

Tetraploid Mutants and Chromosome Mechanisms.

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The discussion which has been evoked in several recent papers, on the manner of origin of *Oenothera gigas*, calls for additional facts as well as certain comments and criticisms. Several years ago (Gates, 1909a) in a somewhat detailed study of the nuclear and cell size in *O. gigas* as compared with its parent, *O. Lamarckiana*, I expressed the view that the doubling in the chromosome number had probably occurred as the result of a suspended mitosis in the fertilized egg or in an early division of the young embryo. This view was based upon several facts, one of which was the absence of triploid ($3X$) mutants in *Oenothera*; and another, the absence of triploid species among all the plants whose chromosome numbers are known, combined with the occurrence of a considerable list of tetraploid species, i. e., species having double the chromosome number of their nearest relatives.

This view placed the essential mutational change in a different part of the life cycle of *O. Lamarckiana* from that which the mutation theory of de Vries would suggest, namely in the fertilized egg rather than during the reduction divisions in the spore mother cells.

Accordingly, Stomps (1910) stated his belief that *O. gigas* originated from the union of two "unreduced" or diploid germ cells rather than from a transformation occurring at or after the time of fertilization. He cited (p. 59) as evidence for this view an observation of de Vries' pupil, Geerts (1909, p. 52), who found a megaspore mother cell of *O. Lamarckiana* having twenty-eight instead of fourteen chromosomes. Stomps expressed the opinion that such a megaspore mother cell would undergo the usual chromosome reduction and would then go through the embryo sac morphology, producing an egg with fourteen chromosomes. He further assumed that such an egg was fertilized by a male cell derived from a diploid pollen grain, to produce the *gigas* mutant with twenty-eight chromosomes. Instead of this rather roundabout method, involving the assumed occurrence of diploid pollen grains, I suggested (Gates, 1911a, p. 934) that it was at least equally probable that the type of megaspore mother cell observed by Geerts developed an embryo immediately, thus omitting both reduction and fertilization. This was based upon the well-known fact that higher chromosome numbers are frequently associated with some form of apogamy, a list of such cases having been given in my earlier paper on the subject (1909a, p. 545). I also cited in that paper several instances in which the number of chromosomes had

been doubled experimentally by means of a suspended mitosis after the split in the chromosomes had taken place.

Soon after the publication of my earlier paper, Strasburger (1910) stated his complete agreement with my point of view, and like me, believed that tetraploid species in general originate from the failure of a mitosis to be completed in the fertilized egg or in one of the early divisions of the young embryo. He said (p. 409), „Er (Gates) kommt zu dem Ergebnis, das ich auch für das Wahrscheinlichste halte, dass die Doppelzahl der Chromosomen von *O. gigas* ihren Ursprung hatte in einer Teilung der Chromosomen, die nicht von Zellteilung begleitet war, bald nach der Befruchtung.“ And in conclusion (p. 445) he writes, „Die Wahrscheinlichkeit spricht dafür, dass der Ort eines solchen Vorgangs (the chromosome doubling) das befruchtete, noch ungeteilte Ei ist.“

In the paper above-mentioned, I cited the following as analogous cases of species having tetraploid chromosome numbers which had probably originated in a manner similar to that of *O. gigas*, though in some cases complicated by the occurrence of more than 4 X chromosomes: Several species belonging to the Eualchemillas, *Antennaria*, *Drosera longifolia*, *Hieracium excellens*, *H. flagellare*, *Nephrodium molle*, several varieties of *Athyrium filix-foemina*, and certain varieties of *Lastrea pseudo-mas*. To this list Strasburger (1910) added a long series of cases in plants and animals. The following table includes this list together with a number of other cases which have been reported since.

Table I.

	Reproduction	Chromosomes		Author
		Reduced number	Unreduced number	
<i>Wikstroemia canescens</i>	Sexual	9	18	Strasburger, 1910
<i>W. indica</i>	apogamous	—	26–28 gemini ¹⁾	„
<i>Rosa livida</i> ²⁾	sexual	8	16	„
<i>R. cinnamomea</i>	„	8	16	„
<i>R. canina</i> (many forms)	„	8	16	„
<i>R. canina</i> (one form) .	apogamous	16 or 17	33 or 34	Rosenberg, 1909
<i>R. glauca</i> (one form) .	„	16 or 17	33 or 34	„
<i>Taraxacum officinale</i> .	—	—	over 26	Juel, 1905
<i>T. confertum</i>	—	8	about 16	Rosenberg, 1909
<i>Houttuynia cordata</i> . .	partheno- genetic	—	52—56	Shibata & Miyaka, 1908

1) Gemini larger than in *W. canescens*, the cells, as well as the stigmas and ovules being also larger.

2) Strasburger (1910, p. 407) also refers to the fact that in the genus *Rubus* there are commonly six gemini in the germ cells, while in several *Rosa*

Table I. contd.

	Reproduction	Chromosomes		Author
		Reduced number	Unreduced number	
<i>Thalictrum purpurascens</i>	partheno-genetic	24	48	Overton, 1909
<i>T. minus</i>	sexual	12	24	"
<i>Rumex Acetosa</i>	apogamous	8	16	Roth, 1906
<i>R. hispanicus</i>	"	8	16	"
<i>R. arifolius</i>	"	8	16	"
<i>R. nivalis</i>	"	8	16	"
<i>R. Acetosella</i> ³⁾	"	—	16 gemini	"
<i>R. scutatus</i> ⁴⁾	—	—	12 gemini	"
<i>R. cordifolius</i> ⁵⁾	—	—	40 gemini	"
<i>R. crispus</i>	"	—	—	"
<i>R. Patientia</i>	"	—	—	"
<i>Funkia ovata</i>	sexual	—	48 ⁶⁾	Sykes, 1908
<i>F. Sieboldiana</i>	"	—	48	"

Table I. contd.

	Reproduction	Chromosomes		Author
		Reduced number	Unreduced number	
<i>Ascaris megalcephala univalens</i>	sexual	1	2	Boveri, 1887
<i>A. m. bivalens</i>	"	2	4	"
<i>A. lumbricoides univalens</i>	"	12	24	"
<i>A. l. bivalens</i>	"	24	48	"
<i>Styelopsis</i> ⁷⁾	—	—	8 or 4	Julin.
<i>Planaria</i>	—	—	6 or 3	Stevens
<i>Helix pomatia</i>	—	—	48 or 24	—
<i>Echinus microtuberculatus</i>	—	9	18	Boveri, 1888

species he found 8 gemini, and remarks that if the Aphanes group of the genus Alchemilla have been derived from such ancestors, they should be regarded as tetraploid and the Eualchemillas as octoploid in character. He suggests that a similar explanation may apply to the Elatostemas and Urticas.

3) Strasburger points out (1910, p. 429) that in this case the chromosomes of the tetraploid species are half the size of those in the diploid species, while the nuclei are the same size in both, from which he concludes that in this case the tetraploid number originated through a transverse division of the chromosomes.

4) Nuclear size same as in previous species.

5) Nuclei larger than in the section Acetosa. Also the species with low chromosome numbers do not hybridize, while species with high numbers cross readily.

6) This number is tetraploid as compared with many other Liliaceae, and probably originated through a transverse division of the chromosomes.

7) See Strasburger (1910, p. 442).

Table I. contd.

	Reproduction	Chromosomes		Author
		Reduced number	Unreduced number	
<i>E. microtuberculatus</i> .	—	18	36	Boveri, 1902 & Stephens, 1902
<i>Cyclops</i> , spp.	—	—	6—22 ⁸⁾	H. Braun
<i>Mnium hornum</i>	normal	6	12	M. Wilson, 1911
<i>M. hornum bivalens</i> . .	aposporous	12	—	É. & É. Marchal, 1911
<i>Bryum capillare</i>	normal	10	20	"
<i>B. capillare bivalens</i> .	aposporous	20	—	"
<i>Amblystegium serpens</i> .	normal	12	24	"
<i>A. serpens bivalens</i> . .	aposporous	24	48 ⁹⁾	"
<i>Musa sapientum</i> var. „Dole“	Sterile	8	16	Tischler, 1910
<i>M. s.</i> var. „Radjah Siam“	"	16	32	"
<i>M. s.</i> var. „Kladi“ . . .	"	24	48	"
<i>Crepis tectorum</i>	—	4	8	Juel, 1905
<i>C. japonica</i>	—	8	16	Tahara, 1910
<i>Dahlia coronata</i>	—	—	32	Ishikawa, 1911
<i>Dahlia</i> , nine varieties .	—	—	64	Ishikawa, 1911
<i>Saxifraga sponhemica</i> .	—	15	30	Pace, 1912 (p. 317)
<i>S. granulata</i>	—	30	60	Juel, 1907
<i>Artemia salina</i> , from Cagliari	sexual	—	42	Artom, 1911
<i>A. salina</i> , from Capodistria	partheno-genetic	—	84	"
<i>Primula floribunda</i> . .	sexual	9	18	Digby, 1912
<i>P. verticillata</i>	"	9	18	"
<i>P. verticillata</i> × <i>P. floribunda</i> (= <i>P. verticillata</i> F ₁)	"	9	18	"
<i>P. kewensis</i> (type) . . .	—	9	18	"
(= <i>P. floribunda</i> × <i>P. verticillata</i>)	self-sterile (no pin-flowers)	9	18	"
<i>P. kewensis</i> (seedling) (from a pin-flower) ¹⁰⁾	fertile	18	36	"

8) This range of chromosome numbers occurred in different species, with corresponding differences in nuclear size.

9) That is, twelve "bi-gemini" or partly fused groups of four chromosomes. In each case the nuclei and cells of the tetraploid forms are obviously larger, following the rule developed by me in the case of *O. gigas*, in 1909.

10) This single pin-flower appeared as a bud mutation on a plant which bore

Table I. contd.

	Reproduction	Chromosomes		Author
		Reduced number	Unreduced number	
<i>P. kewensis farinosa</i> (by selection)	fertile	18	36	Digby, 1912
<i>P. kewensis farinosa</i> (from <i>P. verticillata</i> \times <i>P. floribunda isabellina</i>)	"	18	36	"
<i>P. floribunda isabellina</i> \times <i>P. kewensis</i> (type) (= <i>P. floribunda isabellina</i> F ₁)	"	9	18	"
<i>P. kewensis</i> (type) \times <i>P. floribunda isabellina</i>	sterile	—	—	"
<i>P. floribunda isabellina</i> \times <i>P. kewensis</i> (seedling) (= <i>P. floribunda isabellina</i> F ₁)	fertile	9	18	"
<i>Triticum vulgare</i>	self-pollinating	8	16	Nakao, 1911
<i>Secale cereale</i>	"	8	16	"
<i>Hordeum distichum</i>	"	7	14	"
<i>Triticum dicoecoides</i>	"	8	16	Bally, 1912
<i>Aegilops orata</i>	"	16	32	"

The Marchals in the year previous to Strasburger's paper (1909) published a second paper on experimental apospory in the Mosses, in which among other things, it was shown that the tetraploid races possessed proportionally larger nuclei and cells, accompanied by larger dimensions of certain organs, particularly the sex organs. In a third important paper (1911) these authors reach further interesting conclusions, some of which may be referred to here. It was found that in the sporophyte of *Amblystegium serpens bivalens*, produced aposporously by wounding the capsule of the moss, the chromosomes were in groups of four ("bi-gemini"). As a result of extensive experiments with many mosses, it was found that in the dioecious species, regeneration of the gametophyte from the sporophyte gives rise to diploid gametophytes, which are physiologically bisexual, but sterile; while in monoecious species a diploid gametophyte is produced which has normal sexuality and

only thrum flowers. Self-sterility obviously accounts for the failure of the original *P. kewensis* to set seed.

is fertile, its (tetraploid) sporophyte producing diploid spores which permanently fix the race.

One of the most interesting facts discovered was a single case (*Phasium cuspidatum*) in which the doubling in the number of chromosomes, or rather the aposporous production of a diploid gametophyte directly from the sporophyte, was accompanied by mutational changes in the external characters. This mutant produced no sex organs and was consequently sterile, but reproduced by means of groups of cells resembling propagula, such as are found normally in certain other mosses. This result shows, as I have held, that mutational changes may occur at other points in the life cycle than the reduction divisions.

Another interesting paper dealing with polyploid chromosome numbers, is that of Tischler (1910), who found in the banana (*Musa sapientum*) three races having reduced chromosome numbers as follows: "Dole" 8, "Radjah Siam" 16, and "Kladi" 24. He further found that the volumes of the nuclei were in the ratio 1 : 2 : 3, confirming the law I obtained with *O. gigas* and *O. Lamarckiana*. Since the bananas are sterile, it is not evident how the tetraploid and hexaploid conditions could have been arrived at through the union of unreduced germ cells.

Tahara (1910) has found 16 chromosomes as sporophyte number in *Crepis japonica*, which is the tetraploid number as compared with 8 chromosomes reported by Juel (1905) in *C. tectorum*. Ishikawa (1911) has also shown recently that while nine varieties of *Dahlia* examined by him possessed 64 chromosomes, one species, *D. coronata*, had only 32. Judging from his figures, the cells of the tetraploid races are somewhat larger, though the individual chromosomes are distinctly smaller. This condition does not fit the anticipation either for a longitudinal or a transverse split of the chromosomes.

Very recently, Miss Pace (1912) has added another to the list of tetraploid species by determining 15 as the X number of chromosomes for *Saxifraga sponhemica*, Juel (1907) having already found 30 as the X number in *S. granulata*. And Bally (1912) has found the X number of chromosomes in *Aegilops orata* to be 16, which is double the X number (8) in *Triticum vulgare* and *T. dicoccoides*. The determination of the number for wheat is a confirmation of Nakao (1911), who found the X numbers to be 8 for wheat and rye, and 7 for barley. *Aegilops orata* is so closely related to *Triticum vulgare* that the two cross freely and have been included by some writers in the same genus. Bally found the heterotypic chromosomes in *T. dicoccoides* to be short and plump, while in *Aegilops* they were elongated and with a hook for attachment to the spindle fibres. He states that the latter were also about half

as large. It is not clear from his figures whether there is an accompanying difference in the size of cells and nuclei. Hybrids between these species should be very favourable for tracing the distribution of the chromosomes in meiosis.

Another paper to which reference must be made, is that of Artom (1911), who found similar conditions in the Crustacean *Artemia salina*, the sexual form from Cagliari having 42 chromosomes, while the parthenogenetic form from Capodistria possessed 84. Of all the papers hitherto cited, in which the question is considered, Artom's is the only one which refers the origin of the doubling to the union of two diploid germ cells rather than to the region of the fertilized egg¹¹).

Keeble (1912) has given an interesting account of the origin and structure of a giant *Primula sinensis* which originated as a mutant in a culture of "White Queen Star". The cells were found to be gigantic though the chromosome number (24) remained unchanged. Gregory (1909) found the same relation to exist in normal and giant Star Primulas. Keeble (l. c., p. 172) suggests that the cell giantism "may be due to a reduction in the normal rate of cell-division". It seems to me more probable that the original change or mutation was in the size of the cell, and that the slower rate of growth was a secondary effect. This view is based on the fact that *Oenothera gigas*, in which the chromosome number is doubled, is also slower in its rate of growth.

Several most interesting parallels to the case of *Oenothera gigas* are furnished by the Primulas recently investigated by Miss Digby (1912). The two species, *P. floribunda* and *P. verticillata*, each have 18 chromosomes as $2X$ number. *P. floribunda* \times *P. verticillata* gave the hybrid *P. kewensis* which produced only thrum flowers and was therefore sterile, having also 18 chromosomes like the parents. It was multiplied by cuttings for about five years, when a single pin flower appeared on one individual. This was pollinated from a thrum flower and gave rise to the fertile race of *P. kewensis*, having 36 chromosomes, from which a variety, *P. kewensis farinosa*, having also the tetraploid number of chromosomes, was afterwards obtained by selection.

Of equal interest is the further fact that the reciprocal cross, *P. verticillata* \times *P. floribunda isabellina*, also gave *P. kewensis farinosa*, having 36 chromosomes. Thus the doubling is not a

11) I must also refer here to a recent observation of Geoffrey Smith (1912) in which he found (in accordance with Guyer's results) that in hybrid pigeons normal synapsis failed to take place in spermatogenesis, the chromosomes failing to form bivalents and being irregularly distributed in the heterotypic mitosis. The homotypic mitosis was almost wholly suppressed, the secondary spermatocytes forming directly spermatids and spermatozoa, which are therefore of twice the normal size.

chance occurrence, and obviously the most probable place to look for the origin of the tetraploid number is in the fertilised egg, for it is too great a strain on one's credulity to assume that in both these independent cases the union happened to be between a diploid egg and a diploid male cell. It might be assumed that only tetraploid seedlings germinated, but this is certainly contrary to the probabilities when we consider that, in other crosses, both *P. floribunda* \times *P. verticillata* and the reciprocal cross gave hybrids agreeing with the female parent and having the regular diploid number of chromosomes. The further fact is of interest, that though *P. floribunda* \times *P. verticillata* and its reciprocal have both given matroclinous hybrids, they have also, in other crosses, both given rise to races of *P. kewensis*.

(Schluss folgt.)

Mikrokryoskopische Versuche.

Von Carl Drucker und Erling Schreiner.

Die Veranlassung zur Ausarbeitung einer mikrokryoskopischen Methode gab der Umstand, dass oft, insbesondere bei biologischen Aufgaben, nur eine kleine Flüssigkeitsmenge zur Verfügung steht. Diejenigen Verfahren zur Bestimmung osmotischer Konzentrationen¹⁾, die bisher die geringsten Substanzmengen beanspruchten, sind erstens die vortreffliche Dampfdruckmethode von Barger²⁾ und zweitens die spezielle Form der Beckmann'schen Gefrierpunktmessung, die von Guye und Bogdan³⁾ angegeben und von Burian und Drucker⁴⁾ modifiziert worden ist. In dieser Gestalt verlangt der Apparat noch ca. 1 resp. 1.5 ccm Lösung, aber auch das ist in vielen Fällen noch erheblich mehr als vorhanden ist.

Die Anwendung eines kleinen elektrischen Thermometers in der eben erwähnten Anordnung war das erste Mittel, durch das wir den Substanzbedarf zu vermindern versuchten. Nach einigen Versuchen haben wir aber darauf verzichtet und uns entschlossen, die Temperaturmessung außerhalb des Versuchsobjektes vorzunehmen. Dadurch bekommt die Arbeitsweise Ähnlichkeit mit der allgemein gebräuchlichen Schmelzpunktsbestimmung reiner Stoffe, wie sie der Chemiker täglich ausführt; sie unterscheidet sich von ihr durch größere Feinheit der Temperaturmessung, eine andere Indexerscheinung und andere Eigentümlichkeiten, die wesentlich

1) Dieser Ausdruck bedarf wohl keiner Erläuterung, da er nicht nur in der physikochemischen Literatur schon lange bekannt, sondern auch später von Hamburger nochmals ausdrücklich definiert worden ist.

2) Journ. Chem. Soc. 85, 286 (1904).

3) Journ. chim. phys. 1, 385 (1903).

4) Centralbl. f. Physiol. 23, Nr. 22 (1910).

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