occurs in both *T. turgidum* and *T. aestivum*. A diploid species with the constitution *BB* has been looked for but never found. At one time *Aegilops speltoides* (= *Triticum speltoides*) was thought to be the carrier of the *B* genome, but cytogenetic and electrophoretic evidence is against this hypothesis, which is no longer accepted in its original form. The genome constitution currently assigned to *Ae. speltoides* is *SS*. As regards the missing *BB* diploid, one possibility is that it is now extinct. Another possibility is that there never was a *BB* diploid. The *B* genome in *T. turgidum* may have diverged from some other related genome, perhaps *S*, within tetraploid *T. turgidum* (Feldman 1976).

The phylogeny of the polyploid series leading to bread wheat can be summarized as follows. (1) Hybridization and amphiploidy between wild einkorn (*AA*) and an unidentified diploid carrying *B* or a precursor of *B* to yield wild emmer (*AABB*). (2) Changes brought about by selection under domestication from wild emmer to cultivated emmer with hulled grains and then to cultivated durum wheat with free-threshing grains. (3) Hybridization and amphiploidy between cultivated emmer and *Aegilops squarrosa* (*DD*) to produce bread wheat (*AABBDD*). (4) Selective changes in cultivation from hulled bread wheat to free-threshing bread wheat.

These events took place in western and southwestern Asia. This area is an important center of early agriculture as is well known. Carbonized grains of *T. monococcum*, *T. turgidum*, and *T. aestivum* are found in various archeological sites in this area. The ages of the oldest known grains of the three species are about 9000 B.P. (Feldman 1976).

Wild emmer occurs today in western Asia from Israel and Lebanon to the Tigris river and Caspian sea (Harlan and Zohary 1966). Durum wheats have mostly been grown in the Mediterranean region with its relatively mild climate (Zohary et al. 1969). *Aegilops squarrosa* ranges from the Caspian region into the central Asian steppes as far east as Tashkent and Alma Ata (Zohary et al. 1969). It evidently includes a

variety of ecotypes, including those adapted to highly continental climates. The ecological adaptations of *Ae. squarrosa* represented that species' most important contribution to bread wheat. The *D* genome in hexaploid bread wheat accounts for its wide ecological amplitude and its ability to be grown in cold dry steppe climates (Zohary et al. 1969; Harlan, personal communication).

It is interesting to note that this process is continued in the artificially synthesized allooctoploid, *Triticale*, an amphiploid derivative of *T. aestivum* (6*x*) × *Secale cereale* (2*x*), which can be grown in northern latitudes and montane altitudes.

Triticum timopheevii has the genomic constitution *AAGG* (table 25.1) and thus represents another tetraploid product of *T. monococcum*. The other diploid parent could be *Ae. speltoides* (*SS*) or some related species such as *Ae bicornis* (S^bS^b). The *S* genome is close to the *G* genome. It is assumed on this phylogenetic hypothesis that the *S* genome changed to *G* within tetraploid *T. timopheevii* (Feldman 1976).

The larger number of species in the old genus *Aegilops* includes diploids, tetraploids, and hexaploids. Five genomes and a larger number of subgenomes are recognized in *Aegilops*. At the diploid level the five genome groups mostly coincide with taxonomic sections of the genus. The main genomes, subgenomes, and their diploid carriers are listed in table 25.2. Some subgenomes (M^{cr}, D^2, S^v, etc.) are known only in polyploids; these are not listed in table 25.2.

The genomic constitution of the polyploid species of *Aegilops* is given in table 25.3. The crisscross phylogenetic derivation of the polyploid species can be visualized by reference to this table. Thus two diploid species

Table 25.2. Genomes and their diploid carriers in *Aegilops*. (Kihara 1954; Zohary and Feldman 1962)

Genome group	Subgenome	Diploid species
Mt		Ae. mutica
S	S^b	Ae. bicornis
	S^1	Ae. sharonensis, longissima
	S	Ae. speltoides, ligustica
D		Ae. squarrosa
C	*C*	Ae. caudata
	C^u	Ae. umbellata
M	*M*	Ae. comosa
	M^u	Ae. uniaristata

Table 25.3. Genome constitution of polyploid species of *Aegilops*. (Zohary and Feldman 1962)

Polyploid species	Genome constitution
Ae. crassa (4*x*)	$DDM^{cr}M^{cr}$
Ae. crassa (6*x*)	$DDD^2D^2M^{cr}M^{cr}$
Ae. juvenalis	$DDC^uC^uM^jM^j$
Ae. ventricosa	DDM^vM^v
Ae. cylindrica	*DDCC*
Ae. variabilis and Ae. kotschyi	$C^uC^uS^vS^v$
Ae. triuncialis	C^uC^uCC
Ae. columnaris	$C^uC^uM^eM^e$
Ae. biuncialis	$C^uC^uM^bM^b$
Ae. triaristata (4*x*)	$C^uC^uM^tM^t$
Ae. triaristata (6*x*)	$C^uC^uM^tM^tM^{t2}M^{t2}$
Ae. ovata	$C^uC^uM^oM^o$

carrying the *DD* and *MM* genomes have produced tetraploids with the constitution *DDMM* One of these diploids (*DD*) and another (*CC*) have then produced another tetraploid *DDCC*, and so on. The different tetraploid species often have one common and one different diploid ancestor. The process of recombination of genomes is continued at the hexaploid level.

The reticulate pattern of relationships in *Triticum-Aegilops* is presented here in terms of the addition of different genomes by amphiploidy. This is not the whole story, however. There is evidence, both direct and indirect, for natural hybridization and introgression between some of the species involved. This hybridization has altered the morphological characters and probably also the genomes of these species (Zohary and Feldman 1962; Pazy and Zohary 1965; Zohary et al. 1969; Feldman 1976).

Old Polyploid Complexes

In the course of time the diploid species of a polyploid complex may die out. Or the lower polyploids may become extinct too, leaving the higher polyploids behind as the only living representatives of the complex.

The Bromus carinatus group (Gramineae) illustrates a polyploid com-

plex which has reached an advanced stage of development. This group reaches high ploidy levels, *B. arizonicus* being 12*x*, but has suffered much extinction at the diploid and tetraploid levels. The ancestry of the 12*x* and 8*x* species has been worked out by Stebbins and collaborators (Stebbins and Tobgy 1944; Stebbins, Tobgy, and Harlan 1944; Stebbins 1947b, 1956).

The *Bromus carinatus* complex belongs to the section *Ceratochloa* of the genus but contains genomes from two related sections, *Bromopsis* and *Neobromus*. The plants are perennial grasses, often bunch grasses, of North and South America. The basic number is $x = 7$.

There are no known diploid or tetraploid species in *Bromus* section *Ceratochloa*. *Bromus catharticus* and its relatives in South America are allohexaploids carrying genomes derived from diploid species which are now extinct (figure 25.5).

Bromus carinatus and *B. marginatus* in North America are alloоctoploids. Three of their four genomes are homologous with those in the South American hexaploids. The fourth *L* genome is believed on cytological and morphological evidence to be derived from some North American diploid species of the section *Bromopsis* (figure 25.5). The amphiploid origin of the octoploids probably took place in western North America in the late Tertiary, perhaps the Pliocene. It is necessary to suppose that some hexaploid species homologous with the present-day South American hexaploids occurred in North America in former times (Stebbins and Tobgy 1944; Stebbins 1947b).

Bromus arizonicus is an amphiploid at the 12*x* level. It, too, is homologous with the South American hexaploids in three of its six genomes (figure 25.5). The other three genomes in *B. arizonicus* are probably derived from an allohexaploid in the related section *Neobromus* (figure 25.5) (Stebbins, Tobgy, and Harlan 1944).

The 12-ploid species, *Bromus arizonicus*, is a common and aggressive weed throughout much of its range in Arizona and California. Its diploid and tetraploid ancestors are extinct. Its hexaploid ancestor in the section *Ceratochloa* became extinct in North America, perhaps during adverse climatic changes in Pliocene-Pliestocene time, and survives today under more moderate climatic conditions in South America. Yet the 12-ploid derivative of these extinct diploids and lower polyploids is a successful and aggressive species today, showing how continued amphiploid doubling can give an old polyploid complex a new lease on life (Stebbins 1947b, 1956).

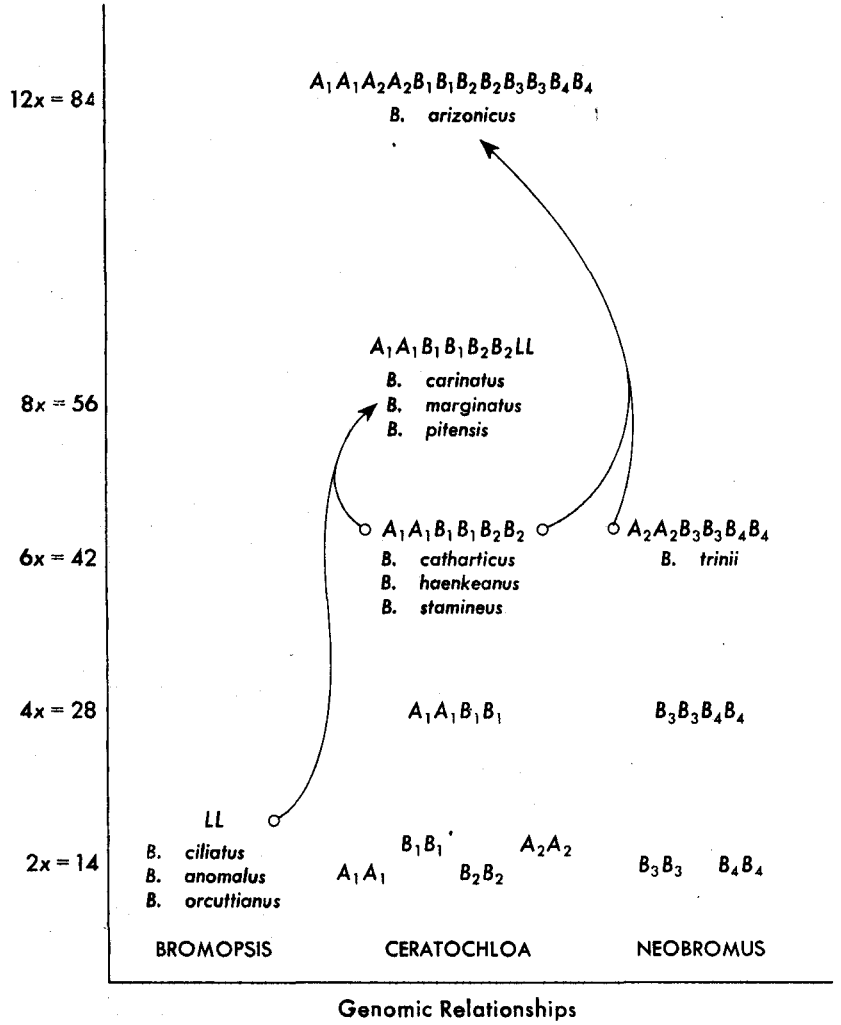

Figure 25.5. Phylogenetic relationships of high polyploid species of *Bromus*. Some of the basic genomes are unknown at the diploid or tetraploid level. (Redrawn from Stebbins 1956)

Vestiges of Ancient Polyploid Complexes

Stebbins (1971, 1980) has called attention to an inverse correlation between degree of advancement in morphology and that in ploidy level in various angiosperm families. Within the plant family, the morphologically primitive genera have basic chromosome numbers that are poly-

ploid. Conversely, the genera with more specialized morphological characters have diploid basic numbers.

Some examples are the following (Stebbins 1980):

	Morphologically primitive, old-polyploid basic numbers	Morphologically specialized, diploid basic numbers
Liliaceae	*Tofieldia*	*Trillium, Scilla*
Winteraceae	*Drimys*	*Tasmannia*
Polemoniaceae	*Cantua, Cobaea*	*Gilia, Phlox*
Hydrophyllaceae	*Wigandia*	*Nemophila*
Compositae	Heliantheae	Cichorieae

The evolutionarily advanced genera in these families have retained the ancestral diploid condition. The retention of diploidy was probably an important factor in their ability to attain high levels of evolutionary advancement. The high-number genera in the same families, on the other hand, are old polyploids, and often remnants of old polyploid complexes, which have remained conservative (Stebbins 1971, 1980).

Some whole families of woody dicotyledons have high basic chromosome numbers which have been plausibly considered by various authors to represent an old polyploid condition (Stebbins 1950, 1971; Tischler 1954; Darlington 1954b):

Magnoliaceae	$x = 19$
Trochodendraceae	$x = 19$
Cercidiphyllaceae	$x = 19$
Salicaceae	$x = 19$
Hippocastanaceae	$x = 20$
Platanaceae	$x = 21$

Most of the main groups of pteridophytes have basic numbers in the polyploid range, and in some groups the basic numbers are in the high polyploid range (Manton 1950; Löve, Löve, and Pichi Sermolli 1977). For example:

Polypodium, etc. (Polypodiaceae)	$x = 37$
Psilotum (Psilotaceae)	$x = 50, 52$
Tmesipterus (Psilotaceae)	$x = 104$

Equisetum (Equisetaceae)	$x = 108$
Ophioglossum (Ophioglossaceae)	$x = 120$

The most likely conclusion is that many groups of recent pteridophytes are the surviving remnants of geologically ancient polyploid complexes (Manton 1950).

Irreversibility

The evolutionary trend from diploid to tetraploid to higher polyploid is in the main an irreversible trend. This trend can be reversed partially by polyploid drop (see chapters 22 and 27). Thus in *Hesperis*, where $x = 7$, tetraploid species have gametic numbers of $n = 14$, 13, and 12.

Some workers have suggested the possibility of abrupt and complete reversals from the tetraploid to the diploid condition by means of polyhaploids (Raven and Thompson 1964; De Wet 1968). The haploid or polyhaploid progeny of a tetraploid parent is, of course, diploid. Such polyhaploids do arise spontaneously in polyploid plant populations. The polyhaploid derivative of an allotetraploid is, however, by definition and by observation, a chromosomally sterile diploid hybrid whose main chance of reproducing sexually is by doubling once again. Polyhaploids offer little hope for reversals in polyploid trends.

Suppression of Variability

The polyploid condition places certain restrictions on the generation of mutational and recombinational variability, as compared with the diploid condition, and these restrictions become tighter at the higher polyploid levels. The expression of new mutations is suppressed by gene duplication and polysomic inheritance. The formation of new recombination types is restricted by these factors and by preferential pairing.

Tischler points out that seedling mutants are common in *Triticum monococcum* (2*x*), are much rarer in *T. durum* (4*x*), and are quite rare in *T. aestivum* (6*x*) (Tischler 1953).

The generation of variability is restricted but not blocked completely

by the polyploid condition. Segmental allopolyploids can segregate to a limited extent for the interspecific gene differences. Polyploids can segregate mutant types rarely in polysomic ratios. Nevertheless, the variation-producing mechanism of the sexual process is inhibited in polyploids as compared with diploids.

The ability of polyploid species to respond to changing environmental conditions is therefore expected to be less efficient than that of diploid species. Certainly new polyploids are often very successful, more so than their diploid relatives, in various types of habitats, as we have seen in chapter 24. They are successful by virtue of a genetic system which permits a particular hybrid genotype to breed true. But this genetic system also imposes restrictions on the release of new variations and thereby sets limitations on the evolutionary potential of the polyploid lineage.

As the mainly irreversible trend to higher ploidy levels continues in the phyletic lineage, these limitations of evolutionary potential must become greater. The polyploid system, as Stebbins states (1950:366), is capable of producing numerous related species or even genera with generally similar characteristics, but has apparently played no role in the origin of new families or orders.

Diploidization

Old polyploids tend to be more diploid-like than newly formed polyploids. This change is known as diploidization. Diploidization affects both the cytological behavior and the genic constitution of polyploids.

A new or raw polyploid is expected to have a high frequency of multivalents, if it is an autopolyploid, and some multivalent formation, if a segmental allopolyploid. The multivalents reduce the fertility of the polyploid. Natural or artificial selection for fertility will favor genes, where these are available in the gene pool, that promote bivalent formation at the expense of multivalent formation.

Gilles and Randolph (1951) compared the multivalent frequency in an autotetraploid line of maize (*Zea mays*, $x = 10$) at the beginning and the end of a 10-year period of selection for fertility. The newly induced autotetraploid plants had 8–10 IV in 89% of the pollen mother cells, whereas their tenth-generation descendants had 8–10 IV in only 52% of the cells. The frequency of bivalents increased as the quadrivalent frequency decreased. The artificial selection for fertility which brought about this change probably involved an unconscious selection for genic factors influencing the mode of chromosome pairing at meiosis.

Selection for meiotic genes must be important in the history of many natural amphiploids. There is much homology between the different genomes in hexaploid wheat, *Triticum aestivum*. Yet the homeologous chromosomes do not normally pair; instead they form bivalents consisting of homologous chromosomes. This meiotic behavior is due to a gene on the long arm of chromosome 5 of wheat. When this gene is absent, multivalents are formed. The *5B* gene, when present, inhibits multivalent formation and promotes homologous bivalent pairing (Riley 1960).

Duplicate factors are common in new amphiploids and present in old ones. The duplicate loci are a consequence of the summation of related genomes. The duplicate factors may not be necessary for the functioning of the organism. One duplicate locus is then free to diverge from its original function. If the divergent gene finds another related function which is beneficial for the organism it will be preserved by selection.

An interesting case of divergence between originally duplicate factors is found in the allotetraploid cottons, *Gossypium hirsutum* and *G. barbadense*. Their genome constitution is *AADD*. The *AA* diploids are Old World cultivated cottons, and the *DD* diploids are wild American species.

A linkage group including the gene *R* for anthocyanin pigment and the gene *Cl* for inflorescence congestion occurs in both the *A* and *D* genomes and again in the *AADD* tetraploids. The *R* gene is present as a single locus in the *AA* diploids and the *DD* diploids, but as two loci (R_1 and R_2) in the *AADD* tetraploids. Similarly the gene *Cl* is present as a single locus in the *AA* diploids, and probably also in the *DD* diploids, but occurs in two loci (Cl_1 and Cl_2) in the *AADD* tetraploids. The genomic location of these genes in the tetraploids is R_2—Cl_2 in the *A* genome, and R_1—Cl_1 in the *D* genome (Stephens 1951a, 1951b).

The genes R_1 and R_2, and Cl_1 and Cl_2, were undoubtedly duplicate factors when tetraploid cotton first originated. But they are not duplicate factors in modern tetraploid cotton. Instead R_1 and R_2 interact as a pair of complementary factors, and so do Cl_1 and Cl_2 (Stephens 1951a, 1951b).

The evolutionary trend to higher levels of polyploidy is accompanied by greater difficulties of meiosis and greater restrictions on segregation and recombination. The process of diploidization works against these

tendencies. This process enables medium or high polyploids to behave genetically like diploids to a greater or lesser extent.

We can suspect that diploidization is a factor making it possible for some polyploid complexes to evolve to high ploidy levels. Likewise it is probably a factor in the ability of some genera with high basic numbers (e.g., *Epilobium*, $x = 18$; *Equisetum*, $x = 108$) to speciate extensively on their old polyploid levels. Diploidization, in short, can give old polyploids a new lease on life.