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Tables Illustrating Biparental Crossing-Over in Genetics[1]

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Students of elementary genetics frequently are called upon to calculate the theoretical distribution into phenotypic and genotypic classes, of populations resulting from divers crosses with linked genes, say (A and B). In some of these crosses, the dominant factors exhibit "coupling"; in such crosses, the respective parents are AB/AB and ab/ab, and the F_1 generation has the formula AB/ab. Other crosses show a condition known as "repulsion"; the two parents exhibit a converse condition; one parent has the formula Ab/Ab, and the other aB/aB; and the F_1 generation the formula Ab/aB. Still other crosses may involve parents that are like the F_1 individuals of the two crosses just mentioned: one parent is AB/ab, and the other parent Ab/aB. In all types of crossing, the linkage (or its converse, crossing-over) is for any two genes fairly constant. The percentages of the four classes of the populations resulting from different kinds of crosses (coupling, repulsion, etc.) will, however, differ at the same linkage-percentage, as is well exhibited in Tables I to IV.

As every student of genetics knows, the degree of linkage (or, conversely, crossing-over) can easily be found by first back-crossing the F_1 individual on a homozygous linked double recessive (here, ab/ab), and then counting the progeny in linked and cross-over classes. In many creatures, whether of XX,XY or WZ,ZZ genetic type, the heterogametic sex shows no crossing-over. In some other species (especially of plants) crossing-over occurs in *both* types of gametogenesis; and it is to this type of crossing-over that this paper applies. Moreover, in this paper the dominance of each linked gene is assumed as *complete* (segregation of

[1]The present paper is in correction and extension of one published in Volume 1 of FIELD & LABORATORY, 1932. It is prepared primarily for the use of my students in Genetics.

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3 : 1 in the F_2) ; and the factors are *independent* in the sense of not being complementary.

Formerly, when the theoretical distribution of progeny of such crosses was to be calculated, a Punnett Square, four divisions to a side, was made, and the linked and cross-over gametes (with their frequency-factors or percentages) laid out on both axes. (*Cf.* Sinnott & Dunn, 3d. ed., 1939, p. 203.) If the sum of the factors on each axis was 10, the products of these factors for each class of progeny represented the actual percentages of the population. If, however, the sum of the factors on an axis was more than 10 or less than 10, a correction-factor was necessary for conversion into percentages. If irregular values for linkage and crossing-over (like L=87% ; CO=13%) obtained, the factors were written as decimal fractions (0.87, 0.13, 0.13, 0.87) on the axes; and (since the sum of these factors is 2.00, or 200%) the products of these factors, and thereby the sums for each phenotypic and genotypic class, *had to be divided by four* (since $2.00 \times 2.00 = 4.00$, or 400%).

In the present formulae (Table I) I have used the actual percentage values for linkage and crossing-over, and the sum of the factors on each axis is 2.00. I have therefore used in the formulae the solidus or virgula (/) to indicate that the value set forth in the formula is to be divided by 4 to give the actual theoretical percentage of the population belonging to a given phenotypic or genotypic class. For ready comparison, the formulae of each type of cross are set out for each class in parallel columns.

TABLE I

Formulae for PHENOTYPES *in Progeny of the Crosses* (A), (B), *and* (C).

Type	(A)	(B)	(C)
AB	$(3x^2 + 4xy + 2y^2)/4$	$(2x^2 + 4xy + 3y^2)/4$	$(2x^2 + 5xy + 2y^2)/4$
Ab, aB	$(2xy + y^2)/4$	$(x^2 + 2xy)/4$	$(x^2 + xy + y^2)/4$
ab	$x^2/4$	$y^2/4$	$xy/4$

Formulae for GENOTYPES *in Progeny of the Crosses* (A), (B), *and* (C)

Genotype	(A)	(B)	(C)
AB/AB	$x^2/4$	$y^2/4$	$xy/4$
AB/Ab	$2xy/4$	$2xy/4$	$(x^2 + y^2)/4$
AB/aB	$2xy/4$	$2xy/4$	$(x^2 + y^2)/4$
Ab/ab	$2xy/4$	$2xy/4$	$(x^2 + y^2)/4$
aB/ab	$2xy/4$	$2xy/4$	$(x^2 + y^2)/4$
AB/ab	$2x^2/4$	$2y^2/4$	$2xy/4$
Ab/aB	$2y^2/4$	$2x^2/4$	$2xy/4$
Ab/Ab	$y^2/4$	$x^2/4$	$xy/4$
aB/aB	$y^2/4$	$x^2/4$	$xy/4$
ab/ab	$x^2/4$	$y^2/4$	$xy/4$

In Table I, Cross A involves AB/ab × AB/ab; Cross B, Ab/aB × Ab/aB; and Cross C involves a cross of AB/ab × Ab/aB. The first cross is one of coupling, and the second one of repulsion. The values of x and y are the percentage-values for linkage and crossing-over, respectively. Thus, in a case where the CO-% is 11, the value of y is .11; and the value of x is 1.00—.11=.89. Since x+y always equals 100% (or 1.00), a cross-over of 7% would mean a linkage of 93%.

Inspection of Tables II-IV shows that with 50% crossing-over we have the equivalent of free segregation, with its ratio (for dihybrids) of 9 : 3 : 3 : 1. In progeny of Cross A (Table II), with *complete* linkage (0.0% crossing-over) there are no intermediate classes (Ab, aB.) In Cross B, there is no double recessive (ab/ab) class at 0.0% crossing-over. Cross C shows no ab/ab individuals at 0.0% crossing-over. Many relations between the theoretical percentages for each class will appear to the student in the tables.

If the percentage of crossing-over is known, and the type of cross is known, the distribution of the progeny by classes can be seen at once on inspection of the proper table. One can derive a very rough approximation of the CO-% of a Cross A population by study of its ab/ab class. The intervals between the values of the ab/ab class at different CO-percentages in Cross B are too small to be of much value in determining the CO-% on inspection.

Tables II and III are of help in quickly calculating from F_2 populations the approximate percentage of crossing-over. Thus, in Sinnott & Dunn's "Problem 293" (3d ed., 1939, p. 213f.), Punnett's sweet-pea linkage data (coupling, n=716) showed 28% of the population evenly distributed between the two intermediate classes. [This, by our Table II, indicates between 34% and 35% of CO.] In the repulsion experiment on sweet-peas (n=1494), 40% of the population was equally distributed in the two intermediate classes [by our Table III this indicated a CO of between 40% and 44%]. Such approximations are, of course, only rough ones; but enough has been said to indicate use of the tables instead of the laborious and involved formula of Immer (1930), when only a rough approximation of the value is desired. The values given in the tables are theoretical ones, which assume that there is no fertility-differential in favor of any gamete-type, or survival-differential in favor of any zygote-type.

TABLE II. SEGREGATION OF PHENOTYPES IN THE CROSS AB/ab × AB/ab, BOTH PARENTS SHOWING CROSS-OVER, AT DIVERS VALUES

CO-%	AB	Ab	aB	ab/ab
0	75.00	0.00	0.00	25.00
1	74.50	0.50	0.50	24.50
2	74.01	0.99	0.99	24.01
3	73.52	1.48	1.48	23.52
4	73.04	1.96	1.96	23.04
5	72.56	2.44	2.44	22.56
6	72.09	2.91	2.91	22.09
7	71.62	3.38	3.38	21.62
8	71.16	3.84	3.84	21.16
9	70.70	4.30	4.30	20.70
10	70.25	4.75	4.75	20.25
11	69.80	5.20	5.20	19.80
12	69.36	5.64	5.64	19.36
13	68.92	6.08	6.08	18.92
14	68.49	6.51	6.51	18.49
15	68.06	6.94	6.94	18.06
16	67.64	7.36	7.36	17.64
17	67.22	7.78	7.78	17.22
18	66.81	8.19	8.19	16.81
19	66.40	8.60	8.60	16.40
20	66.00	9.00	9.00	16.00
21	65.60	9.40	9.40	15.60
22	65.21	9.79	9.79	15.21
23	64.82	10.18	10.18	14.82
24	64.44	10.56	10.56	14.44
25	64.06	10.94	10.94	14.06
26	63.69	11.31	11.31	13.69
27	63.32	11.68	11.68	13.32
28	62.96	12.04	12.04	12.96
29	62.60	12.40	12.40	12.60
30	62.25	12.75	12.75	12.25
31	61.90	13.10	13.10	11.90
32	61.56	13.44	13.44	11.56
33	61.22	13.78	13.78	11.22
34	60.89	14.11	14.11	10.89
35	60.56	14.44	14.44	10.56
36	60.24	14.76	14.76	10.24
37	59.92	15.08	15.08	9.92
38	59.61	15.39	15.39	9.61
39	59.30	15.70	15.70	9.30
40	59.00	16.00	16.00	9.00
41	58.70	16.30	16.30	8.70
42	58.41	16.59	16.59	8.41
43	58.12	16.88	16.88	8.12
44	57.84	17.16	17.16	7.84
45	57.56	17.44	17.44	7.56
46	57.29	17.71	17.71	7.29
47	57.02	17.98	17.98	7.02
48	56.76	18.24	18.24	6.76
49	56.50	18.50	18.50	6.50
50	56.25	18.75	18.75	6.25

TABLE III. SEGREGATION OF PHENOTYPES IN THE CROSS Ab/aB × Ab/aB, BOTH PARENTS SHOWING CROSS-OVER, AT DIVERS VALUES

CO-%	AB	Ab	aB	ab/ab
0	50.00	25.00	25.00	0.00
1	50.002	24.998	24.998	0.002
2	50.01	24.99	24.99	0.01
3	50.02	24.98	24.98	0.02
4	50.04	24.96	24.96	0.04
5	50.06	24.94	24.94	0.06
6	50.09	24.91	24.91	0.09
7	50.12	24.88	24.88	0.12
8	50.16	24.84	24.84	0.16
9	50.20	24.80	24.80	0.20
10	50.25	24.75	24.75	0.25
11	50.30	24.70	24.70	0.30
12	50.36	24.64	24.64	0.36
13	50.42	24.58	24.58	0.42
14	50.49	24.51	24.51	0.49
15	50.56	24.44	24.44	0.56
16	50.64	24.36	24.36	0.64
17	50.72	24.28	24 28	0.72
18	50.81	24.19	24.19	0.81
19	50.90	24.10	24.10	0.90
20	51.00	24.00	24.00	1.00
21	51.10	23.90	23.90	1.10
22	51.21	23.79	23.79	1.21
23	51.32	23.68	23.68	1.32
24	51.44	23.56	23.56	1.44
25	51.56	23.44	23.44	1.56
26	51.69	23.31	23.31	1.69
27	51.82	23.18	23.18	1.82
28	51.96	23.04	23.04	1.96
29	52.10	22.90	22.90	2.10
30	52.25	22.75	22.75	2.25
31	52.40	22.60	22.60	2.40
32	52.56	22.44	22.44	2.56
33	52.72	22.28	22.28	2.72
34	52.89	22.11	22.11	2.89
35	53.06	21.94	21.94	3.06
36	53.24	21.76	21.76	3.24
37	53.42	21.58	21.58	3.42
38	53.61	21.39	21.39	3.61
39	53.80	21.20	21.20	3.80
40	54.00	21.00	21.00	4.00
41	54.20	20.80	20.80	4.20
42	54.41	20.59	20.59	4.41
43	54.62	20.38	20.38	4.62
44	54.84	20.16	20.16	4.84
45	55.06	19.94	19.94	5.06
46	55 29	19.71	19.71	5.29
47	55.52	19.48	19.48	5.52
48	55.76	19.24	19.24	5.76
49	56.00	19.00	19.00	6.00
50	56.25	18.75	18.75	6.25

TABLE IV. SEGREGATION OF PHENOTYPES IN THE CROSS AB/ab × Ab/aB, BOTH PARENTS SHOWING CROSSING-OVER, AT DIVERS VALUES

CO-%	AB	Ab	aB	ab/ab
0	50.00	25.00	25.00	0.00
1	50.25	24.75	24.75	0.25
2	50.49	24.51	24.51	0.49
3	50.73	24.27	24.27	0.73
4	50.96	24.04	24.04	0.96
5	51.19	23.81	23.81	1.19
6	51.41	23.59	23.59	1.41
7	51.63	23.37	23.37	1.63
8	51.84	23.16	23.16	1.84
9	52.05	22.95	22.95	2.05
10	52.25	22.75	22.75	2.25
11	52.45	22.55	22.55	2.45
12	52.64	22.36	22.36	2.64
13	52.83	22.17	22.17	2.83
14	53.01	21.99	21.99	3.01
15	53.19	21.81	21.81	3.19
16	53.36	21.64	21.64	3.36
17	53.53	21.47	21.47	3.53
18	53.69	21.31	21.31	3.69
19	53.85	21.15	21.15	3.85
20	54.00	21.00	21.00	4.00
21	54.15	20.85	20.85	4.15
22	54.29	20.71	20.71	4.29
23	54.43	20.57	20.57	4.43
24	54.56	20.44	20.44	4.56
25	54.69	20.31	20.31	4.69
26	54.81	20.19	20.19	4.81
27	54.93	20.07	20.07	4.93
28	55.04	19.96	19.96	5.04
29	55.15	19.85	19.85	5.15
30	55.25	19.75	19.75	5.25
31	55.35	19.65	19.65	5.35
32	55.44	19.56	19.56	5.44
33	55.53	19.47	19.47	5.53
34	55.61	19.39	19.39	5.61
35	55.69	19.31	19.31	5.69
36	55.76	19.24	19.24	5.76
37	55.83	19.17	19.17	5.83
38	55.89	19.11	19.11	5.89
39	55.95	19.05	19.05	5.95
40	56.00	19.00	19.00	6.00
41	56.05	18.95	18.95	6.05
42	56.09	18.91	18.91	6.09
43	56.13	18.87	18.87	6.13
44	56.16	18.84	18.84	6.16
45	56.19	18.81	18.81	6.19
46	56.21	18.79	18.79	6.21
47	56.23	18.77	18.77	6.23
48	56.24	18.76	18.76	6.24
49	56.247	18.752	18.752	6.247
50	56.25	18.75	18.75	6.25

TABLE V. CONSTANTS FOR RAPID DETERMINATION OF PERCENTAGES FOR GENOTYPIC CLASSES IN THE THREE CASES GIVEN ABOVE, AT DIVERS CROSS-OVER VALUES

NOTE: When two constants are given in a formula, add them; then divide by four, and point off in the quotient proper decimal places.

CO-%	x^2	$2x^2$	xy	2xy	y^2	$2y^2$
1	9801	19602	99	198	1	2
2	9604	19208	196	392	4	8
3	9409	18818	291	582	9	18
4	9216	18432	384	768	16	32
5	9025	18050	475	950	25	50
6	8836	17672	564	1128	36	72
7	8649	17298	651	1302	49	98
8	8464	16928	736	1472	64	128
9	8281	16562	819	1638	81	162
10	8100	16200	900	1800	100	200
11	7921	15842	979	1958	121	242
12	7744	15488	1056	2112	144	288
13	7569	15138	1131	2262	169	338
14	7396	14792	1204	2408	196	392
15	7225	14450	1275	2550	225	450
16	7056	14112	1344	2688	256	512
17	6889	13778	1411	2822	289	578
18	6724	13448	1476	2952	324	648
19	6561	13122	1539	3078	361	722
20	6400	12800	1600	3200	400	800
21	6241	12482	1659	3318	441	882
22	6084	12168	1716	3432	484	968
23	5929	11858	1771	3542	529	1058
24	5776	11552	1824	3648	576	1152
25	5625	11250	1875	3750	625	1250
26	5476	10952	1924	3848	676	1352
27	5329	10658	1971	3942	729	1458
28	5184	10368	2016	4032	784	1568
29	5041	10082	2059	4118	841	1682
30	4900	9800	2100	4200	900	1800
31	4761	9522	2139	4278	961	1922
32	4624	9248	2176	4352	1024	2048
33	4489	8978	2211	4422	1089	2178
34	4356	8712	2244	4488	1156	2312
35	4225	8450	2275	4550	1225	2450
36	4096	8192	2304	4608	1296	2592
37	3969	7938	2331	4662	1369	2738
38	3844	7688	2356	4712	1444	2888
39	3721	7442	2379	4758	1521	3042
40	3600	7200	2400	4800	1600	3200
41	3481	6962	2419	4838	1681	3362
42	3364	6728	2436	4872	1764	3528
43	3249	6498	2451	4902	1849	3698
44	3136	6272	2464	4928	1936	3872
45	3025	6050	2475	4950	2025	4050
46	2916	5832	2484	4968	2116	4232
47	2809	5618	2491	4982	2209	4418
48	2704	5408	2496	4992	2304	4608
49	2601	5202	2499	4998	2401	4802