THE RELATION OF MUTATIONAL CHARACTERS TO CELL SIZE¹

W. W. TUPPER and H. H. BARTLETT
University of Michigan, Ann Arbor, Michigan

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In continuation of a former study published in this journal, the writers have made a large number of measurements of the cells of various mutations and of the species from which they arose, in order to determine to what extent the characters of a mutation are dependent upon the size and shape of the individual cells that compose it, and, conversely, to what extent the characters depend upon the arrangement of the cells. The literature that has a direct bearing upon this problem is not extensive, and is summarized in the following classification of the cases thus far investigated:

(1) The mutation arises through a doubling in the number of chromosomes.

- (a) The cells show a marked increase in size, concomitant with the increase in chromosome number, and the characters of the giant mutation are to at least a large extent correlated with this increase. Examples: *Amblystegium serpens bivalens*, *A. subtile bivalens*, and analogous varieties in *Mnium*, *Bryum*, and *Amblystegium* (ÉL. & ÉM. MARCHAL 1911), *Oenothera Lamarckiana* mut. *gigas* (GATES 1909), *Oe. stenomeris* mut. *gigas* (TUPPER and BARTLETT 1916), *Solanum Lycopersicum gigas* and *S. nigrum gigas*, experimentally induced bud sports arising from hyperchromatic meristematic cells of the normal forms of these two species (WINKLER 1916).
- (b) The character of the mutation can not be correlated with the change in the cells. Example: The dwarf tetraploid variety of *Phascom cuspidatum* (ÉL. & ÉM. MARCHAL 1911).

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FIGURE 1.—*Oenothera pratensis* f. *typica*, belonging to the dimorphic progeny of the cross *mut. latifolia* $\times$ f. *typica*. The *latifolia* twin is shown in fig. 2.

FIGURE 2.—*Oenothera pratincola* mut. *latifolia*, belonging to the dimorphic progeny of the cross mut. *latifolia* $\times$ f. *typica*. The *typica* twin is shown in fig. 1.

(2) The mutation does not arise through a doubling of the chromosome number.

- (a) The cells of the mutation are nevertheless gigantic, and with the increase in cell size may be correlated the new characters of the mutation. Examples: Certain ones of the giant mu-

tations of *Primula sinensis* (GREGORY 1911, KEEBLE 1912).

- (b) The cells of the mutation show either no change in size, or too slight a change to account for the deviation of the mutation from the parent species. Example: The mutations of *Oenothera Reynoldsii* (LA RUE and BARTLETT 1918).

This paper deals with *Oenothera pratincola* and two of its mutations. The three forms are referred to throughout as f. *typica*, mut. *latifolia*, and mut. *gigas* (?). The species has been the subject of former papers (BARTLETT 1914, 1915 a, b) in which it is described and figured. Mut. *latifolia* has been partially characterized, and its breeding behavior described, but it has not been figured before. It may be considered as a half dwarf, with many distinctive features in addition to its lower stature. It has relatively broader leaves than f. *typica*, very weak stems, which are unable to bear up the heavy foliage, and are therefore frequently more or less decumbent, and enormous stigmas, often more than a centimeter long, and proportionately thick, which are protruded from the apex of the bud before the flower opens. This unique mutation is one of several derivatives from *Oe. pratincola* that behave in inheritance as follows:

Mutation $\times$ mutation $\rightarrow$ mutation + type.

Mutation $\times$ type $\rightarrow$ mutation + type.

Type $\times$ mutation $\rightarrow$ type.

That is to say, every progeny grown from seeds of mut. *latifolia*, whether self-pollinated or crossed with f. *typica*, consists of a mixture of mut. *latifolia* and f. *typica*. This mode of inheritance is known not only among certain mutations of *Oe. pratincola* (BARTLETT 1915 b), but also among those of *Oe. stenomeres* (BARTLETT 1915 c) and *Oe. Lamarckiana* (DE VRIES 1916). The two forms composing the dimorphic progeny of mut. *latifolia* are shown in figs. 1 and 2. It is an especially noteworthy fact that although mut. *latifolia* is a half dwarf, the individuals of f. *typica* contained in its progeny are in every way normal, not only as regards size, but also in other characters. In spite of the passage of *typica* germ-plasm through an entirely different generation, the characters of f. *typica* come out entirely unmodified. It may be that a cytological explanation of this phenomenon will be forthcoming. The analogy in behavior between mut. *latifolia* and *Oe. lata* de Vries suggests that the former, like the latter, may have 15 chromosomes, for it has recently been shown (LUTZ 1917) that most of the mutations of *Oe. Lamarckiana* giving a dimorphic progeny, of which

one of the forms is the specific type, are characterized by the presence of an extra chromosome.

The same strains that frequently give rise to mut. *latifolia* have several times thrown mutations that are referred with some doubt to mut. *gigas*. It is probable that the only conclusive method of determining that a given mutation is mut. *gigas* and not mut. *semigigas* is to make a count of the chromosomes. This has not been done in the case of any of the three plants referred to in this paper as mut. *gigas* (?), and it has therefore seemed wise to follow the name by a question mark. The putative *gigas* plants have not been all alike. One of them differed little if at all from an authentic specimen of mut. *gigas* in which ARZBERGER (BARTLETT 1915 b) had determined the chromosome number to be 28. The two others were very similar to one another, and looked much as if they might be *gigas* forms corresponding to one of the half dwarf mutations with normal (or at least not double) chromosome number. Only the apparently normal, tall individual gave a progeny from self-pollinated seeds, and the two daughter plants were both semi-dwarfs. The same individual gave very large progenies of seemingly tetraploid plants, tall in stature, when reciprocally crossed with *Oe. stenomerus* mut. *gigas*.

It will be remembered that it is only comparatively recently, as a result of the researches of LUTZ (1912) and of STOMPS (1912) that triploid mutations have been distinguished from tetraploid. The former have been found to be remarkably sterile. As a rule, pollen is lacking, or at any rate well formed and functional grains are very few. The putative mut. *gigas* of this paper is indeed very self-sterile, but not for the reason that there is any lack of good functional pollen. The latter is fairly abundant, mostly of the square form so characteristic of tetraploid mutations, not only in *Oenothera* (LUTZ 1917) but also in *Solanum* and *Lycopersicon* (WINKLER 1916), and is functional on the stigmas of *Oe. stenomerus* mut. *gigas*. The hybrids with the latter have beautiful and abundant pollen. In the absence of chromosome counts, the best designation for the cell giants of *Oe. pratincola* would seem to be mut. *gigas* (?). From the standpoint of this paper it makes little difference whether they are tetraploid or triploid.

The six individual plants that furnished material for our measurements were grown in 1915 at the Glen Dale (Maryland) experiment garden of the Office of Physiological and Fermentation Investigations of the BUREAU OF PLANT INDUSTRY. In the tables that follow they are designated a, b, c, d, e and f. Since some few readers may wish to

locate these plants in the pedigrees that have been published (BARTLETT 1915 a, b) or will be published in future papers, the culture number of each is given.

Plant a was a fine individual of *f. typica*, occurring in a progeny from mut. *latifolia* $\times$ *f. typica* (culture no., Lex. C-22-(13 $\times$ 10)-53). Two of its sister plants are shown in figures 1 and 2.

Plant b was a well developed individual of mut. *latifolia*, in a progeny from self-pollinated mut. *latifolia* (culture no., Lex. C-22-13-246).

Plant c was mut. *latifolia*, in a progeny of mut. *latifolia* $\times$ mut. *angustifolia*. The pollen of the latter mutation is exactly equivalent to that of *f. typica*, as has been stated elsewhere (BARTLETT 1915 b, p. 438) (culture no., Lex. C-22-(13 $\times$ 19)-69).

Plant d was mut. *gigas* (?) in a progeny from self-pollinated mut. *latifolia* (culture no., Lex. E-36-51). It was tall, and in this respect, as well as in general aspect, resembled the authentic mut. *gigas* of a former paper (BARTLETT 1915 b). It had the thick stems and foliage, and the large flowers which generally occur in *gigas* forms. The buds had a length, before opening, of 72-75 mm, with a greatest diameter at the base of the cone of 7.5 mm. Corresponding measurements for a sister plant of *f. typica* were 55 and 5 mm, respectively. The average length of the open flowers, measured from the base of the ovary to the tips of the calyx, was 65 mm in *f. typica* and 86 mm in mut. *gigas*. The following measurements give the average of five representative flowers of each type:

	<i>F. typica</i>	Mut. <i>gigas</i> (?)
Ovary	11	13.3
Hypanthium	31	46
Calyx segments	23.5	27
Free tips of calyx	4.5	6
Petals, length and breadth.....	21.3 $\times$ 24	26 $\times$ 33

Plant d was almost self-sterile, but gave large progenies when reciprocally crossed with *Oe. stenomerus* mut. *gigas*.

Plant e likewise occurred in a progeny from self-pollinated mut. *latifolia*, and was one of the half dwarf *gigas* (?) types. Its flowers were as large as those of plant d, and except for its low stature and bushy branching it had all the earmarks of a mut. *gigas* (culture no., Lex. C-22-13-41).

Plant f was another half dwarf *gigas* (?), occurring in the same progeny as plant c (culture no., Lex. C-22-(11 $\times$ 19)-14).

The reader's attention is called to the fact that every one of the six

plants had mut. *latifolia* as a seed parent, and a pollen parent of which the pollen has been shown to be exactly equivalent to that of f. *typica*. The same individual of mut. *latifolia*, variously pollinated, was the mother of all except plant d, which belonged to a different strain from the rest. In connection with the frequent origin of the cell giants from mut. *latifolia*, it is interesting to find a parallel in the relationship between *Oe. semigigas* Stomps and *Oe. lata* de Vries, two of the mutations from *Oe. Lamarckiana*. Three out of eight individuals of *Oe. semigigas* discovered by Miss LUTZ (1912) were derived from *Oe. lata* as a seed parent, an unduly large number when it is considered how small are progenies of this form in comparison with those of *Oe. Lamarckiana*. In view of the large number of individuals that have been grown from *Oe. pratincola* f. *typica*, it has not produced giants with anywhere near the same frequency as mut. *latifolia*. If there is some causal relationship between the great frequency with which 15-chromosomed *Oe. lata* produces *Oe. semigigas*, and the presence of the odd chromosome, one might anticipate the discovery not only that mut. *latifolia* has 15 chromosomes, as its behavior in inheritance would indicate, but also that the cell giants of this paper are forms with 21 rather than 28 chromosomes.

Measurements (from which the areas of these cells were calculated) were made of the length and breadth of the epidermal cells overlying the midvein in the upper third of the outer surface of the calyx segments (tables 1, 2, and 3), of the length and width of the epidermal cells of the upper surface of the petals (tables 4 and 7), of the length of the epidermal cells in the upper third of the filament (table 5), and the diameter of the pollen grains (table 6). In order to get comparable results, it was necessary to select cells for measurement from exactly the same position on the different plants. The epidermal cells of the calyx, for example, are of two very different types. Those lying over the midvein are regular and oblong, with the long sides fairly parallel. The others are too irregular to measure, unless with a planimeter, or by the method of weighing outline camera drawings. Even the regular cells had to be measured in the upper third of the calyx (any other restricted region would have done equally well) in order to eliminate the error that would have come from not measuring the same number of cells from each aliquot part of the length, if the entire calyx segment had been used. Epidermal cells in general were found to vary greatly in size, according to their position. The petal cells were measured in the upper third of the petal, away from the edge. In the case of the

pollen, the dimension taken was the diameter of the central body of the grain, exclusive of the germination points.

The flowers of plants a, b and c were chosen to be as nearly as possible of the same size. Material was taken from unopened buds in which the length of the cone, from hypanthium to the ends of the free calyx tips, was 22 mm. In the case of plants d, e and f, the bud cones had a length of 26 mm. The calyx segments and petals of plants d, e and f were roughly half again as great in area as those of plants a, b and c.

The tables follow.

TABLE 1

Length of epidermal cells of the calyx in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).

Length in mm	F. <i>typica</i>	Mut. <i>latifolia</i>		Mut. <i>gigas</i> (?)		
	Plant a	b	c	d	e	f
.024-.039		1				
.040-.055	1	6	1			
.056-.071	9	20	1			1
.072-.087	13	35	26		13	6
.088-.103	18	15	34	3	10	7
.104-.119	8	13	17	5	12	11
.120-.135	0	5	17	9	26	21
.136-.151	1	4	4	9	13	19
.152-.167		1		9	9	12
.168-.183				8	7	7
.184-.199				2	3	6
.200-.215				2	3	8
.216-.231				2	2	1
.232-.247				0	0	0
.248-.263				0	0	0
.264-.279				1	1	1
.280-.295					1	

TABLE 2

Width of epidermal cells of the calyx in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).

Width in mm	F. <i>typica</i>	Mut. <i>latifolia</i>		Mut. <i>gigas</i> (?)		
	Plant a	b	c	d	e	f
.008-.015	2					
.016-.023	11	26	10			
.024-.031	22	59	62			7
.032-.039	14	11	25	6	36	28
.040-.047	1	4	3	18	17	50
.048-.055				18	12	13
.056-.063				8	2	2
.064-.071				0	2	
.072-.079				1		

TABLE 3

Area of epidermal cells of the calyx in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).

Area in mm ²	F. <i>typica</i>	Mut. <i>latifolia</i>		Mut. <i>gigas</i> (?)		
	Plant a	b	c	d	e	f
.00032-.00095		3				
.00096-.00159	9	17	4			
.00160-.00223	19	38	17		4	
.00224-.00287	10	25	25		7	2
.00288-.00351	6	11	35		23	9
.00352-.00415	5	6	16	2	15	8
.00416-.00479	1		3	3	12	11
.00480-.00543				5	4	20
.00544-.00607				9	8	16
.00608-.00671				6	9	10
.00672-.00735				5	5	10
.00736-.00799				4	1	2
.00800-.00863				6	8	3
.00864-.00927				6	2	5
.00928-.00991				1	1	3
.00992-.01095				3	1	1

TABLE 4

Length of epidermal cells of petal in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).

Length in mm	F. <i>typica</i>	Mut. <i>latifolia</i>		Mut. <i>gigas</i> (?)		
	Plant a	b	c	d	e	f
.032-.039	6					6
.040-.047	22	5	3			12
.048-.055	32	13	17	1	1	12
.056-.063	21	24	25	4	8	12
.064-.071	14	22	28	10	17	18
.072-.079	4	17	16	20	19	21
.080-.087	1	17	7	24	21	15
.088-.095		1	3	19	16	4
.096-.103		1	1	12	11	2
.104-.111				7	4	5
.112-.119				3	2	1
.120-.127					1	2
.128-.135						0
.136-.143						1
.144-.151						0
.152-.159						2

TABLE 5

Length of epidermal cells of filament in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).

Length in mm	F. typica	Mut. latifolia		Mut. gigas (?)		
	Plant a	b	c	d	e	f
.048-.063	1	5	5			1
.064-.071	17	26	28			5
.080-.095	45	43	45	3		14
.096-.111	26	28	14	14	2	15
.112-.127	6	7	6	33	8	24
.128-.143	4		2	24	18	18
.144-.159	1			13	8	14
.160-.175				10	7	7
.176-.191				1	4	2
.192-.207				2	1	
.208-.223					2	

TABLE 6

Diameter of subglobose body, and number of germination pits, of pollen of Oe. pratincola f. typica, mut. latifolia, and mut. gigas (?).

Diameter in mm	F. typica	Mut. latifolia		Mut. gigas (?)		
	Plant a	b	c	d	e	f
.088-.095	14		1			
.096-.103	16	3	18			
.104-.111		13	23			
.112-.119		12	7			1
.120-.127		2	1	4	2	13
.128-.135				10	13	28
.136-.143				24	56	8
.144-.151				42	27	
.152-.159				15	2	
.160-.167				5		
Number of germination pits	Plant a	b	c	d	e	f
3	30	30	50	22	30	12
4				67	63	37
5				11	6	1
6					1	

TABLE 7

Summary of tables 1-6, together with data on the average width of the epidermal cells of the petals, based in each case upon 15 counts of the number of cells in 0.2 mm. (All measurements are in mm.)

	F. typica	Mut. latifolia		Mut. gigas (?)		
	Plant a	b	c	d	e	f
<i>Calyx cells:</i> Mean length σ CV	.089 .0182 $\pm$.0012 20.47 $\pm$ 1.38	.085 .0244 $\pm$.0012 28.69 $\pm$ 1.37	.101 .0189 $\pm$.0009 18.75 $\pm$.89	.153 .0337 $\pm$.0023 22.00 $\pm$ 1.48	.134 .0402 $\pm$.0019 30.00 $\pm$ 1.43	.144 .0379 $\pm$.0018 26.29 $\pm$ 1.38
Mean width σ CV	.028 .00688 $\pm$.00046 24.58 $\pm$ 1.66	.027 .00546 $\pm$.00026 20.21 $\pm$.96	.030 .00523 $\pm$.00025 17.43 $\pm$.83	.050 .01026 $\pm$.00069 20.52 $\pm$ 1.37	.038 .00947 $\pm$.00045 24.90 $\pm$ 1.19	.042 .00673 $\pm$.00033 16.02 $\pm$.76
Mean area σ CV	.0025 .00071 $\pm$.00005 28.44 $\pm$ 1.92	.0023 .00068 $\pm$.00003 29.63 $\pm$ 1.41	.0030 .00076 $\pm$.00004 25.45 $\pm$ 1.21	.0077 .00246 $\pm$.00012 31.93 $\pm$ 1.52	.0051 .00208 $\pm$.00010 40.83 $\pm$ 1.95	.0060 .00185 $\pm$.00009 30.90 $\pm$ 1.47
<i>Petal cells:</i> Mean length σ CV	.054 .0099 $\pm$.0005 18.25 $\pm$.87	.067 .0106 $\pm$.0005 15.85 $\pm$.76	.066 .0115 $\pm$.0005 17.39 $\pm$.83	.086 .0135 $\pm$.0006 15.74 $\pm$.75	.083 .0144 $\pm$.0007 17.42 $\pm$.83	.078 .0178 $\pm$.0008 22.85 $\pm$ 1.08
Mean width Mean area	.013 .00070	.017 .00114	.018 .00119	.020 .00172	.020 .00166	.018 .00140
<i>Filament cells:</i> Mean length σ CV	.101 .01839 $\pm$.00088 18.21 $\pm$.87	.097 .01631 $\pm$.00075 17.02 $\pm$.78	.086 .01632 $\pm$.00078 18.98 $\pm$.91	.130 .02179 $\pm$.00104 16.76 $\pm$.80	.132 .02889 $\pm$.00195 22.22 $\pm$ 1.50	.122 .02697 $\pm$.00129 22.11 $\pm$ 1.05
<i>Pollen:</i> Mean diameter σ CV	.096 .00398 $\pm$.00004 4.17 $\pm$.47	.111 .00610 $\pm$.00007 5.50 $\pm$.62	.106 .00626 $\pm$.00004 5.90 $\pm$.40	.146 .00897 $\pm$.00004 6.14 $\pm$.29	.141 .00588 $\pm$.00003 4.17 $\pm$.20	.131 .00555 $\pm$.00004 4.23 $\pm$.29

Bearing in mind that the individuals of *f. typica* (plant a) and *mut. latifolia* (plants b and c) were all descended from the same mother, variously pollinated, but in every case with pollen equivalent to that of *f. typica*, several interesting conclusions can be drawn.

(1) The half dwarf habit of *mut. latifolia* is not due to its being composed of smaller cells, but rather to its being composed of fewer cells.

(2) When a significant difference exists between the sizes of corresponding cells of the two forms, as in the case of the petal epidermis and pollen, the cells of the mutation are decidedly the larger.

(3) The half dwarf habit of *mut. latifolia* results from a life cycle shortened not as to duration but as to number of cell divisions.

The measurements of the supposed *gigas* mutations confirm previous work of GATES (1909) and the writers (TUPPER and BARTLETT 1916), which showed that the individual cells were markedly larger than those of the parent species. The data now at hand are ample to show that although the *gigas* mutations are larger in all parts than the forms from which they were derived, the increase in size of plants or organs is by no means comparable with the increase in cell size. Thus, if the petals of *f. typica* (plant a of the tables) and *mut. gigas* (?) (plant d) were composed of equal numbers of cells, the area of the latter would be roughly $2\frac{1}{2}$ instead of $1\frac{1}{2}$ times as great as the former. Similarly, the calyx segments would have three times the area, instead of less than twice. Although the cells of all tissues are indeed larger in *mut. gigas* than in homologous tissues of the parent form, there is a compensation for the larger cells in the smaller number of cells of which organs and the entire individual are composed. In indubitable *gigas* plants the net result is an increase in the size of the plant, although a smaller number of cell divisions take place in the production of an individual than is the case in *f. typica*. It has been remarked by both DE VRIES (1913) and GATES (1915) that the growth rate of diploid forms is higher than that of tetraploid forms, and that the latter therefore attain maturity more slowly than the former. Obviously the difference would be accentuated if it were not for the fact that fewer divisions are necessary to produce a *gigas* individual. A longer period of time for the accomplishment of fewer cell divisions indicates clearly that a retardation of metabolic processes must accompany increase in cell size. With increase in cell size, the surface of the cell would not increase in proportion to the volume, with the result that respiration and nutrition would certainly be retarded. These considerations are familiar through the classical essay of SACHS (1893) on the factors limiting cell size. When we con-

sider the evolutionary possibilities of the process of doubling the chromosome number, it becomes clear that they are very limited. Since increase in chromosome number (as long as the chromosomes remain of the same size) must of necessity result in an increase of cell size, it is clear that relatively few doublings would suffice to overstep the limitations placed on cell size by the functions that it has to perform. The whole question has been well reviewed recently by WINKLER (1916).

Our studies of plants e and f have shown that a presumable *gigas* mutation (or if not a *gigas*, at any rate a *semigigas*) may be a cell giant and at the same time a half dwarf. In such a case the number of cells must be very much less than in either f. *typica* or mut. *gigas*. Such plants have smaller cells than more typical mut. *gigas* (plant d), and have a much smaller stature, but some organs (e.g. the petals) are quite as large.

The general conclusions to be drawn from a comparison of f. *typica* and mut. *gigas* (?) are as follows:

- (1) The supposed tetraploid forms have much larger cells.
- (2) They have characters of organization as well as of proportion that differentiate them from f. *typica*.
- (3) It is impossible, on account of the complex interrelations of structural and physiological characters, to be sure which characters are directly and which only indirectly due to the doubling of the number of chromosomes.
- (4) That some characters may be independent of the doubling, and due to an independent mutation at the time of origin of the tetraploid number, is possibly indicated by the fact that the supposed *gigas* mutations differ widely among themselves, some of them appearing to belong to the category of half dwarfs.

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