

## CHROMOSOMAL CHANGES—MECHANISM FOR EVOLUTION?

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*Polyploidy (an increase in the number of whole chromosome sets) is defined, illustrated, and explained. Mechanisms of polyploidy are discussed and the effects are examined for any possible role in progressive evolution. Although polyploidy may introduce changes in size, osmotic pressure, fertility, and other factors, these same changes are often unfavorable to the polypliod and are not the kinds of changes required for major evolutionary steps.*

*Aneuploidy (addition or subtraction of a single chromosome) is shown to be the basis of several disorders in the human body. Rather than adding extra genetic material from which to evolve new traits, aneuploidy is usually harmful to the species, and not creative in its effect.*

*Rearrangements of chromosome parts (translocation and inversions) are also seen to be generally harmful.*

*Although the various types of chromosomal changes may produce some striking modifications in the organism, they can hardly be regarded as important evolutionary mechanism.*

What about chromosomal changes as a mechanism for "big jump" evolution? Is it possible that the changes demanded by progressive evolution have come about in this way? Is this a possible mechanism for euglena to man development?

At first glance, chromosomal changes would seem to be a rather promising mechanism. There is no doubt that new variations in some respects comparable to species can arise through chromosomal changes. Moreover, changes in the number of chromosomes or in the arrangement of the genes within the chromosome do bring about profound effects—in many cases greater than the effects brought about by point mutations (changes in DNA).

### Change Through Polyploidy

One of the most promising mechanisms for change of a considerable magnitude is polyploidy—an increase in the number of chromosome sets, so that whereas the normal individual has  $2n$  chromosomes, the polypliod individual will have  $3n$ ,  $4n$ ,  $6n$ , or  $8n$ . There is no question that polyploidy is a means of producing what are ordinarily regarded as new species, and it is for this reason that evolutionists have been intrigued with the possibility of polyploidy as a mechanism for evolution. Goldschmidt went so far as to suggest that chromosomal changes are the only mechanism by which changes of the magnitude demanded by evolution can take place.

New species produced by polyploidy generally meet many of the criteria which have been set up for a good species. They either do not interbreed with their parent forms, or the resulting hybrids are partially, to completely sterile. They are fertile when bred among themselves, though rarely are they as fertile as the parent forms from which they have been derived.

In some cases the polypliod is derived from a single species—in this case it is referred to as an *autopolypliod*. In other cases two separate species serve as the parent of the new form—in these the forms are referred to as *allopolypliods*.

Mayr<sup>1</sup> tells us that polyploidy is the only proven mechanism of instantaneous speciation in sexually reproducing organisms; and, Stebbins<sup>2</sup> says that polyploidy is one way and perhaps the only way in which an interspecific barrier can arise in one step and thus give an opportunity to a new line to "evolve" independently and to diverge from the parental type.

There is no doubt that this mechanism is the common way in which new species have arisen: there are probably several hundred instances in the literature in which new species have arisen either by allopolyploidy or autopolyploidy. Many of these have been produced in the laboratory, either by exposing the organism to radiation, or by treating it with some chemical substance such as colchicine (an alkaloid drug derived from the corm of *Colchicum autumnale*, the autumn crocus). The latter drug interferes with metabolism and cell division with the result that two sets of chromosomes go to a single daughter cell.

We do not know what causes polyploidy in nature, and it is difficult under field conditions to determine the parents of a given plant or animal which we are examining. Presumably many cases of natural polyploidy are due to an abnormal meiosis which results in production of either diploid eggs or sperm. If a diploid egg is fertilized by a monoploid sperm the resultant organism is *triploid*; if a diploid egg is fertilized by a diploid sperm, the resulting organism is *tetraploid*.

### Two Possible Natural Polypliods

One form which is believed to be the result of natural polypliod is rice grass or cord grass, *Spartina townsendii* H. and J. Groves, which was

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first collected in 1870 at the edge of Southampton Water in England. Since that time it has spread over much of the south coast of England and to France. It seems to have arisen as a cross between *S. stricta* Roth, which is a European species, and *S. alterniflora* Loisel, an American species. The latter was apparently introduced from America with a shipment of merchandise. *Spartina townsendii* is fertile and breeds practically true.

*Spartina alterniflora* has a chromosome number of 70, *S. stricta* has a chromosome number of 56 and *S. townsendii* has a chromosome number of 126. It appears, therefore, to be a tetraploid which carries a complete chromosome set from both parents. It should be pointed out that the evidence for the origin of *S. townsendii* is circumstantial, and **no experimental production** of this species has been reported.

Another species believed to have developed as a natural polyploid is *Primula kewensis* which is thought to have arisen from a spontaneous cross at Kew, just outside London, between *P. verticillata* and *P. floribunda*. Both parent forms have a chromosome number of 18. The hybrid between the two proved to be only partly fertile and was cultivated vegetatively for a number of years until a shoot appeared which proved to be fertile. The fertile form usually has 36 chromosomes—apparently a pair of each set of chromosomes from each parent. It might be noted that this form would have died out completely had it not been cultivated vegetatively; it could not have maintained itself without human interference and care.

Also there are a number of irregularities about the chromosome behavior of *P. kewensis* which would make it quite unable to survive under natural conditions. Thus according to C. D. Darlington,<sup>3</sup>

In *Primula kewensis*, corresponding chromosomes of the diploid parents, *P. floribunda* and *P. verticillata*, are not sufficiently different to inhibit their pairing in the diploid hybrid. Such a lack of differentiation is associated with two abnormalities in the tetraploid: (1) chromosomes of opposite parents occasionally pair (in quadrivalents or bivalents) and pass to opposite poles. The progeny therefore differ in the proportions of the chromosomes of the two species present. Moreover, owing presumably to this pairing being accompanied by crossing over, the normal type can never again be recovered from its aberrant offspring. (2) Quadrivalents are formed which sometimes divide unequally (as in the auto-tetraploid *Datura* and *Primula sinensis*) giving therefore, gametes with 17 and 19 chromosomes instead of 18, and progeny with 34, 35,

and 37 chromosomes instead of 36. These differ from the normal tetraploid both owing to a change in proportion within the set of nine and owing to a change in the proportionate influence of the two species. Such plants, particularly those with 34 chromosomes, which have 2 chromosomes of one type and 4 of the other 8 types, are *less fertile* (Emphasis added) than the normal tetraploid.

Natural selection therefore would not only eliminate the 34 chromosome plants, but also *P. kewensis* since its overall fertility is reduced by these aberrant offspring.

#### Effects of Polyploidy

What are the effects of polyploidy? This is the crucial question so far as any consideration of polyploidy as a possible mechanism for progressive evolution is concerned. Does it bring about changes of the nature which would be demanded by progressive evolution?

It is generally observed that experimentally produced polyploids are larger than their diploid relatives; and, it is for this reason that polyploids are much sought after by seed men who hope to produce larger flowers and fruits. Gigantism may not be a permanent effect—in the course of time some polyploids become smaller in size.

It has also been suggested that polyploids are better able to stand severe climates, but Stebbins does not believe this is necessarily the case.<sup>4</sup> It is true that the number of polyploids increases as one goes north or to higher altitudes, and it is also true that polyploids have a wider geographical range than what is assumed to have been the range of their diploid ancestors. Stebbins believes that these observations are either without significance or are by no means universal.<sup>5</sup> It is generally agreed that polyploids possess a wider range of tolerance for climate and edaphic conditions; they can stand wider ranges of temperature and water supply than can their presumed diploid ancestors.

Polyploidy tends to decrease osmotic pressure though this does not always happen and cannot be regarded as a generalization. This particular characteristic would be unfavorable since a plant with a high osmotic pressure is able to get more water from the soil than a plant with low osmotic pressure—desert plants typically have a high osmotic pressure and plants that grow in wet places usually have a low osmotic pressure.

#### Losses of Viability and Fertility

Autopolyploids generally show a lower growth rate than do their assumed diploid ancestors. They flower later than do the diploids. Both these characteristics would seem to be unfavorable. However, polyploids flower over a longer

period of time and this presumably is a favorable characteristic. In polyploids the amount of branching is reduced and the leaves are generally thicker. Under some conditions these might be favorable characteristics; under other conditions, unfavorable.<sup>6</sup>

One particularly significant characteristic of polyploids is the fact that they usually have a lower reproductive rate than their diploid relatives. This is especially marked in triploids, but appears also in tetraploid. In one study with barley triploids, Kerber<sup>7</sup> reports an average fertility of 11.6%. Stebbins reports that the reduction in pollen and seed fertility in autopolyploidy as compared with their supposed diploid ancestors ranges from 5% to 20% in some maize to almost 100% in one of the cottons.<sup>8</sup>

Such losses of viability and fertility is significant when we consider the suggestion that polyploidy is supposed to be an important mechanism for evolution. Yet, the importance of polyploidy seems much reduced if it results in the formation of inviable and partially sterile forms. Any significant reduction in reproductive rate will necessarily be harmful so far as survival is concerned.

It is generally agreed that in most cases polyploids can survive only if the individual is capable of perpetuating itself in some other way. Tetraploid plants can survive, for instance, if they reproduce by clones, stolons, rhizomes, bulbs, or "winter buds." Polyploid forms may survive in animals in hermaphroditic and parthenogenetic species.

It should be noted that in some instances polyploids do appear to regain their fertility after several generations. It appears that some eventually become stabilized and are able to reproduce at a normal rate. However, until this condition is reached, vegetative reproduction is almost a "must."

Another important difficulty which reduces the importance of polyploidy as a possible mechanism for evolution is the fact that it is limited almost exclusively to flowering plants. Multiple sets of chromosomes have been reported in some of the other plant forms but this is rare. And furthermore, polyploidy rarely occurs in animals.

Wallace<sup>9</sup> points out that, for an animal polyploid species to develop successfully, a complicated combination of rare events—hybridization and doubling of the chromosome number—would have to occur simultaneously in each of two individuals, one male and one female, living in the same locale. In addition, these two individuals would have to choose each other as mates in preference to normal individuals of the parental species living in the same region, and their off-

spring, too, would have to prefer one another and mate brother and sister for a number of generations. Animal species then could adopt polyploidy, Wallace believes, only as a consequence of the coincidence of four, five, or six extremely rare events.

Mayr<sup>10</sup> says that while polyploidy is the only proved mechanism of instantaneous speciation in sexually reproducing organisms, and while it is common among plants, it is of no significance in animals.

#### Polyploidy Evaluated as Mechanism

In any case, the critical question is whether the changes polyploidy brings about are the types of changes which are needed in progressive evolution. To this question, the answer seems to be a clear "no." We note gigantism; we note a possible better adaptation to climatic condition, but we do not find the types of changes which would be required for euglena to man evolution.

Stebbins<sup>11</sup> believes that the long continued evolution needed to differentiate genera, families, orders, and phyla, appears to have taken place chiefly on the diploid, or at least on the homoploid level, in those forms which have had a polyploid origin. The little evidence that exists for evolution by means of polyploids, he feels, is a bit hazardous at present and not too impressive. He says that even with this evidence it does not appear that progressive evolution is furthered by polyploidy.

Stebbins points out, further, that none of the trends in floral specialization which have been so important in plant evolution are caused or promoted by polyploidy, and he concludes that polyploidy does not originate a major new departure. Indeed, he says, polyploidy is a complicating force rather than one which promotes progressive evolution. He characterizes the species originating by polyploidy as being, for the most part, very similar to the diploid ancestors in external morphology and in ecological preferences, or else they contain recombination of the characteristics found in those ancestors.

Cameron<sup>12</sup> believes that polyploidy is an evolutionary dead end, and that ultimately polyploids will succumb as a result of their inability to go back to the diploid condition, and because genetic variation seems to be hampered by the high number of chromosomes.

Ehrlich and Holm<sup>13</sup> say that such mechanisms as polyploidy are often considered disadvantageous from a long range point of view. Interestingly enough, however, they argue that since these mechanisms are extremely common in both plants and animals they must have some selective advantage.

Goldschmidt and his pupils cling to the importance of polyploidy and similar mechanisms. They believe that real evolution can take place only by changes involving whole chromosomes. In commenting on Goldschmidt's views, Mayr says<sup>14</sup> that the fact that some geneticists can come to conclusions diametrically opposed to those of other geneticists is striking evidence of our ignorance of the actual facts.

### Chromosomal Changes as Mechanism

What about other chromosomal changes as a mechanism for evolution? Some have suggested the addition or subtraction of a single chromosome, *aneuploidy*, as a mechanism for progressive change. Most people who suggest this mechanism are interested in the possibility provided by the addition of a chromosome to the normal chromosomal complement. They suggest that this extra chromosome may provide additional genetic material which can make possible the changes which progressive evolution demands. Most instances of aneuploidy represent a decrease in chromosome number,<sup>15</sup> but let us look at the evolutionary possibilities of the addition of one or more chromosomes.

Evidence which comes from a study of human chromosomal abnormalities is most interesting: (a) We now know that many if not most cases of Down's syndrome (Mongoloid idiocy) are due to an extra chromosome. These individuals have 47 chromosomes instead of the normal 46. The extra chromosome is one of the smallest of the human chromosomes (number 21).

(b) Investigators have also found two sexual disorders in man that are due to abnormal chromosome numbers. Klinefelter's syndrome is due to an extra "X chromosome, and Turner's syndrome is due to the absence of one of the sex chromosomes. In both cases the individuals are sterile, suffer from hormonal abnormalities which affect their sexual phenotype, and are generally mentally retarded.

(c) Recent studies on males with an extra "Y chromosome suggest that this condition may be associated with psychopathic criminality and aggressiveness.

(d) Two other conditions in which there is an extra chromosome have recently been described in man. One condition is Trisome 18 in which there is an extra chromosome (number 18) and the other, Trisome D, is probably the result of another extra chromosome (number 15). Both are associated with multiple congenital anomalies and the survival rate is poor.

If such evidence which we have from the results of the addition or subtraction of a single chromosome from the normal human comple-

ment of 46 is any indication, it seems unlikely that this mechanism is of any significance in evolution. Ehrlich and Helm say<sup>16</sup> that there are numerous examples suggestive of progressive increases in chromosome number but unfortunately little experimental evidence.

White<sup>17</sup> believes that the formation of supernumerary chromosomes is the chief method by which chromosome number has increased. A supernumerary chromosome is one which is absent in some individuals of the species altogether without noticeably affecting the appearance of the organism. It is suggested that supernumerary chromosomes may be more or less "blanks" to which genetic material can be added, which will provide for progressive evolution. At the present time, there is no evidence that supernumerary chromosomes are anything else than an abnormal temporary situation in the cell; and, there is no indication that active parts of chromosomes ever become translocated to such a chromosome.

### Translocation and Inversions

There remains to discuss the possibility that rearrangements may be mechanisms for evolution. These include translocation and inversions. Translocation are instances in which a piece of one chromosome is attached to a non-homologous chromosome. Inversions are instances in which the order of the genes on the chromosome is reversed.

Such rearrangements do change the organism and often in a striking way. The changes are often more marked than those to be seen in gene mutations. However, they are almost always harmful—harmful to a degree even greater than the changes brought about by mutation.

Muller says<sup>18</sup> that only those rearrangements can survive which involve a breakage of one or more chromosomes at least two points, together with a union of the pieces so formed by their broken ends in a new order leaving the originally free ends, or telomeres, still free, and leaving one spindle fiber attachment or centromere on each chromosome. This limits drastically the number of rearrangements that can survive.

Stebbins says<sup>19</sup> that while inversions alter the genetic mechanism they do so in such a way as to produce more constancy and fitness at the expense of flexibility. Thus the organism is not able to meet even relatively minor changes in the environment.

Many cytogeneticists believe that chromosomal rearrangements may result in the development of new species. While we have little laboratory evidence bearing on the problem, comparison of

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could not be separated, save after a study of their enclosed organic remains.

This quotation illustrates the "reasoning in a circle" that has been prevalent from Geike's day to the present. Biology in many instances did not offer the positive proof required to substantiate the evolutionary hypothesis. Scientists looked to geology—to the order of the fossils in the strata—to furnish the essential evidence. When the strata showed a contrary order, however, they fell back upon the overthrust hypothesis to explain the embarrassing discrepancy; thus employing evolutionary concepts they hoped to demonstrate, to try actually to show the strata in the wrong order.

In this study we have not intended to present a blanket denial of all thrust faults. We have shown, however, that when such faults exist, they are accompanied with physical evidence of differential movement. In the specific case of the Empire Mountain range (where Permian

rock lies atop Cretaceous) we have demonstrated the **lack of any conclusive evidence** for a thrust. The only conclusion we can reach from such data is that no thrust occurred. The area was once mapped as a thrust fault on paleontological evidence **alone** and physical data have evidently been disregarded.

The authors suggest that many such supposed "thrust faults" must be re-analyzed on the basis of physical evidence alone. The lesson seems clear enough that thrust faulting must be judged hereafter solely upon the physical criteria and aside from any evolutionary preconceptions.

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the chromosomal patterns of various *Drosophila* species has led many to believe that, in at least some cases, the differences between the species are due to translocation or inversions.

The critical question, however, is whether the changes brought about are the type of changes which progressive evolution requires, and to this question the answer seems to be "no." Also to be considered is the fact that chromosomal changes are usually lethal. It is unlikely that an animal, in which a translocation or inversion has occurred, will meet an individual of the opposite sex which has the same chromosomal change with whom he can then mate.

Huxley concludes<sup>20</sup> that chromosomal rearrangements are rarely if ever the sole cause of evolutionary diversion. He says that, for one thing, they have very little prospect of becoming established. Then, too, he says their presence in non-interbreeding groups is normally accompanied by numerous single gene differences which are themselves often responsible for much of the group incompatibility. He believes that they can, therefore, be regarded only as secondary agents in bringing about speciation.

#### Conclusions

In summary, we shall have to say that the various types of chromosomal changes can hardly be regarded as important evolutionary mechanisms. True, they do bring about striking changes in the organism—changes that are greater than those brought about by mutations. However, along with this goes the fact that most of the changes show even greater lethality than do mutations.

Only polyploidy and chromosomal rearrangement show any promise as a mechanism for evolution, and in the final analysis these contribute nothing that is really new. Moreover both usually result in a substantial reduction in viability and fertility.

#### References

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