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THE INHERITANCE OF HULL-LESSNESS IN OAT HYBRIDS[1]

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THE purpose of this paper is to set forth some results obtained in certain crosses between the hull-less types of oats and some of the hulled forms.

The hull-less types belong to the species *Avena nuda*. The origin of these forms is not definitely known, although, according to Carleton,[2] they appear to have come from central and eastern Asia. Reports are to the effect that a certain form of this oat has been cultivated in China for a thousand years or longer. These types are not generally cultivated in any other countries and perhaps due to this fact little study has been made of the various hull-less types and their possible origin. From some observations made on our material it seems quite possible that these hull-less forms may have originated through mutative changes. For example, in a pure line of the variety Sixty Day certain spikelets suddenly appeared which were very similar to the true hull-less forms in having the caryopsis loosely held in the glumes and an increased number of flowers per spikelet. These seeds were tested, but did not reproduce this hull-less tendency. A large number of similar cases have been observed particularly with hybrids, although none of these

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[1] Paper No. 68, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

[2] "The Small Grains," 1916.

has been tested as to its inheritance as yet, but it is planned to do so.

Trabut[3] says in regard to the possible origin of hull-less oats that "the study of the domestication of Avena presents, from the genetic point of view, some rather substantial arguments in favor of an ambient medium, a modifying agent causing fluctuations which end in the formation of varieties well characterized and fixed by selection."

PREVIOUS WORK

A number of investigators have studied hybrids between varieties of *Avena nuda* and *Avena sativa*. Norton[4] was the first investigator in America to hybridize these forms. He reports that

> the spikelet of the naked varieties usually has more than three grains, while in the hulled types three grains is the limit. The first generation plants produced a head naked at the top and hulled at the bottom. In the second generation, one fourth of the progeny were typical naked plants, one fourth were hulled, and one half like the first generation hybrids. The naked plants all had long spikelets with more than three grains, while the hulled plants had spikelets with the usual two or three grains. In future generations no exception to this rule has been found except that one second generation plant of a cross between European Hull-less and Garton's Tartar King which seems to have become fixed in the intermediate hybrid type. In this example we have an extremely rare case of the fixation of a heterozygote or hybrid type.

Gaines[5] reports having made some hybrids between hulled and hull-less oats and first separated the F_2 types into two groups, hulled and hull-less. In making such a grouping the heterozygous types were put into the group which it resembled most. He obtained from one cross 48.7 per cent. hulled and 51.3 per cent. hull-less plants and says, "this indicates an intermediate about half-way between hulled and hull-less for the heterozygous types. As was mentioned above, the separation was made arbitrarily into hulled and hull-less, according to the type any given plant most nearly resembled."

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[3] *Journal of Heredity*, Vol. 5, p. 84, 1914. Translation of original paper.

[4] American Breeders' Association, Vol. III, p. 285, 1907.

[5] Washington Agr. Expt. Sta. Bul. 135, p. 58, 1917.

In another cross Gaines found 77.1 per cent. hulled to 22.9 per cent. hull-less, which caused him to conclude that the two crosses were not similar in their behavior. This would seem to be the case from the data at hand, yet in 1914 Gaines made a number of other crosses, among which according to the pedigree numbers is another one between these two sorts, Black (Wash. No. 665) and Hulless (Wash. No. 680) which gave, this time, results very similar to all the other crosses reported as made that year, which indicated a 1:2:1 ratio. Gaines did not offer any explanation as to the different behavior of these two crosses between the same two sorts.

From these experiments Gaines concludes,

> the percentage of hulled type suggests a simple Mendelian recessive although in every case there are a few too many hulled plants. The percentage of hull-less plants is not only very irregular in the different crosses but is also irregular in the different families within the same cross with the exception of the two families of Sixty Day × Hull-less, which gave a ratio approaching 1:2:1. The intermediate types showed great variation. Plants could be found with only one or two spikelets that showed the hull-less character. Others could be found that showed the hulled character in only one or two spikelets, and plants were obtained with every degree of hull-lessness between these extremes. However, most of the intermediates produced more than half hulled oats. A curve fitted to these intermediate variations in Black Tartarian × Hull-less shows larger numbers at either extreme and few numbers showing per cents. of hulled oats ranging from 30 to 50. This is just the opposite of what we would expect if the hull-less character was caused by a single Mendelian unit which produced an intermediate in the F_1.

In a paper by Zinn and Surface[6] results are given of a cross between a hull-less and hulled oat. The sorts used were *Avena sativa patula* var. Victor, and *Avena sativa nuda* var. *inermis*. The results indicate that their forms agree very closely with those reported by Norton and Gaines. The following paragraph gives part of their conclusions.

> The F_1 generation is distinctly intermediate in most characters. In regard to the glumes, both naked and firmly hulled grain as well as intermediate forms are found on the same panicle and even in the same

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[6] *Journal of Agricultural Research*, Vol. X, No. 6, pp. 310–311, 1917.

spikelet. As shown in Table I, the spikelets near the top of the panicle are either entirely naked or nearly so, while those spikelets near the base of the panicle tend to be firmly hulled. A similar but less marked relation is to be observed between the spikelets at the tip and base of each whorl.

In the F_2 generation a large number of intermediate forms appear. In addition to the two parental hull types, four intermediate classes were distinguished. These intermediate forms contain all gradations from the plants with perfectly hulled grain to the perfectly naked forms.

As shown in Table II, the inheritance of the hull characters presents a simple Mendelian relation giving 1 hulled, 2 intermediate, 1 naked. Likewise, in respect to grain color, there are 3 black plants to 1 white, in the second generation.

Material and Methods

In connection with some experiments in oat breeding a number of hybrids between the hulled and hull-less forms have been made. While in these crosses the inheritance of other characters such as color of glumes, pubescence, awns and the like, are very interesting, the present paper will be confined to the discussion of the inheritance of the hull-less and hulled characteristics. A more complete discussion of the various characters is being prepared for a later publication.

The authors want to take this opportunity to express their appreciation for the valuable assistance in note-taking and tabulation of results rendered by W. T. Craig and Miss A. M. Atwater. Their work has been of great aid in conducting these experiments.

The hull-less oat used for the various hybrids was typical of the *Avena nuda* group and differs from the *Avena sativa* forms by three important characters: (1) The lemma, or flowering glume, and palet do not clasp the kernel as in other forms, and the kernel is therefore loose, or free, within the hull; (2) The rachillæ of the three to many-grained spikelet are so elongated that the uppermost grains are borne above the empty glumes; (3) The glumes and the lemmas are similar in texture. The illustration (Fig. 1) will give a fair idea of the par-

FIG. 1. THE FEMALE PARENT (*Avena nuda*) USED IN SERIES 382.

ticular characteristics which separate *Avena nuda* from the hulled species. This type is typical of the hull-less forms used in the following hybrids.

The hulled forms were all varieties of *Avena sativa* with one exception. In this case *Avena fatua* was used

Fig. 2. The Male Parent (*Avena sativa*) Used in Series 382.

as the hulled parent. Fig. 2 shows the hulled variety, Sixty Day, used in one of the crosses. It is typical of a hulled oat.

The first crosses of this sort were made in 1910 and the F_1 plants grown in the greenhouse the following winter. The first cross was between Hulless and Black Tartarian. Here the hull-less form was used as the female parent. The male parent possessed, as indicated by its name, black glumes, and was a typical hulled oat. The other cross was between Danish Island and Hulless in which the hulled type was used as the female parent. In each case the F_1 type was typical of the F_1 types as described by the authors mentioned above. This form is intermediate in that both kinds of kernels, hulled and hull-less, are found on the same head. The type of panicle resembles the hull-less parent more than it does the hulled and may be considered as intermediate in type. There are some spikelets with hulled and some with hull-less kernels and also some with both hulled and hull-less kernels. As a usual thing the hulled spikelets occur towards the base of the panicle while the hull-less kernels occur near the terminal spikelet which is almost invariably hull-less if such kernels are present at all in the panicle.

There are fewer hulled than hull-less kernels on the F_1 types. The percentage of hulled kernels does not usually run very high. In Fig. 3 is shown a typical form of F_1 panicle of a cross between a hulled and hull-less oat.

The F_2 generation of these two crosses were grown in the field in the summer of 1913. The plants were then sorted into two groups, hulled and hull-less, or hull-less like. All those plants having any indication of hull-lessness were placed in the hull-less class. The result of these counts was as follows:

Series Number	Varieties Crossed	Hull-less	Hulled
111	Hulless × Black Tartarian	129	37
51	Danish Island × Hulless	364	93
		493	130

Although the ratio deviates considerably from 3:1 it indicates that this character behaves as a simple monohybrid and that there is one factor pair concerned. In

FIG. 3. F_1 INTERMEDIATE TYPE OF A CROSS BETWEEN HULL-LESS AND HULLED. Series 382.

order to test this out more fully all plants from which good seed could be obtained were grown in the following year. The results obtained from these plants showed without doubt that the segregation followed a simple monohybrid ratio. That is, the pure hulled and hull-less plants bred true to these characteristics, while the intermediate types reproduced the three types again. The second generation plants tested as to their composition gave the following results in the third generation:

Series Number	Varieties Crossed	Pure Hulled	Inter-mediate	Pure Hull-less
111	Hulless × Black Tartarian	37	85	38
51	Danish Island × Hulless	115	216	114
		152	301	152

It is apparent from these results that certain plants were classed as intermediate in the second generation, which were in reality pure hulled plants. It is evident that the hulled-hull-less character is inherited in a simple Mendelian fashion so far as its general behavior is considered.

The heterozygous plants produced in the third generation were examined as to the relative amounts of hulled and hull-less kernels present. This was done by threshing a representative head from each plant by hand and counting the hulled and naked kernels and expressing the result as the percentage of hulled kernels.

In order to determine whether the results from a single head fairly represented the type of the plant a number of plants were examined and recorded a head at a time. The percentage of hulled kernels for a representative head was then compared with that for the entire plant. The average percentage was the same for the results from single heads as it was for the entire plant. Although there was some deviation in the individual determinations, the correlation between the two methods is very high.

The result of determining the percentage of hulled kernels was to indicate the great variation existing, which was from a very low to a very high percentage. As a result of these observations it was apparent that while in the hybrids under consideration the usual 1:2:1 ratio was observed, some factor or factors were present which affected the heterozygous forms in such a way as to modify the amount of hulled or hull-less kernels present.

In order to determine this effect in a more definite way it was planned to sow seed from heterozygous individuals which differed as to the percentage of hulled kernels present. A rather large number of such seeds were planted in 1915. The plants were severely injured by a storm, so that accurate percentage determinations could not be made.

In the meantime, however, a number of other crosses had been made in which the *Avena nuda* was used as one parent. The following sorts were crossed with the naked oats: Swedish Select, Sixty Day and *Avena fatua*. Other crosses are being studied but these will be reported on later.

As regards the hull-less character the F_1 individuals of these crosses were all similar to the description of the first generation given earlier in this paper. Regarding the other characters, the cross between the hull-less form and *Avena fatua* showed some very interesting variations. These will not now be discussed.

Seeds of these various F_1 plants were sown and the resulting plants harvested. From each plant a head was saved and threshed separately by hand and the plants then sorted into hulled, intermediate and hull-less. The result of the several crosses is given here:

Series Number.	Varieties Crossed	Hulled	Intermediate	Hull-less
379	Hulless × *Avena fatua*	68	111	78
202	Hulless × Swedish Select	41	90	36
382	Hulless × Sixty Day	75	193	53
	Observed	184	394	168
	Expected	186.5	373	186.5

The probable error is ±7.98 and the observed numbers agree fairly well with the expected numbers. The number of hull-less plants is too low and the number of intermediates too high. It is possible that in some cases

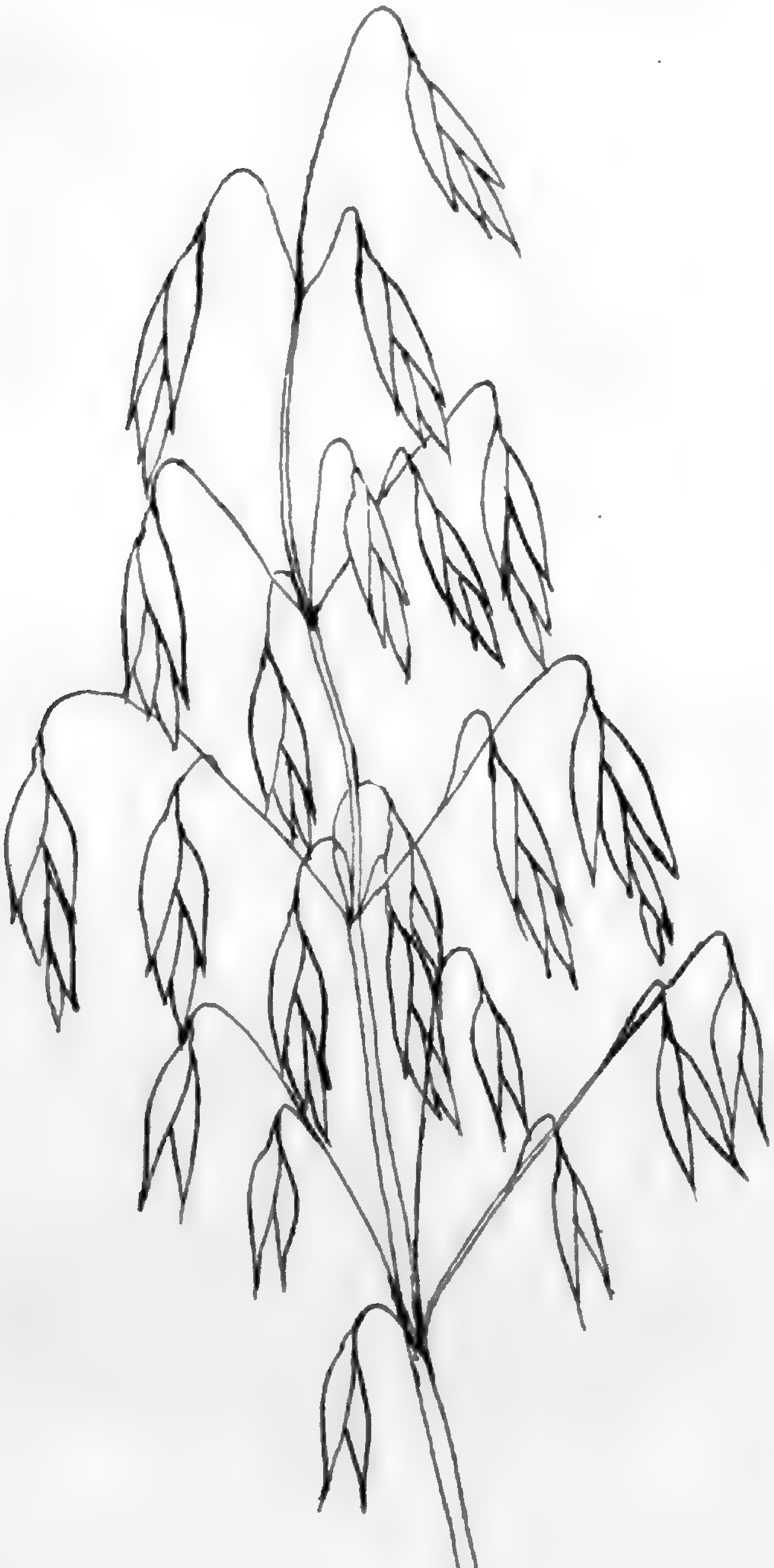

FIG. 4. HETEROZYGOUS TYPE F_4 POSSESSING 10 PER CENT. OF HULLED KERNELS. Series 382.

hull-less plants may have been recorded as intermediates although the error from this source is not large. When the results are considered on a 1:3 basis and the hull-less and intermediates are grouped together we find that there is a percentage of 24.66 ± 1.07 hulled plants.

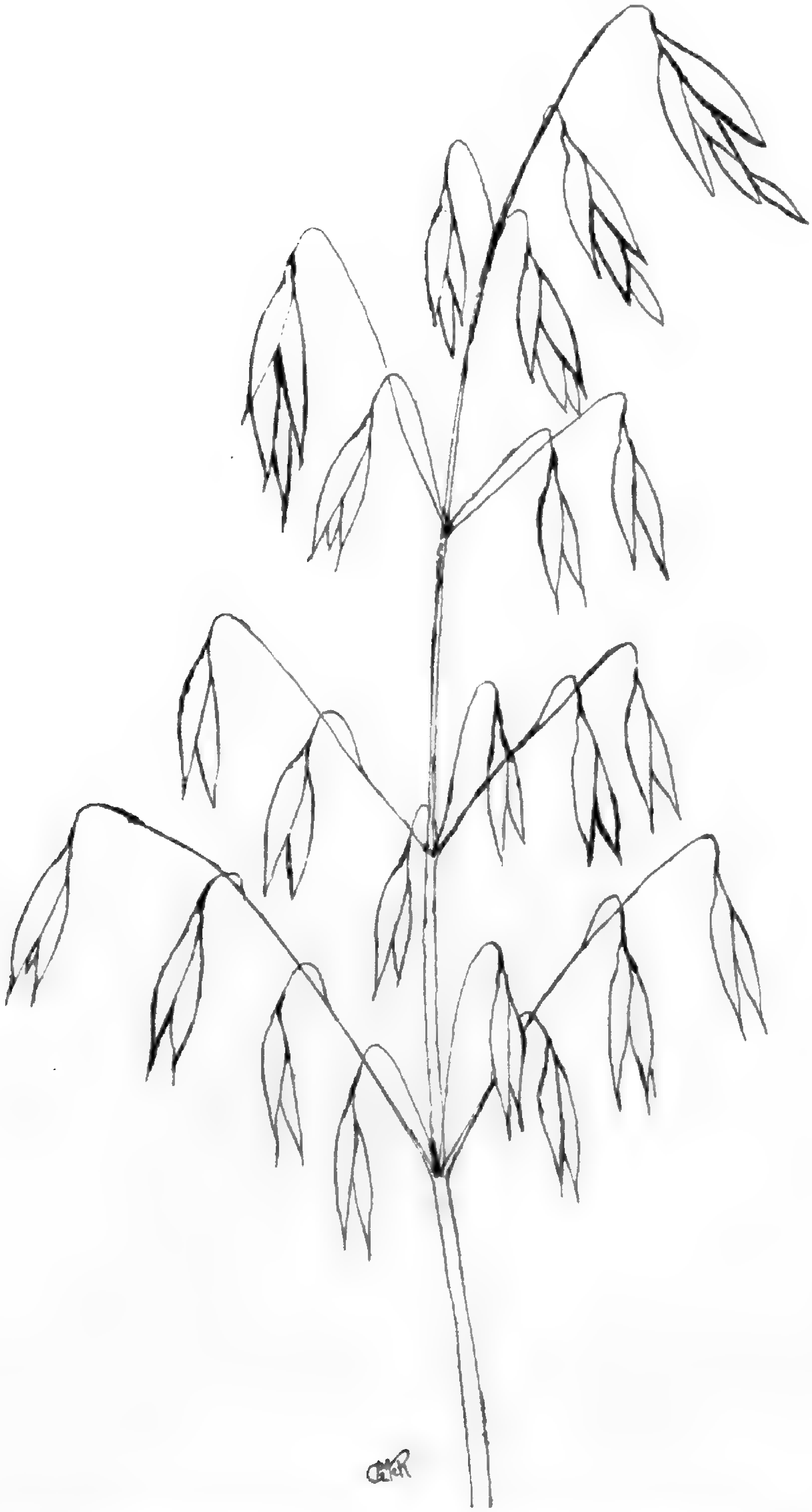

FIG. 5. HETEROZYGOUS TYPE F_4 POSSESSING 87.9 PER CENT. OF HULLED KERNELS. Series 382.

The results of these different hybrids show that hull-lessness is inherited in a simple monohybrid manner and that without doubt the difference between hulled and hull-less oats in this regard is represented by one pair of factors. An analysis of the different heterozygous or intermediate individuals of these second generation plants showed that for these hybrids also there was a great amount of variation in the percentage of hulled or hull-less kernels in the individual plants, the variation ranging all the way from less than 5 per cent. to 95 per cent. or more. In Figs. 4 and 5 are shown two forms of heterozygous plants, one very low and one very high, in percentage of hulled kernels. These percentages were obtained from the heterozygous individuals by sorting the kernels from one head of each plant into hulled and hull-less as outlined earlier. The percentage of hulled kernels on the heterozygous plants of the second generation for the three series is given in Table I.

TABLE I

SHOWING PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PLANTS OF THE SECOND GENERATION IN CROSSES BETWEEN HULLED AND HULL-LESS OATS.

Series Number	Varieties Crossed	Percentage of Hulled																			
		2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5	87.5	92.5	97.5
379	Hulless × *Avena fatua*		2	3	5	4	4	3	4	4	7	5	5	8	4	6	5	7	10	13	15
202	Hulless × Swedish Select	10	4	4	3	5	8	2	1	7	6	3	4	2	5	3	3	6	3	4	6
382	Hulless × Sixty Day	5	5	5	4	4	6	6	8	20	15	22	21	15	13	17	11	7	4	4	1
		15	11	12	12	13	18	11	13	31	28	30	30	25	22	26	19	20	17	21	22

From this table it is seen that there is considerable difference in the percentage of hulled kernels on the different heterozygous plant. The range is from a very low percentage or one which indicates nearly all hull-less to a very high percentage or one which is nearly all hulled. There is no general grouping near the middle of the series, as might be expected with the exception of series 382. This may be due to lack of numbers or to a segregation of the different types which give percentages ranging from low to high without any tendency to grouping. That it is not due to lack of numbers is probably borne out by the fact that in series 51, where over 900 plants of the third generation were sorted into the different classes, there was no indication of a grouping near the middle classes, in fact, the slight indication of grouping was near the lower values. The distribution is as follows:

TABLE II

Showing Percentage of Hulled Kernels in the Heterozygous Plants of the Third Generation in a Cross Between Danish Island and a Hull-less Oat.

Percentage of Hulled Kernels	Frequency	Percentage of Hulled Kernels	Frequency
0 – 4.9	89	50.0 – 54.9	42
5.0 – 9.9	80	55.0 – 59.9	48
10.0 – 14.9	60	60.0 – 64.9	43
15.0 – 19.9	49	65.0 – 69.9	26
20.0 – 24.9	59	70.0 – 74.9	35
25.0 – 29.9	48	75.0 – 79.9	33
30.0 – 34.9	47	80.0 – 84.9	32
35.0 – 39.9	53	85.0 – 89.9	26
40.0 – 44.9	52	90.0 – 94.9	21
45.0 – 49.9	46	95.0 – 99.9	15

It was planned to carry some of this work further to answer in general two questions which are: (1) Does the percentage of hulled plants obtained from any heterozygous parent vary with the percentage of hulled kernels possessed by that parent? (2) Do the hulled and hull-less kernels of a heterozygous plant give approximately the same results in their offspring?

In order to obtain data on these questions two of the series have been continued. The hull-less-*Avena fatua* series has not been carried further as yet but it is planned to do so.

Results from Series 202—Swedish Select × Hulless

The first series to be discussed is the Swedish Select-Hull-less cross. Seed from two hulled and two hull-less plants of the second generation were grown in the third generation and each bred true to type. In addition to these plants twenty heterozygous plants were selected for planting. These varied as to the amount of hulled kernels. The range was from 3.2 per cent. to 92.0 per cent. The number of seed was not large, therefore the number of plants obtained was not as large as desired, yet from the consistency of the results certain conclusions are justified. The offspring from these twenty plants were sorted into the three classes, hulled, intermediate and hull-less. The intermediate plants were again threshed and the percentage of hulled kernels determined.

In Table III is given the percentage of hulled condition in the parent plant, the segregation into the three groups, the percentage of hulled kernels in the heterozygous offspring, the grouping into hulled and hull-less and (where both hull-less and intermediate plants are grouped together) the percentage of hulled plants with the probable error.

TABLE III

SHOWING SEGREGATION IN F_3 OF CERTAIN F_2 PLANTS TOGETHER WITH THE PERCENTAGE OF HULLED SEED IN PARENT TYPE AND THE AVERAGE PERCENTAGE IN THE HETEROZYGOUS OFFSPRING.

	Segregation Obtained from Plants Sown and Resulting Percentage of Hulled Kernels on Intermediate Forms.							
	Per Cent. of Hulled Kernels in Plants Sown	Hulled	Intermediate	Hull-less	Per Cent. Hulled in Intermediate Offspring	Hulled	Hull-less and Intermediate	Per Cent. Hulled and P. E.
202al–4...	44.9	27	63	22	44.8	27	85	24.11 ± 2.76
6...	25.0	34	51	40	21.0	34	91	27.20 ± 2.61
9...	20.9	27	35	60	12.8	27	95	22.13 ± 2.64
10...	83.0	42	63	34	39.5	42	97	30.22 ± 2.48
11...	92.0	42	62	17	52.6	42	79	34.71 ± 2.65
22...	65.1	13	36	7	60.6	13	43	23.21 ± 3.90
25...	90.3	14	36	9	55.3	14	45	23.73 ± 3.80
26...	76.6	14	37	21	56.3	14	58	19.44 ± 3.44
29...	30.7	12	19	15	44.1	12	34	26.09 ± 4.31
31...	56.8	16	43	21	47.6	16	64	20.00 ± 3.27
38...	10.5	21	26	40	22.3	21	66	24.14 ± 3.13
40...	82.4	19	33	19	53.6	19	52	26.76 ± 3.47
46...	16.7	14	20	22	24.7	14	42	25.00 ± 3.90
51...	56.6	25	41	10	47.1	25	51	32.89 ± 3.35
60...	74.3	7	10	4	46.0	7	14	33.33 ± 6.37
66...	3.2	10	26	32	22.7	10	58	14.71 ± 3.54
77...	65.4	15	21	14	34.9	15	35	30.00 ± 4.13
92...	35.3	12	10	8	36.0	12	18	40.00 ± 5.33
120...	44.7	14	18	8	33.9	14	26	35.00 ± 4.62
121...	9.5	13	11	23	20.2	13	34	27.66 ± 4.26
Totals......		391	661	426		391	1087	26.45 ± .76
Expected....		369.5	739	369.5				

The results of the segregation into the three classes gave 391 hulled, 661 intermediate and 426 hull-less. Here the hull-less plants are too great in number, while the number in the intermediate class is too small. The expected numbers are 369.5:739:369.5, with a probable error of ± 11.23. It is possible that some intermediate plants were classed as hull-less. Such a condition is possible since some intermediates are found bearing only one or two hulled kernels, and if these should be lost through shattering, such plants would be classed as hull-less when in reality they are intermediates. When the grouping is made into the two groups, hulled and hull-less, it is seen that the 3 to 1 ratio is approximated very closely, as there are 391 hulled plants to 1087 hull-less, giving a percentage of 26.45 ± .76 hulled.

An examination of this table shows further that some of the families do not give ratios close to 1:2:1. This is true with regard to certain families particularly with certain of those coming from plants low in percentage of hulled, and some of those relatively high in this respect. The results of some of these families have been brought together in Table IV.

TABLE IV

SHOWING SEGREGATION OF OFFSPRING COMING FROM SOME INDIVIDUALS LOW OR HIGH IN THE PERCENTAGE OF HULLED KERNELS.

Family Number	Percentage of Hulled Seed in Plants Sown	Segregation of Offspring Into Different Types.		
		Hulled	Intermediate	Hull-less
6	25.	34	51	40
9	20.9	27	35	60
38	10.5	21	26	40
46	16.7	14	20	22
66	3.2	10	26	32
121	9.5	13	11	23
	Total..........	119	169	217
10	83.	42	63	34
11	92.	42	62	17
25	90.3	14	36	9
26	76.6	14	37	21
40	82.4	19	33	19
	Total..........	131	231	100

In this table the plants from parents having 25 or less per cent. of hulled kernels give 119 hulled: 169 intermediate: 217 hull-less. From this result it appears that those plants having a low percentage of hulled or high percentage of hull-less kernels tend to produce a relatively high number of hull-less plants. On the other hand, those plants having more than 75 per cent. of hulled kernels do not give results so striking. There are more hulled than hull-less plants, yet not strikingly so, and the hulled do not run higher than the intermediates. It may be, however, that the degree of hull-lessness as expressed by the percentage may influence the segregation in the following generations. This can not be definitely stated from this cross, and further evidence will be needed.

TABLE V

SHOWING THE RELATION BETWEEN THE PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PARENT PLANTS AND THE PERCENTAGE OF HULLED KERNELS ON ITS OFFSPRING

Percentage of Hulled Oats on Plants Sown	Percentage of Hulled Oats on Offspring																				
	0–4.9	5.0–9.9	10.0–14.9	15.0–19.9	20.0–24.9	25.0–29.9	30.0–34.9	3.50–39.9	40.0–44.9	45.0–49.9	50.0–54.9	55.0–59.9	60.0–64.9	65.0–69.9	70.0–74.9	75.0–79.9	80.0–84.9	85.0–89.9	90.0–94.9	95.0–99.9	
3.2	12	3		3	1	1				1		1			1	1		1	1		26
9.5	1	1	2	2	2	1		1	1												11
10.5		5	2	3	6	6	1	1	1		1										26
16.7	2	3		3	4	2	1	2		2				1							20
20.9	9	10	7	4		1	2			1	1										35
25.0	5	12	4	6	5	2	9	2	4	1			1								51
30.7	1	1		1		1	2	2	2	2	1	1	1	1	2	1					19
35.3		2		1	1	1	1	1	1						1				1		10
44.7	1	1	1		2	4	3				3	2	1								18
44.9	4	3	6		3	1	6	3	2	3	4	7	7	6	0	6	2				63
56.6	1	3	1	1	3		3	2	6	3	3	2	3	3	1	2	2	1		1	41
56.8			5	1	1	4	3	2	2	4	2	5	6	2		3	2	1			43
65.1	2	3									6	4	2	4	2	6	4	1	2		36
65.4	1	5	1	1	1	4			2	1			1		1		1	1	1		21
74.3	1	1		1			1			1	1		1	1			1	1			10
76.6			1	2	3	2	1	1	1	3	4	5		1	1	1	6	4		1	37
82.4			1	1	2		2	3	3	4	3	3	1	1	2	2	2	1	2		33
83.0	5	1	2	8	4	5	2	7	5	2	5	3	3	5	2	1	2		1		63
90.3	4	2	2			1				3		3	1	7	1	5	3	3	1		36
92.0	1	4	2	1	3	3	2	3	2	5	5	6	4	2	4	4	7	1	3		62
	50	60	37	39	41	39	39	30	32	36	39	42	32	34	18	32	32	15	12	2	661

The relation between the percentage of hulled kernels on the parent and the percentage of hulled kernels on the heterozygous offspring for this series is shown by the correlation table given above. The correlation coefficient is. 421 ± .022, which shows a very definite relation between the percentage of hulled in the parent and offspring.

This relation is also better shown by means of a curve (Fig. 6) in which the parents are represented by the dotted line beginning with the lowest and increasing to the highest value. On the same ordinate is plotted the average value for the heterozygous offspring, and to this line has been fitted a straight line whose equation is $y = 20.1999 + 1.9579x$.

Certain of these families show a decided grouping; for example that represented by 20.9 per cent. shows a decided tendency to be grouped in the lower classes, while that represented by 65.1 per cent., with five exceptions, shows a grouping around the higher classes.

RESULTS OF SERIES 382—SIXTY DAY × HULL-LESS

From the second generation of this cross six heterozygous plants were selected for further study. The results of three of these will be discussed here. These plants possessed different amounts of hulled kernels, which expressed in percentages were as follows, 73.3, 37.7, 49.3. Thus, there was one high, one low and one medium plant. The offspring of these gave the following results when grouped in the three classes:

	Hulled	Intermediate	Hull-less
382al–7......	23	55	20
8......	15	37	24
9......	53	105	49
	91	197	93

These figures agree very well with the expected 1:2:1 ratio. Single heads of the heterozygous plants of these three families were threshed and the percentage of hulled kernels per plant determined as before. The three families gave the following distribution:

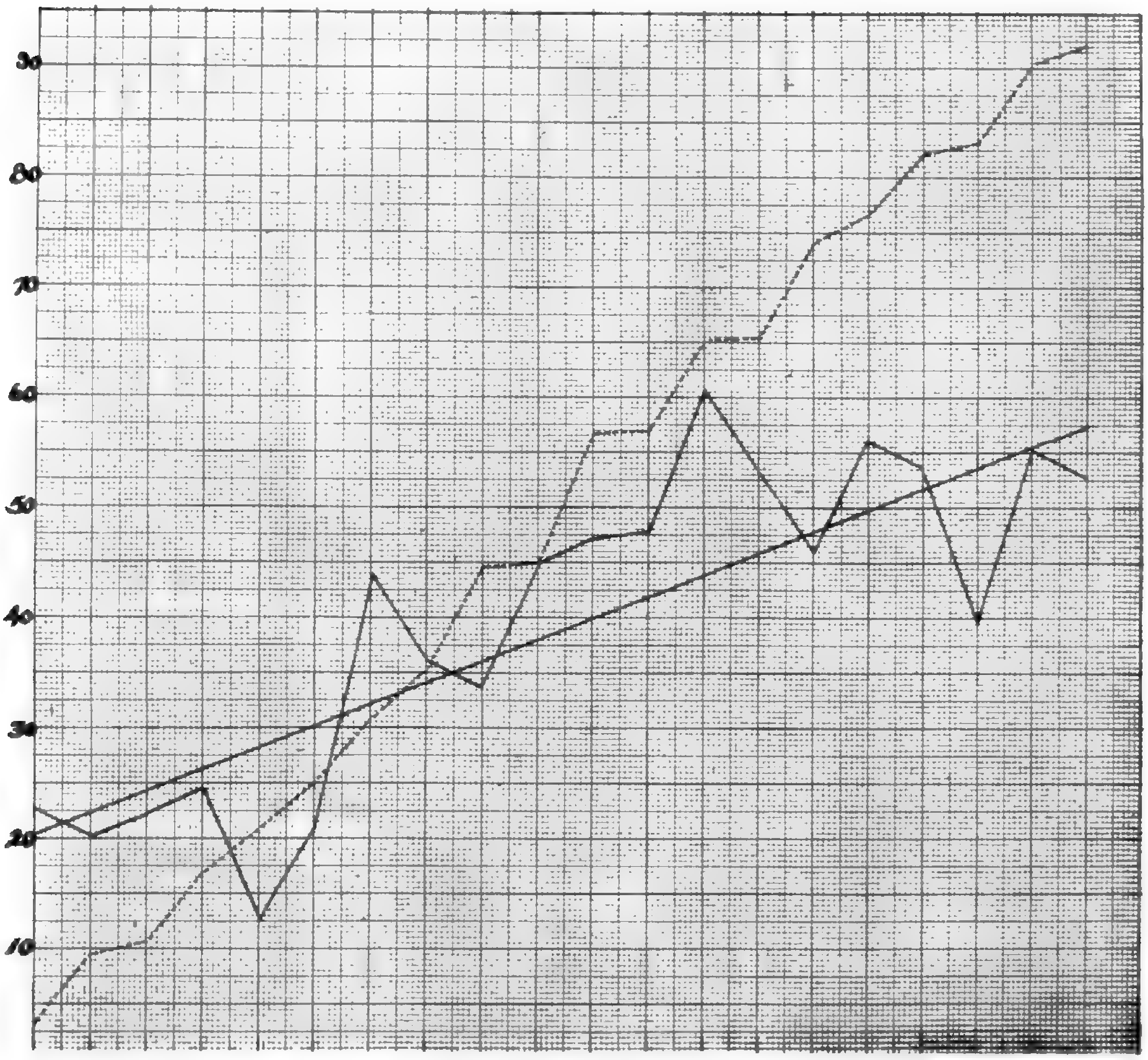

Fig. 6. These curves show the relation between the percentage of hulled grain on the heterozygous plant used as parent and the average percentage of hulled kernels on its heterozygous offspring. Dotted line represents the value for the parents and the solid line that of the heterozygous offspring. Series 202.

From these distributions it is clear that the percentage of hulled kernels on the parent form influences the amount of the hulled condition. The average percentage of the offspring in each case agrees closely with that of the parent forms.

From these three families several plants differing in their percentage values were selected to continue the study in the fourth generation. As observed from the frequency distribution just given it is noted that series 7 is of high value, while 8 is relatively low and 9 varies from very low to high. The plants selected then in general represented the types of their lines; that is, those from 7 were generally high, those from 8 generally low, and those from 9 both low and high. The offspring of these various selections are arranged in a table similar to that for series 202.

Series No.	Percentage Hulled Seed in Plants Sown	Percentage of Hulled in Offspring																				Totals	Average Per Cent. of Hulled Kernels on Offspring
		0–4.9	5.0–9.9	10.0–14.9	15.0–19.9	20.0–24.9	25.0–29.9	30.0–34.9	35.0–39.9	40.0–44.9	45.0–49.9	50.0–54.9	55.0–59.9	60.0–64.9	65.0–69.9	70.0–74.9	75.0–79.9	80.0–84.9	85.0–89.9	90.0–94.9	95.0–99.9		
382al–7	73.3					1				1	3	5	5	5	6	12	10	6	1			55	67.3
8	37.7	1	1	2	3	3	6	4	5	2	5	2	1	2								37	33.7
9	49.3	1	1	3	6	7	6	5	4	4	14	5	8	11	11	7	8	1	1	2		105	50.1
		2	2	5	9	11	12	9	9	7	22	12	14	18	17	19	18	7	2	2			

TABLE VI

SHOWING SEGREGATION IN F_4 OF CERTAIN F_3 PLANTS TOGETHER WITH THE PERCENTAGE OF HULLED SEED IN PARENT TYPE AND THE AVERAGE PERCENTAGE IN THE HETEROZYGOUS OFFSPRING

	Segregation Obtained from Plants Sown and Resulting Percentage of Hulled Kernels on Intermediate Forms.							
	Per Cent. of Hulled Kernels in Plants Sown	Hulled	Intermediate	Hull-less	Per Cent. Hulled in Intermediate Offspring	Hulled	Hull-less and Intermediate	Per Cent. Hulled and P. E.
382al-7-10. .	63.6	22	31	25	63.1	22	56	28.21 ± 3.31
11. .	53.0	24	34	10	46.0	24	44	35.29 ± 3.54
32. .	77.0	28	38	22	70.5	28	60	31.82 ± 3.11
33. .	70.3	21	53	26	62.7	21	79	21.00 ± 2.92
37. .	80.0	8	31	19	57.5	8	50	13.79 ± 3.84
45. .	81.7	13	27	13	75.1	13	40	24.53 ± 4.01
55. .	63.0	19	39	28	67.8	19	67	22.09 ± 3.15
8-14. .	43.6	26	34	19	37.6	26	53	32.91 ± 3.29
17. .	38.2	28	63	23	44.1	28	86	24.56 ± 2.74
22. .	23.2	15	36	14	25.3	15	50	23.08 ± 3.62
23. .	17.0	4	9	9	19.2	4	18	18.18 ± 6.23
28. .	60.8	12	30	13	49.8	12	43	21.82 ± 3.94
35. .	17.2	22	43	24	20.5	22	67	24.72 ± 3.10
61. .	59.6	13	27	11	50.6	13	38	25.49 ± 4.09
64. .	9.8	16	36	14	25.3	16	50	24.24 ± 3.60
9- 9. .	14.0	4	29	7	19.2	4	36	10.00 ± 4.62
44. .	62.4	24	50	15	49.1	24	65	26.97 ± 3.10
94. .	23.6	15	21	20	22.2	15	41	26.79 ± 3.90
166. .	79.7	16	27	22	81.2	16	49	24.62 ± 3.62
175. .	87.9	19	32	17	67.2	19	49	27.94 ± 3.54
Totals		349	690	351		349	1041	25.11 ± .78
Expected . . .		347.5	695	347.5		347.5	1042.5	

The total number of plants in the hulled, intermediate and hull-less classes agree very closely with the expected numbers. The same is true for the 3:1 grouping, since the percentage of hulled is 25.11 ± .78, which shows without doubt that the various families give offspring which follow the 1:2:1 expectancy.

In this series there is little evidence that the percentage condition of the parent plant affects the type of segregation in the following generation. In general the segregation of the various families follows a 1:2:1 ratio regardless of the percentage condition of the parent.

To show the relation between the hulled condition of the parent forms and that of the heterozygous offspring a correlation table was made in which the different families were arranged according to their percentage values. The coefficient of correlation here is .726 ± .012, which

TABLE VII

SHOWING THE RELATION BETWEEN THE PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PARENT PLANTS AND THE PERCENTAGE OF HULLED KERNELS ON ITS OFFSPRING

Percentage of Hulled Oats on Plants Sown	Percentage of Hulled Oats on Offspring																				
	0–4.9	5.0–9.9	10.0–14.9	15.0–19.9	20.0–24.9	25.0–29.9	30.0–34.9	35.0–39.9	40.0–44.9	45.0–49.9	50.0–54.9	55.0–59.9	60.0–64.9	65.0–69.9	70.0–74.9	75.0–79.9	80.0–84.9	85.0–89.9	90.0–94.9	95.0–99.9	
9.8	2	2	4	5	4	5	7	2	3	2											36
14.0	2	7	7	3	1	2	2	1	2	2											29
17.0	1		2	1	3	1	1														9
17.2	2	7	6	11	4	5	3	1	3					1							43
23.2	2	2	4	5	4	7	2	3	2												36
23.6	2			6	7	2	1	1			1										20
38.2					2	3	12	11	11	8	7	3	1	3						2	63
43.6			2		5	2	4	5	6	6	1	2	1								34
53.0		1	1	2	1	3		2	2	6	5	6	1	2	1		1				34
59.6						1		4	2	4	8	4	2	1	1						27
60.8				1		2	1	3	4	3	6	2	3	3	2						30
62.4	4	2	2	1			1	4	2	3	5	9	6	4	4	1			2		50
63.0	1						2			1	2	5	1	6	5	8	5	1	2		39
63.6				1			2	1	1	2	2	2	1	9	1	2	6	1			31
70.3						1	1	2	2		7	9	7	9	5	6	1	3			53
77.0			1				1			1		4	1	5	9	6	5	3	1		37
79.7								1		1	1			2	1	4	4	1	10	2	27
80.0	1	1				3			1	3	4	1	3	6	2	3	1	1		1	31
81.7											1		3	3	5	8	3	3	1		27
87.9				1				1		2	4	2	4	3	2	2	5	4	1		31
	17	22	29	37	31	35	45	41	42	46	54	49	34	57	38	40	31	17	17	5	687

is considerably higher than it was with the 202 series. One reason for this may be that perhaps there is a difference between this series and the former or that the result is caused by grouping the three families. When a correlation table is made for each of the three families separately, correlation coefficients of .296 ± .039, .623 ± .025 and .741 ± .024 are obtained. Thus it is seen that within any family correlation exists to a greater or less degree. Putting the three families in one table does increase the correlation somewhat over the average value for each alone. Another and possibly more plausible reason is the fact that these plants are of the fourth generation, while those of 202 are of the third.

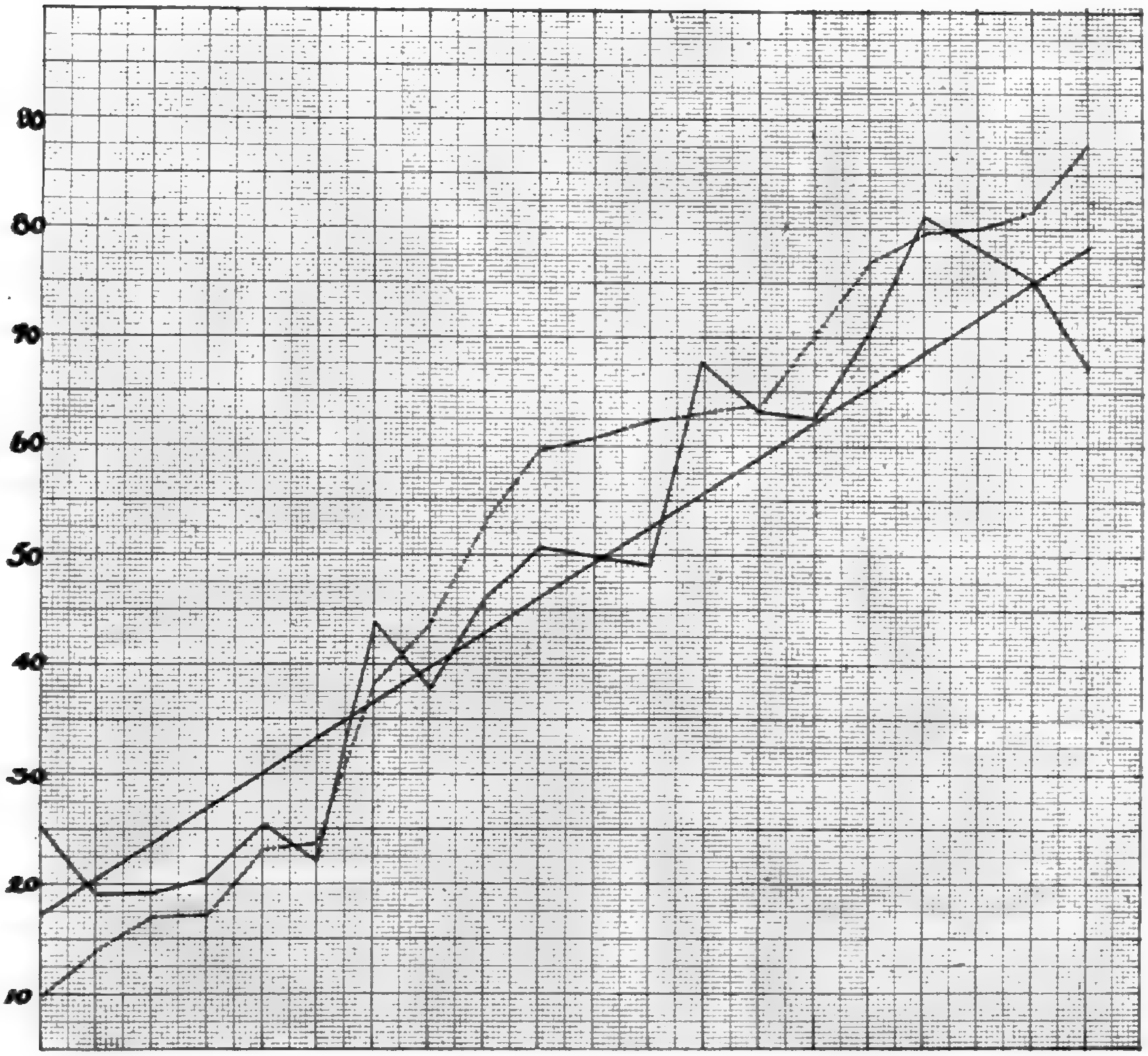

FIG. 7. These curves show the relation between the percentage of hulled grain on the heterozygous plant used as parent and the average percentage of hulled kernels on its heterozygous offspring. Dotted line represents the value for the parents and the solid line that of the hetrozygous offspring. Series 382.

The three parent series from which these were taken were of three types as mentioned before, therefore the parent plants selected from them carried the tendency to produce high or low as the case may be, and when they are all arranged in a correlation table naturally a high coefficient is obtained. In other words, the three parent forms were more nearly homozygous, so to speak, for high or low values. More will be said on this point later.

This relationship was further shown by means of a graph showing the relation between the parent percentage condition and the average value for the offspring, the same as was done in Fig. 7.

In this case the relationship is higher than in the former series. The equation to the straight line is $y = 17.2411 + 3.2062x$.

That the plants arising from heterozygous plants having a low or high percentage of hulled kernels did not segregate in a manner indicating any influence of the hulled condition of the parent plant, as was the case to some extent with series 202, is shown in Table VIII.

TABLE VIII

SEGREGATION OBTAINED WHEN SOWING SEED FROM HETEROZYGOUS PLANTS HAVING LOW OR HIGH PERCENTAGES OF HULLED SEED

Percentage of Hulled Kernels in Plants Sown	Segregation of Offspring Into Different Types		
	Hulled	Intermediate	Hull-less
9.8	16	34	14
14.0	4	29	7
17.0	4	9	9
17.2	22	43	24
23.2	15	36	14
23.6	15	21	20
	76	172	88
77.0	28	38	22
79.7	16	27	22
80.0	8	31	19
81.7	13	27	13
87.9	19	32	17
	84	155	93

It is clear that the percentage of hulled seeds does not seem to influence the segregation as far as these data are concerned.

HULLED COMPARED WITH HULL-LESS KERNELS

In order to learn whether there was any difference in the ratios produced by the hull-less kernels from the heterozygous plants the seed from the third generation plants used was separated and planted separately; that is, the hulled and hull-less from family 382*a*1–7–45 was planted separately so that the ratio may be determined on each lot of plants. This was done for all the families. These results are given in Table IX.

TABLE IX

RESULTS OBTAINED FROM SOWING HULLED AND HULL-LESS SEED FROM THE SAME HETEROZYGOUS INDIVIDUAL SEPARATELY

Family No.	Segregation Obtained from Hulled Seeds			Segregation Obtained from Hull-less Seeds		
	Hulled Plants	Intermediate Plants	Hull-less Plants	Hulled Plants	Intermediate Plants	Hull-less Plants
382a1–7– 45	11	26	12	2	1	1
7– 10	18	22	20	4	9	5
7– 11	19	27	10	5	7	0
7– 32	18	28	17	10	10	5
7– 33	20	39	21	1	14	5
7– 37	8	25	19	0	6	0
7– 55	14	31	25	5	8	3
8– 14	18	19	8	8	15	11
8– 17	10	28	12	18	35	11
8– 22	3	7	4	12	29	10
8– 23	4	6	6	0	3	3
8– 28	9	18	8	3	12	5
8– 35	5	16	7	17	27	17
8– 61	9	19	9	4	8	2
8– 64	3	7	4	13	29	10
9– 9	3	6	3	1	23	4
9– 44	16	35	13	8	15	2
9– 94	7	8	7	8	13	13
9–166	13	22	14	3	5	8
9–175	19	30	16	0	2	1
Totals	227	419	235	122	271	116
Expected Nos.	220.25	440.5	220.25	127.25	254.5	127.25

In many of the cases the numbers are too small to give good ratios, yet the important point is obtained from the summation of the two series. In each case these agree very closely with the expected numbers. If there was any difference we might expect the hulled kernels to produce relatively more hulled plants and the hull-less relatively more hull-less. The facts are the reverse. In the series from the hulled kernels the hull-less plants are in the majority and the opposite is true for the hulled plants from the hull-less seed. It is very evident that there is no relation between the kind of kernel (hulled or hull-less) sown from a heterozygous plant and the offspring produced.

General Discussion

From the foregoing data it seems without doubt that the inheritance of the hulled condition follows a simple Mendelian ratio giving in general 1 hulled, 2 intermediate, 1 hull-less. This is in accord with the results obtained by Norton, Gaines, Zinn and Surface, and others.

In regard to the relation between the hulled condition of the heterozygous parent plants and of the offspring, it is clear that there is a very close agreement in regard to the hulled percentage. When high or low plants are selected they produce heterozygous offspring giving high or low percentage. In most cases, however, the usual 1:2:1 ratio is obtained. This is true in general in all cases of the 382 series but not so for 202. Whether the 202 series behaves differently or whether in reality it will agree with 382 will have to be determined with further work.

The percentage relation shows that there is a variation from very low to a very high percentage. Owing to this fact and that any heterozygous plant tends to reproduce a simple monohybrid ratio, in which the heterozygous plants tend to follow the percentage relation, it seems at first that we are dealing with a case of multiple factors, in which one primary factor pair determines the hulled or hull-less condition and the other factors influence the hulled condition of those plants only that are heterozygous for the primary factors. This may be so, as the results of selecting high or low individuals seem to indicate. If, however, we assume a multiple factor series to account for the facts, it is evident that, assuming all the factors involved to have equal value, we must have an F_1 type that is very nearly intermediate as regards its percentage condition. This we have not observed in any of our series. The F_1 type, while being generally intermediate, is not so as regards its hulled condition, for it always contains fewer hulled kernels than hull-less. Thus, so far as the percentage relation is concerned, we do not have a strict intermediate. To be sure, there is a reduction of the multiple-flowered spikelet and other changes which cause the F_1 type to appear as an intermediate.

With the usual multiple factor hypothesis assuming ordinary segregation, there must be a larger number of individuals ranging from 30 to 70 per cent. than we have at the extremes. With series 379 and 202 we do not have any indication of such a condition. On the other hand, there is a slight suggestion that series 382 does tend more nearly to a frequency distribution such as would usually be expected with the ordinary multiple factor hypothesis. When the third generation distribution of series 202 is observed (Correlation Table V) it is apparent that there is more of a tendency to pile up nearer the lower values. When the size of the classes is doubled a decided skew curve is obtained with the mode at class 0–9.9. As stated above, the seed sown to obtain the plants used in this distribution was selected from plants of high, low, or medium value, and this may influence to some extent the type of distribution. Yet, when one examines the percentages of the plants used as parents, it is apparent that they are fairly evenly distributed. If, as suggested above, the nearly dominant primary factor pair influences the hulled or hull-less condition and the other factors influence the hulled condition of plants heterozygous for the primary factor, then we would expect a piling up near the lower values.

With series 382 there is a tendency for both the third and fourth generation percentage distributions to be grouped around the middle classes. This is especially true with regard to the fourth generation, especially when the size of the classes is doubled.

The results of the different series are rather conflicting and it does not seem possible at present to explain all of them on a simple multiple factor hypothesis. It seems quite possible to explain series 382 on this basis (except the first generation) but the other types do not at present seem capable of such an explanation.

The distribution in Table II, which is the third generation of a cross between Danish Island and Hull-less, is skewed much the same as for the third generation of series 202. No doubt for these series there is some disturbing factor which causes such distributions and more data will be needed before a suitable explanation can be found to fit all of these cases. It may be that, since in crosses between two hulled sorts we have found some hull-less spikelets, we have combinations such that there is a tendency to produce an excess of hull-less kernels. This would influence the type of distribution considerably.

At first one might assume that those individuals nearer the lower part of the distribution were like the F_1 types, however, from all the plants tested where the percentage of hulled kernels has been low the frequency distribution of the percentage of hulled kernels from the heterozygous plants has been low in general and has not ranged from very low to very high, as would be the case with seed from F_1 plants. These facts would help support the statement just made, which is to the effect that it is possible certain crosses tend to produce an excess of hull-less kernels.

SUMMARY

From the results presented it is evident that hull-lessness exhibits a simple Mendelian ratio of 1 hulled, 2 intermediate, 1 hull-less.

The intermediates show all gradations of hull-lessness from those nearly hulled to those nearly hull-less.

The percentage of hulled kernels on the heterozygous plants seem, to indicate to some extent the percentage of hulled kernels on the heterozygous offspring.

No matter what percentage of hulled kernels is present on the heterozygous individual, it tends in general to produce a 1:2:1 ratio.

The hulled and hull-less kernels from intermediate plants reproduce similar 1:2:1 ratios.

ENVIRONMENTAL REACTIONS OF PHRYNOSOMA[1]

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I. INTRODUCTION

1. *General Distribution.*—The horned lizards, more familiarly known as the "horned toads," of the southwestern portion of the United States and the northern states of Mexico form a very distinct group of the family Iguanidæ. Unlike most other comparatively large reptilian genera, this particular genus (*Phrynosoma*) is limited to a very special environment, and it is only in a region of relative aridity that these animals find a favorable habitat. Within the limits set by the above condition the specific habitats of the various species and varieties of the genus vary greatly, ranging all the way from the extreme aridity and great heat of Death Valley in southern California (*Phrynosoma calidiarum* Cope) to the comparative moisture and cold of the northern Rockies (*Phrynosoma douglassii* Bell and varieties). The species especially discussed in this paper are all found in the Southwest, under varying environmental conditions.

Phrynosoma modestum, the specimens of which were taken near Albuquerque, New Mexico, close to the lower edge of the "mesa" or clinoplane region, at an altitude of about 1,700 meters, is distributed throughout New Mexico, and to a certain extent in the adjoining states, wherever conditions are similar to those in the above typical habitat. The rainfall here averages about 30 cm. annually, while the yearly evaporation from a free water surface is in the neighborhood of 200 cm. The soil is

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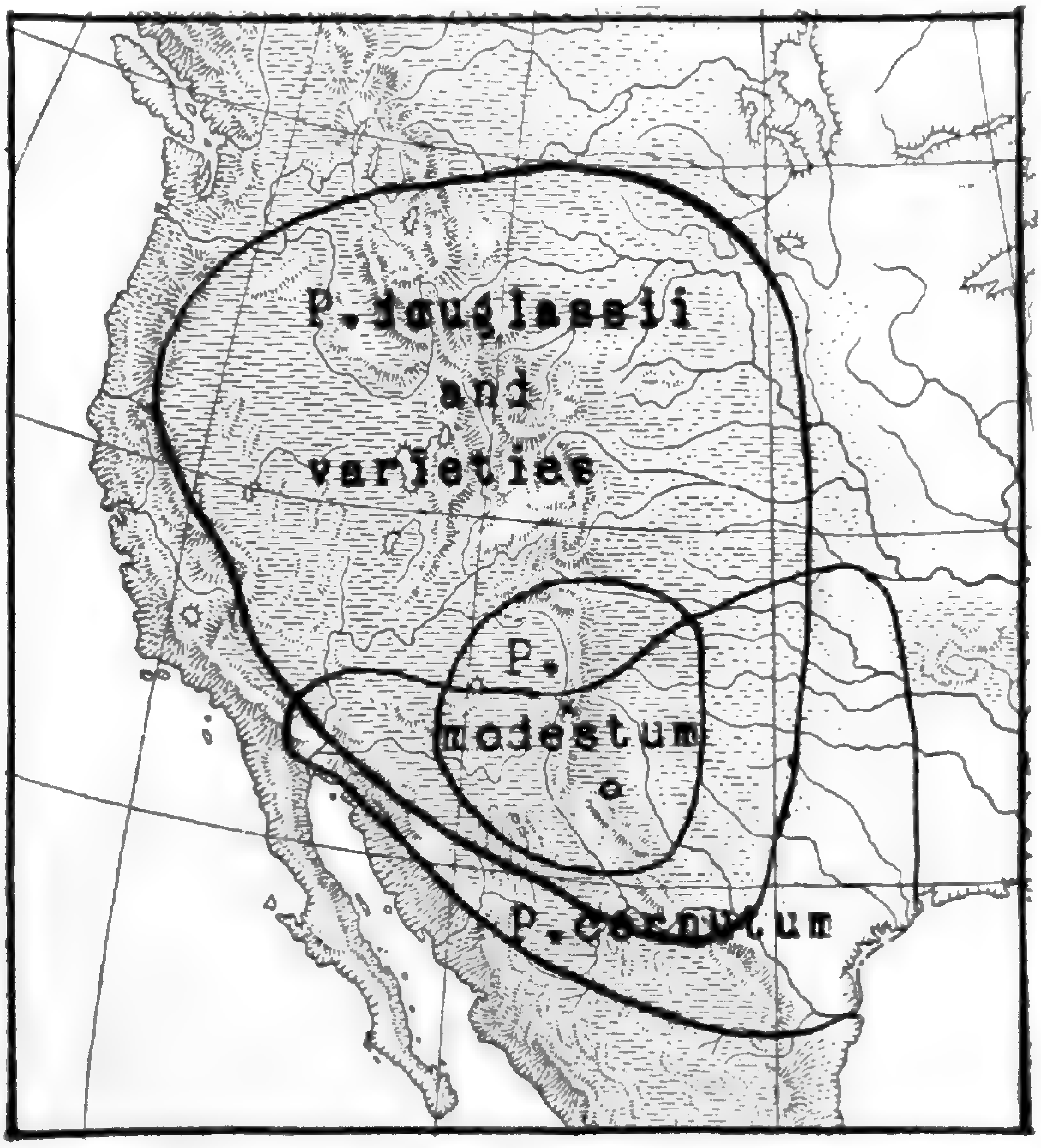
[1] Contribution from the Zoological Laboratory of the University of Illinois.

rather loose and friable, consisting principally of "Tijeras fine sandy loam" and containing, near the surface, a relatively large proportion of fine angular gravel and wind-blown sand. The color is a yellowish or yellowish brown. The vegetation is sparse, consisting of scattered grasses, *Chrysothamnus, Gutierrezia, Salsola, Yucca,* etc. This species is not found in the adjoining valley of the Rio Grande, nor in the mountains (Sandias) which border the "mesa" on the east (2,200 meters and above), where moister conditions prevail. In the mountains the rainfall is probably twice as great, on the average, as on the "mesa," although accurate data are not available, and the evaporation is much less, due to the lower temperatures which prevail. In the valley the water table is very near the surface of the soil (actual soil surface or above to 5 meters below the surface). Standing water is not found on the clinoplane except after very heavy rains, which sometimes fail for months.

Phrynosoma douglassii ornatissimum, specimens of which were obtained with the above, has a much less restricted habitat, both locally and regionally. It is distributed over a great deal of the eastern slope of the Rocky Mountains, even as far north as Canada, and, locally, extends into both of the regions described above as bordering on the clinoplane. It is, indeed, more abundant in either of these than in the clinoplane region between, indicating that the determining factor in the distribution in this case is similar in the lower valley and on the mountain side. As mentioned above, the aridity of these two regions is much less than that of the clinoplane. The soil differences are also marked, in that the moister soils are more dense and contain more humus, derived from the more abundant vegetation. However, the variation in both regions is very great, from heavy clay to fine sand in the valley and from native rock to fine sand in the mountain.

Phrynosoma cornutum does not occur in the same local area as that occupied by the species previously mentioned, although it also is of wide distribution. This species is found throughout Texas and eastern and southern New Mexico, and has been reported from Nebraska, Arkansas, etc. In general, it appears to inhabit regions in which the mean summer temperature is slightly higher than that required by the other two species. The specimens here considered were obtained at Alamogordo, in the Otero Basin, New Mexico, where the mean temperature is higher by about 5° C. than at Albuquerque.



Map showing the approximate geographical distribution of the species discussed in this paper.

2. *General Habits.*—The general habits of the three species here considered are much the same, so no separate description will be attempted. The following discussion will apply, perhaps, more accurately to *Phrynosoma modestum* than to either of the other species, but will, in general, be true of all. They are not, essentially, heat-loving animals, although tolerant of desert condi-

tions. They are found more abundantly during the earlier summer months, and during the autumnal rainy season, when the aerial temperature does not exceed 32° C. During these periods the animals move about actively all day, spending the night in protected nooks under vegetation, in the burrows of other animals, or buried beneath the surface of the soil. As the daily maximum temperature becomes greater they are to be found only in the early morning and in the later afternoon when the heat is less intense. During the heated part of the day the lizard is at rest, almost if not quite buried under the superficial layers of the soil. This position is reached in a characteristic manner. The snout is directed downward and moved rapidly from side to side, the body extremely flattened, while the legs take part in a rapid horizontally clawing movement. The net result of this series of movements is to cover the animal with the loose soil, the depth varying according to the temperature, the character of the soil, and other external conditions, as well as the individual. The same method of burrowing is employed in preparation for hibernation, when the animal may bury itself under several inches of loose soil. In attempting to escape from enemies, other lizards have been observed to dig in a similar manner, and it is probable that *Phrynosoma* also escapes in this way.

3. *Food Relations.*—The food consists of various insects with which the animals come into contact, ants being more readily eaten by the smaller individuals and beetles (*Eleodiini*) forming a considerable portion of the diet of the larger ones. No food is taken unless it is living or at least moving. Sand grains set in motion by a heavy wind or otherwise are often snapped up, and sand grains are accordingly found in the feces.

4. *Water Relations.*—None of the species of *Phrynosoma* have been observed by the writer to drink water, and it is doubtful if water, independent of that contained in the insect food, is ever ingested. Many individuals are found in situations where there is never any standing

water except after the very infrequent heavy rains. Very little water is excreted ordinarily, as when fed on ants, beetles, etc., the feces are eliminated as a dry mass containing practically no water, and the urine is composed of an equally dry mass largely made up of crystals of uric acid. When fed on a moist diet, such as grasshopper nymphs from a moist habitat, the feces become softer and are often accompanied by a considerable amount of mucilaginous liquid. The urine, however, remains as usual. The idea that the excretion of waste nitrogen as uric acid is an adaptation on the part of the Reptilia for life in arid regions is well borne out by the conditions in these animals. Urinary analyses made by the writer in the laboratory of physiological chemistry of the University of Illinois give the following results (1917*b*):

Constituents	Milligrams per gram
Total nitrogen (N_2)	260.0
Ammonia nitrogen	1.4
Urea nitrogen	0.0
Uric acid	765.0
Uric acid nitrogen	255.0
Ash	87.5
Phosphorus as P_2O_5	3.5

It will be observed that uric acid accounts for practically all of the nitrogen contained in the urine and that urea is entirely absent. In this respect the urine of the horned lizard differs from that of the aquatic and semiaquatic reptiles, which contains a considerable amount of urea, as does that of birds, another group in which the uric acid content is high.

5. *Reproduction.*—It is in connection with *Phrynosoma cornutum* that the long-disputed question as to the viviparity or oviparity of the members of this genus may be opened again. Cope (1898) states that *Phrynosoma* is oviparous, which is denied by Ditmars (1908) and Watson (1911), the latter of whom bases his statement on observations of *P. douglassii*. On July 5, 1917, some twenty specimens of *P. cornutum* were received at the vivarium

of the University of Illinois from Alamogordo, New Mexico, and placed in a sand-bottomed wire screen cage. On July 7, between 11 A.M. and 1 P.M., twenty-three eggs were deposited in the sand on the bottom of the cage. The eggs were about 1 cm. in length, ovoid in shape, and covered with a grayish-white shell of leathery texture. Some were opened and found to contain living embryos of about 2 mm. length. Several times thereafter, during a period of two weeks, eggs were found in the cage, always lots of about twenty. The deposition of the eggs was never observed. None of the eggs hatched, although living embryos were found in eggs opened a week after deposition. Such embryos were about 6 mm. in length. *P. douglassii* has not been observed to lay eggs, although a few eggs of *P. modestum* were discovered in the cage in which these animals were kept. These were found in small numbers only and differed from those just described in being light yellow in color and having no leathery shell. They were probably abortive. As the observations of Watson and Ditmars appear to be well founded, it is possible that the genus is divided with respect to the retention or deposition of the eggs, or that in the same species different conditions may alter the length of time the egg is retained in the maternal body, as is the case among the adders.

II. ENVIRONMENTAL FACTORS

As has been concluded (1917*a*), it is dangerous to ascribe to any one factor or group of factors the supreme rôle in determining the seasonal or general distribution of a species. These factors are certainly not the same for all species even in the same environment, and before definite conclusions can be drawn a careful analysis of the habitat must be made, and experimental data must be obtained as to the reactions of the animals in gradients involving the factors capable of variation. Unfortunately, it is not possible or practicable to construct effective gradients involving all environmental conditions, and in such cases we must rely on careful observation and analysis. Such a review as has just been given of the habitat and habits of the horned lizards may indicate to us the probable external conditions variations of which are of importance in the daily and seasonal life of the individual and of the species. The following are the most apparent of such external conditions:

1. Temperature.
    - (*a*) Air.
    - (*b*) Soil.
    - (*c*) Maxima and minima.
2. Water.
    - (*a*) Relative humidity and evaporating power of air.
    - (*b*) Soil moisture.
    - (*c*) Food in relation to its water content.
3. Soil.
    - (*a*) Texture as influenced by
        1. Composition.
        2. Moisture content.
        3. Vegetation.
    - (*b*) Color.
4. Food.
    - (*a*) Character.
    - (*b*) Abundance or scarcity.
5. Light.
    - (*a*) Quality.
    - (*b*) Quantity.
    - (*c*) Rhythm.

In the natural habitat it is rare that one of the above conditions varies without an accompanying variation in one or more of the others; for example, a variation in temperature of the air is accompanied by a variation in the relative humidity and in the evaporating power of the air, and may be followed by an alteration of soil temperature and soil moisture, as well as soil texture. Thus it is difficult to consider these conditions separately.

1. *Temperature.*—That temperature affects profoundly the daily life of the animal and limits its activities is shown by the relation of daily variation in temperature to the change from diurnal to crepuscular habit and to the burrowing activities initiated by high or low temperatures. Minimum temperature is probably associated most closely with the phenomena of hibernation. According to Bachmetjew (1901) the minimum winter temperature which can be survived by hibernating insects depends on the degree of elimination of water from the tissues and the consequent lowering of the freezing point of the body fluids. Tower (1917) states that in the case of potato beetles those animals acclimated to desert conditions (retention of water) are killed at higher temperatures than those of a more humid climate. In the experiments to be described gradients in air temperature and in soil temperature (substratum temperature) were established and the reactions of animals in such gradients were recorded.

2. *Water.*—The water relation must always be important in an animal adapted to arid conditions, even though this relation may seem to be negative. As indicated by the examination of excreta and observation of the water relations of *Phrynosoma* it would appear that the absence of water as such would not have a limiting effect on the distribution of the animals. It is probably necessary, however, that a certain minimum amount of water be supplied in the food, and that the evaporating power of the air must not exceed a certain maximum for any great length of time. It is to be doubted that any vertebrate may subsist indefinitely without some small water supply in addition to metabolic water. As shown in previous experiments (1917*a*), the reaction of *Phrynosoma* in a gradient of the evaporating power of air is not definite unless the gradient be very steep. Daily variation in the normal habitat is very large.

3. *Soil.*—The apparent importance of the burrowing reaction in the life history of the members of this genus

points to a corresponding importance of the texture of the soil. Evidently this must be such as to render the success of the burrowing reaction comparatively easy, a condition which is met only in soils of a low moisture content, and little humus, containing a considerable amount of loosely aggregated particles of sand or fine gravel. In a heavy clay or loam it would be impossible for the animal to burrow deep enough to get below the zone of killing temperatures during hibernation. This would also be impossible in a compact sod. Unfortunately, the problem of the soil relation involves an extensive seasonal study which, so far, it has been impossible to carry out.

While the color and markings of the animals vary with the individual and the species, and the color of the individual changes from time to time, it may be said in general that the color of the horned lizard is very similar to that of the soil of its normal habitat. Experiments of the author and others have shown that high temperature, darkness or high evaporating power of the air causes a centripetal movement of the melanophoric pigment, while the opposite conditions cause a darkening. Thus, in general, individuals observed after a rain are darker in color than at other times. The soil is also darker when wet, which might lead the observer to suppose that the change had taken place as a direct adjustment to the color change of the substratum, while the actual cause is the change in the evaporating power of the air. Within the limits of the conditions of the habitat, variations in the evaporating power of the air are the most potent factors in the production of color changes. No direct connection between the color of the animal and that of the substratum has been verified experimentally by the author. Redfield (1917), in a recently published paper on the color changes in *Phrynosoma cornutum*, has stated that there is a direct approximation of the color of the animal to that of the substratum, and that the light rays reaching the retina form the stimulus for such changes. The mechanism for the approximation of the color of the animal to that of the substratum is, according to Redfield, subordinate to the daily rhythm of color change occasioned by changes in light and temperature, and to changes brought about by the emotional condition of the animal.

4. *Food.*—An adequate study of this factor would require much more extended observation than has been possible. Some suggestions as to the character of food required have been made above.

5. *Light.*—An estimation of the effect of light of varying intensity and quality in the natural habitat would be very difficult, but it is probable that the relations of light in the life of such animals have been greatly underestimated. Experiments with a gradient of the color of light are included here.

III. Experimental Results

1. *Air Temperature Gradients.*—Two series of experiments were performed in which air varying in temperature was passed across the experimental cage previously (1917*a*) described. In the first series the air passing across one third of the cage was heated to a temperature of about 38° by being passed through coils immersed in hot water, that passing across the next third was heated to about 33°, while the remaining third was supplied with air at about 29°. The air was unmodified except as to temperature and the rate of flow was the same in each case. Typical results of this series (*Phrynosoma modestum* only) are shown statistically in Table I.

In the second series the air for the hottest third was heated to a temperature in the neighborhood of 50°, which is about the maximum soil surface temperature on unprotected sand exposed to the direct rays of the sun. This temperature was obtained by passing the air through heated iron pipes. A medium temperature was obtained by passing the air through coils immersed in hot water, as above, while the lowest temperature was that of the

TABLE I

EXPERIMENT 34. SHOWING THE REACTIONS OF *Phrynosoma modestum* IN AN AIR TEMPERATURE GRADIENT

Ten animals were placed in the cage, and observations of their position taken at one-minute intervals. The temperatures taken at intervals along the cage are indicated at the heads of the respective columns.

Minutes	Temperatures					
	Experiment 34*a*			Experiment 34*b*		
	29°	33°	38°	38°	33°	29°
1	3	3	4	3	4	3
2	4	2	4	3	5	2
3	4	2	4	3	6	1
4	4	2	4	4	4	2
5	3	2	5	4	4	2
6	3	2	5	4	5	1
7	3	4	3	4	5	1
8	3	4	3	4	5	1
9	3	4	3	4	5	1
10	3	4	3	4	5	1
11	3	4	3	4	5	1
12	4	3	3	4	5	1
13	2	4	4	4	5	1
14	2	4	4	4	4	2
15	2	4	4	3	5	2
16	2	4	4	3	5	2
17	2	4	4	3	5	2
18	2	3	5	4	5	1
19	2	3	5	4	5	1
20	2	3	5	4	5	1
21	2	3	5	5	4	1
22	1	5	4	5	4	1
23	1	5	4	5	4	1
24	1	5	4	4	5	1
25	1	5	4	3	6	1
26	1	4	5	3	6	1
27	1	4	5	3	6	1
28	1	4	5	3	6	1
29	1	4	5	3	6	1
30	1	4	5	3	6	1

unmodified air, about 30°. These temperatures varied somewhat in the various experiments, as shown by the records, but were fairly constant throughout a single experimental period.

The records of Experiments 34*a* and 34*b* show, for *Phrynosoma modestum*, that the optimum air temperature is in the neighborhood of 35° or 36°. The graphic records of Experiments 86 and 88 (Pl. I) show similar results. It will be noticed in the record of the former

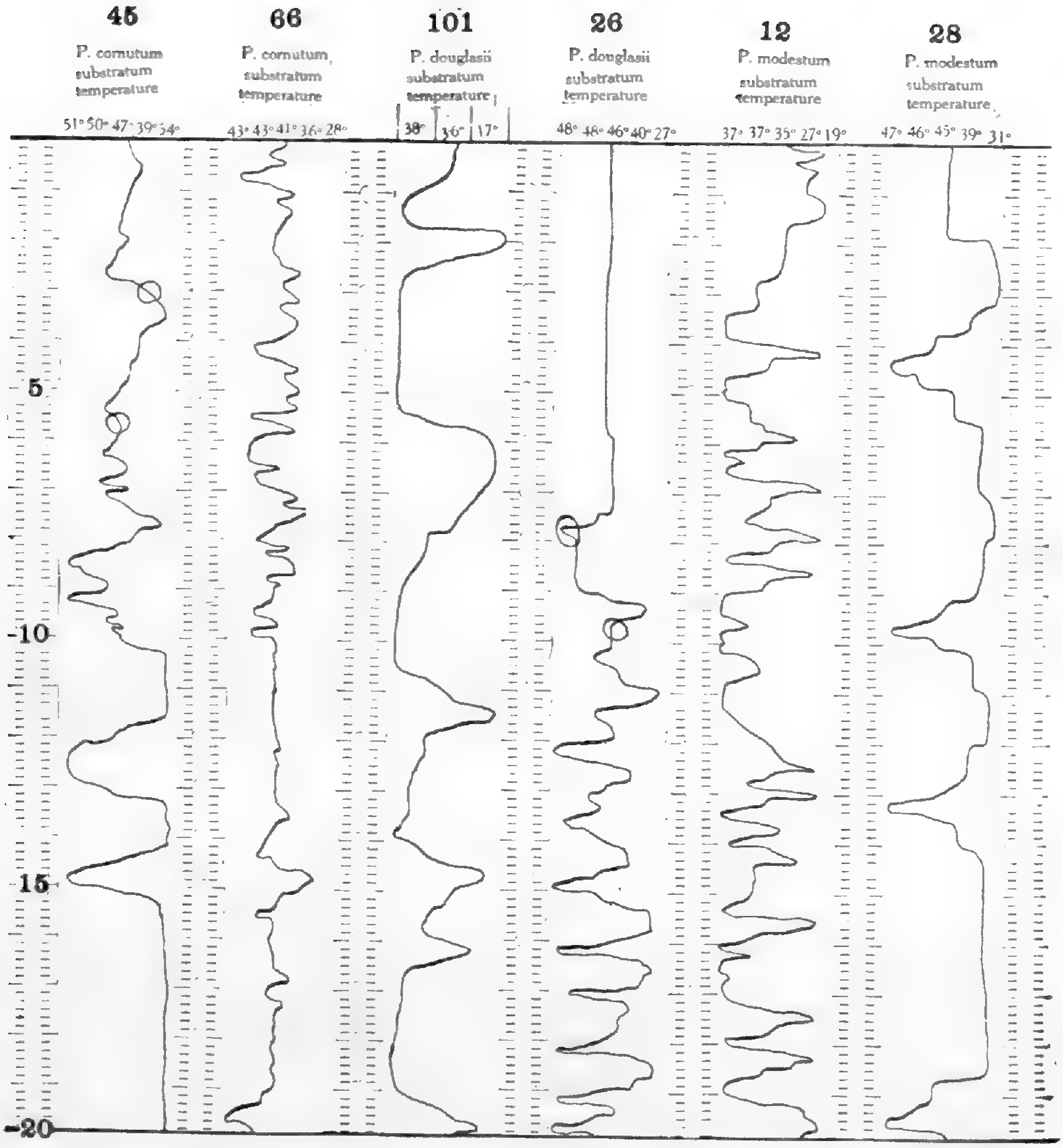
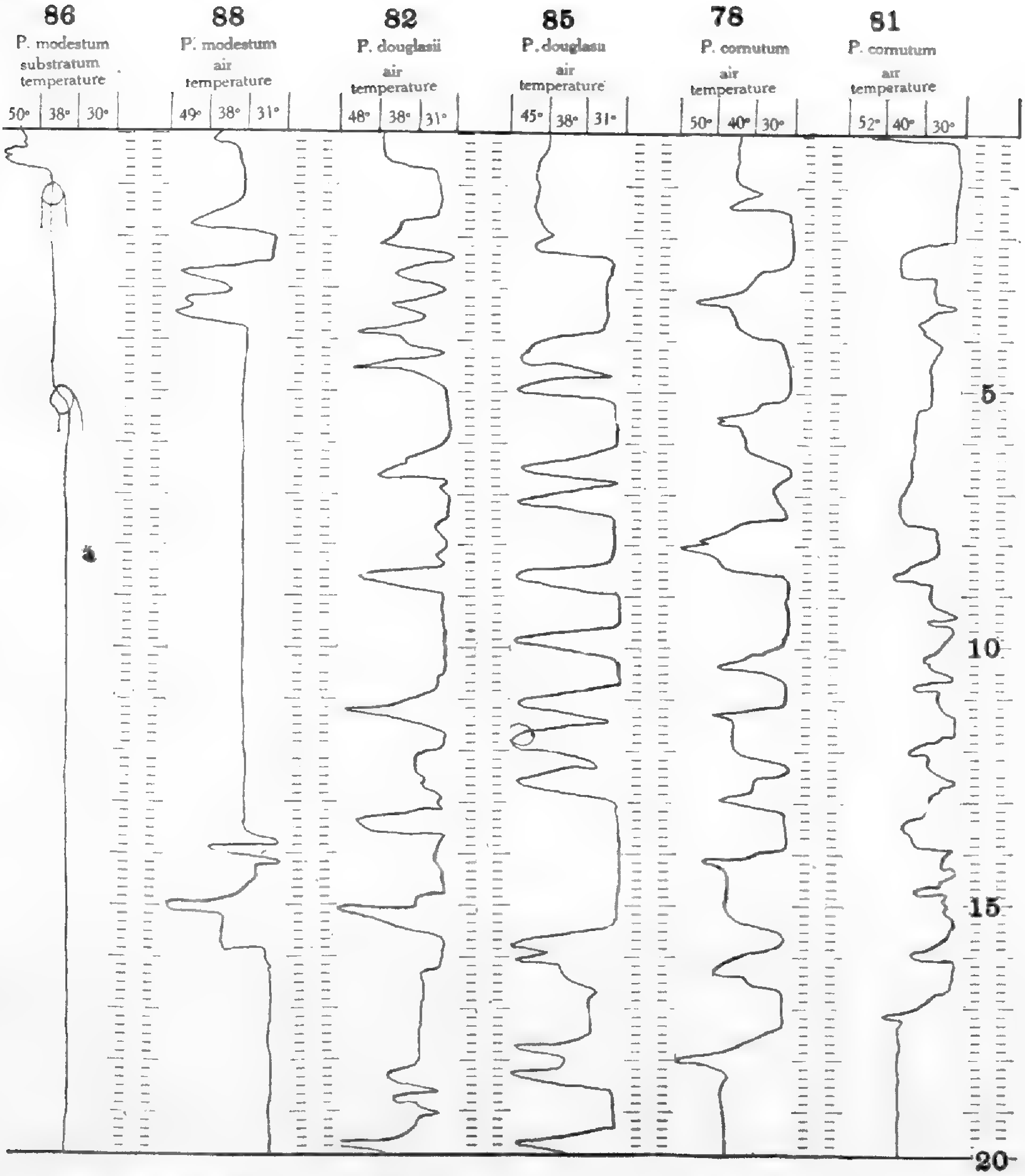


PLATE I. Illustrating the reactions of ***Phrynosoma*** in gradients of air temperature and substratum temperature. Experiments No. 45, 66, 101, 26, 12, 28, 86, 88, 82, 85, 78, 81.

In the chart, each section between the numbered scales represents the record of a twenty-minute experiment, the distance between the scales representing the length of the cage, and the vertical length of the chart the time, twenty minutes, each division on the scale representing ten seconds. The curve represents the movements of the animal under observation, and as the time component is vertical and the space component horizontal, the parts of the curve most nearly horizontal represent the most rapid movements, while the vertical parts of the curve indicate that the animal remained in the same position during the length of time indicated on the adjacent scale. The character of the experiment is in each case noted above the graph, as is the temperature of the various parts of the cage. In some the temperature was taken in five places along the cage and in others in only three places, as indicated. The circles found in the graphic records of certain experiments indicate that the animal attempted to burrow at the times indicated.

Controls, *i. e.*, experiments in which all portions of the cage were at the same temperature, were carried out in all cases, but the regular curves obtained have been omitted to save space.

Experiment 45.—For the first two minutes the animal was comparatively quiet, and after the close of this period moved toward the hot end of the cage, to return immediately, and then attempted to burrow. Just after the fifth minute the animal again moved toward the higher temperature and again burrowed. Thereafter the movements were of greater amplitude but less frequent, until the animal finally came to rest near the cooler end of the cage, where it remained until the end of the experimental period.



Experiment 66 shows a record of almost the same character, except that all movements were of lesser amplitude.

Experiment 101.—Phrynosoma douglassii here remained for the greater part of the time at a temperature of about 38°, making infrequent excursions into the region of lower temperature.

Experiment 26.—Same species as above. The temperatures here were higher, and the animal avoided the highest temperatures.

Experiments 12 and 28 show results similar to the two just preceding, in one the avoidance of low temperatures and in the other the avoidance of higher temperatures.

Experiment 86.—This is the record of the movements of a very sluggish individual, which burrowed twice at a temperature a little above that chosen by other members of the species.

Experiment 88.—This animal showed alternate periods of rest at an optimum temperature and activity involving incursions into both temperature extremes represented in the gradient.

Experiments 82 and 85 are good examples of the type in which there is great activity, but very short stays in the unfavorable temperatures.

Experiment 78.—This record shows avoidance and turning away from the higher temperatures. The farther the animal penetrated into the high temperature area before turning, the longer was the subsequent inactive period in the region of optimum temperature.

Experiment 81.—This animal was very sensitive to the higher temperatures and never reached the hot end, although very active at times.

that the animal burrowed, first at a temperature of about 38° and later at a slightly lower temperature (indicated by the circles in the first and sixth minutes of the record). This burrowing reaction was found to take place very often, throughout the whole series, usually at the upper limit of the optimum temperature range. This agrees with the phenomena observed in the field, of burrowing as the air temperature rises in the course of the day.

Phrynosoma douglassii, as shown in the graphic records of Experiments 82 and 85 (Pl. I), seems to choose a somewhat lower temperature, between 30° and 35°, although there is a considerable amount of individual variation.

Phrynosoma cornutum, the behavior of which in the gradient is illustrated by the records of Experiments 78 and 81 (Pl. I), appears to show a preference for a temperature slightly higher than that shown by the other species.

2. *Substratum Temperature Gradients.*—For the purpose of establishing this gradient the cage was placed in a water bath so arranged that hot water flowed into the latter at one end and cold water at the other, the water being directed backward and forward beneath the cage, and running out near the center, in such a manner as to produce a gradient in the temperature of the cage bottom. The temperature of the substratum was taken at intervals along the edge of the cage by thermometers whose bulbs were just covered by the sand in the bottom.

The statistical records of Experiments 43, 126 and 127 (Table II) show an optimum substratum temperature for *Phrynosoma modestum* of about 40°, or about 5° higher than the optimum air temperature for the same species. In this species the response to changes of temperature of the substratum is very definite, and by varying the temperatures of the gradient, the animals can be driven repeatedly from one end of the cage to the other as the temperature is raised or lowered. The lizards often burrowed at or near the upper limit of the optimum temperature, and, less often, at the temperatures below the optimum. The graphic records of Experiments 10 and 28 (Pl. I) show similar results.

TABLE II

EXPERIMENTS 43 AND 127. SHOWING THE REACTIONS OF *Phrynosoma modestum* IN A GRADIENT OF THE TEMPERATURE OF THE SUBSTRATUM

The method of recording is the same as that employed in Table I.

Minutes	Temperatures					
	Experiment 43			Experiment 127		
	45°	41°	36°	25°	40°	52°
1	2	4	2	2	6	2
2	2	4	2	1 *1**	8	0
3	2	4	2	1 *1*	8	0
4	2	5	1	*1*	8	1
5	2	5	1	*1*	8	1
6	2	4	2	*1*	8	1
7	2	5	1	*1*	8	1
8	3	4	1	*1*	9	0
9	1	6	1	*1*	9	0
10	1	5	2	*1*	9	0
11	1	5	2	*1*	*1** 8	0
12	2	5	1	*1*	*1* 8	0
13	2	5	1			
14	1	6	1			
15	1	5	2			
16	1	5	2			
17	0	6	2			
18	0	6	2			
19	0	6	2			
20	0	7	1			

* The individuals indicated by the *italic numerals* burrowed in the space indicated.

The individuals of *Phrynosoma douglassii* gave practically the same figures for the optimum substratum temperature. The graphic records of Experiments 101 and 26 indicate the behavior of this animal in the gradient. Statistical records of the behavior of *Phrynosoma douglassii* and *Phrynosoma cornutum* in this gradient were not made, because of the size of the animals, which prevented the introduction of any number into the cage at the same time.

Phrynosoma cornutum, as illustrated by the records of Experiments 45 and 66 (Pl. I), chose a higher substratum temperature than either of the other species, averaging nearly five degrees above that shown by the other curves.

In summing up the results of the air temperature and substratum temperature experiments (over one hundred) in relation to those of the evaporation gradient previously reported (1917*a*), it is found that the animals choose conditions which are very near the normal conditions in the usual habitat at the time of the greatest activity. These conditions represent the optimum for the animals. For example, as reported in a previous paper, the evaporation optimum for *Phrynosoma modestum* appears to be near 3 c.c. per hour, as measured by the standard atmometer, which is very near the average outdoor evaporation as observed in the natural habitat of the animal at the season and at the time of day when the animal is most active. If the temperature under such conditions be observed, it will be found that the average atmospheric temperature, 1 cm. from the surface of the soil, in the sun, is in the neighborhood of 35°, and that of the surface layer of the soil about 40°. These temperatures vary greatly, of course, with other features of the weather, such as air movements, clouds, etc., but the above figures represent a normal condition. Of the variables mentioned here, substratum temperature has much the greatest effect on the behavior of the animal.

3. *Moisture of Substratum Gradient.*—Although it was impossible to establish and observe an effective gradient in general soil conditions, several experiments were performed on the direct effect of a soil moisture gradient. The gradient in water content of the substratum was obtained by placing a layer of torpedo sand saturated with water on the bottom of one third of the cage, a mixture of saturated sand and dry sand in the adjoining third, and dry sand in the remainder of the cage. In none of the species observed was any marked preference for any portion of the cage exhibited. Soil moisture, as such, does not seem to affect the movements of the animals, although, in the natural habitat, the high evaporating power of the air produces a considerable degree of temperature difference between dry soil and wet soil by the

vaporization of the water from the latter. This difference was not reproduced under experimental conditions. Typical results of this series of experiments are shown in the graphs of Experiments 91 and 97 (Pl. II).

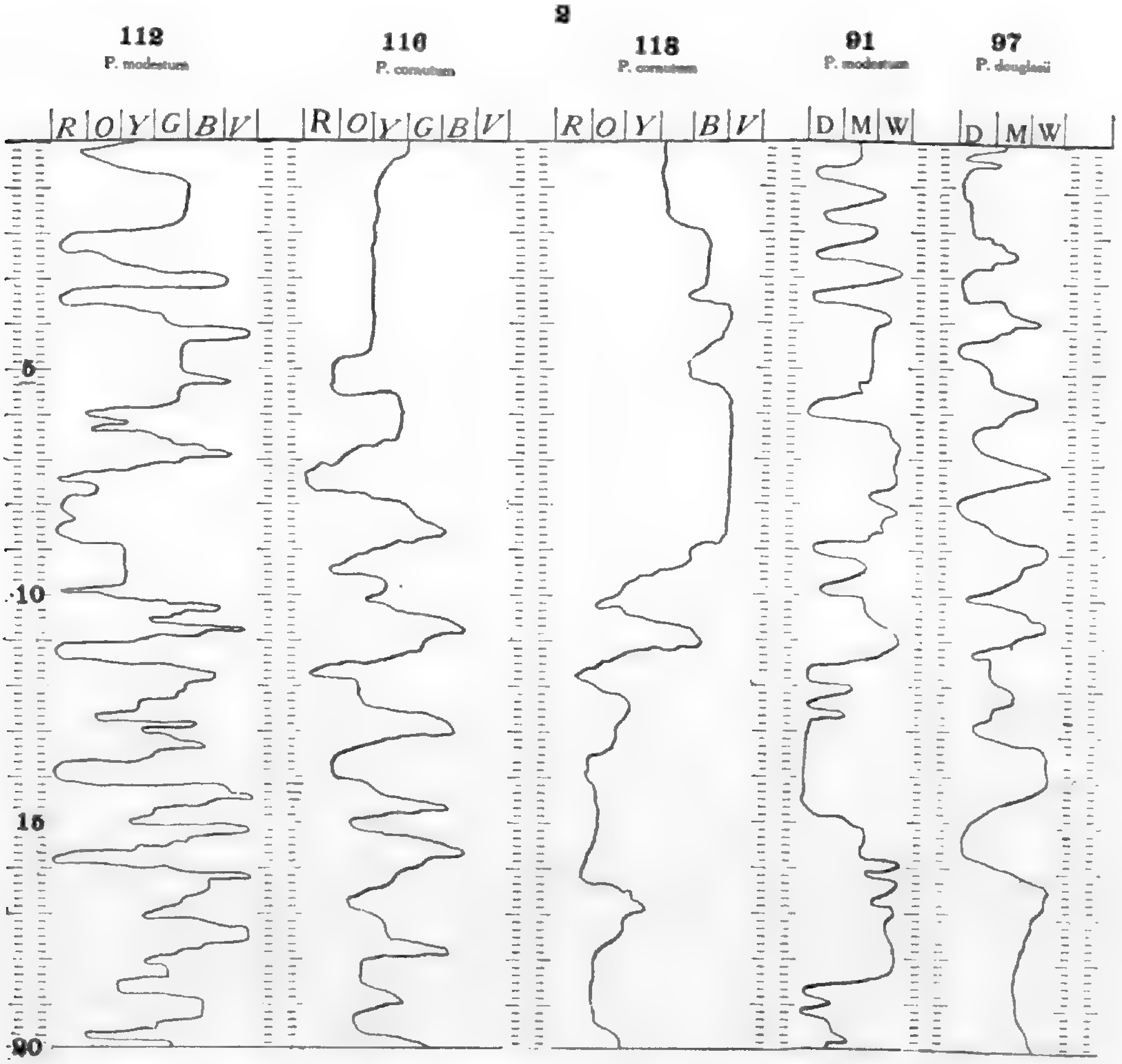


Plate II. Illustrating the reactions of *Phrynosoma* in gradients of wave-length (color) of light and moisture of substratum. Experiments 112, 116, 118, 91 and 97.

Experiment 112.—In this and the two experiments following, the letters *R, O, Y, G, B* and *V* above the graphs represent the color of the light screen over the corresponding portion of the cage. The graphs may be interpreted in the same manner as those illustrated in Plate I. In this experiment the animal avoided the violet section, turning away from it rather quickly in each instance, The greater part of the time was spent in the green and the yellow.

Experiment 116.—This animal avoided the violet and even the blue very markedly and entered the red only twice. The optimum seems to be in the yellow and the green.

Experiment 118.—Avoidance of both the violet and the red is characteristic of this curve. This animal, however, did not avoid the blue and the orange, in which it spent a considerable amount of time.

Experiments 91 and 97.—Here the letters *D, M,* and *W* refer to dry, medium and wet thirds of the cage. The graphs show no preference for either on the part of the animal.

4. *Gradient in the Color of Light (Wave-Length).*—Although it would be difficult to estimate the effect of the various light components in the natural habitat, a series of light experiments has been included. For use as a color gradient the cage used in the other experiments was covered with an accessory lid composed of a series of six equal strips of gelatine ray filter in the principal colors (violet, blue, green, yellow, orange, red). Three forty-watt electric lamps were placed above the cage within the observation hood, so that the light was approximately equally distributed throughout the cage, each sixth being illuminated principally by rays of a narrow range of wave-length.

Experiment 112 illustrates the movements of *Phrynosoma modestum* in such a gradient. The longest rays were avoided, as well as the shortest, although the animal remained for greater lengths of time in the red section than in the violet. The optimum seems to lie in the green and the yellow.

Phrynosoma cornutum (Experiments 116 and 118, Pl. II) avoided both red and violet, with an optimum near the middle of the spectrum. *Phrynosoma douglassii* did not respond regularly and seemed little affected.

The color reactions are probably not as significant as those involving some of the other factors here considered. Direct sunlight in the arid regions contains a rather larger amount of the light of the shorter wave-lengths than elsewhere, and it is possible that the avoidance of violet light as shown in these experiments is of significance in explaining the avoidance of sunlight under certain conditions, but it is more probable that temperature is the dominating factor in this reaction.

IV. SUMMARY AND CONCLUSIONS

1. Of the temperature conditions capable of being tested in the gradient, the temperature of the substratum calls forth the most definite response. In addition to the

indication of an optimum by the movements of the animal, definite motor responses of a specialized character (burrowing) are made to certain temperature conditions just above or just below this optimum. The temperature of the air calls forth similar reactions but not as readily or as definitely as that of the soil, the reaction to the former being overshadowed by the response to the latter when a difference exists. The temperature of the substratum is evidently of very great importance in the daily movements of the horned lizards, and probably plays an important rôle in the control of distribution. The temperature of the soil is probably also of great importance in connection with the deposition and hatching of the eggs in those species which are oviparous. The differences between the optimum temperatures of the various species considered are in the direction and of the magnitude of the temperature differences normal to their respective habitats. While the limits of temperature variation favorable for the completion of the life cycle of the animal could not be subjected to experiment of the type here used, it is evident that at least the minimum is of great importance in connection with the phenomena of hibernation, and the maximum is probably of similar importance in relation to the estivation which takes place more or less regularly.

2. In the gradient of the evaporating power of air definite responses were obtained only in the case of one species (*Phrynosoma modestum*), and here only when the gradient was steep. The daily and seasonal variation in this factor is very large in the natural habitat. The reactions of the animals to temperature changes act in such a way as to prevent the exposure of the organism to excessive desiccation. The effect of soil moisture is felt indirectly, through the alteration of the temperature and the texture of the soil, the latter of which is important in relation to the burrowing habit. It is probable that there is a certain minimum water content of food, below which the animal can not survive. This must be very

low, however, considering the character of the normal food. The excretion of water is reduced to a minimum by the character of the nitrogenous excreta, which are almost exclusively in the form of insoluble uric acid.

3. An important factor in the distribution of these animals is the texture of the soil, which must be suitable for burrowing, as this is the reaction of the animal to unfavorable conditions generally, and specifically to temperatures inducing hibernation and estivation. The soil texture is affected adversely by increases in moisture content, and by increases in the amount of vegetation present. The color of the soil is probably important from the standpoint of invisibility and it is probable that there is some degree of approximation of the color of the animal to that of the substratum. It is difficult to see how this fact could be of much use to the animals, especially in the case of such profusely armored species as *Phrynosoma cornutum.*

4. The rôle of light in the daily and seasonal life of the horned lizards has not been shown, although they are positively phototactic and avoid extremes in a color gradient. The optimum in this gradient lies in the green and in the yellow. This may be correlated with the predominant colors of soil and vegetation in the natural habitat.

V. ACKNOWLEDGMENTS AND BIBLIOGRAPHY

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MIGRATION AS A FACTOR IN EVOLUTION: ITS ECOLOGICAL DYNAMICS, II.

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III. The Migrational Factors in Evolution

1. *Introduction*

From the preceding discussion of the principles of animal activity which underlie their behavior, attention is now directed in greater detail to suggestions for their application to migration. Emphasis is placed upon those relations which show the main causes of stress, the cycles of circulation caused by diversity, and the interaction, equilibrium, and adjustment operating between the various systems. I have not attempted to go into detail on the quantitative relations, although there is much physical and some ecological data, already organized, which illustrate the method of application. There is, however, but little quantitative distributional data which are at present available. The elaboration of this phase is urgently needed. Limiting factors retard and prevent the migration and diffusion of animals; these are the "barriers" so frequently mentioned by students of geographical distribution. As previously mentioned, two major systems or agencies are involved in this process, the animal and the environment. The locomotor activity of the animal is a phase of its general responses. The migrations of most animals are therefore not different, in any important features, from the ordinary daily life of the animals; that is, migrations are incidental and included within the ordinary responses. Anticipating somewhat, and speaking broadly, if animal responses are of evolutionary value so must be the migratory ones. In detail there are innumerable animal peculiarities which influence migration, depending on the stage of development of the animal, its physiological and ecological conditions and characteristics, and the status of its environment. The large number of factors involved in this is no doubt an important conservative influence and checks the speed of interaction.

The word migration is used in several senses, so that for our purpose it is now necessary to define this more definitely. By migration is here meant the movement of animals from one place to another, and this includes, not only the causes and conditions of their migration, but their methods as well and the immediate result upon the animal. If all migrating animals perished at the end of their journey the study of its influence would be relatively simple.

In deference to those who are mainly interested in the animal and who are less interested in the environment it has been customary in many zoological writings to discuss animals first, and their environment later. But as zoology progresses and as explanations are resolved more and more into the sciences upon which it rests, greater and greater prominence is given to the physical causes and conditions of the environment. Viewed broadly, zoology should be made to fit into the general world system in such a manner as will best aid in understanding it, irrespective of our traditional habits of mind. For this reason this phase of the discussion will begin with the environment, as a factor in *passive migration or transportation,* and will lead up to the animal as a factor in its own migrations.

In the orientation of the major features of the world Powell recognized: the atmosphere, the hydrosphere, the lithosphere and the biosphere. These self-explanatory, relatively homogeneous, physically and mechanically distinct, and interacting systems, furnish the medium in which animals live and perform their migrations. We may look upon these three physical systems as a result of existing temperature conditions of the earth. Increase the temperature to a certain amount and the atmosphere would be rarefied, the hydrosphere would disappear into the atmosphere as water vapor, and the solid earth would become fluid. Or, reverse the process, beginning with its present state, and should the earth cool progressively, the hydrosphere would become frozen to the solid phase and atmosphere would likewise be transformed to the solid state, and all these systems would become one. The present resolved and differentiated state is thus dependent on the present temperature conditions. The relation of equilibria between these three systems is one of the major problems for the application of the phase rule, and their methods of interaction is an unlimited field for the application of Bancroft's law, and both of these are of the greatest importance to all concerned with the gross environments of organisms.

In view of the dominating influence of temperature, we must not overlook the fact that temperature is only one of the essential conditions of life. It is important to observe that the present stratum of the earth's surface where organisms live is a remarkably narrow one, and only moderate departure above or below the condition in this stratum at once becomes limiting factors to organic activity. Chamberlin ('06, pp. 1–2) states this impressively as follows:

> The narrowness of the range to which temperatures must be confined to permit progressive organic and intellectual evolution takes on its true meaning only when we recall that the natural temperature range on the earth's surface is sixteen times as great as this, while that affecting the solar family is at least sixty times as great. For a hundred million years, more or less, this narrow range of temperature has been maintained quite without break of continuity, unless geologists and biologists are altogether in error in their inductions.

The maintenance of such a dynamic system of equilibrium of the environment and of the organism, and the inertia of their systems—the tendency to continue or persist in a given state—may well cause wonder and stimulate thought.

In the following analysis of the larger units which influence migration, those agencies will be used which serve as the basis for the smaller systems of action, and some of their main cycles of activity and methods of interaction will be indicated briefly.

2. *Atmospheric Agencies in Transportation*

The instability of the air, its numerous cycles of activity or circulation, hourly, daily, seasonally, annually, and those of longer duration, furnish an agency which has transported animals from one locality to another for ages. Gentle breezes carry small animals, while violent tornadoes carry larger ones. Small eggs, desiccated rotifers, entomostraca, and other small aquatic animals, have been transported long distances by the wind, and have thus found many favorable habitats, otherwise not available to them. The wind, reinforced by streams, even temporary ones, has transported animals long distances, as have the waves of the sea and inland waters. The winds, supplementing the flight of animals, have carried them thousands of miles beyond their normal range, as in the case of birds and insects. A vast literature has grown up recording the details of these findings, and yet about the only evolutionary conclusion which can be safely drawn from the multitude of facts is that by these processes animals have tried out and acclimated themselves to a vast number of isolated habitats which have tended to give them a varied and widespread range, and to that degree it has aided in their perpetuation.

The most definite evidence of atmospheric influence in evolution is perhaps the direct influence of climate and of climatic changes. Fortunately, for our present purpose, and mainly through the researches of Chamberlin (1897–1901) and Huntington ('15, pp. vi–vii), secular climatic cycles have been investigated. Chamberlin has related these intimately to the changes in the hydrosphere and lithosphere, and he has indicated their modes of interaction in a strictly dynamic manner. He shows that during a period of land elevation and mountain formation, with cold, dry, diverse climatic differences and zonal arrangements on land and with a deepening of the sea, these conditions tend to change progressively toward a moist, warm, uniform and tropical condition, which is related to the land equilibrium developed during base-level on land, and a marine condition of extensive shallow seas. The process of adjustment to these strains beautifully illustrates Bancroft's law. It is not an accident that mountains are centers of origin and dispersal of animals, nor are they solely refuges where endemic forms escape the competition of the lowlands. Mountain regions in their elevation subject whole populations to severe climatic and other stresses of many kinds, depending on the physical and vegetational diversity of the region, and doubtless thus many animals become extinct, while others as individuals or as a race become acclimated to the new and changed conditions and thus survive.

It seems strange that, although dynamic principles are shown in almost ideal form in the unstable air, yet, as a whole, this phase of science seems to be somewhat backward in the formulation of the ideas of processes, so that their greater successful application is seen in geology. It appears that the reciprocal dynamic relations which exist between barometric lows and highs (both temporary and permanent) makes them dynamic centers of action (Fassig, '99) in a cycle of circulation and adjustment to stress. This idea is one which may profitably be extended to the interpretation of successive phases in the establishment of climatic dominance. The change from the Ice Age to that of the present, and the accompanying change of storm tracks (Adams, '09, pp. 45–46) are comparable to the seasonal change from winter to summer dominance, while passing through the transitional March weather stage. Furthermore, the summer and winter dominance are dynamic equilibria established by a balancing among the various highs and lows (Adams, '15*a*, pp. 69–71). These transitional periods illustrate Bancroft's law in the process of establishing new relative equilibria. The dynamic centers are to be looked upon as concentrating, transforming and radiating centers, whose recognition and cycles of activity are an essential part in the application of Bancroft's law to the development of atmospheric equilibria.

3. *Hydrospheric Agencies in Transportation*

The waters of the earth are more dense than the air but are yet quite mobile, and undergo relatively rapid cycles of circulation, both in the sea and in inland waters.

(*a*) *Marine.*—The great currents of the sea, the tides, and the wind-formed waves, are very active agents in the transportation of animals. Not only are marine animals extensively transported, but also, in the long run, large numbers of land kinds, as the animals on oceanic islands testify, as shown by Wallace. And just as the processes of erosion operate upon land, and tend to reduce such areas to sea level, so the sea itself possesses its own cycles of transformation of its bottom and shores, tending to flatten them out to the equilibrium of the deep sea floor, transporting materials and redistributing them in response to its stresses, eroding here, depositing there, and always making changes in the conditions which not only transport animals, but as well, by the migration of the physical conditions, lead animals from one locality to another. Land animals are largely influenced by the surface conditions, while the marine ones are largely by sub-surface conditions.

(*b*) *Inland Water Bodies.*—Bodies of inland standing water, in their broad features, are smaller editions of the seas, as far as their waves, circulation and transporting powers are concerned. Their chemical character, whether fresh or saline, has more influence upon animals than the mechanics or their methods of circulation. The most marked influence of the inland waters is their relatively small area, isolation, even though they may overflow into streams. Inland waters are in general relatively ephemeral in character compared with marine waters, because with progressive erosion of the land they tend to become extinct through deposition and ultimate drainage.

(*c*) *Running Waters.*—The transporting power of running water is easily evident. The constant direction of flow, its duration (as some drainage lines are of extreme antiquity), and repeated transportation, have subjected animals again and again to new conditions, and carried them to new localities. Streams transport both land and aquatic animals and by their persistence, activity, and the thoroughgoing fashion in which they work over the land surface, are one of the most powerful agencies of transportation. Streams undergo changes depending on the dynamic status of the stream. The greater stress to which the stream is subjected by uplift, the greater its velocity and its relative transporting power, and the nearer it erodes to base-level, the less current and relative transporting power it possesses. Most animals counteract the transporting power of the stream by definite responses to the current, and thus maintain their position and are not carried away.

4. *Lithospheric Agencies in Transportation*

The lithosphere includes the solid earth, which to the ordinary mind is the ideal of stability. The transporting power of the solid is, however, usually at a very slow rate, but this is not always the case, because of the suddenness of fracture. The solid ice of the glacier moves slowly and yet travels long distances, but usually does not transport an abundance of animals. Avalanches move with greater speed, but they operate in rather limited areas. Landslides transport, slowly or rapidly, large masses of land containing animals. All of these processes are dominated by gravity, and tend to transport animals from a higher to a lower altitude. Perhaps the most powerful motion of the solid earth is seen in the crustal movements, associated with the cycle of isostacy, which elevates and depresses the surface of the land in relation to sea level. In this is seen an essential condition which has made all land life possible, because without such movements all the land would have been washed into the larger dominating sea. The great land elevations, such as those which produce plateaus and mountains, have transported whole faunas, covering thousands of square miles, upward, and have subjected them to great stress, through long periods of time. Such elevations as arise in a region unfavorable to animals, may improve them, as in the case of high mountains, rising on a dry desert, but often such elevations, which are departures from the favorable thin surface stratum, are in the direction of unfavorable conditions and of limiting factors. Broadly speaking, depressions below sea level are similarly limiting to marine organisms, and these have operated on a magnificent scale. The mountain tops, like the deeps of the sea, are relatively animal deserts, both are extreme departures from the conditions which are normal to most animals.

The most rapid physical agency in the transportation of animals on land is the influence of running water and that of the wind. These forces operate in short cycles and intensively, in contrast with the movements of the solid earth.

Volcanic activity has probably been only a minor factor in the transportation of animals, although in a secondary way, in conjunction with other agencies, as currents of water, porous materials buoyed by air, may act as a raft in their transportation. But indirectly by building mountains, islands, etc., it has had an influence similar to that of the crustal movements of the earth in forming new habitats, and has thus had a powerful effect.

5. *Biospheric Agencies in Transportation and Migration*

(*a*) *Plants.*—The relatively sedentary and rooted condition of plants caused Cope to aptly call them "earth parasites." With this stable habit and the unstable environment, rooted plants have been forced to develop a line of fracture, as it were, between themselves and the environment, which has permitted them, by their exceptional powers of dispersal, to spread rather freely at some stage, and to thus scatter over much of the available surface of the earth. As far as the actual movements of plants are concerned, unaided by winds, waters, and animals, but solely by growth and similar movements, plants have probably had but relatively small influence upon animal transportation, although secondarily, by the spreading of vegetation and the changed conditions which this causes, they have permitted extensive transportation and migration of animals. The specific gravity of wood, its buoyancy in water, and the various sails, vanes, and structures which favor wind dispersal, and all the hooks and claws which help make various kinds of burrs, and the edible fruits which animals devour, all combine to favor transportation by wind, water, animals, and other active agencies. By these means, animals living within, or on such transported parts, may be buoyed and transported by waves, currents of water or air, and be carried by animals for long distances, and into new localities and conditions.

(*b*) *Animal Migration.*—The movements of animals which take them from one locality to another are exceedingly diverse. They vary not only with the character of the animal, at different stages in its life history both structurally and functionally, and also under varied environmental conditions. The fixed and sessile animals more nearly approach the conditions found commonly among plants, but among animals this habit is confined mainly to aquatic animals, that is, to animals living in a mobile medium, which transports them at some stage.

The most important character which influences the migration of animals is its own powers of movement. These movements are dependent upon the ecology and the physiology of the animal, its structure and its mode of response. The general principles of response have been discussed in the first part of this paper, where the systems of activity, the cycles of activity, the limits of activity, and the interaction of all systems was emphasized. All of these factors should now be recalled. Animals creep, walk, swim, and fly, according to the media in which they live, their structure, and their ecology, and the interaction of all these factors put limitations upon animal movements.

From the standpoint of function, animal movements and migrations have two main influences. By movement the animal subjects itself to new conditions, these conditions have a direct influence upon the animal, and change the direction or its internal changes, and it becomes acclimated or dies; or by its repeated responses and retreating movements, it escapes from the adverse conditions and finally comes to rest in a new relatively favorable condition (Adams, '15, p. 12). This monotonous cycle is repeated with all the variations which diversity of animals and diversity of conditions can produce, and in its essential features it is the same from Protozoa to man.

The geological age in which we live is one in which the land surface, relative to the sea, has accumulated uplift from former ages, and has been newly elevated, and as a result there are many high mountains, and the seas are relatively deep. These are conditions of stress, and the processes of adjustment to strain are in full operation. This is a period of relative diversity of the lands and of the seas, which favors diversity, both in the atmosphere and in the hydrosphere. With the elevation of the land, this diversity is shown both vertically and horizontally. Large areas lie at considerable altitudes and in their departure from the narrow mean surface stratum, are subjecting many animals to stress, and to the process of acclimatization to the high altitude conditions. The climatic diversity shown vertically, also expresses itself longitudinally, by interference with free circulation of temperature, moisture, and other climatic factors, and tends to produce the varied climatic zones, such as tropical, temperate, and polar, as well as the diversity due to humidity. These diversities mean that many minor circulating systems are caused and consequently there are varied local wind systems, further favoring diversity. All of these influences tend to favor local or relatively limited migration, rather than the widespread dispersal of animals subjected to such conditions.

The hydrosphere is influenced similarly. The diversity of the lands favors diversity in inland waters, and the arid climates favor saline waters. Inland waters under these conditions tend to be isolated and varied. In the sea the deepened waters produce stresses similar to those on land produced by altitude, and the elevations and relative increase in the land area interferes with the circulation of marine waters and favors local differences and local stresses. With the deepening of the seas, the shallow waters are restricted and the littoral animals are under increased stress. It is seen, therefore, that the conditions dominant on a world scale are those of stress or strain, now in the process of adjustment. It should be observed that all spheres, the atmosphere, hydrosphere, lithosphere, and the biosphere are involved in the same general interacting process. It is only by viewing the subject broadly that we thus gain this perspective of the status of our own times.

We may now turn to certain details which will help to illustrate the application of these ideas to animal migration. The same grouping of influences will be used which has been applied in the preceding discussion of passive migration.

(*a*) *Atmospheric Influences.*—The atmospheric factors which influence active animal migrations are mainly those which are dependent upon: chemical composition (largely oxygen, CO_2 and volcanic gases); temperature; pressure; humidity; and mechanical effects, as they are combined in climatic changes. All of these influences undergo differences which influence, by acceleration or interference, the movements and migrations, acclimatization and ecological attunement of animals. Furthermore, these influences, or their systems, do not act independently but at the same time, so that their laws of interaction are the main rules of the game.

(*b*) *Hydrospheric Influence.*—The hydrospheric influences are similar to those of the air, depending on: composition (salts and gases); temperature; pressure; and mechanical effects (waves, tides, circulating currents). In this geological age of stress and diversity, on account of the mobility of this medium, it has transmitted its pressure with slight friction to animals. Upon land the active streams are a direct response to the steep slopes down which they flow, and they visualize at once the reality of this active media which has kept fishes and other animals busy moving up stream for millions of years. Bodies of standing water, by their isolation, except when connected with streams, tend to retard active animal migration. Such bodies are likely to abound in the early stages of uplift and to decline as drainage lines develop. The diversity of climate into humid and arid as previously mentioned, tends to favor diversity, chemically, in bodies of standing water. These inland waters, while discontinuous to many aquatic animals, are not so to many flying and running kinds.

In the sea, the narrowing of the continental shelf tends to crowd the shore animals, and favors isolation and diversity of habitat, and retards ready migration for many animals. The hastened erosion, however, tends to increase the continental shelf and its continuity. The deeper water shows relative diversity and tends toward stagnation in its currents because of the relative increase of the land area.

(*c*) *Lithospheric Influences.*—The interdependence of the physical spheres is so marked that by this time, in the discussion of the air and water, the solid earth has been included in part. The rigidity of the lithosphere is so great that its adjustments to strain are in general relatively slow and of long duration. The density of the medium is so great that animals inhabit only a shallow surface stratum, the upper part of the zone of weathering processes, in or on the soil. Animals living in the soil are influenced by its density, its physical and chemical composition, temperature, and its movements. Those living on it are relatively independent of the qualities just mentioned, but are much influenced by the relief of the surface, by the climate and vegetation, and are more truly air rather than earth dwellers. The elevation of the land above sea in itself, and not as modified by climate and topography, probably has little direct influence, except in its degree of stability with regard to erosion. The greater the altitude and the steeper the slope, the greater the physical stress and the rapidity of erosion. Ice and landslides exert pressure and drive animals before them, and are largely dependent on elevation and slope. The cycle of degradation of the land, particularly its topographic diversity, greatly influences the degree of freedom in the movement of land animals.

(*d*) *Plant Influences.*—The stresses of the physical environment in the air, water and earth, impose pressure upon the vegetation. Since the largest number of animals are directly dependent, and a smaller number indirectly upon plants, much of this pressure is transmitted to animals. The climatic diversity, seasonal and secular cycles, influence the amount of animal food. Some animals, during adverse seasonal conditions and scanty food supply pass into an inactive state, and tide over such a season, and most animals not possessing such tend to migrate. Thus upon the plains the bison wandered with the seasonal changes of pasture, just as mountain sheep and goats migrate up and down the slopes as their pasture varies with the season. The succession of vegetation upon all surfaces, drives out some animals, just as it invites others to follow with it, as when, with the development of forest, the animals of the open find conditions unfavorable. The kind of vegetation, whether herbaceous, woody, conifer or deciduous, etc., has an important influence upon the movements of many animals. The cycles of vegetation also change the physical conditions, the temperature, humidity, soil conditions, and thus influence animals.

(*e*) *Animal Migrations.*—The individual migrations of animals, caused by their own spontaneity, and that by other animals, are exceedingly varied. All the factors which influence individual movements, as indicated in the first part of this paper, now apply in detail, and in addition there is the pressure exerted by animals living associated with them. Simple animals require a favorable

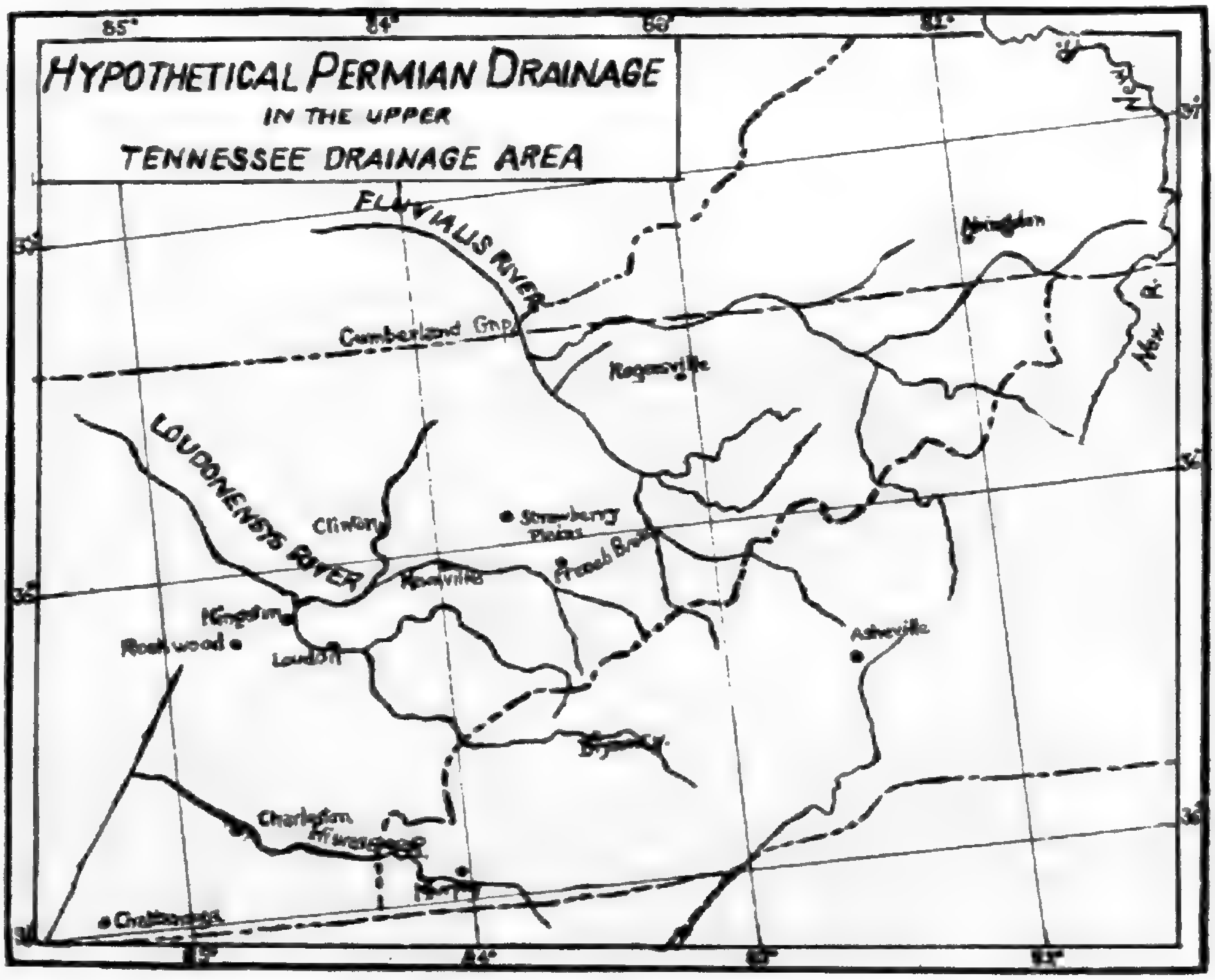

Fig. 1. Map showing the hypothetical Permian drainage of the Upper Tennessee drainage area. Compare with the present drainage shown in Fig. 2.

environment as truly as complex ones. It is known that many animals decline in vigor if kept in the same medium, but if the medium is kept fresh, or the animal moves about freely and secures a fresh medium, it thrives. Freedom of movement thus permits the animal to move away from influences which interfere with its system, and thus minimizes the disturbance. The continuation of this process tends, with freedom, to bring the animal ultimately into favorable non-interfering conditions if such exist. With these ideas in mind we need to recall that the atmospheric, hydrospheric, lithospheric and vegetational pressure all combine to encroach upon the animal, and to interefere or reinforce its activities and movements. The normal movements of the animal, and the ordinary routine of environmental changes, are thus in process of continual adjustment. Thus with the migration of the animal habitat, whether caused by a change in the atmosphere, hydrosphere, lithosphere, vegetation,

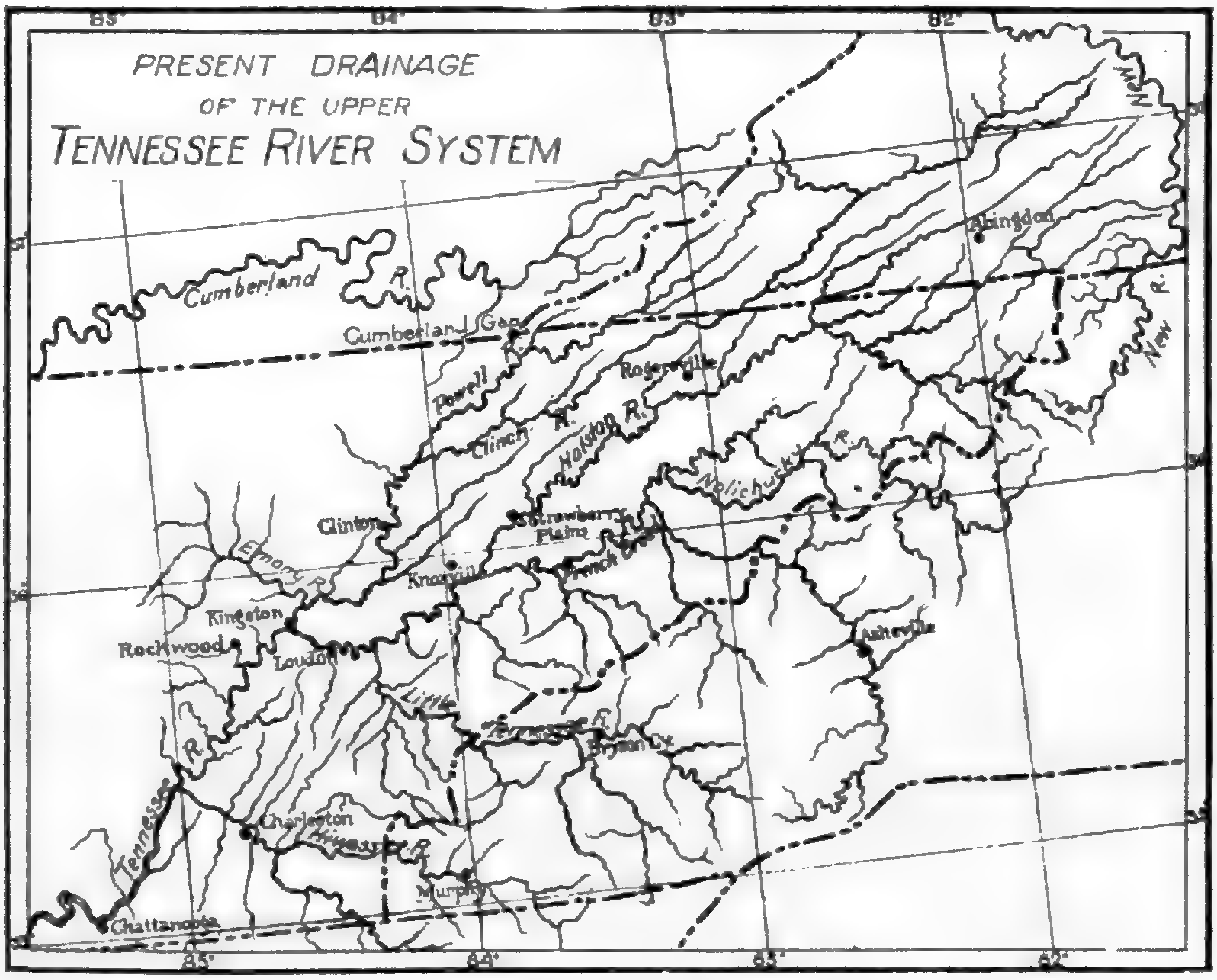

FIG. 2. The drainage of the upper Tennessee River system.

or any combination of these, the animals also tend to migrate with it and they are thus led about all over the surface of the earth. In this we see the importance of cycles of climatic changes, cycles of crustal movements of the earth, changes in circulation of the sea, and the succession of plant and animal associations. It is to the changes of this character that the student of paleontological evidences and causes of evolution gives much thought, and it is to the present evidences of these changes to which the field ecologist gives much attention.

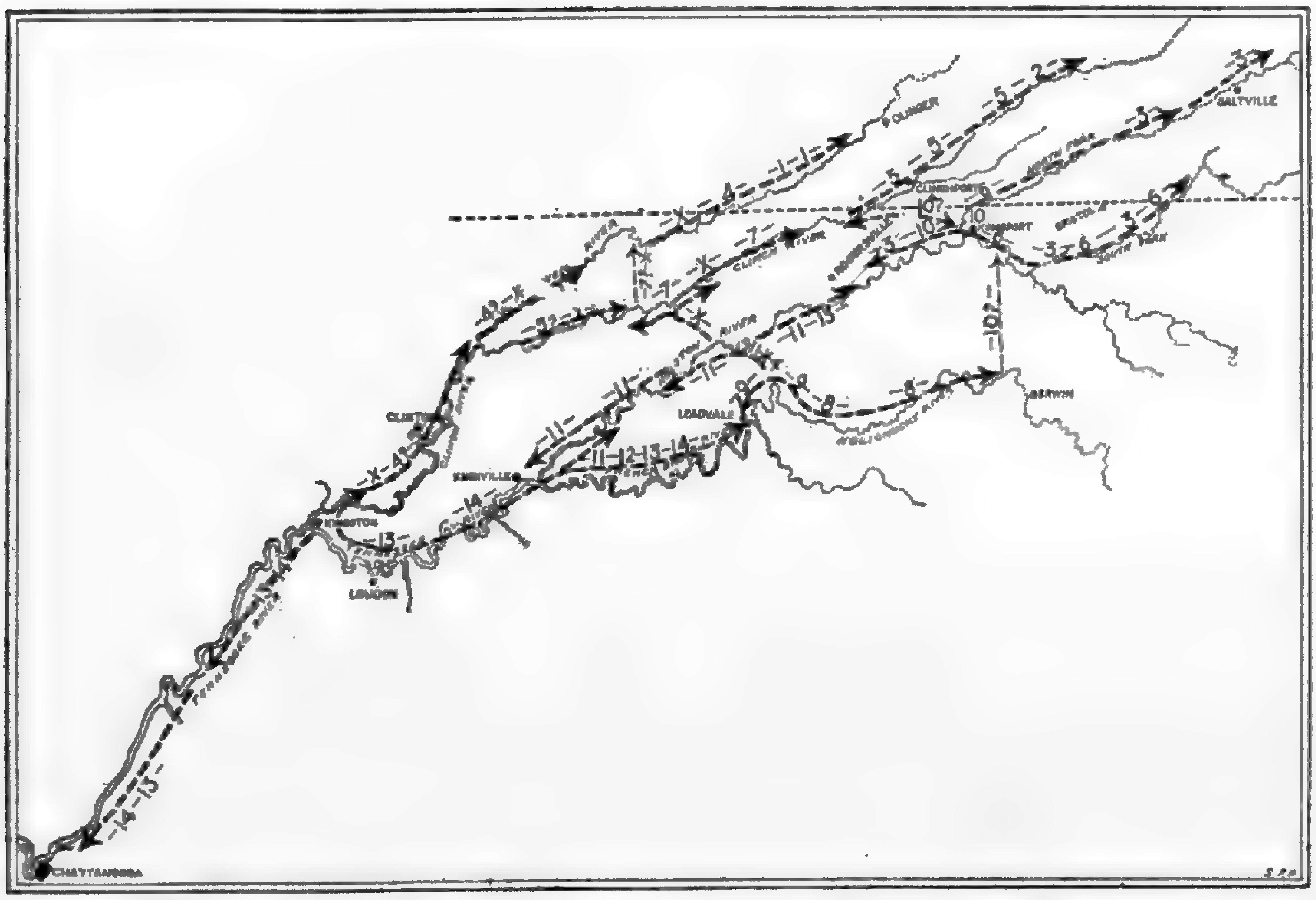

Fig. 3. Map showing the hypothetical migrations of the snails of the genus *Io* in the upper Tennessee River system, as influenced by drainage changes. The numbers refer to the kind of shell illustrated in Fig. 5.

In my study of migrations of the fresh-water snail *Io*, in the drainage of the upper Tennessee River system (Adams, '15*b*), it was found that there were great cycles of change in the history of the streams, and that there were probably corresponding migrations of the snails. This is shown if we compare the map of ancient hypothetical drainage, Fig. 1, with that of the present, Fig. 2, and the supposed migration of the snails, Fig. 3, and compare these with the map of their present distribution,

Fig. 4. The shells of these snails are shown in Fig. 5. The presence of these snails in the headwaters of streams appears to be due to the ordinary creeping movements of the snails taken in connection with the up-stream migration or growth of the stream habitat, because, on the other hand, the current tends only to favor a down-stream dispersal. Such animals, therefore, appear to be led about *by the migration of their habitat.* This sort of migration is comparable to those land migrations which have clearly taken place during climatic migrations, as during the ice age, and during similar changes in humidity, and with base-leveling changes (Woodworth, '94; Adams, '01).

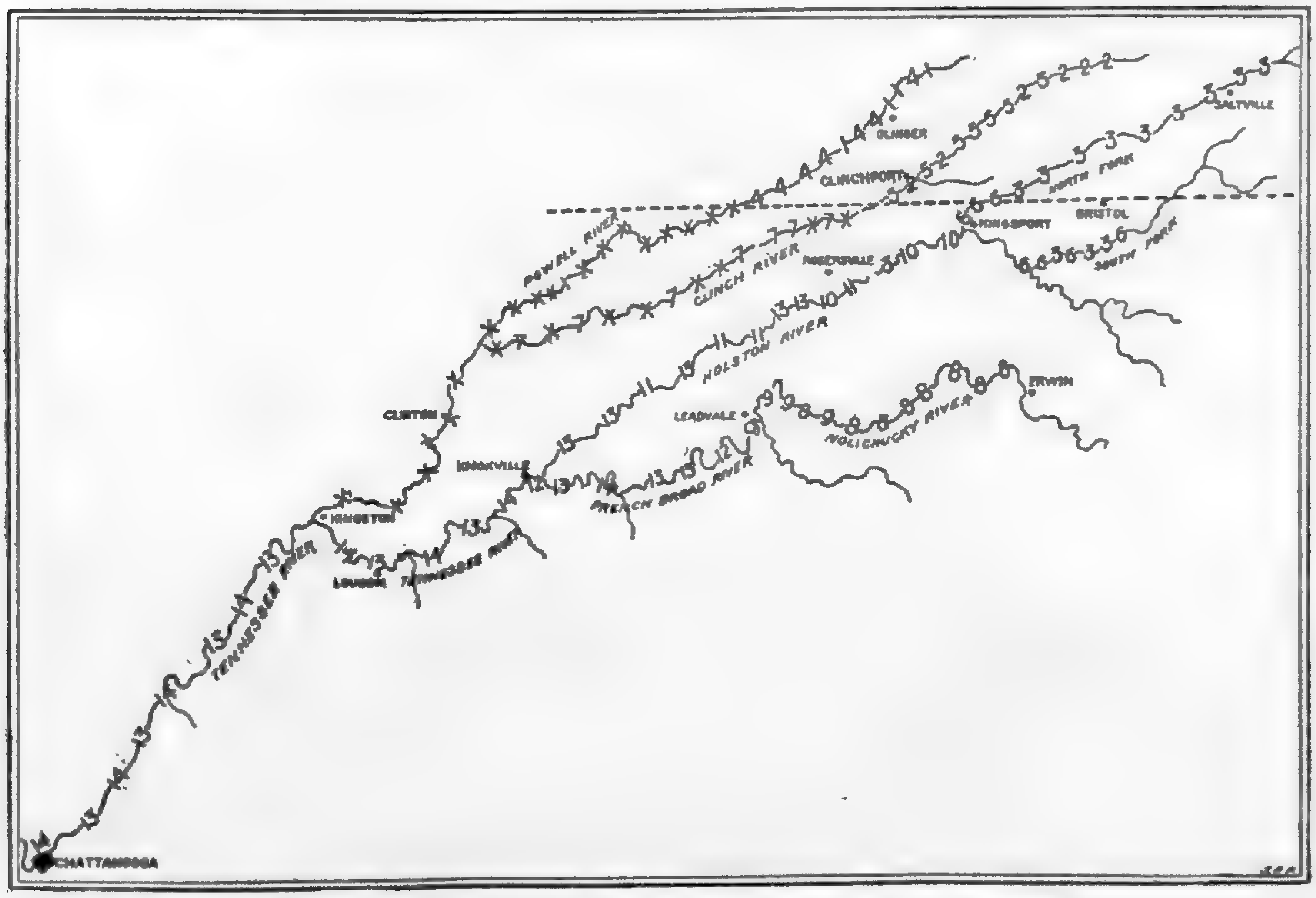

FIG. 4. Map showing the present distribution of the forms of the snail *Io* in the upper Tennessee River system. The numbers refer to the kind of shell illustrated in Fig. 5.

The competition among different kinds of animals has long been recognized as an important factor in animal migrations. Overcrowding produces a condition of stress, and as a result of this stimulus, animals tend to migrate and become diffused from the region of pressure in all possible directions. Thus new conditions are encountered which necessitate changes on the part of the animal, and thus this process continues indefinitely.

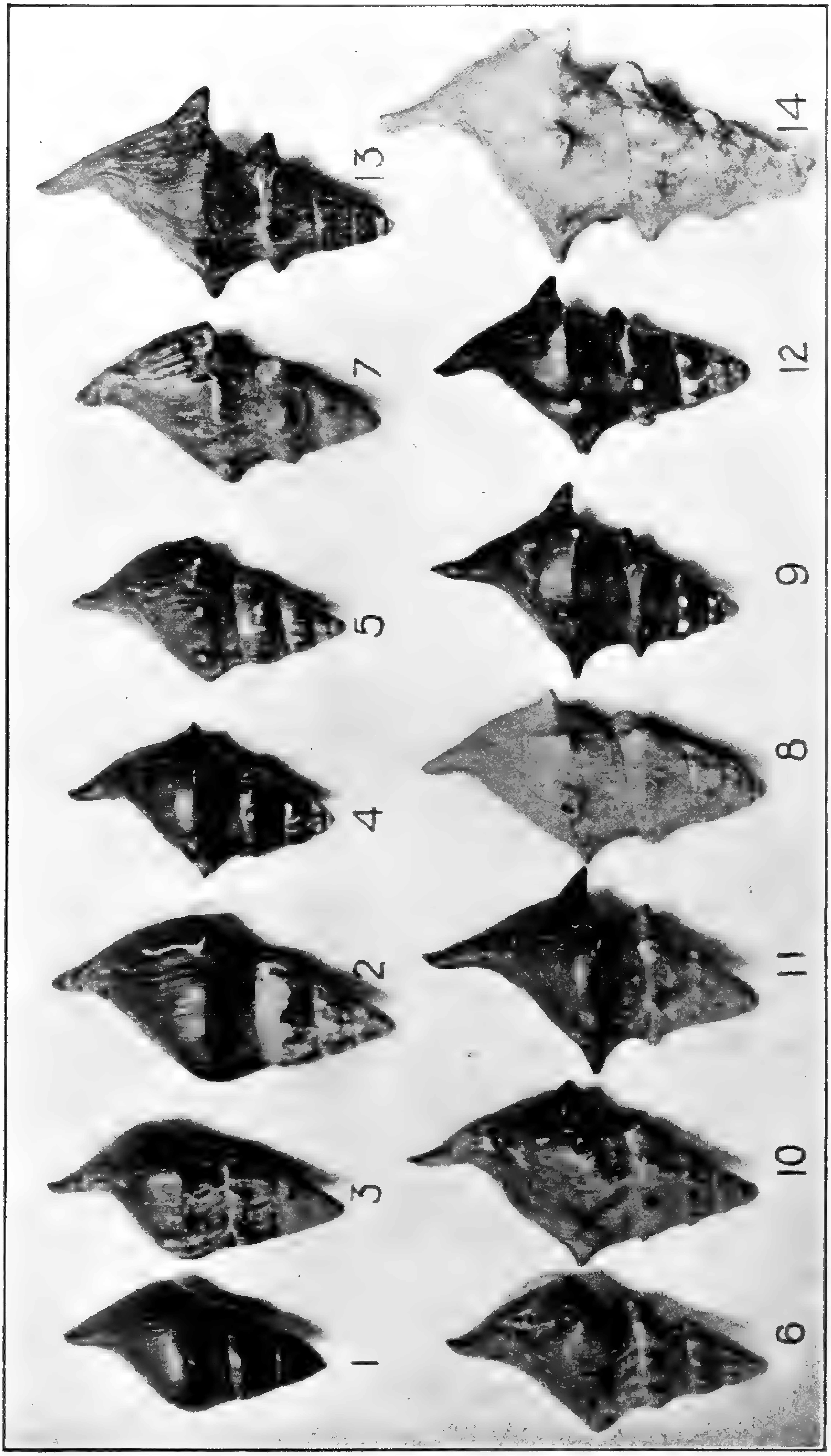

Fig. 5. Illustrations of the main forms of shells in the genus *Io*, whose hypothetical migrations are indicated in Fig. 3.

IV. Summary and Conclusions

The animal should be looked upon as a *dynamic system* which tends to continue in its course of action until changed from within or until diverted by external interference with its system, and until a condition of relative equilibrium is developed by balancing all influences. The behavior of animals should be viewed as a *process* of rhythmical activity.

The *cycle of activity* of the animal agent is a unit of fundamental importance. To study cycles, their *dynamic status,* their degree of relative equilibrium must be determined. In this manner the conditions of stress, the processes of adjustment to strain, and the conditions of relative equilibrium may be recognized and determined. These determinations should be applied to all cycles of activity, that of the life history, and all others. The use of these ideas enables one to apply Bancroft's law—that a system tends to change to minimize external disturbance—to animal activities, and thus one is enabled to explain a large number of diverse observations. Supplementary to Bancroft's law are the influences which tend to accelerate or reinforce, without other change, the condition of the animal.

The *activities of animals* cause them to collide with their environment. Conditions under which animals have become accustomed or attuned are those of relative equilibrium. With departure from these conditions, the animals are stimulated, their system is interfered with, and the animal tends to change until the interference is minimized. The hindrance thus placed upon animal activities are its "limiting factors," and these are to be viewed according to Bancroft's law. This law is not limited to the actions of the individual animal, but includes also the race, and those of animal associations. The Vernon-DeVries law of the *diminishing influence of the environment progressively during ontogeny,* is an example of limiting factors according to Bancroft's law. This law of Vernon's is of great value in the study of migration in relation to evolution because it suggests the *critical period* at which the stress of the new environment may have its *greatest direct influence upon the new generation* and thus influence its heredity.

The next important category above the animal system is the *law of interacting systems.* The main models of interacting systems are:

1. The physical model of interacting forces, recalling in this connection the law of *inertia,* the tendency of a body to continue in its present state at rest, or in motion, and the law of reinforcement or acceleration.

2. Bancroft's law is that a system tends to change in such manner as to minimize external disturbance. This should be applied to the interaction of all systems. This is a law concerned with responses to stress and to the process of adjustment, and it shows development or evolution of *equilibria.*

3. The phase rule applies to the *result* of responding to stress or *equilibria.* This is thus complementary to Bancroft's law; one is concerned with the condition of stress, and the other with the condition of equilibria.

These laws appear to be universal and not limited solely to the non-living. Irritability may not be causally explained, but *it seems to obey these general laws in the same manner as causal changes.* Applying these laws to animal migration, we see that the present geological age is one of physical stress, and that the process of adjustment to strain is now in operation. The physical stress applies to the air, water, earth and to their interactions. This is an age of physical diversity—tending toward one of simplicity and uniformity. With diversity there are many local cycles of activity in all features of the environment. These cycles of circulation influence the *transportation* of animals, and their active *migrations.* By transportation and migration animals encounter new conditions, new stresses, and change to minimize the disturbance and acclimate themselves to the limit of their possibilities; and they repeat this cycle with unending monotony and persistence.

December 15, 1917.

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Although these books by Spencer are in many ways not representative of the more recent conceptions, yet strange as it may seem to some, I have seen no better general discussion of biological problems which uses so many thoroughgoing dynamic conceptions. After familiarity with more modern views, these books may be read with great profit, particularly his discussions of cycles, relative equilibria, and his general conception of life processes. See footnote on page 488. Bancroft and Child make no reference to Spencer. Cf. Höffding, Darwin and Modern Science, 1910, pp. 450–455.

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ERRATA

P. 471, line 23 from top, third word should read "the."
P. 472, line 5, for "ontology," read "ontogeny."
P. 482, line 29, for "really," read "readily."

SOME STUDIES IN BLOSSOM COLOR INHERITANCE IN TOBACCO, WITH SPECIAL REFERENCE TO N. SYLVESTRIS AND N. TABACUM

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The blossoms of varieties of *Nicotiana tabacum* exhibit three distinct colors, white, carmine and pink.[1]

In the writer's crossing experiments, two white-flowered nicotianas were used, *N. sylvestris,* a species with long, slender, pure white blossoms, and a variety of *N. tabacum* from Honduras (S. P. I. No. 30887), with rather small, pure white blossoms of the *tabacum* type. The pink-flowered variety generally used was the Connecticut Broadleaf variety, although the varieties 70-leaf Cuban, a mammoth type of Cuban which appeared as a mutation in Connecticut in 1912, and Maryland Mammoth also were used. The carmine-blossomed tobacco[2] is a variety of *tabacum* sold by various seedsmen for ornamental purposes under the name giant red-flowering tobacco. This variety breeds true to blossom color and crosses readily with all the commercial varieties of *tabacum.*

Crosses of Pink-flowered Varieties with Carmine-flowered Varieties

In the crosses Pink ♀ × Carmine ♂ and their reciprocals, Carmine, without exception, has been perfectly

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[1] The colors carmine and pink have been compared with Ridgway's Color Standards and Color Nomenclature, 1912 edition. The carmine is practically identical with Ridgway's carmine, shown on Plate 1. The pink matches almost exactly his Hellebore Red, shown on Plate 38.

[2] There seems to be little definite information at hand concerning the origin of the carmine-flowered varieties of *N. tabacum.* O. Comes, in his monograph "Delle Razze Dei Tabacchi," *Atti. Del R'Inst. d'Incoraggiamento di Napoli,* Serie 6, 1905, pp. 77–306, speaks of the Nepal tobacco, a variety of *N. tabacum,* as having intensely red blossoms. The Rano variety is also said to have distinctly red blossoms.

dominant, so that all the blossoms of first generation plants bear carmine flowers.

TABLE I

FIRST GENERATION PLANTS OF CROSS CARMINE × PINK

Year	Row	Cross	No. of Plants	Remarks
1915	26A	Carmine ♀ × Pink (Md. Mammoth) ♂......	21	All carmine
1916	21C	Pink (70 leaf Cuban) ♀ × Carmine ♂......	27	" "
1916	26A	Carmine ♀ × Pink (70 leaf Cuban) ♂......	22	" "
1916	35A	Pink (Conn. Broadleaf) ♀ × Carmine ♂....	26	" "
1917	114A	Pink (Conn. Broadleaf) ♀ × Carmine ♂....	50	" "
Total			146	All carmine

TABLE II

SECOND GENERATION PLANTS OF CROSS CARMINE × PINK

Year	Row	Cross	No. of Plants	Red	Pink
1915	27B	Carmine ♀ × Pink (Md. Mammoth) ♂...	15	13	2
1916	19B	Pink (Conn. Broadleaf) ♀ × Carmine ♂...	39	30	9
1917	90B	Pink (Conn. Broadleaf) ♀ × Carmine ♂...	10	6	4
1917	91B	Pink (Conn. Broadleaf) ♀ × Carmine ♂...	42	29	13
1917	107C	Pink (Conn. Broadleaf) ♀ × Carmine ♂...	23	19	4
1917		Pink (Conn. Broadleaf) ♀ × Carmine ♂...	153	114	39
Total			282	211	71

From the data shown in Tables I and II, it is evident that the characters pink and carmine behave as typical unit characters, with carmine completely dominant. Segregation takes place in the 2d generation into carmine and pink blossomed plants very close to the theoretical ratio of 3 to 1.

A heterozygous plant of the first generation of the cross Pink (Conn. Broadleaf) ♀ × Carmine ♂ was then crossed with homozygous carmine. Of 115 plants obtained in this cross, all were carmine in color, which is in accord with the expected result.

Heterozygous plants of the first generation were now crossed with recessive pink with the following results.

From these results it is evident that the theoretical ratio 1:1 which obtains in such a cross is very closely approached.

TABLE III

Crosses Between Heterozygous Plants of the First Generation of the Cross (Pink ♀ × Carmine ♂) and Pink

Year.	Row.	Cross.	No. of Plants	Red	Pink
1915	18A	A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (White Burley Mammoth) ♂	19	7	12
1915	22	A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (White Burley Mammoth) ♂	41	17	24
1915	26B	A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (Md. Mammoth) ♂	19	11	8
1915	28B	A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (White Burley Mammoth) ♂	16	7	9
1917		A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (White Burley Mammoth) ♂	197	91	106
1917		A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (Conn. Broadleaf) ♂............	249	130	119
Total..			541	263	278

In further studies of the cross Carmine × Pink, the progenies of many extracted, recessive pink-flowered plants of the second generation have been grown, and all have produced pink-flowered lines. Of the carmine-flowered plants of the second generation, some (the heterozygous) have again broken up into Carmine and Pink, while others (homozygous) have given pure Carmine lines.

Crosses Involving Carmine of Pink with White

In crosses involving Carmine or Pink with White, white has behaved as a recessive, whether the cross has been made with the white-flowered species *N. sylvestris,* or with the white-flowered variety of *N. tabacum* S. P. I. No. 30887 from Honduras. Carmine, however, is not perfectly dominant in these crosses for plants of the first generation are somewhat lighter red than the carmine itself. In the cross Pink × White (*N. sylvestris*) the blossoms of the first generation are somewhat paler than the usual pink of the tabacum varieties. In crosses between pink-flowered varieties of *N. tabacum* and White (S. P. I. No. 30887 from Honduras) white has behaved as a recessive. The intensity of the dominant pink depends upon the pink variety used. In some crosses, the blossoms of the first generation plants are similar in color to the pink of the pink parent. In other crosses, the pink of the first generation plants may be noticeably deeper than that of the pink-flowered parent.

A number of heterozygous plants of the first generation of the cross Pink (Conn. Broadleaf) ♀ × Carmine ♂ have been used as mother plants and crossed with the recessive white *N. sylvestris,* with the following results:

42 plants, of which 25 were carmine blossomed and 17 pink blossomed.

41 plants, of which 23 were carmine blossomed and 18 pink blossomed.

Here we have a total of 83 plants, of which 48 possessed Carmine blossoms and 35 possessed Pink blossoms, showing an approximation to the 1:1 ratio. In crosses involving the species *N. sylvestris,* some difficulties are involved, since the first generation plants are usually sterile or nearly so. However, this sterility has been overcome in the cross in which a first generation plant of the cross (Pink (Conn. Broadleaf) ♀ × Carmine ♂) was pollinated with the pollen of *N. sylvestris.* In the second generation of this cross, whites, pinks and carmines appeared. A number of carmine plants were selected and their progenies studied. One known as no. 12, proved to be homozygous for carmine and has bred true to this color for several generations. A sister plant no. 9 with carmine blossoms proved to be heterozygous. In a progeny of 32 plants obtained from this plant, 26 were carmine and 6 were pink blossomed, approximating the theoretical ratio 3:1.

In the cross Carmine × White, using the white-flowered variety of *N. tabacum* S. P. I. No. 30887 from Honduras, the plants produce an abundance of fertile seed. As has been stated, carmine is dominant over white, but it is not a perfect dominance as in the cross Carmine × Pink, for the blossoms of the first generation plants are somewhat paler than pure carmine. In the second generation there is a segregation into whites, and various degrees of pinks and reds, ranging from light pink to pure carmine. Of 278 second generation plants of this cross, grown in 1917, the blossom colors were grouped as follows:

White	65
Dark pink	26
Light pink	38
Lighter than carmine	95
Carmine	54
Total	278

It is evident that the recessive whites which were easily determined approximated very closely the theoretical 25 per cent. Owing, however, to the uncertainty of analyzing correctly the varied pinks and reds, the carmines which probably represent the homozygous dominants are somewhat below the theoretical 25 per cent. It is quite probable that this class is somewhat smaller than it should be, owing to the difficulty of distinguishing with certainty all the homozygous carmines from the heterozygous somewhat paler carmines.

A number of extracted, recessive whites of the second generation of this cross have been grown and all have produced white-blossomed progenies. These white-blossomed plants have proved somewhat puzzling, however, for some seemed to reveal a hint of color, like an almost imperceptible sheen, that could be detected only in certain lights. So fugacious was this suggestion of color, that I felt inclined to ascribe it to the imagination, until certain crosses were made with pink-flowered varieties as follows:

From the cross Pink (Maryland Mammoth) ♀ × White (extracted) ♂, 54 first generation plants were obtained, of which 17 were carmine, 18 were pink as in the Mammoth, and 19 somewhat lighter than carmine.

In the reciprocal of this cross, *i. e.*, White (extracted) ♀ × Pink (Md. Mammoth) ♂, 43 plants were obtained, of which 20 were carmine, and 23 were pink blossomed as in the Mammoth.

This same extracted white-flowered plant was also crossed with Pink (Conn. Broadleaf) as follows:

From the cross Pink (Conn. Broadleaf) ♀ × White (extracted) ♂, 51 first generation plants were obtained, of which 12 were carmine or approaching it, and 39 were pink approximating the pink of the Broadleaf parent. It is apparent that the extracted white used in these crosses has somehow retained the factor of Carmine which reappeared in the cross with Pink.

From the results reported in this paper, the Mendelian behavior of the cross Carmine × Pink is particularly striking, and for those who wish to demonstrate before students interested in questions of heredity simple Mendelian behavior in a monohybrid, this particular tobacco cross is especially suitable. Not only is the technique of crossing easy, but a single fertile capsule from a cross will produce several thousand seed. Furthermore, tobacco plants may be readily grown to the flowering stage, in five or six inch pots under greenhouse conditions.

SUMMARY

Among the varieties of tabacum, carmine and pink in crosses behave as unit characters, carmine being dominant. In the second generation perfect Mendelian segregation follows, approximating very closely the theoretical ratio of three carmines to one pink. The extracted recessive pinks and the homozygous carmines breed true. The heterozygous carmines again break up into carmine and pink. If a heterozygous plant of the first generation is crossed with a pure carmine, the progeny will all produce carmine blossoms. If it is crossed with a pink, carmines and pinks will appear in the progeny, approximating the ratio 1 to 1.

In crosses involving carmine or pink with white, white behaves as a recessive, appearing in the second generation.

SHORTER ARTICLES AND DISCUSSION

A BIOLOGICAL SURVEY OF DESCRIBED CERCARIÆ IN THE UNITED STATES*

Among the earlier American zoologists Joseph Leidy alone was a student of cercariæ. From his time to very recent years American cercariæ have received little attention. This may have been due to the greater demands made by other groups of animals, or possibly to the minute size of the larvæ and a failure to appreciate the exact differences of their structure. It could not have been due to a lack of knowledge of the presence of cercariæ, for the European records were abundant and the classical studies of Leuckart, Ercolani and Looss had demonstrated the life-history relations of cercariæ and adult flukes. Moreover, the large number of adult trematode records showed that the larvæ must be fairly abundant.

Within the past few years a revival of study in this larval group has revealed a large number of forms, so that now there are some sixty named species. Only eight of these have dates prior to 1914. The majority of described cercariæ have been worked over by Cort, Faust and O'Roke.

A study of the descriptions of earlier named species shows them to be very general, so that they apply not to the species at all but to larger groups, genera or perhaps even subfamilies. For example, the record of a monostome with three eye-spots instead of characterizing a species merely distinguishes the trioculate from the binoculate group of species. A parallel is found in the diplostomulum commonly known as *Diplostomum cuticula* von Nordmann 1832, which has been recorded from a variety of vertebrate hosts and from equally variable habitats. There is great probability of the existence of several new species concealed beneath these generalized data. Such cases illustrate the futility of generalized descriptions.

Cort emphasizes the value of the excretory system of the cercaria as a basis of description. The conservatism of the system is urged as a basis on which fundamental group relationships of the trematodes can be discovered. Advantage in using this

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* Contributions from the Zoological Laboratory of the University of Illinois, No. 113.

TABLE I

RECORD OF DESCRIBED CERCARIÆ IN THE UNITED STATES

Name	Host	Locality and Date	Per Cent. Infection
Monostomes			
1. *C. urbanensis* Cort, 1914	*Physa gyrina* Say	Urbana, Ill., 1913	5.0
2. *C. konadensis* Faust, 1917	*Lymnæa proxima* Lea	Corvallis, Mont., 1916	31.3
3. *C. pellucida* Faust, 1917	*Physa gyrina* Say	Ft. Missoula, Mont., 1916	5.5
4. *C. pellucida* Faust, 1917	*Lymnæa proxima* Lea	Corvallis, Mont., 1916	31.3
5. *C. robusta* Faust, 1918	*Physa gyrina* Say	DeKalb, Ill., 1917	60.0
6. *C. aurita* Faust, 1918	*Goniobasis pulchella* (Anthony)	Homer, Ill., 1917	8.3
7. *C. hyalocauda* Haldeman, 1842	*Physa heterostropha* (Say)	Philadelphia, Pa., 1842 ?	?
8. *C. hyalocauda* Haldeman, 1842	" " "	Philadelphia, Pa., 1880	?
9. *C. lucania* Leidy, 1877	*Planorbis parvus* Say	Philadelphia, Pa., 1877 ?	Heavy
Amphistomes			
10. *C. inhabilis* Cort, 1914	*Planorbis trivolvis* Say	Lawrence, Kan., 1913	11.1
11. *C. inhabilis* Cort, 1914	" " "	Urbana, Ill., 1913	Few
12. *C. inhabilis* Cort, 1914	" " "	Lawrence, Kan., 1915	4.5
13. *C. diastropha* Cort, 1914	" " "	Chicago, Ill., 1913	5.0
14. *C. diastropha* Cort, 1914	" " "	Lawrence, Kan., 1915	4.0
15. *C. cortii* O'Roke, 1917	" " "	Cherryvale, Kan., 1915	4.0
16. *C. gorgonocephala* Ward, 1916	Free in plankton, host unknown	Put-in-Bay, O., 1901	Single specimen
Distomes			
17. *C. megalura* Cort, 1914	*Pleurocerca elevatum* Say	Sangamon River, Ill., 1913	1.4
18. *C. megalura* Cort, 1914	*Goniobasis virginica* Say	Princeton, N. J., 1908	?
19. *C. gracilescens* Faust pro *C. gracilis* O'Roke, 1917, preocc.	*Physa integra* Hald.	Chanute, Kan., 1915	4.0
20. *C. magnacauda* O'Roke, 1917	*Planorbis trivolvis* Say	Lawrence, Kan., 1915	5.0
21. *C. agilis* Leidy, 1858	"In company with *Planorbis*, *Paludina*, and *Lymnæa*"	Delaware, R., ?	?
22. *C. ascoidea* Leidy, 1877	*Planorbis parvus* Say	Philadelphia, Pa., 1877 ?	Heavy
23. *C. ascoidea* Leidy, 1877	*Lymnæa elodes* Say	Philadelphia, Pa., 1877 ?	?
24. *C. trigonura* Cort, 1914	*Campeloma decisum* (Say)	Hartford, Conn., 1913	11.0
25. *C. wrightii* Ward, 1916	In aquarium, host unknown	Toronto, Can., 1885	Single specimen

TABLE I—*Continued*

Name	Host	Locality and Date	Per Cent. Infection
Distomes			
26. *C. anchoroides* Ward, 1916[1]	Free-swimming, host unknown	Lake St. Clair, 1894	—
27. *C. douthitti* Cort, 1914	*Lymnæa reflexa* Say	Chicago, Ill., 1913	10.3
28. *C. douthitti* Cort, 1914	*Lymnæa stagnalis appressa* Say	Douglas Lake, Mich., 1915–1916	?
29. *C. douthitti* Cort, 1914	*Lymnæa stagnalis perambla* Walker	Douglas Lake, Mich., 1915–1916	?
30. *C. gracillima* Faust, 1917	*Physa gyrina* Say	Bitter Root River, Mont., 1916	19.4
31. *C. gracillima* Faust, 1917	*Lymnæa proxima* Lea	Missoula, Mont., 1916	3.1
32. *C. tuberistoma* Faust, 1917	*Physa gyrina* Say	Corvallis, Mont., 1916	5.3
33. *C. gigas* Faust, 1918	*Planorbis trivolvis* Say	DeKalb, Ill., 1917	56.0
34. *C. gigas* Faust, 1918	" "	Urbana, Ill., 1917	100.0
35. *C. gigas* Faust, 1918	*Physa gyrina* Say	Pine Creek, Ill., 1917	23.0
36. *C. minima* pro *C. minor* Faust, 1918 preocc.	" " "	DeKalb, Ill., 1917	6.0
37. *C. inversa* O'Roke, 1917	" " "	Lawrence, Kan., 1915	2.0
38. *C. echinocauda* O'Roke, 1917	" " "	Lakeview, Kan., 1915	6.0
39. *C. quieta* O'Roke, 1917	*Planorbis trivolvis* Say	Lawrence, Kan., 1915	15.4
40. *C. elephantis* Cort, 1918	" "	Douglas Lake, Mich., 1914–1916	?
41. *C. emarginatæ* Cort, 1918	*Lymnæa emarginata angulata* Sowerby	Douglas Lake, Mich., 1914–1916	?
42. *C. douglasi* Cort, 1918	*Physa ancillaria* Say	Douglas Lake, Mich., 1914–1916	?
43. *C. tardigrada* Leidy, 1858	*Anodonta (fluviatilis) cataracta* Say	Philadelphia, Pa. ? ?	?
44. *C. tardigrada* Leidy, 1858	*Anodonta (lacustris) marginata* Say	Philadelphia, Pa. ? ?	?
45. *Cercariæum helicis* Leidy, 1847	*Helix albolabris* Say	Philadelphia, Pa. ? ?	?
46. *C. helicis* Leidy, 1847[2]	*Helix alternata* Say	Philadelphia, Pa. ? ?	?
47. *C. leptacantha* Cort, 1914	*Campeloma decisum* Say	Hartford, Conn., 1913	8.3
48. *C. caryi* Cort, 1914	*Goniobasis virginica* Say	Princeton, N. J., 1909	?
49. *C. brevicæca* Cort, 1914	*Physa anatina* Lea	Manhattan, Kan., 1913	3.2
50. *C. crenata* Faust, 1917	*Lymnæa proxima* Lea	Ft. Missoula, Mont., 1916	13.6
51. *C. isocotylea* Cort, 1914	*Planorbis trivolvis* Say	Urbana, Ill., 1914	18.0
52. *C. isocotylea* Cort, 1914	" "	Urbana, Ill., 1916–1917	50.0
53. *C. isocotylea* Cort, 1914	" "	DeKalb, Ill., 1917	6.0
54. *C. polyadena* Cort, 1914	*Lymnæa reflexa* Say	Chicago, Ill., 1913	2.6

TABLE I—*Continued*

Name	Host	Locality and Date	Per Cent. Infection
Distomes			
55. *C. dendritica* Faust, 1917	*Lymnæa proxima* Lea	Ft. Missoula, Mont., 1916	35.7
56. *C. dendritica* Faust, 1917	" " "	Bitter Root River, Mont., 1916	10.3
57. *C. glandulosa* Faust, 1917	*Physa gyrina* Say	Corvallis, Mont., 1916	40.0
58. *C. diaphana* Faust, 1917	*Lymnæa proxima* Lea	Corvallis, Mont., 1916	31.3
59. *C. micropharynx* Faust, 1917	" " "	Missoula, Mont., 1916	56.3
60. *C. racemosa* Faust, 1917	" " "	Ft. Missoula, Mont., 1916	10.3
61. *C. hemilophura* Cort, 1914	*Physa gyrina* Say	Rockford, Ill., 1913	5.0
62. *C. stilifera* Faust, 1918	" " "	Pine Creek, Ill., 1917	6.6
63. *C. haskelli* O'Roke, 1917	" " "	Lawrence, Kan., 1915	3.0
64. *C. gregaria* O'Roke, 1917	*Planorbis trivolvis* Say	Cherryvale, Kan., 1915	21.7
65. *C. kansiensis* O'Roke, 1917	" " "	Pratt, Kan., 1915	75.0
66. *C. Lissorchis fairporti* Magath, 1918	" " "	Fairport, Iowa, 1917	10.0
67. *C. platyura* Leidy, 1890	*Lymnæa* sp.?	Fort Bridger, Wyo. ?	Free in pool
68. *C. reflexæ* Cort, 1914	*Lymnæa reflexa* Say	Chicago, Ill., 1913	21.0
69. *C. rubra* Cort, 1914[3]	*Campeloma decisum* (Say)	Hartford, Conn., 1913	16.6
70. *C. trivolvis* Cort, 1914	*Planorbis trivolvis* Say	Urbana, Ill., 1913	Few
71. *C. trivolvis* Cort, 1914	" " "	DeKalb, Ill., 1917	23.3
72. *C. biflexa* Faust, 1917	*Physa gyrina* Say	Ft. Missoula, Mont., 1916	7.0
73. *C. trisolenata* Faust, 1917	" " "	Ft. Missoula, Mont., 1916	49.1
74. *C. trisolenata* Faust, 1917	*Planorbis trivolvis* Say	Ft. Missoula, Mont., 1916	75.0
75. *C. chisolenata* Faust, 1918	*Physa gyrina* Say	Pine Creek, Ill., 1917	8.3
76. *C acanthostoma* Faust, 1918	" " "	Urbana, Ill., 1917	100.0
77. *C. acanthostoma* Faust, 1918	*Planorbis trivolvis* Say	Urbana, Ill., 1917	100.0
78. *C. fusiformis* O'Roke, 1917	*Physa gyrina* Say	Lawrence, Kan., 1915	1.0
Holostomes			
79. *C. flabelliformis* Faust, 1917	*Physa gyrina* Say	Corvallis, Mont., 1916	23.3
80. *C.* (*Tetracotyle*) *typica* Diesing, by Leidy, 1890	*Galba catascopium* (Say)	Philadelphia, Pa. ? ?	?
81. *C.* sp. by Rettger, 1896	*Lymnæa stagnalis* (Linn.)	Terre Haute, Ind. ?	?

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[1] Recently the writer has described two species closely related to *C. anchoroides: C. brookoveri*, from Campeloma sp., Cedar Point, Lake Erie, 1912, and *C. macrostoma*, free in an aquarium, Urbana, Ill., 1917.

[2] Possibly Agamo distomum.

[3] Agamo distomum.

system lies in the fact that it can be studied entirely in the living cercariæ. The writer has used this method with profit, but in addition has worked out a method of staining the genital organs in the preserved larvæ. This method can be utilized when the worker has access only to preserved larvæ. While the excretory system is indeed a conservative system, the genital system is probably more conservative and less likely to change from cercarial to adult stage. It has been found to be remarkably similar in the large, yet variable in minor, details in groups of cercariæ known to be related through other organs or systems. The best description of a cercaria is probably that which includes both the excretory system as worked out in the living animal and the genital cell masses as depicted in carefully preserved and stained material.

A mere superficial description of the worm is a distinct burden on the literature. The cercaria should be carefully studied in minute detail or not at all. It is the nicety of technic and care in observation which have yielded the number of species now known and bids fair to increase the number vastly in the next few years. It is necessary, then, to urge the investigator in this group to use the utmost care in his work, to describe the minute parts of the organs, and to record the complete biological data available that these records may be of use in life-history investigations.

In order to place the more important biological data of described cercariæ in the United States in a convenient form, a table has been prepared to cover the groups, the authors and dates of the naming of the species, the hosts, localities and dates of collections and the per cent. of infection (see Table I). The same data have been collated from the standpoint of the host in Table II.

A study of the described species shows that the great bulk are distome larvæ. Most of these fall into three groups, the stylet, echinostome and forked-tailed cercariæ. The former group bear evidence of relationship to the Plagiorchiidæ; the echinostome cercariæ are known to be larval Echinostomidæ, and the forked-tailed cercariæ are probably larval schistosomes. The life history of only one species in the group has been worked out with certainty, that of *Cercaria Lissorchis fairporti*, with *Planorbis trivolvis* as larval host, a chironomid larva as intermediate host, and *Ictiobus* spp. as definitive hosts. Of the species recorded

TABLE II

RECORD OF MOLLUSK INFECTION WITH CERCARIÆ

Host Species	Total No. Species	Mono-stome	Amphis-tome	Distome	Holo-stome	Distinct Localities
Planorbis trivolvis	14	0	3	11	0	7
Planorbis parvus	3	1	0	2	0	1
Campeloma decisum	3	0	0	3	0	1
Lymnæa sp.	1	0	0	1	0	1
Lymnæa proxima	8	2	0	6	0	1
Lymnæa emarginata angulata	1	0	0	1	0	1
Lymnæa elodes	1	0	0	1	0	1
Lymnæa stagnalis	1	0	0	0	1	1
Lymnæa stagnalis appressa	1	0	0	1	0	1
Lymnæa stagnalis perambla	1	0	0	1	0	1
Lymnæa reflexa	3	0	0	3	0	1
Physa gyrina	19	3	0	15	1	5
Physa anatina	1	0	0	1	0	1
Physa heterostropha	1	1	0	0	0	1
Physa integra	1	0	0	1	0	1
Physa ancillaria	1	0	0	1	0	1
Goniobasis pulchella	1	1	0	0	0	1
Goniobasis virginica	2	0	0	2	0	1
Pleurocerca elevatum	1	0	0	1	0	1
Galba catascopium	1	0	0	0	1	1
Helix alternata	1	0	0	1	0	1
Helix albolabris	1	0	0	1	0	1
Anodonta cataracta	1	0	0	1	0	1
Anodonta marginata	1	0	0	1	0	1
Free-swimming only	3	0	1	2	0	3
Total No. distinct host records	72	8	4	57	3	
In two or more hosts	11	2	0	9	0	
Net species	61	6	4	48	3	

for the United States only one, *C.* (*Tetracotyle*) *typica* Diesing, 1858, is recorded for another locality than North America.

The larval hosts are without exception mollusks. All except two, *Anodonta cataracta* and *A. marginata,* are Gasteropoda. Several of the species have been found in two snails, although none have been recorded as infecting three or more hosts. Usually where the species occurs in two hosts the infection of the one is more widely spread and heavier than that of the other. Several records show the parasitism of several species of cercariæ within the same host species in the same locality. In fact, the writer found as many as four trematode species within the same host individual (*Planorbis trivolvis*) at DeKalb, Illinois, in August, 1917. The occurrence of two cercariæ species in the same host individual is commonly found in the records. In this case one of the parasites usually has a heavier hold on the host than the other and constitutes the major infection.

Limited geographical areas have been covered in the surveys for cercariæ. Two drainage systems of the Atlantic slope, isolated regions around the Great Lakes, a portion of the upper Columbia and an isolated region in Wyoming, together with more widely investigated areas in the Mississippi basin, constitute the localities in which collections have been made. The entire south, southeast and southwest constitute vast unexplored areas, the former two of which should yield a great number of species. In addition, the variation of species of flukes in snails from one season to another makes it highly probable that many more species occur in the Mollusca of the areas surveyed than the records show. Table I shows that one distome species, *Cercaria megalura*, has been found in *Goniobasis virginica* from the Atlantic slope, and in *Pleurocerca elevatum* from the Mississippi basin; and that *C. inhabilis* and *C. diastropha* have been found on both the eastern and western slopes of the Mississippi drainage. On the other hand, none of the species described for the Bitter Root Valley have been recorded east of the Rocky Mountains.

Records of percentage of infection from larval flukes vary from a few hundredths of a per cent. for certain cercariæ described by Sisnitzin in 1911 from the Black Sea to a heavy infection of every individual of a particular species in a locality. The lowest infection record for the United States is one per cent. (*C. fusiformis* in *Physa gyrina*). On the other hand, several heavy infections have been recorded, including three with total infection. The mollusks most heavily infected are the ubiquitous species, *Planorbis trivolvis* and *Physa gyrina,* and the western species, *Lymnæa proxima.* In the case of the *Planorbis* and the *Lymnæa* the average heavy infection is caused by distome cercariæ. The heavy infection among the physas is caused by monostome and holostome larvæ.

Table II, which summarizes the infection from the host point of view, shows that *Lymnæa proxima* has the greatest number of species per habitat. *Planorbis trivolvis* has been found to be infected in the greatest number of localities, while *Physa gyrina* is the only mollusk to harbor three groups of *Digenea.* Of the sixty named species listed in Tables I and II eleven are recorded from two hosts.

Accompanying the cercariæ in the mollusks are the parthenitæ (sporocysts and rediæ) of these cercariæ. The cercariæ develop parthenogenetically within these parthenitæ. Typically, as in the life history of *Fasciola hepatica,* the sporocyst and redia generations both occur, but in several groups, notably in the stylet cercariæ and the furcocercariæ the redia stage has been omitted or replaced by another sporocyst stage.

Sporocysts and rediæ have not been sufficiently distinguished. The sporocyst is an adult which has lost its digestive tube, while a redia is an adult which possesses both a rhabdocœle gut and a pharyngeal sphincter. In certain sporocysts the sphincter still remains, as in *C. dendritica.* In other sporocysts, as in some furcocercariæ, while no definitely differentiated sphincter is present, the anterior end of the sac is muscular, turning in and out like the finger of a glove. This may easily be mistaken for a rhabdocœle gut.

The cercariæ develop within the parthenitæ and usually at the time of maturity break out of the parent and work their way through the tissues of the host into the water. In case no suitable host is at hand in which the larvæ may continue development they ordinarily encyst. Groups like the furcocercariæ, however, are not known to encyst. On the other hand, the writer has found encysted larvæ of *C. biflexa* within the larval host and encysted larvæ of *C. micropharynx* even within the parent sporocysts.

The parthenitæ of monostome, amphistome and holostome cercariæ are rediæ. Parthenitæ of certain groups of distome cercariæ are sporocysts and of other groups of distome cercariæ are rediæ, although some of the records are conflicting. This shows the need of the accurate determination of the parthenita of each cercaria, since the parthenita is a distinct generation in the life history of the species.

In order that the records may not be confusing the writer proposes the name *Cercaria gracilescens* for *C. gracilis* O'Roke 1917, preoccupied by La Valette 1855, and *C. minima* for *C. minor* Faust 1918, preoccupied by Lebour 1912.

In conclusion, the effect of the larva on the mollusk must be emphasized. It is an observable fact that heavily infected snails die sooner than uninfected ones. The cause of this mortality is both the mechanical disruption of the tissues of the infected mollusk and the pathological changes within the cells of the infected animal. A pathologico-chemical study of this relationship would be of great value to parasitologist and malacologist alike.

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ON REGENERATION AND THE RE-FORMATION OF LUNULES IN MELLITA[1]

THE ambulacral lunules of the genus *Mellita* are characteristically developed by the inclusion of reëntrant marginal notches; except that in *M. sexiesperforata* these lunules, like the interambulacral lunule in this and in related genera, is formed by resorption through the test.[2] In a few species the ambulacral lunules are permanently maintained as open marginal notches, and Jackson[3] has called attention to the fact that in *Encope annectans* Jackson, the adult interambulacral lunule is represented by mere dorsal and ventral furrows, not sufficiently deep to meet and form a hole through the test. In view of the possibly exceptional character of the formation of the ambulacral lunules in *M. sexiesperforata,* note may be made of the manner in which the lunules of this species are re-formed during regenerative changes consequent upon natural injury. For in collections of *Mellita* comprising half-a-dozen or more individuals of adult size it is rarely found that every specimen presents a complete and regular marginal outline. The degree of irregularity is in most instances not large, but in some cases amounts, at the deepest point, to a radial deficiency of 13 mm. in a specimen 12 cm. in transverse diameter. I have found no irregularities of this character in specimens less than 8 cm. in transverse diameter. The nature of these deficiencies is such as to suggest that they have been inflicted by other bottom-feeding animals, possibly fishes. The wound-surfaces seem, however, to be readily covered over; and the various degrees of alteration toward a more perfect outline, exhibited in different specimens, show that relatively complete restitution is possible.

It is a noteworthy fact that these injuries are almost entirely confined to that end of the animal which is morphologically the posterior (cf. Figs. 1, 2, 3). It seems to me possible that this fact may be understood upon the assumption that when burrowing the anatomically anterior end of the "sea plate," which is somewhat more sharply pointed than the posterior, is the one

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[1] Contributions from the Bermuda Biological Station for Research.

[2] Agassiz, A., "Revision of the Echini," pp. 320–324. Clark, H. L., 1904, "Echinoderms of the Woods Hole Region," *Bull. U. S. Bur. Fish.* for 1902, pp. 545–576 (p. 565).

[3] Jackson, R. T., 1917, *Proc. U. S. Nat. Mus.*, Vol. 53, pp. 489–501 (p. 494).

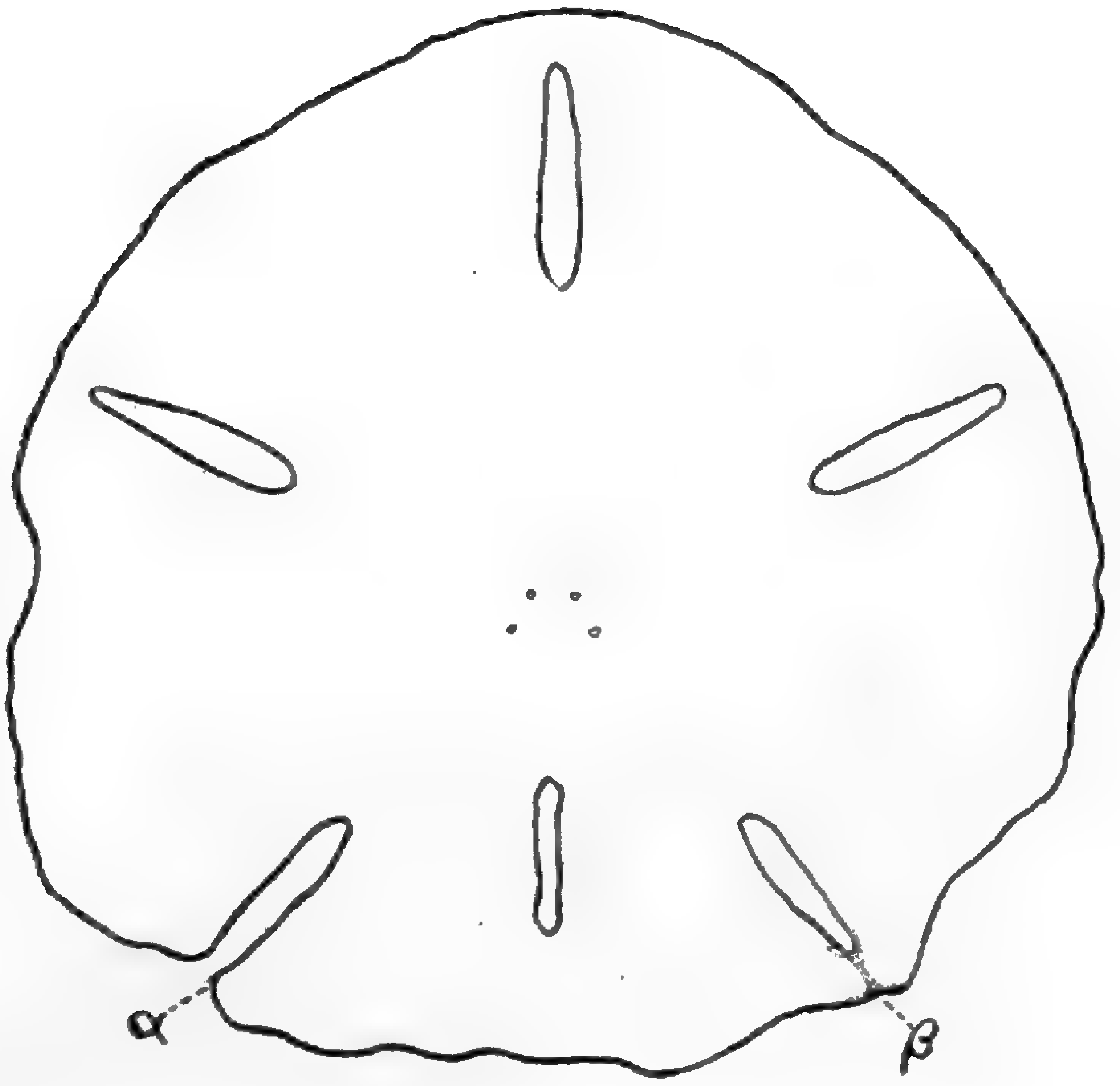

FIG. 1.

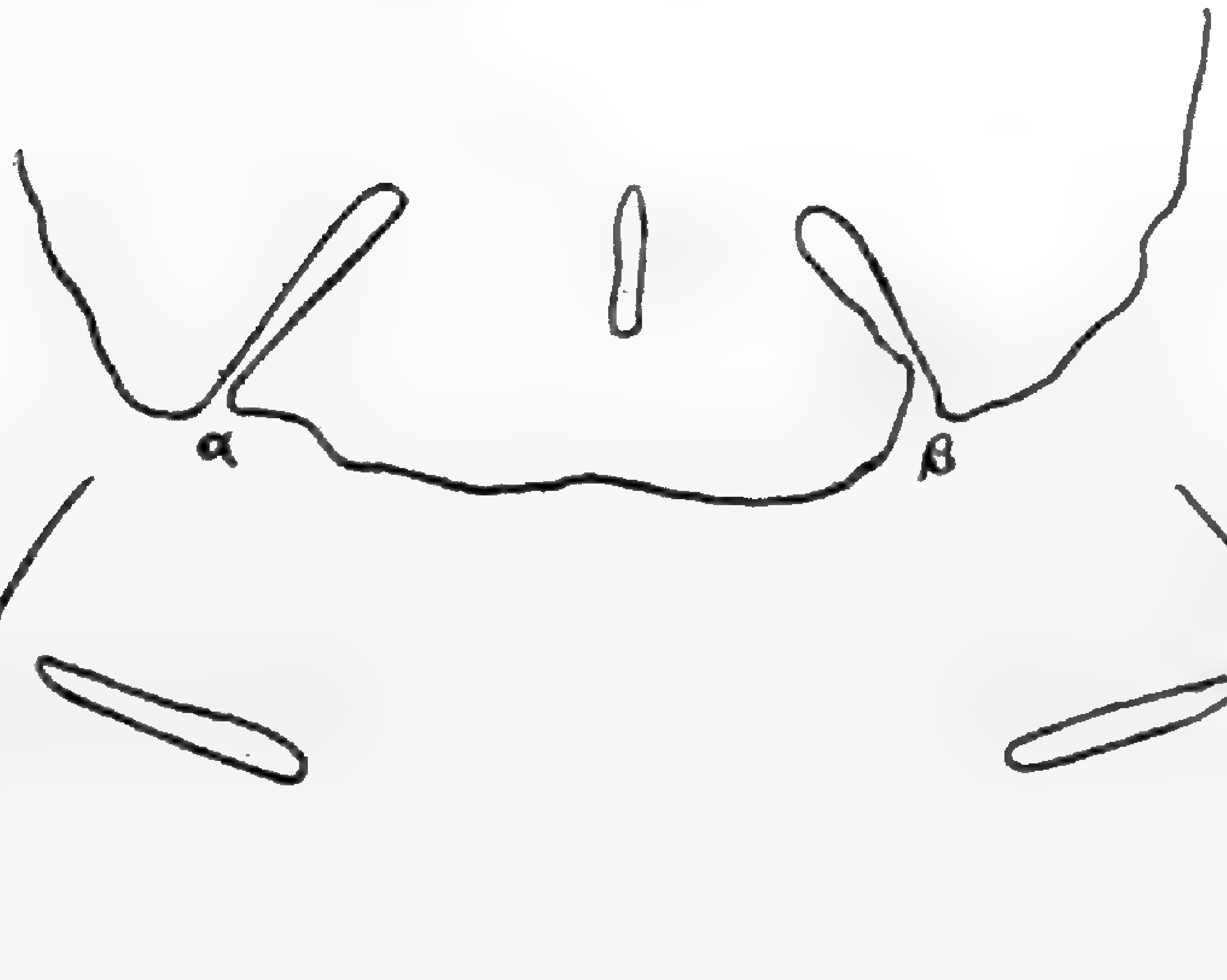

FIG. 2.

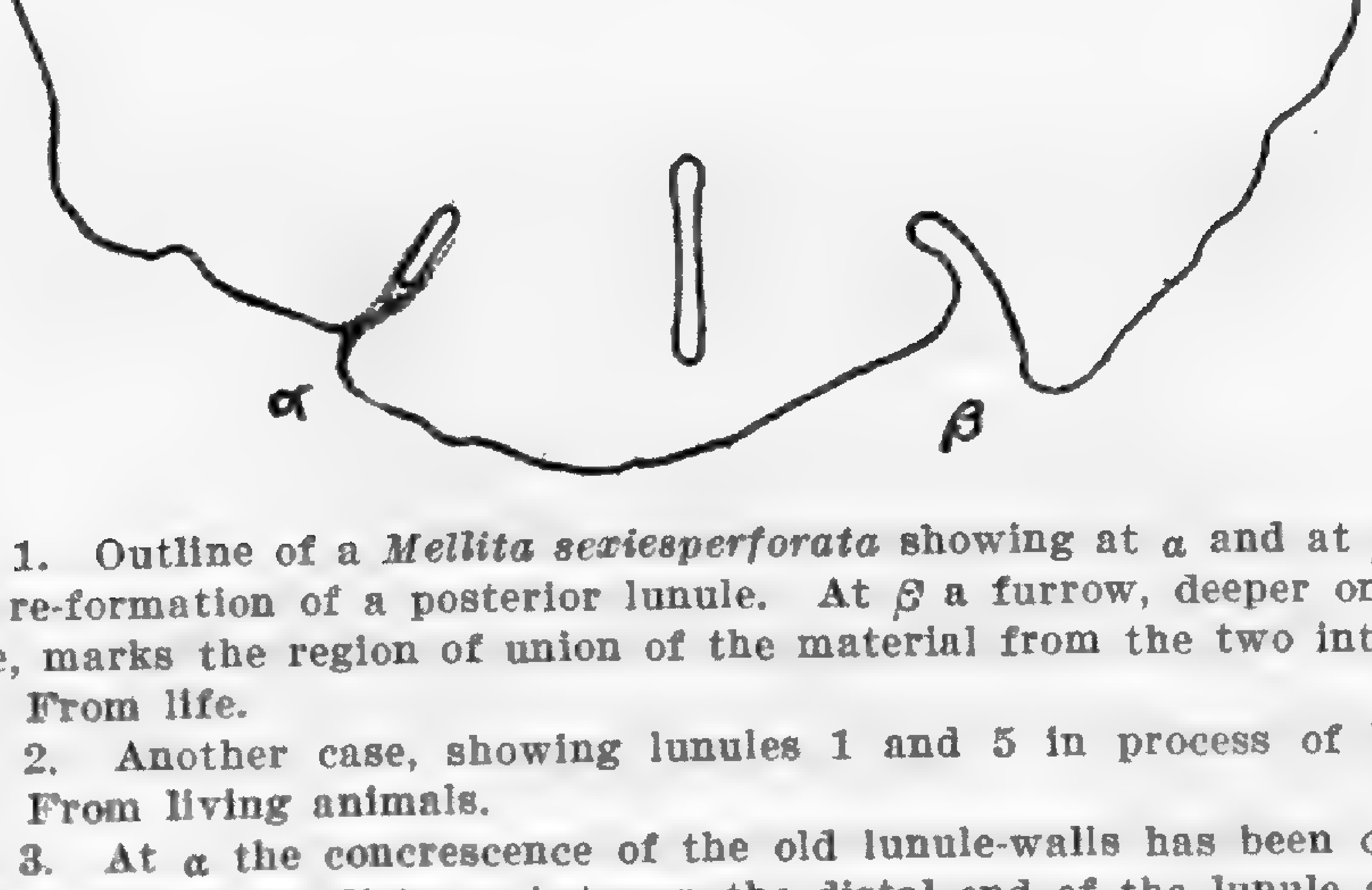

FIG. 3.

FIG. 1. Outline of a *Mellita sexiesperforata* showing at α and at β two stages in the re-formation of a posterior lunule. At β a furrow, deeper on the ventral surface, marks the region of union of the material from the two interambulacra. (× 1.) From life.

FIG. 2. Another case, showing lunules 1 and 5 in process of being closed. (× 1.) From living animals.

FIG. 3. At α the concrescence of the old lunule-walls has been carried to an extent such that the distance between the distal end of the lunule and the margin of the disc is actually greater than in the case of a lunule normally formed. Here also the furrow indicated by shading is deeper on the ventral surface. At β, deformation of a lunule through growth after injury. (× 1.) From life.

which is carried ahead.[4] These animals do burrow beneath the surface of the sand when the weather is at all stormy, and, if this assumption be valid, the posterior end might then be exposed (or even separated somewhat from the bottom) to a greater extent than at other times. If the process of emergence from the sand is somewhat different from, or quicker than, that involved in burrowing, one could understand why the anterior end is rarely, if ever, damaged, as might otherwise be expected if differential exposure of some kind alone determines the incidence of injuries; there are, of course, other possibilities.

However they originate, the restorative phenomena which these posterior injuries entail show that the ambulacral lunules of *M. sexiesperforata* May, in regeneration, follow a method of formation resembling, in a measure, that adhered to in the normal development of these lunules by other mellitas. The individuals herewith depicted in outline (Figs. 1, 2, 3) exhibit several stages in a process of lunule-completion through the concrescence of the growing edges of the disc. It is difficult to decide whether this process is of a specific regulatory character, "aiming at" the reconstitution of the lunules, or whether it represents merely the inevitable consequence of ordinary (though accelerated) growth at the margin of the mellita disc, and is, perhaps, for this reason, devoid of any recapitulatory significance. An inspection of Fig. 1 will show that at α there is evident a decided out-bulging of the disk-margin, at the point of union with the old outline of the lunule. This out-bulging, seen also at β in Fig. 2, and at β in Fig. 3, shows definite growth of the tissue toward the opposite lunule-wall in interambulacrum *V*. At β in Fig. 1 an outgrowth of this type has met and fused with a less extensive outgrowth from the opposite lunule-boundary; here, as at α in Fig. 2, it will be noted that the lateral extension of interambulacral area *V* is not confined merely to the margin of the disc, but affects also the whole lateral wall of the lunule on that side,—provided the injury be sufficiently extensive—so that closure of the lunule is slow. If the original disturbance be small, as at β in Fig. 1, this and other similar cases show that reparation may be relatively complete. On the other hand, more extensive injury, as at β in Fig. 3, seems to result in "regeneration" which is not so quickly effective as, for example, in β, Fig. 1; under these circumstances the posterior extension of the substance of interambulacrum *I*,

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[4] Cf. Cole, L. J., 1913, *Jour. Exp. Zool.*, Vol. 14, pp. 1–32.

not met by growth from interambulacrum *V*, produces a relatively considerable distortion of the old lunule. Moreover, the coalescence of the lunule-walls may be carried to a length which seems greater than it need be, as a *a* in Fig. 3. For these reasons the idea of a specific regulatory character in the re-formation of the lunule seems unnecessary.

It would be of interest to observe the effect, upon the course of regeneration, of an injury deep enough to remove the area of a lunule down to its proximal border; I have seen no cases of this kind, nor any in which the interambulacral lunule had been affected.

Morgan[5] was unable to find in the literature any mention of regeneration among echini. The present observations may consequently help to fill a gap at that point, since I am not aware that any one has previously commented upon the matter, although the conditions described are perhaps well known to other students of echinoderms. For *M. pentapora* cases have indeed been noted in which a lunule, unclosed, extended to the periphery of the disc; but these instances have been referred either to accidental injury or to delayed growth, and "repair" phenomena seem not to have been observed. In *M. sexiesperforata* regeneration (of a sort) does undoubtedly occur, giving evidence of a respectable degree of plasticity in a stony structure where such might not be expected.

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[5] "Regeneration" (1901), p. 105.

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AN EARLY PAPER ON MAIZE CROSSES

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IN the writer's opinion the paper of McCluer, entitled "Corn Crossing,"[1] has lacked adequate appreciation by later investigators. This paper is referred to by East (3), Shull (7) and Collins (1) in various articles, but only with reference to McCluer's observations on the superiority of F_1 hybrids in point of yield, as compared with their parents. The other matter of genetic interest in the paper seems to have attracted little attention, perhaps because of the more extensive earlier experiments ('89–91) of Kellerman and Swingle (4), and the more important later ones of Correns (2).

However, with respect to the superior yield of F_1 hybrids, McCluer's paper exceeds in interest the more frequently quoted ones of Morrow and Gardner[2] in respect to the wider variety of types selected for crossing, and especially in the fact of the progeny of the F_1 plants having been followed out in the yields of the F_2 generation, which, in all but a very few cases, were found to be distinctly less than the yields of the F_1 plants. This seems to have been, historically speaking, the first demonstration of the inferiority in yield of F_2 segregates, as compared with first generation hybrids. McCluer's experiments involved a wider range of types of maize than did those of Morrow and Gardner, and comprised dent, sweet,

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[1] Ill. Ex. Sta. Bull. 21, May, 1892.

[2] Ill. Ex. Sta. Bull. 25, 179–80, and 31, 359–60.

pop and soft corn varieties in eighteen different crosses. He was thus enabled to make observations on the inheritance of characters other than those resulting in yield.

In 1889 McCluer began his hybridization work with corn, crossing a number of strains of dent maize, without at first, however, making crosses between varieties of different colors. In addition he utilized the following characters in thirteen crosses made in 1889, and in five crosses made in 1890 obtained in the former year 36 and in the latter year 158 ears.

Sugary endosperm	×	starchy endosperm.
White endosperm	×	yellow endosperm and the reciprocal.
Starchy endosperm	×	corneous endosperm and the reciprocal.
Corneous endosperm	×	sugary endosperm.
Non-colored aleurone	×	purple aleurone.

Expressing these crosses in the following notation, according to presence and absence, for convenience, without regard to the actual gametic composition of the parents, which of course can only be inferred, we have:

A. Yellow endosperm.
a. White endosperm.
B. Starchy endosperm.
b. Sugary endosperm.
C. Colored aleurone.
c. Non-colored aleurone.
C. Corneous endosperm.

McCluer's crosses then classify according to the formulas on the following page.

Leaving it understood that this is simply a classification in shorthand formulas, of the visible characters, without predicating their gametic composition, which was unknown to McCluer, since he far antedated the days of pure lines, Mendelism and factorial analyses, we are struck by the number of factors with which he experimented, and with his clean observations on the results. Being a horticulturist, he was led to be interested in these various types of maize, to which Morrow and Gardner, as agronomists, gave no attention.

Cross	Phenotype Characters	Variety		Phenotype Characters	Variety
1	abc	Mammoth	×	ABc	Leaming
2	abc	Triumph	×	ABc	"
3	abc	8-rowed	×	ABc	"
4	abc	Mammoth	×	Abc	Golden Coin (Sweet)
5	abc	Triumph	×	Abc	" " "
6	abc	8-rowed	×	Abc	" " "
7	abc	Mammoth	×	Abc	Stowell's Evergreen
8	abc	Triumph	×	Abc	" "
9	abc	8-rowed	×	Abc	" "
10	abc	White Dent (unnamed)	×	ADc	Queen's Golden Pop
11	ADc	Queen's Golden Pop	×	ABc	White Dent (unnamed)
12	ADc	" " "	×	abC	Black Mexican
13	ABc	White Dent (unnamed)	×	abC	" "
14	ABc	Brazilian Flour	×	Abc	Gold Coin (Sweet)
15	ADc	Pearl (pop)	×	ADc	Queen's Golden (Pop)
16	aBc	Burr's White Dent	×	aBc	Brazilian Flour
17	aBc	Yellow Dent variety	×	aBc	White Dent variety
18	aBc	White Dent variety	×	aBc	Yellow Dent variety

McCluer found no xenia effect to be produced, where, as he says, ears "of the same color" but of different types are crossed.

> The typical ear of Stowell's Evergreen differs very decidedly from typical ears of either 8-rowed, Triumph or Mammoth, but the ears produced by pollen of Stowell's on either of the others, did not differ from the female type in any way, more than did many ears left to be fertilized naturally.

In other words, he observed that the "maternal" tissues beyond the endosperm were not affected by the crossing.

McCluer found that in F_1 ears, of crosses between yellow and non-yellow endosperm, the dominant yellow of the F_1 kernels was never as dark as in the yellow parent, whether the latter were the pollen or the seed parent. This fact was observed in crosses 1, 2, 3, 10, 11, 13, 17 and 18. Since McCluer remarks that the effect was not uniform in yellow dent × white dent crosses and their reciprocals, he may in these cases have unconsciously run across the phenomenon of two yellows, as reported in 1911 by East and Hays (3), pp. 46–56. It is probable, however, that most of the instances were cases of the heterozygous yellows, being lighter than the homozygous yellows, as reported by East and Hayes, *loc. cit.*, pp. 55–6. In McCluer's crosses, 14, 17 and 18 at least, he was evidently working with endosperm color factors, the behavior of which was identical with those reported by East and Hayes in their crosses as given in the citation above.

McCluer made a considerable number of observations on xenia, but remarks (italics mine), "*The results obtained from planting crossed seed have been of more importance than the immediate effect of crossing,* not so much in themselves perhaps as in the conclusions which may be drawn from them." Such a point of view could only have been arrived at by one with something of an instinct for genetic studies.

McCluer remarks upon the great uniformity of what we should call F_1 hybrids. He says:

> Of 142 plots planted with sweet corn, pop-corn and their crosses, it is safe to say, there was as much uniformity in any one of the crossed plots, as in any, and very much more than was found in most of the plots planted with pure varieties.

Some interesting notes were made as to the characteristics of some of the F_1 plots. For example, it seems that the plots in which Leaming was used as the pollen parent decidedly resembled that parent; that in crosses between Queen's Golden × White Dent, the F_1 plants resembled the pollen parent, whereas in the reciprocal cross, the plants were intermediate between the two parents. An interesting result came from the cross between Queen's Golden and Pearl pop-corn. The stalks were intermediate between the parents, but larger than the average of the two parents. This characteristic extended to the growth of the cob, so that the F_1 ears were distinctly larger than the average of the ears of either of the parents—a fact very well illustrated in Plate 2 of the bulletin. Plots of F_1, hybrids between White Dent × Black Mexican, decidedly resembled the white dent. An extraordinary result seems to have been obtained in this cross. The F_1 seeds—*i. e.*, the seeds of the white dent ear pollinated with Black Mexican pollen, show the usual dominance of purple aleurone in the F_1 kernels. But the starchy character, ordinarily completely dominant in F_1 seeds of starchy × sugary endosperm crosses, is not dominant in all the kernels. So far as the F_1 ear illustrated on Plate 1 indicates, on which there are four tolerably complete rows in sight, there is a ratio of wrinkled to smooth kernels of 73:50, or approximately 1:1, which would go to indicate that the seed parent was probably heterozygous as to starchy endosperm. The wrinkled seeds from this ear produced ears, to judge again from the plate, for there is no detailed description, that were pure wrinkled in their kernels, whereas the smooth kernels from the F_1 ear produced ears on which both smooth and wrinkled F_2 kernels were borne. Three such ears are illustrated. On each of these ears three complete rows of kernels are visible in the illustration. Counts of these kernels, as nearly as they can be made from the illustrations, show: In ear No. 3 (*i. e.*, the ear showing the immediate effects of the cross and bearing the F_1 kernels) the ratio of smooth seeds to wrinkled seeds is as 73:50.

It was eight years later that the papers of Mendel were rediscovered, and at this time no scientific knowledge of the genetic behavior of corn existed at all. McCluer obtained, however, very definite evidence that the ears "borne by hybrid corn plants grown the first year from the cross," as he puts it, or as we should say to-day, plants of the F_1 generation, were larger on the average than the average ear borne by the parents, and that the yield was greater. Taking McCluer's tabulations of his results on p. 97 of Bull. 21, and revising its notation to correspond with present usage, we have the data given on page 102.

From this early experiment the result of crossing, so far as the yield of the F_1 generation is concerned, is fairly well indicated, since in fourteen cases out of eighteen the F_1 hybrids yield more than the average of the two parents, although in only seven cases did the yield of the F_1 hybrid exceed that of both the parents. McCluer also emphasizes the inferior condition of the self-fertilized plots.

Cross	Wt. (Oz.) of 10 Ears of the Male Parent	Wt. (Oz.) of 10 Ears of the Female Parent	Av. Wt. (Oz.) 10 Ears of the Two Parents	Wt. (Oz.) of 10 Ears Borne by the F_1 Generation (F_2) Seed
Queen's Golden (1) × White Dent	34.50	81.00	57.75	76.00
White Dent × Queen's Golden	81.00	34.50	57.75	64.00
Queen's Golden × Black Mexican (2)	34.50	36.00	35.25	47.50
Common Pearl (1) × Queen's Golden	27.50	34.50	31.00	42.00
Mammoth (2) × Leaming (3)	61.50	87.50	74.50	91.00
Mammoth × Leaming	61.50	87.50	74.50	82.00
Mammoth × Leaming	61.50	87.50	74.50	80.50
Triumph × Leaming	46.50	87.50	67.00	83.00
Eight-rowed (2) × Leaming	41.00	87.50	64.25	72.00
Brazilian Flour Corn × Gold Coin (2)	39.00	63.00	57.00	78 00
White Dent × Black Mexican	81.00	36.00	58.50	51.00
Eight-rowed × Stowell's Evergreen (2)	41.00	57.50	49.25	47.00
Triumph (2) × Stowell's Evergreen	46.50	57.50	52.00	52.50
Mammoth × Stowell's Evergreen	61.50	57.50	59.50	61.00
Gold Coin × Stowell's Evergreen	62.50	57.50	60 00	62.50
Triumph × Gold Coin	46.50	62.50	54.50	58.50
Eight-rowed × Gold Coin	41.00	62.50	51.75	56.00
Eight-rowed × Gold Coin	41.00	62.50	51.75	58.00
Average	50.50	63.30	57.20	64.50

(1) Pop corn, (2) sweet corn, (3) dent corn.

Plots grown from self-fertilized seed, were in most cases notably inferior in size and vigor to the plots grown from crossed seed, or from seed simply selected. The table does not give so convincing an illustration of the bad effects of self-fertilization, as the plots themselves did when growing, or as the corn did when husked and thrown into piles. One plot from self-fertilized seed had nearly half the stalks deformed in such manner that instead of standing up straight, they turned off nearly at a right angle, at or near the joint where the ear was produced, thus throwing the tassel on a level with or below the ear. Many of the tassels were very deficient in pollen. In another plot from self-fertilized seed, nearly all the tassels were abortive. All the plots from self-fertilized seed produced a greater proportion of barren stalks, and of poorly filled ears, than the plots of the same varieties, either from crossed seed or from seed naturally fertilized. The table giving the weight of ten selected ears of corn from self-fertilized seed, and of ten ears from crossed or selected seed, does not give a correct idea of the inferiority of the corn from the self-fertilized seed, because it does not take into account, either the greater proportion of barren stalks, or of small poorly filled ears (pp. 96 and 98).

The results of this experiment at the time simply led to the conclusion that continued selection of corn, leading to a certain amount of inbreeding, was likely, like close fertilization consciously practised, to lead to "deterioration," and that cross fertilization, as it occurs ordinarily in corn, is desirable for the best results. No suggestion is offered by McCluer as to utilizing this fact in a practical way. It remained for Messrs. Morrow and Gardner, also of the Illinois Station, to derive this conclusion from their experiments. In Bulletin 25 of the Illinois Station, pp. 179–180, results are given of crosses made between dent corn varieties exclusively, which, while less extensive and varied than McCluer's, are confirmatory of his experiments. The following table, adapted from Bull. 25, p. 180 (1893), presents these results:

Variety	Bu. Air-dry Corn per Acre	
Burr's White	64.2	
Cranberry	61.6	
Average	62.9	
Cross		64.1
Burr's White	64.2	
Helm's Improved	79.2	
Average	71.7	
Cross		73.1
Leaming	73.6	
Golden Beauty	65.1	
Average	69.3	
Cross		86.2
Champion White Pearl	60.6	
Leaming	73.6	
Average	67.1	
Cross		76.2
Burr's White	64.2	
Edmunds	58.4	
Average	61.3	
Cross		78.5

In each of the above cases the yield from the cross exceeded the average yield of the two parents, although not in all cases exceeding that of each parent.

In Bulletin 31, pp. 359–60 (1894), the result of Morrow and Gardner's second experiment in crossing corn is given.

Champion White Pearl	37.3	
Burr's White	38.6	
Average	38.0	
Cross		28.4
Leaming	34.6	
Burr's White	38.6	
Average	36.6	
Cross		41.7
Edmund's	28.3	
Murdock	35.7	
Average	32.0	
Cross		41.4
Edmund's	28.3	
Burr's White	38.6	
Average	33.5	
Cross		37.8

In three out of the four cases above the cross outyielded the average yield of the two parents.

Some observations were made by McCluer, (p. 86), as to effect of crossing on the number of rows of kernels, the results being an approximately intermediate condition in the F_1 hybrids with respect to this character.

Parents	No. of Rows
Leaming	18–24
Mammoth Sweet	12–16
F_1 hybrids	14–18
Leaming	18–24
Eight-rowed Sweet	8
F_1 hybrids	10–14
Leaming	18–24
Triumph	8
F_1 hybrids	10–16

McCluer remarks upon the difference in reciprocal pop-corn—dent-corn crosses, to the effect that when the pop corn was used as a pollen parent, the F_1 kernels were more flinty than when the dent corn was used as the pollen parent.

So far as the writer knows, McCluer is the first person known to have made a cross between two different types of corn, who paid close enough attention to the results of such a cross to lead him to illustrate the parent ears, the

Fig. 1.

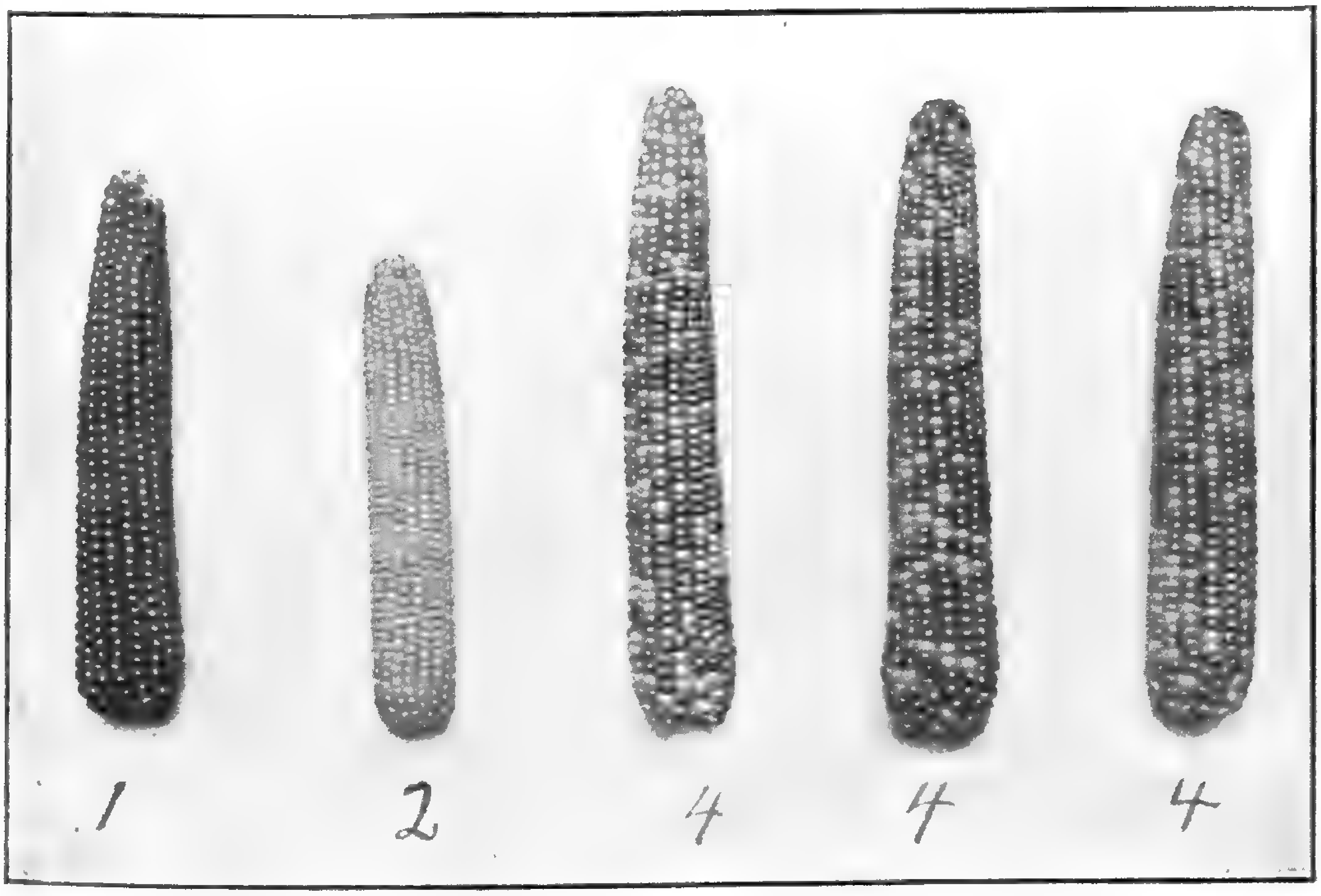

Fig. 2.

ears produced as the result of the cross (F_1) and the second generation hybrid ears (F_2), together for comparison (Figs. 1 and 2; McCluer's Plates 1 and 2). Each of these is a dent-sweet-corn cross, and the results, both of F_1 dominance and of segregation in the F_2 ears, is very plainly shown. In McCluer's Plate 4 the results of segregation are shown, so far as the reappearance of parental types is concerned. Of course, in all these crosses, it must be remembered that the parental types were not selfed strains, but were undoubtedly heterozygous for some of the factors under observation. This is shown in the white corn ear, coming out of a cross between Leaming (yellow dent) and Mammoth Sweet.

> The ears shown as types of the varieties used in crossing are selected typical specimens of the varieties, and the ears shown as grown from the crossed seed are typical of the cross-bred corn (p. 95).

McCluer makes the penetrating remark regarding the production of F_2 seeds that

> The self-fertilized ears showed the same modification of kernels as those naturally fertilized, proving that *each kernel of the crossed corn, had in itself the power to produce both sweet and dent corn* (p. 95).

In the writer's opinion, *this is the most remarkable expression upon the nature of heterozygosis made before Mendel's time.*

The reappearance of parental types is referred to as follows:

> Where the parent varieties were widely different, as in the crosses between sweet and dent, the progeny has tended strongly to run back to the parent forms, while at the same time taking on other forms different from either (p. 95).

A further indirect comment on the superiority in size on the part of F_1 hybrids is seen in McCluer's statement that

> Nearly all the corn grown a second year from the crosses is smaller than that grown the first year, though most of it is yet larger than the average size of the parent varieties (p. 96).

McCluer comments emphatically on the inferior condition of the self-fertilized plants and remarks:

> The table giving the weight of ten selected ears of corn from self-fertilized seed, and of ten ears from crossed, or from selected seed, does not give a correct idea of the inferiority of the corn from self-fertilized seed, because it does not take into account, either the greater proportion of abortive stalks, or of small and poorly filled ears (p. 98).

The fact is noticed that some varieties, when crossed, give rise to plants of increased size, while others do not.

Among other incidental matters, McCluer calls attention to the necessity for "A more perfect knowledge of the development of the races and varieties of corn," and wisely remarks regarding the farmer's part in corn breeding:

> In the production of new varieties by crossing, it will seldom be desirable to cross two varieties that are very widely different from each other. It is probable that, on the whole, selection, with occasional partial changes of seed, will give more permanent as well as more satisfactory results for the general farmer, than would the continual crossing and breaking-up of well fixed types; though there does seem reason to believe that the crossing of such distinct and well-fixed types, will, for the time being at least, give larger corn and better yields (p. 98).

From McCluer's observations on the results in the second generation of the hybrids he comes to the following intelligent conclusion:

> This work gives us a clew to the relative prospects of improvement in other lines by cross-breeding. A variety or type that is strongly fixed is more apt to transmit characters than one poorly or not at all fixed. If we should try to improve corn by crossing the product of two of these cross-bred groups of corn, we should expect to get as a result a few superior ears, with a very large proportion of inferior ones. Even in our well-selected varieties that have been picked for years with reference to given points of excellence, the tendency to run back to inferior forms is so strong, that the grower would save hardly one-tenth of his crop for his own seed. If our well-selected varieties deteriorate thus, when constantly and carefully selected, two varieties that have been long selected for opposite or widely different qualities, must, when crossed, tend to neutralize most strongly the very traits which we have, with so much pains, brought out and maintained.
>
> If, on the other hand, the varieties crossed have long been selected on the same or very similar lines, there seems to be no reason why occasional crossing will not tend to fix more strongly the desired characters.

Here, of course, McCluer quite naturally overlooks the fact of dominance, and adheres, although with a more rational reason than most plant breeders of his time, to the idea of fixation of type through the effects of selection. McCluer, however, here as throughout his paper, shows the inherent instincts of a geneticist, and his paper, although an obscure contribution to the literature of plant breeding, deserves special notice on that account.

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HYBRIDS AMONG SPECIES OF SPIROGYRA[1]

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CONJUGATION between filaments of different species of *Spirogyra* have been reported by several students of the algæ. Bessey (1884) reported and figured zygospores formed by the crossing of *S. majuscula* and *S. protecta.* He noted that the spores formed by the cross in either direction corresponded to the spore type of the female filament. This has been confirmed by all subsequent observers and we shall see later that this is a necessary result of the process of fertilization as it occurs in *Spirogyra.* This cross is of particular interest because the vegetative cells of *majuscula* have plain end walls, while those of *protecta* have replicate end walls. Consequently there is nothing in the physiology of these two species, representative of the two divisions of the genus, that interferes with conjugation. Wolle (1888) figures a cross between *S. maxima* and *S. ? nitida* under the name of *S. maxima* var. *inæqualis.* West and West (1898) figured a cross between two of the smaller species of *Spirogyra* but did not give their names. Andrews (1911) figured and described a cross between *S. crassa,* one of our largest species, with several chromatophores in each cell, and *S. communis,* one of the smallest of our species, with a single chromatophore. Here again the spore formed resembles that normal to the female filament. Evidently differences in size, in number of chromatophores, shape of zygospore, and character of the end walls of the vegetative cells are not impediments to crossing. In the collections from central Illinois which I have studied I have found hybrid zygospores formed between three pairs of

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[1] Papers from the Department of Botany, The Ohio State University, No. 104.

species: *S. communis* × *S. varians* from one locality, *S. varians* × *S. porticalis* from two localities, and *S. maxima* × *S. submaxima* from one locality.

The phenomenon of hybridization in this genus is evidently quite rare, as shown both by the small number of references to it in the literature and by the few cases that have come under my observation. From the collections made in Illinois, Massachusetts, Michigan, Ohio and New York, I have 854 records of conjugating *Spirogyras* and only five records of conjugation between different species from four localities, all in central Illinois.

In this paper I wish to record, not only the finding of conjugation between species, but what seem to be the progeny of such crosses. It has been found impossible to cultivate these forms in the laboratory so that there is no experimental proof of their origin. Nevertheless, they have been found associated with filaments that were crossing and with filaments of the two parent species that were conjugating normally. There were few other species present in these collections, and there are no species in central Illinois that could possibly be confused with them. Under the circumstances it seems impossible to account for the strange mixture of forms in these five collections except on the basis of a hybrid origin.

Spirogyra varians × *S. communis*

In collections taken from Campus Creek, two miles southwest of Charleston, Ill., during the latter part of May, 1913, specimens of typical *S. varians* and *S. communis* occur together with filaments that resembled one or the other of these species but whose dimensions exclude them from these species. In going over these collections in 1915 filaments of *varians* were found conjugating with *communis*, and hybrid zygospores were found in both kinds of filaments. This suggested that the unnamable forms were the progeny of hybrid zygospores.

S. varians has vegetative cells .30–40 μ × 30–120 μ, a single chromatophore making one to five turns in the cell.

The sporiferous cell is usually inflated on the conjugating side and the spores are frequently placed obliquely. In conjugating filaments cells that fail to mate usually become greatly distended. The spores are ellipsoid, 32–40 μ × 50–100 μ (Fig. 1). This species is highly variable, but I have examined many collections containing it and have seen none that resemble the hybrids.

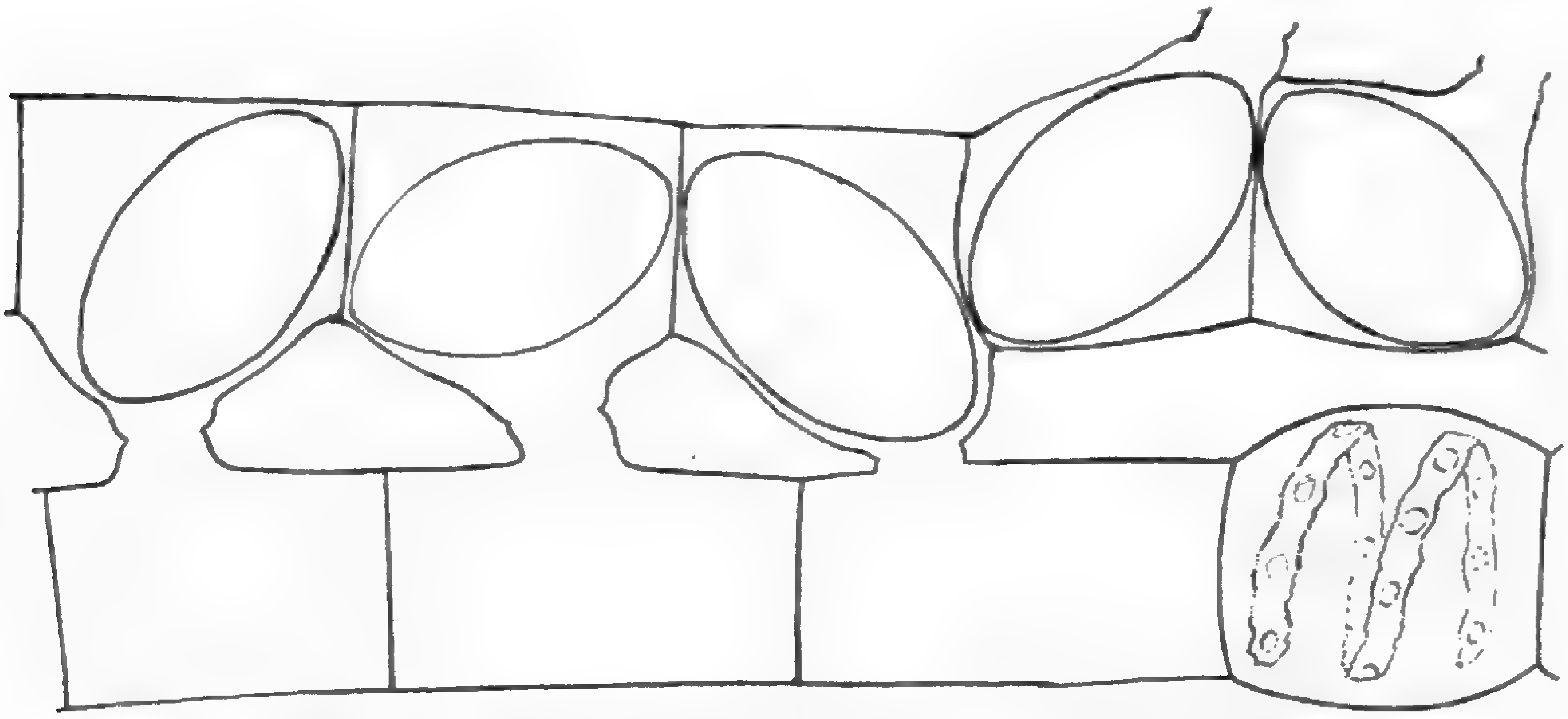

Fig. 1. Typical *S. varians* showing spore form, sporiferous cells inflated on the conjugating side, and an inflated sterile cell. Camera lucida drawing, same scale as the succeeding figures.

S. communis has vegetative cells 18–26 μ × 35–90 μ, a single chromatophore making two to four turns in the cell. The sporiferous cell is cylindrical and the spores are placed longitudinally in the cells. Cells in conjugating filaments that fail to mate usually remain cylindrical. The spores are ellipsoid, 19–26 μ × 35–90 μ (Fig. 2).

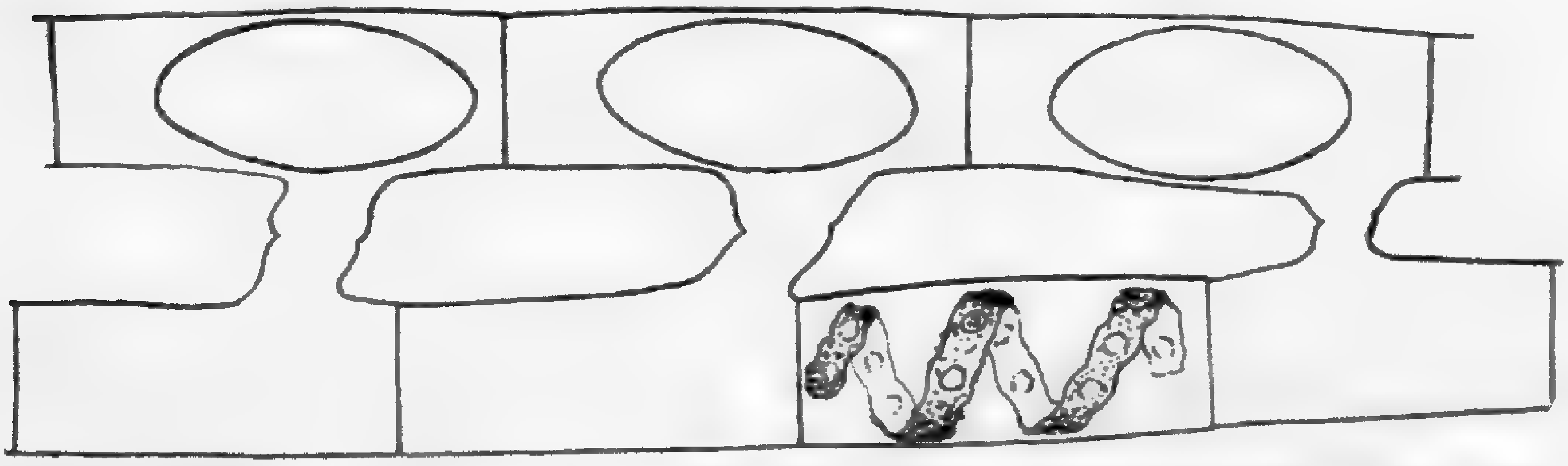

Fig. 2 Typical *S. communis* showing form of zygospore, sporiferous cell and sterile cell.

The collections in question showed in addition to the typical filaments others with the characters of *varians*,

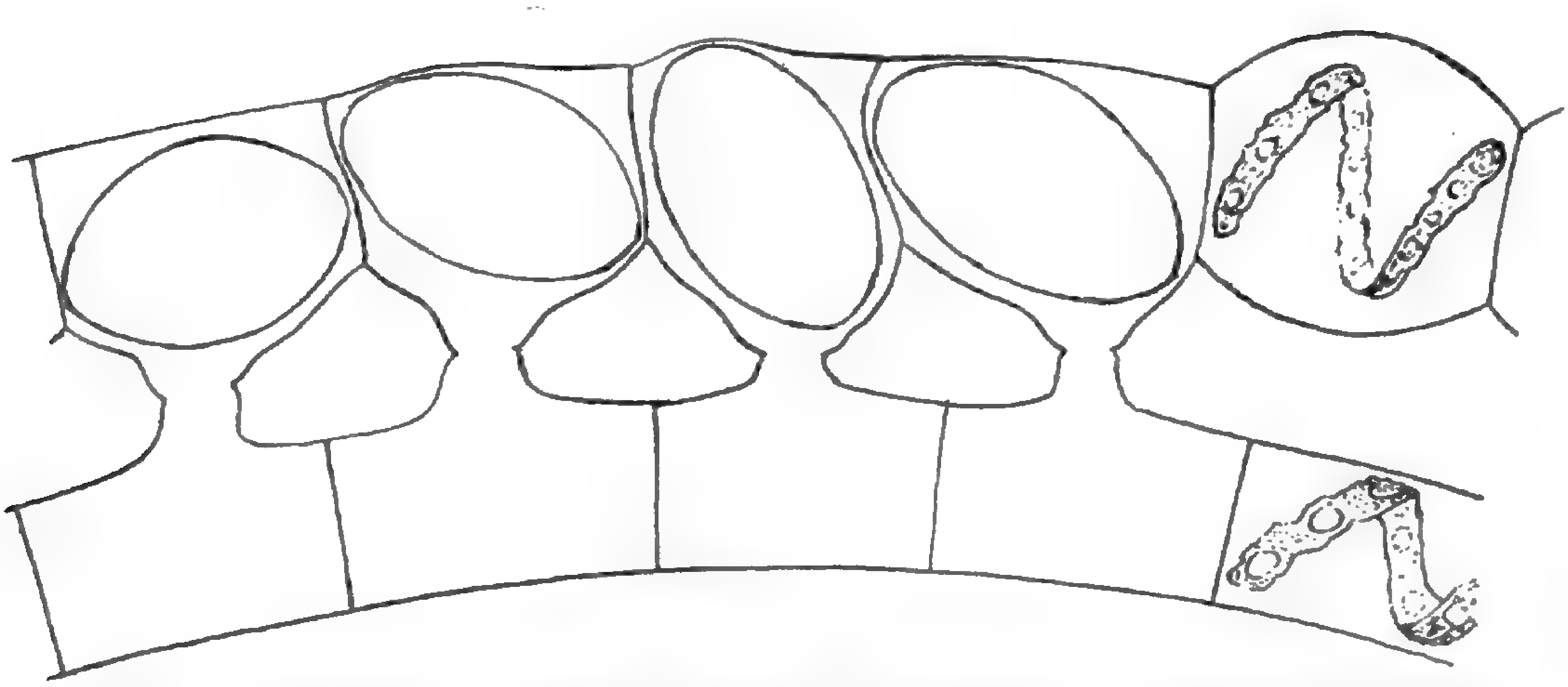

FIG. 3. *S. varians* × *S. communis* showing dimensions of communis, otherwise resembling *varians*.

but with dimensions similar or near to *communis* (Fig. 3) and still others with the form characters of *communis*, but the dimensions of *varians* (Fig. 4). The figures are camera drawings all made from Coll. No. 1877, May 27, 1913.

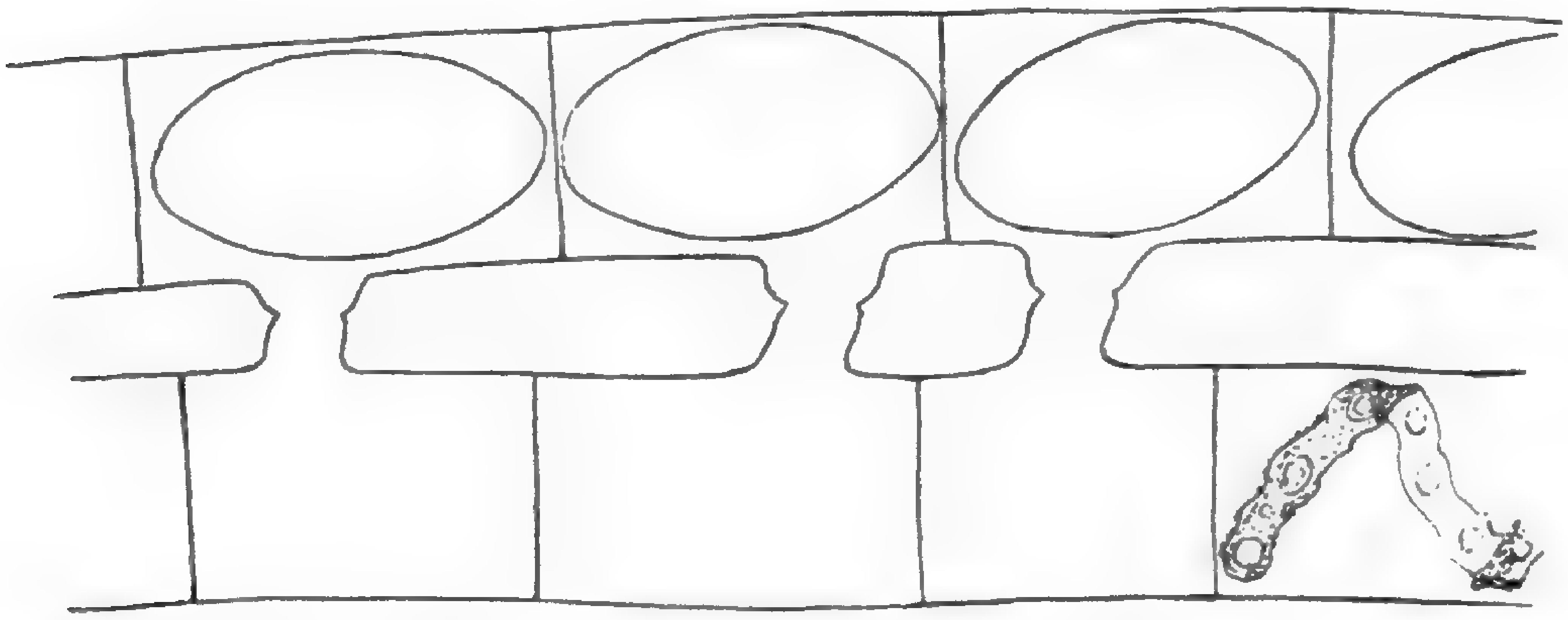

FIG. 4. *S. varians* × *S. communis* showing dimensions of varians, otherwise resembling *communis*.

Spirogyra varians × *S. porticalis*

In collections from a small stream that flows under the Clover Leaf R. R., just east of the station at Lerna, Ill., collections made during May, 1913, and April, 1914, *Spirogyra varians* was found conjugating with *S. porticalis*. Accompanying the typical *varians* and *porticalis* filaments were fruiting filaments which could not be placed satisfactorily in either species, but which possessed various combinations of the characteristics of both species.

In collections from Cossel Creek, about one mile west of Charleston, Ill., made during May, 1914, and April, 1915, a similar mixture of forms was found associated with filaments of typical *varians* and *porticalis*. It was the discovery of these latter collections in 1915 that led me to go over the collections from Campus Creek, Lerna, and the previous collections from Cossel Creek. In all cases the forms seemed quite explicable on the assumption that hybridization had occurred in previous years as it was occurring when the collections were made and that the progeny of the hybrid zygospores showed various combinations of the characteristics of the parent species.

FERTILIZATION IN SPIROGYRA

Fertilization in *Spirogyra* takes place by the fusion of two gametes through a tube formed by the union of emergences from two adjoining cells in the same or different filaments. The zygospore matures its wall within three or four days after the passage of the gametes.

In the large species, *S. ellipsospora,* I have watched the movement and fusion of the gametes. The male gamete withdraws slightly from the gametangium wall; its chromatophores disintegrate and the whole gamete appears to have a foam structure. Opposite the tube a small lobe develops and this moves through the tube to the female gamete. On reaching the surface of the female gamete the cytoplasm of the female gamete at the point of contact spreads, drawing its chromatophores apart. The male gamete penetrates the cytoplasm and at the end of the process lies entirely inside the female gamete. Its chlorophyll then turns brown and stains the cytoplasm, so that it can be seen through the maturing spore wall for several days. During this period it gradually spreads out and coalesces with the cytoplasm of the female gamete.

Since the cytoplasm that secretes the zygospore wall is thus only the cytoplasm of the female gamete, its form and markings are determined entirely by that gamete.

All the recorded facts concerning hybrid zygospores are in harmony with this observation.

The male and female nuclei, however, do not fuse until some time later, perhaps two to four weeks. The character of the zygospore is therefore entirely dependent upon the female parent. This is well brought out by all the published figures of hybrid zygospores as well as by my own observations. After the formation of the fusion nucleus various observers—Chmielewski (1890), Tröndle (1907), Karsten (1909) and Kurssanow (1911) (*Zygnema*)—report the occurrence of a double mitosis of which the second division is heterotypic. This results in the formation of four nuclei, of which three degenerate (Tröndle, 1911). The degeneration of three of the nuclei has been observed also by Kurssanov in *Zygnema*. The remaining nucleus becomes the final nucleus of the zygospore.

In a hybrid zygospore, therefore, the first fusion nucleus would contain the hereditary factors for the alternate characters of both species; in the subsequent reduction division and degeneration of three of the nuclei the final zygospore nucleus would contain one of the several possible combinations of these hereditary qualities. The vegetative filament derived from a hybrid zygospore would present some combination of its vegetative characters, such as cell dimensions, number of chromatophores and character of the end walls. The factors for spore characters would not become visible until it conjugated, and then only the characters carried by the female filaments would become visible since the spore characters are entirely matriclinal. In the adjoining diagram (Fig. 5) the zygospores are figured in typical forms. The two characters most important in separating the species are: (1) The dimensions of the filaments (*varians* averages about 33, *communis* about 22); (2) the lateral inflation of the sporiferous cell in *varians* in contrast with the cylindrical sporiferous cell of *communis*. If we represent the factor for the dimensions of *varians* by *A* and of *com-*

munis by *a,* and the factor for the inflated sporiferous cell of *varians* by *B* and cylindrical sporiferous cell of *communis* by *b,* then the fusion nucleus in the zygospore would have the composition *AaBb.* At the subsequent reduction division these four characters might be distributed in four different ways: *AB* typical *varians; Ab varians* dimensions and *communis* type of sporiferous cell; *aB—communis* dimensions and *varians* type of sporiferous cell; and *ab*—typical *communis.* All four of these possibilities are represented by filaments in Collection 1877 from Campus Creek. Furthermore, the fertile cells of individual filaments and the zygospores formed are similar throughout a particular filament, as would be expected on the basis of the origin of the final zygospore nucleus. This hypothesis, therefore, accounts for all the facts at present known concerning this series of collections.

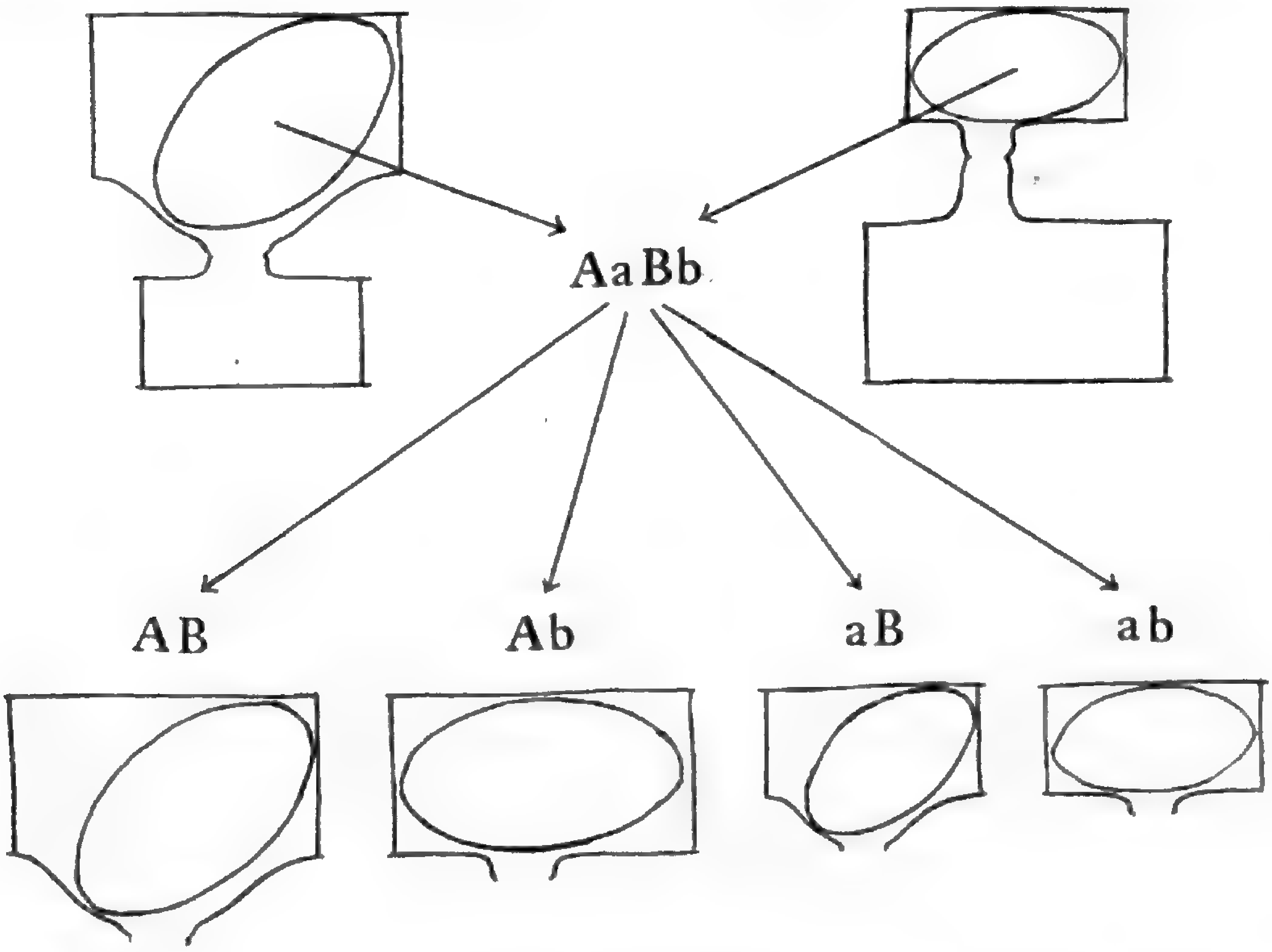

FIG. 5. Diagram illustrating the hybrid progeny of a cross between *S. varians* and *S. communis.*

The forms occurring in the two series of collections from Lerna and Cossel Creek can be similarly accounted for. In this case, however, the two species, *S. varians* and *S. porticalis,* evidently differ in three characters. The characteristics of *varians* have been given above.

S. porticalis (Fig. 6) has vegetative cells 40–50 μ × 66–200 μ containing a single chromatophore, making three to four turns. The fertile cells are cylindrical and the zygospore is ovoid, 38–50 μ × 50–83 μ. It, therefore, differs from *S. varians* in dimensions of the vegetative cells, in the absence of inflated fertile cells, and in the ovoid form of the zygospore. In both series of collections all of the eight possible combinations of these three characters occur.

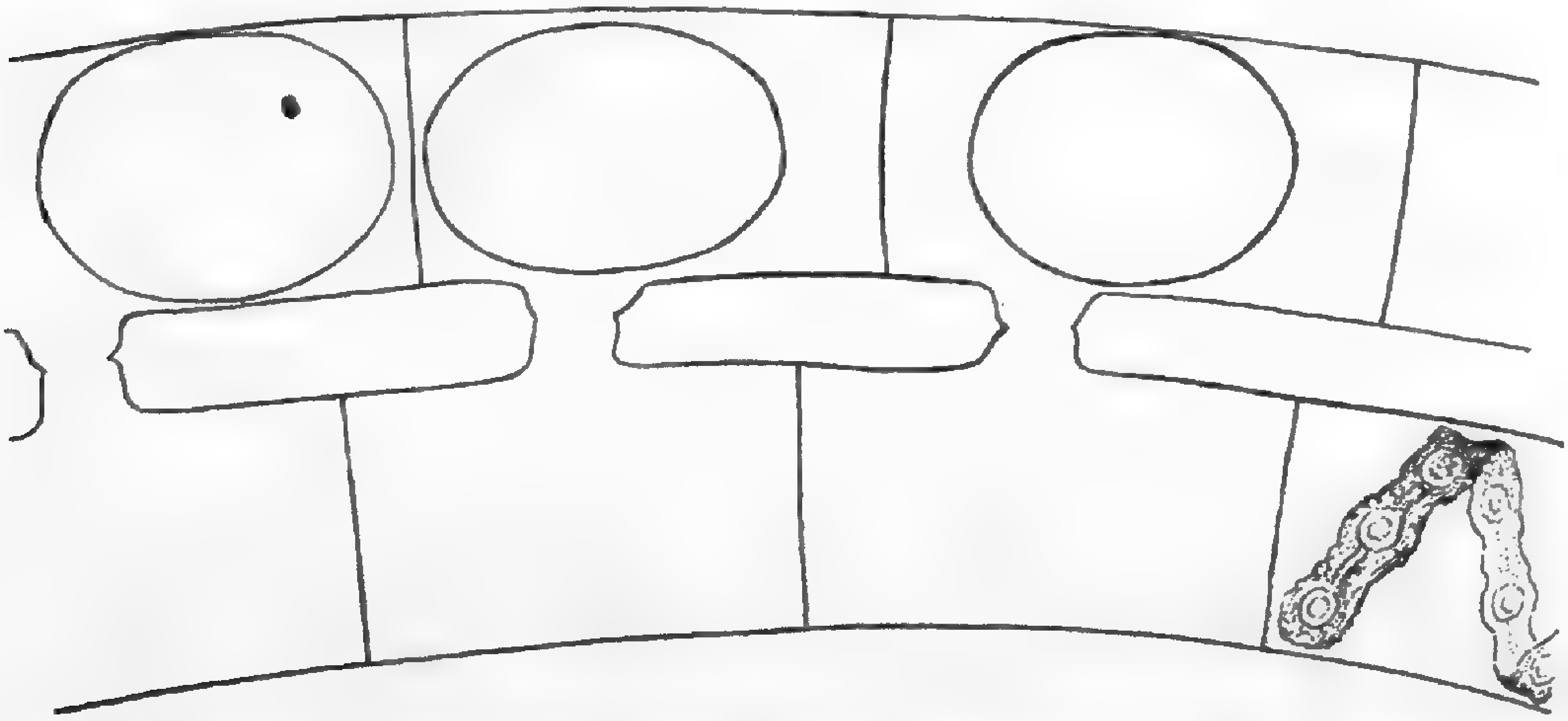

Fig. 6. Typical *S. porticalis* showing single chromatophore, ovoid spores and cylindrical sporiferous cells.

In the accompanying diagram (Fig. 7) the dimension factor for *varians* and *porticalis* are represented by *A* and *a,* respectively. The factor for the *varians* type of fertile cell by *B,* and for the *porticalis* type by *b.* The factor for the ellipsoid spore by *C* and for the ovoid spore by *c.* The nucleus formed by the fusion of the two gamete nuclei therefore contains all the factors (*Aa, Bb, Cc*). The final zygospore nucleus contains any one of eight possible combinations: *ABC,* typical *varians; AbC, varians* dimensions and spore form, with *porticalis* fertile-cell form; *Abc, varians* dimensions, with *porticalis* fertile-cell form and spore form; *ABc, varians* dimensions and

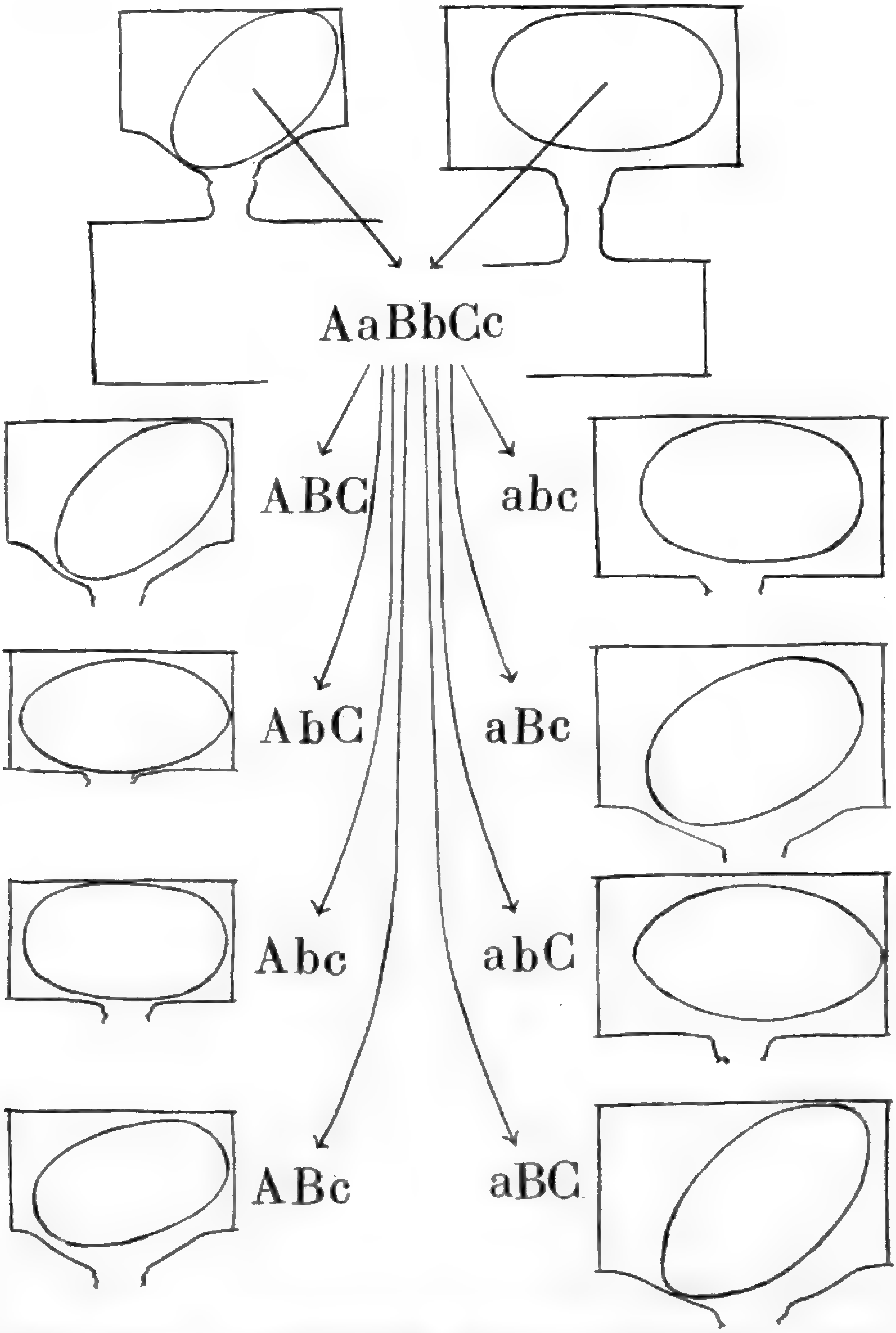

FIG. 7. Diagram to illustrate hybrid progeny of a cross between *S. varians* and *S. porticalis.*

fertile-cell form, with *porticalis* spore form; *abc,* typical *porticalis; aBc, porticalis* dimensions and spore form, with *varians* fertile-cell form; *abC, porticalis* dimensions and fertile-cell form, with *varians* spore form; *aBC, porticalis* dimensions, with *varians* fertile-cell and spore form.

The female filaments derived from these several zygospores should show these eight possible combinations when they fruit. These forms have all been found in the two series of collections in each of two successive years, and there seems to be no question but what they are the products of hybridization and segregation. Since the inheritance is entirely matriclinal, segregation occurs in the first generation.

As to the relative numbers of the several types it is impossible to count filaments in a collection. Theoretically they should be present in about equal numbers if all the filaments are of hybrid origin. In all the collections, however, there were filaments conjugating in the usual way, so that any attempt at counting filaments would be useless even though it were practically possible.

SUMMARY

1. Hybridization between *Spirogyra communis* and *S. varians* and between *S. varians* and *S. porticalis* have been observed. The forms probably derived from these crosses have also been found.

2. Hybrids are exceedingly rare among species of *Spirogyra.*

3. They have been observed only in a few species.

4. Hybrid zygospores may be formed between species even though they have very different vegetative and spore characters.

5. The nuclei derived from the two gametes do not fuse until after the zygospore wall matures. The form of the zygospore is determined entirely by the female gamete.

6. The fusion nucleus of a hybrid zygospore contains factors for all the various characters of both species.

When the reduction division takes place these factors are segregated in various combinations in the final spore nucleus.

7. When the filaments derived from hybrid zygospores fruit their hybrid character becomes evident in the dimensions of the filament, the character of the sporiferous cell and the form of the zygospores.

8. Inheritance is matriclinal and therefore the segregation becomes evident in the first generation.

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SYNTHETIC PINK-EYED SELF WHITE GUINEA-PIGS[1]

DR. HEMAN L. IBSEN

Introduction

In the fall of 1914 Professor W. E. Castle kindly sent to the Department of Experimental Breeding, University of Wisconsin, five guinea-pigs representing some of the rarer color varieties, suggesting that their genetic make-up be studied independently. These animals were subsequently turned over to the writer for investigation. During the winter two of them died without offspring and hence only three were left the following spring. Two of these proved to be what has been called by Castle red-eyed agoutis and the third was a "pink-and-red-eyed" tortoise. The factors involved in the production of these animals will be described below in more detail.

Castle (1914) had already described the different factors found in these animals and had given some indication of their relationships to other factors. At this time he stated that red-eyed was allelomorphic to albinism, and that pink-eyed was recessive to the usual dark-eyed condition. In 1915 Wright showed that red-eyed formed an allelomorphic series with albinism and dilute and intense pigmentation. This made the account of the relationships of the factors fairly complete.

At about this time it occurred to the writer that with the proper combination of the newly described factors and other factors it should be possible to produce an animal which to all appearances would be an ordinary albino, but entirely different genetically from what have hitherto been known as albinos. Matings were imme-

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[1] Papers from the Department of Genetics, Wisconsin Agricultural Experiment Station, No. 13. Published with the approval of the Director of the Station.

diately started with this in view, but since there were only three animals to work with at the start progress was necessarily slow at first.

In the meantime Detlefsen (1916) had described some pink-eyed white mice carrying the color factor. He believed they were due to the combination of the dominant self white condition and the pink-eyed, but in his paper this was not fully demonstrated.

Castle (1916) refers to two pink-eyed white guinea-pigs, presumably albinos, which were born to pigmented parents. The male parent was tested with true albinos, but all of the eleven offspring obtained were pigmented. Castle therefore supposes that the two pink-eyed white offspring were not true albinos, but "pink-and-red-eyed" animals lacking the factor for the extension of black or chocolate pigment. This is undoubtedly the correct explanation, as the evidence presented in this paper will demonstrate. Castle, however, must have discarded his pink-eyed whites before he realized their importance since he makes no mention of testing them genetically.

Before going into further detail it may be well to describe briefly the various factors directly concerned in the production of the pink-eyed self whites. Some of those indirectly concerned are also described in order to give the proper orientation.

Description of Factors

B, the factor for black pigmentation. When unmodified by other factors black pigment is found only in the eyelids, mammae, external genitals and the skin of the ears and feet.

b, the factor for chocolate (or brown) pigmentation.

E, the factor for extension of black or chocolate throughout the pigmented part of the coat. The unpigmented parts are of course white.

e^p, the partial extension factor. This factor causes black or chocolate to be only partially extended and therefore to appear in blotches, the remainder

1 ♀1118.1 ♀1866.2 ♂1830.1

2 ♂849.1 ♂1258.1

3 Litter 1514 ♂1202.1 ♀1171.3

4 ♂1202.1 ♀1171.3

5 ♀1118.1 ♂1202.1 ♂1587.1

of the pigmented part being red. Guinea-pigs spotted black and red in this manner are commonly known as tortoises.

e, the non-extension of black or chocolate. In this case black or chocolate are found only in the places mentioned under *B*, *i. e.*, in the eyelids, etc. E, e^p and e form an allelomorphic series (Ibsen, 1916). They are given in the order of their dominance.

C, intense pigmentation.

C_d, dilute pigmentation. Yellow is dilute red.

C_r, red-eyed or non-yellow. In a C_r animal red (or yellow) is never present in the coat and black or chocolate are somewhat dilute. Owing to the absence of red the amount of pigment in the eyes is decreased, thereby partially allowing the blood to show through. It is because of this reddish tint to the eyes that they have been called red-eyed by Wright (1915). However, it seems more proper to call them non-yellows since the absence of yellow in the coat is the more general and striking effect produced by the factor. A C_r tortoise is therefore black-and-white because the red spots of the ordinary tortoise are here absent. An eC animal is a self red, but an animal with the composition eC_r is a self white, owing to the absence of red pigment. Such an animal will be referred to in the text as a "non-extended (e) non-yellow (C_r)."

FIG. 1. From left to right: ♀ 1118.1, a pink-eyed non-extended non-yellow; ♀ 1866.2, an albino carrying both black (*B*) and the extension factor (*E*): ♂ 1830.1, an albino lacking both black and extension and therefore *be*. Owing to the pink color of the skin of the ears of ♀ 1118.1 and ♂ 1830.1, and also because of the direction of the light, causing them to cast shadows, the ears appear darker than they really are. The pink eyes also appear dark.

FIG. 2. Guinea-pig, ♂ 849.1 is a *bb* dark-eyed non-extended non-yellow. ♂ 1258.1 is a dark-eyed non-extended non-yellow carrying black (*B*).

FIG. 3. Guinea pigs ♂ 1202.1, a pink-eyed non-extended non-yellow (ppC_rC_ree), ♀ 1171.3, an albino heterozygous for partial extension (e^p), and three of their offspring, litter 1514.

FIG. 4. A nearer and clearer view of ♂ 1202.1 and ♀ 1171.3, already shown in Fig. 3.

FIG. 5. Guinea-pigs ♂ 1202.1 and ♀ 1118.1, both pink-eyed non-extended non-yellows and one of their 24 offspring, ♂ 1587.1, also a pink-eyed non-extended non-yellow.

The C_r factor has been described in some detail because it plays an important part in the production of the synthetic pink-eyed self whites. C and C_d are dominant to C_r, while it in turn is dominant to C_a.

C_a, albinism. Albino guinea-pigs generally tend to have some pigmentation on the nose, ears and feet. This varies in amount depending on the other factors present. A *be* albino is almost if not quite devoid of pigment (♂1830.1, Fig. 1), while a *BE* albino is heavily pigmented at its extremities (♀1866.2, Fig. 1). In all cases, however, the eyes are pink and the greater part of the coat is white.

P, dark-eyed.

p, pink-eyed. The eyes are as pink as those found in albinos. Black (*B*) or chocolate (*b*) are also affected, becoming quite dilute, while red is unaffected.

It will be seen from the description of the factors given above that if we can obtain an animal which is a non-extended non-yellow, eC_r, and therefore a self white, and which in addition is *pp*, or pink-eyed, we shall have a pink-eyed self white (eC_rp), which is not an albino in the ordinary sense of the word as applied to guinea-pigs, but which nevertheless to all appearances in an albino (see ♀1118.1, Fig. 1). There is one difference, however. Albinos vary considerably in the amount of pigment in the ears, nose and feet depending on whether E, e^p, or B are present or absent. The synthetic pink-eyed self whites on the other hand cannot carry E or e^p, but may carry B. The pink-eyed factor (p) dilutes black pigment (B) to such an extent that it is impossible to tell by the appearance of the animal whether or not black is present. All the synthetic pink-eyed self whites are therefore a pure white and fulfil the guinea-pig fancier's requirements for a good albino better than most true albinos do.

BREEDING OPERATIONS

As previously stated there were three animals with which to begin breeding operations in the production of the synthetic pink-eyed self whites. These were two non-yellow agoutis, ♂360.1 and ♀361.1, and a pink-eyed non-yellow tortoise, ♀363.1. By various test matings these were proven to be of the following gametic compositions: ♂360.1, $AaPpC_rC_re^pe^p$,[2] ♀361.1, $AaPPC_rC_re^pe^p$, and ♀363.1, $aappC_rC_re^pe^p$. It will be seen that all three were homozygous for e^p, the factor for the partial extension of black or chocolate. On this account it would be impossible by mating the animals together to produce the pink-eyed self whites since the desired animals must lack the extension factor and therefore be ee.

What seemed the best method of procedure was to mate ♀363.1 ($ppC_rC_re^pe^p$) to a self red ($PPCCee$), and then to inbreed the F_1's ($PpCC_re^pe$). These all looked like ordinary tortoises. Since this was a tri-hybrid cross and since the desired animals were to be homozygous recessives, it would theoretically be necessary to have 64 offspring for the production of one of the desired type. This proved to be a very slow process and was finally discarded in favor of other less methodical matings, which were more rapid in their results. The most successful will be described in some detail.

A heterozygous tortoise ♂572.1, of the composition $PpCC_re^pe$ obtained by mating ♂360.1 to a self red, was mated to a yellow-and-white female, 629.3, carrying albinism (PPC_dC_aee). One of their offspring, ♂849.1 (Fig. 2), was at first mistaken for an albino, but more careful examination proved him to be a dark-eyed non-extended non-yellow. The reason for mistaking him for an albino was that he did not carry black (B).[3] His

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[2] A is the factor for agouti.

[3] In a dark-eyed non-extended non-yellow (PeC_r) the presence or absence of black (B) is as easily detected as it is in an albino or a self red. In Fig. 2 ♂ 1258.1 carries black while ♂ 849.1 does not. In addition to having much lighter colored extremities a bb non-extended non-yellow also has much pinker eyes than one which carries black. For this reason it may be mistaken for an albino.

gametic composition turned out to be PpC_rC_aee. He was mated to a pink-eyed tortoise, ♀734.2,[4] whose composition judging by her offspring, must have been $ppC_dC_re^pe$. This cross may be represented as follows:

	♂ 849.1	×	♀ 734.2
	PpC_rC_aee		$ppC_dC_re^pe$
Gametes	PC_re PC_ae pC_re pC_ae		pC_de^p pC_de pC_re^p pC_re

Offspring		Obtained
$PpC_dC_re^pe$ $PpC_dC_ae^pe$	Dark-eyed tortoise	1
$ppC_dC_re^pe$ $ppC_dC_ae^pe$	Pink-eyed tortoise	2
PpC_dC_ree PpC_dC_aee	Dark-eyed self-yellow	2
ppC_dC_ree ppC_dC_aee	Pink-eyed self-yellow	2
$PpC_rC_re^pe$ $PpC_rC_ae^pe$	Dark-eyed non-yellow tortoise	2
$ppC_rC_re^pe$ $ppC_rC_ae^pe$	Pink-eyed non-yellow tortoise	0
PpC_rC_ree PpC_rC_aee	Dark-eyed non-extended non-yellow	1
ppC_rC_ree ppC_rC_aee	*Pink-eyed non-extended non-yellow*	2
Total		12

It will be seen that according to expectation there should be equal numbers of 8 different phenotypes. The 12 offspring actually obtained are remarkably close to expectation.

At the time this cross was made the gametic composition of the mother, ♀734.2, was not definitely known. When, therefore, the two pink-eyed non-extended non-yellows were born one could not be certain that they were not just ordinary albinos. The only definite method

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[4] Ancestry of ♀ 734.2:

- ♀ 734.2, $ppC_dC_re^pe$
  - ♂ 346.1, $PpC_dC_re^pe$
    - ♂ 179.1, $PPCC_dee$
    - ♀ 363.1, $ppC_rC_re^pe^p$
  - ♀ 549.3, $PpC_rC_re^pe^p$
    - ♂ 360.1, $PpC_rC_re^pe^p$
    - ♀ 361.1, $PPC_rC_re^pe^p$

to test this was to mate them to true albinos, and this was accordingly done.

One of these animals, ♀1118.1 (Figs. 1 and 5), mated to an albino,[5] ♂596.3 (PPC_aC_aee), had 4 dark-eyed non-extended non-yellow offspring and 2 albinos. This would make her composition ppC_rC_aee and the cross may be represented as follows:

♂ 596.3 × ♀ 1118.1
PPC_aC_aee ppC_rC_aee
Gametes: PC_ae pC_re
pC_ae
Offspring: PpC_rC_aee, dark-eyed non-extended non-yellow;
PpC_aC_aee, albino.

The other animal, ♂1202.1 (Figs. 3, 4 and 5), was mated to an albino (♀ 1171.3, Figs. 3 and 4) of the composition $PPC_aC_ae^pe$. There were 12 offspring. Of these 6 were dark-eyed non-yellow tortoises and the other 6 were dark-eyed non-extended non-yellows (see litter 1514, Fig. 3). This would indicate that ♂1202.1 was of the composition ppC_rC_ree, and the cross would be as follows:

♂ 1202.1 × ♀ 1171.3
ppC_rC_ree $PPC_aC_ae^pe$
Gametes: pC_re PC_ae^p
PC_ae
Offspring: $PpC_rC_ae^pe$, dark-eyed non-yellow tortoise;[6]
PpC_rC_aee, dark-eyed non-extended non-yellow.

It will thus be seen that the two pink-eyed non-extended non-yellows were not of the same composition, the male, 1202.1 being homozygous for C_r, while the female, 1118.1, was C_rC_a. This is what one might expect by reason of their parentage.

According to expectation, these pink-eyed non-extended non-yellows when bred together should have

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[5] The albinos used in these test matings were unquestionably homozygous dark-eyed (PP) since they came from stock that has never been known to carry the pink-eyed factor (p).

[6] These dark-eyed non-yellow tortoises as well as the dark-eyed non-extended non-yellows are being inbred, and the results from these matings will be reported at some future date.

nothing but pink-eyed non-extended non-yellow offspring. Thus:

	♂ 1202.1	×	♀ 1118.1
	ppC_rC_ree		ppC_rC_aee
Gametes:	pC_re		pC_re pC_ae

Offspring: $\left.\begin{matrix} ppC_rC_ree \\ ppC_rC_aee \end{matrix}\right\}$ pink-eyed non-extended non-yellows.

The mating has been made and thus far there have been 24 offspring, all of them pink-eyed non-extended non-yellows (see Fig. 4). Some of these offspring are being tested by being mated to albinos, but as yet their composition with respect to the presence of albinism is not definitely known. It may be of interest to mention that one of them when mated to a *PPEE* albino had one dark-eyed *self black* offspring. The other two offspring in the same litter were black-and-white, due to the fact that neither parent was homozygous for entire pigmentation (*S*).[7]

Discussion

In most domesticated mammals an albino, as ordinarily understood by breeders, is a completely self white animal with pink eyes. Albino rabbits are of this type. In addition there is the Himalayan variety which also has pink eyes, but the coat instead of being entirely white is pigmented at the animal's extremities. This condition is dominant to albinism and recessive to the fully pigmented condition, thus forming part of an allelomorphic series (Sturtevant, 1913). Guinea-pig fanciers also have what they call a Himalayan variety. Here, however, the genetic relationship differs from that found in rabbits. Himalayan guinea-pigs are undoubtedly true albinos carrying the factor for black (*B*) and the exten-

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[7] An *S* animal is entirely pigmented, while one that is *ss* shows some white spotting and is therefore not entirely pigmented. In this connection it may be of interest to note that in a non-yellow tortoise the white spotting may be due to two different causes, (1) because of the non-yellow factor (C_r) the yellow of the ordinary tortoise is here white, and (2) if the animal is *ss* it will show some white spotting on this account also.

sion factor (*E*) which extends the black. The presence of these two factors tends to make the extremities heavily pigmented.

The albino guinea-pig, according to the fanciers' standard, should be as completely white as the albinos of other species. This, however, has never been entirely attained, even though much selection has been practised. Albinos most nearly approaching the standard lack both black and extension factor and are therefore *eb*. When mature they ordinarily show, nevertheless, a lightly pigmented rim along the edges of the ears. The synthetic pink-eyed whites, produced as explained in the earlier part of this paper, are, on the other hand, pure white, and they therefore satisfy the fanciers' standard in this respect. They would meet his desires, furthermore, in that they breed true for this character.

There are other means besides those already mentioned whereby pink-eyed self white guinea-pigs could be produced which would satisfy the fancier's standard. One method would be to combine a self white condition described by Castle (1905) with the pink-eyed. Self whites of this type, however, do not breed true. Very frequently they throw spotted offspring. They seem to be merely an extreme form of white spotting, all of the animal being unpigmented except the eyes. Pink-eyed self-whites of this type would necessarily on this account be very unstable in the transmission of their coat character.

Another method would be to produce a "pink-eyed" (*pp*) albino. The pink-eyed factor in this case would cause the pigmentation ordinarily found in albinos to become invisible. We have produced an animal of this type. When mated to pink-eyed it had nothing but pink-eyed offspring, and when mated to albinos it had only albino offspring. It was pure white in color.

It seems quite probable that synthetic pink-eyed self whites may also be produced in rats. Castle (1914) has already described yellow varieties and pink-eyed varieties, and Whiting (1916) has stated that the non-yellow factor has been found in some animals.

In conclusion it may be said that we have furnished one more proof of the fact that the phenotypic appearance of an animal may entirely mislead one as to its gametic composition. The synthetic pink-eyed self white guinea-pig may also serve another purpose. By proper matings an animal can be produced which carries all the known recessive color factors in guinea-pigs except albinism, and animals of this type should be most useful in determining the possible linkage relations between the factors.

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PARTHENOGENESIS AND CROSSING-OVER IN THE GROUSE LOCUST APOTETTIX[1]

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Introduction

There have been found among the grouse locusts, genus *Paratettix*,[2] in nature, fourteen factors for color patterns, all in one series of multiple allelomorphs. A fifteenth factor, a modified S, in the same series, has originated in the laboratory by means as yet not understood. Another factor, θ, for melanism, discovered in nature, has been found to segregate independently of the multiple allelomorph group (Nabours, '14, '17). Still another factor, ϕ, for red-all-over, yet to be described, also from nature, behaving precisely as does θ, though segregating independently of both it and the multiple allelomorph series, has been bred in considerable numbers. In one species of the genus *Tettigidea*,[3] bred in our laboratory, there have been described a series of five multiple allelomorphic factors for patterns, and an independently segregating color factor of the behavior of θ, or ϕ, in *Paratettix* (Bellamy, '17). In these experiments, involving several hundred kinds of matings and many thousands of individuals, with only the two exceptions, both as yet unexplained, segregation has taken place as expected.

Among another genus, *Apotettix*,[4] of the grouse locusts

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[1] Paper 25 from the Zoological Laboratory, Kansas Agricultural College and Experiment Station.

[2] *Paratettix texanus* Hancock. Kindly identified by both Dr. J. L. Hancock and Mr. Jas. A. G. Rehn.

[3] *Tettigidea parvipennis pennata* Hancock.

[4] Identified by Mr. Rehn as *Apotettix eurycephalus* Hancock, and by Doctor Hancock as follows: "nearer the Mexican species *Apotettix convexus Morse*, than the nearly allied Texan species, *Apotettix eurycephalus* Hancock. Inasmuch as you have used material from both Texas and Mexico in your experiments, it is possible you have hybridized the two." The natural history of this group has been described (Hancock '02).

there have been discovered in nature eleven factors for color patterns, all in the same series, but evidently only a few, if any, are allelomorphs. Pending further consideration, the patterns are designated as AA, GG, KK, MM, OO, RR, TT, WW, XX, YY and ZZ, respectively (all conspicuous, except AA which is of a mottled gray ground color and well protected). These patterns are as sharply defined and distinct, each from any other, as are those of *Paratettix*. Any two make a readily recognizable hybrid pattern, with the elements of each parent pattern seemingly equally represented, except that the part of a hybrid pattern produced by the factor A, when it is a member, is less clearly perceived, and such hybrids can not be, in every case, superficially distinguished from the pure, or homozygous, pattern of the more apparent member. For instance, it requires trained and careful scrutiny to distinguish between AK and KK, AW and WW, AY and YY, etc. It appears that the pattern AA, if it be the result of only the one factor, is quite different from the others, not only in its manifestation in the hybrid of which it may be a member, but also, as will be shown later, in that it appears to result from crossing-over among the others. On the other hand, KW, KY, WY, and most other hybrid patterns not containing A as a member are sharply distinct, each making a composite picture of both components. Even in case of linkage, where three, four or more factors are combined, the individual presents the composite appearance of all the patterns involved. For example, in $\mathrm{K}\widehat{\mathrm{MR}}$, $\widehat{\mathrm{KM}}\mathrm{R}$ or $\widehat{\mathrm{KR}}\mathrm{M}$, $\mathrm{K}\widehat{\mathrm{YZ}}$ and $\widehat{\mathrm{KR}}\widehat{\mathrm{YZ}}$ individuals all the patterns concerned are clearly visible and apparently equally represented. In respect to representation of patterns in the hybrids, as well as in the actual resemblance of a few of the patterns, there is striking parallelism between some of the members of this genus and some of those of *Paratettix*.

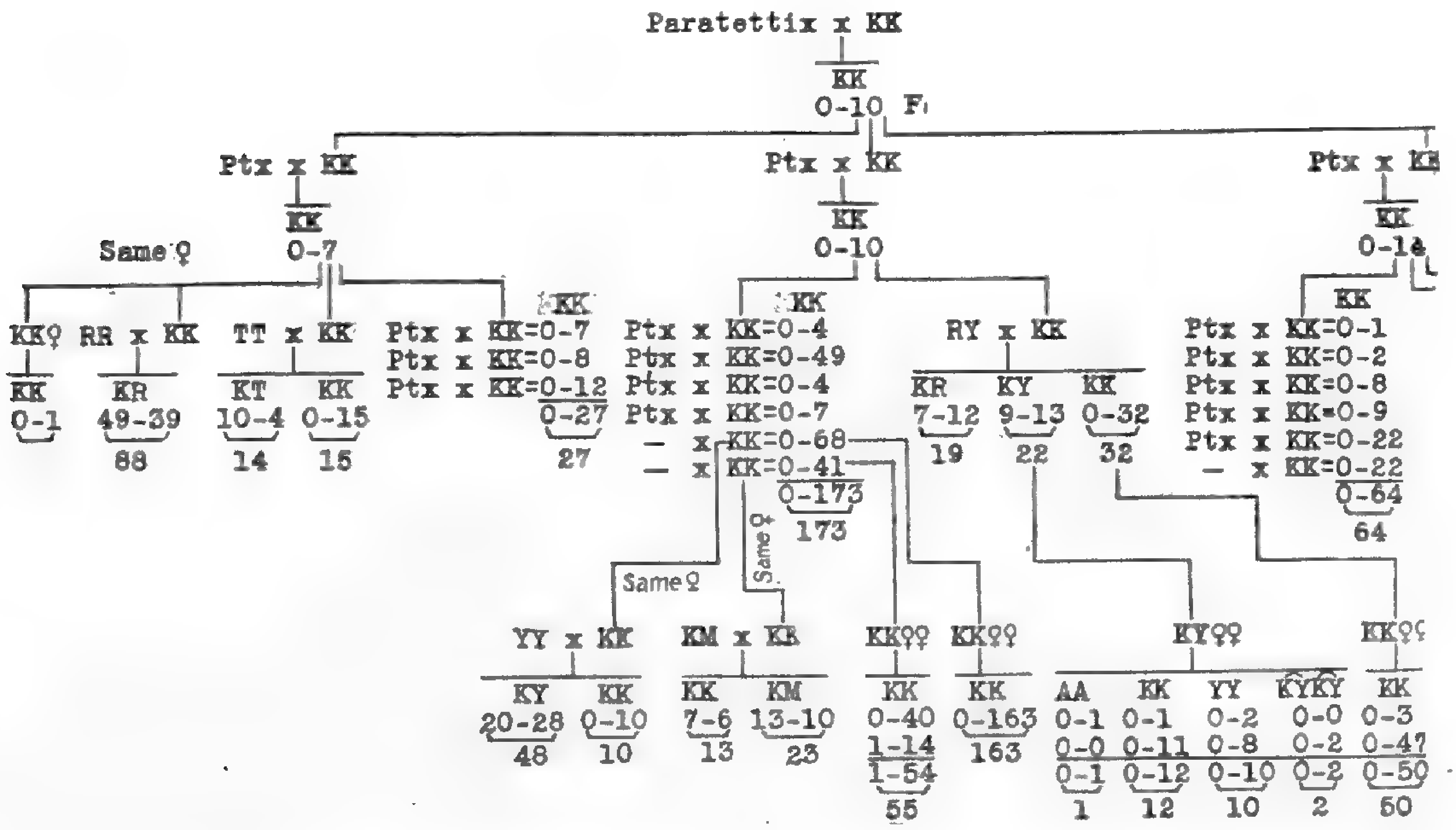
However, as already suggested, in contrast with the inheritance behavior in *Paratettix*, most of the factors in *Apotettix* show from small to considerable percentages of crossing-over. The discovery of crossing-over, with the further disclosure that these forms breed parthenogenetically, as well as bisexually, prompts me to submit a preliminary report in advance of a more extended presentation of the data and illustrations which can not be made ready this year.

The Adams fund has cared for the expenses, and I have had the generous and open-minded support of director, now president, W. M. Jardine. Mr. A. W. Bellamy gave effectual assistance during the earlier stages of the experiment.

Parthenogenesis and Crossing-over in the Female

The discovery of parthenogenesis in *Apotettix* was the result of attempts at cross-breeding the members of this genus with those of the genus *Paratettix*. It was observed that when an *Apotettix* male was used with a *Paratettix* female no progeny ever resulted, but the female of the reciprocal gave offspring, exclusively females, and of her own color pattern if she were homozygous, or segregated into her components and cross-overs if she were heterozygous. Then it was soon ascertained (see chart) that the *Apotettix* females which had never been exposed to males of any kind at any time behaved in this respect precisely as did those exposed to *Paratettix* males. Copulation between members of the two genera was never observed. Confirming these observations, Dr. J. L. Hancock kindly examined specimens for me and concluded that on account of structural differences the members of the one group could not mate with those of the other.

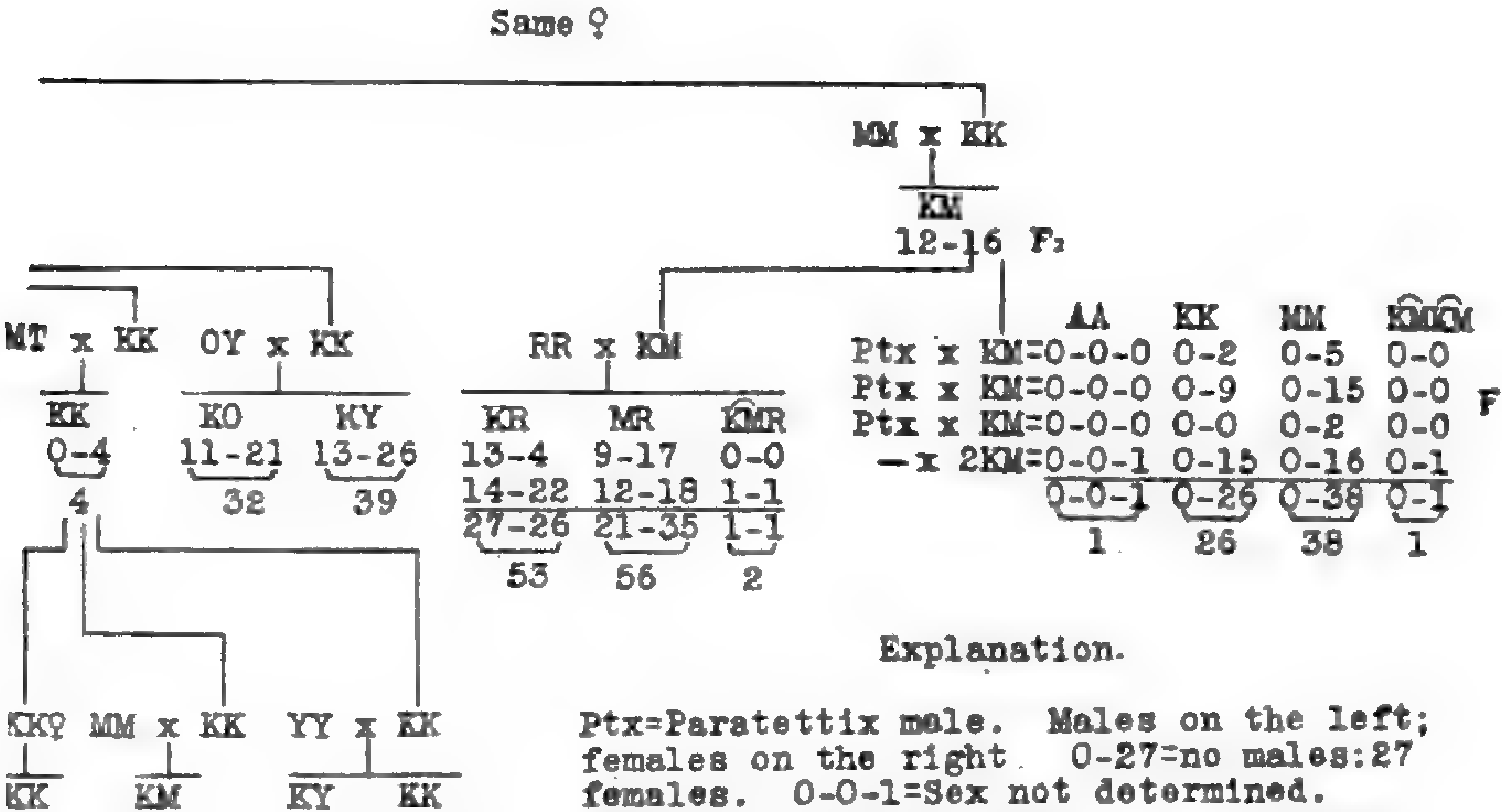
The chart illustrates a portion of the experiment which definitely determined that parthenogenesis occurs. It also shows crossing-over in the females. Following the chart, the first KK female, exposed to a *Paratettix* male of strongly contrasting pattern, produced 10 offspring, all females and of her own pattern. Three of these F_1



individuals were separately exposed to *Paratettix* males and gave 7, 10 and 14, respectively, and again all were KK females like the female parents and grandparent. One of these F_1 females was subsequently mated to a male of the strongly contrasting pattern MM, of her own genus, and then she produced 12 males and 16 females of the composite pattern KM.

From left to right, in F_2, a female KK was mated to an RR male and gave, in F_3, 49 ♂♂ : 39 ♀♀ of the intermediate KR pattern. About three weeks after the death of the male this KK female was removed to another cage, where she produced a few offspring, the only one recorded being a KK female. The next F_2 KK female was mated to a TT male of a strongly contrasting pattern. She produced 10 ♂♂ : 4 ♀♀ of the hybrid pattern KT, and 15 KK's, all females and without a trace of the TT pattern. The following three F_2 KK females were placed with *Paratettix* males and produced 7, 8 and 12 KK females, respectively. The next four F_2 KK females were also exposed to *Paratettix* males, and gave 4, 49, 4 and 7 offspring, all like the female parents; while the remaining two sisters, without exposure to males of any kind at any time, gave, in F_3, 68 and 41 KK females, respectively.

One of these, the one having produced 68 offspring



Explanation.

Ptx=Paratettix male. Males on the left; females on the right. 0-27=no males:27 females. 0-0-1=Sex not determined. 49-39=49 males:39 females. All other letters refer to factors in Apotettix and patterns.

parthenogenetically, was mated to a YY male and gave KY 20♂♂:28♀♀ and 10 KK ♀♀ without a trace of the YY pattern. The other F_2 KK female, which had given 41 offspring parthenogenetically, when mated to a KM male, gave KK 7♂♂:6♀♀, and KM 13♂♂:10♀♀. It is obviously impossible to determine if all the KK offspring from this mating were produced bisexually, or some of them parthenogenetically. However, since parthenogenetically produced individuals are, with rare exceptions, females, the result is somewhat checked by the proportion of 7♂♂:6♀♀. From the 68 F_3 offspring several females were allowed to reproduce without exposure to males of any kind at any time, and 163 KK females resulted in F_4. From the 41 KK F_3 individuals one which had never associated with any male gave 40 KK females in F_4, and another, also parthenogenetically, gave 14 females and 1 male, all KK's.

The following F_2 KK female was mated with an RY male and gave KR 7♂♂:12♀♀, KY 9♂♂:13♀♀, and 32 ♀♀ of the pattern of the KK parent. Two of these F_3 KK females were further tested parthenogenetically and produced, in F_4, a total of 50 offspring, all like themselves. Two of the KY ♀♀ were bred parthenogenetically and gave, both combined, 1 AA:12 KK:10 YY:2 $\widehat{KY}\widehat{KY}$, all females, thus exhibiting the crossovers AA and $\widehat{KY}\widehat{KY}$, as well as the expected segregates KK and YY.

The five next F_2 KK females placed with *Paratettix* males produced 1, 2, 8, 9 and 22 offspring, respectively, all KK females. The sixth female of this group, exposed to no male whatsoever, behaved precisely as did those individuals which had been with *Paratettix* males. Another of these F_2 KK females was placed with an MT male with 4 KK female offspring resulting in F_3, none evidencing any M or T part in the parentage. Three of these were bred further and gave offspring in F_4 as follows: one, without any male, 2 KK females; the second, mated to an MM male, 3 KM females showing the male parentage unmistakably; and the third, mated to a YY male, 1 KY female showing male parentage clearly, and 3 KK females indicating none of the male characteristics and plainly parthenogenetic. On account of the extremely small numbers involved, I suggest there is no special significance to the absence of males in the two last described matings. An eighth F_2 KK female, of this group, was mated to an OY male and gave KO 11♂♂:21♀♀ and KY 13♂♂:26♀♀.

The following two matings show RR males mated to KM females and giving KR 27♂♂:26♀♀, MR 21♂♂:35♀♀ and the crossovers K͡MR 1♂:1♀. Three of the KM females were placed with *Paratettix* males, but the offspring exhibited no more evidence of male parentage than those produced by the two KM sisters without exposure to any male. The combined result from the five KM sisters was AA 1:KK 26:MM 38:K͡MK͡M 1, all females, except that the sex of the AA individual was not determined. As in the case of the KY females already noted, this furnishes a very interesting exhibition of segregation as well as crossing-over in parthenogenetic individuals.

Subsequently from KK females, individually and in groups, but not exposed to males of any kind at any time, there have been given 2,726 female and 4 male offspring, all KKs, some of them having arrived at the fifth parthenogenetic generation. Including the KK females represented in the chart, and others exposed to males without effect, there have been produced parthenogenetically from KK females, a total of 3,289 females and 5 males, all of the KK pattern. Other females than KK (some of the data presented below) have produced 1,181 females and 2 males, making a total of 4,470 females and 7 males of various patterns produced parthenogenetically (August 1, 1918). Individuals of all the patterns, except AA which has not been adequately tested, have given offspring by parthenogenesis. It is not known if any one breeds in this way more readily than any other, the KK's having been used up to the present time more than the rest. Furthermore, it has not been determined whether, or not the capacity for parthenogenesis is in any sense an inheritable character. There are, however, great differences among individuals in this respect, even from the same F_2, or F_3, parthenogenetic batch.

Note: ♂♂ on the left.
♀♀ on the right.

(1)
MM ♀ ♀

	MM
	0–1
	0–1
	0–7
	0–12
	0–15
	0–37
	0–23
Total	0–96

(2)
RR ♀ ♀

	RR
	0–1
	0–16
	0–61
	0–7
	0–24
	0–35
	2–24
Total	2–168

(3)
YY ♀ ♀

	YY
	0–2
	0–4
	0–5
	0–22
	0–8
Total	0–41

(4)
$\widehat{YZ}\widehat{YZ}$ ♀ ♀

	$\widehat{YZ}\widehat{YZ}$
	0–18
	0–7
	0–19
Total	0–44

(5)
$\widehat{MR}\widehat{MR}$ ♀

	$\widehat{MR}\widehat{MR}$
	0–1
	0–16
Total	0–17

(6)
KM ♀ ♀

	AA	KK	MM	$\widehat{KM}\widehat{KM}$
	0–0–0	0–1	0–3	0–1
	0–0–0	0–5	0–5	0–0
	0–0–0	0–13	0–12	0–0
Total	0–0–0	0–19	0–20	0–1
From Chart	0–0–1	0–26	0–38	0–1
Total	0–0–1	0–45	0–58	0–2

(7)
KY ♀ ♀

	AA	KK	YY	$\widehat{KY}\widehat{KY}$
	0–0	0–6	0–2	0–0
	0–0	0–3	0–3	0–0
	0–0	0–1	0–0	0–0
	0–0	0–4	0–9	0–0
Total	0–0	0–14	0–14	0–0
From Chart	0–1	0–12	0–10	0–2
Total	0–1	0–26	0–24	0–2

(8)

$K\overset{\frown}{YZ}$ ♀ ♀

	KK	$\overset{\frown}{YZ}\overset{\frown}{YZ}$	$\overset{\frown}{KY}\overset{\frown}{KY}$	ZZ
	0–3	0–11	0–0	0–1
	0–14	0–8	0–1	0–1
	0–4	0–6	0–1	0–1
Total	0–21	0–25	0–2	0–3

(9)

MR ♀

AA	MM	RR	$\overset{\frown}{MR}\overset{\frown}{MR}$
0–2	0–11	0–4	0–2

A few other results from breeding *Apotettix* females parthenogenetically are given in the above tables, which also include the segregation and crossing-over in the KY and KM females shown in the chart.

Further crossing-over is indicated in the parthenogenetic $K\overset{\frown}{YZ}$ females (8) and the MR female (9). The latter indicates more than 21 per cent. of crossing-over, but the total crossing-over shown in 296 offspring from MR females, produced both bisexually and parthenogenetically, amounts to only 20, or less than 7 per cent. A few other simple hybrid females, some parthenogenetically and others bisexually, have produced cross-overs as follows:

From GM females 279 individuals with 11 crossovers, about 4 per cent.
From KM females 517 individuals with 5 crossovers, about 1 per cent.
From KY females 205 individuals with 12 crossovers, about 6 per cent.
From RY females 33 individuals with 3 crossovers, about 10 per cent.
From TY females 70 individuals with 8 crossovers, about 12 per cent.
From RT females 125 individuals with no crossovers.

There is every indication that as the numbers available become larger these percentage figures will be different; therefore it seems inadvisable to project at this time even a tentative diagram illustrating crossing-over percentages.

Crossing-over in the Male

Crossing-over in the females, in parthenogenetic as well as bisexual reproduction, is shown in the chart, and tables (1–9), and there are numerous other cases to be presented later in both bisexual and parthenogenetic breeding. While it appears that the crossovers in the females greatly exceed those in the males, the data are as yet insufficient to justify a final judgment. A few of the considerable number of cases of crossing-over in males are herewith given:

(10)

$\mathrm{A}\widehat{\mathrm{YZ}} \times \mathrm{AK}$

AA	AK	$\mathrm{A}\widehat{\mathrm{YZ}}$	$\mathrm{K}\widehat{\mathrm{YZ}}$	AZ
3–2	3–2	2–3	6–1	0–1
5	5	5	7	1

(11)

$\mathrm{O}\widehat{\mathrm{TY}} \times \mathrm{KK}$

KO	$\widehat{\mathrm{KT}}\mathrm{Y}$	KT
9–12	11–17	2–1
21	28	3

(12)

$\mathrm{MR} \times \mathrm{GK}$

GM	GR	KM	KR	$\mathrm{K}\widehat{\mathrm{MR}}$
1–4	3–5	1–5	1–2	0–1
5	8	6	3	1

(13)

$\mathrm{KM} \times \mathrm{RR}$

KR	MR	$\widehat{\mathrm{KM}}\mathrm{R}$	AR RR
6–7–5	3–14–4	0–1	0–2
18	21	1	2

(14)

$\widehat{\mathrm{KY}}\mathrm{M} \times \mathrm{RT}$

MR	MT	$\widehat{\mathrm{KY}}\mathrm{R}$	$\widehat{\mathrm{KY}}\mathrm{T}$	$\widehat{\mathrm{KM}}\mathrm{T}$
8–15	14–9	16–20	14–4	0–1
23	23	36	28	1

The KM × RR mating (13) is of interest and a sample of a frequent occurrence. The $\widehat{\mathrm{KM}}\mathrm{R}$ individual, of unmistakable pattern, could not be accounted for otherwise than by assuming crossing-over in the male, but since AR and RR were so much alike and were not bred further, we can not know whether both of these were AR, the A gamete coming from crossing-over in the male, or whether they were RR produced parthenogenetically by the RR parent, or one was produced by the former and the other by the latter method.

Discussion

Are the female gametes in this group of grouse locusts all of the same kind with respect to the necessity of fertilization, or do some of them require the spermatozoon, in order to develop, and others not? The latter situation is suggested by the fact that mated individuals frequently reproduce bisexually and parthenogenetically at the same time. Also, often, when an individual which has been reproducing parthenogenetically is mated she thenceforth gives offspring, some exhibiting, and others not, male parentage. In an unmated female perhaps the eggs that require fertilization disintegrate either before or after oviposition. (The eggs are oviposited in the ground. This matter can be, and is being, investigated.) On the other hand, it as often happens that when an individual reproducing parthenogenetically is mated she thenceforth gives offspring all showing male parentage. Also, though less readily, a mated female reproducing exclusively bisexually, when placed to herself, will, after a few weeks, give offspring parthenogenetically. Although the end result data which might give light on this point have not as yet been adequately developed, I venture the suggestion that with respect to the need of fertilization the mature eggs are approximately the same, and that it is the time of the entrance of the spermatozoon which determines the matter. If a spermatozoon enters the egg at the proper stage of its maturation the pronuclei unite; if no spermatozoon enters, or one enters too late, the egg either proceeds parthenogenetically, or fails to develop altogether.

The diploid number of chromosomes in the *Apotettix* female appears to be fourteen. This number has been clearly demonstrated in the late metaphase plate of an oogonial division in an individual derived bisexually. In a preparation of somatic cells of a female produced parthenogenetically, nine apparently whole chromosomes and some fragments were observed in one (Mr. A. H. Hersh, unpublished.) The females of some other members of the Tettigidæ have fourteen chromosomes (Robertson, '16). In some forms of the Tettigidæ the males have been shown to have thirteen chromosomes as the complete number (Harman, '15, and Robertson, '16).

The "maneuvers of the chromosomes" theory of Morgan may very well account for the observed end results presented in this paper, though the possibility of some other explanation is not by any means excluded. Even if the results herein entitled "crossing-over" should at some time be found actually not to be connected with the maneuvers of the chromosomes, the term might still be retained as an adequate expression of whatever does occur. The discussion of the mechanism, physiological processes, or both, involved in the parthenogenesis must await further investigation.

In nature, individuals of the pattern AA, of a mottled gray ground color, in striking contrast with, and much less conspicuous than, the rest, exceed in numbers all the others combined. This situation has been accounted for in the past by the assumption that the brilliant patterns rendered the individuals possessing them so conspicuous that they more readily fell prey to enemies, while the inconspicuous and protected AA individuals were largely unmolested. Now, since it has been demonstrated that crossing-over among the forms of conspicuous patterns produces the A gametes as well, the cause of the preponderance of AA patterns in nature may, in part at least, call for an entirely different explanation. AA may be the primitive form and the others have originated from it, by mutation or in some other way. The form AA seems to correspond to the so-called "normal" or "wild type," though all the others have also been found exclusively in nature, none (in *Apotettix*) having so far originated in the laboratory.

CONCLUSIONS

1. Through complete isolation of females from males of any kind, in some cases for as many as three generations, and, in addition, by genetic behavior, it has been demonstrated that these forms of *Apotettix* are gynogenetically, except rarely parthenogenetic (tychoparthenogenetic).

2. Segregation is demonstrated as occurring in heterozygous individuals reproducing by parthenogenesis, as well, and apparently to the same extent, as in those females reproducing bisexually.

3. Crossing-over is demonstrated as occurring in heterozygous individuals reproducing by parthenogenesis, as well, and apparently to the same extent, as in those females reproducing bisexually.

4. Crossing-over occurs in the male, as well, but apparently not to the same extent, as in the female.

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THE EVOLUTION OF ARTHROPODS AND THEIR RELATIVES WITH ESPECIAL REFERENCE TO INSECTS [1]

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The two lines of descent which have culminated in the production of some of the most active and "dynamic" of living creatures, and those in which the psychic faculties have attained their highest degree of perfection, are represented by the vertebrate group Mammalia, at whose apex is man, and the invertebrate group Arthropoda, at whose apex are the Insecta. Since these are the great rival groups, contending for the possession of the earth, the tracing of the paths by which they have arrived at their present dominating positions affords one of the most fascinating chapters of the study of organic evolution. Concerning the ancestry of man, there is some degree of agreement of opinion in modern works upon the subject; but the recent investigations of Handlirsch, 1904–1908, are not in accord with those of his predecessors in the study of insect phylogeny, and since his views have received a surprisingly widespread acceptance, his work has served to revive the discussion of the ultimate derivation of the insectan type of animals.

There can be but little doubt that the insects and their arthropodan relatives are the descendants of ancestors related to the worm-like forms. These in turn were derived from lower worm-like ancestors resembling the members of the Rotifera-Platyhelminthes group. In the present state of our knowledge of the subject, it is hardly possible to state with any degree of certainty whether the ancestors of the worm-like forms were ultimately

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[1] Contribution from the Entomological Laboratory of the Massachusetts Agricultural College, Amherst, Mass.

derived from the Cœlenterata-Porifera group—*i. e.,* from a cœlenterate (cnidarian ?) type of animal through *Ctenophora*-like (?) forms; or more directly from a colonial protozoan type through forms comparable to the "Mesozoa" and their relatives, such as *Dicyema,* etc.; although there is a strong probability that the lower worm-like forms arose from ancestors occupying a position intermediate between these types of animals. From the standpoint of evolution, the Rotifera and Platyhelminthes (also such worms as *Dinophilus,* etc.) are among the most important of the lower worm-like forms, since they have departed as little as any from the condition characteristic of the ancestors of the "Annelida" and many other invertebrates; and even the line of descent of the vertebrates themselves may ultimately lead back to forms not unlike the members of this group. A higher stage of development is represented by the "Annelida" (including the Sternaspididæ, *Gephyrea,* etc.), which are a group of the greatest phylogenetic importance due to the fact that their line of development is approached by, or is paralleled by, those of many other invertebrate groups, and to the fact that they have retained a great number of characteristics apparently typical of the ancestors of the Arthropoda. Their forebears probably occupied a position intermediate between the Rotifera and the Platyhelminthes, and indeed, some investigators have even placed the "archiannelid" *Dinophilus* among the planarian Platyhelminthes, although its closest affinities seem to be with the annelidan worms *Protodrilus* and *Polygordius.*

From their annelid-like forebears, there have branched off two important lines of descent, which have approached very close to the arthropodan type, and which have even been classed among the Arthropoda by some investigators. One of these lines of development is represented by the Onychophora, which are suggestively arthropod-like in many particulars, although they have retained many annelidan characters; while the other line is represented by the Myzostomida, which are regarded by some authorities as occupying a position intermediate between the chætopod Annelida and the Tardigrada.

The position of the Tardigrada is still a subject of considerable discussion, and the decision of the matter depends largely upon the settling of the question whether the apparent simplicity of their organization is due to the retention of a primitively simple condition, or to a secondarily acquired simplicity brought about by reduction or degeneracy, etc. If the simplicity of the Tardigrada is a primitive one, there is much to be said in favor of placing them next to the Myzostomida in the Myzostomida-Onychophora group; but whether the Linguatulida should also be included in this group seems very doubtful.

From the resemblance of the adults to Eriophyid mites, and of the immature forms to such short-bodied mites as *Phytoptus*, etc., many recent authorities would place the Linguatulida near the Acarina—a highly modified group far removed from the base of the arthropodan stem. If this view is correct, the apparent simplicity of the Linguatulida is to be regarded as the result of a reduction or degeneration rather than the retention of a primitive condition, in forms so far removed from the base of the arthropodan stem; and if the simplicity of the Tardigrada is primitive, while that of the Linguatulida has been secondarily acquired through reduction or degeneracy, the apparent resemblance between the Tardigrada and Linguatulida must be regarded as the result of convergence, or parallelism, rather than of consanguinity. Under these conditions the Linguatulida could not be grouped with the Tardigrada, if the latter are placed next to the Myzostomida in the Myzostomida-Onychophora group; but if the apparent simplicity of the Tardigrada is also due to reduction or degeneracy, they too might be placed with the Linguatulida near the mites—although this does not appear to be very probable from our present knowledge of the subject. It is quite apparent, however, that the matter needs considerable further investigation before this question can be definitely determined.

The affinities of the molluscan group are somewhat obscure, but the study of their immature stages would indicate that the Mollusca are rather distantly related to the Chætopoda, *Gephyrea,* "Polyzoa," and other annelid-like forms. If this be true, their line of development apparently likewise extends back to forebears similar to the members of the Rotifera-Platyhelminthes group (which are very like the ancestors of the "Annelida" also), and the ancestors of the Echinodermata and Hemichordata may possibly be traced back to a similar stock (or to forms closely related to them) as well.

The Hemichordata are regarded by many authorities as a group which has departed but little structurally from the ancestral condition of the forms leading up to the vertebrate type of animal. From a study of their larvæ, some investigators have concluded that the Hemichordata are related to the Echinodermata; but this brings us no nearer to the solution of the problem, since the Echinodermata occupy an isolated position, and their ultimate affinities are very obscure. Although the Echinoderm line of development may lead back more directly to the Cœlenterata, there is a possibility of their forebears being quite closely related to the members of the Rotifera-Platyhelminthes group which have departed but little from the condition characteristic of the ancestors of the "Annelida" and other invertebrate groups; and even if the Echinodermata are to be regarded as the descendants of Cœlenterata-like forebears, it must be remembered that the ancestors of the Rotifera-Platyhelminthes group were themselves very closely related to the Cœlenterata, and would probably have been classed as such, rather than as colonial Protozoa.

It is quite possible to regard the line of development of the Echinodermata as related to the other two lines of development in question, and as branching off near, or even further down in the developmental scale, than the points of origin of the lines of descent of the Hemichordata and the worm-like forms. It is also possible to suppose that in the hemichordatan line there have been carried over certain developmental tendencies from their common ancestry, such as the preservation of a "tornaria" larva characteristic of the Echinodermata, while in other respects the Hemichordatan line of development has paralleled that of the worm-like forms more closely, having taken over more of the tendencies which were to find opportunities for fuller expression in the worm-like forms from their ultimately common inheritance. Under these conditions the Hemichordata are related to both the Echinodermata and the worm-like forms, but their line of development has accompanied that of the worm-like forms much more closely and for a longer distance before each branched off along its own path of specialization. If the lines of development of the Hemichordata and of the worm-like forms have an ultimately common ancestry, and if both lines of descent have "travelled along the same developmental road" for a considerable distance before each branched off along its own path of specialization, it is not surprising that we find many structural resemblances in the two lines of descent, and the resemblance of such Hemichordata as *Cephalodiscus, Rhabdopleura, Phoronis,* etc., to certain "Polyzoa," may be as much the result of consanguinity as of "convergent development." This view enables us to harmonize the apparently discordant theories concerning the ultimate origin of the Vertebrata—all of which may contain a portion of the truth, as is frequently the case in the different hypotheses put forward to explain certain observed phenomena. Thus, according to this conception, we may derive the Vertebrata from forms similar to the Hemichordata, and still account for the annelid-like (and arachnid-like) features which appear in certain of the lower representatives of the vertebrate group, since tendencies present in the ancestors which ultimately gave rise to both the Annelida and the Hemichordata are quite likely to appear in both Annelida and Hemichordata (or in forms descended from them, such as the Arachnida and the Vertebrata).[2]

One of the chief difficulties in the way of reaching a proper understanding of the mutual interrelationships of the different lines of development is the attempt to arrange these lines in the form of a dichotomously branching tree drawn in one plane—which is almost as impossible as the attempt to arrange all animals in a single linear developmental series; for it must be borne in mind that these different lines of development frequently approach one another from different directions, so that it would be necessary to represent their relationships by a figure drawn in *three* dimensions, rather than in a single plane. If this is done, it becomes easier to understand that the line of development of the "Annelida," for example, is paralleled (on different sides) by those of several other groups, and that all of these lines of descent may lead back to a common ancestry, or that their points of origin may be near the point at which the line of descent of the "Annelida" arose.

In discussing the ultimate relationships of the Vertebrata, Echinodermata, Mollusca, etc., the lack of intermediate forms annectent between the different developmental series, or connecting them with the supposedly ancestral forms, has made the subject of their affinities extremely speculative; and it is not until we come to the consideration of arthropod phylogeny that the evidence is at all satisfactory, and even here important gaps in the developmental chain leave much to be desired.

As was previously stated, the members of the Myzostomida-Onychophora group have developed many characters strongly suggestive of arthropod affinities; but they

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[2] This statement should not be interpreted as implying that recent vertebrates are descended from living Hemichordata, etc., but it is merely intended to indicate that the Hemichordata have departed but little from the probable ancestral condition of the Vertebrata, and the same holds true for similar statements throughout this paper.

have become too greatly modified along their own lines of specialization in regard to those particular structures most frequently used in comparative morphology to be of much value for a phylogenetic study of the development of the different parts of the body in the lower arthropods. Among the "Annelida," on the other hand, we find some very promising material for such a study, especially among the chætopodan annelids, such as the Syllidæ (*e. g., Dujardinia rotifera,* etc.), which have segmented appendages, while others of the group have developed structures no less interesting from the standpoint of phylogeny, indicating that they have departed but little from the ancestral condition of the arthropods. The segmentation of the body of these annelids,[3] the nature and relative positions of the heart and the digestive, nervous and other systems, very readily lend themselves to such an interpretation, and it is not a difficult matter to derive the head region of a primitive arthropod from that of the annelid type (Bernard, 1892), or to derive the appendages of such an arthropod from those of the annelidan type, as has been recently discussed by Borradale, 1917.

In connection with the discussion of the derivation of the appendages of the lower arthropods from structures comparable to the parapodia of the annelids, it may be remarked that the attempt of Lankester, 1872, to derive the Arthropoda more directly from the Rotifera, such as the remarkable *Pedalion mira* (whose appendages and the "arms" of the male *Asplanchna* he compares to the movable spines of *Triarthra* and *Polyarthra*), has not been productive of as important results as those obtained from the comparison of the annelidan structures with those of the arthropods. This, however, is merely to be expected, since the annelids have developed far

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[3] Just as some annelids are many-segmented, while the bodies of others are composed of fewer segments, it is quite reasonable to suppose that the ancestors of the arthropods exhibited a considerable range in the number of segments composing their bodies—and even among the most primitive arthropods there is a wide range in the number of segments composing their bodies.

more features in common with the lower arthropods than have such primitive forms as the Rotifera. On the other hand, the Annelida themselves (and hence ultimately the Arthropoda also) are the descendants of Rotifera-like (and Platyhelminthes-like) forebears, and it is quite possible that certain rotifers might develop features which later find opportunity for fuller expression in the forms descended from them (*e. g.*, the striated muscles of *Pedalion*); but, since the general organization of a rotifer's body is not so similar to that of the lower arthropods as is the case in the annelids in question, for the present at least it seems preferable to regard the slight resemblances between the appendages of the Rotifera and the lower Arthropoda mentioned above as the result of "convergence" (parallelism) in development rather than to consider it as a precocious development of structures later to be developed in the arthropod descendants of ancestors ultimately arising from rotiferan forebears. I would not utterly deny the latter possibility, however, since it may be quite possible that arthropods are to be derived more directly from Rotifera-like forebears (*e. g., Hexarthra polyptera,* etc.) through forms related to the Tardigrada and *Nauplius*-like ancestors; but the great mass of evidence from comparative anatomy, embryology, etc., points to an "annelid ancestry" for the Arthropoda, and until other hitherto undiscovered forms have been found to indicate some other derivation for the group, we are safe in assuming that the "Annelida" represent as nearly as any known forms the ancestral condition of the Arthropoda.

In taking up the consideration of the evolution of the Arthropoda themselves, the question naturally arises as to what arthropods have departed the least from the probable ancestral condition of the group as a whole. Some investigators would claim that since the *Nauplius* larva is of such widespread occurrence among the lower arthropods, that it represents an ancestral type; but it must be borne in mind that a free-swimming larva is usually very greatly modified in adaptation to its own mode of life and environmental conditions, and frequently represents an interpolated stage having no great phylogenetic significance (in comparison with the developmental stages of the embryo). Furthermore, it is extremely probable that the ancestral arthropods were not of one single type at all, but doubtless differed very greatly among themselves in size, the number of segments composing their bodies, etc., just as is the case among certain annelidan groups, or as is the case among the assemblage of lower arthropods comprising the most primitive members of the group next to be discussed.

The assemblage of lower arthropods comprising the Copepoda, Branchiopoda and their immediate relatives may be referred to as the Copepoda-Branchiopoda group. Its members include some of the most primitive of the arthropods, and it may be regarded as representing as nearly as any the forms giving rise to the different arthropodan lines of development. The Ostracoda represent a line of development which branched off at an early date, and should also be included in the group; but they are not structurally so important as the Branchiopoda, etc., for a phylogenetic study of the lines of descent to which the ancestral arthropoda gave rise. The Cirrepedia likewise represent a group which branched off from this stem at an early date, but they are too degenerate, and have followed their own line of specialization too far to be included among the primitive representatives of the Copepoda-Branchiopoda group. The Trilobita are very closely related to the Apodiæ and Branchiopoda in general, for such trilobites as *Nathorstia transitans* are somewhat annectent between the trilobites and the branchiopod *Opabina regalis* described by Walcott, 1912, and such trilobites as *Marella splendens* are very like certain Apodidæ, etc.; but the closest affinities of the Trilobita appear to be with the group next to be considered, and although the trilobites have preserved many very primitive features which might entitle them to a position in the ancestral "Copepoda-Branchiopoda" group, it is preferable to consider them as members of the Trilobita-Merostomata group, with which they have much more in common.

The Trilobita-Merostomata group is composed of the Trilobita, Eurypterida, and Xiphosura, with their immediate relatives, and includes the forms which have departed the least from the ancestral condition of the arachnoids in general. The Trilobita are extremely closely related to the Merostomata, some of which (such for example as the fossil merostome *Bunodes lunula,* which has been admirably restored by Patten, 1912, or the cambrian merostomes, *Sidneyia inexpectans, Emeraldella brocki,* etc., described by Walcott, 1911–1912) bear well-developed antennæ very similar to those of the trilobites; so that the division of the Arthropoda into "Teleiocerata" and "Chelicerata" by Heymons, 1901, or into "Antennata" and "Chelicerota" by Boerner, 1909, can not be strictly applied when we take these forms into consideration. Walcott, 1912, considers that such merostomes as *Molaria spinifera* are connected with the trilobites through such intermediate forms as *Nathorstia transitans*—a trilobite also related to the Branchiopoda. Walcott also considers that the merostome *Sidneyia* represents a transition form between the trilobites and the eurypterids, and that the merostomes *Beltina* and *Sidneyia* are related to the ancestors of living Xiphosura; so that according to his views the trilobites are descended from branchiopods, while the eurypterids are descended from trilobites through such merostomes as his "Aglaspina" and "Limulava," from which living Xiphosura are descended.

In discussing the lower arachnoid forms, it is necessary to take into consideration the Pantopoda, which have apparently retained certain features strongly suggestive of crustacean affinities, while certain other features suggest that they are related to the arachnoid forms. Boerner, 1902, however, thinks that the Pantopoda are structurally quite far removed from the arachnids examined by him, and since he has made a very extensive study of the different arachnoid forms, his opinion should have considerable weight. Since their line of development does not approach very closely to those of the other forms here discussed, the study of the Pantopoda is not of as great phylogenetic importance as that of those forms which occupy a position annectent between the other groups, or whose lines of descent approach those of the other groups. For the purpose of the present paper, it is therefore sufficient to say that the Pantopoda represent a highly aberrant group whose line of descent branched off at an early date, somewhere near the Trilobita-Merostomata group, and that they have followed a widely divergent path of specialization.

The scorpions are descended from forms very like the eurypterid members of the Trilobita-Merostomata group, and such eurypterids as *Glyptoscorpius* occupy a position annectent between the two groups. On the other hand, the scorpions, together with the Pedipalpi, are in many respects very like the ancestors of the higher arachnids, so that they form an ancestral group, the Scorpionida-Pedipalpi, intermediate between the Trilobita-Merostomata group and the higher arachnids. In the Scorpionida-Pedipalpi group should be included the closely allied pseudoscorpions and probably the *Koenenia*-like forms and the Solifugæ also.

Of the higher groups of arachnids, the spiders (Araneæ) are apparently quite closely related to the amblypigid (tarantulid) branch of the Pedipalpi, while the Phalangidea (Opiliones) and *Acarina* are more closely related to the pseudoscorpions and Solifugæ, although it has been suggested that the Cryptostemmatidæ occupy a position intermediate between the Pedipalpi (to which they are somewhat more closely allied) and the Phalangidea. The Linguatulida have been placed near the mites by many recent authorities on account of the supposed resemblance of their larvæ to such short-bodied mites as *Phytoptus,* etc., and the apparent resemblance of the adults to eriophyid mites, so that provisionally, at least, the Linguatulida may be regarded as strongly aberrant mites, while the Tardigrada are probably not related to them, but to the Myzostomida, as has been previously discussed.

Since the arachnoid path of evolution has led off in a direction widely divergent from the path followed in the development of the Insecta, it is very difficult to understand how Thorell came to the conclusion that such highly developed arachnids (*i. e.,* those occupying a position far along the divergent line of development) as the Solifugæ are intimately related to insects. Furthermore, since the trilobite trend of development leads off toward the merostomes and the divergent evolutionary path of the arachnoid forms, it is necessary to search further back than the trilobites for a group standing more nearly in the direct line of development eventually resulting in the evolution of the insectan type, and for this purpose the study of the branchiopod representatives of the Copepoda-Branchiopoda group is much more valuable.

The members of the Copepoda-Branchiopoda group which seem to be the nearest to the stem forms at the base of the line of descent which ultimately leads up to the insect type of development are the Notostraca (Apodidæ) and anostracan Branchiopoda, which are likewise very closely related to the trilobites, so that certain ancestral features are to be found in the trilobites also, having been inherited from their common forebears; but, as was stated above, the trend of trilobite development is toward the production of the eurypterid and arachnoid type of development, and therefore leads away from the line of development which eventually results in the production of the insect type. Walcott, 1912, agrees with Bernard, 1892, in regarding the Apodidæ as among the lowest representatives of the Arthropoda (although certain copepods are also extremely primitive) and suggests that the fossil annelids, *Canadia spinosa* (in which the head is bent down "so that the mouth faces posteriorly" in the position assumed by Bernard, 1892, to be that of the annelids which gradually took on the character of head region leading up to the arthropod type), and the Crustacea "were derived from the same general type of animal." The Copepoda represent a line of development which branched off near that of the Branchiopoda, at the base of the arthropod stem; and the Argulidæ (which are grouped with the Copepoda by Calman, 1909) are regarded by some authorities as annectent between the Copepoda and the Branchiopoda. The Ostracoda are related to both the conchostracan and cladoceran Branchiopoda (following Calman's classification) and the ancestors of the ostracods doubtless arose from forms intermediate between the Cladocera and Conchostraca. The Cirrepedia are apparently descended from ancestors related to both the Ostracoda and Copepoda, and their line of development branched off at an early date to follow their own strongly aberrant part of development.

Such anostracan branchiopods as the fossil *Opabina regalis,* whose structure according to Walcott, 1912, "is very suggestive of an annelidan ancestor," and such notostracan branchiopods as the fossil *Burgessia bella* (which has sessile eyes and hepatic glands in a carapace resembling that of *Lepidurus*) serve to indicate what the first arthropods were probably like, and they occupy a position near the base of the stem-forms whose lines of development were eventually to produce the insectan type of arthropod. The fossil notostracan branchiopod *Waptia* occupies a position annectent between the above-mentioned branchiopods and the malacostracan group next to be considered.

The leptostracan (phyllocarid) group occupies a position intermediate between the rest of the Malacostraca and the branchiopods described above. They have also carried over from their common branchiopod ancestry certain features likewise inherited by the trilobites; but.

as was previously stated, the trilobites do not stand in the direct line of descent of the Leptostraca, and those characters which they possess in common were inherited from their common branchiopod ancestry, and can not be interpreted as indicating that the trilobites represent the ancestral forms giving rise to the lepostracan type. The fossil leptostracan *Hymenocaris* is evidently related to the fossil branchiopod *Waptia* (which occupies a position intermediate between the branchiopods and Leptotraca), but *Hymenocaris* is clearly a leptostracan, and resembles such living forms as *Nebalia*, while the fossil leptostracans *Carnavonia* and *Tuzoia* resemble such living Leptostraca as *Nebaliopsis typica* in the character of the carapace, etc. The closer affinities of the fossil Ceratiocaridæ, etc., have not been determined, due to the imperfect preservation of the limbs, etc., but they clearly belong to the leptostracan group. There is much to be said in favor of including the Leptostraca in the next group of the Malacostraca to be considered, but from the standpoint of a phylogenetic study it is preferable to consider the Leptostraca (together with other primitive forms not yet described) as nearer the ancestral forms from which the other Malacostraca were derived.

A further stage of development is represented by the Anomostraca-Cumacea group which includes the Syncarida and a portion of the Peracarida of Calman's classification, together with their immediate relatives. The Anomostraca (Anaspidacea and Bathynellacea of Chappius, 1915), Mysidacea and Cumacea are very closely interrelated, and all of them exhibit affinities with the Leptostraca, so that the members of the leptostracan group might well be included here also; but they have been treated as a separate group, to emphasize the fact that they occupy a position annectent between the Branchiopoda and the Malacostraca (with which their strongest affinities lie). Although the members of Anomostraca-Cumacea group are extremely closely related to the Tanaidacea, the closest affinities of the Tanaidacea are with the Isopoda (and Amphipoda), so that it is preferable to consider them with the latter group. The Anomostraca-Cumacea group is of the greatest phylogenetic importance, since its members have departed as little as any known forms from the probable ancestral condition of the higher Crustacea, Insecta and "Myriopoda" (*sensu lato*).

The Mysidacea have retained some primitive characters indicating their connection with the Leptostraca-like forms which preceded them, and they are quite like the ancestors of the eucaridan (euphausiacean and decapodan) members of the higher crustacean groups. They are also probably related more remotely to the ancestors of the aberrant hoplocaridan (stomatopodan) line of development, and through such forms as the Cumacea they are connected with the ancestors of the Tanaidacea (and therefore of the Isopoda also). They are not so important for a phylogenetic study of the insects, etc., however, as the Anomostraca and Cumacea (with the Tanaidacea) are. The Cumacea occupy a position intermediate between the Mysidacea and the Tanaidacea, being somewhat more closely allied to the latter. They are also related to the Anomostraca (Syncarida), as is true of the Mysidacea, the interrelations of the different members of the group being rather complicated.

From the standpoint of the study of the phylogeny of the insects and their relatives the Anomostraca and Cumacea (together with the Tanaidacea) are by far the most important forms, since the ancestors of the insects and their relatives were doubtless descended from forms closely related to the Anomostraca, Cumacea, and Tanaidacea. Of these three, the Anomostraca are apparently the most ancient (fossil remains of the others have not yet been found), and have doubtless departed as little as any from the ancestral forms which were eventually to give rise to the isopods, insects and "myriopods." The fossil Pleurocaridæ (*e. g.*, *Acanthotelson*, etc.) are nearer to the living genera *Koonunga*, *Anaspides*, *Para-*

naspides, etc., while the fossil "Gampsonychidæ" (*e. g.,* "*Gampsonyx,*" *Palæocaris* and *Gasocaris*) are nearer the living genus *Bathynella.* Such fossil forms as *Præanaspides* found in the Carboniferous rocks is extremely like the living *Anaspides* which has apparently preserved many ancestral characters, but little modified, to the present time. The Anomostraca are related to the Leptostraca, but no forms intermediate between them and the Leptostraca have yet been described, and it is possible that the line of descent of the Anomostraca leads back to the branchiopods through Leptostraca-like forms not yet discovered. Superficially, at least, such slender branchiopods as *Yohoia tenuis,* etc., resemble certain members of the Anomostraca, and it is possible that the slenderer, more cylindrical Anomostraca, such as *Bathynella,* may have inherited the tendency toward the slender form of body from anostracan branchiopods of the *Yohoia* type. In *Bathynella* the eyes have become completely lost, but in *Koonunga* sessile eyes are found and their presence suggests that sessile-eyed forms may have developed from the *Koonunga* type. In *Anaspides* the eyes are stalked.

From ancestors occupying a position intermediate between the Anomostraca and Cumacea (and also related to the Mysidacea) have arisen the lines of descent leading to the isopod Crustacea, Insecta, and "Myriopoda" (s. l.). The Tanaidacea (Chelifera) which occupy a position near the base of the isopod stem are very closely related to the Anomostraca, Cumacea and Mysidacea, and, together with the Isopoda and Amphipoda (which are descended from ancestors very similar to them), they might be included in the Anomostraca-Cumacea group; but if the Isopoda-Amphipoda group is considered separately, the Tanaidacea must be included in the latter group, since their closest affinities are with the Isopoda. The Amphipoda are quite closely related to the Isopoda, and their ancestors may also have arisen from forms intermediate between the Anomostraca and Cumacea (and also related to the Mysidacea), so that the sessile-eyed character occurring in the group might be regarded as a retention of the tendency toward the formation of sessile eyes exhibited by such primitive forms as *Koonunga,* while the slender body form present in such Amphipoda as the caprellids, *Rhabdosoma,* etc., may possibly be due to the retention of the tendency toward the slender form of body (such as that present in the more primitive *Bathynella*) in forms which are otherwise rather highly modified. The Isopoda-Amphipoda group originated very close to the point of origin of the insect line of development, and the two lines have paralleled one another extremely closely. Since the members of the Isopoda-Amphipoda group have not travelled so far along the path of specialization in following the same developmental road with the insects, they have retained many primitive features characteristic of the ancestors of the insects (and "myriopods"), and such forms as *Apseudes* are particularly interesting for a phylogenetic study of insects and their immediate relatives.

The Symphyla-Pauropoda group (composed of such forms as *Scolopendrella, Scutigerella, Pauropus, Eurypauropus,* and their immediate relatives) contains the forms which appear to be very near the base of the "myriopod" stem, and which have retained a great number of features characteristic of the ancestors of insects, so that a study of the structures of the Isopoda-Amphipoda group and the Symphyla-Pauropoda group are of the greatest importance for a proper conception of the nature of the first insects to be evolved. The Symphyla-Pauropoda group probably also arose from forms occupying a position intermediate between the Anomostraca and Cumacea, and likewise closely related to the Tanaidacea which originated from similar forebears. Such Anomostraca as *Bathynella* have not departed far from the ancestral condition of the Symphyla-Pauropoda group, and although they have developed many modifications along their own line of specialization, they are as near as any known forms to the ancestors of the Symphyla, etc. The Symphyla-Pauropoda group in turn has departed but slightly from the ancestral condition of the "Myriopoda" as a whole, although the ancestral "Myriopoda" comprised forms with bodies composed of more numerous segments as well as those made up of fewer segments. From ancestors similar to the members of the Symphyla-Pauropoda group one line of development has led to the chilopod type of myriopod, while the other has led to the diplopod type. From their ancestors related to the members of the Symphyla-Pauropoda group, the Chilopoda have carried over many characters also inherited by the ancestors of insects, so that a structural study of the Chilopoda is of considerable value from the standpoint of insect phylogeny (as is true to a lesser degree of the Diplopoda also).

As was stated above, the ancestors of the Insecta were related to the members of both the Isopoda-Amphipoda group (including the Tanaidacea) and the Symphyla-Pauropoda group, so that the lines of descent of all three groups (insects, isopods and Symphyla) doubtless had a common origin in forms intermediate between the Cumacea and Anomostraca (and also related to the Mysidacea), and all of the three groups have inherited from their common ancestry many characters also carried over in the lines of development of the other two of the three groups in question. The common ancestors of the three groups just mentioned (insects, isopods and Symphyla) were not of any one single type, but doubtless differed quite markedly among themselves in the number of segments composing their bodies, the slender or stouter and flatter character of the body and other features. Some of them were more like the Tanaidacea, while others were more like *Bathynella* and other members of the Anomostraca, etc., and this should be clearly borne in mind in attempting to determine what the ancestors of the insects, etc., were like; for the greatest obstacle to arriving at the realization of the true nature of the ancestors of insects and their relatives has been the attempt to derive them all from one type of creature —which is manifestly impossible, since even the lowest representatives of any group differ markedly among themselves, and their ancestors also must have differed markedly among themselves (although not to such a great extent as their progeny do).

Although such Anomostraca as *Bathynella* have become specialized along their own lines of development, they have retained many features which suggest what some of the ancestors of the insects and Symphyla must have been like, and I think it very probable that the ancestors of *Scolopendrella* and the Protura were quite similar in many respects to *Bathynella,* while other apterygotan insects, such as *Machilis,* have carried over more characters from the tanaidacean side of their common ancestry. Therefore, if we accept the idea that some of the common ancestors of insects, isopods and Symphyla occupied a position intermediate between the lines of development of the Anomostraca and the Cumacea-Tanaidacea, and differed a little less among themselves than the Anomostraca do from the Cumacea-Tanaidacea, it becomes perfectly clear that some apterygotan insects could inherit from the tanaidacean side of their common ancestry characters which also appear in the isopods which are derived from Tanaidacea-like forebears; while on the other hand, other apterygotan insects could inherit from the *Bathynella* side of their common ancestry certain characters which also appear in the Symphyla or other forms descended from *Bathynella*-like forebears.

The Protura (such as *Acerentomon, Eosentomon,* etc.) are the most primitive representatives of the Insecta, and have inherited from their common ancestry many features also preserved in the "Myriopoda"; and the embryological development of the apterygotan group to which they belong has much in common with that of the "Myriopoda," as has been pointed out by Philiptschenko, 1912, Lignau, 1911, Chamberlain, 1917, Heymons, and others. The retention of the stumps of three pairs of legs on the abdominal region (in addition to the three pairs of thoracic legs) at first caused some zoologists to doubt that the Protura are really insects (since the idea that such forms with vestigial abdominal legs could not be true "hexapods" if they had more than six limbs seemed to stand in the way of their realizing the true insectan nature of the Protura), but the overwhelming evidence of their structural organization has convinced all recent entomologists that the Protura are true insects. As pointed out in a recent paper (Crampton, 1916) the Protura are quite closely related to such other Apterygota as *Tomocerus;* and, with the Entomobryids and Sminthurids, they constitute the non-styli-bearing division of the Apterygota.

Of the styli-bearing Apterygota, the next group to be considered, which may be referred to as the Campodeoid group, comprises the Rhabdura (*e. g., Campodea*), the Dicellura (*e. g., Projapyx, Japyx,* etc.) and their immediate relatives. Dicellura, such as *Projapyx, Anajapyx,* etc., have segmented cerci, and occupy a position intermediate between the Rhabdura, such as *Campodea,* and the other Dicellura, although their closest affinities are clearly with the Dicellura. The Campodeoid group, whose members have entognathous mouth parts and vestigial abdominal legs suggestive of the proturan structures, occupy a position intermediate between the lower apterygotan Protura and the higher apterygotan forms, such as *Nicoletia, Lepisma,* etc., which also belong to the styli-bearing apterygotan subdivision which includes the Campodeoid group as well (Crampton, 1916). The Campodeoid group, while inheriting certain features from the symphylan side of their common ancestry, have inherited in addition certain other features more typical of the crustacean side—which likewise reappear in the isopod-amphipod descendants of their common ancestors.

The Lepismoid group, composed of the lepismids, machilids, and their immediate relatives, is quite closely connected with the Campodeoid group in the styli-bearing subdivision of the Apterygota; but their mouth parts are ectognathous, and in their general organization they approach remarkably closely to the lower Pterygota; so that they may be said to occupy a position annectent between the lower Pterygota and the Campodeoid group. The members of the Lepismoid group seem to have inherited more characters from the crustacean side of their common ancestry than from the symphylan side, while the members of the Proturan group seem to have inherited more characters from the symphylan side, and the members of the Campodeoid group appear to partake to some extent of characters occurring in both the crustacean (isopod) and symphylan sides of their common ancestry.

It might be possible to explain the presence of both crustacean (isopod) and symphylan characters in the insectan stem by supposing that the crustacean, insectan and symphylan "currents" in the "onward flow of life," although acquiring more and more of a distinct individuality as their "waters" emerge from the common stream at their source, nevertheless have an intermingling or commingling of contiguous waters as they flow side by side, before ultimately diverging too greatly for such an intermingling. This idea, however, might in a sense be interpreted as meaning that the Symphyla-like insects were descended from Symphyla, and the Crustacea-like insects from Crustacea (*i. e.*, isopod Crustacea), whereas insects as a whole were probably not "polyphyletic," but all insects were derived from a common ancestral source. The forms composing this common ancestral source, however, differed among themselves very greatly, although the amount of divergence was probably not too great to prevent their being grouped in a single class—or possibly even in a single subclass or order. In this ancestral-insectan group, there were doubtless isopod-like insects which resembled the most insect-like representatives of the ancestral isopods, while the Symphyla-like members of the ancestral-insectan group must have resembled the most insect-like representatives of the ancestral Symphyla. In other words, at the common level at which the lines of descent of the isopods, insects and Symphyla originated, some of the ancestral insects (which differed greatly among themselves) occupying the "hereditary territory" contiguous to that of the ancestral Symphyla would inherit certain developmental tendencies in common with or similar to those also inherited by certain Symphyla; and similarly, some of the ancestral insects occupying the "hereditary territory" contiguous to that of the ancestral isopods would inherit certain developmental tendencies similar to those of certain isopods and the same principle would apply to successively larger, as well as to the smaller groups in any evolutionary study. According to this view, certain developmental or "inherent" tendencies exhibited by the isopods or myriopods might also appear in insects if the opportunity of manifesting themselves should arise, and this would merely imply that these tendencies were inherited from an ultimately common ancestry, rather than that some insects were descended from isopods while other insects were descended from Symphyla, etc. Some evolutionists might object to the use of such terms as "inherent tendencies" on the ground that they savor too strongly of "vitalism"; but, so far as I can see, the expression "inherent tendencies" means much the same thing as a part of "heredity," and one implies no more of a predilection toward vitalism than the other does.

Although their closest affinities are with the Campodeoid group and the Apterygota in general, certain members of the Lepismoid group are structurally remarkably similar in many respects to such primitive Pterygota as the stone-flies and may-flies, so that Handlirsch, 1906, who has completely disregarded the close interrelationships of the Apterygota, and their evident ancestral character (with reference to the winged insects) in his attempt to derive the Pterygota more directly from trilobites, is forced to assume that the lepismids may represent degenerate Pterygota! Their whole sturctural organization clearly proclaims in no uncertain terms that the closest affinities of the lepismids are with the rest of the Apterygota, with which they are connected by intermediate forms, and a careful study of the comparative anatomy and embryology of the Apterygota, "Myriopoda" and Crustacea can result in no other conclusion than that the Apterygota have departed as little as any known forms from the condition characteristic of the ancestors of the Pterygota. The lepismids are therefore no more to be considered as degenerate Pterygota, than apes are to be considered as degenerate men—unless one reverses the whole scheme of evolution; and under such conditions there would be nothing to prevent any one from assuming that trilobites are degenerate lepismids, or any other equally improbable reversing of the evolutionary sequences!

In connection with the supposedly "degenerate" condition of the Apterygota, I would take issue with the implication carried in such statements as that by Tothill, 1916 (p. 376), who would claim that the Apterygota "are highly specialized animals as indicated by the frequent reduction of mouth parts, visual organs, tracheæ, etc.; and by the development of peculiar structures such as the caudal spring and collophore." In the first place, it is inadmissible to judge the ancestral character of any group by the condition of its most highly specialized members, as Tothill appears to do in the case of the Apterygota, since any arthropodan group, no matter how low it may be in the scale of development (*e. g.*, Copepoda, etc.) may include certain members which have become very highly specialized along their own lines of development without affecting the general position of the group as a whole; and in a phylogenetic study we must consider the most primitive representatives of the group, rather than the most highly specialized ones, if such a study is to yield any tangible results. If Tothill had therefore considered such lowly organized Apterygota as *Eosentomon, Anajapyx,* etc., instead of the highly specialized *Anurida, Sminthurus,* etc., I am sure that his opinion of the "degenerate" condition of the Apterygota as compared with the Pterygota would have been quite the opposite of that expressed in his paper. Furthermore, there are practically no arthropods known which are primitive in all respects, and, as is the case throughout the whole realm of zoology, forms which have retained many features in an exceedingly primitive condition may be very highly specialized in other respects; so that one must take into consideration the composite primitive features of the group as a whole; and, just as the most primitive members of the Pterygota are studied in an attempt to determine their ancestry, so the most primitive members of the Apterygota must be considered in such a phylogenetic study.

Even in the matter of the nature of their eyes, such forms as *Machilis* (which are related to *Lepisma*) can hardly be called "degenerate," and in the face of the fact that in the trilobites themselves there occur at least three types of eyes—"isolated eyes or ocelli, aggregate eyes of biconvex lenses, and compound eyes" (Tothill, p. 321, quoted from Lindstrom, 1901), it is very improbable that the type of eyes found in *Lepisma* are of a higher type than the compound eyes of the Pterygota. As far as their mouth parts are concerned, I find the lepismids much more primitive than the Pterygota (with the possible exception of nymphal ephemerids) and Boerner, 1908–1909, has called attention to crustacean structures so similar to those found in the maxillæ, etc., of apterygotan insects, that there can be no doubt that the mouth parts of the Apterygota in general instead of being "degenerate" have retained many more primitive features than those of most lower Pterygota.

As far as the number of abdominal segments is concerned, some Apterygota, instead of having fewer segments, have even retained twelve, and in these forms, such as the Protura, there is also a postembryonic increase in the number of segments (from nine to twelve in the abdomen) comparable to the increase of segments in the "Myriopoda," so that Tothill's statement that "in the Hexapoda numerous investigations have shown the segments arise only during the egg stage" does not hold in the case of the Protura. There is also one other point in Tothill's paper which might easily lead to error unless properly explained: namely, that his discussion of the nature of the appendages of the abdomen in a "larval" *Stenodictya* is based upon a figure taken from Handlirsch's book, the supposition being that it represents the restoration of an actual fossil larva, whereas in reality the figure is purely a figment of Handlirsch's imagination, for no known insects have biramous abdominal legs, and even the supposedly biramous condition of such specialized structures as the maxillæ of insects is now thought to be a secondarily acquired feature, and not a retention of an originally biramous condition (Borradale, 1917). Tothill's suggestion of a derivation of winged insects directly from Chilopoda (which represent a side branch from the symphyloid main stem of myriopod development) without reference to the apterygotan forms is open to all of the objections raised against deriving winged insects from apterygotan forms without having any of the advantages of the latter hypothesis, and if the latter is untenable, the idea of deriving winged insects from chilopods is infinitely more so!

Despite the fact that trilobites are on a divergent branch leading away from the main line of insectan development (*i. e.,* leading off to the arachnoid development) Handlirsch, 1906, would derive winged insects directly from trilobites, wholly ignoring the Apterygota, Symphyla, Tanaidacea, and all of the other anatomically intermediate forms—which would be exactly on a par with an attempt to derive the "Nordic" race of men directly from lemurs (or rather from *cats,* whose line of development has deviated from the main line of evolution leading to the development of the human type) wholly ignoring the Mongolians, Australoids, Neanderthaloids, Heidelberg man, *Pithecanthropus,* the great apes, and all other anatomically intermediate types! His line of argument is somewhat as follows: winged insects occurred at an extremely early period, and no fossil Apterygota dating back to so ancient a period has yet been discovered; therefore Apterygota are more probably a recent degenerate offshoot, rather than forms standing more nearly in the line of development of winged insects—a line of reasoning which caused the earlier Coleopterologists to reverse the evolutionary sequence and attempt to derive true beetles from the snout beetles, until further discoveries brought to light the fact that true beetles were geologically as ancient, or more ancient, than the snout-beetle type, which comparative anatomy clearly showed must have been derived from, and therefore could not be ancestral to, the true beetles! As experience has shown, the paleontological evidence, which at best is of a most fragmentary and incomplete nature, must supplement that of comparative anatomy (of adults or embryos)—and even in the case of the paleontological evidence it depends wholly upon comparative anatomy here also; and furthermore many fossils were themselves as highly specialized along their own lines of development as the most primitive living forms are (some of which have retained just as many ancestral characters and are as little modified in certain respects as those forms which fell by the wayside at an early date). Paucity in numbers of individuals among the Apterygota, their usually small size and fragile nature, have all contributed to make their fossil remains extremely rare, and under these conditions the lack of remains from earlier strata can not offset the weighty argument of comparative anatomy and embryology in favor of regarding them as the nearest representatives of the type ancestral to winged insects.

As for deriving winged insects directly from trilobites on the ground of the faint resemblance of trilobites to insects in regard to their possession of a certain type of eye structure, antennæ, and lateral projections of the tergal region (woefully inadequate resemblances in comparison with the multitude of resemblances between insects and their real ancestral forms), it may be said that these same structures are likewise shared by such fossil merostomes as *Bunodes lunula* and on precisely the same grounds, insects should be derived from merostomes also (a manifest impossibility) since these have the same ancestral qualifications of great antiquity, and they possess the trilobite type of antennæ, eyes and lateral tergal projections! When one studies the embryological development of insects, however, it is evident that their ancestors had *two* pairs of antennæ instead of the one pair apparent in trilobites, and the insectan type of head is nothing like that of a trilobite in which the head region is not set off by a marked constriction with well-defined mandibles, maxillæ and underlip of the insectan type, while the head region and mouth parts of isopod and amphipod Crustacea, etc. (with their two pair of antennæ, insectan type of head, mandibles, maxillæ and underlip), are clearly similar in character to what the ancestors of insects must have been like, and the same holds true of the legs and terminal appendages, etc., in these Crustacea. Therefore, as far as comparative anatomy is concerned the Crustacea, with their progeny the Symphyla, etc., are, beyond any possibility of doubt, the nearest forms to the ancestors of insects in general, and this is also borne out by embryology, which, however, can not be applied in the case of the trilobites; so that here we must depend largely upon comparative anatomy, whose verdict is unmistakably in favor of the Crustacea, Symphyla and Apterygota as the ancestral forms leading up to the pterygotan type, and is unmistakably against considering the trilobites anywhere near the immediate ancestors of winged insects or even in their direct line of descent. On this account, it is most astonishing that nearly all recent writers (Schuchert, 1915, Ruedemann, 1916, Lull, 1917, etc.) have accepted without reservation such startlingly revolutionary ideas as those proposed by Handlirsch—and upon such meagerly insufficient grounds when one looks into the subject at all! Such implicit faith in this age of skepticism speaks volumes for the weight of Handlirsch's authority among paleontologists, but the true morphologist prefers the direct evidence of his own observation to any "*petitio ad auctoritatem*" especially when such startlingly revolutionary ideas as those which Handlirsch proposes are based upon no firmer foundation than a vague resemblance which will not even bear the test of close scrutiny.

When one turns to the published figures of the earliest fossil insects for some light upon the nature of their body structures, his eye is met by a dreary succession of disembodied wings, and in the rare instances in which the body parts are also figured, only the vague outlines are given with a nonchalant disregard for the vital details so necessary for any phylogenetic study; and one can not help wondering what impression the "pterophilous" paleontologists would have of their subject if the tables had been reversed and they had been presented with merely the vaguest outlines of a series of wings containing no veins or other important structures, in the expectation that such figures would be of any value for a phylogenetic study! Furthermore, many living "synthetic" types are quite devoid of wings (as it true of immature forms also) and the study of these forms is in some cases even more important than that of the wing-bearing ones (*e. g.*, *Timema, Grylloblatta,* nymphal Plecoptera, *Lepisma,* etc.), but how are we to compare them with a series of disembodied wings? So far as one can judge from the figures of fossil insects, we have living to-day certain lowly organized forms which are in many respects just as primitive as these fossil forms (which are also specialized to some extent) and when the paleontologist returns again and again to a comparison with living forms for an interpretation of fossil structures, the suspicion becomes a conviction that a study of the primitive characters of various lowly organized living insects is just as instructive from a phylogenetic point of view, and is infinitely more satisfactory than a laborious reconstruction of fossil fragments.

The different theories concerning the origin of the wings of pterygotan insects were discussed in a recent paper (Crampton, 1916) in which it was pointed out that it is possible to consider that the wings of insects were derived from paranotal outgrowths of the tergal region of apterygotan forms, Crustacea, etc., which are ultimately homologous with the paranotal outgrowths of the trilobites, without attempting to derive the wings from these trilobitan structures without the intermediation of other ancestral forms. Not only do the lepismids exhibit paranotal structures (lateral tergal outgrowths) which are homologous with the precursors of wings, but the lepismoid forms (*Lepisma, Nicoletia, Machilis,* etc.) approach remarkably closely to the pterygotan type in many respects, and may be considered as annectent between the remainder of the Apterygota and the lower Pterygota.

The lowest representatives of the Pterygota, or winged insects, constitute the Perlid-Ephemerid group, composed of the Plecoptera, Ephemerida, and their immediate relatives. The modern representatives of the group are in many respects fully as primitive as certain of their fossil relatives, although it is necessary to turn to some such extinct forms as the "Protephemeroidea" and Palæodictyoptera to find the connecting forms annectent between the Plecoptera and the ephemerids. The immature Plecoptera are remarkably similar to lepismids in the nature of the head outline, mouth parts, thoracic sclerites, etc. (Crampton, 1917*a*), and even in regard to their terminal abdominal structures the lepismids are very like Plecoptera (Crampton, 1918*a*), but the Plecoptera have lost the median terminal filament, which, however, is still retained in the ephemerid members of the group. The ephemerids, and the Odonata, represent somewhat aberrant types of development which branched off at an early date to follow their own paths of specialization, although they have not proceeded very far along this road. The Plecoptera, on the other hand, have carried over in their line of inheritance a great many characters which were to become further developed in the higher groups of insects, and they appear to have departed as little as any from the ancestral condition of these groups, so that they are as important as any synthetic types, with the possible exception of the Palæodictyoptera, for a phylogenetic of winged insects in general. The great antiquity of fossil Plecoptera is also in harmony with the idea that the Plecoptera are quite like the ancestors of the higher forms, and since the anatomical and phylogenetic data are in complete harmony in this respect, we are justified in assuming that the Plecoptera have departed as little as any forms from the ancestral condition of the groups next to be considered.

The Plecoptera, embiids, and Dermaptera originated from essentially similar ancestors, which were not far removed from present-day Plecoptera, and their lines of descent have followed a common developmental road for a considerable distance, before first the embiids, and a little later the Dermaptera branched off to follow their own paths of specialization (Crampton, 1917*a*). The *Hemimerus*-like forms branched off from the Dermapteron stock at an early date, and a little later, the Coleopteron type was differentiated. The Strepsiptera were possibly differentiated from a similar stock still later. The terms "earlier" or "later" as used above are employed in the sense of indicating the relatively lower or higher level along a line of development, at which a group branched off, and is based upon the comparative anatomical primitiveness of the group under consideration. In the case of the Coleoptera, Handlirsch maintains that they are paleontologically older than the Dermaptera, and if subsequent findings should corroborate this view, it would be necessary to search for the origin of the Coleopteron line of development lower down on the Plecopteron stem than the point at which the Dermaptera branched off to follow their own path of specialization, but the Dermaptera are so much more lowly organized than the Coleoptera, to which they are anatomically very similar (see also Crampton, 1918*b*), that I am inclined to believe that the lack of earlier Dermapteron remains is due to the incompleteness of the fossil record, rather than to the absence of Dermapteron forms antedating the Coleoptera.

The Isoptera, blattids and mantids seem to have originated from a stock similar to the members of the Plecopteron group mentioned above (Crampton, 1917*a*) and they apparently branched off at a very early date to follow their own developmental road for a short distance before each of the three separated to follow its own path of development. The Isoptera are anatomically intermediate between the members of the Plecopteron group. and the rest of the blattid group (with which the Isoptera seem to have somewhat stronger affinities than with the members of the Plecopteron group, although they are related to the embiids and Dermaptera quite closely). This might be taken to indicate that the Isoptera are more primitive than the blattids, as is borne out by certain of their anatomical features; but on the whole, the blattids seem to be somewhat more lowly organized and, according to Handlirsch, the Isoptera are paleontologically much younger than the blattids. It is quite probable that the Zoraptera described by Silvestri, 1913, are an offshoot of the isopteron stock.

The orthopteroid insects, grylloblattids and phasmids were descended from ancestors very similar to *Grylloblatta* recently described by Walker, 1914, and such phasmids as *Timema* are also very near the base of the orthopteroid stem. These insects have inherited many characters from the plecopteroid side of their ancestry, and they also share many features in common with the blattoid group mentioned above (see Crampton, 1917*a*). Their line of descent is apparently ultimately traceable to a plecopteroid ancestry (as is probably also the case with the blattoid forms), but their line of development branched off very near that of the blattoid group, and they continued to parallel the path of development of the latter group for a considerable distance before diverging along their own branch of specialization. The grylloblattids seem to be somewhat closer to the ancestors of the gryllids and "locustids," while the phasmids may be nearer to the ancestors of the "acridids," although the line of development of the latter may have branched off from a "locustid" stock. The *Phyllium*-like forms seem to be modified phasmids which have certain features in common with the grasshopper group.

The plecopteroid, blattoid and orthopteroid groups are all very primitive, and are so intimately connected by intermediate forms or synthetic types that they are to be considered as representing one section of the Pterygota, to which the term "Plecopteradelphia" was applied (Crampton, 1916*a*) to indicate that they are the immediate descendants of Plecoptera-like ancestors and the ephemerids and Odonata should doubtless be included in the same section of the Pterygota. There is a bare possibility that the blattoid forms rather than the Plecoptera are nearer the ancestral type from which the others were derived, but the close resemblance of immature Plecoptera to lepismids, and the very primitive organization of the Plecoptera, make it very probable that they, rather than the blattids, represent very closely the ancestral forms which gave rise to the blattids themselves, and the other types mentioned above. The higher insects were also apparently descended from forms ultimately derived from ancestors related to the Plecoptera, but they have "clustered together" in another division forming the "Neuropteradelphia" (Crampton, 1916*a*) or forms grouped about the Neuroptera in the second section of winged insects next to be considered.

The members of the second section (or "Neuropteradelphia") fall into two principal groups. One of these, comprising the psocids, Thysanoptera, and hemipteroid forms, were probably descended from ancestors not unlike the psocids, and it is also quite possible that the Mallophaga, and the Anopleura or "Siphunculata," represent offshoots of this stock. This group had a common origin with the neuropteroid insects (probably from Plecoptera-like forebears) and the two paths of development have extended side by side for a considerable distance, both having numerous characters in common.

The Neuropteron group comprises the Neuroptera, Trichoptera, and Mecoptera, with their immediate relatives. They and their descendants are very closely related to the members of the psocid group mentioned above, and the two lines soon merge in a common ancestry when traced back toward the plecopteroid stem. The Neuroptera seem to be a very ancient type, and have inherited certain primitive characters which would indicate that their line of development branched off at a comparatively low level. Both the Trichoptera and the Mecoptera are descended from ancestors quite like the present-day Neuroptera, while the Lepidoptera branched off near the trichopteron line of descent, and the Diptera branched off near the mecopteron line (see also Crampton, 1917*b*). The Siphonaptera were apparently descended from ancestors not unlike phorid Diptera.

The Hymenoptera represent a somewhat aberrant group having affinities with both the members of the psocid and neuropteron groups. Their line of descent probably originated near the point at which the psocids and Neuroptera branched off, and they inherited many features also present in the members of both of these groups, so that their line of development must have accompanied or extended beside those of the other two for a considerable distance before it branched off to follow its own path of specialization.

SUMMARY

The points which should be especially emphasized in regard to the evolution of the insectan branch of the arthropod lines of development may be briefly summarized as follows:

The ancestors of arthropods were not of any one type, but varied in regard to the number of segments composing their bodies, the outline of the body, etc.; and while some of them may have been as small as the tardigrades, it is more probable that the types would be included between the extremes represented by the Onychophora and the Annelida, or even between the extremes included within the annelidan group itself.

The first arthropods also were not of one single type, but possibly varied as greatly among themselves as a branchiopod-like copepod would differ from a copepod-like branchiopod, etc. It is very probable that the stem forms eventually giving rise to the line of development leading up to the production of the insectan type of arthropod would be included in the branchiopod group.

The next stage in the evolution of the insectan type of arthropod is represented by forms related to the leptostracan group, although the Leptostraca do not include all of the types representing this stage of development. It is possible that the Trilobita may be considered as somewhat near these forms, since they exhibit a few characters in common with them, but the trilobitan line of descent is not directly in line with the insectan path of development, since it diverges toward the evolution of the merostomes and eurypterids leading off toward the arachnoid type of development and away from the insectan type.

A further stage of development is represented by the members of the group including the Anomostraca, Cumacea and Tanaidacea. While they doubtless also resembled the other members of this group in certain respects, it is quite possible that the ancestors of insects and "myriopods" varied between the extremes represented by *Bathynella* among the Anomostraca and by such forms as *Apseudes,* etc., among the Tanaidacea, from which the Isopoda, etc., were also descended. *Bathynella,* with no eyes, with its cylindrical body, reduced legs and "stumpy" pair of pleopods, basal limb appendages suggesting the precursors of styli, short terminal appendages, etc., must be very like the ancestors of the Protura and Scolopenrelloid forms; while such Tanaidacea as *Apseudes,* with its flagelliform terminal uropods, and the type of head appendages, etc., present in the Isopoda in general suggest the type of ancestors giving rise to those Apterygota which are provided with flagelliform terminal appendages.

The members of the Symphyla-Pauropoda group have retained many characters present in the ancestors of the "Myriopoda" and Insecta. The Chilopoda are an offshoot from this stock and do not stand quite as near the direct line of development of the insectan type.

The Apterygota are the nearest known representatives of the ancestors of winged insects, and while the first insects to be evolved possibly were of types resembling both the proturan forms and the campodeoid forms (or even the machiloid forms), the lepismid type approaches as nearly as any known forms to the lowest representatives of the Pterygota.

The first winged insects resembled the lepismids in many respects, and their nearest living representatives are the ephemerids and Plecoptera. The Plecoptera and the fossil Palæodictyoptera stand at the base of the lines of descent of the higher forms, and, since the line of descent of the Plecoptera has accompanied those of the higher forms for a longer distance, they are even more important than the Palæodictyoptera for a phylogenetic study of the evolution of higher insects. Most higher forms cluster about the Plecoptera and Neuroptera as nuclei representing synthetic types of the greatest importance, and both types are of considerable antiquity, although the Neuroptera were possibly ultimately descended from forms not unlike the Plecoptera (and ephemerids).

It is quite improbable that insects or arthropods in general (as well as the more inclusive groups) are of a polyphyletic origin. The ancestors of insects, for example, were of several types, some resembling the ancestors of isopods, while others resembled the ancestors of the Symphyla, etc., and the lines of development of all three extend for some distance side by side before each begins to diverge from the others. Those insects resembling Symphyla were not descended from symphylid forebears nor were those insects which resemble isopods descended from isopod forebears, but the symphylid and isopod characters which appear in certain insects were inherited from their ultimately common ancestry, and the relative positions of the different ancestors of insects in the "hereditary areas" of this common ancestry (*i. e.*, whether their hereditary areas were contiguous to those of the ancestors of isopods or to the ancestors of the Symphyla, etc.) determines whether certain of the insects descended from them shall resemble isopods or Symphyla, etc., and the same principle applies in the successively larger as well as in the smaller groups of living things.

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SHORTER ARTICLES AND DISCUSSION

ON THE RESISTANCE OF FUNDULUS TO CONCENTRATED SEA WATER[1]

I. THERE is at Bermuda a Fundulus, described by Günther ('79) under the name *F. bermudæ,* which is very closely related to *F. heteroclitus,* if not indeed specifically identical with it.[2] The common habitat of this Fundulus is along the shores of mangrove swamps, in water normally having a salinity of 35–36 per mille (Cl = 20 ± per mille; sp. gr. about $1.0225^{27\frac{1}{4}°}$). When this Fundulus was placed in sea water which was allowed to evaporate at laboratory temperature (about 27°) a good number of specimens were found to resist a concentration of about $^{15}/_{8}\,M$ sea water (Cl = 67 per mille). According to Loeb ('13, '16), *F. heteroclitus* at Woods Hole may be brought to live in a concentration equivalent to $^{10}/_{8}\,M$ or $^{11}/_{8}\,M$, if the water be slowly evaporated, but a $^{12}/_{8}\,M$ concentration is rapidly fatal. Sea water at Woods Hole is at about $M/2$ (salinity = 32 per mille ±), with a freezing-point depression of 1.81° (Scott, '13), whereas the Bermuda sea water is nearly $^{9}/_{16}\,M$, with (according to Knudsen's Table, 5) a freezing-point depression of 1.95.° McClendon ('11) found the Δ of Tortugas water (S = 36 per mille ±) to be 2.03°.

Is the considerable difference noted in the resistance of *Fundulus* taken from these differing environments to be regarded as an instance of adaptation brought about in nature?

II. Tests were made at different seasons to discover the upper limit of concentration which the Bermuda fundulus will tolerate. One of these experiments may be cited as an example:

Experiment 4.—Aug. 20, 1917. Six fundulus were placed in each of three glass aquaria containing 2 liters of sea water ($\mathrm{Cl} = 19.65^0/_{00}$; $\mathrm{S} = 35.50^0/_{00}$) brought from the mangrove creek in which the fundulus were collected. The water was allowed to evaporate at room temperature (28°). In aquarium No. 1, two fishes were still alive on Sept. 7,

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[1] Contributions from the Bermuda Biological Station for Research, No. 102.

[2] Some of the specimens used in these experiments were examined by Mr. Samuel Garman, of the Museum of Comparative Zoology, who pronounces them to be *Fundulus heteroclitus,* var. *bermudæ* Goode and Bean.

at which time the water was so concentrated that the salinity titration (of an aliquot part of a dilution with distilled water) gave $Cl = 66.69^{0}/_{00}$. These two fishes lived until Sept. 11, when the Cl content of the water was $72^{0}/_{00}$. Similarly, in the other two aquaria the maximal concentrations were $Cl = 66.83, 66.90^{0}/_{00}$.

Other tests gave comparable results, about one third of the fundulus living until the Cl content of the water was nearly 67 per mille ($= {}^{15}/_{8}$ *M* sea water). Provided the process of evaporation occupied at least two weeks, slowing the evaporation of the water did not seem to augment the resistance of the fishes. Fundulus "adapted" by slow evaporation lived in ${}^{14}/_{8}$ to ${}^{15}/_{8}$ *M* solutions for a week or more. When a concentration of about $Cl = 70$ per mille (${}^{16}/_{8}$ *M*) was reached, the fishes usually died very rapidly, although an occasional one survived until the Cl content was 75 per mille, whereas at Woods Hole, according to Loeb, the rapidly fatal concentration is ${}^{12}/_{8}$ *M*. In each case the maximal concentration endured for any length of time is about three times that normally experienced by the fish.

III. While Loeb found the resistance of *F. heteroclitus* to be only slightly enhanced by a series of "adapting" experiences in waters of gradually increasing concentration, it might nevertheless be argued that a more gradual series of changes, leading to normal life in more saline water, would be more efficacious. There are several facts which dispose of this supposition, aside from the somewhat disproportionately great increase in absolute resistance which is exhibited by the Bermuda form.

The Bermuda fundulus is found not only in the mangrove creeks, but also in certain landlocked brackish ponds (*e. g.*, Warwick Pond, Trott's Pond) where the salinity is usually 14.5–23 per mille ($Cl = 8.0$–12.7 per mille), although it varies somewhat with the rainfall. The level in these ponds rises and falls slightly with the ocean tide, but there is no variation in salinity synchronous with this. Fundulus were taken from these ponds and placed in sea water which was allowed to evaporate slowly, and others were put in pond water which was allowed to evaporate. The lethal concentrations in these two series were practically identical, namely, at about $Cl = 65$–70 per mille, one third of the individuals usually surviving until the Cl content reached 66–67 per mille, which is essentially the same maximal concentration as that found with the individuals living normally in undiluted sea water. *F. bermudæ* will live for a long time in rain water containing but a trace of salts, and those from the brackish ponds will live equally well when suddenly transferred to sea water of full salinity (36 per mille).

Now, the fundulus living in the brackish ponds have been there for an indefinitely long period. They reproduce there, and must be regarded as "adapted" to the low salinity of the ponds. There is consequently no reason to expect, on the adaptation hypothesis, that they should be as resistant to concentrated sea water as the individuals living in Fairyland Creek, for example, where the water is of normal salinity. Yet this appears to be the case. It is true that this species inhabits other brackish swamp pools at Bermuda, where the salinity undergoes considerable changes. But if the high resistance of the isolated-pond fundulus were to be explained as the result of a persisting mechanism inherited from ancestors adapted to withstand changes in salinity, then it will be noted that the appeal to adaptation in the first place becomes not merely superfluous, but inconsistent.

IV. There is another explanation available, which probably accounts for the high resistance of the sea-water and brackish-pond fundulus to concentrated solutions. This explanation considers that the conditions of temperature and the composition of the water (especially in the brackish ponds) have shifted the protoplasmic equilibria which determine the composition (and hence the permeability and the resistance) of the limiting membranes of the fish's body.

Loeb and Wasteneys ('12, '15) found that fundulus taken from a temperature of 10° died in the course of several hours when kept at 29°, in a few minutes at 35°; whereas those maintained at 27° would live indefinitely if transferred to 35°. The fundulus at Bermuda living in the mangrove creeks are at a temperature of 26°–27° (during the summer months). They withstood for some hours a temperature of at least 37°, and died when heated to 40.9°. In the shallow landlocked ponds the surface temperature was 30°–33°. Fundulus from these ponds withstood for several hours a temperature of 39°–40°, and died when heated to 42.6°. The upper temperature limit was also determined for fundulus from the brackish ponds which (at 27°) had for two weeks been living in $^{10.5}/_{8}\,M$ sea water; they withstood 40°, and died at 42.5°. Other individuals living for the same period in $^{8}/_{8}\,M$ sea water withstood 40°, and died quickly at 41.5°. There is thus seen in fundulus the correspondence usually found in every thermal species between the temperature at which the animal lives and the maximal temperature which it can successfully withstand (cf. Mayer, '14).

The alkalinity of the waters inhabited by the Bermuda fundulus is quite various. In the mangrove creeks the reaction of the water along the shore may vary a little with the state of the tide, but is usually not far from $p_H = 8.1$. In the landlocked brackish ponds, however, the alkalinity is commonly much higher than this. In one pond, where many algæ were growing, the alkalinity was conspicuously high, $p_H = 9.0$–9.2 (except after rains);[3] and in another, with a sparser growth of water plants, the reaction usually observed was $p_H = 8.7$. Rain water had at this time a consistent reaction of $p_H = 5.9$–6.0, but after contact with the soil and limestone it quickly becomes alkaline, so that the water in cave pools, or dripping from growing stalactites, was found to have a reaction of $p_H = 7.9$–8.0. The high alkalinity of the pond waters may be important in determining the survival of fundulus in abnormal solutions.

If the idea is correct that the composition (*e. g.*, the calcium content) and (?) the temperature of the sea water or pond water are responsible for the high resistance of the brackish-pond fundulus to concentrated sea water, then we should expect that NaCl solutions would be less toxic for the Bermuda fundulus than for the northern variety, which, according to Loeb, and Wasteneys ('12), is killed by 1 *M* NaCl in less than one half hour (at about 18°–20°, it is inferred). The pure NaCl solution increases the permeability of the surface membranes of fundulus. At 25°–27°, 50 per cent. of the Bermuda fundulus lived forty-five minutes in 1 *M* NaCl solution, when the specimens were taken from the mangrove creeks. Individuals from the landlocked brackish ponds lived about the same length of time (even after rapid washing, three times, in changes of NaCl solution). At 20° they lived a little longer. This result is in agreement with that obtained experimentally by Loeb ('16, p. 332), namely, that fundulus adapted to higher concentrations of sea water became more resistant to pure NaCl solutions; those brought artificially to live in $^{10}\!/_{8}$ *M* sea water could live two to

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[3] Moore and his co-workers ('14) state that the photosynthetic activities of algæ are capable of increasing the alkalinity of sea water until $p_H = 9.0$; I have been able to confirm this statement through experiments with the green alga *Valonia*.

three days in $\frac{6}{8}$ M NaCl, which killed fundulus taken directly from the sea in less than four hours. But in the present case the fundulus from the brackish ponds lived about equally well in pure NaCl solution. The cause of this behavior, which would not be expected from an adaptational standpoint, is believed to lie in the direct effect of the calcium or some other element of the pond water. In $\frac{6}{8}$ M NaCl solution fundulus from the mangrove creeks and those from a brackish pond lived respectively 3.5 and 4.0 hours, roughly, at 20°. The experiments with 1 M NaCl seemed more valuable for the purposes of this inquiry, because of the more rapid toxic effects, secondary complications being thus more easily avoided.

V. The fact that the Bermuda fundulus, closely related to *F. heteroclitus,* but living usually in water of greater salinity than that inhabited by the Woods Hole variety, seems also able to withstand a distinctly higher concentration of evaporated sea water than the latter will tolerate, is therefore not to be considered an expression of adaptation to life in more saline water. Other members of the same species at Bermuda which are confined to brackish ponds of low salinity, and have for at least several generations been restricted to this environment, are equally resistant to concentrated sea water, and to pure NaCl solutions, and more resistant than the fundulus at Woods Hole, indicating that the resistance of the Bermuda form is due to a direct action of certain constituents of the waters in which it lives upon the composition of its surface membranes.[4]

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[4] The observations here briefly reported in a preliminary way have been temporarily interrupted, but it is hoped to continue them in the near future, as some indication was noted of a lowered resistance to pure NaCl correlated with a decreased alkalinity of the pond-waters, during the winter months. The determinations of alkalinity were made with the aid of apparatus purchased through a grant to the Station from the C. M. Warren Fund of the American Academy of Arts and Sciences.

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PEMBROKE,
BERMUDA, January, 1918.

A NOTE ON THE FATE OF INDIVIDUALS HOMOZYGOUS FOR CERTAIN COLOR FACTORS IN MICE

ISBEN and Steigleder have reported on certain breeding experiments with mice which produce evidence in support of the view advanced by Castle and the writer in 1910, and later strengthened by Kirkham, 1917, that homozygous yellow mice were formed but perished during embryonic life.

At the time that they were collecting their data, the writer was, on a smaller scale, carrying on similar experiments. In the course of these experiments, certain data confirmatory to the results of Isben and Steigleder and of Kirkham were obtained. It seems best at this time to put these results on record.

The embryos referred to as ''abnormal'' may be considered as falling in Isben's and Steigleder's Class A of dead embryos, that is to say, those in which development ceased shortly after implantation as contrasted with those in which death had resulted probably from overcrowding within the uterus during the latter part of the period of gestation.

Three types of matings to control the results in yellow × yellow crosses were made. In all cases, the non-yellow animals used were taken from the same stock as that producing the yellows. The control matings made were as follows: Yellow female × non-yellow male, non-yellow female × yellow male and finally non-yellows crossed *inter se.* The numbers obtained are small and are grouped together in the following table:

TABLE I

♀	♂	Normal	Abnormal
11696 Brown	× 11713 Yellow	11	—
11776 Brown	× 11717 Yellow	7	—
11438 Brown	× Brown	7	—
11442 Yellow	× Brown	6	1
11562 Yellow	× Brown	9	—
10619 Yellow	× Brown or Black	2	—
		42	1

The *one* abnormal embryo consisted of a small apparently embryonic mass, with a blood clot closely jammed in between two normal embryos. It will be noted that from these matings 97.6 per cent. of the embryos are normal and 2.4 per cent. abnormal.

When yellows are crossed *inter se* a very different result is obtained, as may be seen from the following table, which shows the result of such matings:

TABLE II

♀	♂	Normal	Abnormal
Yellow D	× Yellow	4	1
Yellow H	× Yellow	7	3
Yellow F	× Yellow	7	2
Yellow G	× Yellow	6	3
11867	× 11711	6	0
11786	× Yellow	8	2
Yellow E	× Yellow	7	1
Yellow B	× Yellow	10	0
11151	× 11162	2	1
12916	× Yellow	5	0
Yellow J	× Yellow	7	3
11149	× Yellow	4	2
Yellow A	× Yellow	7	0
Yellow C	× Yellow	4	1
11926	× 11477	3	0
12672	× — 99 Sooty Yellow	4	2
		91	21

18.7 Per cent. abnormal,
81.3 Per cent. normal.

From this table it will be seen that 81.3 per cent. of the embryos produced are normal, and 18.7 per cent. are abnormal. If one considers in addition the fact that Kirkham obtained embryological evidence that certain embryos broke down even before implantation, it seems probable that the fate of the homozygous yellow mouse is known.

One other point of some interest should be noted. In 1915 the writer reported on the hereditary behavior of black-eyed white spotting in mice. At that time it was found that this character behaved in a similar manner to yellow in that no animal homozygous for it was obtained. Later it was found (1917) that black-eyed white spotting was, however, entirely independent of yellow in heredity, although its behavior was analogous.

If the uteri of black-eyed white females which are pregnant by black-eyed white males are examined they are, in some cases, found to contain a certain number of abnormal embryos of the same gross appearance as those occurring in the yellow × yellow matings. The numbers obtained are small but striking.

TABLE III

♀		♂	Normal	Abnormal
Black-eyed White A	×	Black-eyed White	3	1
11413	×	11466	1	5
Black-eyed White B	×	Black-eyed White	5	0
— 73	×	Black-eyed White	7	0
			16	6

The percentage of abnormal embryos is 27.2. While this last mentioned cross should be repeated, it nevertheless indicates that, like the homozygous yellow embryo, the homozygous black-eyed white embryo breaks down, in most cases at least, after its implantation in the uterus.

C. C. Little

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THE VARIETIES OF HELIANTHUS TUBEROSUS

The girasole, Jerusalem artichoke or sunroot, *Helianthus tuberosus* of Linnæus, has been in cultivation more than three hundred years. It is native in North America, and its tubers were well known as a source of food to the Indians in pre-Columbian times. In spite of its long history and value as a "root-crop," this plant has received little attention from breeders in modern times, and it still remains to be seen what may be done with it, with intensive study and improved methods. At the present time we can say that it is enormously prolific, and the tubers are excellent food for man and beast. Recent experiments indicate that they may be an important source of sugar in the form of syrup. The very large tops can be used as fodder. For these and other reasons it is desirable to investigate the existing varieties, and place on record their principal characteristics. This year, in Boulder, Colorado, I have grown all those listed below, excepting the first:

(*a*) *typicus.*—I take as typical of the original *H. tuberosus* the plant figured by Fabius Columna in his account of little-known and rare plants, published in 1616. This figure is cited by Linnæus. It is labelled Flos Solis Farnesianus, Aster Peruanus tuberosus, *i. e.*, the Farnesian sunflower, or tuberous Peruvian aster. It did not, of course, originate in Peru. The figure shows that the plant was much branched, the branches highly floriferous; tubers quite large, potato-shaped or oblong; leaves short-stalked, with broad base, the margin quite coarsely crenate-dentate; rays about 16, not very long; involucral bracts recurved. I have never seen a plant with exactly this combination of characters, but the peculiarities recur separately in different varieties.

(*b*) *nebrascensis.*—Received from the Rev. J. M. Bates, who found it growing wild at Red Cloud, Nebraska. It is like typicus in its general appearance, with many floriferous branches. Compared with *albus* (described below) it differs conspicuously by the shiny upper surface of leaves and the less densely hairy stems. It flowers earlier than the cultivated forms with large tubers. The heads in bud have the involucral bracts spreading (as in *typicus*), dark basally, much less hirsute than in *albus*. The ligules are much longer than in the varieties with large tubers, their length about 42 mm. (30 or less in the large-tubered forms), so the flowers are very handsome. The tubers are produced at the ends of the rhizomes, mostly distant from the stem, and are elongate, broad or narrow, cylindrical, but usually not claviform, and not compressed at end. The thin skin is pale brown.

(*c*) *alexandri.*—Growing wild in Michigan, and received from the late Mr. S. Alexander, who regarded it as a distinct species. It resembles the tall cultivated forms in not being conspicuously branched or bushy, as are the two varieties described above. Compared with *albus* it differs by the opposite leaves, less densely hairy stem, bases of leaf-blades more abruptly truncate, yet upper part of petiole much more broadly winged; leaves longer in proportion to breadth. hairs on midrib beneath subappressed (erect in *albus*). The upper surface of leaves is dull, as in *albus*. The ligules are long, as in *nebrascensis*, and are not rarely quilled. The stigmas begin to emerge while the anthers are fully extended, which is not the case with the other forms. The tubers are elongate, at the ends of the rhizomes, claviform, subcylindrical, more or less compressed apically. They are white, with a very thin brownish skin, the color being like that of *albus*.

(*d*) *purpurellus*.—Sent out by the firm of John Lewis Childs as "Pink Helianthi." A request for information concerning its origin brought no answer. It is a small-tubered form, presumably still in the state in which it occurs wild. The mode of growth and general appearance are as in *nebrascensis*, but the leaves are perfectly dull above. The large leaves are coarsely dentate, with very broad base, but the petiole is not so broadly winged apically as in *alexandri*. The rays are long, as in *nebrascensis*. This is the first of the varieties to come into flower; one head was out on August 21. The tubers are comparatively short, fusiform, cylindrical, not much attenuate at ends; they are about 50–70 mm. long and 15–18 mm. in diameter, produced at ends of rhizomes. The color is deep pinkish-purple, as in variety *purpureus*.

✓ (*e*) *fusiformis*.—The "Rose" variety of Sutton and Sons, Reading, England. We are indebted to the Sutton firm for kindly supplying us with material of their cultivated varieties. This is a remarkable form, very distinct from all the others. When it first comes up, it grows slowly, and tends to spread out on the ground. When mature it is about 7 feet high, only about two-thirds the height of *albus* and *purpureus*. The stems are entirely green, not purple above as in *albus*. The leaves turn yellow in the fall, without any of the red so conspicuous in *albus*. After frost, most of the stems give way somewhere above the middle and the part above hangs downward, forming an acute angle with the standing stem. This rarely occurs in *albus*, but not in *purpureus*, nor in the wild forms. The leaves are long, with a cuneate base, which is very distinctive. The margin is irregularly dentate. The involucral bracts are paler and much longer than in *albus*. The plants were just coming into flower September 22, and are later than any of the other forms. The tubers are large, of variable shape, but more or less fusiform, with only occasional lateral knobs. The diameter is about 45 mm., the length two or three times as much. The surface is pale brown, practically the color of *nebrascensis*, with a faint rosy suffusion. The tubers of one plant weighed 8 lbs.

✓ (*f*) *albus*.—We first got this, a number of years ago, from Dreer of Philadelphia. Mr. L. Sutton tells me that his firm first offered it in 1915, having obtained it from some one who said it had been sent him by a friend in South Amreica. He believes it had not been grown in England before this. Dreer had it much earlier in this country, having obtained it from Mr. A. E. Coleman of Enonville, Va. Mr. Coleman states that he knows nothing of the origin of the variety, and hardly thinks any record was kept. This variety is very tall, and usually not very conspicuously branched. The upper

Fig. 1. *Helianthus tuberosus* var. *fusiformis* at Boulder.

part of the stem is purple, and in the fall the upper leaves turn very red. The leaves have the blades broadly angled or subcuneate at base, the larger leaves forming an angle greater than a right angle; the petioles are not broadly winged apically. Thus this differs greatly from the wild *alexandri*, and in addition the margins are sharply though rather finely dentate, while in *alexandri* they are crenate. The axillary branches have a purplish-black callus at base above; in *nebrascensis* this callus is reddish. The petioles are conspicuously longer than in *nebrascensis*. The heads in bud have the phyllaries or involucral bracts erect, not spreading as in *nebrascensis* and *typicus*. The ligules are about 30 mm. long and 9.5 broad; those of *purpureus* are considerably broader, 30 mm. long and 11 broad. The tubers are very large and knobby, irregularly subglobose, and mostly among the roots, close to the base of the stem. One plant of Sutton's white, dug Nov. 3, had 12 lbs. of tubers. The color of the tubers is white.

A subvariety of *albus*, with more deeply serrate leaves, was kindly sent by Mr. G. C. Worthen, who purchased the tubers in Boston. The growth and other characters do not differ, and the tubers are the same, the buds perhaps a little more tinged with purplish.

(*g*) *purpureus*.—Received from Sutton, who states that it is the variety long cultivated in England. It is a tall plant, with the same appearance and manner of growth as *albus*. On June 30 I noted that as compared with *albus* it had paler, larger leaves, and the veins were more impressed. It was in good flower by Sept. 22. The phyllaries are notably spreading or deflexed; the ligules are broader than in *albus*. Both *purpureus* and *fusiformis* have an orange flush at the base of the ligules, which is lacking in *albus*. The ends of the disc-bracts are broader and more hairy in *fusi-*

FIG. 2. *Helianthus tuberosus* var. *albus* (var. *fusiformis* at extreme left). The flowers are *Helianthus annuus*.

formis than in *albus;* in *purpureus* they are much as in *fusiformis*, but the difference from *albus* is hardly so marked. The stems show no red color. The tubers are like those of *albus*, but are rosy-purple, the same color as those of *purpurellus.* One plant produced seven lbs. of tubers.

It will be seen from the above, that all the varieties differ in a number of characteristics. At the same time, they agree in various particulars. Thus *purpureus* and *purpurellus* in the color of the tubers, *purpureus* and *albus* in their shape. We do not know how far the cultivated varieties owe their characters to aboriginal ancestors; but it is practically certain that no wild form has tubers as large as those of the cultivated ones.[1] It is also certain that the excellent (from our standpoint) character of having the tubers clustered about the crown, making them easy to harvest, could not have existed in a wild ancestor, in which it would be extremely detrimental. On the other hand, the tubers of *albus* and *purpureus* are very knobby, and so hard to prepare for the table; those of the wild forms are essentially smooth (like a sweet potato), but too small. The variety *fusiformis* combines large tubers with, at least in large measure,

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[1] There is some reason for thinking that the Indians had a cultivated form with rather large tubers.

the better shape of the wild varieties. If *purpurellus,* shaped like a Zeppelin, could be crossed with another form to secure a large tuber while conserving the form, the result would be valuable. It still remains to determine the chemical constituents of the several varieties, and this will be done during the winter.

From the standpoint of genetics, an interesting feature is the distribution of the anthocyanin pigments. The variety *purpureus,* with a great quantity of anthrocyanin in the skin of the tubers, lacks this coloring in the leaves and stems. The variety *albus* has it in the leaves and stems, but not in the tubers. The physiological significance of this is at present unexplained.

One of the greatest difficulties in the way of plant breeding comes from the impossibility, in so many cases, of making sure of the history or oven the identity of the varieties used. The same thing may go under several names, or the same name may be applied to different things. In the case of species, it is usually possible to unravel the synonymy by reference to the original descriptions, or to refer to the type specimens. With horticultural varieties, there is usually no type and no formal description. The history, in the majority of cases, is lost. When a new variety is introduced, the firm putting it on the market rarely states where it came from, and often, after a few years, can not recollect. There is no way to ascertain definitely that what is sold today under a certain name is identical with the plant bearing that name a number of years ago. These conditions lead to many misunderstandings and difficulties of all sorts, and to much waste of time and energy. They are no longer tolerable, when the production of new plants is of such prime importance to mankind. What we need is an organization or office, with suitable means of publication, to study and report on every plant put upon the market as new. Each should be carefully described in botanical language, and if necessary figured. Its origin, if ascertainable, should be precisely stated, with full details. Any firm refusing to submit its alleged novelties to such a test, and to permit the reports to be made, would be under grave suspicion of fraud. Not only would plant breeders be greatly benefited, but the general plant-buying public would be saved enough useless expense and annoyance to much more than pay the cost of the undertaking.

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ADAPTATION AND THE PROBLEM OF "ORGANIC PURPOSEFULNESS"[1]

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I. THE REALITY OF THE PROBLEM

DESPITE the "revolutions of thought," which succeed one another with rather bewildering rapidity these days, we may occasionally listen with profit to the voice of a past generation. And I can not believe that we are yet in a position to wholly reject Herbert Spencer's well-known characterization of life as a "continuous adjustment of internal relations to external relations." Now it is this process of adjustment to which we give the name adaptation, and the special structures or functions by which the adjustments are carried out are called adaptations.

By earlier biologists and philosophers these facts of adaptation and adaptedness were regarded as among the most fundamental phenomena of life. It was facts such as these that furnished ammunition for Paley and a whole succession of natural theologians. It was these which Lamarck sought to explain by his theory of evolution through functional activity, and which Darwin attributed to the action of natural selection. And it is in this same realm of facts that the vitalists find their rea-

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[1] In its main outlines, this paper was written about five years ago. It was submitted for publication February, 1918, and since then has undergone relatively little revision. For this reason, adequate reference has not been made to certain recent papers.

sons for attempting to remove biology from its place among the natural sciences.

Now it is a curious circumstance that recent developments of the evolution theory have carried us continually farther from an explanation of adaptation. Natural selection, in the Darwinian sense, has been relegated to a secondary position, while the Lamarckian principle is denied *in toto* by many. On the other hand, all that the mutationist can tell us in regard to the matter is that such useful characters as spring full-fledged into existence are not likely to be eliminated. Thereupon, the vitalist takes fresh hope and asserts the inadequacy of what he calls "mechanistic" biology to account for progressive evolution.

Of course, one way to solve a problem is to deny that the problem exists. And this is what is being done by various persons who are interested in minimizing the difference between the living and the non-living. Thus one physiological botanist, Livingston,[1a] tells us that anything organic or inorganic is adapted to do just those things which in reality it is found to do. And he seems to think it quite as reasonable to speak of the adaptation of fragments of pumice to float on water, as of the adaptation of a flower to insure the visits of insects. The "concept of purposeful adaptation," which still plays such an extensive rôle in biology, is due to the fact that "ours is a developmentally young science," retaining "features of its early youth." Sooner or later this concept will be "totally abandoned, even as the same concept has already been abandoned by the other natural sciences."

Now it may well be that a more mature state of science will enable us to dispense with such naïve expressions as imply that an organ has a function to perform in the economy of an animal. And it may be that growing enlightenment will lead us to replace such a primitive notion as that of life by chemical affinities, electric charges and what not. But until that happy (or unhappy!) day

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[1a] AMERICAN NATURALIST, January, 1913.

arrives, I think that most biologists will continue to regard the origin of adaptive characters in animals and plants as offering a real and important problem for solution.

Again, Parker,[2] while going to no such lengths as this in denying the significance of organic adaptation, expresses his belief that

> the majority of animal reactions are, in all probability, neither conspicuously advantageous nor disadvantageous to the life of the individual. They are dependent chiefly on the material composition of the given organism, and, so long as they are relatively indifferent to the continuance of life, they pass without special consequence. . . . The world at large affords an environment in which each animal has a wide range for possible reactions, and of a number of responses that might be made to a given set of conditions, one may be quite as appropriate for the continuance of life as another. In other words, versatility seems to be a more truthful description of actual conditions in animal life than the rather rigid state implied in the idea of adaptive responses.

It may be freely granted that much ingenuity has been displayed in discovering adaptations which probably do not exist. And it is doubtless true that many organisms may live indifferently under a wide range of conditions, or may eat indifferently a wide range of foods. But is not this condition of versatility itself a fact of adaptation? The "continued adjustment of internal relations to external relations" implies that the external relations change. Man, it is true, may live indifferently on the equator or within the Arctic circle. But would any one maintain that the physiological states which adapted him to these unlike conditions did not differ widely in the two localities? I may make a meal equally well of meat or of vegetables. But the digestive fluids secreted for the occasion would differ in the two cases.

Again, because two wholly unlike plants grow side by side in the same soil, it does not follow that they are adjusted in quite diverse ways to the *same set of conditions*. The environment of an organism doubtless comprises the totality of things which surround it. But the *effective* environment comprises only those things with which

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[2] AMERICAN NATURALIST, January, 1913.

the organism comes into functional relation. And as the organism evolves, these effective elements become different.

As I see the situation at present, the fact of organic adaptation remains the central one in evolution, and indeed the central one in biology. I shall give no further time, therefore, to justifying a rather laborious attempt to show how this fact may be accounted for without carrying us outside the limits of natural science. Before passing on to this discussion, I will merely remark that I place in the category of adaptation anything which increases the adjustment of the organism to the conditions of its existence, whether or not this may ever have a determining influence in the preservation of life. Many such adjustments have arisen in our own race which certainly can have played no part in the survival of the individual or the race. An example of this is the case dwelt upon by Spencer, of the correspondence between the nicety of tactile discrimination on various parts of our skin and the relative frequency of contact with foreign objects on these surfaces. And such cases could be multiplied indefinitely. Nevertheless, much recent biological speculation has been vitiated by the identification of adaptation with self-preservation.

II. Adaptation and "Contingency"

If an intelligent animal is confronted with the necessity of taking action to avoid injury or secure food, two ways only would seem to be open to it:

1. It may consciously adapt its actions to this end, or
2. It may go through a series of more or less random movements until it happens to make one which is fitted to the needs of the situation.

On first thought, it might seem that these two modes of procedure were radically distinct, and indeed, in a sense they are. Considered historically, however, the second may be regarded as a step in the development of the first, or, to express the same thought otherwise, intelligent action is in every case the outcome of earlier experimentation. We can foresee the results of an action, only in so far as they have been experienced before, either in a situation identical with the present one, or at least in situations having certain elements in common with it. Furthermore, in the early life of the individual, the movements of the so-called "voluntary" muscles were in a high degree random and undirected. The association between a given muscular contraction and a given result in consciousness must, in the first instance, have been purely arbitrary, and could not have been anticipated prior to experience.

Thus to restate somewhat paradoxically our original proposition, an intelligent animal attains a sought-for end, either by blundering into it or by directing its course on the basis of past blunders. In either case, the association between the means employed and the end attained is, in the last resort, accidental. At the outset, the idea of the end did not in any direct way call forth the means to its realization, however purposive the action may appear when fully perfected.

Let us extend our argument to those fields of organic activity from which intelligence seems to be largely or wholly excluded. In instinctive actions, even more than in intelligent ones, a series of movements proceeds unfalteringly to a given end, as if directed by the latter. In earlier days the adaptive instincts of certain lower animals furnished some of the most telling arguments for the special interposition of an all-wise Providence. To-day, as biologists, we commonly explain these movements on the basis of an inherited "mechanism." We may believe, with Loeb and others, that we have to do with a chain of reflexes, each serving as a stimulus to call forth its successor at the appropriate moment.

How this mechanism arose is a disputed point, but there are two principal hypotheses as to its origin: (1) Instinctive actions are ones which originated, intelligently or otherwise, in the course of individual experience, and finally became fixed through heredity; and

(2) they are the result of natural selection, acting on congenital tendencies toward such movements as proved to be adaptive.

Without discussing the merits of these rival theories, which are by no means mutually exclusive, I merely wish to point out that both of them assume a complete *contingency* as regards the relation of means to end. On the assumption that instinct is inherited habit, the actions, before becoming habitual, must have been performed either intelligently or as a result of blind groping. In either case, their adaptedness to the end in view was, at the outset, accidental, as we have already seen. On the assumption that instincts have arisen through natural selection, chance tendencies toward movements of an adaptive sort were perpetuated. Here, the complete contingency is obvious, unless we assume some directing influence determining the nature of the variations. I shall return to this last point later.

Still lower than instincts, in the scale of organic behavior, we have the various responses to stimuli which are known as "tropisms" or "taxes." Under this head are included the locomotion of the organism to or from a source of stimulation, or, in the case of a fixed organism, the assumption of a definite position, or the arrangement of its parts, with relation to the direction of the stimulus.

Here, again, we have two rival hypotheses, which are not, it seems to me, wholly antagonistic. According to one view, the organisms are "fatally" turned to or from the source of light, heat, or the like by the unequal stimulation of the opposite sides of the body. When the appropriate orientation has been brought about, the two sides of the organism are equally affected, and further locomotion will be in line with the source of stimulation.

The other view lays stress on those cases in which organisms are not drawn directly towards or away from a stimulus, but undergo random movements, having no primary relation to it. In what are regarded as the most primitive cases the stimulus which results in a change of behavior is usually a noxious one, leading to a backing out or turning aside. When forward movement is resumed, it is a matter of chance whether the organism remains in favorable surroundings or finds its way back to the unfavorable ones. If the latter, the "avoiding reaction" recurs, and the performance is repeated until it leads to a more fortunate issue. The invariable "pull" or "push" of the tropism theory is not regarded as the primary phenomenon, though an observer who viewed only the end results of the process might easily believe that they had been brought about by such a directing influence.

Here, again, it is not my purpose to discuss the merits of these rival hypotheses. It is possible, indeed, that they should be regarded as complementary, rather than antagonistic. Jennings admits that responses which originally were performed according to the method of "trial and error" may, through the abbreviating influence of habit, come to be determined more directly by the stimulus. But, however we may view the method of origin of these responses to stimuli, it seems plain that any adaptiveness that we meet with is contingent in the sense in which I have already used the term. According to the investigations of Jennings, the organism reaches an optimum environment by chance, and remains there because it is stimulated to change its course whenever it begins to pass out of this environment. That unfavorable stimuli should provoke these changes of behavior need not be attributed to any "primary purposefulness" in living matter, since we can be perfectly sure that any organisms behaving differently would be speedily eliminated.

Again, I take it that the chief advocate of the theory of direct orientation would be the last to assume a principle of primary adaptedness, and would admit that any utility connected with these "tropisms" must have been, in the first instance, a pure coincidence. In the case of an organism, "irresistibly" drawn toward a favorable stimulus, as a growing plant toward the light, we might seem to have an instance of such a directly purposive action, *i. e.*, the determination of the means by the end. But several things must here be taken into consideration. (1) It not infrequently happens that organisms are drawn in an equally irresistible manner toward a fatal stimulus, *e. g.*, the moth to the flame; (2) we can not feel sure, in every case, that the attainment of the goal is not the outcome of random movements, unperceived by the observer; (3) even where the response is indubitably adaptive, and as direct and unfailing as a simple reflex, it may be the outcome of a mechanism developed through natural selection, *i. e.*, the survival of random variations which were as frequently unadaptive as they were adaptive. The fact that some organisms still make suicidal responses to less familiar stimuli favors this last view.

Next, we may consider the phenomena of metabolism, growth and development. We group these things together, because they can hardly be considered separately. Growth is the outcome of metabolism, and development of metabolism and growth.

The phenomena revealed through studies of normal physiology and embryology are obviously highly "purposive," in the sense that they have relation to the attainment of an end, that end being the preservation of the individual and the race. Nevertheless, they are believed by most biologists to be the outcome of a "mechanism" the functioning of which presents no greater difficulties, apart from complexity, than the working of a clock or a steam-engine.

When we come to consider the origin of this mechanism, we may mention three chief hypotheses, which have been or still are held. (1) It may have been specially created by a super-mundane power in each individual species of organism; (2) it may have gradually developed out of simple beginnings by the "selection" or survival of random variations which were as likely to be unadaptive as adaptive; or (3) it may have gradually developed out of simple beginnings through (*a*) direct responses to environmental stimuli, or (*b*) the effects of functioning upon the functioning parts themselves.

The first of these alternatives has been well-nigh discarded by scientist and layman alike, and need not be further considered here. I will point out in passing, however, that certain elements of the "special creation" hypothesis have recently been put forward in the name of science. Of this more anon.

The second alternative, that of natural selection, is admitted by most biologists to be one of the factors concerned in the production of adaptive mechanisms, though it is doubtful whether any two thinkers would agree as to the importance to be assigned to it. The essence of this hypothesis is the contingency of the individual variations in relation to the need to be satisfied. If the variations are *directed,* in the sense of tending preponderatingly toward the satisfaction of this need, then our explanation is shifted to a totally new basis. It is this directive tendency, not natural selection, which is the effective agency in evolution. The consequences which would follow such an assumption will be discussed later.

The third of our alternative hypotheses has figured historically as the chief rival of natural selection, though by many (*e. g.,* by Darwin himself), both principles were accepted. One of the merits of the Lamarckian principle, in the eyes of some of its adherents,[3] is its apparent rejection of contingency or chance, a fatal weakness, so they believe, in the natural selection theory. But a little thought will show us that the Lamarckian principle, no less than the Darwinian, is based upon chance, as regards the relation between the need and the means to its fulfilment.[3a]

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[3] August Pauly, "Darwinismus und Lamarckismus," 1905; R. H. Francé, "Der heutige Stand der Darwin'schen Fragen," 1907.

[3a] It is true that both of the writers cited in the preceding footnote clearly recognize this *accidental* character of adaptive responses in their inception, though failing to realize the significance of this fact for biological philosophy. (See my review of Pauly, in *Journal of Philosophy, Psychology and Scientific Methods,* August 27, 1908.)

Let us consider (*a*) the case of modification through direct environmental stimuli. There is much vague talk about the "environmental mould," in which the "plastic" organism is supposed to be "cast"; but those who have given much study to the subject recognize that modifications produced by the environment are in the nature of reactions to stimuli. In many cases, these reactions are plainly adaptive, in the sense of furthering the life or comfort of the individual or the race, as when a callosity is developed in consequence of continued friction, or an antitoxin is generated to combat a bacterial poison. The fact, however, that there are varying degrees in the adaptiveness of these responses, and indeed that many of them appear to be wholly unadaptive, suggests the probability that the truly adaptive ones, when at all constant, have resulted from the selection of "accidental" variations. This can, of course, be true only of responses to environmental stimuli which have presented themselves frequently in the history of the race. Cases in which the organism has responded adaptively to stimuli quite new to racial experience are not, however, entirely unknown. These will be discussed in a later section. It may be said in passing, however, that the only conceivable scientific explanation of such cases involves the principle of "trial and error," which, of course, is based upon complete contingency as regards the relation of means and end.

Let us pass to (*b*) the effects of functioning upon the functioning parts themselves. It is held by the Lamarckians that organs or parts grow or diminish through use and disuse, and that the perfected mechanisms which now arouse our admiration and wonder are the outcome of past functional activity. Many upholders of this view introduce the idea of a conscious struggle toward a desired end. The perfecting of the parts they regard as a voluntary process. Thus is "blind chance" cast out as a factor in evolution. But such reasoning rests on insufficient analysis. Granting the part played by voluntary action (*e. g.*, exercise or practice) in the postnatal development of many higher organisms, we need only refer the reader to what we have already said about the "contingent" character of even intelligent action. But it seems likely that the claims of the psycho-vitalists (*e. g.*, Pauly and Francé) are largely fantastic, and that voluntary struggle toward an end has not played the important rôle in organogenesis which they imagine that it has. The greater part of the functioning of the organism probably consists in blind responses to external or internal stimuli—blind in the sense of having no conscious end in view. Thus regarded, they are in no way different from the responses already considered under (*a*), save that we there dealt with the effects of external stimuli alone.

Accordingly, we may repeat here that so far as these functional responses—and the organs they perfect—are adaptive, their adaptiveness must have arisen, in the first instance, by the selection of contingent variations. Under this head are to be included (1) the preservation of those individuals which chanced to make appropriate responses (natural selection); and (2) the making habitual on successive generations of individuals of responses which chanced to fulfil a given need when first experienced (Lamarckism). The only other alternative would seem to be some sort of inscrutable foreknowledge on the part of the organism of every need to be experienced, and of the way in which this need could be satisfied. Such a conception would obviously carry us beyond the field of scientific explanation, but I shall none the less consider it in its proper place.

It is not my purpose here to discuss the arguments for or against either the Darwinian or the Lamarckian principle. It is my object merely to point out that *both theories rest on the selection, in one way or another, of variations which were originally contingent or accidental, in the sense of not being directly determined by the need to be fulfilled.* And, indeed, this is true of all of the other rival or subsidiary hypotheses of evolution, so far as they may be regarded as scientific theories at all.

The theory of mutation, in its original form, postulated large and abrupt variations as the material for selection, a modification which does not affect the principle essentially. In its later form, it merely insists that these variations must be of the discontinuous or Mendelian type, assuming that all other variations are non-inheritable. Those who maintain the importance of isolation in evolution can not, of course, regard this as a *vera causa* of adaptive change. The actual changes must be either "spontaneous" variations or mutations or else modifications due to environment. Thus, we must resort finally to either the Lamarckian or the Darwinian principle to account for such of them as prove to be useful. "Orthogenesis," so far as it is not a vague appeal to a "perfecting principle," "élan vital" or the like, is a mere assertion that variations may accumulate in a given direction independently of selection. Wherever the variations are sufficiently adaptive, however, we are not justified in excluding selection. When non-adaptive, such a process presents no greater difficulty in principle than the continuous growth of a crystal or the continuous deepening of a canyon by erosion.

Most of us are prepared to admit that much in the organic world is non-adaptive. We may even grant that a large proportion of the diagnostic characters of species and genera belong to this category. Such characters, while they may baffle the investigator, are in general not such as would have suggested the operation of a supernatural factor in evolution. In this paper we are concerned with the problem of organic adaptation, and shall leave aside the origin of characters which are useless to the organism.

In the foregoing analysis, I have regarded adaptive response, whether of structure or function, as being invariably a secondary phenomenon. The connection between the need of the organism and the means adequate to satisfy this is believed to have always been, at the out-

set, an "accidental" one. In those cases where the correct response appears to ensue unhesitatingly, we have had to suppose either (1) that the observer has overlooked "trial and error" stages preceding the response in question, or (2) that the response is the outcome of an inherited mechanism, based upon racial experience, and therefore ultimately upon some form of selection.

III. VITALISM[4]

Let us now consider the claims of a school of thinkers who argue for the existence of a primary purposefulness in living things, and who deny that any conceivable mechanism can account for certain of the phenomena observed. As the most conspicuous representative of this school we naturally turn to Hans Driesch, who has made a more determined attempt than any other vitalist to reduce his beliefs to a unified system of philosophy.

Driesch's three "proofs" of vitalism may be summarized as follows:

1. In the earlier development of some organisms, rather low in the scale of life, any part of the embryo, provided that it be of a sufficient size, will, if artificially detached, produce the entire organism. This he regards as conclusive disproof of the supposition that the spatially arranged diversities of the adult organism depend for their origin upon diversities of a *spatial* sort in the embryo. Such a spatial prearrangement of the parts as is postulated by the Weismannian "germ plasm" theory, and other preformationist hypotheses, he assumes to be essential to any mechanical theory whatever.

But, Driesch claims, the spatial diversities of the adult organism must depend upon preexisting diversities of *some* sort, therefore he invokes a non-spatial agent, "entelechy," to account for them. Now "entelechy" must be a manifoldness, since it is conjured up to explain other manifoldness, but this manifoldness is *intensive*,

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[4] In this section, I have made free use of a review of Driesch's "Science and Philosophy of the Organisms," which I wrote some years ago (*Journal of Philosophy, Psychology and Scientific Methods*, June 9, 1910). I have not thought it necessary, however, to indicate the extent of these quotations.

not extensive. As an illustration of an "intensive manifoldness" he instances one of our own states of consciousness, in which many elements are presented simultaneously, though not spatially separated from one another. But entelechy is not to be identified with mind. It is an unknown something which stands in the same relation to our mental life as it does to other organic phenomena.

2. Driesch's next "proof" of vitalism is somewhat similar to the first, though it rests upon the facts of normal life history, instead of upon artificial disturbances of this. The primitive germ cells, each of which, according to the hypothesis he combats, should contain the "machine" or spatial prearrangement of parts necessary for the development of an entire organism, undergo in the gonads an extensive series of divisions, leading to the formation of the mature ova and spermatozoa. "Can you imagine," he asks, "a very complicated machine, differing in the three dimensions of space, to be divided hundreds of times and in spite of that to remain always the same whole?"[5]

3. The last "proof" of vitalism is based upon an analysis of animal behavior. Driesch makes much of the fact that an action of a higher animal, particularly of an intelligent one, is something more than the sum of many simpler elements, each depending upon an element in the complex of stimuli to which the organism responds in a given case. The response of the organism is a unified whole, corresponding to a total situation in the outer world. A slight change in this complex of physical stimuli, provided that it has *significance* for the organism, may result in a totally different kind of response. On the other hand, an entirely different set of physical elements—having, however, the same *meaning* for the organism—may call forth precisely the same response. In other words, there is no functionality (in the mathematical sense) between the response and the stimulus.

This line of argument, different as it may seem, rests

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[5] "Science and Philosophy of the Organism," Vol. I, p. 225.

upon the same fundamental assumption as the two preceding ones, namely, that a truly mechanical theory must find in the cause as many separate elements as we observe in the effect. The structural diversities of the adult organism must rest upon corresponding structural diversities, present from the beginning in the germ. The functional diversities, constituting a complex act of behavior must rest upon corresponding functional diversities in the stimuli which make up the total effective situation. If no such correspondence can be shown, we must invoke some principle of a totally different nature from those which we employ as explanations in the inorganic world.

Now, such a conclusion as this seems to rest upon an insufficient consideration of what really happens in the inorganic world. In a sense, the solar system was present potentially in the original homogeneous nebula, while the various continents and oceans, mountains, lakes and rivers of the world we live in were all present potentially in the molten globe which in some way detached itself from the parent mass. But there was certainly no "preformation" of these final products of cosmic evolution. The diversity which was introduced was totally new. In the language of biology the world's development was strictly "epigenetic." And yet the process was none the less mechanical, as every vitalist will allow. Why then does Driesch insist that a mechanism adequate to account for an animal's ontogeny must present a part-for-part correspondence with the adult organism? For it is only a mechanism, *as thus conceived,* that is disposed of by his "proofs" of vitalism. His experiments compel him to dismiss the notion of a *spatial* prearrangement of parts. Therefore, he jumps to the conclusion that there must be a *non-spatial* prearrangement of parts—an "intensive manifoldness." But why should there be any prearrangement of parts at all? Is it not a fallacious philosophy which insists on such an exact numerical correspondence between the elements of the cause and the elements of the effect?[6]

Despite these logical difficulties, Driesch's third "proof" of vitalism contains such an unmistakable element of plausibility that some further consideration may profitably be given to it here. His contention is summed up in the phrase "individuality of correspondence" between stimulus and reaction. "It is not the single constituents of the stimulus," he says, "on which the single constituents of the effect depend, but one whole depends on the other whole, both 'wholes' being conceivable in a logical sense exclusively" (II, 81). Why is it that we react to *objects* rather than to sensuous images? "The dog, 'this dog,' 'my dog,'" to quote Driesch, "is 'the same' stimulus, seen from any side or at any angle whatever: it always is recognized as 'the same,' though the actual retinal image differs in every case" (II, 73). Experience and association, he thinks, afford an insufficient basis of explanation here. There must be something capable of resolving past experience into its elements and making wholly new combinations of them.

Driesch challenges his opponents even to conceive of a machine that could accomplish results such as these. This introduction of the word "machine" would seem to prejudice the case in his favor at once. But is he not really challenging us to imagine how phenomena that require sense organs and a nervous system for their performance could be performed by some other type of mechanism which is simpler and more fully understood by us. Confessedly we can not do so. Looking at the subject in an unbiased way, it would seem that the nervous system had the appearance of a finely wrought mechanism to a higher degree than any other portion of the body. It is truly one of almost infinite complexity, and one that is largely inaccessible to experimental observation. But certain significant facts have been demon-

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[6] Spaulding (*Philosophical Review,* July, 1909) and Jennings (*Johns Hopkins University Circular,* No. 10, 1914) have already called attention to the fallacy of this aspect of Driesch's argument.

strated none the less. Sherrington has described in some degree the mechanism of inhibition, and has ascertained some of the factors which determine which of two simultaneous stimuli shall prove effective in a given reflex. Do not such data at least help us to conceive the possibility of a nervous system whose activities may be understood without the aid of an entelechy to make its decisions for it?

The emancipation of the organism from the controlling influence of immediate stimuli is admitted to be one of the salient features in animal evolution. Now, in order that present activities may be directed with reference to future results, the stimuli must become more and more symbolic, *i. e.*, they must acquire a "meaning." That one thing may "stand for" something else, and call up the responses proper to that something else may readily be understood in terms of association. At least there would seem to be no desperate need for invoking "entelechy" at this point. If this be granted, why should we expect any correspondence between the sensuous elements of the stimulus and the elements of the response? The effects of a given "individualized stimulus" are dependent rather upon the aggregate of associative processes which this stimulus calls up. And this aggregate is altogether an empirical one, not a logical one as Driesch supposes. The connections that bind it together may be quite arbitrary and accidental. It is partly the product of individual experience, partly of racial experience—this last on any theory of inheritance. That several widely different stimuli, having the same meaning (*i. e.*, having certain important associations in common), can bring about essentially the same response would seem, on the face of it, no more difficult to understand "mechanically" than that several very differently shaped keys can open the same lock.

The weakness of Driesch's "third proof of vitalism" would seem, therefore, to be twofold. (1) He appears to believe that an explanation, in order to be mechanical, must find a definite correspondence between separate factors of the cause and separate factors of the effect,[7] and (2) he appears to believe that in any mechanical explanation of action the character of the response must be determined by the immediate sensuous stimuli themselves, without regard to the representative (associational) character of these stimuli.

Driesch, like other vitalists, lays great stress upon "adaptive" or "regulative" phenomena, though he makes no claim that these necessarily demonstrate the truth of vitalism. Indeed, it will be noted that the three foregoing "proofs" rest on quite other grounds. We may safely say, however, that for most biologists the great stumbling-block to a consistent mechanical explanation has been this central fact of organic "purposefulness." In pre-Darwinian days the whole subject was a mystery, which science cheerfully handed over to theology for solution. Later, we grew accustomed to the idea that much which seemed purposeful in nature was the outcome of "chance." But for many there was always a considerable residuum which defied solution. For there certainly seem to be cases of adaptive response to wholly new situations, that can not be accounted for on the basis of an evolved mechanism. And furthermore, it is now obvious that no single theory of evolution yet proposed, nor, indeed, all of them combined, can adequately account for much that has come to pass.

In the face of these perplexities, it is but natural that many have taken refuge once more in various intangible forces and principles, almost wholly devoid of positive attributes, and agreeing only in their alleged competence

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[7] It must be admitted that explanations of this type have been put forward by avowed mechanists. Thus Loeb ("Mechanistic Conception of Life," p. 80), in discussing the present writer's experiments upon the color changes of flatfishes, concludes that there is an actual reproduction on the skin, through the brain, of the retinal images of the background. I think that a careful reading of my own discussion of these experiments sufficiently disposes of this contention (*Journal of Experimental Zoology*, May, 1911). The yet more extensive experiments of Mast (*Bulletin of the Bureau of Fisheries*, Vol. XXXIV, are likewise conclusive against this view.

to "explain" otherwise inexplicable facts. Of these Driesch's "entelechy" and Bergson's "élan vital" are but types.

Much less discordant with our scientific habits of thought are the utterances of some of the so-called "psycho-vitalists," to whom allusion has already been made. These writers do not have recourse to metaphysical principles, wholly beyond the realm of experience. They invoke the familiar facts of conscious purpose, intelligence and will. Organic happenings *seem* purposive, they think, because they *are* purposive, in the same sense that our own voluntary actions are purposive. Such a view carries the realm of mental life far beyond the bounds which we are wont to assign to it. Its logical outcome is a thoroughgoing panpsychism, an outcome which some of its advocates are quite ready to accept.

Now, it seems to the writer that a panpsychic view of nature can be stated in such terms as not only to be plausible, but to meet certain of our most fundamental intellectual needs. But such a view is at best a philosophical creed, not a scientific explanation, and should never be offered as a substitute for the latter.

The introduction of will, purpose, etc., in the rôle of scientific explanations may have one of two implications. Either (1) it may be assumed that a given physical configuration, plus these psychical concomitants, is able to accomplish what would be impossible for the *same* physical configuration minus these psychical concomitants (interactionism); or (2) it may be assumed that only that type of physical configuration which is invariably bound up with certain psychical factors is competent to call forth the result in question (parallelism). According to the second point of view, the question whether the same result would have ensued without the agency of purpose or will is an absurdity. If purpose and will had been lacking, the physical antecedents would of necessity have also been different.

It is needless to say that both of the foregoing positions have been upheld by philosophers. It is my wish to point out, however, that on neither assumption does the introduction of conscious purpose supply a missing link in our explanation of the "teleological" in nature. Whether or not we admit the efficacy of mental states, independently of their physical concomitants, we have already seen that conscious purpose must proceed on the basis of experimentation. It must have learned through trial that a given means will lead to the attainment of a given end. The existence of any primary foreknowledge of the relation of means to end is contradicted in our own every-day experience.

It may be useful to introduce a description by a psychologist[8] of what actually occurs when we are trying to solve a problem:

> Our only command over it is by the effort we make to keep the painful unfilled gap in consciousness. . . . Two circumstances are important to notice: the first is, that volition has no power of calling up images, but only of rejecting and selecting from those offered by spontaneous redintegration [= association]. But the rapidity with which this selection is made, owing to the familiarity of the ways in which spontaneous redintegration runs, gives the process of reasoning the appearance of evoking images that are foreseen to be conformable to the purpose. There is no seeing them before they are offered; there is no summoning them before they are seen. The other circumstance is, that every kind of reasoning is nothing, in its simplest form, but attention.

It is, therefore, a false theory of our own purposeful actions that is projected backward into organic nature by the psycho-vitalists. The existence of instinctive acts, which fit means to ends, prior to experience, in no way invalidates what I have said. For these may be assumed to be based, in some way, on past racial experience. And, in any case, so far as an action is instinctive, it can not be *consciously purposive*. Assuming that instinctive actions are performed consciously, at all, which some would perhaps deny, it is not likely that anything beyond the next succeeding step in the series is at any moment present to consciousness. The biological meaning of the entire performance (say the building of

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[8] Hodgson, quoted by James ("Principles of Psychology," Vol. I, p. 589).

a nest) can not be understood by the organism. Each step is desired and willed on its own account alone. The end *takes care of itself,* by virtue of a preestablished mechanism.

Thus purpose, in the psychological sense of the word, can not be predicated of a complex instinctive act, even though the individual steps be consciously performed. Least of all can it be predicated of a process of organic regulation or reparation, the object of which can never be consciously in view. It was doubtless in part considerations like these which led Driesch to deny the mental nature of "entelechy" altogether and to remove it to a transcendental sphere in which it was no longer subject to the exacting demands of experienced reality. Indeed, he tells us that "there *must* be a something in them [morphogenetic, adaptive and instinctive entelechies] that has an analogy not to knowing and willing in general . . . *but to the willing of specific unexperienced realities,* and to knowing the specific means of attaining them" (II, p. 142). We think more favorably of Driesch's good sense when he admits that the position of his doctrine is at this point "rather desperate." Nor is Bergson's case a bit better when he naïvely attempts to clear up certain of the most baffling phenomena of instinct by invoking the aid of "intuition" or "sympathy."[9] The psycho-vitalists introduce an agent which is to some degree intelligible, even though it is inadequate. The agents which Driesch and Bergson conjure up are neither adequate nor intelligible.

In the writings of these and some other vitalists the "vital principle," by whatever name called, is distinctly credited with powers which we should ordinarily term clairvoyant. Indeed, we are forced to conclude that it must be able to "tap" sources of information which are closed even to the highest finite intelligence. This, of course, is mysticism pure and simple, though such a reproach admittedly does not constitute its refutation for all minds.

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[9] "Creative Evolution" (trans.), pp. 173–175.

It may be interesting perhaps to consider where such assumptions would lead us. Suppose that we adopt the absolutist idea of an Infinite Knower, having cognizance of the future as well as the past, or rather including both future and past in one eternal present. By getting into connection with this, our entelechy could doubtless solve any problem which confronted it. But how, on such an assumption, could we account for the multitudinous *mis*-adaptations which confront us? How should we explain an instinct which led to the harboring of baneful parasites in an ant community or a regenerative process which resulted in the formation of the wrong organ? Perhaps these perplexing cases would be merged into the general mystery of the origin of evil, and there, indeed, may be where they belong.

But we are not compelled to accept an absolutist interpretation of things. As scientists, we may find it more easy to believe in the evolution of God, in a "*Dieu qui se fait.*"[10] Well and good, but then the essence of this view is the *newness* of everything that happens. No mind, however infinite, could foresee the future, for the simple reason that the future is not determined until it comes to pass. Even our deity must learn by experience, and "entelechy" would have to do the same. In that case neither would be of much service in attempting to explain organic purposefulness. Had we previously learned to expect any great amount of consistency among the various views of M. Bergson, it would have been a source of surprise to us to find him coupling together this idea of "creative evolution" with a transcendental "élan vital," which provides the organism with useful structures without the guidance of experience.

Such a departure as I have made from the field of legitimate scientific discussion may shock those of my readers who shy at anything suggestive of metaphysics or theology. But we have been told with increasing frequency of late that our accepted scientific methods

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[10] I believe that this expression is Bergson's.

have broken down in the face of vital phenomena, and that the only path of escape was one which logically led to mysticism. For this reason it seemed worth while to inquire whether even this abandonment of our scientific principles would lighten our difficulties.

Now, while we believe the solutions offered by the vitalists to be but pseudo-solutions, we must admit that the issues they have raised are real ones. It is to the great credit of this school, and of Driesch in particular, that they have awakened some of us biologists from our "dogmatic slumber" and forced these problems upon our attention. The problems are real ones in the pragmatic sense of determining our attitude, both theoretical and practical, toward biological investigation in general. Most important of all, vitalism has unearthed a number of highly interesting experimental data, which it challenges its opponents to explain. To this extent it may lay claim to the rank of a "working hypothesis."

Let us consider some of the points at issue between vitalism and what I shall call "scientific biology." In what follows, I have stated what I believe to be the typical attitude of each side, though it is likely that no two persons would agree in every particular.

1. Scientific biology is strictly deterministic. It admits the possibility of only one result from a given set of antecedents. Vitalism is indeterministic, holding that from precisely the same antecedent situation more than one result is possible. Driesch saves the principle of "univocal determination" by saying that in cases where different results follow the same physical causes, there must have been a difference in "entelechy." But Johnstone,[11] a disciple of Driesch, throws over even this formal adherence to scientific method, and asserts boldly that there must be "uncaused differences" in the organic world. He illustrates this belief from the variability among the millions of eggs spawned by a single flounder. The usual explanation, based upon differences in exter-

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[11] "The Philosophy of Biology," 1914.

nal conditions or on imperfections in the mechanisms of cell-division he holds to be inadequate. Now, in his belief, it is these "spontaneous" variations (using the former word literally) that furnish the raw material for evolution.

Jennings[12] sees in this postulate of indeterminism the fundamental fallacy of vitalism. It certainly is the feature that would most seriously affect us as investigators. For whether variations are regarded as uncaused or as caused by an agent beyond the ken of scientific investigation matters little. Any attempt to account for them by experimental or observational means must be futile.

2. Scientific biology endeavors to explain organic phenomena on the basis of antecedent physical conditions, though admitting that our knowledge of cause and effect is in the last resort empirical, to the extent that much which happens could not have been predicted in advance. Vitalism explains organic phenomena—or a certain part of them—on the basis of ends to be realized, and gives to these ends a determining influence in providing the means to their realization. Since the *a tergo* "push" of physical causation would only by rare chance be directed in harmony with these ends, vitalism introduces a non-physical agent to guide or control the former. Driesch goes to great lengths to explain how "entelechy" can play this rôle without coming into conflict with the law of the conservation of energy.

In a certain sense the existence of such "ends" must be admitted by all biologists. Attainment of the typical form, self-preservation, racial preservation, etc., are "ends" in the sense that organic processes in general are observed to trend in those directions. Furthermore, disturbances of this normal trend often seem to be corrected automatically. Phenomena strictly analogous in this respect can, of course, be instanced from the inorganic world. All we have to do is to designate the observed goal of such a process as the "end" and the

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[12] *Science*, June 16, 1911; October 4, 1912.

causally determined steps become the means to its realization. The difference between such a physical process and a vital one, as conceived by Driesch, is that in the latter a given sequence of events *may or may not* come to pass, depending on the whim of "entelechy." The issue here, then, is practically the same as that first raised, namely, that of determinism versus indeterminism.

3. Scientific biology declares that vital phenomena are chemico-physical, in the sense that they are the inevitable outcome of the particular material aggregations which we term organisms.[13] It grants that in these manifold chemical syntheses entirely new properties have emerged, though insisting that the same may be said of any union of elements whatever. Vitalism denies that any possible configuration of material particles, without the aid of an immaterial principle, can account for the phenomena observed. It is for this reason that "vitalism" is commonly set in opposition to "mechanism." Driesch's three "proofs" of vitalism are concerned with this last aspect of the theory. We have seen that all three are based on the assumption that we must find a diversity in the cause, corresponding to each diversity in the effect. And it has been pointed out that this does not hold true even of admittedly physico-chemical systems.

Now, I do not claim that the bare word "mechanism," however hallowed by scientific usage, has any greater explanatory value than "entelechy." Indeed, I do not see why we should be called on to furnish a *mechanical* explanation, *sensu stricto,* of biological phenomena at all. Not all natural science is mechanics; some of it is chemistry. And I believe it is equally true that still another part is biology, a science quite distinct from either. But I think we can claim the possibility of a scientific explanation in the sense indicated by the foregoing antitheses, and it is with this in mind that I have grappled with the problem of organic "purposefulness."

(*To be concluded*)

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[13] It is not, however, necessarily "materialistic" in a metaphysical sense.

GIGANTISM IN NICOTIANA TABACUM AND ITS ALTERNATIVE INHERITANCE

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Introduction

Within recent years observers working with different varieties of *Nicotiana tabacum* grown commercially in the United States and elsewhere have recorded the sudden appearance of occasional giant plants of abnormally high leaf number. Except in height and number of leaves, which may be increased several times above the usual number, these giant plants in general appearance do not depart widely from the varietal type from which they took their origin. The great increase in number of leaves, together with a greatly elongated main stem, is accompanied by a period of vegetative vigor of such long duration that blossoming does not normally take place when the plants are growing in the field. In order to obtain seed from such plants, the usual practise has been to transplant the roots and stub, or even the plants entire, to the greenhouse in the fall, where vegetative vigor is resumed with the final production of normal blossoms and seed during the winter. Plants of this habit of growth have been recorded in the Sumatra, Maryland. Cuban and Connecticut Havana types of tobacco.

Occurrence of Gigantism in Different Varieties

The first published record of gigantism in tobacco appears to have been made in 1905 by Hunger (1905), working with tobacco in Sumatra in connection with an investigation of the mosaic disease.

Garner (1912) mentioned a Maryland Mammoth type, the origin of which was associated with a cross between two common varieties of Maryland tobacco.

Hayes and Beinhart (1914) reported the occurrence of giant plants in the Cuban shade tobacco and the Connecticut Havana type in Connecticut.

In addition to Hunger's observation previously mentioned, Honing (1914) brought out other interesting facts concerning the occurrence and behavior of giant plants in Sumatra (Deli) and Java.

Hayes (1915) further discussed the occurrence of giant plants in the Cuban and Connecticut Havana types of tobacco grown in New England.

Hunger, in the paper referred to, states that the largest giant plant observed by him developed 123 leaves and reached a height of nearly five meters. These plants were entirely sterile, or, if blooming took place, the number of blossoms was greatly reduced. Honing states that the behavior of these giant Sumatra plants with respect to the transmission of their peculiarities is variable. In one instance he observed that a line of these plants finally disappeared entirely. With respect to number of leaves, Honing's studies of the Deli tobacco indicates that several more or less distinct types exist. Even though line selections of these have been grown under bag for several generations, plants possessing high leaf number have occasionally appeared. Mammoth plants have also appeared in the Sumatra variety grown in the United States from seed obtained from Sumatra. In 1912 two plants of this type appeared in a plot of about 100 plants grown at Arlington, Va. These plants appeared in the second year's planting from seed obtained from Sumatra. One of these, when removed to the greenhouse, had reached a height of eleven feet and had produced about 100 leaves, with no indication of blooming. It was not possible to determine to what extent these plants transmitted their characteristics to their progeny since both died after being cut back and removed to the greenhouse.

In 1906 and 1907 giant or mammoth plants were obtained in Maryland tobacco, as mentioned above.[1] The

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[1] A discussion of the commercial value of these types of Maryland tobacco will be found in Bulletin 188, of the Maryland Agricultural Experiment Station, entitled, "Types and Varieties of Maryland Tobacco," by W. W. Garner and D. E. Brown, 1914, pp. 135–152.

type known as the Broadleaf Mammoth was first observed in 1906 in a selection line of Maryland Broadleaf begun in 1904. Of 100 plants grown in 1906, five were typical mammoth plants producing many leaves and showing no tendency to bloom at the end of the season. Subsequent generations of these plants were grown successively in 1907, 1908 and 1909, and all reproduced the characteristic habits of growth of the original parent isolated in 1906. This mammoth type, as the name indicates, differed materially in shape of leaf from the better known Narrowleaf Mammoth.

The so-called Narrowleaf Mammoth appeared in 1907 in second generation plants of a cross made in 1905 between a Broadleaf type and a Narrowleaf type of Maryland tobacco. From a single mammoth plant found in 1907, 157 plants were grown in 1908, all of which were mammoth plants. Two of these plants which were allowed to grow until frost without topping had produced 109 and 111 leaves, respectively, with no indication of blooming. The Narrowleaf Mammoth has been propagated from seed and grown on a commercial scale in Maryland up to the present time, and under normal field conditions still retains its characteristics of high leaf number and the non-blooming habit.

A third mammoth type appeared in 1907 in second generation plants of a cross made in 1905 between Maryland Broadleaf and the White Burley variety of Kentucky. In a crop of 30,000 to 40,000 plants but one mammoth plant was found. Unfortunately, this plant was harvested inadvertently by laborers and lost.

From the previous discussion it is evident that gigantism has occurred rather widely in the varieties of *Nicotiana tabacum*. It would appear from Honing's work that Mammoth Sumatra plants are not constant in their inheritance and that intermediate forms exist. The accumulated experience of various observers working with all Mammoth types which have appeared in the United States, however, has shown a constant inheritance of

Mammoth characteristics from generation to generation. Intermediate forms have not been observed.

BEHAVIOR OF GIGANTISM IN CROSSES

Since Mammoth forms are now grown commercially in the United States and promise to become valuable new varieties, it has been considered desirable to determine the possibility of combining the Mammoth character of indeterminate growth or gigantism with other characters of commercial value by crossing Mammoth types with ordinary varieties.

The Maryland Narrowleaf Mammoth has been crossed with a number of pure lines of the more distinct varieties of *Nicotiana tabacum*, including White Burley, Yellow Pryor, Little Oronoco, Connecticut Broadleaf, and the very distinct variety known as *N. Chinensis* (S. P. I., No. 42,355). In all these crosses the Mammoth characteristic behaves as a unit character and is recessive to normal size and normal blossoming habit of the ordinary varieties.

A Maryland Mammoth and a Burley Mammoth, secured as the result of the cross Maryland Mammoth ♀ × White Burley ♂, have also been crossed with the distinct species, *N. sylvestris* and *N. glutinosa*. In these crosses the F_1 plants invariably have blossomed normally as where crosses were made with varieties of *N. tabacum*.

Under normal field conditions, first generation plants of all Mammoth crosses have blossomed in practically the same period required by the ordinary varieties of *N. tabacum*. The plants, however, are usually somewhat taller and, on an average, produce a somewhat higher leaf number than the ordinary varieties, showing that the F_1 plants are more or less intermediate between the normal and the Mammoth parents. This relation of leaf number is shown in Table I.

In crosses between Little Dutch and Maryland Mammoth, the F_1 plants were also somewhat larger and produced more leaves than the Little Dutch parent. F_1

TABLE I

Comparison of Number of Leaves of F_1 Plants of Crosses between Maryland Mammoth and Normal Varieties

Variety	Leaf Number Classes									
	23	25	27	29	31	33	35	37	39	41
Yellow Pryor	2	7	1							
Md. Mammoth ♀ × Yellow Pryor ♂			1	1	1	6	7	2	2	
Little Oronoco	1	1	2	3	3					
Md. Mammoth ♀ × Little Oro. ♂					1	3	2	11	4	1
White Burley	1	4								
Md. Mammoth ♀ × White Burley ♂						1	6	10	5	1

plants of the cross Maryland Mammoth ♀ × *N. Chinensis* ♂ (S. P. I., 42,355) were grown in 1918, and records of dates of blooming were made for comparison with the dates of blooming of the parent *N. Chinensis*, which is an unusually small and early maturing variety of *N. tabacum*. From the following table it is evident that the parent *N. Chinensis* blossomed somewhat earlier than the F_1 plants of the cross with Maryland Mammoth:

TABLE II

Number of Days Elapsing from Transplanting to Date of First Bloom of F_1 Plants of Cross Maryland Mammoth ♀ × N. Chinensis ♂ and Plants of the Parent Variety of N. Chinensis

Variety	Classes									
	45	47	49	51	53	55	57	59	61	63
N. Chinensis	8	5	11	2	10	1	6	0	2	5
Md. Mammoth ♀ × N. Chinensis ♂				1	14	1	14	2	1	11

In the cross Maryland Mammoth × White Burley, Mammoth Burley types have consistently appeared in the F_2 progenies, and have since remained true to Mammoth character. These have been crossed with a number of different types and varieties of *N. tabacum*. During the summer of 1918 considerable data were secured at Arlington, Va., showing the segregation of plants of Mammoth character in the F_2 of many crosses.

Let us first consider the behavior of different Mammoth types when intercrossed. In these lines the Maryland

Mammoth (narrowleaf type) has been crossed with Stewart Cuban (a giant type previously mentioned as originating in Connecticut in Cuban shade-grown tobacco), and also with a Mammoth Burley type, which was secured in the F_2 generation of the cross Maryland Mammoth × White Burley. In the cross Maryland Mammoth × Stewart Cuban, many plants of the F_1 generation were grown, all of which were of Mammoth habit of growth. Selections of these F_1 plants were grown and bred true to the Mammoth habit.

In the cross Maryland Mammoth ♀ × Burley Mammoth ♂ many F_1 plants were grown at Arlington, Va., in 1918. Of a total of 558 individuals, all were of Mammoth habit and of this number twenty-one were yellowish green like the normal White Burley variety, and 237 were full green in color like the Maryland Mammoth parent.

In a study of the reappearance of Mammoth types in the F_2 generation of crosses involving Mammoth and normal forms, several different combinations have been made. In one group both parents were of Burley type. In the second group one of the parents was normal green and the other of Burley type. In the third group both parents were green.

In the first group, involving Burley color in both parents, one of the parents was the Burley Mammoth secured in the F_2 generation of the cross Maryland Mammoth × White Burley. From the cross Mammoth Burley ♀ × ordinary White Burley ♂, 638 F_2 plants were grown, of which 158 were Mammoth. This is a very close approximation to the theoretical Mendelian ratio $638/4 = 159.2$, which should obtain in a cross involving two simple contrasted Mendelian characters.

From the cross White Burley type of 30A,[2] ♀ × Burley Mammoth ♂, 348 F_2 plants were obtained, of which eighty were of Mammoth habit of growth. This figure closely approximates the theoretical Mendelian ratio $348/4 = 87$.

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[2] The type designated as White Burley type of 30A is a tall, vigorous Burley type originally obtained from the cross Connecticut Broadleaf × White Burley.

Of the total number of Mammoth plants, *i. e.*, 986, appearing in the F_2 of these crosses, only two were Green Mammoth, the rest being typically of Burley character. Whether these two exceptions represent mixtures or reversions can not be stated.

In the second group, one of the parents involved in the original cross was Green, the other being of Burley character.

From the cross Connecticut Broadleaf ♀ × Burley Mammoth ♂, 305 F_2 plants were grown, of which sixty-nine were of Mammoth habit. This approximates the theoretical ratio $305/4 = 76.2$. From the cross Maryland Mammoth ♀ × White Burley type of 30A ♂, 152 F_2 plants were grown, of which forty were of Mammoth habit. This figure is very close to the theoretical ratio $152/4 = 38$. Of the total number of Mammoth plants, *i. e.*, 457, which appeared in the two crosses Connecticut Broadleaf ♀ × Burley Mammoth ♂ and Maryland Mammoth ♀ × White Burley type 30A ♂, only two were of Burley color, the rest being green.

We will now consider the third group, which involves normal green color in both parents.

From the cross Connecticut Broadleaf ♀ × Maryland Mammoth ♂, 175 F_2 plants were grown, of which thirty-nine were of Mammoth habit.

From the cross Maryland Mammoth ♀ × Yellow Pryor ♂, eighty-three F_2 plants were grown, of which twenty-five were Mammoth.

From the cross Little Dutch ♀ × Maryland Mammoth ♂, 119 F_2 plants were grown, of which twenty-eight were Mammoth. A total of 377 plants were grown in these crosses, of which ninety-two were Mammoth plants. This is a very close approximation to the expected ratio $377/4 = 94.2$.

Considering all the crosses in the three groups involving the Mammoth character in one of the parents a total of 1,820 F_2 plants were grown, of which 439 were of Mammoth character. This is a fair approximation to the expected ratio 1820/4 = 455, if the Mammoth habit behaved as a simple Mendelian character in contrast with the normal blossoming habit.

From these data it would appear that the Mammoth character is recessive in its inheritance and reappears in the F_2 generation in numbers approximating closely the expected ratio for a simple Mendelian recessive.

THE ORIGIN AND BEHAVIOR OF A NEW MAMMOTH TYPE OF TOBACCO IN A LINE DESCENDING FROM A SPECIES HYBRID

In an earlier paragraph it has been mentioned that the Maryland Narrowleaf Mammoth and a Burley Mammoth appeared in the F_2 generation of certain crosses. In the writer's experience a giant type appeared in third generation plants descending from a species cross.

In 1914 the blossoms of a first generation plant of the cross Connecticut Broadleaf (pink) ♀ × Giant Red flowering (carmine) ♂ were pollinated with the pollen of *Nicotiana sylvestris* (white).[3] Although first generation plants of crosses between the species *N. tabacum* and *N. sylvestris* are likely to be sterile, or nearly so, considerable fertile seed were obtained from F_1 generation of this particular cross. In the second generation there was a noticeable segregation into plants with pink, white and carmine blossoms. The size and shape of the blossoms of the plants of the F_2 generation were also very variable and various abnormalities were noted. Some plants were completely self-sterile and others produced blossoms with supernumerary petals. A number of plants producing the largest and finest carmine-colored blossoms were selected for further inheritance studies. The progenies of two of these mother plants, nos. 9 and 12, were grown in the field at Arlington, Va., during the season of 1916.

The mother plant, no. 9, proved to be heterozygous, breaking up into carmines and pinks, approximating the theoretical ratio of three carmines to one pink. All the plants of this line were normal in size and habit of growth.

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[3] The so-called Giant Red flowering tobacco sold by seedsmen for ornamental purposes, is only a variety of *N. tabacum* with deep carmine blossoms.

The sister plant, no. 12, which proved to be homozygous for carmine, behaved differently, giving rise to a progeny of plants which were very variable in height.[4] A number of these plants appeared to possess the Mammoth habit of indeterminate growth and gave no evidence of blossoming. On October 26, 1916, the heights of the plants, all of which had blossomed except those of Mammoth habit of growth, were as follows:

TABLE III.

HEIGHTS OF THE PLANTS IN THE PROGENY OF SISTER PLANT NO. 12

	Height classes		
	3 to 5 ft.	5 to 7 ft.	7 to 9 ft.
Number in class....	12 (blossomed)	16 (blossomed)	3 (Mammoth)

The shortest plants in this progeny were first to blossom and produced an average of only 20 to 25 leaves, including the first bald sucker. Other plants of intermediate heights blossomed considerably later and produced an average of 35 to 40 leaves, including the first bald sucker. Those plants of Mammoth habit of growth which showed no indications of blossoming had produced considerably more than 40 leaves.

Two of these Mammoth plants, nos. 12 (a) and 12 (b), each seven feet in height, were transplanted in the greenhouse October 21 without cutting them back. Both plants blossomed December 8, producing carmine blossoms. Plant no. 12 (a) had produced 70 to 75 leaves, not including many bract-like leaves below the flowerhead. Plant no. 12 (b) produced 60 to 65 leaves, including all small ones below the flowerhead.

In addition to these two Mammoth plants the seed of several of the taller sister plants, nos. 12 (c) and 12 (d), in class 2, which had blossomed late, producing 35 to 40 leaves, were saved separately. The progenies of all were grown in the field at Arlington Farm, Va., in 1917. A

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[4] The leaves of the mother plant no. 12 were characterized by coarse, thick, broad and rounded blades abruptly contracted at the base to a long, almost naked or slightly winged petiole. This striking type of leaf has remained constant in the progeny of no. 12, and also in the progenies of no. 12 (a), 12 (b), 12 (c) and 12 (d), descending from this mother plant.

total of 60 plants was grown from the Mammoth mother plant, no. 12 (a), all of which were of Mammoth type, with an average height of seven to seven and a half feet. On September 11 a few of the tallest plants were eight feet in height. On this date an average of 50 to 55 leaves had been produced and none showed any evidence of blossoming. A progeny of 60 plants (see row 38A, 1917) was also grown from the Mammoth mother plant, no. 12 (b). On September 11 these plants averaged six and a half to seven feet in height and resembled the progeny of no. 12 (a) in all respects except that they were not quite as tall.

From the mother plant, no. 12 (c), which was one of the late blossoming plants, producing an average of 35 to 40 leaves, 49 plants were grown. On September 13 the heights of 48 of these plants and their blossoming habits were noted as follows:

TABLE IV

HEIGHTS OF 48 PLANTS IN THE PROGENY OF MOTHER PLANT NO. 12 (c) SELECTED FROM CLASS 2, OF TABLE III

	Height of classes					
	5 to 7 ft.		7 to 9 ft.		1 to 11 ft	
	Normal	Mamm.	Normal	Mamm.	Normal	Mamm.
Number in class ..	2	2	20	12	12	0

The height of one plant which blossomed was not obtained and is not included in the table.

In this progeny of 49 plants it is evident that 14 plants possessed Mammoth characteristics of continuous growth and showed no evidence of blossoming, while 35 plants, some of which were of giant stature, blossomed. From the late blossoming mother plant, no. 12 (d), a progeny of 48 plants was grown. The heights of 42 of these plants were also measured on September 13 and their blossoming habits noted as follows:

TABLE V

FREQUENCY DISTRIBUTION OF HEIGHTS OF 42 PLANTS IN PROGENY OF MOTHER PLANT NO. 12 (d) SELECTED FROM CLASS 2 OF TABLE III

	Height of class							
	3 to 5 ft.		5 to 7 ft.		7 to 9 ft		9 to 11 ft.	
	Normal	Mamm.	Normal	Mamm.	Normal	Mamm	Normal	Mamm.
Number in class	0	1	17	0	19	0	4	1

Six other plants were grown in this progeny which are not included in the table since their heights were not obtained. All blossomed, however.

In addition to these individual progenies of the sister plants, nos. 12 (a), (b), (c) and (d), selected from the progeny of the mother plant, no. 12, in 1916, a mixed lot of seed was harvested from several other sister plants which had blossomed. Fifty-six plants were grown from this mixed lot of seed, all averaging six to six and a half feet in height, and all blossoming. In this lot of plants there were no indications of Mammoth types and so far as could be determined with the eye, no intermediate forms were present.

From the inheritance behavior of the sister plants, nos. 12 (a), (b), (c) and (d), it is evident that pure Mammoth types, breeding true, and intermediate inconstant types appeared simultaneously in the progeny of the original mother plant, no. 12. These intermediate plants behaved as hybrid forms, in that they gave rise in their progeny to a certain percentage of typical Mammoth, non-blossoming types. Since the progenies of the two sister plants, nos. 12 (c) and (d), were handled under similar conditions from the time the seed were sown, it is evident that the mother plant, no. 12 (c), yielding 14 Mammoth plants in a total of 49 plants, was considerably more prolific in Mammoth individuals than the sister plant, no. 12 (d), which yielded only two Mammoth individuals in a total of 48 plants.

It is of interest to note that Lodewijks (1911) in working with tobacco in Java, has observed the occurrence of Mammoth types which breed true and also intermediate or inconstant races which break up into Mammoth or Giant forms approximating the theoretical Mendelian ratio of 25 per cent.

Lodewijks regards these inconstant races as hybrid mutations and states the results of his investigations as follows, a translation of which will also be given:

TRANSLATION

I. Occasionally giant plants which breed true to type occur in Vorstenland tobacco.

II. Evidently giant intermediate races also occur.

> III. In my experiments I obtained either an atavist of an inconstant intermediate race or a hybrid-giant.
>
> IV. As none of the giant plants in my experiments have reached the flowering stage, it is not certain which of the two mentioned possibilities is the chief. It would seem to be the latter, however, as seed of the few-leaved mother plant of the second generation produced exclusively plants while seed of the many-leaved plant produced nearly 25% giant and many-leaved and few-leaved plants.
>
> V. It is probable, therefore, that a second instance is present of a mutation arising as a hybrid.

Honing (1914), in his studies of the aberrant types occurring in Sumatra and Java tobacco, states that in some instances 100 per cent. of the progeny of normal plants were of the Mammoth type. According to Honing even the Mammoth plants were not always constant in their inheritance, and intermediate races were also present.

From Lodewijk's observations in Java, and the writer's observations at Arlington Farm, Va., it is evident that intermediate races, as well as Mammoth types which breed true, may appear in a progeny. Concerning the actual mode of origin of these intermediate and Mammoth races nothing definite is known. Hayes and Beinhart (1914), speaking of the origin of a Mammoth Cuban type in Connecticut in 1912, say:

> This mutation must have taken place after fertilization, *i. e.,* after the union of the male and female reproductive cells. If the mutation had taken place in either the male or female cell before fertilization, the mutant would have been a first generation hybrid, and would have given a variable progeny the following season.

They assume that if one gamete alone were affected, a progeny of hybrid character would have resulted, but if we assume that one gamete can become so affected, it is quite as reasonable to assume that both may sometime be changed in the same manner. If such were the case, Mammoth plants breeding true to this indeterminate habit of growth would be expected.

If, as Lodewijk finds, intermediate races behave as true Mendelian hybrids, producing the theoretical ratio of 25 per cent. true Mammoth plants which breed true, there is strong reason to believe that the change responsible for Mammoth habit of growth has affected one gamete only. If this gamete unites with a normal gamete, then the simple Mendelian ratio would follow, just as in the case of an artificial cross between gametes produced by a Mammoth plant and those of a normal plant. In the one case a portion or all the gametes bearing the Mammoth character are produced by a normal plant. In the other case, Mammoth plants themselves produce gametes with potential Mammoth characters. In the experience of Honing, normal plants have even produced progenies containing 100 per cent. mammoth plants. This behavior would indicate that all the gametes produced by a mother plant may sometimes become modified to express the Mammoth habit of growth. Although Honing has observed the complete disappearance of a line of Mammoth plants which gave rise to progenies of blossoming plants, this behavior has not been definitely observed in this country except as a response to obscure environmental conditions. It is possible that the behavior of Honing's inconstant Mammoths is of this nature rather than an internal gametic change, permanently affecting the heredity of the Mammoth feature. Until this question is more definitely settled, Honing's inconstant Mammoth can not be disposed of.

Since inconstant, intermediate plants behaving as Mendelian hybrids with respect to Mammoth character, and sister plants of pure type are known to arise suddenly in the same progeny, there is reason to believe that the change responsible for Mammoth behavior may affect one or both gametes, as the case may be. This inconstant behavior of these mutant hybrids is particularly significant since it appears in every way similar to the actual behavior of a controlled cross between a Mammoth and a normal plant. Of course, if it is possible for one or more gametes produced by a normal plant to become so modified as to originate a hybrid-mutant or a pure line mutant, then it is quite as probable that all the gametes in a single blossom, or the gametes produced by all the blossoms of a normal plant, may become so modified. Honing's observations at least would indicate that this does occur.

In those instances where an occasional Mammoth appears in the progeny of a normal plant, it is usually assumed that the change responsible for the Mammoth character was associated in some way directly with the gametes themselves. In those instances where many or even all the plants in the progeny of a normal plant produce Mammoths, the question becomes more involved and difficult of interpretation. It is very difficult to see how all the gametes of a normal plant can become simultaneously modified to produce by their union Mammoth plants, unless we assume that the change takes place at some stage preceding the development of the gametes. Should the change take place in a mother cell of the anther preceding tetrad formation, *i. e.*, by the addition or subtraction of some factor in the chromosome material, it is reasonable to suppose that the four pollen grains resulting from the division of this mother cell may be similarly affected, and bear the Mammoth character. It is possible, however, that the change may take place very much earlier, so that a part or even all the sporogenous cells will be affected. If this condition occurred, it is easy to see how great numbers or even all the pollen grains arising from their division would bear the Mammoth character. Since the development of the megasporangium is in every way parallel to the development of the microsporangium or anther, similar changes would affect one or more egg-cells, depending upon whether the change responsible for Mammoth character took place immediately in the egg-cell itself, in the mother cells, or very much earlier, so that all the sporogenous cells, and hence all the egg-cells arising from them, are affected. Such changes affecting great numbers or all the gametes in a single flower, or even in the entire flower head itself, would produce the phenomenon of a more or less complete acquirement of Mammoth character in the progeny of a normal plant. It may be stated here that East (1917) has offered the same suggestion concerning the origin of variations in cell-divisions preceding the formation of the gametes themselves.

THE PRODUCTION OF NEW MAMMOTH FORMS BY HYBRIDIZATION

Two Mammoth types of tobacco are now grown commercially in the United States, the Maryland Narrowleaf Mammoth in Maryland, and to a lesser extent the Stewart Cuban in the Connecticut Valley. Promising Mammoth types have also originated in Havana Seed tobacco in Connecticut. Beinhart (1918, however, in a brief discussion of the occurrence of Mammoth types in the Connecticut Valley, states that practical methods of seed production and special cultural methods must be worked out before the Stewart Cuban Mammoth and the Havana Seed Mammoth can be successfully grown on a commercial scale. Although these Mammoths originated spontaneously from commercial types, there is every reason to believe that valuable new types can be secured by crossing with the ordinary commercial types of tobacco. Since in crosses with ordinary varieties gigantism is recessive in its inheritance, the problem of producing new giant types by hybridization and recombination has not been difficult. Several Mammoth types have already been secured in crosses with Connecticut Broadleaf, Little Dutch and White Burley. If by this means it is possible to combine the habit of gigantism, which insures greatly increased yields, with the desirable quality characteristics of ordinary varieties, very valuable commercial types can be obtained.

SUMMARY

1. Gigantism has occurred in several different commercial varieties of tobacco, including Maryland types, Cuban, Connecticut Havana and Sumatra. It has also been associated with certain varietal crosses and species crosses.

2. Not only giant or mammoth types which breed true, but intermediate or hybrid types occur spontaneously which subsequently give rise to a greater or less proportion of mammoth forms.

3. In crosses with normal varieties the mammoth character is recessive, and F_1 plants invariably blossom. The F_1 plants average a somewhat higher leaf number than the normal parent which entered into the cross.

4. In the F_2 generation mammoth plants occur in proportions approaching the theoretical ratio of 25 per cent. obtaining in a single Mendelian cross involving two contrasted unit characters.

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THE MENDELIAN BEHAVIOR OF AUREA CHARACTER IN A CROSS BETWEEN TWO VARIETIES OF NICOTIANA RUSTICA

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Introduction

The species of tobacco *Nicotiana rustica* comprises a number of more or less distinct varieties. One of the more characteristic varieties which was received from Russia (S. P. I. 35080) is a light, yellowish-green type with distinctly white stems and midribs. In these respects this type of *N. rustica* resembles the well-known White Burley variety of *N. tabacum.* According to Splendore,[1] who has described it in detail, this white-stemmed variety of *N. rustica* is grown commercially in Russia (Makorka, Bakoun, Kolmak, Tseco, etc.) as a pipe and cigarette tobacco. In this variety of *N. rustica,* the stems of young plants—especially if they have been somewhat etiolated by crowding—are almost snow white. A cross section of the stems of such plants one month old reveals the fact that this whiteness is not merely superficial, but extends entirely through the stems, whereas in green varieties of *N. rustica* the internal structure of the stems is green throughout. The cotyledons are decidedly chlorotic and the leaves have a pale yellowish-green, chlorotic appearance which becomes more marked as the plants approach maturity. As a matter of convenience, the writer has applied the term "aurea" to this peculiar, varietal form of chlorosis.[2]

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[1] Splendore, A., "Due Particolore Forme Di N. Rustica Brasilia Chwitzent e Kapa Magiara," *Boll. Tech. Della Colt. Dei Tabachi del R. Inst. sperimentale, Scafati* (Salerno), XI, No. 2, 1912.

[2] This type of *aurea* appears to be quite distinct from the type of *aurea* described by Lodewijks as having occurred suddenly in plants of *N. taba-*

DOMINANCE OF GREEN PLANT COLOR IN F¹ PLANTS OF CROSSES

In 1914 the writer made reciprocal crosses of this white-stemmed, chlorotic *aurea* type of *N. rustica,* with green-stemmed, green-leaved type, and several hundred F^1 plants were grown in the field at Arlington, Va., during the season of 1915. All the F^1 plants were green in color, whichever type was used as the seed-bearing parent. It was at once evident that the white-stemmed, chlorotic, *aurea* character behaved as a simple recessive to normal greenness of stem and leaf. To determine more fully the Mendelian behavior of this cross an analysis of the F^2 and F^3 generations was made.

SEGREGATION IN F² PLANTS

In the F^2 generation, green- and white-stemmed *aurea* plants appeared. So distinct is the white-stemmed recessive that four or five weeks after germination, the young plants can be readily distinguished from the green-stemmed types. This made the growing and handling of large numbers of plants a comparatively easy matter, since it was only necessary to grow them to the size of small seedlings and obtain counts when they were four or five weeks old. In the following table an analysis of 25,000 F^1 plants is shown.

From this data it is evident that the recessive white-stemmed *aurea* type of *rustica* appeared in numbers approximating very closely the theoretical Mendelian ratio of 25 per cent., since in a population of 25,000 plants, 24.31 per cent. were of the white-stemmed, *aurea* type.

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cum in Java. He found that this type of *aurea* was inconstant in its inheritance, since *aurea* mother plants always gave progenies consisting of green and *aurea* plants. In crosses between *aurea* and green plants the F^1 generation always included *aurea* and green plants. From the inconstant inheritance of this character he concludes that this *aurea* form originated as a mutant with an essentially hybrid constitution. See Lodewijks, J. A., "Erblichkeitsversuche mit Tabak," *Zeitschr. für Induktive Abstammungs. Vererbungslehre,* Vol. 5, 1911, pp. 139–172.

TABLE I

Ratios of Green-stemmed and Recessive White-stemmed aurea Plants in the F^1 Generation of the Cross 35080 (White-stemmed) ♀ × No. 1 from India (Green-stemmed) ♂

Date of Count	Total Number Counted	Number of Green-stemmed	Number of White-stemmed *aurea*	Percent. of White-stemmed *aurea*
June 19, 1918	4,188	3,178	1,010	24.1
May 16, 1918	1,167	887	280	23.9
May 17, 1918	417	308	109	24.9
June 24, 1918	1,955	1,476	479	24.5
June 25, 1918	279	231	48	17.2
July 1, 1918	1,072	818	254	23.6
July 16, 1918	747	594	153	20.4
July 18, 1918	1,246	930	316	25.3
Sept. 3, 1918	2,114	1,597	517	24.4
Oct. 18, 1918	2,253	1,707	546	24.2
Oct. 21, 1918	2,673	2,035	638	23.8
Oct. 24, 1918	4,556	3,400	1,156	25.3
Oct. 26, 1918	2,333	1,760	573	24.5
Totals	25,000	18,921	6.079	24.31

Behavior of F^2 Green Plants and White-stemmed Extracted *aurea* Recessive

Of twenty-eight F^2 green plants selected at random the character of the inheritance in the progenies of those showing segregation was noted as follows:

TABLE II

Ratios of Green-stemmed and White-stemmed aurea Plants Appearing in the Progenies of Heterozygous Green-stemmed Plants in the F^2 Generation

Number of Mother Plant	Total Number of Progeny Counted	Number of Green-stemmed Plants	Number of White-stemmed *aurea* Plants
1	414	300	114
4	401	300	101
5	462	345	117
6	392	300	92
7	887	649	238
10	403	304	99
11	395	300	95
12	386	300	86
14	399	300	99
17	390	300	90
21	410	310	100
23	397	300	97
24	660	503	157
27	995	747	248
28	739	561	178
33	393	300	93
Totals	8,123	6,119	2,004

The green F^2 individuals Nos. 2, 3, 9, 13, 15, 16, 18, 19, 20, 25, 29, 30 were homozygous for greenness and gave pure green progenies. A progeny of several thousand plants was grown from each individual.

Of 8,123 plants descending from heterozygous green individuals analyzed in Table II, 2,004 or 24.6 per cent. were white-stemmed recessives. It is evident that these figures for the extracted recessives also approach very closely the theoretical 25 per cent. Mendelian ratio which obtains for contrasted characters in simple hybrids. This ratio of 24.6 per cent. extracted recessives of the *aurea* type descending from green heterozygous F^2 individuals, is very close to the ratio 24.3 per cent. obtained in a count of 25,000 individuals descending from F^1 plants. Since 12 of the 28 green F^2 plants tested were homozygous for greenness and gave all green progenies, it is evident that these were extracted dominants.

The progenies of 20 extracted white-stemmed *aurea* recessives of the F^2 generation were also studied. Several thousand plants were grown from each of the 20 individuals, and all proved homozygous for the *aurea* character, etc.

Behavior of Back Crosses

First generation plants of the original cross No. 35080 (white-stemmed *aurea*) ♀ × No. 1 from India (green-stemmed *Rustica*) ♂ were now crossed with the parent green-stemmed and white-stemmed *aurea* types.

In the back cross with the recessive white-stemmed *aurea* parent 591 plants were obtained of which 303 were green-stemmed individuals, and 288 were *aurea*. These figures approach the theoretical 1:1 ratio which may be expected in such crosses.

In the back cross with the dominant green-stemmed type, 280 plants were obtained, all of which were green-stemmed.

From these results obtained with the cross between the green-stemmed types of *N. rustica* and the distinctive white-stemmed *aurea* type, it is evident that we are dealing with a clear-cut instance of Mendelian behavior, in which greenness of stem and leaf is contrasted with the character of white stems and a yellowish, chlorotic appearance of the leaves. Since these characteristics are readily distinguished in plants in the seedling stage, only five or six weeks after germination, this cross is especially favorable for the demonstration of simple Mendelian behavior in all its phases. The technique of crossing is simple, and many thousands of seedlings may be grown in a comparatively small area in a short time.

SUMMARY

In crosses between a distinctive white-stemmed *aurea* type and green-stemmed type of *N. rustica* the following Mendelian relations were found:

In F^1 plants the white-stemmed *aurea* type is recessive to the green-stemmed type.

F^2 plants segregate into green-stemmed and white-stemmed *aurea* plants. Approximately 25 per cent. of the plants are *aurea* recessive. Some of the green plants are homozygous for greenness of stems, etc., and some are heterozygous, again segregating into green and white-stemmed *aurea* types with the same ratios obtained in the F^1 generation. The extracted *aurea* recessives of the F^2 generation are homozygous with respect to the character of white stems, etc., peculiar to this type.

In back crosses between a heterozygous F^1 plant and the dominant green-stemmed type, the progeny consists of 100 per cent. green-stemmed plants.

In back crosses with the recessive *aurea* type, the progeny consists of green-stemmed and white-stemmed *aurea* plants in approximately the expected ratio of 1 to 1.

SOME FACTOR RELATIONS IN MAIZE WITH REFERENCE TO LINKAGE

D. F. JONES AND C. A. GALLASTEGUI

CONNECTICUT AGRICULTURAL EXPERIMENT STATION

IN view of the many distinct Mendelizing characters known in maize (*Zea mays* L.) it has been rather surprising that so few cases of linkage have been reported in this plant up to the present time. The number of chromosome pairs, about ten, is not large for plants and about twenty distinct contrasting factors are known of which the inheritance can be easily followed and about as many more which offer some difficulty in following in transmission but which can be used more or less satisfactorily in carrying on experiments on linkage. The writers have made no systematic search for cases of linkage in maize, but having found, almost accidentally, what seems to be a fairly good case of linkage between the tunicate factor which determines the production or inhibition of the glumes covering the seeds and the factor for starchy or sweet endosperm, the results are reported here in the hope that they may be of use to others who may be pursuing investigations along this line.

Collins and Kempton (1911) were the first to record a case of linkage in maize. Their results involved the relation of endosperm texture, as contrasted in our ordinary starchy varieties with the waxy condition found in Chinese varieties, to the color of the aleurone layer. They did not determine which of the several factors concerned with aleurone color was involved in this linkage. More recently Bregger (1918) has given additional proof of this case of linkage. He has determined the amount of crossing-over and has also shown that it is the C aleurone factor (East and Hayes, 1911; Emerson, 1918) which is the one involved. At about the same time Lindstrom (1917) reported the second case of linkage, that of one of the factors of chlorophyll color G, with another aleurone color factor, this time the R factor, which in the presence of a suitable basic factorial combination produces red color in the aleurone cells. More recently Lindstrom (1918) has found another chlorophyll factor L linked with R and G. L is completely linked with R and both show about the same amount of breaks in the linkage with G. This makes the first group of three factors so far reported in maize.

LINKAGE BETWEEN TUNICATE EAR AND STARCHY-SWEET ENDOSPERM FACTORS

The curious type of maize, known generally in this country as pod corn (*Zea mays tunicata* Sturtevant) is considered by Collins (1917) not to be a pure type, but a heterozygous condition somewhat analogous to the blue Andalusian fowl. When selfed seed of the typical podded ears are planted Collins finds that three types of plants are produced: one type like the typical podded parent; one with normal ears without the enclosing glumes; and one anomalous type of a plant which does not produce seed in lateral inflorescences, but in perfect flowers in the tassels. On these last plants lateral inflorescences with much elongated glumes are produced, but are sterile. All these three types have been secured in about the ratio of 1:2:1 as expected on the assumption that a single Mendelizing difference is involved and the heterozygote is distinguishable from both homozygotes.

Our own rather limited experience with this type of maize confirms Collins's conclusions. In 1915 seed of a typical podded ear was planted (there was no record whether it had been selfed or not). All three types which Collins described later were obtained. A number of typical podded plants were self-pollinated and grown the next year in the hope of getting a pure podded strain. At that time no thought was given to the possibility of its being a heterozygous type. The plants with seeds in the tassels were thought to be extreme variations from the usual type. Nine selfed ears were obtained and grown the following year and all gave some plants with podless ears and others with seeds in the tassels as well as plants of the typical pod type. No record was made of the numbers in each class, but it was noted as rather surprising that all of the nine ears gave some normal non-pod plants.

An attempt was made to self-pollinate some of the plants with the peculiar terminal inflorescences which were easily recognized as the type which produced seed, but no seed was obtained where they were enclosed in a bag. Very little good pollen is produced in these tassels and probably all or most of the seeds which are produced on open-pollinated plants result from crossing with foreign pollen. One tassel with a number of such open-pollinated seeds was saved and the seed planted. No normal non-pod ears were obtained. Most of the ears were of the typical pod type or half-tunicate as named by Collins. All of these results bear out the assumption of Collins that the podded maize considered by Sturtevant (1899) as a separate species and stated by him to have been known for 300 years is not a constant type and has little more claim to specific rank than the blue Andalusian fowl.

One of the half-tunicate ears produced from the open-pollinated seed of the perfect flowered segregate was self-pollinated, and when examined this ear was found to have segregated into starchy and sweet seeds, showing that the plant which had furnished the pollen had sweet seeds. Since all the podded maize which had been grown up to that time was starchy and all of the sweet maize was non-podded, the cross involved the tunicate character and starchy endosperm from the female parent, and non-tunicate, sweet endosperm from the male. The starchy and sweet seeds were planted separately. There were 173 of the starchy and forty-three of the sweet seeds. Not a perfect 3:1 ratio, but reasonably close. All of the seeds were planted, but since not all of each type produced a mature plant, it is legitimate to correct the observed results according to the theoretical starchy-sweet ratio. The results obtained and corrected in this way are as follows:

	Starchy Tunicate	Starchy Non-tunicate	Sweet Tunicate	Sweet Non-tunicate
Found.	113	4	7	25
Corrected Starchy-sweet ratio	108.0	3.8	8.2	29.1
Expected. 11:1:1:11 gametic ratio	105.8	6.0	6.0	31.3

The numbers are small, but the distribution obtained is clearly different from a 9:3:3:1 ratio. The agreement with the nearest theoretical results, assuming linkage, is close ($P = .615$). The per cent. of crossing-over, 8.3, indicated by these figures is low. In the other cases of linkage reported, the percentages of crossing-over were much higher, 25.7 per cent. in the waxy endosperm-aleurone color combinations and 20 per cent. in the aleurone color-chlorophyll color combination with the exception of the one case where complete linkage has so far been found.

In making the classification all of the plants which showed the tunicate character, whether of the half-tunicate or full-tunicate type, were classed as tunicate, as contrasted to the normal plants. Segregation was clear between these two classes and there was little possibility of confusion even when the ears were immature. On the other hand, it was not always easy to distinguish full-tunicate from half-tunicate plants, as the tassels of the former class do not always produce seed, and the ears, which are quite characteristic when fully developed, are not so distinct when immature, and many of these plants were late in maturing. Any error of classification here does not affect the linkage results, however. There is one source of error in that the plants suckered profusely; many of these bore ears and tassels and were difficult to distinguish from the main stalk. The plants were grown in hills, and when classifying them it was not always possible to tell which was plant and which was sucker, so that the same plants may have been included in the count more than once.

The figures for the segregation with respect to the tunicate character together with the figures from a similar ear, which instead of segregating starchy and sweet segregated for yellow and white endosperm, are given as follows:

		Normal	Half-tunicate	Full-tunicate
Ear 1	Sweet	25	6	1
	Starchy	4	70	43
Ear 2	White	10	19	14
	Yellow	36	58	29
Found		75	153	87
Expected 1 : 2 : 1 ratio		79	158	79

With regard to this second ear, which was similar to the first except that it was crossed with yellow, starchy, non-tunicate instead of white, sweet maize, it is to be noted that there is no indication of linkage between the factors for tunicate ear and yellow endosperm. The figures obtained compared to the expectancy are given herewith:

	Yellow Tunicate	Yellow Non-tunicate	White Tunicate	White Non-tunicate
Found	87	36	33	10
Corrected Yellow-white ratio	88.1	36.4	31.9	9.7
Expected 9 : 3 : 3 : 1 ratio $P = .739$	93.4	31.1	31.1	10.4

EVIDENCE FOR LINKAGE BETWEEN ALEURONE COLOR FACTORS

Another case of linkage is suggested by the results of East and Hayes (1911) in the inheritance of aleurone color. From crosses of colorless aleurone by purple they obtained marked deviations from the expected ratios which they could not account for. At that time the first cases of gametic coupling had just been published by Bateson and Punnett and the subject of linkage was not well understood nor its true significance realized. These writers considered the possibility of gametic coupling as a disturbing factor, but came to the conclusion that this phenomenon could not be concerned in their aberrant results.

One of the crosses studied involved two aleurone factors, the basic color factor C and the factor P (Emerson's Pr factor), with R present coming from both parents. This cross was expected to give a ratio of 9 purples : 3 red : 4 non-colored, but actually showed a large excess of purples and deficiency of reds. East and Hayes considered the possibility of linkage between the P and R factors, but since R, according to their theory, was homozygous, crossing-over between these two factors would make no visible difference in the F_2 results. On the other hand, since PC entered the cross from one side and pc from the other, the cross-over class pC, if there is linkage, would be red because of the presence of R. Hence any possibility of linkage should be looked for between the P and C factors. Such a situation would account for an excess of purples and a deficiency of reds in the cross under consideration. Another cross involving, in addition to the P and C factors, a color inhibiting factor likewise showed an excess of purples and a deficiency of reds.

Since it is always rather difficult to prove linkage from F_2 distributions alone, in this case it would be even more difficult because only one of the cross-over classes, if such it is, can be distinguished. The data of East and Hayes, as far as numbers go, do not agree with expectation from linkage with any amount of crossing-over, and since other crosses involving the same factors have been reported which seem to show independence, it is doubtful whether or not linkage really exists in respect to these two factors. It is more probable that the deviations from theory are to be looked for in either incomplete analysis of the factor relations or faulty classification of the seeds. Red seeds gradate somewhat into purple and there may be a tendency to include reds among purples. If this were the case, however, wrongly classified purple seeds should sometimes give all red progeny or red and white progeny in the next generation. East and Hayes found no cases of this kind. The possibility of linkage between the P and C factors should be kept in mind until this point can be definitely settled.

Other Factorial Relations

Looking over East and Hayes's data for other cases of linkage or independence of factors there seems to be good evidence that the C aleurone and R aleurone factors are not linked, and also that the factor for sweet endosperm is not linked with either the R or P aleurone factors. In a factorial analysis of the characters of an organism with reference to linkage it is just as important to know the cases where no linkage is shown as those cases where it is shown. Collins and Kempton (1913) give data which indicate independence between sweet and waxy endosperm factors and in another paper (1917) independence between the *tunicata* and *ramosa* factors. East (1910) gives data which indicate that the two factors for yellow endosperm color are not linked with each other and it is quite probable that both of them are independent of the factor for sweet endosperm.

With this evidence we can attempt a beginning at an analysis of the factorial relations in maize. Three independent groups of factors can be tentatively proposed as follows:

Group I	Group II	Group III
Ww Endosperm Cc Aleurone Pp Aleurone (?)	Gg Chlorophyll Ll Chlorophyll Rr Aleurone	Ss Endosperm Tt Tunicate

The fact of no linkage between the Cc aleurone and the Rr aleurone color factors separates groups I and II. No linkage between Ww and Ss endosperm factors separates groups I and III. No linkage between the Ss endosperm and Rr aleurone factors separate groups II and III.

Since the number of known factor differences in maize is already some three or four times the number of chromosomes, more definite knowledge of the behavior of all these factors in relation to each other will be awaited with interest. Especially since maize is one of the best materials from the plant side to which the chromosome hypothesis, as worked out in Drosophila, can look for contradiction or support.

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HOOKE'S MICROGRAPHIA

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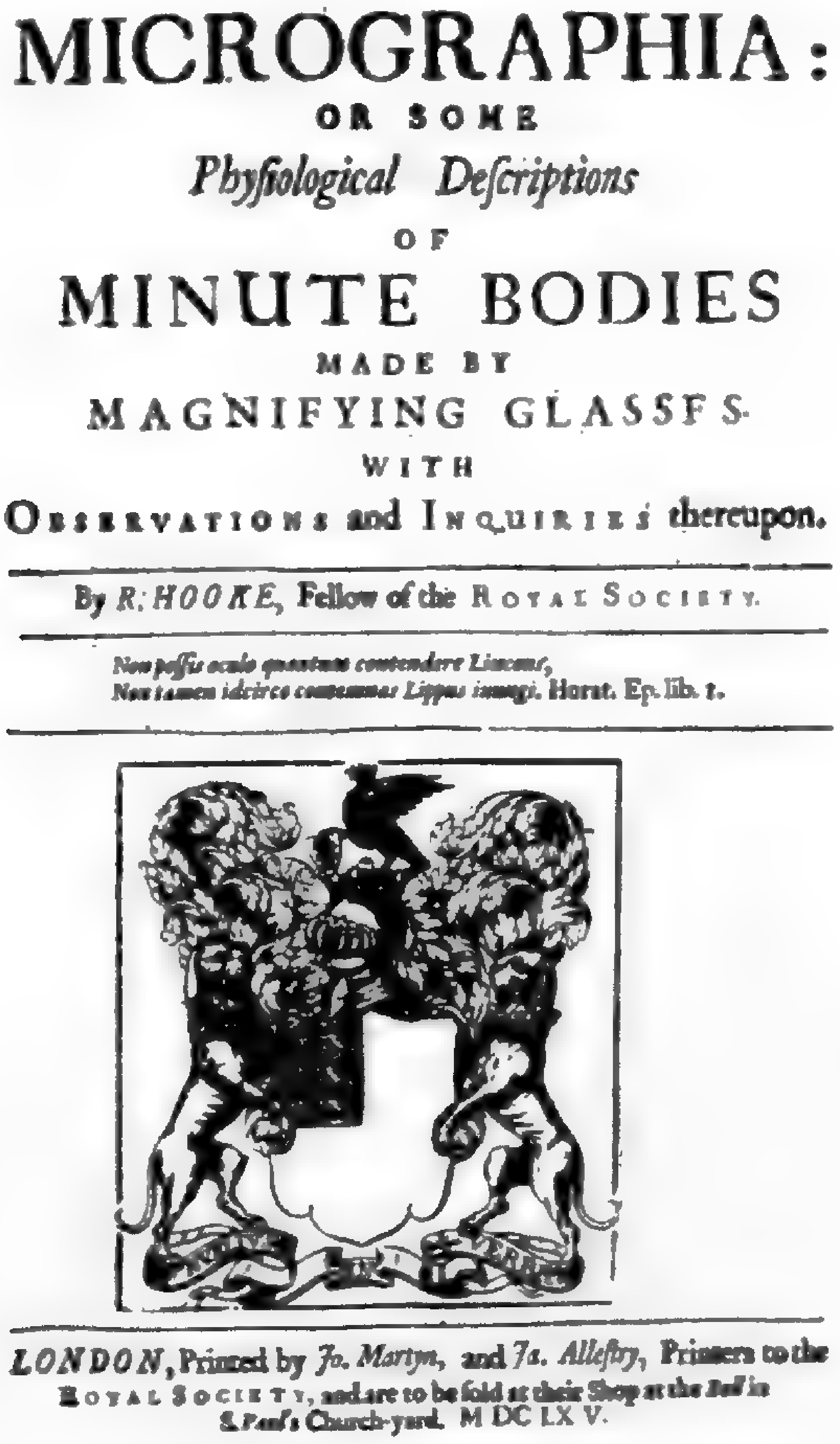
Biological research in general during the latter part of the seventeenth century begins to be permeated with an attention to details and with an intensive critical analysis which is conspicuous by its absence in practically all but the masterpieces of previous times. Nor is the explanation far to seek. The improvement of simple lenses and the invention of the compound microscope provided a method of increasing the apparent size of things which, in addition to revealing a new world of "animalcules" beyond the range of unaided vision, brought to the attention of students finer details of structure of the higher animals and plants. But, as Sachs has emphasized, the use of magnifying glasses contributed an advantage of still another kind—it taught those who employed them to see scientifically and exactly. In equipping the eye with increased powers the attention was concentrated on definite points and observation had to be accompanied by conscious critical reflection in order to make the object, which is observed in part only by the microscope, clear to the mental eye in all the relations of the parts to each other and to the whole. Therefore, in marked contrast with the very slow progress in obtaining a mental mastery over the macroscopic morphological features of plants and animals is the work of the early students with the microscope such as Hooke and Grew in England, Malpighi in Italy, and Swammerdam and Leeuwenhoek in Holland.

The earliest clear appreciation of the importance of studying nature with instruments which increase the powers of the senses in general and the vision in particular, is found in a remarkable book by a remarkable man—the "Micrographia" of Robert Hooke, published by the Royal Society of London in 1665 (cf. Fig. 1). The point of view of the author is well illustrated in the following extracts from the preface:

> *It is the great prerogative of Mankind above other Creatures, that we are not only able to* behold *the works of Nature, or barely to* sustein *our lives by them, but we have also the power of* considering, comparing, altering, assisting, *and* improving *them to various uses. And as this is the peculiar priviledge of humane Nature in general, so it is capable of being so far advanced by the helps of Art, and Experience, as to make some Men excel others in their Observations, and Deductions, almost as much as they do Beasts. By the addition of such* artificial Instruments *and* methods, *there may be, in some manner, a reparation made for the mischiefs, and imperfection, mankind has drawn upon it self, by negligence, and intemperance, and a wilful and superstitious deserting the Prescripts and Rules of Nature, whereby every man, both from a deriv'd corruption, innate and born with him, and from his breeding and converse with men, is very subject to slip into all sorts of errors.*

. . . .



MICROGRAPHIA:
OR SOME
Phyſiological Deſcriptions
OF
MINUTE BODIES
MADE BY
MAGNIFYING GLASSES
WITH
OBSERVATIONS and INQUIRIES thereupon.

By *R. HOOKE*, Fellow of the ROYAL SOCIETY.

Non poſſis oculo quantum contendere Linceus,
Non tamen idcirco contemnas Lippus inungi. Horat. Ep. lib. 1.

LONDON, Printed by *Jo. Martyn*, and *Ja. Alleſtry*, Printers to the
ROYAL SOCIETY, and are to be ſold at their Shop at the *Bell* in
S. *Paul's* Church-yard. M DC LX V.

FIG. 1.

The next care to be taken, in respect of the Senses, is a supplying of their infirmities with Instruments, *and, as it were, the adding of* artificial Organs *to the* natural; *this in one of them has been of late years accomplisht with prodigious benefit to all sorts of useful knowledge, by the invention of Optical Glasses. By the means of* Telescopes, *there is nothing so* far distant *but may be represented to our view; and by the help of* Microscopes, *there is nothing so* small, *as to escape our inquiry; hence there is a new visible World discovered to the understanding. By this means the Heavens are open'd, and a vast number of new Stars, and new Motions, and new Productions appear in them, to which all the antient Astronomers were utterly Strangers. By this the Earth it self, which lyes so neer us, under our feet, shews quite a new thing to us, and in every* little particle *of its matter, we now behold almost as great a variety of Creatures, as we were able before to reckon up in the whole* Universe *it self.*

It seems not improbable, but that by these helps the subtilty of the composition of Bodies, the structure of their parts, the various texture of their matter, the instruments and manner of their inward motions, and all the other possible appearances of things, may come to be more fully discovered; all which the antient Peripateticks *were content to comprehend in two general and (unless further explain'd) useless words of* Matter *and* Form. *From whence there may arise many admirable advantages, towards the increase of the* Operative, *and the* Mechanick *Knowledge, to which this Age seems so much inclined, because we may perhaps be inabled to discern all the secret workings of Nature, almost*

Fig. 2.

> *in the same manner as we do those that are the productions of Art, and are manag'd by Wheels, and Engines, and Springs, that were devised by humane Wit.*
>
> *In this kind I here present to the World my imperfect Indeavours; which though they shall prove no other way considerable, yet, I hope, they may be in some measure useful to the main Design of a* reformation *in Philosophy. . . . .*
>
> . . . .
>
> *As for my part, I have obtained my end, if these my small Labours shall be thought fit to take up some place in the large stock of* natural Observations, *which so many hands are busie in providing. If I have contributed the* meanest foundations *whereon others may raise nobler* Superstructures, *I am abundantly satisfied; and all my ambition is, that I may serve to the great Philosophers of this Age, as the makers and the grinders of my Glasses did to me; that I may prepare and furnish them with some* Materials, *which they may afterwards order and manage with better skill, and to far greater advantage.*
>
> . . . .
>
> *Toward the prosecution of this method in* Physical Inquiries, *I have here and there* gleaned *up an* handful *of Observations, in the collection of most of which I made use of* Microscopes, *and some other* Glasses *and* Instruments *that improve the sense; which way I have herein taken, not that there are not multitudes of useful and pleasant Observables, yet uncollected, obvious enough without helps of Art, but only to promote the use of Mechanical helps for the Senses, both in the surveying the already visible World, and for the discovery of many others hitherto unknown, and to make us, with the great Conqueror, to be affected that we have not yet overcome one World when there are so many others to be discovered, every considerable improvemnt of* Telescopes *or* Microscopes *producing new Worlds and* Terra-Incognita's *to our view.*

The author of this work was a versatile genius who applied his powers to a wide field of endeavor—physics, chemistry, mathematics, mechanics, architecture and philosophy—fields which long since have expanded beyond the grasp of one man, and which, even in his own time and by himself, might more profitably have been coped with singly. It is impossible to adequately survey Hooke's varied career within the limits imposed by this paper, but the following extracts from his biography, appended by Richard Waller to Hooke's "Posthumous Works," show what manner of man he was (cf. Fig. 5).

Dr. *Robert Hooke* was Born at *Freshwater*, a Peninsula on the West side of the Isle of *Wight*, on the eighteenth of *July*, being *Saturday*, 1635, at twelve a Clock at Noon, and Christened the twenty sixth following by his own Father Minister of that Parish.

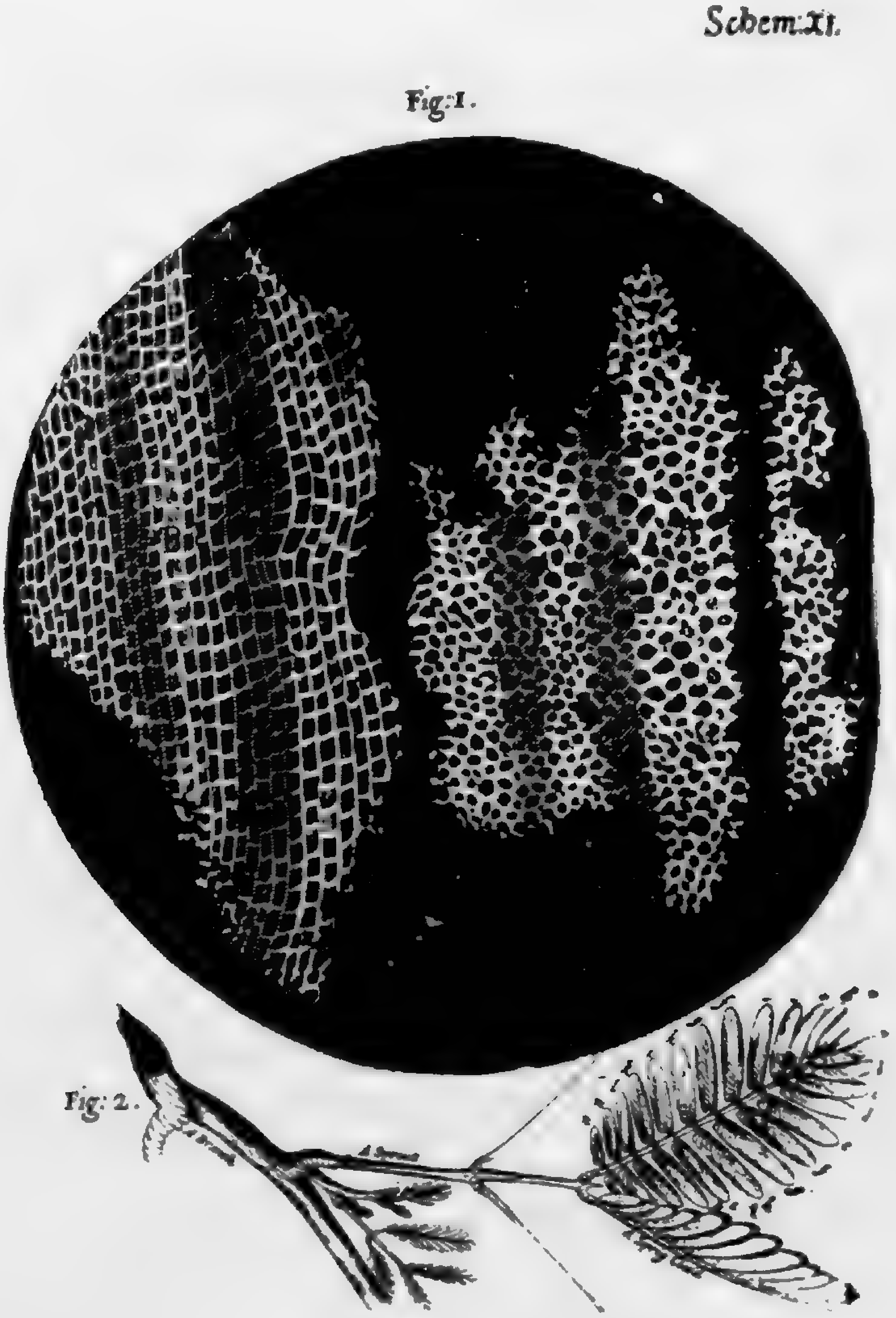
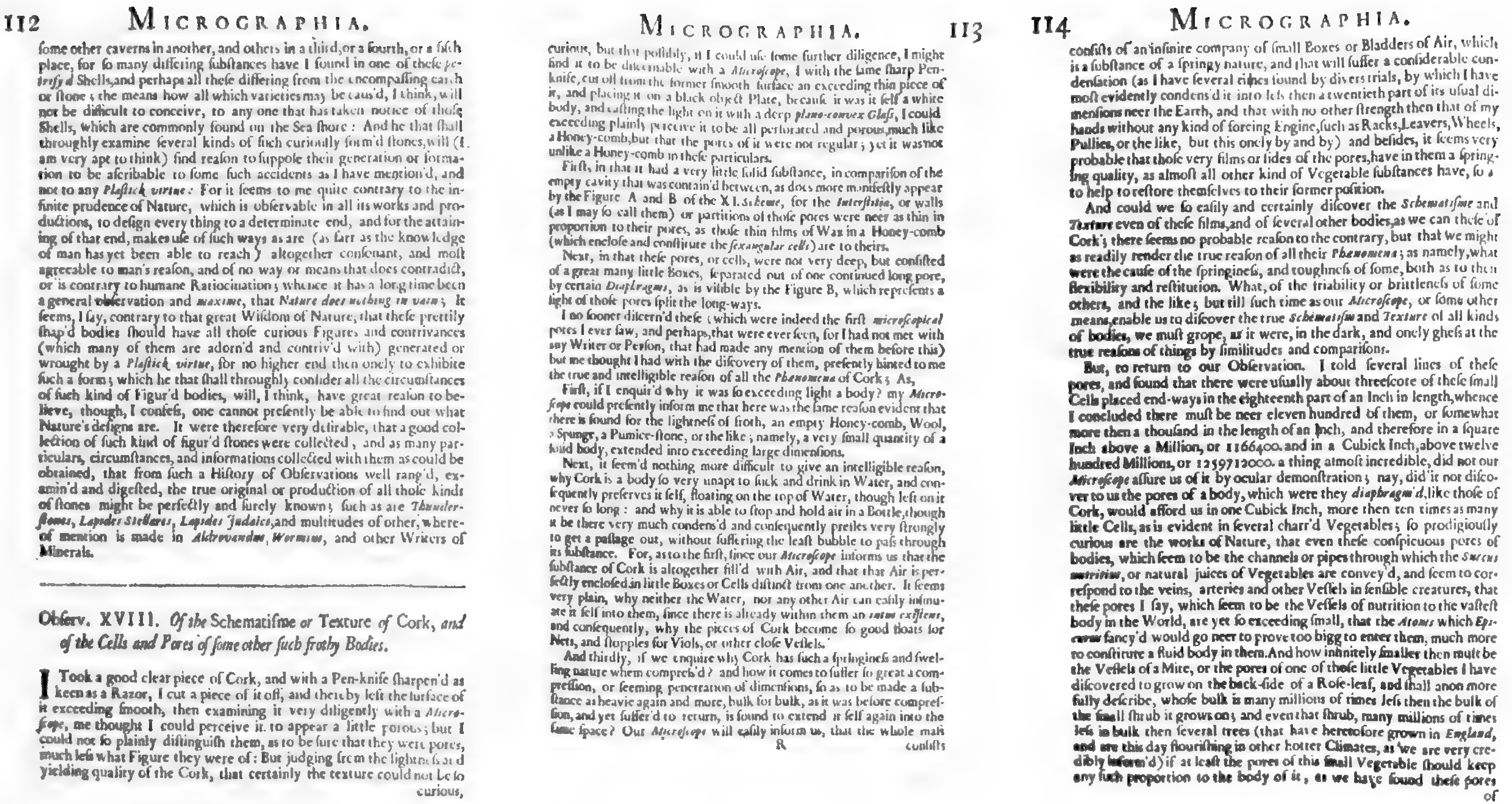


FIG. 3.

. . . .

From *Westminster-School* he went to the University of *Oxford*, in 1653. but as 'tis often the Fate of Persons great in Learning to be small in other Circumstances, his were but mean. I find that he was a Student of *Christ-Church*, tho' not of the Foundation, but was, as I have heard, a Servitor of one Mr. *Goodman*, and took his Degree of ***Master of Arts*** several Years after, about 1662, or 1663.

About the Year 1655, he began to shew himself to the World, and that he had not spent his Juvenile Years in vain; for there being a Concourse at that time of extraordinary Persons at *Oxford*, each of which afterwards were particularly distinguish'd for the great Light



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ſome other caverns in another, and others in a third, or a fourth, or a fifth place, for ſo many differing ſubſtances have I found in one of theſe *petrify'd* Shells, and perhaps all theſe differing from the encompaſſing earth or ſtone; the means how all which varieties may be cauſ'd, I think, will not be difficult to conceive, to any one that has taken notice of thoſe Shells, which are commonly found on the Sea ſhore: And he that ſhall throughly examine ſeveral kinds of ſuch curiouſly form'd ſtones, will (I am very apt to think) find reaſon to ſuppoſe their generation or formation to be aſcribable to ſome ſuch accidents as I have mention'd, and not to any *Plaſtick virtue*: For it ſeems to me quite contrary to the infinite prudence of Nature, which is obſervable in all its works and productions, to deſign every thing to a determinate end, and for the attaining of that end, makes uſe of ſuch ways as are (as farr as the knowledge of man has yet been able to reach) altogether conſonant, and moſt agreeable to man's reaſon, and of no way or means that does contradict, or is contrary to humane Ratiocination; whence it has a long time been a general obſervation and *maxime*, that *Nature does nothing in vain*; It ſeems, I ſay, contrary to that great Wiſdom of Nature, that theſe prettily ſhap'd bodies ſhould have all thoſe curious Figures and contrivances (which many of them are adorn'd and contriv'd with) generated or wrought by a *Plaſtick virtue*, for no higher end then onely to exhibite ſuch a form; which he that ſhall throughly conſider all the circumſtances of ſuch kind of Figur'd bodies, will, I think, have great reaſon to believe, though, I confeſs, one cannot preſently be able to find out what Nature's deſigns are. It were therefore very deſirable, that a good collection of ſuch kind of figur'd ſtones were collected, and as many particulars, circumſtances, and informations collected with them as could be obtained, that from ſuch a Hiſtory of Obſervations well rang'd, examin'd and digeſted, the true original or production of all thoſe kinds of ſtones might be perfectly and ſurely known; ſuch as are *Thunder-ſtones*, *Lapides Stellares*, *Lapides Judaici*, and multitudes of other, whereof mention is made in *Aldrovandus*, *Wormius*, and other Writers of Minerals.

Obſerv. XVIII. *Of the* Schematiſme *or* Texture *of* Cork, *and of the Cells and Pores of ſome other ſuch frothy Bodies.*

I Took a good clear piece of Cork, and with a Pen-knife ſharpen'd as keen as a Razor, I cut a piece of it off, and thereby left the ſurface of it exceeding ſmooth, then examining it very diligently with a *Microſcope*, me thought I could perceive it to appear a little porous; but I could not ſo plainly diſtinguiſh them, as to be ſure that they were pores, much leſs what Figure they were of: But judging from the lightneſs and yielding quality of the Cork, that certainly the texture could not be ſo

curious,

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curious, but that poſſibly, if I could uſe ſome further diligence, I might find it to be diſcernable with a *Microſcope*, I with the ſame ſharp Penknife, cut off from the former ſmooth ſurface an exceeding thin piece of it, and placing it on a black object Plate, becauſe it was it ſelf a white body, and caſting the light on it with a deep *plano-convex Glaſs*, I could exceeding plainly perceive it to be all perforated and porous, much like a Honey-comb, but that the pores of it were not regular; yet it was not unlike a Honey-comb in theſe particulars.

Firſt, in that it had a very little ſolid ſubſtance, in compariſon of the empty cavity that was contain'd between, as does more manifeſtly appear by the Figure A and B of the XI. *Scheme*, for the *Interſtitia*, or walls (as I may ſo call them) or partitions of thoſe pores were neer as thin in proportion to their pores, as thoſe thin films of Wax in a Honey-comb (which encloſe and conſtitute the *ſexangular cells*) are to theirs.

Next, in that theſe pores, or cells, were not very deep, but conſiſted of a great many little Boxes, ſeparated out of one continued long pore, by certain *Diaphragms*, as is viſible by the Figure B, which repreſents a ſight of thoſe pores ſplit the long-ways.

I no ſooner diſcern'd theſe (which were indeed the firſt *microſcopical* pores I ever ſaw, and perhaps, that were ever ſeen, for I had not met with any Writer or Perſon, that had made any mention of them before this) but me thought I had with the diſcovery of them, preſently hinted to me the true and intelligible reaſon of all the *Phænomena* of Cork; As,

Firſt, if I enquir'd why it was ſo exceeding light a body? my *Microſcope* could preſently inform me that here was the ſame reaſon evident that there is found for the lightneſs of froth, an empty Honey-comb, Wool, a Spunge, a Pumice-ſtone, or the like; namely, a very ſmall quantity of a ſolid body, extended into exceeding large dimenſions.

Next, it ſeem'd nothing more difficult to give an intelligible reaſon, why Cork is a body ſo very unapt to ſuck and drink in Water, and conſequently preſerves it ſelf, floating on the top of Water, though left on it never ſo long: and why it is able to ſtop and hold air in a Bottle, though it be there very much condens'd and conſequently preſſes very ſtrongly to get a paſſage out, without ſuffering the leaſt bubble to paſs through its ſubſtance. For, as to the firſt, ſince our *Microſcope* informs us that the ſubſtance of Cork is altogether fill'd with Air, and that that Air is perfectly encloſed in little Boxes or Cells diſtinct from one another. It ſeems very plain, why neither the Water, nor any other Air can eaſily inſinuate it ſelf into them, ſince there is already within them an *intus exiſtens*, and conſequently, why the pieces of Cork become ſo good floats for Nets, and ſtopples for Viols, or other cloſe Veſſels.

And thirdly, if we enquire why Cork has ſuch a ſpringineſs and ſwelling nature when compreſs'd? and how it comes to ſuffer ſo great a compreſſion, or ſeeming penetration of dimenſions, ſo as to be made a ſubſtance as heavie again and more, bulk for bulk, as it was before compreſſion, and yet ſuffer'd to return, is found to extend it ſelf again into the ſame ſpace? Our *Microſcope* will eaſily inform us, that the whole maſs

R conſiſts

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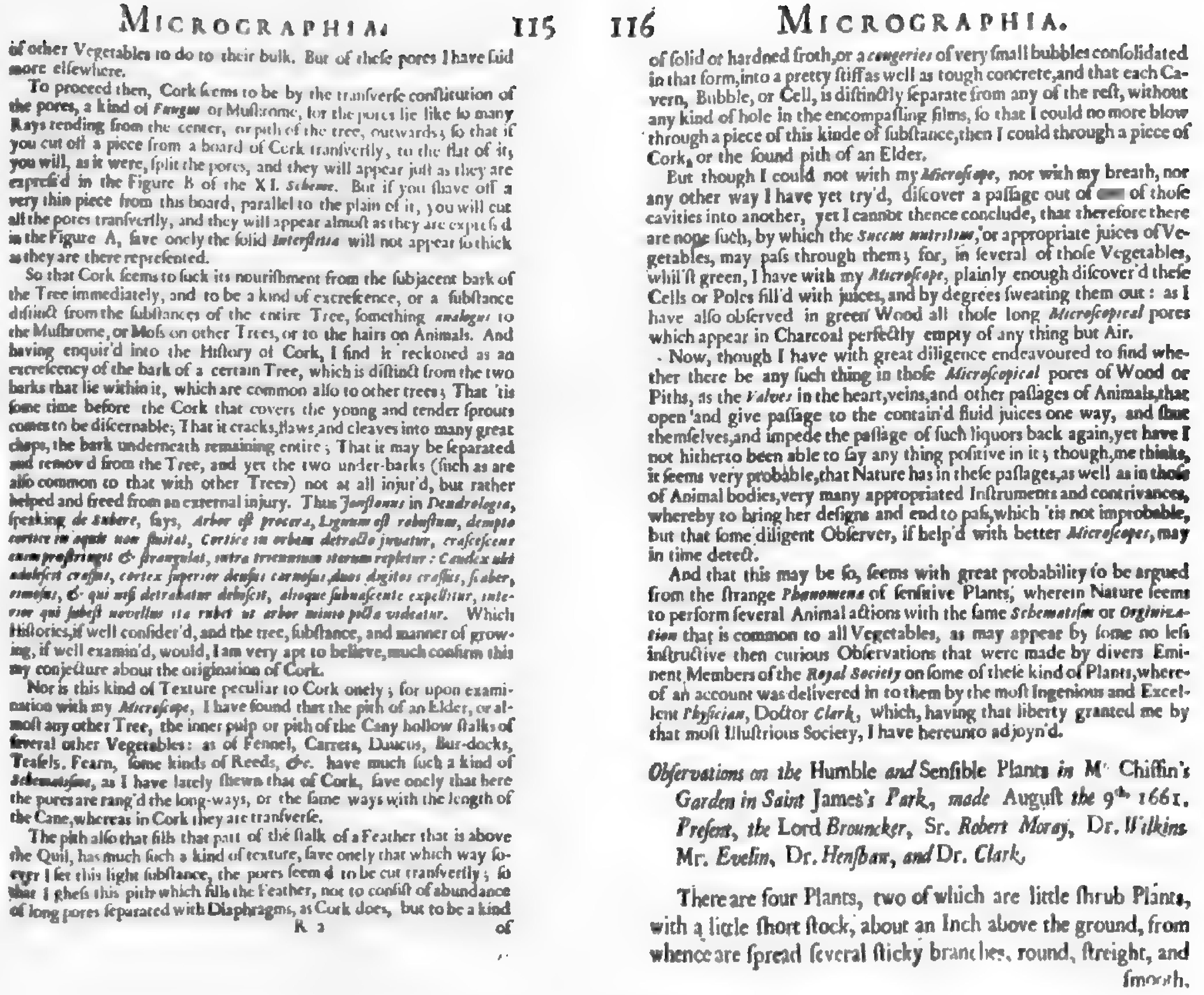
conſiſts of an infinite company of ſmall Boxes or Bladders of Air, which is a ſubſtance of a ſpringy nature, and that will ſuffer a conſiderable condenſation (as I have ſeveral times found by divers trials, by which I have moſt evidently condens'd it into leſs then a twentieth part of its uſual dimenſions neer the Earth, and that with no other ſtrength then that of my hands without any kind of forcing Engine, ſuch as Racks, Leavers, Wheels, Pullies, or the like, but this onely by and by) and beſides, it ſeems very probable that thoſe very films or ſides of the pores, have in them a ſpringing quality, as almoſt all other kind of Vegetable ſubſtances have, ſo as to help to reſtore themſelves to their former poſition.

And could we ſo eaſily and certainly diſcover the *Schematiſme* and *Texture* even of theſe films, and of ſeveral other bodies, as we can theſe of Cork; there ſeems no probable reaſon to the contrary, but that we might as readily render the true reaſon of all their *Phænomena*; as namely, what were the cauſe of the ſpringineſs, and toughneſs of ſome, both as to their flexibility and reſtitution. What, of the friability or brittleneſs of ſome others, and the like; but till ſuch time as our *Microſcope*, or ſome other means, enable us to diſcover the true *Schematiſm* and *Texture* of all kinds of bodies, we muſt grope, as it were, in the dark, and onely gheſs at the true reaſons of things by ſimilitudes and compariſons.

But, to return to our Obſervation. I told ſeveral lines of theſe pores, and found that there were uſually about threeſcore of theſe ſmall Cells placed end-ways in the eighteenth part of an Inch in length, whence I concluded there muſt be neer eleven hundred of them, or ſomewhat more then a thouſand in the length of an Inch, and therefore in a ſquare Inch above a Million, or 1166400. and in a Cubick Inch, above twelve hundred Millions, or 1259712000. a thing almoſt incredible, did not our *Microſcope* aſſure us of it by ocular demonſtration; nay, did it not diſcover to us the pores of a body, which were they *diaphragm'd*, like thoſe of Cork, would afford us in one Cubick Inch, more then ten times as many little Cells, as is evident in ſeveral charr'd Vegetables; ſo prodigiouſly curious are the works of Nature, that even theſe conſpicuous pores of bodies, which ſeem to be the channels or pipes through which the *Succus nutritius*, or natural juices of Vegetables are convey'd, and ſeem to correſpond to the veins, arteries and other Veſſels in ſenſible creatures, that theſe pores I ſay, which ſeem to be the Veſſels of nutrition to the vaſteſt body in the World, are yet ſo exceeding ſmall, that the *Atoms* which *Epicurus* fancy'd would go neer to prove too bigg to enter them, much more to conſtitute a fluid body in them. And how infinitely ſmaller then muſt be the Veſſels of a Mite, or the pores of one of thoſe little Vegetables I have diſcovered to grow on the back-ſide of a Roſe-leaf, and ſhall anon more fully deſcribe, whoſe bulk is many millions of times leſs then the bulk of the ſmall ſhrub it grows on; and even that ſhrub, many millions of times leſs in bulk then ſeveral trees (that have heretofore grown in *England*, and are this day flouriſhing in other hotter Climates, as we are very credibly inform'd) if at leaſt the pores of this ſmall Vegetable ſhould keep any ſuch proportion to the body of it, as we have found theſe pores

of

FIG. 4. (PART 1.)



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of other Vegetables to do to their bulk. But of theſe pores I have ſaid more elſewhere.

To proceed then, Cork ſeems to be by the tranſverſe conſtitution of the pores, a kind of *Fungus* or Muſhrome, for the pores lie like ſo many Rays tending from the center, or pith of the tree, outwards; ſo that if you cut off a piece from a board of Cork tranſverſly, to the flat of it, you will, as it were, ſplit the pores, and they will appear juſt as they are expreſs'd in the Figure B of the XI. *Scheme*. But if you ſhave off a very thin piece from this board, parallel to the plain of it, you will cut all the pores tranſverſly, and they will appear almoſt as they are expreſs'd in the Figure A, ſave onely the ſolid *Interſtitia* will not appear ſo thick as they are there repreſented.

So that Cork ſeems to ſuck its nouriſhment from the ſubjacent bark of the Tree immediately, and to be a kind of excreſcence, or a ſubſtance diſtinct from the ſubſtances of the entire Tree, ſomething *analogus* to the Muſhrome, or Moſs on other Trees, or to the hairs on Animals. And having enquir'd into the Hiſtory of Cork, I find it reckoned as an excreſcency of the bark of a certain Tree, which is diſtinct from the two barks that lie within it, which are common alſo to other trees; That 'tis ſome time before the Cork that covers the young and tender ſprouts comes to be diſcernable; That it cracks, flaws, and cleaves into many great chaps, the bark underneath remaining entire; That it may be ſeparated and remov'd from the Tree, and yet the two under-barks (ſuch as are alſo common to that with other Trees) not at all injur'd, but rather helped and freed from an external injury. Thus *Jonſtonus* in *Dendrologia*, ſpeaking *de Subere*, ſays, *Arbor eſt procera, Lignum eſt robuſtum, dempto cortice in aquis non fluitat, Cortice in orbem detracto juvatur, craſceſcens enim praſtringit & ſtrangulat, intra triennium iterum repletur: Caudex ubi adoleſcit craſſus, cortex ſuperior denſus carnoſus, duos digitos craſſus, ſcaber, rimoſus, & qui niſi detrahatur dehiſcit, alioque ſubnaſcente expellitur, interior qui ſubeſt novellus ita rubet ut arbor minio picta videatur.* Which Hiſtories, if well conſider'd, and the tree, ſubſtance, and manner of growing, if well examin'd, would, I am very apt to believe, much confirm this my conjecture about the origination of Cork.

Nor is this kind of Texture peculiar to Cork onely; for upon examination with my *Microſcope*, I have found that the pith of an Elder, or almoſt any other Tree, the inner pulp or pith of the Cany hollow ſtalks of ſeveral other Vegetables: as of Fennel, Carrets, Daucus, Bur-docks, Teaſels, Fearn, ſome kinds of Reeds, *&c.* have much ſuch a kind of *Schematiſme*, as I have lately ſhewn that of Cork, ſave onely that here the pores are rang'd the long-ways, or the ſame ways with the length of the Cane, whereas in Cork they are tranſverſe.

The pith alſo that fills that part of the ſtalk of a Feather that is above the Quil, has much ſuch a kind of texture, ſave onely that which way ſoever I ſet this light ſubſtance, the pores ſeem'd to be cut tranſverſly; ſo that I gheſs this pith which fills the Feather, not to conſiſt of abundance of long pores ſeparated with Diaphragms, as Cork does, but to be a kind

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of ſolid or hardned froth, or a *congeries* of very ſmall bubbles conſolidated in that form, into a pretty ſtiff as well as tough concrete, and that each Cavern, Bubble, or Cell, is diſtinctly ſeparate from any of the reſt, without any kind of hole in the encompaſſing films, ſo that I could no more blow through a piece of this kinde of ſubſtance, then I could through a piece of Cork, or the ſound pith of an Elder.

But though I could not with my *Microſcope*, nor with my breath, nor any other way I have yet try'd, diſcover a paſſage out of [illegible] of thoſe cavities into another, yet I cannot thence conclude, that therefore there are none ſuch, by which the *Succus nutritius*, or appropriate juices of Vegetables, may paſs through them; for, in ſeveral of thoſe Vegetables, whil'ſt green, I have with my *Microſcope*, plainly enough diſcover'd theſe Cells or Poles fill'd with juices, and by degrees ſweating them out: as I have alſo obſerved in green Wood all thoſe long *Microſcopical* pores which appear in Charcoal perfectly empty of any thing but Air.

Now, though I have with great diligence endeavoured to find whether there be any ſuch thing in thoſe *Microſcopical* pores of Wood or Piths, as the *Valves* in the heart, veins, and other paſſages of Animals, that open and give paſſage to the contain'd fluid juices one way, and ſhut themſelves, and impede the paſſage of ſuch liquors back again, yet have I not hitherto been able to ſay any thing poſitive in it; though, me thinks, it ſeems very probable, that Nature has in theſe paſſages, as well as in thoſe of Animal bodies, very many appropriated Inſtruments and contrivances, whereby to bring her deſigns and end to paſs, which 'tis not improbable, but that ſome diligent Obſerver, if help'd with better *Microſcopes*, may in time detect.

And that this may be ſo, ſeems with great probability to be argued from the ſtrange *Phænomena* of ſenſitive Plants, wherein Nature ſeems to perform ſeveral Animal actions with the ſame *Schematiſm* or *Orginization* that is common to all Vegetables, as may appear by ſome no leſs inſtructive then curious Obſervations that were made by divers Eminent Members of the *Royal Society* on ſome of theſe kind of Plants, whereof an account was delivered in to them by the moſt Ingenious and Excellent *Phyſician*, Doctor *Clark*, which, having that liberty granted me by that moſt Illuſtrious Society, I have hereunto adjoyn'd.

Obſervations on the Humble *and* Senſible Plants *in* Mr Chiffin's *Garden in Saint* James's *Park, made* Auguſt *the* 9th 1661. *Preſent, the* Lord *Brouncker*, Sr. *Robert Moray*, Dr. *Wilkins* Mr. *Evelin*, Dr. *Henſhaw*, *and* Dr. *Clark*.

There are four Plants, two of which are little ſhrub Plants, with a little ſhort ſtock, about an Inch above the ground, from whence are ſpread ſeveral ſticky branches, round, ſtreight, and

ſmooth.

FIG. 4. (PART 2.)

they gave the Learned World by their justly admired Labours; he was soon taken notice of, and for his Facility in Mechanick Inventions much priz'd by them.

. . . .

"The same Year I contriv'd and made many trials about the Art of flying in the Air, and moving very swift on the Land and Water, of which I shew'd several Designs to Dr. *Wilkins* then *Warden* of *Wadham College,* and at the same time made a Module, which, by the help of Springs and Wings, rais'd and sustain'd itself in the Air; but finding by my own trials, and afterwards by Calculation, that the Muscles of a Mans Body were not sufficient to do anything considerable of that kind, I apply'd my Mind to contrive a way to make artificial Muscles; divers designs whereof I shew'd also at the same time to Dr. *Wilkins,* but was in many of my Trials frustrated of my expectations."[1]

What is mentioned here of his attempts about flying, is confirm'd by several Draughts and Schemes upon Paper, of the Methods that might be attempted for that purpose, and of some contrivances for fastening succedaneous Wings, not unlike those of Bats, to the Arms and Legs of a Man, as likewise of a Contrivance to raise him up by means of Horizontal Vanes plac'd a little aslope to the Wind, which being blown round, turn'd an endless Screw in the Center, which help'd to move the Wings, to be manag'd by the Person by this means rais'd aloft. . . .

. . . .

Soon after the beginning of the ROYAL SOCIETY, *viz.* about *April* 1661. a Debate arose in the Society, occasion'd by a small Tract Printed in 1660. about the cause of the rising of Water in slender Glass Pipes, higher than in larger, and that in a certain proportion to their Bores; this Discourse was wrote and Publish'd by *Hooke;* the Explication of which difficult *Phænomenon* made him the more regarded. The sum of his Reasonings upon this Subject he Publish'd afterward, *Micrography Observ.* the 6th. in which there are several very curious and then new Remarks and Hints; as to the Nature of Fluidity and Gravity, which last is farther prosecuted in his Treatise of Springs, with other excellent Subjects, to which the Inquisitive are referr'd for a more ample satisfaction.

This, together with his former Performances, made him much respected by the *R. Society,* and on the fifth of *November* 1662. "Sir *Robert Moray* propos'd a Person that was willing to be entertain'd as a *Curator* by the *Society,* offering to furnish them every day when they met, with three or four considerable Experiments; which Proposition was unanimously receiv'd, Mr. *Hooke* being nam'd to be the Person; and accordingly the next Day of their meeting on the twelfth of *November* he was unanimously accepted and taken as *Curator,* with the Thanks of the *Society* order'd to Mr. *Boyle* for dispensing with him for their

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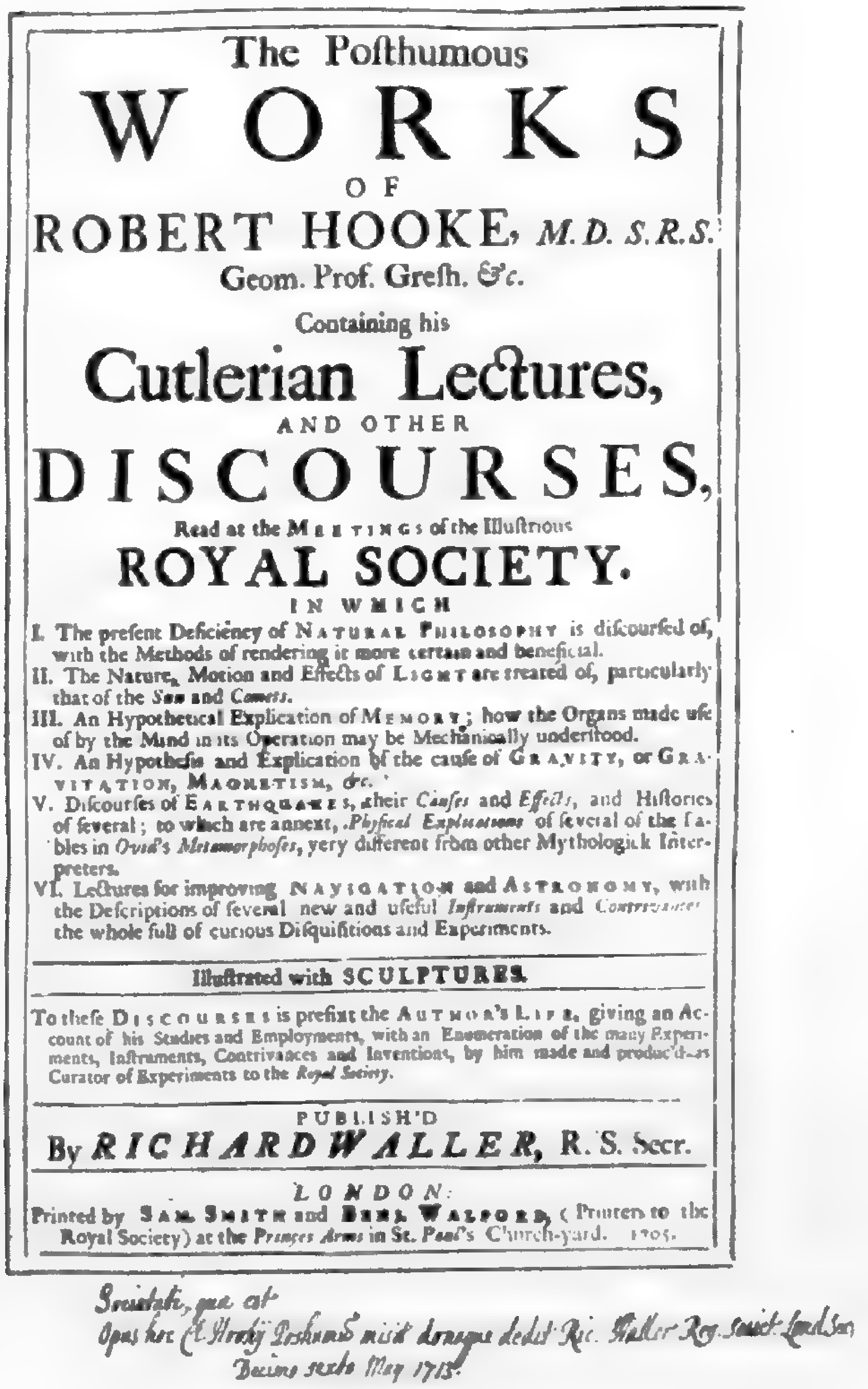
[1] From Hooke's diary.

use, and order'd that Mr. *Hooke* should come and sit among them, and both bring in every Day three or four of his own Experiments, and take care of such others as should be recommended to him by the *Society*."



The Poſthumous
WORKS
OF
ROBERT HOOKE, *M.D. S.R.S.*
Geom. Prof. Greſh. *&c.*
Containing his
Cutlerian Lectures,
AND OTHER
DISCOURSES,
Read at the MEETINGS of the Illuſtrious
ROYAL SOCIETY.
IN WHICH

I. The preſent Deficiency of NATURAL PHILOSOPHY is diſcourſed of, with the Methods of rendering it more certain and beneficial.
II. The Nature, Motion and Effects of LIGHT are treated of, particularly that of the *Sun* and *Comets*.
III. An Hypothetical Explication of MEMORY; how the Organs made uſe of by the Mind in its Operation may be Mechanically underſtood.
IV. An Hypotheſis and Explication of the cauſe of GRAVITY, or GRAVITATION, MAGNETISM, *&c.*
V. Diſcourſes of EARTHQUAKES, their *Cauſes* and *Effects*, and Hiſtories of ſeveral; to which are annext, *Phyſical Explications* of ſeveral of the Fables in *Ovid's Metamorphoſes*, very different from other Mythologick Interpreters.
VI. Lectures for improving NAVIGATION and ASTRONOMY, with the Deſcriptions of ſeveral new and uſeful *Inſtruments* and *Contrivances*; the whole full of curious Diſquiſitions and Experiments.

Illuſtrated with SCULPTURES.

To theſe DISCOURSES is prefixt the AUTHOR'S LIFE, giving an Account of his Studies and Employments, with an Enumeration of the many Experiments, Inſtruments, Contrivances and Inventions, by him made and produc'd as Curator of Experiments to the *Royal Society*.

PUBLISH'D
By *RICHARD WALLER*, R.S. Secr.

LONDON:
Printed by SAM. SMITH and BENJ. WALFORD, (Printers to the Royal Society) at the *Princes Arms* in St. *Paul's* Church-yard. 1705.

Societati, qua est
Opus hoc R. Hookij Posthumum misit donoque dedit Ric. Waller Reg. Societ. Lond. Secr.
Decimo sexto May 1715.

FIG. 5.

From this time the *Societies* Journals gave sufficient Testimonials of his Performances, all which would be too many to particularize here, therefore I shall only touch upon some of the chief. . . .

. . . .

At several Meetings of the *Society* in 1663, and 4. he produc'd his Microscopical Observations, and read the Explications and Discourses made upon them, which were after publish'd in his *Micrographia,* at the beginning of the year 1665.

. . . .

"Sir *John Cutler* having founded a Lecture, and settl'd an Annual Stipend upon *Robert Hooke,* M.A. of fifty Pounds during Life (entrusting the President, Council and Fellows of the said *Society* to direct and appoint the said Mr. *Hooke* as to the Subject and Number of his Lectures) the *Society* order'd several of their Members to wait upon Sir *John Cutler,* with their Thanks for his particular Favour to a worthy Member, and for that Respect and Confidence he hath hereby exprest towards their whole Body, etc."[2]

. . . .

From this time he brought in almost at every Meeting Experiments, Observations, Schemes of new Instruments and Inventions, or something considerable to the advancement of Knowledge, and very frequently read his *Cutlerian* Lectures, of many whereof he publish'd, the most material parts in his Tracts Printed at different times, in Quarto, call'd *Lectures and Collections,* &c. comprizing compendiously in one continu'd Discourse, the chief Matters and Subjects handled in several Lectures.

Thus the generous Ardor with which the ROYAL SOCIETY was inspir'd continued 'till the Year 1665, when, by reason of the great Mortaity then reigning, they were oblig'd to desist and break up their Weekly Meetings till the fourteenth of *March* 166$\frac{5}{6}$. . . .

. . . .

The dreadful Conflagration of a great part of the City of *London* happening in the beginning of *September* 1666. brought another great hindrance to the *Societies* Proceedings; so that they were oblig'd to remove their usual place of Meeting from *Gresham College* to *Arundel* House in the *Strand,* where, by the favour of the then Duke of *Norfolk,* they prosecuted their former Inquiries, their first Meeting at *Arundel* House being on the ninth of *Jan.* 166 .

On the nineteenth of *Sep.* 1666. he produc'd a Module he had design'd for the Rebuilding of the City, with which the *Society* were very well pleas'd, and Sir *John Laurence* the then Late *Lord Major,* address'd himself to the *Society,* expressing the present *Lord Majors and Aldermens* liking thereof, as also their desire that it might be shewn to his *Majesty,* they preferring it far before the Model drawn up by the City Surveyor.

What this Model was, I cannot so well determine, but I have heard that it was design'd in it to have all the chief Streets as from *Leaden-Hall* corner to *Newgate,* and the like, to lie in an exact strait Line, and all the other cross Streets turning out of them at right Angles, all the Churches, publick Buildings, Market-places, and the like, in proper and convenient places, which, no doubt, would have added much to the Beauty and Symmetry of the whole. How this came not to be accepted of I know not, but it is probable this might contribute not a little to his being taken notice off by the Magistrates of the City, and soon after made Surveyor.

The Rebuilding of the City, according to the Act of Parliament, requiring an able Person to set out the Ground to the several Proprietors,

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[2] From the Journal of the Secretary of the Royal Society, November 9, 1664.

Mr. *Hooke* was pitch'd upon, and appointed *City-Surveyor* for that difficult Work, which being very great, took up a large proportion of his Time, to the no small hindrance of his Philosophical Disquisitions. In this Employment he got the most part of that Estate he died possessed of, as was evident by a large Iron Chest of Money found after his Death, which had been lock'd down with the Key in it, with a date of the Time, by which it appear'd to have been so shut up for above thirty Years: In this was contain'd the greatest part of what he left behind him, which was to the value of many thousands in Gold and Silver. That he might by this place justly acquire considerable Estate, I think cannot be deny'd. . . .

. . . .

Mr. *Oldenburgh,* the then Secretary, dying in the time of the Societies Recess, 1677. Mr. *Hooke* was desir'd to take his place, and take the Minutes of what considerable Matters past, which he did on the twenty fifth of *October* 1677. and the same day produc'd his Waterpoise and shew'd the nicety thereof.

From that time he officiated in that Place, as well as his Curatorship, shewing several Experiments and Instruments in order to explain the Gravitation and Alterations in the Air by Vapours, etc. Contriving an Air-poise to shew the different specifick Gravity of the Air by a large thin ball of Glass counter-poised.

. . . .

From this time he made Microscopical Observations on *Animalcules* in Peper-water, and other Seeds steeped in Water, confirming Monsieur *Leuenhook's* Assertions, and propos'd some Improvements of Microscopes.

. . . .

Apr. 25. 1678. he shew'd an Experiment farther to explain the action of a Muscle, " which was by a Chain of small Bladders fastened together, so as by blowing into one Pipe, the whole might be successively fill'd, and by that means contracted, supposing the Fibres of the Muscles which seem'd like a Necklace of Pearl in the Microscope, might be fill'd with a very agill Matter, which he thought most likely to be Air, which being included in so thin Skins, was easily wrought upon by Heat, Cold, or the acting Properties of the Liquors that pass between them, and so perform the lengthening and contracting of the Muscles.

Aug. 1678. he read several Discourses, and shew'd Experiments in order to confirm his Theory of Springs and springy Bodies. . . .

. . . .

Thus I have mention'd some of his Performances. . . . It must be confessed that the latter part of his Life was nothing near so fruitful of Inventions as the former; tho' it is certain he had a design to repeat the most part of his Experiments, and finish the Accounts, Observations and Deductions from them, and had an Order for the Societies bearing the Charge thereof, in *June* 1696. when he propos'd likewise to perfect the Description of all the Instruments he had at any time contriv'd; but by reason of his increasing Weakness and a general Decay, he was absolutely unable to perform it, had he desir'd it never so much.

. . . .

Thus he liv'd a dying Life for a considerable time, being more than a Year very infirm, and such as might be call'd Bed-rid for the greatest part, tho' indeed he seldom all the time went to Bed. . . . being emaciated to the utmost, his Strength wholly worn out, he dy'd on the third of *March* 170$\frac{2}{3}$. being 67 Years, 7 Months, and 13 Days Old.

His Corps was decently and handsomely interr'd in the Church of St. *Hellen* in *London*, all the Members of the ROYAL SOCIETY then in Town attending his Body to the Grave, paying the Respect due to his extraordinary Merit.

As to his Person he was but despicable, being very crooked, tho' I have heard from himself, and others, that he was strait till about 16 Years of Age when he first grew awry, by frequent practicing with a Turn-Lath, and the like incurvating Exercises, being but of a thin weak habit of Body, which increas'd as he grew older, so as to be very remarkable at last: This made him but low of Stature. . . . He went stooping and very fast (till his weakness a few Years before his Death hindred him) having but a light Body to carry, and a great deal of Spirits and Activity, especially in his Youth.

He was of an active, restless, indefatigable Genius even almost to the last, and always slept little to his Death, seldom going to Sleep till two three, or four a Clock in the Morning, and seldomer to Bed, often continuing his Studies all Night, and taking a short Nap in the Day. His Temper was Melancholy, Mistrustful and Jealous, which more increas'd upon him with his Years. He was in the beginning of his being made known to the Learned, very communicative of his Philosophical Discoveries and Inventions, till some Accidents made him to a Crime close and reserv'd. He laid the cause upon some Persons, challenging his Discoveries for their own, taking occasion from his Hints to perfect what he had not; which made him say he would suggest nothing till he had time to perfect it himself, which has been the Reason that many things are lost, which he affirm'd he knew. He had a piercing Judgment into the Dispositions of others, and would sometimes give shrewd Guesses and smart Characters.

. . . .

It must be confess'd that very many of his Inventions were never brought to the perfection they were capable of, nor put in practice till some other Person either Foreigner or of our own Nation cultivated the Invention, which, when Hooke found, it put him upon the finishing that which otherwise possibly might have lain 'till this time in its first

> Defects: Whether this mistake arose from the multiplicity of his Business which did not allow him a sufficient time, or from the fertility of his Invention which hurry'd him on, in the quest of new Entertainments, neglecting the former Discoveries when he was once satisfied of the feazableness and certainty of them, tho' there wanted some small matter to render their use more practicable and general, I know not. . . .

Whatever the answer may be, Hooke's first and best known work, the Micrographia, at once epitomizes the versatility of his genius as well as his apparent inability to see one problem through to a finish. To quote from a review of the work in the *Philosophical Transactions,* No. 2, Monday, April 3, 1665:

> The Ingenious and knowing Author of this *Treatise,* Mr. *Robert Hook,* considering with himself, of what importance a faithful *History of Nature* is to the establishing of a solid Systeme of *Natural Philosophy,* and what advantage *Experimental* and *Mechanical* knowledge hath over the Philosophy of *discourse* and *disputation,* and making it, upon that account, his constant business to bring into that vast Treasury what portion he can, hath lately published a Specimen of his abilities in this kind of study, which certainly is very welcome to the Learned and Inquisitive world, both for the *New discoveries* in *Nature,* and the *New Inventions* of *Art.*
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> . . . .
>
> To this end, he hath made a very curious *Survey* of all kinds of bodies, beginning with the *Point of a Needle,* and proceeding to the *Microscopical* view of the *Edges of Rasors, Fine Lawn, Tabby, Watered Silks, Glass-canes, Glass-drops, Fiery Sparks, Fantastical Colours, Metaline Colours, the Figures of Sand, Gravel in Urine, Diamonds in Flints, Frozen Figures, the Kettering Stone, Charcoal, Wood and other Bodies petrified, the Pores of Cork, and of other substances, Vegetables growing on blighted Leaves, Blew mould and Mushroms, Sponges, and other Fibrous Bodies, Sea-weed, the Surfaces of some Leaves, the stinging points of a Nettle, Cowage, the Beard of a wild Oate, the seed of the Corn-violet, as also of Tyme, Poppy and Purslane.* He continues to describe *Hair, the scales of a Soal, the sting of a Bee, Feathers* in general, and in particular those of *Peacocks; the feet of Flies; & other Insects; the Wings and Head of a Fly; the Teeth of a Snail; the Eggs of Silk-worms; the Blue Fly; a water Insect; the Tufted Gnat; a White Moth; the Shepherds-spider; the Hunting Spider, the Ant; the wandring Mite; the Crab-like insect, the Book-worm, the Flea, the Louse, Mites, Vine-mites.* He concludeth with taking occasion to discourse of two or three very considerable subjects, viz. *The inflexion of the Rays of Lights in the Air; the Fixt starrs; the Moon.*

In representing these particulars to the Readers view, the Author hath not only given proof of his singular skil in delineating all sorts of Bodies (he having drawn all the *Schemes* of these 60 *Microscopical* objects with his own hand) & of his extraordinary care of having them so curiously engraven by the Masters of that Art; but he hath also suggested in the several reflexions, made upon these Objects, such conjecturs, as are likely to excite and quicken the Philosophicall heads to very noble contemplations. Here are found inquiries concerning the *Propagation of Light* through differing mediums; concerning *Gravity;* concerning the *Roundness* of Fruits, stones, and divers artificial bodies; concerning *Springiness* and *Tenacity;* concerning the *Original* of *Fountains;* concerning the *dissolution of Bodies into Liquors;* concerning *Filtration,* and the ascent of Juices in Vegetables, and the use of their *Pores.* Here an attempt is made of solving the strange *Phænomena of Glass-drops;* experiments are alleged to prove the *Expansion* of *Glass* by heat, and the *Contraction* of *heated-Glass* upon cooling; *Des Cartes* his *Hypothesis of colours* is examined: the *cause of Colours,* most likely to the Author, is explained: Reasons are produced, that *Reflection* is not necessary to produce *colours,* nor a *double refraction:* some considerable *Hypotheses* are *offered,* for the explication of Light by Motion; for the producing of all colors by Refraction; for reducing all sorts of colors to two only, *Yellow* and *Blew;* for making the *Air,* a dissolvent of all *Combustible Bodies:* and for the explicating of all the regular figures of *Salt,* where he alleges many notable instances of the *Mathematicks* of *Nature,* as having even in those things which we account vile, rude and coorse, shewed abundance of curiosity and excellent *Geometry* and *Mechanism.* And here he opens a large field for inquiries, and proposeth Models for prosecuting them. . . .

He goes on to offer his thoughts about the Pores of bodies, and a *kind* of *Valves* in wood; about spontaneous generation arising from the Putrefaction of bodies; about the nature of the Vegetation of mold, mushromes, moss, spunges; to the last of which he scarce finds any Body like it in texture. He adds, from the naturall contrivance, that is found in the leaf of a Nettle, how the stinging pain is created, and thence takes occasion to discourse of the poysoning of Darts. He subjoyns a curious description of the shape, *Mechanism* and use of the *sting* of a *Bee;* and shews the admirable Providence of Nature in the contrivance and fabrick of *Feathers* for Flying. He delivers those particulars about the Figure, parts and use of the head, feet, and wings of a Fly, that are not common. He observes the various wayes of the generations of Insects, and discourses handsomely of the means, by which they seem to act so prudently. He taketh notice of the *Mechanical* reason of the *Spider's* Fabrick, and maketh pretty Observations on the hunting Spider, and other Spiders and their Webs. And what he notes of a Flea, Louse, Mites and Vinegar-worms, cannot but exceedingly please the curious Reader.

Having dispatched these Matters, the Author offers his Thoughts for the explicating of many *Phænomena* of the Air, from the *Inflexion,* or from a *Multiplicate Refraction* of the rays of Light within the Body of the *Atmosphere,* and not from a *Refraction* caused by any terminating *superficies* of the Air above, nor from any such exactly defin'd *superficies* within the body of the *Atmosphere.* . . .

He concludeth with two *Celestial Observations;* whereof the *one* imports, what multitudes of Stars are discoverable by the Telescope, and the variety of their magnitudes . . . the other affords a description of a *Vale* in the *Moon,* compared with that of *Hevelius* and *Ricciolo;* where the Reader will find several curious and pleasant Annotations . . . about the variations in the *Moon,* and its *gravitating* principle, together with the use, that may be made of this Instance of a gravity in the *Moon.*

As to the *Inventions of Art,* described in this Book, the curious Reader will there find these following:

1. A *Baroscope,* or an Instrument to shew all the Minute Variations in the *Pressure of the Air;* by which he affirms, that he finds, that before and during the time of rainy weather, the Pressure of the Air is less. . . .
2. A *Hygroscope,* or an Instrument, whereby the *Watery steams,* volatile in the Air, are discerned, which the Nose it self is not able to find. Which is by him full described in the Observations touching the *Beard of a wild Oate,* by the means whereof this Instrument is contrived.
3. An Instrument for *graduating Thermometers,* to make them *Standards* of *Heat* and *Cold.*
4. A *New Engin* for *Grinding Optik Glasses,* by means of which he hopes, that any Spherical Glasses, of what length soever, may be speedily made. . . .
5. A *New Instrument,* by which the *Refraction* of all kinds of Liquors may be exactly measured, thereby to give the Curious an opportunity of making Trials of that kind, to establish the *Laws of Refraction.* . . .

Lastly, this Author despairs not that there may be found many Mechanical Inventions, to improve our Senses of *Hearing, Smelling, Tasting, Touching,* as well as we have improved that of *Seeing* by *Optick Glasses.*

Thus the "Micrographia" is obviously something more than "Some Physiological Descriptions of Minute Bodies made by Magnifying Glasses"—it is a demonstration of the advantages to be gained by the use of artificial devices of precision in studying nature. The book is replete with singular anticipations of later discoveries and inventions by other workers and "it will hardly be deny'd that there are more excellent Philosophical Discoveries and Hints, than in most extant of its bulk." It contains the first study of the "fantastical colours" of thin plates with a partial explanation by interference; a theory of light as a "very short vibrating motion" transverse to straight lines of propagation through a "homogenous medium" (p. 56). Heat is stated to be "a property of a body arising from the motion or agitation of its parts" (p. 37); Fluidity is "but an effect of a very strong and quick shaking motion, whereby the parts are, as it were, loosened from each other, and consequently leave an interjacent space or vacuity" (p. 41); while ideas in regard to combustion are clearly outlined (p. 103) which foreshadow those reached by Mayow.

But the biologist's interest in the "Micrographia" is chiefly in Hooke's application of his improved compound microscope (Fig. 2) to the study of animals and plants. At this time Malpighi, Grew, Leeuwenhoek and Swammerdam were engaged in studies, with simple lenses or compound microscopes, on the secrets of the finer structure of organisms which were to give them higher rank in biological history than Hooke's desultory work in this field. Hooke, as has been said, was interested primarily in demonstrating the usefulness of his microscope and his belief that in inventions for the "improvement of the senses" lay the key to a more profound understanding of nature. This he accomplished and therefore, entirely aside from the other remarkable qualities of the "Micrographia," the book holds a unique place in the history of biology. It paved the way, as it were, for the more special, profound and methodical studies of the contemporary founders of the morphology of organisms by creating a considerable interest in microscopy, and in addition proved to be for over a century the standard source from which writers on the microscope gleaned much information and many figures.[3]

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[3] E. g., L. Joblot, 2d Ed., 1754; H. Baker, 1742; M. F. Ledermüller, 1760–1763; etc. In 1745 Baker reprinted and explained the plates of the Micrographia.

Among the large variety of observations made by Hooke, which are cited in Oldenburg's review just quoted in extenso, one in particular claims the attention of the biologist. This is "Observation XVIII. Of the Schematisme or Texture of Cork, and of the Cells and Pores of some other such frothy Bodies." Here are clearly described for the first time the "little boxes or cells" of organic structure, and his use of the word "cell" is responsible for its application to the protoplasmic units of modern biology. This observation, together with the plate, is presented in facsimile in Figs. 3 and 4. In Hooke's treatise on " The method of Improving Natural Philosophy," included in the volume of his posthumous works (p. 28), this observation on cells is selected by Hooke to illustrate his method of scientific inquiry.

Again, "Observation XXV. Of the stinging points and juice of Nettles, and some other Venomous Plants" is accompanied by a figure of the lower side of a nettle leaf in which the outlines of the epidermal cells are well delineated and, as Miall remarks, "there is something very like a nucleus in one of them, but this may be accidental." However, Hooke did not recognize any relationship between the structures he observed in the nettle and in the cork.

As an appendix to his observations on cork, the author relates some experiments on Mimosa in which he attributes the "motion of this Plant upon touching . . . to a constant *intercourse* betwixt every part of this Plant and its root, either by a *circulation* of its liquor, or a constant pressing of the subtiler parts of it to every extremity of the Plant"—a partial anticipation of the modern idea of turgescence (cf. Figs. 3 and 4). The "Observation on Petrify'd wood and other Petrify'd bodies" is interesting because the author takes quite a modern point of view in regard to fossils (cf. Fig 4, Part I).

And so we might continue—but as the reviewer remarks in the *Journal des Scavans,* December, 1666: "This Book contains more than can be taken notice of in an

Extract,'' and we conclude the survey of this man of the past still using the words of the past:

> All his Errors and Blemishes, were more than made amends for, by the Greatness and Extent of his natural and acquired Parts, and more than common, if not wonderful Sagacity, in diving into the most hidden Secrets of Nature, and in contriving proper Methods of forcing her to confess the Truth, by driving and pursuing the *Proteus* thro' all her Changes, to her last and utmost Recesses; so that what *Ovid* said of *Pythagoras* may not unfittly be apply'd to him.
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> *Mente Deos adiit, et quae Natura negavit*
> *Visibus humanis, oculis ea Pectoris hausit.*
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> There needs no other Proof for this than the great number of Experiments he made, with the Contrivances for them, amounting to some hundreds; his new and useful Instruments and Inventions, which were numerous, his admirable Facility and Clearness, in explaining the Phænomena of Nature, and demonstrating his Assertions; his happy Talent in adapting Theories to the Phænomena observ'd, and contriving easy and plain, not pompous and amusing Experiments to back and prove those Theories; proceeding from Observations to Theories, and from Theories to farther trials, which he often asserted to be the most proper method to succeed in the interpretation of Nature. For these, his happy Qualifications, he was much respected by the most learned Philosophers both at home and abroad: And as with all his Failures, he may be reckon'd among the great Men of the last Age, so had he been free from them, possibly, he might have stood in the Front. But *humanum est errare.*[4]

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[4] Waller, *op. cit.*

SHORTER ARTICLES AND DISCUSSION.

SIAMESE, AN ALBINISTIC COLOR VARIATION IN CATS

COMPARATIVE studies of color inheritance in mammals have shown that pigment production throughout the group is due to similar processes and to genes probably homologous. These studies have shown, for example, that the pink-eyed albino condition seen in white rabbits, white rats, white mice and white guinea-pigs behaves in all cases as a simple recessive in crosses. It is probably due to variation in the same (*i. e.,* in an homologous) genetic locus in all these rodents. In its usual form albinism consists in a complete absence of pigmentation from the ectoderm of the embryo and from all derivatives of that germ-layer in the adult animal. This includes, not only the hair, but also the retina and iris of the eye. Such is the condition seen in the white mouse, the white rat, and the "Polish" or "Russian" rabbit. But this same locus may apparently undergo a different change which, while it behaves as the perfect allelomorph of the pure white albino variation, differs from it in that it allows a certain amount of pigment to be produced, more particularly in the retina of the eye and in the hair at the extremities of the body (nose, ears, tail and feet). At times a small amount of pigment is formed elsewhere throughout the coat. This condition is best known in the "Himalayan" rabbit. Clear white albinism of the Polish rabbit is an allelomorph of Himalayan albinism. In the guinea-pig only the Himalyan type of albinism is known; in rats and mice, only the Polish type is known.

In the guinea-pig, Wright has demonstrated the existence of two other albino allelomorphs, which apparently are distinct mutations of the same genetic locus. These are found in the red-eyed and in the dilute varieties described by him. Among rats Whiting and King have demonstrated the existence of a variety comparable with the dilute varieties of guinea-pigs and which they call "ruby-eyed." It behaves as an allelomorph of ordinary albinism in crosses.

White spotting of colored animals, sometimes called "partial albinism," is an entirely different variation, due to variation in a different locus. True albinism and spotting may by suitable crosses be made to coexist in the same individual. In this way

I have frequently produced *spotted* Himalayan rabbits, which would show particular types of white spotting, as Dutch or English, on the feebly pigmented Himalayan background (as has also Punnett), and Wright has produced whole series of varieties of spotted red-eyed and spotted dilute guinea-pigs.

Among certain rodents pink-eyed varieties occur which are due to variation in a genetic locus wholly distinct from that which is responsible for albinism. Such are the well-known pink-eyed varieties of mice having colored coats. Here the retina and the fur alike have a greatly reduced amount of black and brown pigmentation as compared with normal individuals, though yellow is unaffected. Pink-eyed rats and pink-eyed guinea-pigs are similar in appearance and in genetic behavior to pink-eyed mice. When crossed with the albino variety of the same species, they produce fully colored offspring as regards both eye and coat. The gene for pink-eye is thus seen to be complementary to the gene for albinism, with which it is known to be "linked" in rats and mice. Whether the two are also "linked" in guinea-pigs has not yet been ascertained.

Among mammals other than rodents albino and pink-eyed varieties are not certainly known to occur, though white-spotted and black-eyed white varieties are common. It is thus an open question whether the same genetic loci are found among them as among rodents. Bateson has pointed out similarities between a color variety of cat, the so-called Siamese, and the Himalayan variety of rabbit. Both are born white or nearly white and later become more heavily pigmented. I may add (2) that both are inherited as recessives and (3) that in both varieties yellow pigment is largely or wholly suppressed, which is characteristic of the albino variation, but not of the pink-eye variation of rodents.

Wright has suggested that blondism among human beings (which when extreme in character is commonly known as albinism) is similar in nature to the albinism of rodents, being a graded series of allelomorphs similar to the series which he has described in the guinea-pig.

It thus appears probable that the same genetic locus, which occurs in rodents and which has been called the "color factor," occurs also in other mammals, including man.

The case of the Siamese cat has seemed to me for some years deserving of more careful study. Lacking opportunity for such study myself, I sent out an inquiry several years ago through the pet-stock journals for information about Siamese cat crosses A single reply has just come to hand, but from an authoritative source. A doctor, who prefers to remain anonymous, resident in an extensive institution in England and a fancier of Siamese cats, has employed his leisure, and the unusual opportunities afforded by his position, in studying the genetic behavior of Siamese cats in crosses with other varieties. He regards as characteristics of the Siamese breed a peculiar quality of voice and "cross-eyes," which characters often are seen in first generation crosses and so would seem to be inclined to dominance. But the distinctive Siamese color, he states, is never seen in F_1 individuals, "although quite a number show a midway color. At a glance you would say they were black, but on more careful examination you see they are near the color of the Siamese ears, seal brown. Most first crosses in my experience are black or seal, but some tortoise shell, or tortoise shell and white, or black and white." These statements indicate the usual behavior of yellow and of white-spotting in cat crosses. (See Whiting, 1918.) The Siamese color is evidently an independent character incompletely recessive in F_1. The doctor continues his account with a brief statement concerning a back cross of F_1 with pure Siamese. "I have a first cross female, black seal color, marked cross eyes, Siamese voice. She has been twice mated with a pure Siamese male. In her first litter she had two pure Siamese, perfect Siamese color. Unfortunately both died of distemper when about three months old. Her second mating resulted in one pure Siamese which is still alive. It is about five months old and is perfect in all Siamese points and fit to win [at shows]." Presumably the same sort of back-cross matings as these would produce also kittens similar to the F_1 mother in color character, although no mention is made of them in these notes. The information given suffices to show the segregation of Siamese color as a recessive character in generations later than F_1. The doctor confirms the observation of others as to the deficient pigmentation of the eye, a point of resemblance with allelomorphs of true albinism, as seen, for example, in red-eyed guinea-pigs (Castle and Wright), and in ruby-eyed rats (Whiting). He says: "The reflex which the Siamese cat shows in the dark is worth notice. It looks blood red and must be due to absence of pigment in the retina." A further point of resemblance with albinism is its distinctness from dilution as seen in "blue" varieties. The doctor speaks of having produced four Siamese which are "blue-pointed," presumably as a result of crosses with maltese, which are blue pigmented. An exactly similar combination I have recently secured in crossing rabbits, obtaining Himalayans with blue points in F_2 from a cross between ordinary black-pointed Himalayans and a self-colored rabbit which carried blue as a recessive character.

To summarize, we have the following indications that Siamese coloration in cats is a form of true albinism similar to that of the Himalayan rabbit, and still more closely resembling the ruby-eyed rat and the red-eyed guinea-pig, all of which species possess also more typical forms of albinism, but which are allelomorphs of those mentioned.

(1) Siamese coloration in cats is attended by a deficiency in amount of pigmentation in both coat and eye. (2) Yellow pigment is more affected than black or brown pigment. (3) The pigmentation is less at birth than at a later period. (4) The character is recessive in heredity. (5) It is distinct from "blue" dilution since it can be combined with it by suitable crosses.

Siamese in cats as far as reported occurs only in a non-agouti form, as does Himalayan in rabbits bred for exhibition. But by a cross with agouti rabbits, Himalayan rabbits are obtained in F_2 which have agouti points. As this makes the contrast of points with body less strong, fanciers' standards do not recognize the combination. Nevertheless the experiment shows agouti to be due to a genetic factor distinct from Himalayan. If Siamese in cats is also distinct from agouti, it may be expected that a cross of Siamese with tabby would produce Siamese tabbies in F_2, though the combination would probably not be pleasing to the fancier.

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THE MORPHOLOGICAL BASIS OF SOME EXPERIMENTAL WORK WITH MAIZE

Of all the plants that have been made to contribute to our knowledge of the principles of evolution and heredity in the last twenty years, probably none holds a more conspicuous place than Indian corn. The technique of its manipulation is comparatively simple, and it exhibits an extreme variability, which is almost unique in extending to the endosperm; the behavior of a large number of its characteristics has been found amenable to a Mendelian interpretation and has aided materially in establishing present-day views of heredity. Indeed, maize shares with *Pisum* the distinction of having been the means of the establishing of Mendelism itself, for it was in connection with their work on maize that Correns and De Vries discovered Mendel's paper. Since then its genetic behavior has been studied in detail by a number of investigators, and there is probably no other one plant that furnishes such a wealth of material illustrative of the principles of heredity.

The writer has in recent years had the opportunity of examining in more or less detail this same plant from the morphological point of view, and it has been found that we are far more familiar with the Mendelian behavior of some of its characteristics than we are with the characteristics themselves. This has led to some results illustrative of the need of very close coordination between genetics and morphology.

In one of the numerous experiments made by East and Hayes, an attempt was made to interpret the Mendelian behavior of the irregularity of the rows of grains on the ear of corn. The ratios produced in the breeding experiments[1] were not very significant, and, after suggesting the possibility of "monohybridism with reversed dominance," "fluctuating dominance," etc., they finally conclude that "it seems probable that a more complex set of conditions exists."

If, as is suggested, this irregularity is similar to that in Country Gentleman sweet corn, it was probably another set of conditions that caused the trouble. As the writer has since pointed out,[2] the irregularity in the rows of this variety is the more or less complete expression of a very definite and comparatively simple state of affairs. Each female spikelet of ordinary maize

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[1] "Inheritance in Maize," Bull. Conn. Agr. Expt. Sta., 167, 1911, p. 132.

[2] "The Morphology of the Flowers of *Zea Mays*," *Bull. Torrey Club*, 43: 127–144, 1916.

produces one grain; but in Country Gentleman sweet corn, a second flower, ordinarily aborted, becomes functional, and the spikelet produces two grains. Since there is little or no compensation for this in the length of the cob, and insufficient difference in the size and shape of the grain, the ear is producing a larger volume of embryo and endosperm than is ordinarily produced in the same space. As a result of this crowded condition, the straight rows are more or less obliterated for a more economical arrangement. At times, however, a set of conditions, presumably environmental, may limit the size of the grain or increase the length of the cob sufficiently that the rows are almost straight, although each spikelet is still producing two grains. The genetic experiment, then, was probably dealing with an indefinite expression of a definite characteristic. If the heredity of the two-flowered condition of the spikelet had been tested, a more direct explanation would probably have been afforded.

Again (p. 134), these same authorities explain the occurrence of hermaphrodite flowers upon the basis that "the immature sex organs, so-called, of maize seem endowed with the power of becoming either stamens or carpels." In so far as actual genetic results are concerned, this is, in most cases, at least, a sound working basis, but it is far from exact morphologically. There is no organ in the young maize flower that has the possibility of becoming in some cases a stamen and in others a pistil. The young flower has the ability to become either staminate or pistillate because it contains primordia of both stamens and a pistil, one or the other of which usually does not develop to maturity.[3]

Blaringhem's extensive experiments,[4] in which he attempts to initiate mutation by means of injuries to the plant, fail to take into full account certain very significant facts of morphology. It is probably for this reason that he believes that the acquisition of hermaphrodite flowers in the maize plant is a *progressive* step. On the contrary, every indication points to the fact that the rudimentary stamens and pistils that have been found in the flowers of maize are the vestiges of organs that have been, and not the phylogenetic forerunners of organs that are to be. Moreover, normal behavior shows that in mutilating the plants he had merely promoted the production of suckers, which normally tend to have bisexual inflorescences. Blaringhem's method is ingenious and would, no doubt, give good results in a study of physiology of monoecism; but, the normal plant being under-

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[3] *Ibid.*, pp. 129–134.

[4] Blaringhem, L., "Mutation et traumatismes," Paris, 1908.

stood, and full allowance being made for the recognized effects of inbreeding, it is not believed that there is any clear evidence that he produced a single *new* hereditary characteristic in maize.

But not all of the assumptions of fundamentals upon which geneticists have based their work on maize have been so unhappily chosen as those cited. Most of the work that has been done on the heredity of endosperm characters depends upon the so-called "double fecundation" and upon the degeneracy of three of the four potential megaspores. The former of these facts was observed by Guignard[5] in 1901, but he did not figure it; the latter has been deduced by analogy. Circumstantial evidence was good in both cases, but evidence of this kind is not always dependable. No one would risk much in a financial way on chances like these, but some geneticists have risked years of work. In a recent paper[6] the writer has verified the facts assumed in this work.

The peculiar behavior of reciprocal crosses between varieties of corn differing in the physical nature of the starchy endosperm, has been explained[7] by the assumption that the two hereditary factors presumably carried by the two polar nuclei be dominant to the one factor carried by the sperm entering into the constitution of the primary endosperm nucleus. This idea is in accord with the multiple factor hypothesis, and the phenomenon is one of the few *direct* evidences that we have as to the behavior of a double application of a factor as opposed to a single application of its allelomorph. But so little is known of the morphology and the chemistry of these two kinds of starch and their relation to the surrounding tissues that it is not at all improbable that the explanation advanced may be modified by the results of further investigation.

An interesting light is thrown upon the the multiple factor theory by certain other morphological peculiarities of the grain of corn. The essential idea of the multiple factor hypothesis, in a simple form, is that a single visible effect may be due to two or more factors, only one of which is necessary to produce the same effect, at least in a limited degree. Little is known of the relative natures of the two or more factors that compose the multiple unit in the cases that have been investigated; they may be

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[5] Guignard, L., "La double fécondation dans le Maïs," *Jour. de Bot.*, 15: 37–50, 1901.

[6] "Gametogenesis and Fecundation as the Basis of Xenia and Heredity in the Endosperm of *Zea Mays*," *Bull. Torrey Club*, 46: 73–90, 1919.

[7] Hayes, H. K., and East, E. M., "Further Experiments on Inheritance in Maize," Bull. Conn. Agr. Expt. Sta., 188, pp. 12–13, 1915.

alike, or they may be very different from each other. A grain of corn homozygous for yellow starch and red aleurone is different in color from one having only one of these characteristics. But to a person with defective vision, or when viewed in a light of proper color, these two colors and a combination of the two may appear to be merely different shades of one color. By breeding this stock with a homozygous white, carrying no conflicting factors, we should get what would be to this same defective vision a perfect illustration of the behavior of multiple factors. But it is in reality a case of dihybridism in which we have failed to distinguish between the two sets of allelomorphs. And who can doubt that relatively as great a lack of discrimination may characterize our chemical, physical, or morphological vision in observing some of the classical illustrations to which the multiple factor hypothesis is applicable?

Other examples could be selected from the work that has been done on maize, and doubtless many are available from the investigations made with other plants and with animals, but these will suffice for illustration. Many of the organisms most useful for establishing and testing principles of heredity have an external appearance that may be very deceptive as an indicator of their true structure, and the true structure alone is the key to the deeper significance of their genetic behavior.

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ON HETEROPHYLLY IN WATER PLANTS

THE occurrence of two or more different types of leaf upon one individual, which is so frequently characteristic of water plants, has long attracted the interest of botanists. The most usual case is that in which the submerged leaves are finely divided while the floating or aerial leaves are relatively simple. Lyte's Herbal (1578) contains a vivid description of this type of heterophylly in the water buttercup. Since this description is also noteworthy for its insistence on the influence of external conditions, it may be cited here.

> Amongst the fleeting [floating] herbes, there is also a certayne herbe whiche some call water Lyverworte, at the rootes whereof hang very many hearie strings like rootes, the which doth oftentimes change his uppermost leaves according to the places where as it groweth. That whiche groweth within the water, carrieth, upon slender stalkes, his leaves very small cut, much like the leaves of the common Cammomill,

> but before they be under the water, and growing above about the toppe of the stalkes, it beareth small rounde leaves, somewhat dented, or unevenly cut about. That kind whiche groweth out of the water in the borders of diches, hath none other but the small jagged leaves. That whiche groweth adjoyning to the water, and is sometimes drenched or overwhelmed with water, hath also at the top of the stalkes, small rounde leaves, but much more dented than the round leaves of that whiche groweth alwayes in the water.

Among certain Nymphæaceæ we find a different type of heterophylly in which the submerged leaves are large, thin and translucent, somewhat resembling the seaweed *Ulva.* These leaves are particularly well shown in the yellow water-lily.

To enumerate all the varieties of submerged leaf met with among angiosperms would be too long a task to undertake in the present paper. It must suffice to say that they are either highly divided, ribbon-like, or else thinner and broader than the corresponding air leaves. They are characterized anatomically by the lack of stomates and by the presence of chlorophyll in the epidermis. They are thus well suited for the absorption of carbon dioxide in the dissolved form in which it presents itself to water plants.

In considering the significance of heterophylly, it is a matter of importance to remember that the occurrence of different leaf-forms in a single individual is not confined to aquatics but occurs also in terrestrial plants. Nehemiah Grew, as long ago as 1682, pointed out that in many cases one plant bears leaves

> of Two Kinds or Two distinct *Figures;* as the *Bitter-sweet,* the common *Little Bell, Valerian, Lady-Smocks,* and others. For the *Under leaves* of *Bitter-Sweet,* are Entire; the Upper, with two *Lobes:* the Under *Leaves* of the *Little Bell,* like those of *Pancy;* the Upper, like those of *Carnation,* or of *Sweet William.*

We find parallels to the heterophylly of hydrophytes, not only among terrestrial flowering plants, but also in the case of the distinct "youth forms" of conifers, and even—more remotely— in the "*Chantransia*" stage of such algæ as *Batrachospermum.* Heterophylly is indeed so widespread that no interpretation can be valid unless the condition be treated broadly as a very general attribute of plant life, rather than as a rare and exceptional phenomenon, for which special and individual explanations will suffice.

To the earlier writers, such as Lamarck, the problem of heterophylly presented no difficulties. They regarded the submerged or aerial type of leaf as representing a direct response, on the part of the plant, to the medium. The work of the last thirty years has, however, rendered this simple conception untenable; the theory that now holds the field accords a much less prominent place to adaptation. The first observation that shook the foundations of the idea that leaf form necessarily depended directly on the milieu, was that of Costantin, who showed that, in the case of *Sagittaria,* the aquatic and aerial leaves were already differentiated from one another in the submerged bud; he noticed auricles on a leaf which was only 2 to 3 mm. long. In *Ranunculus heterophyllus,* also, the leaves destined to be aerial are differentiated in the bud.

A large amount of experimental work has been published by various authors on the effect of conditions upon the leaf forms of heterophyllous plants, and, although some of the results are confused and conflicting, a study of the literature seems to justify one general conclusion—namely, that, in many cases, the submerged type of leaf is, in reality, the juvenile form, but can be produced later in the life history in consequence of poor conditions of nutrition; the air leaf, on the other hand, is the product of the plant in full vigor and maturity. This conclusion, which is primarily due to Goebel and his pupils, is substantiated not only by experiments but by observations in the field.

In many heterophyllous plants, the first leaves produced by a seedling, whether it develops on land or in water, conform, more or less, to the submerged type. This is the case for instance, in the Alismaceæ. In *Alisma plantago,* the water plantain, and *Sagittaria sagittifolia,* the arrowhead, the first leaves produced by the seedling (or the germinating tuber) are ribbon-like, even when the young plant is terrestrial. The formation of this type of leaf can be induced again, even in maturity, by conditions which cause a general weakening of the plant. Costantin thirty years ago, recorded that, when the leaves of *Alisma plantago* were cut off in the process of clearing out a water course, or in a laboratory experiment, the next leaves produced were ribbon-like, thus representing a regression to the submerged form. More recently, another worker, Wächter, tried the experiment of cutting off the roots of healthy, terrestrial plants of *Sagittaria natans* bearing leaves with differentiated laminæ. It was necessary to cut the roots away every week, as they grew again so rapidly. The result of this treatment was that the plants were found to revert to the juvenile stage, the new leaves being band shaped. When the experimenter ceased to interfere with the roots, the plants again formed leaves with laminæ. Other plants, with uninjured roots, grown as water-cultures in distilled water, also produced the juvenile leaf form, while those grown in a complete culture solution developed their laminæ normally.

The same observer recorded a case in which a plant of *Hydrocleis nymphoides* Buchenau (Butomaceæ), which had been bearing the mature form of leaf, was observed to revert to the ribbon form. On examination it was found that most of the roots had died off. When a fresh crop of roots was produced, the mature type of leaf occurred again.

Another writer, Montesantos, showed by a series of experiments upon *Limnobium Boscii* (Hydrocharitaceæ) that, in this case also, the heterophylly is not a direct adaptation to land or water life, but that the floating leaves are "Hemmungsbildungen" due to poor nutrition. In the water soldier, *Stratiotes aloides,* also, he showed that the stomateless leaves were primary, but that their production could be induced at later stages by unfavorable conditions.

An experiment tried by Goebel on *Sagittaria sagittifolia* indicated that absence of light in this case inhibits the formation of leaves of the aerial type. An observation of Glück's on *Alisma graminifolium* Ehrh., also points to the same conclusion. But it seems probable that the effect produced in these cases was not due directly to the darkness, but to the state of inadequate nutrition brought about by the lack of light for carbon assimilation.

Among the potamogetons, again, experimental work by Esenbeck has shown that reversion to juvenile leaves can be obtained under conditions of poor nutrition. For example, when a land plant of *P. fluitans,* which had been transferred to deep distilled water, had its adventitious roots repeatedly amputated, regression was obtained to the floating type of leaf and then the submerged type. A similar reversion to thin narrow leaves was brought about in the case of *P. natans* by growing the upper internodes of a shoot as a cutting.

Water lily leaves respond to experimental treatment in just the same way as the monocotyledons already mentioned. In the case of two species of *Castalia,* it has been found possible to induce the mature plants to form submerged leaves, either by removing the floating leaves or by cutting off the roots. This confirms an earlier suggestion, made by an Italian writer, Arcangeli, that the development of the submerged leaves of *Nymphæa lutea* was due to "un indebolimento o diminuzione di energia vitale." This suggestion has received independent, experimental confirmation from Brand, who estimated that a well-developed floating leaf of *Nymphæa lutea* was about eleven times the dry weight of a submerged leaf of the same area.

Another dicotyledon, *Proserpinaca palustris,* which was investigated by Burns, gave experimental results pointing to the same general conclusion as those already quoted. The primitive type of leaf in this plant is always a "water" leaf, but this type of leaf was also produced in the autumn by all the plants, regardless of any external conditions which the experimenter could control. On the other hand, at the time of flowering and in the summer generally, almost every plant, whether growing in water or air, produced the "land" type of leaf—the transition from the "water" to the "land" type taking place earlier on strongly growing than on weak stems. The author considers it evident that the aquatic environment is not the cause of the division of the leaf, nor does it depend on light, temperature, gaseous content of the water or contact stimulus. The only conclusion which he holds to be justified by his experiments is that *Proserpinaca palustris* has two forms, an adult form and a juvenile form; under good vegetative conditions, it tends to produce the adult form with the undivided leaf, the blossom and the fruit, while, if the vegetative conditions are unfavorably influenced, a reversion can be induced to the primitive form with the submerged type of leaf. These results are consistent with those of McCallum, who had dealt with the same species at an earlier date, but his interpretation is slightly different. He is inclined to regard the occurrence of the water form as induced by the checking of transpiration and the increased amount of water which hence accumulates in the protoplasm. This explanation is not inconsistent with the more general view that any condition tending to lower the vitality may be responsible for a reversion to the submerged type of leaf.

In nature, the regression to the juvenile type of leaf sometimes occurs, not only in the case of an entire plant subjected to adverse conditions, but also in the case of lateral shoots from an individual which is otherwise producing the mature form of leaf. Goebel for instance, examined an old example of *Eichhornia azurea* (Pontederiaceæ) which had wintered as a terrestrial plant in a greenhouse; the leaves were of the mature form, differentiated into sheathing base, petiole and lamina, except in the case of a lateral shoot, which, on the contrary, bore the grass like, simple leaves which characterize the young plant. Goebel also describes the occurrence of subdivided leaves of the water type on lateral shoots of normal land plants of *Limnophila heterophylla.* A corresponding reversion has been observed in the case of the side branches of plants of *Proserpinaca palustris* developing *in the air* from a plant whose main stem was producing the mature type of leaf; by removing the growing apex of the stem in June, side branches of the "water type" were induced to develop.

The interest of these lateral shoots, which show a reversion to an *ontogenetically* earlier type of leaf, is enhanced by the fact that C. and F. Darwin in "The Power of Movement in Plants" have recorded a case of the occurrence, on lateral shoots, of leaves whose characters are probably *phylogenetically* earlier than those which the species normally exhibits. Their observations related to the sleep habits of the allied genera, *Melilotus* and *Trifolium.* They noticed in *Melilotus Taurica* that leaves arising from young shoots, produced on plants which had been cut down and kept in pots during the winter in a greenhouse, slept like those of *Trifolium,* with the central leaflet simply bent upwards, while the leaves on the fully grown branches of the same plant afterwards slept according to the normal *Melilotus* method, in which the terminal leaflet rotates at night so as to present one lateral edge to the zenith. They suggest that *Melilotus* may be descended from a form which slept like *Trifolium.*

The idea that the "juvenile" leaves produced on lateral shoots may in some cases represent an ancestral type, is consistent with the facts in the case, for instance, of the Alismaceæ, provided that the "phyllode theory" of the monocotyledonous leaf be accepted in the sense advocated by Professor Henslow and the present writer. According to this theory, the ancestral leaf of this family was ribbon-shaped, while the oval or sagittate blade (or "pseudolamina") represents a later development—a mere expansion of the apex of the petiole. The submerged youth leaves of this family would thus represent a reversion to phylogenetically older forms.

If the interpretation of heterophylly indicated in the present paper holds good at all widely, the teleological view of the submerged leaf must be considerably modified. The present writer would like to suggest that, for the old conception of heterophylly as *induced* by aquatic life, we should substitute the idea that such a difference between the juvenile and mature forms of leaf as would render the juvenile leaf well suited to aquatic life, has been in many cases one of the necessary preliminaries to the migration from land to water, and that the aquatic angiosperms thus include, by a process of sifting,[1] those plants whose terrestrial ancestors were endowed with a strong tendency towards heterophylly.

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COALESCENCE OF THE SHELL-PLATES IN CHITON*

CHITONS are peculiar in the fact that the molluscan shell is here represented by a series of eight distinct dorsal plates, which in different genera overlap and articulate with one another to varying degrees. The full number, 8, seems, however, to be invariably present. While examining recently a series of somewhat over 2,100 individuals of *Chiton tuberculatus* L., I came upon two cases, and two only, exhibiting any irregularity with respect to the number of the shell-plates. These were specimens, a male and a female, found near together on the beach at Cross Bay, Bermuda, in which plates 7 and 8 had in each instance almost completely fused (Figs. 2–6), so that each of these animals seemed at first sight to have but 7 plates; since no records seem previously to have been made of such occurrences, they are here figured and described.

In the two abnormal chitons the fused terminal plates were of similar external appearance, but in individual A, the female, the coalescence of plates 7 and 8 was somewhat less complete than in individual B, the male, as shown by the form of the inner surfaces of the compound plates. It is perhaps accidental that in both cases fusion of the respective plates is somewhat assymetrical, being more complete on the right side. As seen in Fig. 4, the muscular intersegmentum, which ordinarily receives the insertion plates of the eighth valve, is represented by a relatively small tongue of tissue.

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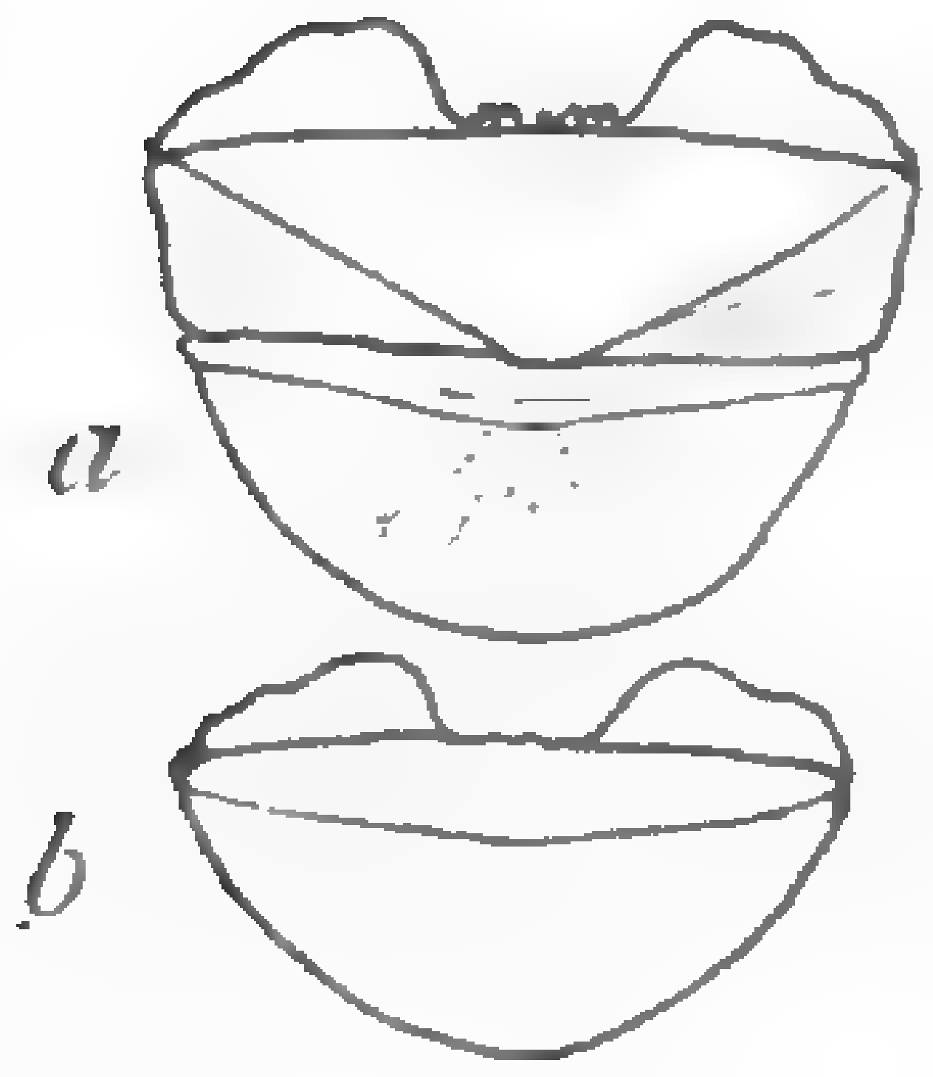
[1] We owe to Dr. H. B. Guppy, F.R.S., the important idea that the habitats of plants are determined by their peculiarities of structure and not *vice versa*. In relation to the occurrence of plants with buoyant seeds and fruits in water-side stations, he writes, "there are gathered at the margins of rivers and ponds, as well as at the sea-border, most of the British plants that could be assisted in the distribution of their seeds by the agency of water. This great sifting experiment has been the work of the ages, and we here get a glimpse at Nature in the act of selecting a station."

* Contributions from the Bermuda Biological Station for Research, No. 104.

It may be of significance that the only instances obtained of fusions of the kind figured, occurred at a sandy beach, on the south side of Bermuda, exposed to the beating of the ocean surf. Individual A, when found, was attached to a rock, but was half-covered by sand left by the tide. Chitons in such situations are frequently buried for a time beneath a foot or more of sand, and under these circumstances the over-lapping edges of the shell-plates are kept tightly pressed together, thus preventing sand-grains from abraiding the soft inter-tegmental mantle. The posterior end of a *Chiton tuberculatus* is less active in turning movements, in curling-up and in similar operations than is the anterior end, so that two valves, once stuck together, might, at the posterior end, have a better chance of remaining together. The incomplete union of the valves, visible when seen from their inner side, suggests that the coalesced plates started out independently. Whether or not this view be valid, it would be of interest to determine if there is any general tendency, in special localities, toward the establishment of races of chiton possessing a reduced number of plates.



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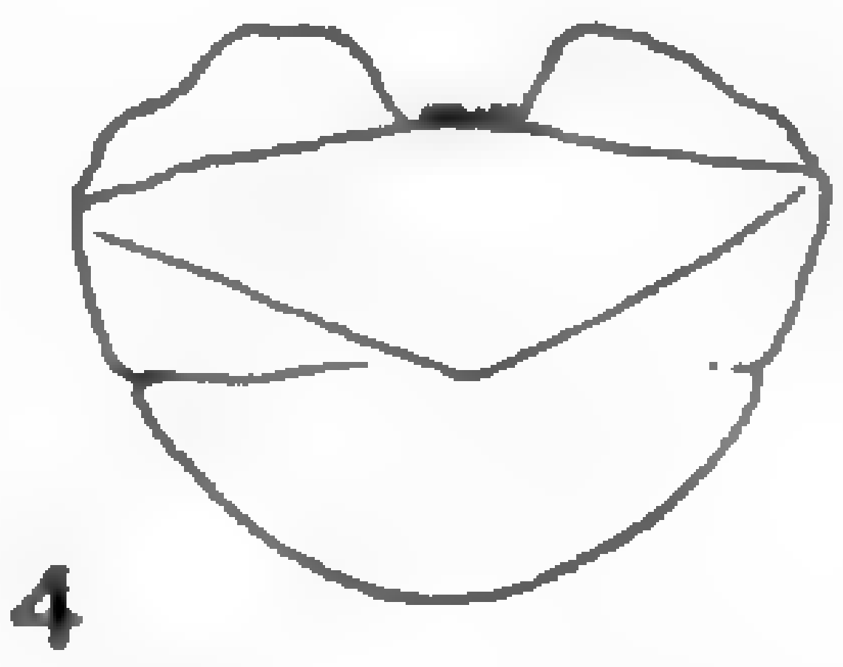

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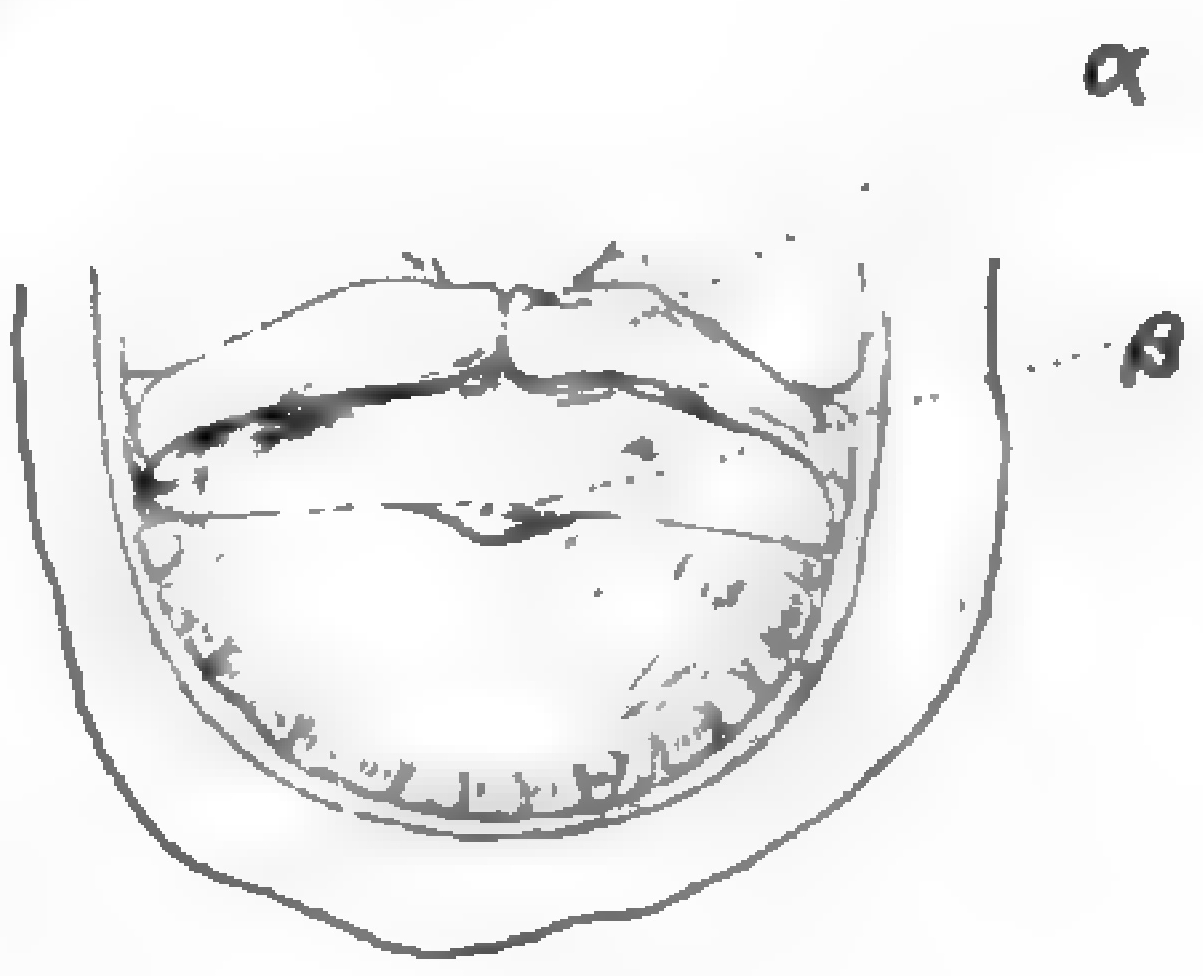

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FIG. 1. Outlines of valves 7 and 8 of a normal *Chiton tuberculatus; a,* in their natural relations; *b,* plate 8 separately. Natural size.

FIG. 2. Compound terminal plate of an abnormal *C. tuberculatus* (individual *A,* ♀) 4.4 cm. long; dorsal view. Natural size.

FIG. 3. The same, ventral view. Natural size.

FIG. 4. Compound terminal plate of an abnormal *C. tuberculatus* (individual *B,* ♂) 4.5 cm. long; dorsal view. Natural size.

FIG. 5. The same, ventral view. Natural size.

FIG. 6. Dorsal aspect of posterior end of *Chiton A,* to show (β) reduction of intersegmentum 7–8; (α) intersegmentum 6–7. Both abnormal chitons estimated to be five years old. Natural size.

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THE EFFECTS OF THE WINTER OF 1917–1918 ON THE OCCURRENCE OF SAGARTIA LUCIÆ VERRILL[1]

IN June, 1902, I published in the AMERICAN NATURALIST some notes on the dispersal of *Sagartia luciæ* that tended to show that this sea-anemone had spread from the neighborhood of New Haven, Conn., along the New England coast as far north as Salem, Mass. This migration was accomplished in approximately a decade, from 1892 to 1901. Since 1902 repeated efforts have been made to discover evidences of this species farther to the north than Salem but without avail. Apparently the species had reached its northernmost limits.

Sagartia luciæ was first noticed in Woods Hole, Mass., in 1898. From that year until the present it has been an extremely abundant species on the stones, mussels and eel grass in the waters of this region. On Pine Island, a narrow ridge of rocky gravel overtopped with coarse vegetation and lying in the swift tidal currents of the Hole, the narrow beaches between tides have been covered with thousands of this species of sea-anemone. When this locality was visited in June, 1918, not a single specimen of *Sagartia luciæ* could be found, though the particular area examined had been covered with many individuals the year before. Nor was this condition due to the relatively early date at which the search was made. Repeated attempts during low tides in July and August never yielded at Pine Island more than two or three specimens at a time, and it was quite clear that *Sagartia luciæ,* once so prevalent in that locality, had suddenly become all but extinct there. The same was true of other situations in and about Woods Hole. In fact, a general search showed that in not a single location where this sea-anemone had been abundant in 1917 could there be found more than a paltry number of specimens in 1918.

The occasion of this sudden and great diminution in the numbers of *Sagartia luciæ* is to be attributed, I believe, to the rigor of the winter of 1917–1918. The cold and ice of this winter were almost unprecedented. Mr. Vinal Edwards, the veteran collector of the laboratory of the United States Bureau of Fisheries at Woods Hole, has kept a continuous record of the weather conditions of this region for a long period and this record shows, as might be expected, that the winter conditions in 1917–1918 were more severe than for many years past. In no win-

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[1] Contributions from the Zoological Laboratory of the Museum of Comparative Zoology at Harvard College.

ter during the last ten years has the sea water been at 0° C. or lower for so long a period as last winter. Beginning with the season of 1908–1909 and proceeding to that of 1917–1918, the number of days for each of the ten winters in which the temperature of the seawater was O° C., or lower, was 3, 40, 44, 63, 3, 55, 0, 65, 36 and 80. Thus 1917–1918 with its 80 days of extremely cold water strikingly outruns any one of the preceding nine years.

This winter was conspicuous for the formation of large amounts of anchor frost in the shallow waters about Woods Hole. This frost or ice can be seen forming on the bottom of shallow bodies of salt water when the temperature of that water is at 0° C., or lower. It is apparently due to the freezing of fresh water that, seeping through the land, rises from the sea bottom and solidifies at once on coming in contact with seawater below its own freezing point. This fresh-water ice is especially destructive to marine animals on the bottom and its great prevalence during the winter of 1917–1918 is probably responsible for the scarcity of sea-urchins and other like forms the following summer. It probably had little or no effect on *Sagartia,* for this sea-anemone lives chiefly between tides and, therefore, above the level at which anchor frost is found, but as a winter phenomenon this ice is a good index of severity and it is severity in the nature of low temperature that is responsible, I believe, for the almost complete elimination of *Sagartia.*

That this sea-anemone was not destroyed by the merely mechanical effect of ice and waves is seen from the fact that the same stretches on Pine Island that were populated with *Sagartia luciæ* were, and still are, covered with many specimens of *Metridium marginatum.* This northern species seems not to have suffered in the least from the severity of the past winter and I, therefore, conclude, since *Metridium* was as much exposed to mechanical injury as *Sagartia* and still survived in ordinary numbers, that *Sagartia* succumbed to low temperature rather than to any other factor in its environment. This is in accord with the general belief, originally expressed by Verrill, that *Sagartia luciæ* is a southern species introduced by some accident into northern waters. Granting this conclusion, it is easy to understand why this species has not migrated farther northward into colder waters and why in severe winters it is almost exterminated in localities such as Woods Hole.

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TAXONOMY AND EVOLUTION

A Rejoinder

The writer has great sympathy with much of what "X" has to say on the above subject in a recent number of the American Naturalist (Vol. xlviii, 369–382).[1] Needless to say, however, he can not agree with all. True there is much in systematic zoology that is slipshod, but till statistics can be produced to show that the percentage of slipshod work produced by systematic zoologists is higher than in other fields of zoology, the writer of this article has a temporary residence in Missouri. He is of the opinion, also, that as great a percentage of the work of the systematic zoologist will stand the test of time as the work of the anatomist or any other worker in the field of zoology and proposes to remain of that opinion until time, the great leveler, proves to the contrary.

Linnæus is apparently not the only genius that has left the back door open and that has "been followed by a crowd of other workers eager to attain to immortality," as witness the great mass of half-digested literature on genetics, say, that has been crowded into the past ten or a dozen years. It would be a sad state of affairs indeed if systematics as a whole were not improving. That there have been occasional backward steps there is no doubt, but on the whole the progress has been forward. I hardly believe that even the systematists are as big fools as "X" pictures them to be, for I have yet to discover in my rambles a systematist who believed that his work was final. Heaven forbid. The czar in zoological nomenclature may arise and issue his fiat, but there will be later czars who will do away with them. For surely "X" would not have us believe that the day will ever dawn in this world when all things are settled. My shorter catechism is somewhat awry, but surely such a happy state is reserved for the Great Beyond.

Without wishing to disparage the modern workers I wish to say that some of the older workers did write "careful descriptions," as witness the following case which has been called to my

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[1] The present paper was written in July, 1914, soon after reading the paper by "X." It was laid away but now that it is more than four years old "going on" five, as children say, it seems best to submit it for publication.

attention. One of the early systematic entomologists described a species, on external characters only, in about three lines. Later entomologists were puzzled because the species had characters common to two widely separated genera; and one systematist said it belonged to one genus, and another said to a widely divergent genus, while a third said it was simply another name for a common form. Yet, behold, when the species was rediscovered it was found to belong to a new genus with characters common to the two widely divergent genera. Now, what's the answer, certainly the original description must have been a good one otherwise how could workers nearly a century later recognize the characters?

Isolated quotations from descriptions of any species look ridiculous (p. 370), but no more so than isolated quotations from the work of ecologist, neurologist or what not. A kindly feeling for my fellow workers in other fields and for the editor of the AMERICAN NATURALIST stays me from quoting at length and verbatim. Fortunately "X" has sufficiently concealed his identity so that I can not quote some of his own discussions until he yawns. Neither is my soul more deeply stirred by contemplating the poor hymenopterist, squinting at his box of dried "bugs" stuck on pins; than it is by the poor hunch-backed short-sighted cytologist (let us say) who, peering through his high power compound microscope, imagines that the world is circumscribed by his field of view and that a cell, or a nucleus, or a chromosome, is all there is to zoology.

"X" seems to deplore the fact of specialization in zoology and at the same time seems to ignore the fact that it is along these lines that the world moves. Why should we not have neurologists, taxonomists, hemipterists, etc., in zoology just as we have masons, carpenters, roofers, painters, tinners, etc. How many railroads would have been built in this world or how much progress would have been made in any other line of human endeavor if every man had to be a jack-of-all-trades? Do we hire a man to build us a house? Most certainly not. We hire a brick mason to lay the foundation, a carpenter to erect the frame, another one to put on the weather boarding, and still another to do the finishing inside; and so on until our house is finished and the whole structure stands only as long as the work of each one of these individual workers will stand. So it seems to me it is in zoology, the systematist lays the foundation upon which the whole structure is raised. And while the whole method of systematic zoology is open to criticism by anatomists, or what not, yet a certain amount of systematic work must be done before the anatomist can develop his work. If we take this position it seems to me that we must grant that the systematist must be far to the forefront, well in advance of the workers in other fields. And certainly this much must be said in his favor that he has turned out enough "new species" in the last few years to keep the rest of the zoologists busy for a year or two.

"X's" whole attitude is that the systematist makes mistakes and that he sticks only to external characters. In regard to the first I would call "X's" attention to the fact that anatomists a little less than 300 years ago believed the arteries carried air, not blood. And it seems to me if we go back about 250 years we find one Robert Hooke describing "little boxes (empty) of cells distinct one from another"; and wasn't it only about half a century ago that the cytologist awakened to the fact that the boxes were not as empty as might seem? Now the question to my mind is this, would we know as much about cytology as we know to-day, if Hooke had not discovered his empty boxes? I think not. And as a necessary corollary would we know as much about the animal world as we now know if systematists had not described new species? I think not. The fundamental basis of systematic work, it seems to me, must always be external characters, though they may be variable and unsatisfactory in many respects. What we all want and what I believe all systematists are striving for though some of their strivings may be misdirected is, among other things, ease of identification which, to my mind, implies reference to external characters. I see a woodpecker sitting in a tree and identify him as a yellow-bellied sapsucker by the fact that he has, among other characters, a white stripe down his wings. Very unscientific, I grant, but highly satisfactory to me if I am collecting not sapsuckers but downy woodpeckers. Also to the sapsucker if the alternate character which enabled me to identify him was the presence of extra small convolutions on his cerebellum.

I make my plea for systematic zoology as systematic zoology, not for its "phylogenetic classification of animals," nor for its bearing on geographical distribution, variation or heredity or anything else. The description of "560 new species of Zonitidæ" may not seem soul-inspiring work to "X," but to the describer it may have been exceedingly so. The description of 560 new species of Zonitidæ makes it possible for some student of variation or of "phylogenetic classification" to work on the Zonitidæ in a way that would not have been possible if these 560 "new species" had not been described, and no one man would have been able to describe the 560 new species and work their embryology, internal anatomy, neurology, ecology, geographical distribulation, behavior, variation, mendelian relations, etc., and live to tell the tale.

Furthermore, if there is any man that has the aptitude to describe "560 new species of Zonitidæ" my benediction is "let him go to it." And while 585 of his "560 new species" may prove to be false alarms that have never been turned in, at the same time it does not seem to have occurred to "X" that he may be doing much less harm thusly employed than if he were rampant with scissors, scalpels and needles or with killing agents, stains and a microtome trying to discover the true inwardness of the Zonitidæ. I do not want to be misjudged by any one who may think that I am making a plea for slipshod work, but I do want to make a plea for the isolated worker who is plodding away in his own particular field without hope of reward or recompense in this day or generation. Let us be very careful about setting our stamp upon a thing as worth while or not worth while. Mendel, the poor isolated monk, working away with his peas, never dared dream, I venture to say, that his work would revolutionize the biological thought of the twentieth century. Thus "X" may have the misfortune to view in a future reincarnation the sad spectacle of the zoologists of say 200 years hence loudly acclaiming the good work of the describer of the 560 new species of Zonitidæ, while at the same time they point with scorn to the work of the anatomist who discovered (?) that the digestive system of the Zonitidæ runs up hill.

The writer has the fortune or misfortune, as pleases your point of view, to be the entomologist of a state experiment station. His principal duties as entomologist are the intensive studies of two widely separated species of extremely injurious insects. This work is carried on under the Adams Fund by grants from the United States Department of Agriculture. Both projects were so outlined as to involve everything about these two insects that could be discovered by the writer; internal and external anatomy, embryology, life history, parasites, etc. Present indications are that it will take an average of about six years to finish (?) each one of these projects. Yet such a seemingly slow rate of progress is made possible only by the fact that some one working somewhere has described these two species and given them names. The one species was described without the describer ever having seen the male! Yet without this inadequate description progress on this problem would have been very greatly delayed. And so it is in every other field that these problems touch. Some one has described somewhere 29 species of parasitic hymenoptera, one of this number preying upon one of the species involved. Yet the describer knew only the adult and that only imperfectly, but his knowledge plus my own sends us one step nearer the complete knowledge of this species which "X" craves. And our knowledge of this species plus some one's knowledge of other related species raises us just one step nearer the truth which should be the goal of all human thought, and all science, zoology not even excepted.

I am interested in the phylogenetic relationship of a group of insects of no great economic importance. Especially am I interested in the genealogical tree of these insects as shown by the groups of characters of one structure. Now such work is made possible because three men in this country have devoted their entire time describing new species and new genera in this group. Without these descriptions many of which might have served as well as the one quoted on page 370, and without the collections of insects which these three men have made it would be impossible for me to make any progress along the line of a genealogical tree, which it is my fond hope will be of some use to the systematists of this group and to zoologists in general.

I have long wondered what could be called trivial characters. A few illustrations of the importance of so-called trivial characters in other fields than systematics may perhaps occur to "X." One of the most important that has come to my notice was that of a cytologist who discovered differences in the chromosomal characters of two different sets of individuals of the "same species" only to discover later that systematists had long distinguished between these two forms on the basis of characters more trivial than whether they were "pink with blue spots" or "blue with pink spots." Again two species of scale insects are separated by the fact that one has the median lobes of the pygidium rounded while the other has the median lobes conical (external characters). Yet one lives on oak trees and has at least four generations annually and the other lives on maple trees and has only a single generation annually. Now if "X" thinks that these facts would have been discovered as easily and as quickly as they have been discovered, if Professor Comstock had not pointed out these "trivial characters" some thirty-odd years ago, he thinks differently than I think. Yet the application of these facts is of vast importance to the horticulturalist and landscape architect or any other artisan who works to beautify our landscapes with trees, or any one who attempts to control these two pests.

I have no doubt that Linnæus was accused of relying on trivial characters for separating some of his genera and species. It would be interesting if history could tell us and it would be still more interesting if we could look into the future, say 100 years, and see what systematists and others will say about the present-day systematists who overlooked such perfectly obvious characters as the extra spines on the hind leg of species "a" as contrasted with "b" and their wonder and amazement that systematists of this our glorious twentieth century should have overlooked such important and obvious characters. So it will be in other fields. The histologist of the future will wonder why we used such crude killing and fixing agents; and will, more than likely, refer to our finest precision microtomes with a shrug much as we refer to the stone hatchets of the men of the Old Stone Age.

I make this somewhat extended plea because it seems to me that "X" has unconsciously done the systematists a great wrong.[2] "X's" attitude may discourage promising young men from entering the field of systematics where their help is greatly needed. Let us therefore lay aside our critical air and our sitting in judgment to decide just what is worth while and what isn't and turn our attention to utilizing the results of other workers in other fields to the greatest extent. The systematist

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[2] That all may see that my plea is entirely unselfish, I will state that I am not a systematist and that I have never described a single "new species." My attitude is simply one of gratitude to the systematists who have helped me with my problems.

is human like the rest of us, he has his limitations like the rest of us, but he believes, I think justly, that his work is pioneer work of great importance; and, if occasionally he gets beyond the limited range of our embryologist's microscope or our anatomist's scalpels and needles, let us not accuse him of wandering along the River of Doubt or being a lineal descendant of the famous Baron Munchausen. But let us look upon the systematist's work as the foundation for the glorious structure, modern zoology, which completed by his other co-workers will stand four square to the wind for all time to come. We do not need to defend systematics on the basis of "(1) the advertisement theory; (2) the recognition mark theory;" although both are perhaps more important than "X" intimates. But what is vastly more important is the fact that systematics is the basis for all real work in zoology. And the morphologist or anatomist who takes the attitude that systematics is to be entirely avoided[3] or, what is worse, is to be simply laughed at is placing himself in the same class as the man who says that there is no such thing as matter in the world. Sooner or later he is going to bump into the fact that systematics must play its part in his field and that systematics is broader than the question whether the "second joint is longer than the third" or whether a species should be called aabus Smith or beabus Jones.

Z.

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[3] Just what does "X" think about the anatomist who discussed at great length the anatomy of, let us say, the "American frog (*Rana temporaria*)" because that was the name given the frog in his perfectly good English "Text-book of Zoology"; when the context shows that the frog he was dealing with was the common leopard frog (*Rana pipiens*)?

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ON THE USE OF THE SUCKING-FISH FOR CATCHING FISH AND TURTLES: STUDIES IN ECHENEIS OR REMORA, II.

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THE FISHERMAN-FISH IN MOZAMBIQUE WATERS

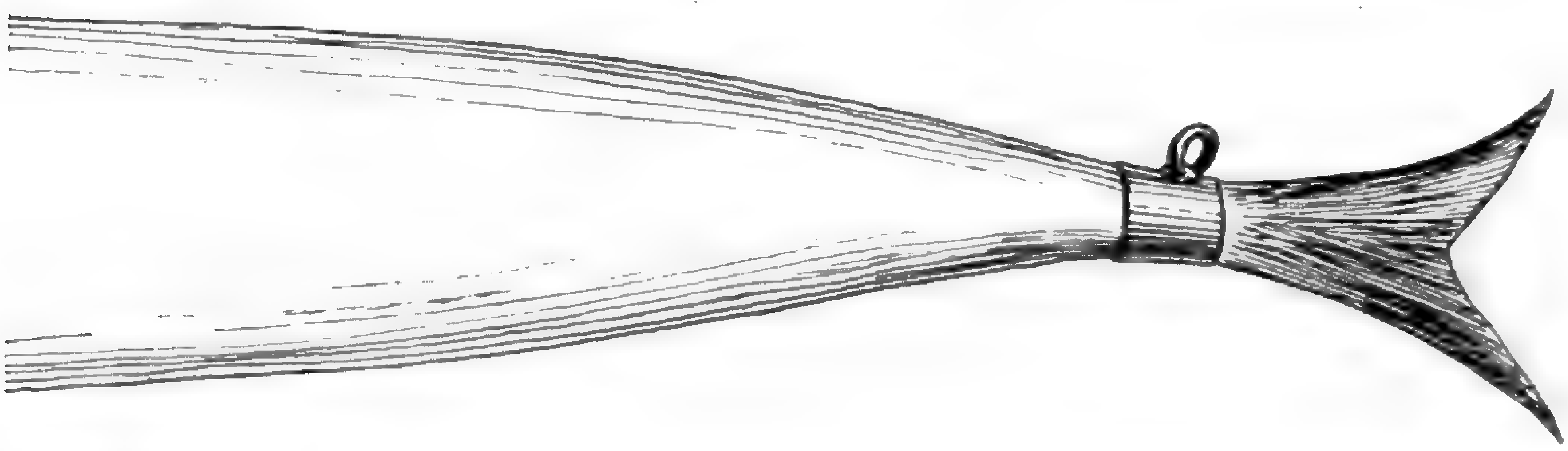
IN the year 1884, Mr. Frederick Holmwood, British Consul at Zanzibar, by publishing an article in the *Proceedings of the Zoological Society of London,* brought this extraordinary use of this remarkable fish to the attention of the scientific world. Chancing on this article, I became greatly interested in the matter and have been led to collect all the available data and to present it herein to those who may be interested.

On a trip in a steam launch from Pemba to Zanzibar, Holmwood had his attention called to a number of remoras which were attached to the sides and bottom of the boat. To these the natives on board gave the name "Chazo." Later at Zanzibar he saw natives digging out diminutive canoes, too small for any normal use, which he was told were for the "Chaza" (so he understood the native word). Now "Chaza" is the word for oysters or other bivalves, hence he thought that these were used to gather such in, but his servant told him that it was a "house" for the "Chazo" or sucking-fish kept by most fishermen in their huts. Later he learned that the native fishermen use the Chazo fish to catch turtles and large fish of any kind. And later still in

Madagascar he was informed that sharks and even large crocodiles were caught by the use of a fish called *Tarundu*[1] which was trained for the purpose. Unfortunately, just here Holmwood gave vent to his incredulity and his informants being greatly incensed refused to talk with him further on this matter.

Holmwood spent considerable time in gaining the confidence of the native fishermen of Zanzibar and was rewarded by being allowed to visit their huts and examine the "Chazo." These he found to be remoras (echeneis?) from 2 to 4.5 feet long and from 2 to 8 pounds in weight. They were kept in the little canoes in the cabins and were so tame as readily to come to the surface of the water at the appearance of their masters, by whom they allowed themselves to be freely handled.

> Each Chazo had a strong iron ring or loop fixed just above the tail [text-figure 1] for the purpose of attaching a line to when being employed in hunting. In some cases these appendages had evidently remained on for years, during which the fish had so grown that the iron had become imbedded in a thick fleshy formation. In two instances the ring had been inserted in the muscular substance at the root of the tail [fin], but generally a simple iron band was welded around the thinnest part of the body a few inches from the tail, which kept it from slipping off. To this was riveted a small movable ring or loop resembling that of a watch-handle. In one case [text-figure 2] this loop was fastened on by servings of brass wire in a similar manner to the rings of a fishing rod.



TEXT-FIGURE 1. Tail of sucker-fish with band and ring. (After Holmwood, 1884.)

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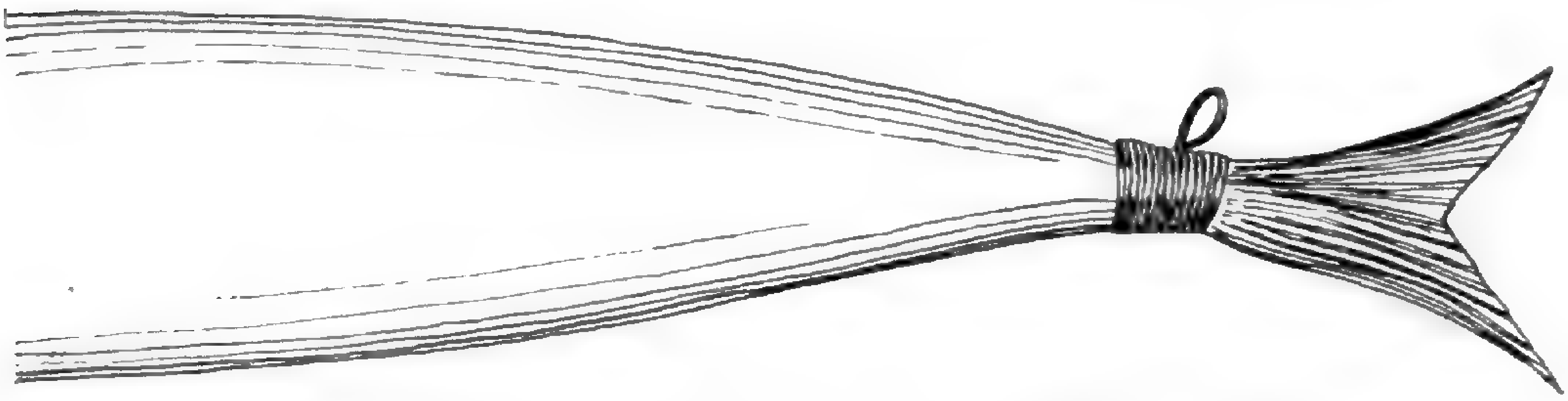
[1] Every effort has been made to trace down the use of the *Tarundu*, but books on the fishes of Madagascar are few, and none of them nor the works of travel consulted have given any clue.

Holmwood purchased one of these fish to send to England but it was killed by a crane. A second one died, probably from lack of a fresh supply of water. He afterwards arranged to buy another on its return from a fishing trip.

> It was brought to me a few weeks later minus its ring, and with a large wound or rent above the tail, part of which was gone. The owner declared that it had caught two turtles, which he showed me lying in his canoe, and that it had afterwards affixed itself to a large shark and, holding on after all the spare line had been paid out, the tail had given way. He stated that the Chazo had then relinquished its hold and returned in its mutilated state to the boat. He assured me that this was not an unusual occurrence and that after a time a fresh ring would be attached and the fish become as useful as before. I endeavored to preserve one of these Chazos in spirits of wine, but failed owing to the inferior quality of the spirit. This specimen measured 2 feet 8 inches in length and weighed 3½ pounds. The sucker contained 23 pairs of lamellæ.



TEXT-FIGURE 2. Tail of sucker-fish with loop and servings. (After Holmwood, 1884.)

Holmwood wanted to go out with the fishermen and see the fishes at work. But as the distance to the fishing-grounds was considerable, as the trips lasted fifteen days, and as the boats were small and lacked accommodations for a European, he was forced to desist. Thus he failed to become an eye witness to this remarkable procedure.[2]

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[2] Under date of 1883, a writer signing himself Phil. Robinson published a pamphlet entitled "Fishes of Fancy—Their Place in Myth, Fable, Fairy Tale, and Folk-Lore." This was issued as a hand book for the great International Fisheries Exhibit of that year in London. In this is a verbatim quotation from an article by Holmwood on the use of the fisherman fish in the official catalogue of the exhibition. After much difficulty this official catalogue was located and in it was found Holmwood's original

Holmwood's interesting account is however not the first for the use of the living fish-hook in Mozambique waters. In the year 1829 Lacépède published his "Histoire Naturelle des Poissons," in which, with reference to foreign fishes, he largely made use of the manuscripts of the lamented naturalist, Commerson. On page 490 of Tome III we read:

> Commerson . . . has written that this fish (*Echeneis naucrates*) frequents very often the coast of Mozambique, and that near to this coast it is employed for fishing for marine turtles in a very remarkable manner, due to the power which the Echeneis possesses of sticking to them. We think that we ought to report here the data which Commerson has collected on this subject so very curious, the only of the kind which has ever been observed. [?]
>
> There is attached to the tail of the living *Naucrates* a ring of diameter sufficiently large not to incommode the fish, and small enough to be retained by the caudal fin. A very long cord is attached to this ring. When the Echeneis has been thus prepared, it is placed in a vessel full of salt water, which is renewed very often, and then the fishermen place this in their boats. They then sail towards those regions frequented by marine turtles. These animals have the habit of sleeping at the surface of the water on which they float, and their sleep is so light that the least noise of an approaching fishing-boat is sufficient to wake them and cause them to flee to great distances or to plunge to great depths. But behold the snare which they set from afar for the first turtle which they perceive asleep. They put into the sea the *Naucrates* furnished with its long cord. The animal, delivered in part from its captivity, seeks to escape by swimming in all directions. There is paid out to it a length of cord equal to the distance which separates the sea turtle from the boat of the fishermen. The *Naucrates* retained by the line, makes at first new efforts to get away from the hand which masters it. Soon, however, perceiving that its efforts are in vain, and that it cannot free itself, it travels around the circle of which its cord is some fashion a radius, in order to meet with some point of adhesion and consequently to find rest. It finds this asylum under the plastron of the floating turtle, to which it attaches itself easily by means of its buckler, and

account. He wrote up for this an account of the fisheries of Zanzibar and concluded by giving a short description of fishing with the "chazo." This gives in very abbreviated form the data included above, and ends with the sentence "I hope to forward a specimen of this interesting fish before the close of the exhibition." However, as indicated previously he was unable to do this.

> gives thus to the fisherman, to whom it serves as a fulcrum, the means of drawing to them the turtle by pulling in the cord.[3]

This account of Commerson-Lacépède's is very circumstantial and exceedingly interesting, but it is not the first account of the fisherman fish, and not even the first for East African waters, for in 1809 and 1810 Henry Salt under orders of the British government made a voyage to Abyssinia by way of the Cape and the Mozambique Channel, stopping at Masuril, a village on the harbor of Mozambique. Of this visit he says under date of September 9, 1809 (his book was published in 1814):

> As he [the Bishop of Masuril] was aware of my wish to collect the rarities of the place, he made me a present . . . of a large sucking-fish (*Echeneis naucrates*) . . . which had just been brought in by a fisherman. All the Portuguese gentlemen, whom I conversed with on the subject, agreed in assuring me that fish of this kind were employed on the coast in catching turtles. The mode of doing this is by confining the fish with a line to the boat, when it is said invariably to dart forwards, and to attach itself by its sucker to the lower shell of the first turtle found in the water, which prevents its sinking, and enables the fisherman to secure his prey. The reason for the fish fastening on to the turtle is supposed to be done (as the Bishop observed) with a view to self-preservation, and its strength is so great that, when once fastened, the turtle is rarely known to escape.

Earlier still (in the latter half of the eighteenth century) a Swede named Andrew Sparrman made a voyage to the Cape of Good Hope, and in that part of his book dealing with the land of Natal, in the French translation published at Paris in 1787 he wrote:

> They [the inhabitants of the country] carry on a very singular method of fishing for turtles. They take alive a fish called Remora, and fixing two cords, one to its head and the other to its tail, they then throw it into the depths of the sea in the region where they judge that there ought to be turtles, and when they perceive that the animal has attached itself to a turtle, which it soon does, they draw in to them the Remora and with it the turtle. It is said that this manner of fishing is also carried on in Madagascar.

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[3] The same account in brief form is found on pages 170–171 of Pasfield Oliver's life of Commerson (1909).

This account is not found in the English translation of Sparrman's voyage, and I have not had access to the original Swedish edition, but it is found in the French edition in a sort of appendix to that section describing South Africa and is credited to Middleton's "Geography." Inspection of volume I (1777) of this latter work revealed the account substantially as given above, but *in quotation marks* with no hint whatever of its ultimate source.

Humboldt (1826) refers to a similar incident related by Captains Dampier and Rogers. Dampier was worked through twice without finding the reference, but a third going through his "Voyages" page by page revealed it as an annex to part 3 of his volume III, "A Discourse of Winds," etc. (6th edition, 1729). Middleton has copied it almost word for word, so it need not be repeated here. It will be of interest, however, to note that Dampier says that this "annexed paper" was "received from my ingenious Friend, Capt. Rogers, who is lately gone to that place ('Natal in Africk'): and hath been there several times before."[4]

It must be remembered that Holmwood wrote of a fish called *Tarundu* used in Madagascar as a living fish hook, and Lacépède quotes Commerson that a sucking fish is so used in the Isle of France as well as in the Mozambique country and lastly that Dampier quotes Rogers as to this use also in Madagascar. Acting on these hints a good deal of time has been spent in hunting for such accounts not only in books on the fishes of these islands but also in books of travel and at this writing three corroboratory accounts have been found. The first is to be found in Pollen's work on the fisheries of Madagascar (1874).

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[4] The index to Rogers' book ("A Cruising Voyage around the World," 1726) does not contain the words echeneis, remora or sucking-fish. Careful examination of the book, and a minute inspection of that part relating to South Africa, gave no results whatever. Dampier's "Voyages" show that he was keenly observant of natural history objects wherever he went, while Rogers paid little or no attention to such matters. It seems likely that the foregoing account was communicated to Dampier by word of mouth or by letter from Rogers.

For Malagassy waters he quotes the use of *Echeneis* as given by Middleton, Commerson-Lacépède and Salt, and for other waters other authors to be referred to later. He is not clear as to its use in his own time but he seems to indicate that in his day it was so used.

Our next reference is dated 1897. In the *Antananarivo Annual* for that date (published by the London Missionary Society at the capital of Madagascar) there is under "Natural History Notes" a translation by James Wills of a native manuscript which reads as follows:

> In the sea off the northwest coast of Madagascar a fish is found called by the people Hamby. It is round and long, somewhat like a lizard, but its tail unfolds for swimming like that of a gold-fish, and it has fins on each side. The length of a full-sized one is about that of a man's arm, and its girth about that of his thigh. Its back fin, from about one quarter of its length up to its head, is just like a brush, and it has a liquid about it, sticky like gum, and when it fastens onto a fish from below with this brush on its head the fish cannot get away, but is held fast. On account of this peculiarity of the *Hamby,* the people of Sambiràno use it to fish with. When they catch one they confine it in a cage of light wood, which they fasten in the sea, and feed the fish daily with cooked rice, or cassava, or small fish; and when they want to use it, they tie a long string round its tail and let it go, following it in a canoe. When it fastens on a fish they pull it in and secure the spoil. There is a sea-turtle called by the people *Fanóhana,*[5] which the *Hamby* is fond of catching, and this the people prize on account of the shell, which is of commercial value.

The above account is given almost word for word by James Sibree in his book "A Naturalist in Madagascar," 1915. Sibree, whose experiences in Madagascar cover a period of fifty years, and who as his book shows was a very close observer, evidently believed in this use of the fish.

The Hunting-Fish of the West Indies

However, the accounts quoted of the remarkable use of the Remora as a hunting fish in the Mozambique country are not the first that we have of such employment. For the very beginning we must go back to the second

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[5] This is probably the tortoise-shell turtle.

voyage of Columbus to the New World in 1494. This account given below is to be found in the writings of Peter Martyr d'Anghera, who was a prominent figure at the court of Ferdinand and Isabella and the foremost letter writer of his day. In 1511 Martyr published at Seville nine books and part of the tenth of his Decade I, the Decade of the Ocean, one of the component parts of his "De Orbe Novo," which has since appeared in many editions and translations. Possibly the best translation available for the general reader is MacNutt's, published by Putnam in 1912, but as better preserving the spirit of the times, I prefer to give Richard Eden's translation made in 1555, the quaint English of which reads as follows:

> At the Ides of Maye, the watche men lokinge owte of the toppe castell of the shyppe towarde the Southe, sawe a multitude of Ilandes standinge thick together, beynge all well replenished with trees, grasse, and herbes, and wel inhabyted. In the shore of the continent, he [Columbus] chaunced into a nauigable ryver whose water was soo hotte, that no man myght endure to abyde his hande therein any tyme. The daye followinge, espyinge a farre off a canoa of fyshermen of th(e) inhabitants, fearinge least they shulde flye at the syght of owre men, he commaunded certyne to assayle them pryuily with the shyppe boates. But they fearinge nothinge, taryed the comminge of owre men. Nowe shal you heare a newe kind of fyshinge. Lyke as we with greyhoundes doo hunt hares, in the playne fieldes so doo they as it were with a huntyng fysshe, take other fysshes. This fysshe was of shape or fourme vnknowen vnto vs: but the body thereof, not muche vnlyke a greate yele: havinge on the hynder parte of the heade, a very towgh skynne, lyke vnto a greate bagge or purse. This fysshe is tyed by the syde of the boate with a corde litte downe soo farre into the water, that the fysshe maye lye close hyd by the keele or bottom of the same, for shee may in no case abyde the sight of the ayer. Thus when they espie any greate fysshe, or tortoyse (whereof there is great abundance bygger then great targettes) they let the corde at lengthe. But when she feeleth her selfe loosed, she enuadeth the fysshe or tortoyse as swiftly as an arrowe. And where she hath once fastened her howld she casteth the purse of skynne whereof we spoke before; And by drawyng the same togyther, so graspeleth her pray, that no mans strength is sufficient to vnloose the same, excepte by lyttle and lyttle drawinge the lyne, shee bee lyfted sumwhat above the brymme of the water. For then, as sone as she seeth the brightness of the ayer, she lettethe goo

her howlde. The praye therefore, beinge nowe drawen nere to the brymme of the water, there leapeth soodenly owte of the boate into the sea soo manye fysshers, as maye suffice to holde faste the praye, vntyll the reste of the coompany haue taken it into the boate. Which thinge doone, they loose so muche of the cord, that the hunting fysshe, may ageyne returne to her place within the water: where by an other corde, they let downe to her a piece of the praye, as we use to rewarde greyhoundes after they have kylled theyr game. This fysshe, they caule *Guaicanum,* but owre men caule it *Reuersum.* They gave owre men foure tortoyses taken by this meanes: And those of such byggenes that they almoste fylled theyr fysshinge boate. For these fysshes are esteemed amonge them for delicate meate. Owre men recompensed them ageyne with other rewardes, and soo let them departe.[6]

Curiously enough a repetition of this story by Martyr himself has been completely overlooked by all who have had occasion to refer to his Reversus story. I myself did not find it until, some two years after making notes and copying his account as quoted above from Eden, I chanced to go over the "Decades" again page by page and stumbled on it. Since Martyr himself has not been quoted directly it will be of interest to give this second account from MacNutt's excellent translation of Decade VIII, Book 8, pages 299–300.

Let us now consider the hunting fish. This fish formerly vexed me somewhat. In my first Decades, addressed to Cardinal Ascanio, I stated amongst other marvels, if I remember properly, that the natives had a fish which was trained to hunt other fish just as we use quadrupeds for hunting other quadrupeds, or birds for hunting other birds. So are the natives accustomed to catch fish by means of other fish. Many people, given to detraction, ridiculed me at Rome in the time of Pope Leo for citing this and other facts. It was only when Giovanni Rufo di Forli, Archbishop of Cosenza, who was informed of all I wrote, returned to Rome after fourteen years' absence as legate of Popes Julius and Leo in Spain, stopped the mouths of many mockers, and restored me my reputation for veracity. In the beginning I also could hardly believe the story, but I received my information from trustworthy men whom I have elsewhere cited, and later from many others.

Everybody has assured me that they have seen fishermen use this fish just as commonly as we chase hares with French dogs, or pursue the wild deer with Molossians. They say that this fish makes good eating.

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[6] This is a literal copy of Arber's literal copy of Eden, save that the old-fashioned ſ-shaped s has had to be replaced by the modern letter.

> It is shaped like an eel, and is no larger. It attacks fish larger than itself, or turtles larger than a shield; it resembles a weasel seizing a pigeon or still larger animal by its throat, and never leaving go until it is dead. Fishermen tie this fish to the side of their barque, holding it with a slender cord. The fish lies at the bottom of the barque, for it must not be exposed to the bright sun, from which it shrinks.
>
> The most extraordinary thing is that it has at the back of its head a sort of very tough pocket. As soon as the fisherman sees any fish swimming near the barque, he gives the signal for attack and lets go the little cord. Like a dog freed from its leash, the fish descends on its prey and turning its head throws the skin pouch over the neck of the victim, if it is a large fish. On the contrary, if it is a turtle, the fish attaches itself to the place where the turtle protrudes from its shell, and never lets go till the fisherman pulls it with the little cord to the side of the barque. If a large fish has been caught (and the fishermen do not trouble about the small ones), the fishermen fasten stout cords to it and pull it into the air, and at that moment the hunting-fish lets go of its prey. If, on the contrary, a turtle has been caught, the fishermen spring into the sea and raise the animal on their shoulders to within reach of their companions. When the prey is in the barque, the hunting-fish returns to its place and never moves, save when they give it a piece of the animal, just as one gives a bit of quail to a falcon: or until they turn it loose after another fish. I have elsewhere spoken at length concerning the method of training it.[7] The Spaniards call this fish Reverso, meaning one who turns round, because it is when turning that it attacks and seizes the prey with its pocket-shaped skin.

This remarkable story of Martyr's has been repeated by many writers from his day almost to this and especially by the Spanish chroniclers of the early political and natural history of the West Indies. Many of these, however, add to the original story certain details which will be of interest to include herein.

The first of these is the historian Oviedo, whose "Sumario" was published but five years (1516) after Martyr's "Decades of the Ocean," and whose "Chronicles" were first published in 1535. My excerpt is taken from the Salamanca edition of 1547, but there is no reason to think that this particular account differs from that found in the earlier editions. We will let Oviedo

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[7] This account does not seem to have been preserved. At any rate it is not to be found in MacNutt's translation.

speak for himself, and his account is all the more interesting and valuable because he gives certain details as to the training and care of the fisherman fish which are absent from the other accounts, and of which he seems possibly to have had some personal knowledge.

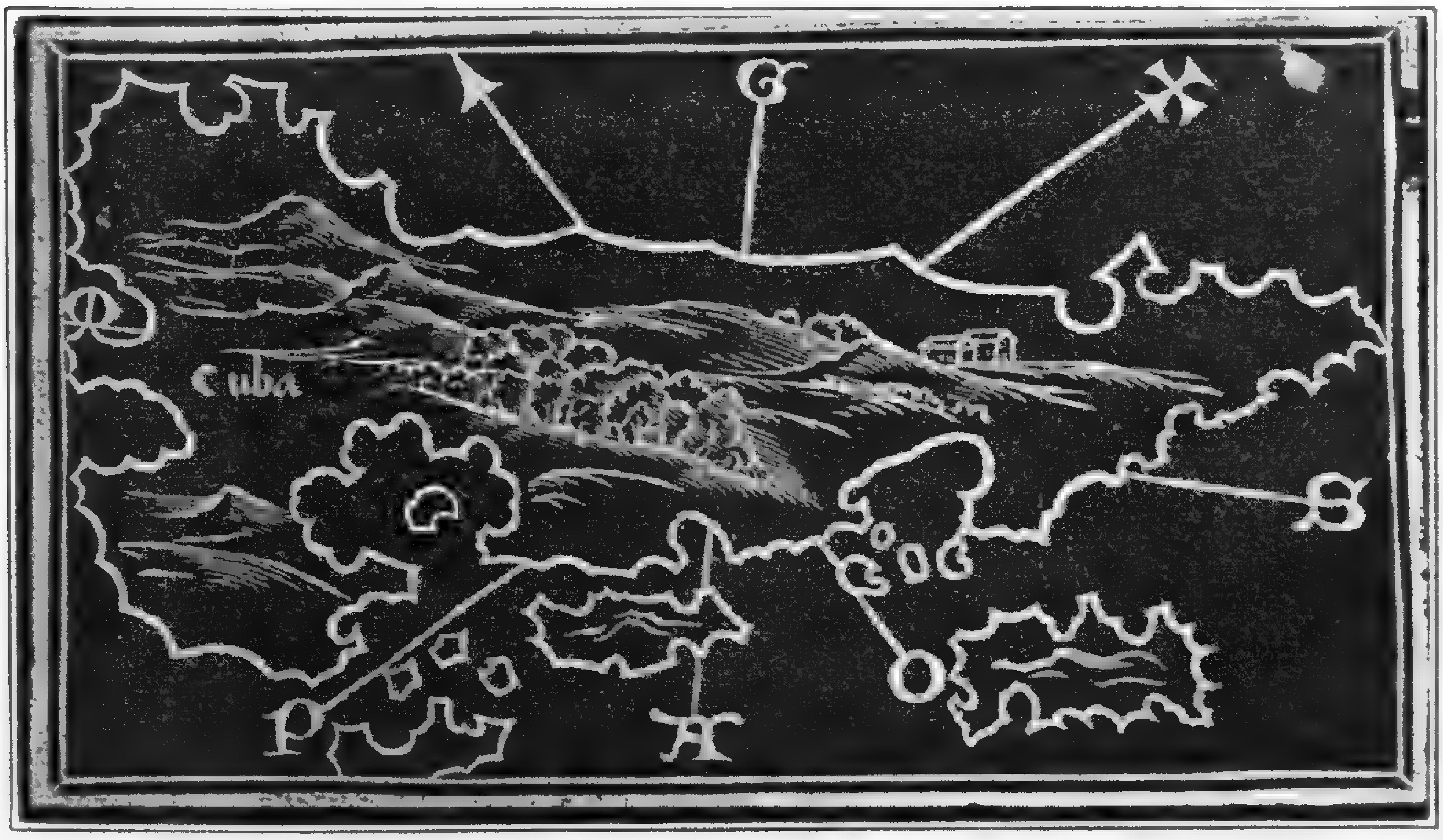
> There is a fishing of these Manati and of the tortoise in the islands of Jamaica and Cuba, which, if what I shall now say were not so public and well known, and if I had not heard it from persons of great reliability, I should not dare to write. And also it is believed that when there were many Indians, natives, on the island Espagnola, they also caught these animals with the Reversus fish. And since the discussion of the history has brought me to speak of the animal, the Manati, it is better that it is to be known that there are some fish as long or longer than a *palma,* which they call the Reversus fish, ugly in appearance but of great spirit and intelligence, which sometimes happens to be caught in their nets along with other fish. This is a great fish and among the best in the sea for eating, because it is dry and firm and without watery parts, or at least it has very few; and many times I have eaten of it and so am able to testify of it.
>
> When the Indians wish to tame and keep any of these Reversus fishes for their use in fishing, they catch it small and keep it always in salt water from the sea, and there they give it food and make it tame, until it is of the size which I have said or a little more, and fit for their fishing. Then they take it out to sea in the canoe or boat, and keep it there in salt water and fasten to it a cord delicate but strong. Then when there is seen a tortoise or any of the large fish which abound in these seas, or some of these Manati or whatever it may be that happens to go on the surface of the water in such a way as to attract attention, the Indian takes this Reversus fish in his hand and strokes it with the other, and tells it to be *manicato,* which means strong and of good courage and to be diligent, and other words exhorting it to bravery, and to see to it that it dare to grapple with the largest and best fish that it may find there [where the fishing is to take place]. And when the Indian sees that the best time has arrived, he lets it go and even throws it in the direction of the large fish. Then the Reversus goes like an arrow and fastens itself on the side of a turtle, or on the belly, or wherever it can, and thus clings to it or to some other large fish. This one, when it feels itself seized by the little Reversus, flees through the sea in one direction or another; and in the meantime the Indian fisherman lengthens the cord to its full length, which is many fathoms, and at the end of this is fastened a stick or cork that it may be for a signal or buoy which will remain on top of the water. In a little while the Manati or turtle, to which the Reversus has attached itself comes to the

shore, and then the Indian fisherman begins to draw the cord into his canoe or boat and when there are but a few fathoms left, he commences to draw it in carefully and slowly, guiding the Reverso and the prisoner to which it is attached until they reach land and the waves of the sea throw them out. The Indians who are engaged in the fishing leap out on land and if the prisoner is a tortoise they turn it over even before it has touched the ground and place it high and dry because they are great swimmers; and if it is a manati they harpoon, wound and kill it. When the fish has been taken to the land it is necessary very carefully and slowly to release the Reverso which the Indians accomplish with soft words, giving it many thanks for what it has effected, and thus they release it from the other large fish which it captured and to which it is so strongly attached that if it were forcibly removed it would be broken to pieces; and thus in the manner I have described are taken these large fish for whose chase and capture it seems that nature has made the Reverso the sheriff and executioner. It has some scales similar to the corrugations [*grades*] such as are found in the palate or upper jaw of man or horse and therewith certain spines very thin, rough and strong, whereby it attaches itself to the fish it seeks. And the Reverso has these scales or corrugations full of these spines over the greater part of the outer body, especially from the head to the middle of the body along the back and not on the belly, but from the middle of the body up; and from this circumstance they call it the Reverso because with its shoulders it seizes, and fixes itself to fishes.

So credulous is this generation of those Indians that they believe the Reverso well understands human speech and all those words of encouragement the Indian says before releasing it for an attack on the tortoise, manati or other fish, and that it understands also the thanks they afterward give it for what it has done. This ignorance arises from a failure to comprehend that this is a natural characteristic, because it happens many times in the great ocean as I have frequently witnessed, that when a shark or tortoise is captured, Reversos, without having been directed, are found attached to these fish and are broken to pieces on detaching them. From which we may infer that it is not in their power to release themselves after they have attached themselves except after an interval of time or from some other cause I have not determined; because one must think that when the shark or tortoise is taken the Reversos attached thereto would flee if they could. The fact is, as I have said above, for each animal there is its constable.

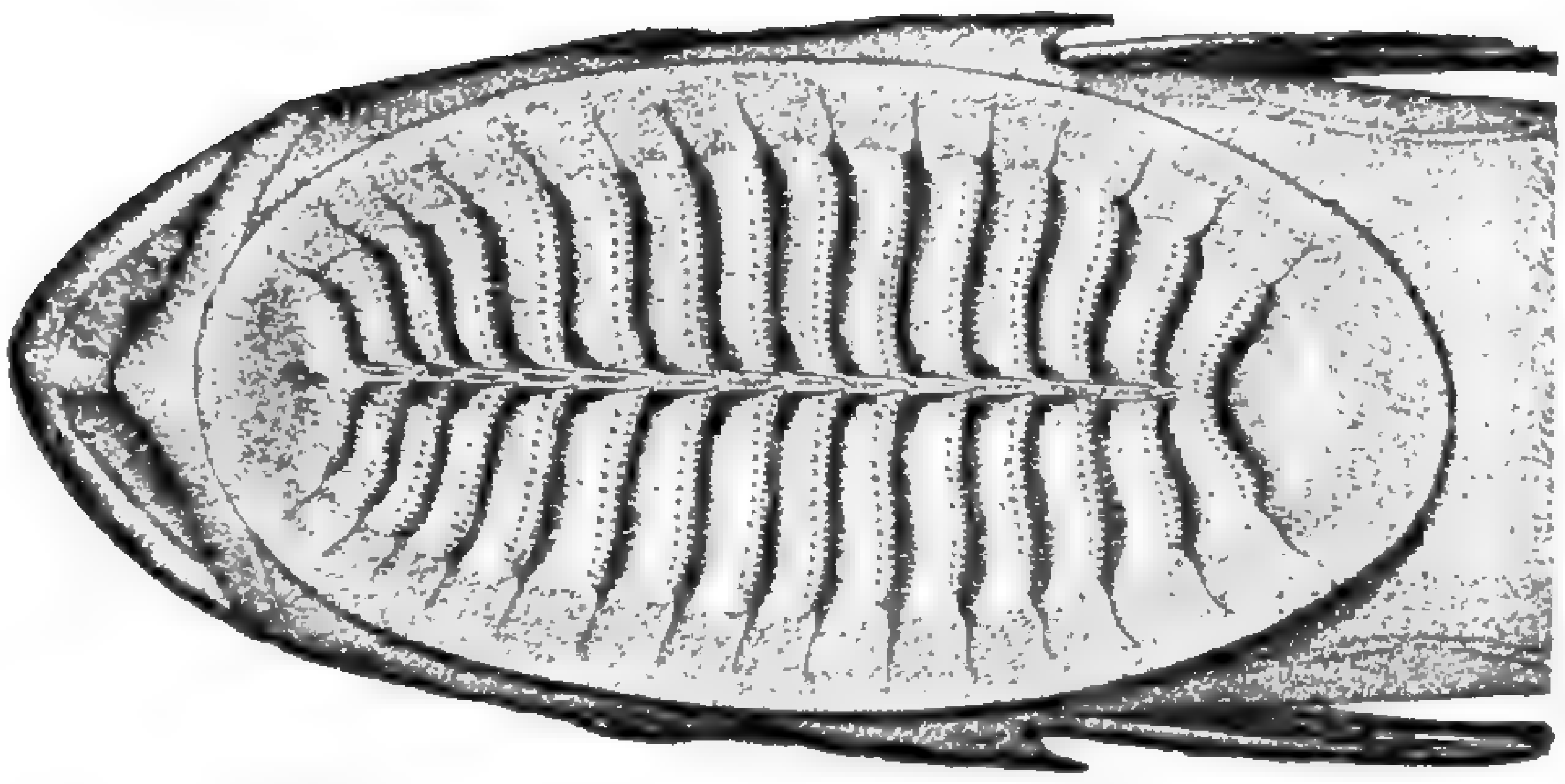
In 1527, Benedetto Bordoni published his "Isolario." In it is a brief account of the fishing in that locality called Queen's Gardens. It seems to be an abbreviated transcript from Peter Martyr and adds nothing new, save a map of Cuba, showing the islands off the southern coast among some of which the fishing with the Guiacan was observed. This seems to be of enough interest to be reproduced herein as text-figure 3.

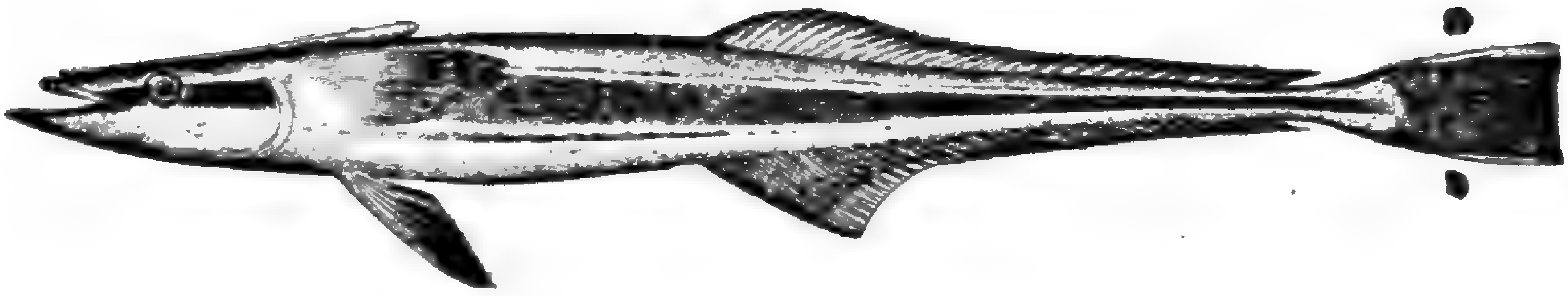
In 1553, Gomara published at Medina del Campo his "Historia General de las Indias." On folio XIIII is found an abbreviated copy of Oviedo's account of the Reversus fish, but as it contains nothing new it need not detain us.



Text-figure 3. The Island of Cuba with the Jardinellas de la Reina to the south. (After Bordoni, 1527.)

The greatest of the encyclopedic writers on natural history in the Renaissance times was the Swiss, Konrad Gesner, who was too good a searcher for the marvellous to let such a story as this escape him. His account (1558) is a somewhat abridged but yet almost literal translation of Peter Martyr. However, he gives us a figure of a hunting scene, showing how this fisherman-fish was used, and this is reproduced herein as Fig. 4, Plate I. The Reversus fish is shaped like an eel and has a great bag or pouch attached on the back of its neck. This pouch has just been thrown over the head of what appears to be a seal (probably meant for a manatee), while a turtle looks on in amazement from one side. In the background in this





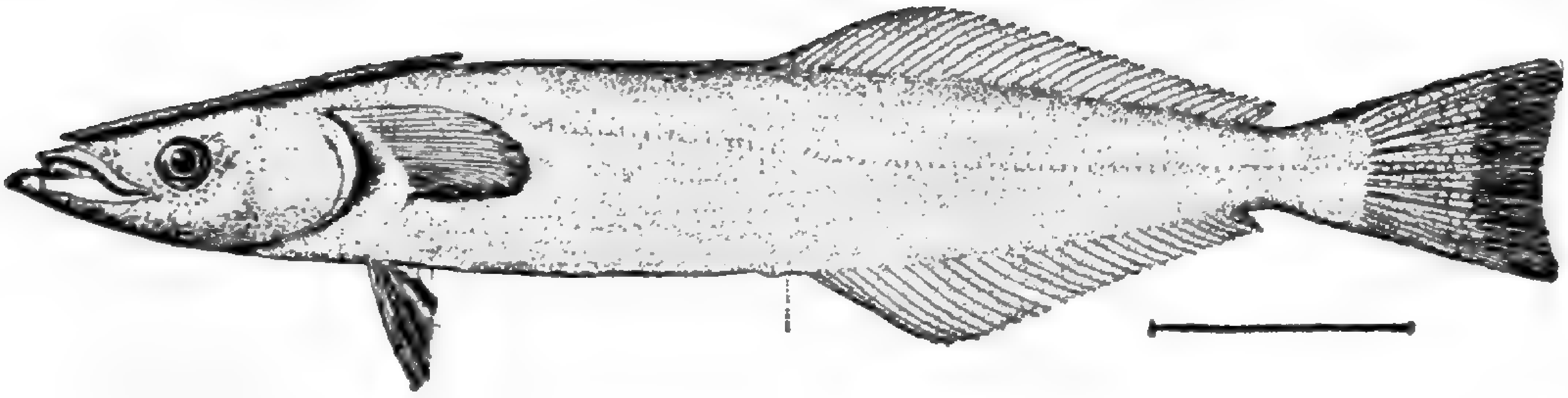


Figura hæc deſumpta eſt ex tabula quadam deſcriptionis orbis terrarum.

PLATE I

FIG. 1. Sucking-disk of Remora. After Jordan and Evermann, 1906.
FIG. 2. *Leptecheneis naucrates.* After Jordan and Evermann.
FIG. 3. *Remora brachyptera.* After Jordan and Evermann.
FIG. 4. The first known figure of fishing with the fisherman fish. After Gesner, 1558.

boat are the fishermen, one of whom holds one end of a line the other end of which is tied around the anterior part of the body of the eel-like fish.[8] In a sort of postscript Gesner refers to another hunting-fish which is similar to but smaller than the above. This reference, however, is not clear.

The first user of the name Guiacan for our fish was Peter Martyr; other and later writers take the name from him. Considerable effort was made to run down this word and to ascertain its meaning. It was finally found in Bachiller y Morales's "Cuba Primitiva" (1883). Here we are told that

> Guiacan was the name the Indians gave to the fish which the Spaniards called Reverso, and which served them in fishing; because tied by the tail, they fixed themselves to the tortoise and other prey which they did not release, rendering thus a useful service.

Earlier than Bachiller y Morales, another writer, Raymond Breton (1665), calls the huntsmen fish "Iliouali" and says that it is a fish which has on its head a membranous plaque, and if it attaches itself to the canoe it can with difficulty be removed save by breaking it into fragments.

That part of Gesner's "Natural History of Animals" which has to do with fishes was worked over in German and published in 1575 as "Das Fischbuch." In it on page L is found the figure of the hunting scene just referred to and an abbreviated account of the use of the fish as a living fish-hook. Here also there is an account of

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[8] Every effort has been made to ascertain the original of this figure. Presumably it is from an insert in some contemporary map or similar publication. Dr. Eastman personally made a search through the rich collection of Americana in the New York Public Library, the able curator of which, Mr. V. G. Paltsits, had to confess himself at a loss. I myself have worked through the collection of reproductions of old maps in the same library but in vain. Finally the question was submitted to Mr. E. A. Reeves, the learned curator of maps of the Royal Geographical Society, London, who courteously made a lengthy search through all the old maps under his care. Finding nothing he passed the question along to the authorities of the British Museum, who in turn could give no help. So the origin of this interesting and oldest figure still remains a mystery.

another Reversus. Apparently herein Gesner has mixed certain data from Oviedo with the legends of another Reversus covered with sharp spines.

It seems that in the writings of these old Spanish historians two fishes are described called Reversus;[9] one the anguilliform kind, having a pouch or sucker on its head, evidently a Remora, or, since it grows larger, an Echeneis; the other the squamous kind covered with scales bearing long spines, evidently the swell fish, Diodon. Concerning these fishes Dr. C. R. Eastman has written several interesting and valuable papers to which the attention of the reader is called. (See Bibliography, Eastman 1915, 1915a, 1916.)

We next hear of the Reversus in the writings of one Antonio Galvano. His book, "The Discoveries of the World from their first Original unto the Yeare of our Lord 1555," was published in the original Portuguese in 1563 under the editorship of his friend, F. Y. Sousa Tavares, and translated and reprinted at London in 1601 by Richard Hakluyt. Neither of these editions being available. I have had to content myself with the Hakluyt Society's reprint[10] found in Vol. 30, 1862, as edited by C. R. D. Bethune. Here there is a short paragraph in which the use of the anguilliform eel is attributed to the squamous form. Nothing new is added and no quotation will be given.

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[9] The reversus or "upside down" fish was undoubtedly so named because when attached to the carapace of a turtle its belly was turned upward or outward, as also when it was attached to the side of a fish—in any case its natural position was reversed. Diodon when it inflates its belly with air floats at the surface belly up, hence it too was a Reversus fish.

[10] It is interesting to note that in the Hakluyt reprint the Reverso story is put in square brackets. This considerably confused me and lest others be similarly thrown off the track it seems well to add this note from Mr. C. K. Jones of the Library of Congress, "Hakluyt, when publishing his 1601 edition was unable to find the original. The Hakluyt Society in preparing its 1862 edition secured a copy of the original publication of 1563 from John Carter Brown; and from this copy the Portuguese text was printed." It seems that Hakluyt included in his 1601 edition the Reverso story from original histories. However, in the original Portuguese text, Mr. Jones finds the Reverso story without brackets.

We next hear of the fisherman-fish in Herrera's "Historia Generale de las Indias Occidentales" published in 1601. In Capt. John Stevens's translation we read:

> They [the Indians] fished on, and took some fishes they called *reves*,[11] the biggest of them about the size of a Pilchard, having a roughness on the belly [?], with which they cling so fast, wheresoever they first take hold, that they must be torn in pieces before they can be torn off again. They ty'd these by the Tail with a small Thread, about two hundred Fathoms more or less in Length, and the Fish swimming away on the Surface of the Water, or but a little under it, when it came to where the Tortoise was in the Water, it clung to the under Shell thereof, and then the Indians drawing the thread, took a Tortoise that would weigh a hundred Weight, or upwards. After the same manner they took Sharks, which are most cruel bloody Fishes that devour Men.

Next comes Ramusio, whose "Della Historia dell' Indie" bears date Venetia, 1606. This appears to be merely a translation into Italian of Oviedo's Spanish work. At any rate it adds nothing to our knowledge of the hunting-fish, and may be passed over with this brief notice.

Another of the "fathers" of ichthyology is Aldrovandi, whose great work was published in 1613. He figures and describes both kinds of the Reversus. In general he follows Peter Martyr, but it is very clear that he copies Gesner. However, he has had Gesner's fishing scene redrawn, as may be seen from the reproduction of it herein (Fig. 5, Plate II). The boat and boatman are omitted, as is the cord around the neck of the fish, the seal-like animal has been replaced by another probably intended to represent a manatee, the turtle is entirely different, and lastly the head of the Reversus is not at all that of Gesner's figure. This is much larger, the teeth are more marked, the upper jaw has a hooked beak; and the bag of skin comes more distinctly off the top of the head, and is smaller at the base and has more longitudinal striations. And yet for all these changes it is plainly Gesner's figure.

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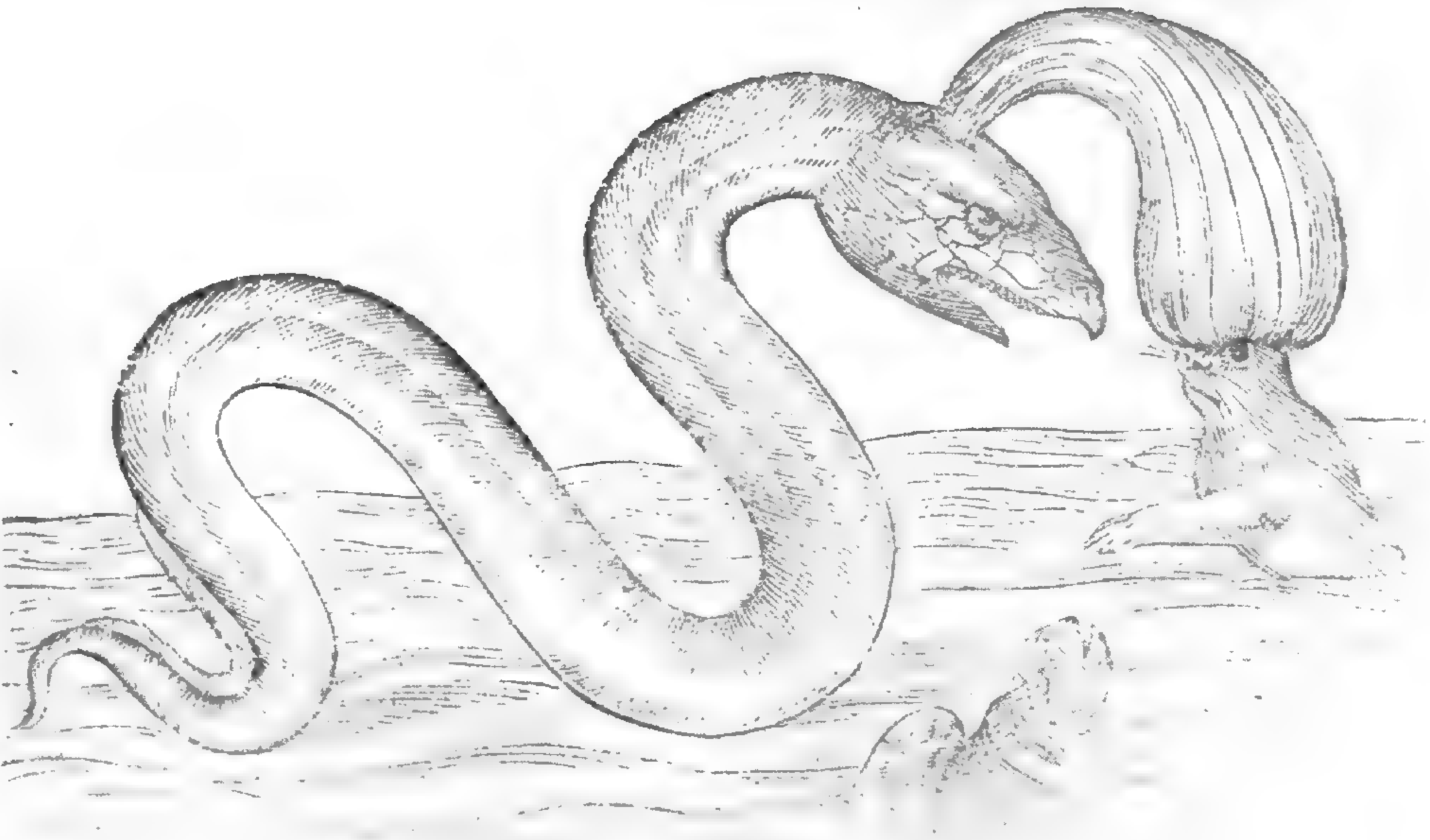
[11] Reves is of course a variant of the word Reversus, an abbreviation possibly.



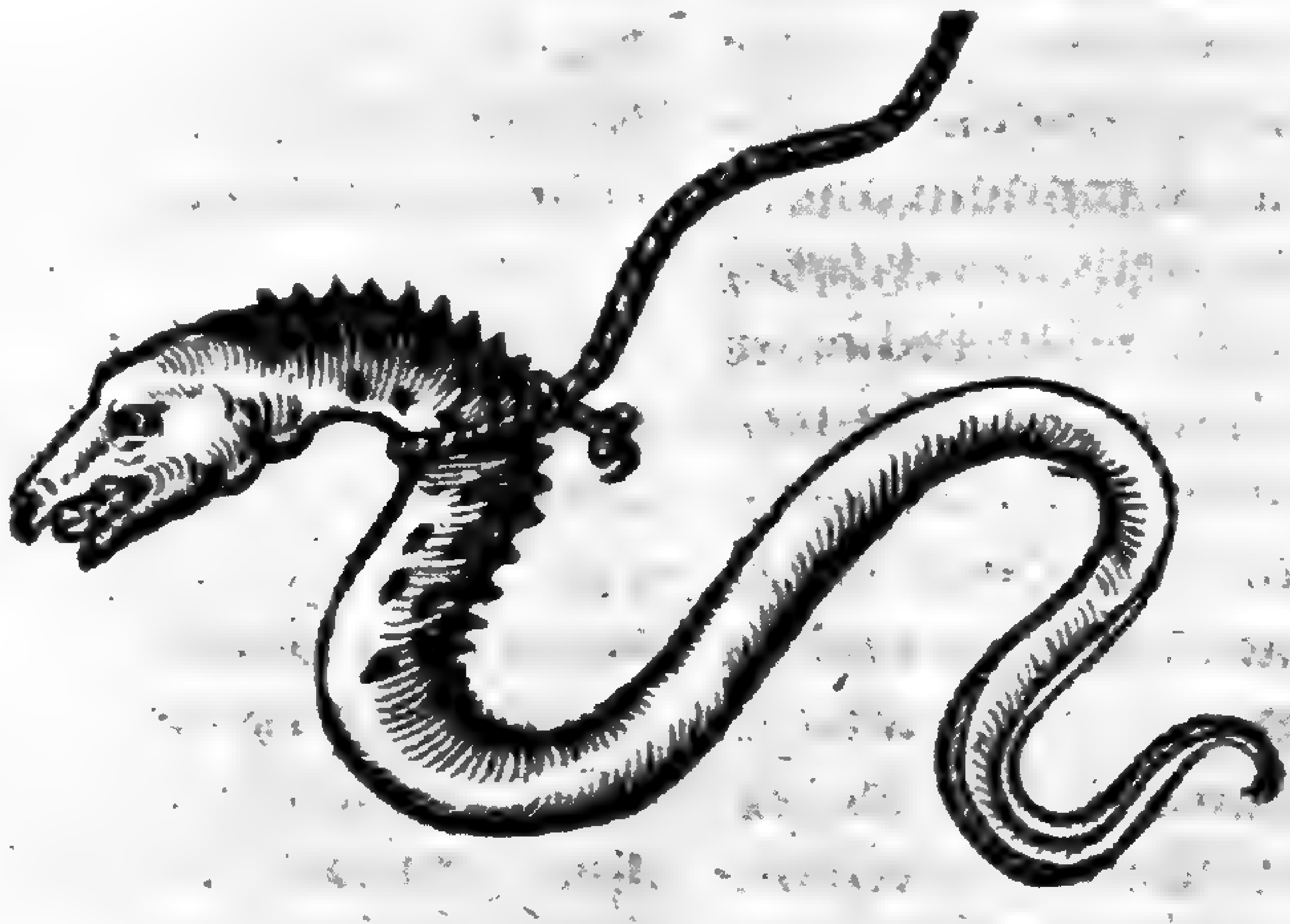


PLATE II

FIG. 5. The Indian anguilliform Reversus. After Aldrovandi, 1613.
FIG. 6. Reversus or Guiacanus, according to Nieremberg, 1635.
FIG. 7. Fishing with the Reversus, from Ogelby's "America," 1671.

In another place Aldrovandi gives a figure of the spinous Reversus, but in his account of this form he gets his data badly mixed since much of it is the data which Peter Martyr ascribes to the anguilliform variety. In neither account does Aldrovandi offer anything new.

We now come to a Spanish work published in Mexico City five years before the Pilgrims landed on Plymouth Rock and when Jamestown was but eight years old. This is Hernandez's work (1615) on the nature and virtues of the plants and animals used in the practise of medicine in New Spain. How he brings in the Remora is not clear, but he attributes his account to Oviedo, the actions of whose anguilliform Reversus he describes in his (Oviedo's) own words. However when he attempts to further describe the fish he gets his account tangled up with that of the porcupine fish. He does not seem to have ever seen either fish.

In 1635, Joannes Eusebius Nieremberg, a Jesuit priest, who was professor of physiology in the Royal Academy of Madrid, published his "Historia Naturae" in folio form. This is a compilation of not very great value, the less so because the references are not set forth clearly. Our interest in his book, in which he quotes Peter Martyr, Oviedo, Hernandez and another to be referred to later, is chiefly centered in his figure of the Reversus or Guiacanus. This is reproduced here as Fig. 6, Plate II. This is plainly Gesner's figure with the addition of a sort of saw-toothed mane on the anterior dorsal region.

Ogilby, whose huge tome was published in 1671, had evidently never seen the Guiacan, but he inserted on page 49 of his "America" such a quaint and interesting figure of his conception (or his artist's) of how this fishing was carried on, that this is reproduced herein as Fig. 7, Plate II.

The Dutchman, Th. van Brussel, in 1799 published a very interesting account of the Reversus; but a careful translation of his Dutch shows that it is but a translation of Martyr and Oviedo, and further that he confuses the anguilliform and squamous forms of the Reversus—a figure of the latter being given. He also need not detain us.

From this time on a long succession of writers repeat the tale. Thus we find it in Shaw's "Zoology," Vol. IV, 1803; Humboldt's "Essai Politique sur l'Ile de Cuba" (1826), his "Receuil d'Observations de Zoologie et Anatomie Comparée (1833) and in the "Personal Narrative" (English translation, 1860). We also find it in most if not all of the "Lives" of Columbus, notably Irving's (1828), Winsor's (1892), and last and best Thacher's (1903).

To these foregoing accounts we may add a brief note which may be of interest. Bernabe Cobo was a Spaniard (born 1582, died 1657) who wrote his "Historia del Nuevo Mundo" and at his death left it in manuscript where it remained until found, edited and published by the Spanish naturalist, Marcos Jimenez de la Espada, towards the close of the last century. Volume II, Sevilla, 1891, contains Cobo's story which turns out to be the familiar paraphrase of Oviedo's account. Absolutely nothing new is added.

We now come to a consideration of the sources of the various accounts of the use of the sucking fish as a living fish-hook in the West Indies. First of all plainly these later accounts are all echoes of Peter Martyr, or of Oviedo, or of both. Then these further questions naturally arise: Is Peter Martyr's "Decade of the Ocean" in 1511 the first account published? And secondly what is the ultimate source of these earliest accounts? In answering these questions I have had three invaluable sources of information. The one is Justin Winsor's keenly critical life of Christopher Columbus, the second is John Boyd Thacher's monumental work on Columbus (Vol. II, 1903) and the third is the continued advice and unfailing help of my friend, the late Dr. Charles R. Eastman.[12] Dr. Eastman became interested in the subject while working on the great "Bibliography of Fishes" published by the American Museum of Natural History, and finding that I was collecting data for a series of papers on Echeneis most courteously turned over to me invaluable material and aided me in every possible way. At the very time when I was slowly tracing these accounts backward towards their ultimate source, Dr. Eastman in the most brilliant fashion ran these stories down to the original recorder himself.

First of all let us see if Martyr's account in 1511 is the *first* published account of the interesting phenomenon. To this the answer must be "No!" Dr. Eastman sent me the following extract from "Libretto de Tutta la Navigatione de Re de Spagna et de le Isole et Terreni Novamente Trovati," Venezia, April, 1504 ["A Little Book in Regard to All the Navigation of the King of Spain to the Islands and Newly Discovered Lands"]:

> Continuing [along the coast of Cuba] they found further onward fishermen in certain of their boats of wood excavated like *zopoli,* who were fishing. In this manner they had a fish of a form unknown to us, which has the body of an eel, and larger, and upon the head it has a certain very tender skin which appears like a large purse. And this fish they drag, tied with a noose to the edge of the boat, because it cannot endure a breath of air. And when they see any large fish or reptile [*biscia*] they loosen the noose, and this fish at once darts like an arrow at the fish or reptile, throwing over them this skin which he has upon his head; which he holds so firmly that they are not able to escape, and he does not leave them if they are not taken from the water, but as soon as he feels the air he leaves his prey and the fishermen quickly seize it. And in the presence of our people they took four large turtles which they gave our people for a very delicate food.

After Dr. Eastman had sent me the above translation from the Libretto, I very carefully worked over Volume II of John Boyd Thacher's monumental life of Columbus

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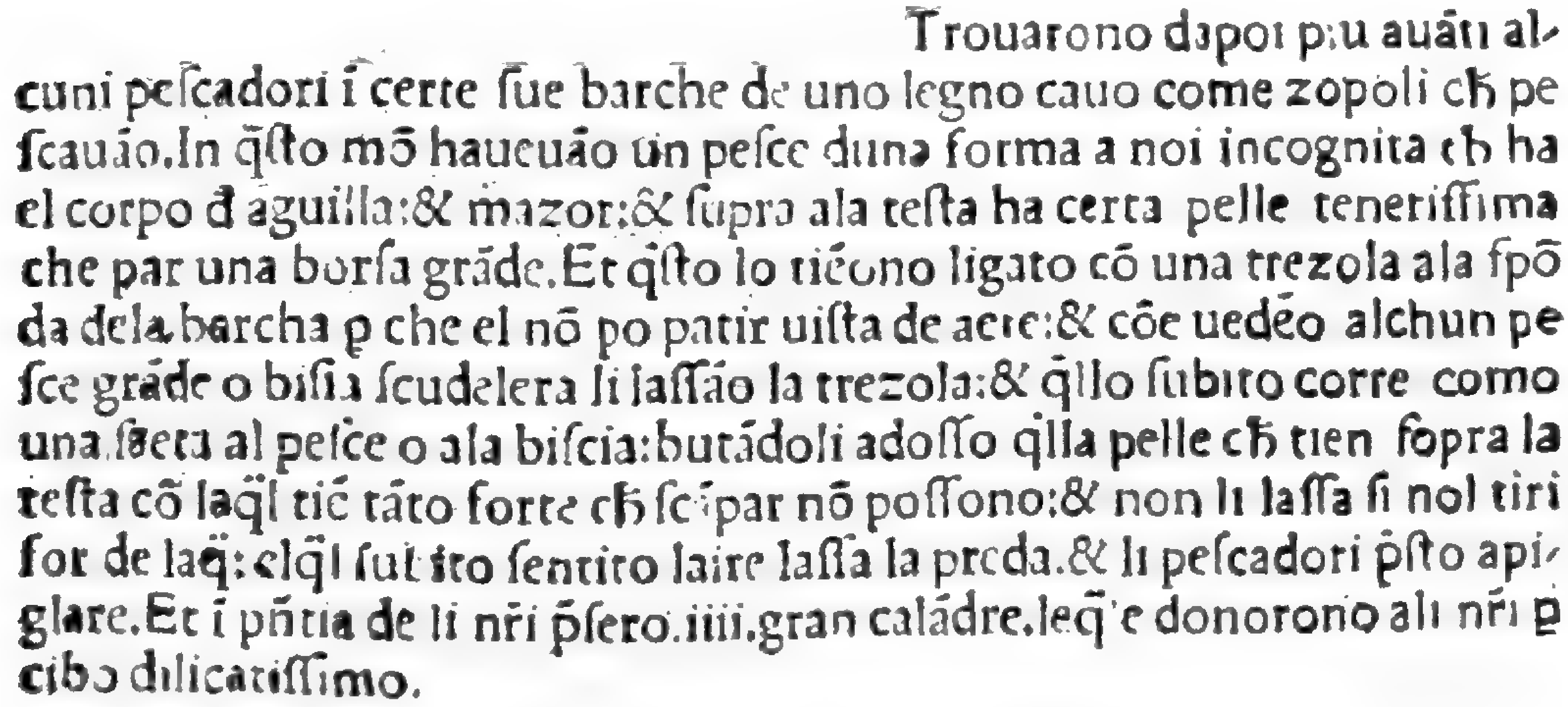
[12] The recital may perhaps not be devoid of either interest or value if the steps are set forth by which Dr. Eastman and myself, working separately and at a great distance from each other, traced this interesting story back to its original narrator. But it should be said here that Dr. Eastman reached the goal first, and that my efforts were chiefly confined to confirming his results, and clearing up certain details.

and from it much of the data following have been obtained. Only one copy of the Libretto is known in the world, and it is preserved in the San Marco Library at Venice. Thacher traced the original manuscript copy of the Libretto to the ownership of a man named Sneyd, living at Newcastle-on-Tyne, but was refused even the sight of it much less a chance to make photographs. However the authorities of the San Marco Library were men of different caliber, and Thacher reproduces in his book the whole Libretto page by page. And I in turn reproduce here as text-figure 4 a part of Thacher's reproduction of the page giving the Reversus story. It is from chapter XV.



Trouarono dapoi piu auãti alcuni peſcadori ĩ certe ſue barche de uno legno cauo come zopoli cħ peſcauão.In q̃ſto mõ haueuão un peſce duna forma a noi incognita cħ ha el corpo đ aguilla:& mazor:& ſupra ala teſta ha certa pelle teneriſſima che par una borſa grãde.Et q̃ſto lo tiẽno ligato cõ una trezola ala ſpõda dela barcha ꝑ che el nõ po patir uiſta de aere:& cõe uedẽo alchun peſce grãde o biſſa ſcudelera li laſſão la trezola:& q̃llo ſubito corre como una ſaeta al peſce o ala biſcia:butãdoli adoſſo q̃lla pelle cħ tien ſopra la teſta cõ laq̃l tiẽ tãto forte cħ ſcāpar nõ poſſono:& non li laſſa ſi nol tiri for de laq̃:elq̃l ſubito ſentito laire laſſa la preda.& li peſcadori p̃ſto apiglare.Et ĩ p̃ñtia de li nr̃i p̃ſero.iiii.gran calãdre.leq̃'e donorono ali nr̃i ꝑ cibo dilicatiſſimo.

TEXT-FIGURE 4. Page from the Libretto, 1504, whereon is contained the first printed account of the fisherman fish. Reproduced from Thacker's "Christopher Columbus," II, 1903.

The Libretto of 1504 was the first collection of voyages to the new world ever printed, and as such is of great interest to scientific men for more reasons than those merely pertaining to this article; hence it may be of interest for us to consider for a few minutes its history, which is as follows.

Peter Martyr, born in Italy, was a courtier and literary man of high standing in the entourage of Ferdinand and Isabella. Thacher says: "Peter Martyr d'Anghera may be said to have composed the matter in this little book, writing it in Latin from a series of letters addressed by him to various noted persons. These letters were written immediately after the events they describe. They bear the first news. They reflect first impressions. . . . This work was put into its present narrative form some time prior to the summer of 1501."

There now enters upon the scene another Italian letter writer, one Angelo Trivigiano, who was secretary to Domenico Pisani, the Venetian ambassador at the Spanish court. Thacher publishes copies of three letters which Trivigiano wrote in 1501 to the Venetian admiral and historian Domenico Malipiero (whose retainer he seems to have been) transmitting copies of various sections of a "voluminous work" on the voyage of Columbus "composed by an able man." Trivigiano nowhere names Peter Martyr as the author, but in all three of the letters he says that the author is the ambassador of the Spanish court to the Sultan of Egypt, and contemporary history informs us that this was no other than Peter Martyr, who left Granada for Egypt, August 14, 1501.

The contents of the Libretto, in Peter Martyr's own words, baring an introductory paragraph by Trivigiano descriptive of the personal appearance of Columbus, was turned over by Malipiero to Albertino Vercelles da Lisona, and by him issued in the Venetian dialect as a printed book on April 10, 1504.[13]

(To be Continued)

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[13] The only other historian of Columbus whom I have found to make mention of the Libretto is Winsor, who says that the first seven books of the first Decade were sent in Italian to Venice and there issued as a printed book of 16 leaves in April, 1504.

THE GERM PLASM OF THE OSTRICH

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A

> The *germ plasm* is fundamental and remarkably conservative . . . when the germ plasm changes it does so as a result either of wholly internal physiological causes, or of very extraordinary environmental stresses acting directly upon the germ cells . . . mixing of germ plasms, in and of itself, does not mutually alter hereditary determiners . . . selection only acts as a mechanical sorter of existing diversities in the germ plasm and not as a cause of alteration in it.

B

> Hereditary determiners or factors fluctuate regularly and frequently, if not indeed usually, and in high correlation with somatic characters . . . mixing of germ plasms in fertilization alters hereditary determiners mutually and hence is, in and of itself, a cause of genetic variations . . . a purely external agent, the continued selection of personal *somatic* qualities, will alter the germ plasm.

IN the above clear, concise phrases, sometimes with supporting amplification, Dr. Raymond Pearl,[1] in the presidential address before the New York Meeting of the American Society of Naturalists, 1916, contrasts the attitude of two sections of American geneticists with regard to the manner of changes in the germ plasm, as affording so much somatic material upon which selection may possibly work in the evolution of animals and plants.

So much evidence is already available for discussion on the merits of the one side or the other that it would appear gratuitous to add more, and one can well appreciate the advice which Pearl gives to get down to *more, and more searching, investigations as to the causes of genetic (factorial) variation.* The case of ostrich breeding in South Africa however affords such direct evidence bearing upon

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[1] "The Selection Problem," AMERICAN NATURALIST, February, 1917, Vol. 51.

most of the dicta that it is thought an account may be welcomed by geneticists. At any rate it may be added to the already voluminous "Experience of Practical Breeders," containing facts which will need to be reckoned with in any explanation of the actual causes of germinal changes. The ostrich affords an example of an animal only recently domesticated and still in the making, and we have before us the practical methods followed and the results obtained, enabling us to deduce in some measure the genetic principles involved. The endeavor will be to see what contribution its germ plasm has to make to each of the contrasting statements at the head of the paper, not forgetting that we know but little of the nature of the germ plasm and its changes except from their manifestation in the soma. It may be there is truth in both attitudes.

I

"The germ plasm is fundamental and remarkably conservative."

Ostrich farming on methodical lines was first undertaken in South Africa about fifty years ago. The beginnings were made with chicks obtained from wild nests, as unless "tamed" from an early age control of the adults is afterwards impossible. So remunerative did the industry prove to be that with the exception of one or two setbacks it advanced with great rapidity until at its zenith, the year before the war, 1913, nearly 1,000,000 domesticated birds were recorded, yielding an export of 1,023,307 lbs. of feathers at a value of $15,000,000, forming with gold and diamonds a triad contributing much to the prosperity of South Africa. With the advent and continuance of the war depression of a most severe character set in among ostrich farmers, and the number of birds has been reduced by about two thirds.

In the early days of the industry very little account was taken of the quality of plumage produced, and any bird reaching sexual maturity (three to four years) was employed as a breeder. Within the past two or three decades however the greatest attention has been devoted to the many characters of the plume and only the best plumage birds have been employed as breeders, the chief reason being the great difference in returns from clippings of high quality compared with those of an ordinary or inferior type. An intensive study has arisen in connection with the various structural details of the feather and also with the measures necessary for their production in the highest state of excellence; among the latter are included both the feeding and management of the birds as well as selection in breeding. It is probably safe to say that no domestic animal has been more intensively and intelligently studied by the farmer than the high grade ostrich, or more pampered in its treatment. Breeding sets, a cock and a hen, known to produce progeny giving superior plumage have frequently realized as much as $5,000.

The "points" of the ostrich plume relate to details concerning the length, width, density, lustre, shapeliness and evenness of the flue (vanes) and the form and strength of the shaft, and a highly technical terminology has arisen in connection therewith. An ostrich produces annually from 200 to 300 commercial feathers, belonging to a dozen or more different classes—whites, byocks, blacks, drabs, floss, tails—each with its many subdivisions. Each individual feather is handled and specially examined several times in the processes of clipping, arranging, sorting and selling, before being exported, and prior to the war two or three hundred millions of feathers were in this manner passed in review.

Under such keenly discriminating circumstances it will be understood that if any plumage variation presented itself it would be at once recognized and brought to general notice. A bird giving rise to a departure of any moment in a desirable direction in connection with any of the feather points mentioned would represent a fortune to its owner. But not a single case has ever been forthcoming. *Without any hesitancy it can be affirmed that in the course of the fifty years during which the ostrich has* *been domesticated it has never produced a feather variation, germinal in its origin, such as could be regarded as of the nature of a sport or mutation.* Feather irregularities and abnormalities are by no means infrequent, but can generally be ascribed to some injury to the feather germ or follicle in the process of quilling, or to malnutrition. Any peculiarity of this nature is usually forwarded to the writer, and some of the more common irregularities have already been described.[2] They are never hereditary peculiarities.

This stability on the part of the various structural details of the feather has continued despite the great changes to which the ostrich has been subject as a domesticated creature. The birds are fed on the most nourishing and stimulating of foods, the farmer having no option in the matter if he is to secure a feather crop of the highest quality; also they may be transferred from the moist coastal planes to the dry and arid interior at an elevation of 5,000 or 6,000 feet, a change involving great variation in temperature, pressure and other conditions. As an epidermal product, growing at the rapid rate of a quarter of an inch daily, the feather is extremely sensitive to changes in nutrition and climatic conditions, often responding to the small differences in blood-pressure between day and night. Yet all the modifications resulting from these influences are somatic; no hereditary germinal alteration has ever manifested itself.

Like so many other African animals, the giraffe, hippo, rhino, elephant and ant-bear, the ostrich is a survival of ancient days, a left-over, and as becomes a creature of long ancestry is fixed and immutable with regard to the many characteristics of its plumage. Numerous germinal changes have appeared in the past and survive to-day in the various feather types recognized by the specialist, all of which breed true; but it can justly be claimed that no further alteration has taken place during the past fifty

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[2] "Experiments with Ostriches, XXI., Feather Irregularities," *Agric. Journ.*, Union of South Africa, August, 1912.

years, in spite of the many environmental changes to which the bird has been subject. As regards the structural details of the feather the germ plasm of the ostrich fully confirms the statement with which the section opens.

II

"Mixing of germ plasm, in and of itself, does not mutually alter hereditary determiners."

If the plumage characters of the ostrich are so immutable what then is the objective in breeding? The original wild stocks with which the farmer commenced in the sixties differed much among themselves in the structural minutiæ of the feather, and the most desirable of the various feather points were distributed among many strains. *The earnest endeavor of the ostrich breeder is to combine in the single plume the best of all the many desirable features originally scattered throughout the wild birds.* The ultimate purpose of every breeder is the same—to produce a plume combining the maxima of all the available feather characters; a plume having the greatest length, width, density and luster and the most perfect shape, supported on a round, strong, slender shaft. On the original birds the largest plumes had for the most part a coarse, loose, unshapely flue, while the most compact, shapely, lustrous, graceful plumes were generally small. The whole effort is to combine the maximum size with all the so-called "quality points"; no other feature of the bird is taken into account in breeding, as none has any commercial value or is known to be in any way correlated with feather production. The problem appears simple, though it is taking years to accomplish; progress is being made each year, but the ideally perfect ostrich plume is not yet.

The genetical methods of the farmer are likewise simple. He proceeds entirely in the belief of a blending inheritance, which though doubtful in theory is succeeding in practise. He starts with a bird which produces plumes the most nearly approaching his ideal, and mates it with another most closely resembling it, but perhaps lacking or surpassing in one or more points; another season he may resort to a different mating to secure other features. From different breeding sets he may rear two or three hundred chicks in a season. The progeny being mostly intermediates and showing much variation he selects when mature the most desirable among them as breeders, or maybe, being weak in some particular point, he will purchase or exchange with another breeder in whose birds the character is strong. By this method, essentially one of hybridization, the ideal plume is being slowly built up. Sometimes by a fortunate mating one breeder will be ahead and sometimes another, a successful competitor at a Feather Show being inundated with orders for breeding birds and chicks and his fortune well assured. Despite the variability in the progeny no breeder can afford to "fix" his strain by a measure of inbreeding, lest while doing this another may get ahead. Taking all the economic and biological circumstances into account the geneticist has little he can contribute to such a practical effort; he can but assist by endeavoring to deduce and explain the principles involved.

The textual application is manifest. *The greatest mixture of germ plasm is going on, but no single hereditary factor or determiner is altered in the process, and has not altered throughout the history of ostrich breeding; only new combinations are formed of factors already available.* The farmer himself has long grasped this and does not look for any change; he knows he can get nothing beyond what the wild bird had to start with; he can create or change nothing, beyond what can be ascribed to good management and feeding. For practical purposes his understanding of the individuality and fixity of the germ factors producing the plume is as clear as that of the most zealous Mendelian; but only in a few instances has he ever heard of the factorial hypothesis, though facts upon which it could have been established were discovered in his farming practise long before 1900, the year of Mendelian reawakening. If his birds, judging by their feather performance, are lacking a certain germ factor he is well aware that he can by no possible means originate the factor nor hope to produce it in any way; he must procure it from some other farmer whose birds display it, and then he may expect to secure it in combination in his own strain.

III

"Selection only acts as a mechanical sorter of existing diversities in the germ plasm and not as a cause of alteration in it."

The term "selection" is employed by the ostrich breeder in South Africa with all that freedom which Pearl finds among the plant and animal breeders in America, but he is never under any delusion that it signifies more than is implied in the simple meaning of the word. He has retained its plain everyday significance and the majority have never heard of Darwin and "The Origin of Species by Means of Natural Selection," nor of the extended meaning which students of evolution are inclined to give the term, as in the phrase, "The Selection Problem." To the ostrich farmer "breeding from selection" simply means that for his breeding sets he picks out birds having the special plumage characters he desires to see in their progeny, or which he expects to get from the combination of the cock and the hen. Selection is merely used in contrast with indiscriminate breeding, as where any cock and hen may be camped off without regard to their plumage value, or in contrast to breeding on the veld where any cock may mate with any hen. He selects partly on the basis of somatic performance and partly on proved germinal production; many birds which themselves give indifferent plumage are yet employed as breeders from being known to produce superior chicks.

From his life-long experience in selective breeding the ostrich farmer clearly grasps that all he is doing is to sort out birds from among his flock with certain characters which he desires to see in combination in their progeny, but he never dreams that any change in the characters themselves will result therefrom. Though perhaps unable to express it in words he knows that the germ plasm of each of his birds contains so many factors, and in his selection of breeders picks out the birds having the factors he desires to give him new combinations, but he has no expectancy that the factors themselves will undergo any change as evidenced by their expression in the progeny. Selection along the prescribed lines is probably as rigid as that which any experimentalist could carry out, and is certainly more so than can be conceived of as taking place in nature, yet long as it has been in operation it has never carried with it an alteration of any of the existing diversities of plumage.

IV

"When the germ plasm changes it does so as a result either of wholly internal physiological causes, or of very extraordinary environmental stresses acting directly upon the germ cells."

The bodily characters of the South African ostrich present a remarkable uniformity except as regards certain details to be described later, but in comparison with the North African bird many striking differences appear. In 1912 the Government of the Union of South Africa imported 132 specimens of the northern ostrich from Nigeria. It was hoped that in these some one or other of the plumage characteristics might be developed to a higher degree than in the southern bird and could with advantage be combined with the latter. Experiments with this end in view are now in progress under the direction of the writer.

The northern ostrich is longer in the legs and neck than the southern, the head reaching a little over eight feet from the ground, about a foot more than in the latter. The color of the skin of immature birds of both sexes and of mature hens is a creamy yellow, while the mature cock is bright red or scarlet on the legs, head and neck, and red and pink over the body generally; in the southern ostrich the skin of the neck, body and legs is a pale yellow in chicks, dark gray in mature hens and dark blue in cocks, while in the sexually ripe cock only the beak, the front part of the head, the naked skin around the eyes and the tarsal scales are a bright scarlet. The crown of the head of the northern bird has a bald oval patch while that of the southern is covered with hair-like feathers similar to those over the rest of the head and neck. The northern egg is larger and rounder, with an enamel-like smoothness, and is practically free from obvious pittings; the southern is deeply pitted all over, smaller and more oval. Knowing as we do the habits and life of the ostrich it is in the highest degree improbable that any of the differences have an adaptive significance or selective value in nature.

When the birds are observed side by side, as can now be done at Grootfontein, the above characters readily serve to separate the northern from the southern ostrich, and may well be held to justify the specific distinction usually accorded them. That the distinguishing features of the former are not environmental but germinal is proved by the fact that they persist under southern conditions and have reappeared in progeny already reared. Numerous cross-breds or hybrids of the first generation have also been obtained, but sufficient time has not yet intervened to secure the second hybrid generation. As regards dimensions, color and the nature of the egg the first generation of cross-breds are intermediates in varying degree between the northern and southern parents, but the bald head patch of the northern is dominant over its absence in the southern, appearing in all the crosses yet reared.

It is clear that the germ plasm of the northern ostrich has undergone marked changes compared with that of its southern representative, or *vice versa,* for one can only think of the various races or species of *Struthio* as derived from a common stock. In terms of the sectional heading we may well enquire whether the changes are due to internal physiological causes or to extraordinary environmental stresses acting upon the germ cells. We have already seen that germinally the South African ostrich is most irresponsive to any environmental changes and we have no reason to suspect that its northern relative is in any way more impressionable. In the climatic and other environmental conditions of North Africa it is difficult to conceive of anything which could, for example, modify the bodily colors as compared with those of the southern bird, or could bring about a perfectly smooth round egg in contrast with an oval pitted one, much less which could either directly or through the soma change the germ cells so as to render the differences hereditary. Of course we know next to nothing of the influence upon the germ cells of extraordinary environmental stresses and to labor the point would be unprofitable. But doubt may certainly be expressed as to whether any external influence could so change them as to bring about the formation of a bald head patch, a feature which it is impossible to regard as having an adaptive significance. It is a new germinal character which has appeared in the northern bird, entirely *sui generis;* there is nothing suggestive of it in the southern ostrich.

We have the hard fact to account for that the germ plasms of the northern and the southern ostrich differ from one another in certain respects as revealed by their manifestation in the soma, and it is also proved that they breed true irrespective of environment. And while in our condition of absolute ignorance no good purpose will be served by dogmatizing it may be permitted to express the conviction that the germ plasm changes as between the northern and southern ostrich have resulted entirely from internal physiological causes. The conviction is strengthened all the more from the facts to be presented in the next section.

B^3

V

"Hereditary determiners or factors fluctuate regularly and frequently, if not indeed usually, and in high correlation with somatic characters."

In a certain measure this statement may be looked upon as opposed to that with which section 1 opens, but no one would maintain either the one or the other to be the exclusive state of the germ plasm, hereditary determiners or factors of all animals and plants. We have abundant evidence that the germ plasm is remarkably conservative for some forms of life (persistent types) while in others it may fluctuate or change frequently (*Drosophila*); also, it is not unreasonable to expect that at any one period the factors for certain parts of an organism may remain fixed while for others they may be in a state of change. We have seen that the factors controlling the structural details of the ostrich plume are peculiarly constant, but the endeavor will now be made to establish that those for the wing feathers numerically, as well as for certain other parts of the bird, are undergoing regular and frequent changes and in determinable directions.

By zoologists the wing of the ostrich is usually regarded as degenerate, on account of its small size compared with the body and legs and the practical absence of any covering of feathers on its inner or under surface. Certain studies recently made have given good reason for concluding that in many other less obvious respects it is still undergoing degeneration. The full details upon which

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[3] The three statements under section B are obviously considered by Dr. Pearl to apply specially to Dr. Castle's claims in connection with his experiments on piebald rats, a condensed account of which appears in the same issue of the NATURALIST as Pearl's paper (p. 102). Instead of regarding them as applicable only to the disputed plus and minus fluctuations in the factor itself it may be permissible to consider them in a broader sense, as referring to the nature of the germ-plasm generally and as contrasted with those in section A. What follows has probably no connection with results such as those which Castle has obtained but nevertheless it is hoped to show that real factorial changes, continuously retrogressive in their nature, are going on in the germ plasm of the ostrich and that there is much likelihood the changes can be influenced by selection.

the claim is based will appear later. Only the outline of the facts can now be given in so far as they bear upon the condition of the germ plasm.

Only a single row of under-coverts usually occurs on the wing of the ostrich, its members alternating with the remiges or wing quills (Fig. 1). In but two specimens out of hundreds examined however has the full number of feathers required for alteration with the complete row of remiges been found. Usually eight to ten are missing from the elbow end of the row, though the number varies, and occasionally two or three vestigial feathers may appear between the normal members and the missing sockets. Single plumes are at times met with in front of the row and are obviously representatives of a second row, while in one farmer's strain an almost complete second row of under-coverts occurs, alternating with the first, and in front of this are five or six members of a third row. One is forced to the conclusion that the ancestral ostrich had the under surface of its wings provided with several rows of under-coverts in the same manner as modern flying birds, and that the rare occurrences mentioned are in the nature of survivals, the germinal factors responsible for their appearance having been largely, though not yet altogether, lost to the race.

The valuable wing quills or remiges ordinarily vary from 33 to 39, having the same average, about 35.5, for both the northern and southern birds. They constitute a fluctuating series about the mode 36, though there is much probability that each separate number in the series will be found to represent a pure line. Assuming that not much numerical variation occurs in the plumes of the ostrich the farmer has never yet bred for quantity, quality has been his only consideration. Recently however a cock bird has been discovered among the government's experimental troops bearing 42 remiges, and it is submitted that this high number represents an ancestral survival rather than a reversion or mutation, and that the wing quills of the African ostrich afford us various stages in degenera-

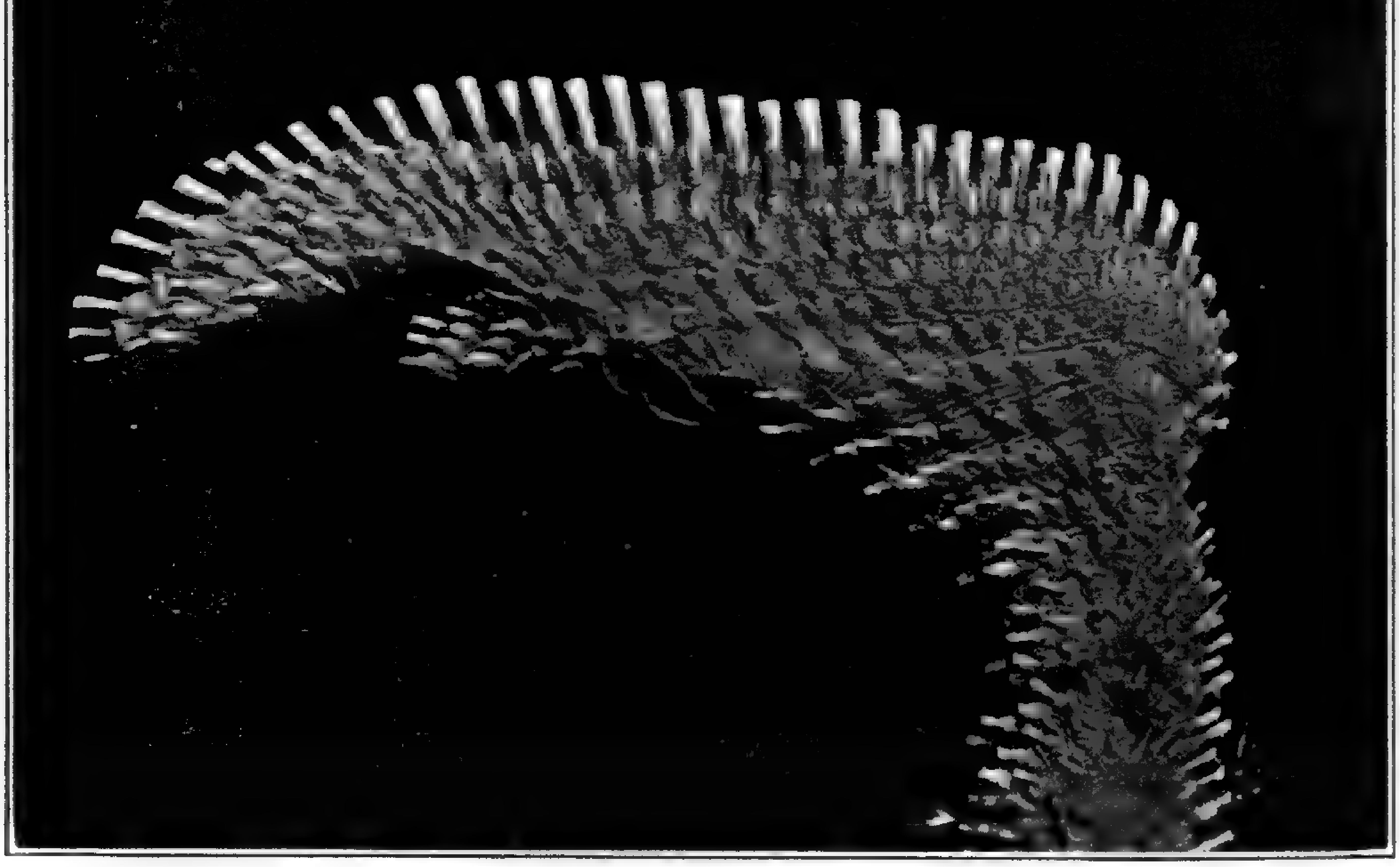

Fig. 1. Under surface of wing of ostrich with plumes clipped off. In by far the majority of ostriches the surface is naked except for the single row of under-coverts which is rarely complete; in the specimen represented six of the coverts are missing from the elbow end of the row. In one farmer's strain an almost complete second row of under-coverts occurs and also a few members of a third row. The third digit is almost buried in the flesh of the wing, but can be seen projecting slightly towards its distal end. The claw which is present on the first and second digits is not clearly shown.

Fig. 2. Outer surface of wing of ostrich, the plumes having been clipped off to show their arrangement in rows. The feathers in the uppermost row, the wing quills or remiges, vary from 42 to 33 in different birds. The members of the first row of upper-coverts alternate with the wing quills and vary with them in number, while the second row of coverts has often a number missing towards the free end of the row, though not in the wing represented. The other rows of coverts, third, fourth and fifth, may also show reduction. The marginal row of the bastard wing may contain from two to seven feathers.

tion from the maximum 42 to the present minimum of 33. As experiments have proved that the high number breeds true, and as the other rows of commercial plumes vary in correlation with the remiges, the discovery has a great industrial bearing; for it now becomes possible to provide the farmer with a pure line of 42-plumed ostriches in place of the degenerate 36-plumed birds with which he farms to-day, and the entire feather crop will surpass the present one by about 25 per cent.

The first row of upper-coverts varies in correlation with the remiges (Fig. 2) but never shows any independent reduction, while the second row has often a number missing from its distal end, and is clearly undergoing reduction here in contrast with the elbow end for the under-coverts. Again, it is usually stated by writers that the ostrich is destitute of an under-covering of down feathers and filoplumes, yet in every northern and southern bird examined, down in all stages of degeneration occurs around the base of the larger plumes of the wing and tail, and in rare cases spreads over a wider area, leading to the conclusion that at one time the ostrich had an under-covering of small feathers like flying birds generally.

The third digit displays certain most unexpected evolutionary stages. While in most cases it is altogether embedded in the flesh of the wing, and can only be seen and felt through the thin skin, yet occasionally its tip projects quite freely, suggesting its former separation, like the first digit which forms the ala spuria. Moreover, in some birds odd feathers are to be found set along the finger, altogether detached from any other series. These are surely to be understood as survivals of a time when the third finger was clawed, free and provided with its own feathers, a primitive condition which is usually held to be represented only in the oldest known fossil bird, *Archæopteryx.*

The legs and toes likewise exhibit degenerative phases. The African ostrich is unique among living birds in having already lost its first, second and fifth toes, only the third and fourth remaining. The outer, fourth toe is far smaller than the inner third toe, and the condition of its claw as well as its smaller size lead one to infer that it also is on the road to disappearance (Fig. 3). In northern birds the claw of the fourth toe is frequently discernible, though altogether functionless, never reaching the ground;

FIG. 3. Tarsus and foot of North African ostrich. The outer, fourth toe is greatly reduced in comparison with the inner, third toe. The former shows a small non-functional claw. A distinct break occurs between the scutellation of the tarsus and that of the middle toe, though in most ostriches the two series of scales are continuous. A second break is beginning to form over the middle joint of the toe, the larger scales being divided into two or three smaller ones.

but on only a few southern birds is it ever seen, and then in a most vestigial state, barely showing beyond the skin.

What may doubtless be regarded as the first steps in the degeneration of the big middle toe are also displayed. Down the front of the tarsus extends a series of large, nearly rectangular scales, continuous all the way from a little below the ankle and passing over the upper surface of the toe, though usually somewhat smaller where the toe joins on to the tarsus. In a few ostriches a distinct break occurs at the joint, several large scales being altogether wanting (Fig. 3), and rarely birds are met with in which a second break takes place over the middle joint of the toe. One may hazard the suggestion that the interruption in the scutellation over the two joints has an adaptive significance, allowing the parts to move more freely, but we have also to face the fact that the single break occurs in but a few while the double break is very rare. It is presumably a new feature in course of introduction into the ostrich race, but not yet established for the members as a whole. It involves however a reduction in the make-up of the toe; it is a minus or retrogressive mutation, and may well be the first hint of impending loss of what will be the only toe when the small fourth has gone.

Although definite experimental data on all these reduction phenomena are not yet available everything points to the fact that the variations breed true and are therefore germinal in their nature; they are certainly not ordinary fluctuating somatic variations. Proof is to hand that the 42-plumed cock has factorial representation for its high number of plumes. Another similarly numbered hen is not yet available, but in crosses with various 36-plumed hens the average number of plumes of the progeny is 39.56 which is midway between the parents, while the mode is 40. Considering the heterozygous nature of the ostrich where number of plumes is concerned a fluctuating series of this kind is what would be expected. Only one farmer's strain has the nearly complete second and third rows of under-coverts, but they are found in all the progeny from the strain; all the members of a flock bred from the same stock have the second row of upper-coverts complete, while in other flocks all the members have a number of plumes absent from the row. Crossing of birds in which the complete loss of the claw on the small toe has taken place with others in which the claw still appears gives results on strictly factorial lines, as also does the crossing of birds with and without a loss of the scales. In a mixed assemblage of any species where only a small proportion display a certain character it may be presumed that the latter will be heterozygous with regard to the particular character, seeing that the chances are much against the mating of two individuals each having the character. The heterozygous nature of the bird can be demonstrated on mating with one in which the character is absent, for if dominant it will appear in half the progeny and be absent from the others. This proportion with regard to the presence of the claw and the loss of the toe scales has been found to hold in all the crosses. Out of a total of 36 chicks hatched from breeding pairs where one parent was clawed and not the other the numbers were actually equal, namely, 18 chicks were clawed and 18 unclawed. Out of 11 chicks reared from a pair where one parent showed no loss of scales on the big toe and the other had a single break, 5 had no break and 6 showed the break.

It may be accepted then that all the degenerative phases represent factorial changes which have come about in the germ plasm of the ostrich. Presumably the changes involve a loss of factors; they are retrogressive or negative mutations. Structures which would be expected to occur either fail to appear or are seen very rarely, and may then be regarded as survivals, the factorial losses not having yet taken place in the particular individuals. Thus, to take the case of the first row of under-coverts, the principle of alternation demands that a complete row of under-coverts should alternate with the row of remiges. The full row actually occurs in a few individuals, and suffices to prove that this was the condition in the ancestral ostrich; more usually eight to ten are missing and also fail to appear in the progeny. It is therefore reasonable to assume that the germ factors originally involved in the production of the eight to ten under-coverts have disappeared from the majority of ostriches though they are retained in a few. The fact that all the intermediate numbers can yet be obtained shows the loss to have been progressive. A similar line of argument can be applied all through. Loss or degeneration is in progress in various directions and differs in degree in different individuals, and the losses are the outward expression of internal changes in the germ plasm.

Where a loss of factors is taking place it could hardly be expected that all the individuals of the race would be affected at one and the same time. The process would be more rapid in some than in others, some would incur the loss at one time and some at another, and the results from crossing would need to be reckoned with. Hence we can understand the great diversity of stages represented in the ostrich where large numbers are available for examination. It may be hard to comprehend how in the first instance germinal changes can be brought about, but if once effected, their repetition and continuance can reasonably be expected. Beginning with one or a few birds it is manifest that as the loss in any direction continues more and more individuals will become affected, until in the end complete loss for the race will be achieved. So far as the investigation of farmer's troops has proceeded it affords strong evidence for the view that only one original 42-plumed bird now exists in South Africa, so that under natural conditions the extinction of this high number of remiges would be imminent. The loss of the claw from the third finger is probably only recent. Some textbooks of zoology[4] assert that a third claw occurs, but it has never been found on the hundreds of southern and northern ostriches coming under my examination, although specially looked for.

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[4] **Parker and Haswell, Vol. II, p. 393.**

In most instances it would appear as if the loss of all the many factors concerned in the production of a single plume takes place simultaneously, as is the case with most meristic structures; for usually the absences are complete plumes. In some birds, however, two or three incompletely formed or vestigial feathers occur between the normal feathers of a row and the absent sockets, as if the loss of the individual plume were taking place piecemeal. This condition can be easily understood if we assume that the constituent factors concerned do not all drop out together, but follow some sort of succession. The factors left at any time would then give rise to the part of the feather for which alone they are responsible, and we should get an imperfect or vestigial feather. In any animal vestiges of a structure will continue to appear so long as any of the factors concerned in the original structure remain. It is submitted that degeneration of any complex structure never takes place in a gradual continuous manner, as is usually supposed, but by successive steps determined by the manner in which the factors drop out; the appearance of continuity will however be conferred if the steps are small enough.

If a sufficient number of individual ostriches were gathered together it could easily be made to appear as if degeneration in any of the recognized directions were taking place in a slow continuous manner, for all stages between the extremes could be obtained. Proceeding by such a method however would give an erroneous impression of what is actually happening. For although all stages do occur they are in reality disconnected, and each stage has been reached in an individual quite irrespective of the others, and represents a separate and distinct germinal loss; furthermore, in the same individual degeneration in any one direction proceeds quite independently of the other directions in which the process is taking place. It is not the wing as a whole which is undergoing degeneration, but the constituent parts of which it is made up, each presumably represented by its own factors and behaving with a large measure of independence. The losses are continuous for the race but discontinuous for the individual; and it is with the individual that heredity is concerned and evolution with the race.

The degeneration phenomena presented by the ostrich in connection with its wings and legs, as well as with its plumage, would appear to provide us with an example of the application of mutative and Mendelian principles to such evolutionary facts as confront the comparative anatomist and paleontologist. So far as concerns the individual bird the retrogressive changes are shown to occur as separate mutations and to follow definite factorial lines, while as concerns the evolution of the race they proceed in a continuous determinate manner. In all probability they take place wholly irrespective of any adaptive significance or consideration for the welfare of the bird, and are intrinsic in their nature and uninfluenced by external conditions. Natural selection has probably played no part in connection with the losses, for the greater changes have already affected the race uniformly and the smaller ones which still vary in degree in different individuals will probably affect the whole in the end. Should the loss of plumage continue to a much further degree and marked degenerative changes be set up in the big middle toe natural selection may then be expected to bring about extinction.

The chief point desired to establish at present is that as regards the number of its wing plumes and in certain other features the ostrich affords strong support for the view that its hereditary determiners or factors are changing regularly and frequently; they are not fixed and constant as are the factors for the structural details of the plumes; one series is in a state of change, the other is non-changing. The great variety and degree of the degenerative stages in the ostrich of to-day admits of no question, and that they are the expression of so many germinal differences may be accepted, seeing that they breed true; that they have been effected simultaneously as we find them is inconceivable, and we are justified in concluding that in the past the germ plasm has changed frequently and presumably over a long period. Moreover, we can hardly admit that the various degenerative phases will remain as they are at present, but that further losses in the same direction will follow, that is, the germ plasm will continue to undergo retrogressive changes of a like character to those already initiated. We may have an appearance of continuous change, but when analyzed it will be found to proceed by means of separate factorial steps. It is conceivable that a continuance of the kind of factorial losses now in progress will result ultimately in the complete disappearance of the wings and legs of the ostrich, allowing that the bird could survive the intermediate stages, a postulate which it must be conceded is of no mean order. May we not suppose that the limbless condition of snakes and some lizards, amphibians and fishes has come about by the successive losses of germinal factors in a similar manner to that which is here shown to be taking place in the ostrich?

The bearing of the germinal changes involved in the degenerative processes upon the thesis of Section IV, may be noted. It is in the highest degree improbable that determinate losses of such a widely embracive nature are taking place in response to any environmental stress acting upon the germ cells; rather they may be regarded as the result of some wholly internal physiological cause. If due to environmental stress one could reasonably expect that in any individual the losses would be taking place in all directions simultaneously, and would have reached about the same degree in all. But among the various rows of feathers, as well as in other parts, the greatest independence in reduction is met with, as if the factors for each were subject to a separate rather than a common influence.

VI

"Mixing of germ plasms in fertilization alters hereditary determiners mutually and hence is, in and of itself,

a cause of genetic variations . . . a purely external agent, the continued selection of personal somatic qualities, will alter the germ plasm."

It seems to be generally allowed that at any period the majority of forms of life are static so far as germinal alterations are concerned, while some are undergoing progressive changes and others retrogressive changes. During the present period the representatives of the widely distributed Ratitæ are unquestionably undergoing marked changes and have been for ages past. The changes are in a negative or retrogressive direction, and express themselves in somatic degeneration, particularly with regard to the wing and shoulder girdle. The living *Apteryx* is a well-known instance of wing degeneration, as also the recently extinct moas, in which no hint of a wing has been found and a trace of the glenoid cavity only in one species. From the data already submitted we are able to learn something as to the manner in which the degenerative processes are proceeding in the wing and leg of the ostrich, and presumably the same method holds for the Ratitæ generally. Factors are evidently in process of dropping out, in regular succession, along definite prescribed lines, the degree varying much when the entire race is taken into account.

All Mendelian writers seem to concede that the factorial changes, plus or minus, are not autonomous on the part of the factors, but are "a result either of wholly internal physiological causes, or of very extraordinary environmental stresses acting directly upon the germ cells." Though the results of Morgan and his associates indicate that it may yet be possible to understand the manner in which the factors undergo their changes it will always be competent for us to enquire as to the cause or causes inducing the changes. To be complete our analysis of variability will need to get beyond the factors to the force or forces acting upon them. In the previous sections good reason has been adduced for supposing that the losses going on in the germ plasm of the ostrich are due to some wholly intrinsic cause, and seeing that it affects all the members of the race and has been operative for a long period we may conclude that it is transmissible and acts continuously from generation to generation. The many stages represented also give some justification for supposing that whatever the cause of the factorial changes may be it varies in intensity in different members of the race, being less active in individuals where the loss of plumes is small as compared with others in which the loss is greater. For example, the causative agent bringing about the loss of the plume factors must be less in intensity or less active in 42-plumed ostriches than in 33-plumed birds. We may with good reason expect that the selection for breeding of the high numbered birds will arrest the rate of degeneration of the race in this particular feature, while on the other hand the selection of the low-numbered birds will tend to accelerate the rate at which the factorial losses are taking place. Where therefore the germ plasm of a race is in a continuously changing phase, as in the ostrich, we can hope to retard or accelerate the changes by selecting individuals differing in the degree to which they are under the influence of the causative agent. It is submitted that in this sense we can say that "a purely external agent, the continued selection of personal *somatic* qualities, will alter the germ plasm."

We can not hope that the continued selection of 42-plumed birds will in the end give to the farmer ostriches with a still higher number of remiges, as the factors for the plumes beyond these have in all probability disappeared from the race, and there is no evidence that the cause of the factorial changes is effective in a plus but only in a minus direction. On the other hand the continued selection of 33-plumed birds may reasonably be expected to accelerate the loss of the remiges, by leading to a more rapid loss of the factors. Owing to the present degenerative forces at work in the ostrich we can by selection hope to modify the germ plasm in a minus direction, though not in a plus direction, beyond the present limits of the race. It will of course be readily appreciated that this possibility differs altogether from that due to the ordinary selection which may go on in a race of organisms where the germ plasm is static, but where all grades of pure lines may be extracted between extreme limits. Where the germ plasm for a race is static, as demonstrated by Jennings in his work on *Paramæcium*, we can readily understand that no further change is possible by selection within a pure line, as nothing inducing factorial changes is present. If where germinal changes are taking place it is not permissible to think of the factors as changing autonomously we have to assume that some causative agent is present, and may vary in degree in different members and thereby form a basis for selective action.

The same considerations can be applied to the statement: "mixing of germ plasms in fertilization alters hereditary determiners mutually and hence is, in and of itself, a cause of genetic variations." When, for example, two germ plasms, in each of which the causative agent producing loss of factors is at its maximum, become mixed in fertilization it is reasonable to expect that the agent will be intensified and the hereditary determiners will be altered mutually, and some of them drop out. The mixing will be, in and of itself, a cause of genetic variation, which will be expressed by a further loss of remiges.

Though the idea of a causative agent inducing changes in the germ plasm, and varying in degree and also transmissible, is altogether hypothetical yet it is stimulating to further experimental effort. Of the hundreds of ostriches examined not one has been found with less than 33 remiges, hence this number must be regarded as the present minimum of the race. There is every reason to expect that a pure line having this number only can be built up. If by breeding these together a further reduction of plumes should take place we should then be fully justified in assuming that the factors concerned with the lost members had dropped out from the germ plasm, especially if later breeding failed to restore them; selection would have induced a definite change in the germ plasm. Also if a pure line with 42 remiges were established and no further increase occurred we should be warranted in concluding that the factors for the plumes beyond this number had already disappeared from the race and could not be restored; the causative agent could not act in a plus direction. It is unfortunate for such investigations that the ostrich is such a slow breeder. Experiments are however being conducted to determine if further reduction in the 33-plumed birds can be induced, while the building up of a pure 42-plumed race is also in progress, the latter having an important industrial bearing.

In many respects the degeneration phenomena in the ostrich appear to be best understood on the conception of autonomous changes and variations in potency of the germ factors. In the case of the dropping out of plumes during the chick stage the reduction in potency has proceeded so far as to result in entire loss of effectiveness only from the chick stage onwards, while complete loss of factors from the germ plasm may be regarded as the final loss of potency. May not a variation of potency of factors be at the root of many of the so-called fluctuating variations? The explanation seeks for the loss of factors among the autonomous changes in the factors themselves, while the idea of a "causative agent" throws the responsibility for the changes upon some influence external to the factors.

Since the above was written certain results have been obtained which strongly support the idea that it may be possible to induce retrogressive changes in the ostrich. As stated, a loss of scales over the large middle toe has already taken place in a small proportion. Out of twenty southern birds of mixed breeding one showed a single break while out of twenty mixed northern birds a single break occurred in three cases and a double break in two. The results given below are derived from the mating of a northern cock without any break and a southern hen in which the break occurs. Of the four offspring reared three are without the break while it occurs in hen No. 179. From the mating of brother and sister four F_2 chicks were hatched, two of which have a double break in the scutellation, one shows a single break and one has no break. Thus the proportional loss of scales has greatly increased in the F_2 generation.

SCUTELLATION IN F_2 CHICKS COMPARED WITH PARENTS AND GRANDPARENTS

	No Break	Break
N. A. cock, No. 9	×	—
S. A. hen, No. 225	—	×
F. Crosses.		
Cross-bred cock, No. 182	×	—
Cross-bred hen, No. 179	—	×
F_2 Chicks.		
No. 1	—	××
No. 2	—	×
No. 3	—	××
No. 4	×	—

From what has been adduced already we may with good reason admit that an inherent tendency exists in the ostrich towards the loss of certain parts of the fore and hind limbs, and the above result may be regarded as highly suggestive that by inbreeding the inherent tendency towards the loss of scales can be accentuated along definite lines. The accumulation of fuller data must be awaited before the suggestion can be regarded as more than tentative.

ADAPTATION AND THE PROBLEM OF "ORGANIC PURPOSEFULNESS." II

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IV. THE PRINCIPLE OF TRIAL AND ERROR IN RELATION TO REGULATIVE PHENOMENA[14]

Driesch and some other vitalists draw their most effective ammunition from the phenomena of experimental embryology and regeneration. How is it that a fragment of a developing organism—any fragment, within certain limits—can produce the whole? How it is that various perversions of the normal course of development do not prevent the attainment of the normal end? How is it that certain adult organs, *e. g.*, the lens of the eye of a triton, when removed by a highly "unnatural" operation, is nevertheless restored, and restored by a process quite different from that in which it is normally produced in embryonic development?

At the outset we must make two admissions: (1) that these processes can not be the result of a mechanism specifically adapted in advance to meet these particular exigencies, and (2) that they can not be satisfactorily explained by assuming any preformation of the parts which are restored. The former supposition is to be re-

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[14] The "trial and error" principle has of late years come into the foreground of biological discussion, largely through the writings of Jennings. It was, so far as I know, first clearly proposed (though not so named) by Spencer (*Principles of Psychology,* Vol. I, pp. 544–545) to account for the origin of adaptive responses to stimuli, and was later developed by Bain. There are important points of agreement between the views of these writers and some of those set forth independently by Roux in his classic essay, "Der Kampf der Theile im Organismus" (1881). More recently, Baldwin (*Mental Development,* 1898, Chapter VII; *Development and Evolution,* 1902, pp. 108–115) has further elaborated the same fundamental idea as that of Spencer and Bain in his theory of "functional selection." Various animal pyschologists (e.g., Lloyd Morgan and Thorndike) have also laid stress on this principle.

jected on account of the unusual and artificial character of the operations, which could never have been provided for by natural selection, nor, so far as we can see, by any other recognized principle of evolution. The latter supposition is sufficiently disposed of by Driesch's analysis (section III) and need not be considered here.

Driesch admits that a physico-chemical machine "might very well be the motive force of organogenesis in general, if only normal, that is to say, if only undisturbed development existed, and if a taking away of parts of our systems led to fragmental development" (II, 139). If, therefore, we can explain these critical cases without invoking any principles beyond those believed to be operative in normal life-history, we have disposed of this line of argument.

In an earlier section of this paper I took the ground that an adaptive or "purposive" response by the organism, if not guided by past individual or racial experience, must be the result of experimentation. I avoided intentionally at the time any consideration of those cases of regeneration and form regulation in which the emergency was totally new, and therefore foreign to the experience of the organism or its ancestors. Here a specially evolved mechanism could hardly be invoked. I suggested, however, that the principle of "trial and error" could be applied to these cases: This suggestion was, of course, not new. Such an extension of this conception had already been made by Jennings,[15] though it is rather surprising to note that he has given it little further consideration in his recent discussions of vitalism. For, to my mind, an explanation involving this principle, seems the only alternative at present to a vitalistic one, or, better stated, it seems to me the only alternative to an abandonment of the search for a scientific explanation.

According to the trial and error principle, as applied to the movements of a lower animal, "behavior that results in interference with the normal metabolic processes

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[15] "Behavior of the Lower Organisms" (1906), Chapter XXI.

is changed, the movement being reversed, while behavior that does not result in interference or that favors the metabolic processes is continued.''[16] The primary ''avoiding reaction,'' in the presence of an unfavorable stimulus, is, of course, comparable with a simple reflex. Its ordinary effect is to remove the organism from the noxious influence. When progressive movements are resumed, they occur at random, so far as their direction is concerned, and they may or may not take the organism into favorable surroundings. If they chance so to do, they are continued indefinitely. If not, the reversal of movement occurs as before. Thus while, to the uncritical observer, the organism seems to ''seek out'' the optimum environment, it really reaches this through a series of accidents. This is as true of a cat, releasing itself from an experimental trap, as it is of a paramœcium escaping from a harmful to an optimum water temperature. In the case of the cat we may be tolerably sure that the animal experiences a feeling of discomfort until the means of escape is discovered, and we find it convenient, if not inevitable, to say that her restless movements are the *result* of this feeling. In the case of the infusorian, we are much less sure of the conscious element, though its introduction is permissible as an act of philosophic faith. In theory, most scientists are probably psychophysical parallelists, but in practise it seems necessary at times to use the language of interactionism. In discussing the voluntary movements of a higher animal, any other course would seem pedantic. But in discussing the simple behavior of a lower organism, such language is commonly branded as ''anthropomorphic.'' Nevertheless, I believe that its employment even here is sometimes useful in forcing us to keep in view the essential unity of animal life. No protest is raised by the physiologist when thoroughly *protozoomorphic* language is applied to a vertebrate. Why then should ''anthropomorphic'' terminology so shock us in describing the be-

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[16] Jennings, *op. cit.*, p. 39.

havior of a *Paramœcium?* Each is the extension of an article of philosophic faith far beyond the realm of experience. But this is no essential part of our present argument. Let us consider whether the trial and error principle may not be applicable to other phenomena than the bodily movements of animals.

Jennings asks:

> Is it possible that interference with the physiological processes may induce changes in other activities,—in chemical processes, in growth, and the like,—and that one of these activities is selected, as in behavior, through the fact that it relieves the interference that caused the change? . . . It is evident, then, that the organism has presented to it, by the condition just sketched, unlimited possibilities for the selection of different chemical processes. The body is a great mass of the most varied chemicals, and in this mass thousands of chemical processes, in every direction,—all those indeed that are possible,—are occurring at all times. There is then no difficulty as to the sufficiency of the material presented for selection, if some means may be found for selecting it (*op. cit.*, p. 346).

Looking for evidence that such a process of selection does actually occur in physiological regulation, Jennings cites the experiments of Pawlow, in which the latter habituated dogs to various kinds of foods and noted the effects upon the digestive juices. In these experiments

> the adaptive changes in the activities of the digestive glands, fitting the digestive juices to the food taken, do not occur at once and completely under a given diet, but are brought about gradually. . . . This slow adaptation is, of course, what should be expected if the process occurs in anything like the manner we have sketched (p. 347).

Jennings concedes:

> It is perhaps more difficult to apply the method of regulation above set forth to processes of growth and regeneration. Yet there is no logical difficulty in its way. The only question would be that of fact, whether the varied growth processes necessarily do, primitively, occur under conditions that interfere with the physiological processes. When a wound is made or an organ removed, is the growth process which follows always of a certain stereotyped character, or are there variations? It is well known, of course, that the latter is the case. . . . Removal of an organ is known to produce great disturbances of most of the processes in the organism and among others in the process of growth. . . . Some of these relieve the disturbance; the variation then ceases and these processes are continued (p. 348).

A line of argument which has points of similarity to the foregoing has been independently developed by Holmes.[17] He believes:

> The harmonious functioning of an organism is mainly secured by a system of automatically acting checks which we may conceive to act in manner more or less remotely analogous to the governor of a steam-engine or the forces which regulate the motions of the planets. . . . In these cases deviation from the normal is the cause which automatically sets up activities by which the normal is regained.

So, too,

> the self-regulation of organisms may . . . be in a measure understood if we assume that their parts stand in a relation of mutual dependence such that the undue growth or functioning of any part is held in check by the reactions thus brought about by other, and especially the contiguous structures. If we suppose that the various cells constituting the body have each a different kind of metabolism, and that the products of each cell are in some way utilized by the neighboring cells, so that each derives an advantage from the particular association in which it occurs, we may understand, in a measure, how this checking may be brought about.

And here an analogy is pointed out with the relations which obtain in "symbiotic" communities, such as those composed of animal cells and certain unicellular algæ.

The conception here developed is in some respects an extension of Roux's intra-selection hypothesis, though Holmes rejects the notion of a "struggle of the parts." This conception, which derives strong support from recent discoveries respecting "hormones," gives a certain measure of concreteness to that rather vague expression, "the organism as a whole." For, despite the many known instances of local autonomy, we can not doubt that the organism does in a high degree act as a whole. But this "wholeness" may not be an irresolvable fact, as has sometimes been assumed. It may be possible to conceive it in terms of chemical and structural integration.[17a]

This hypothesis, as applied to form regulation, would

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[17] *Archiv für Entwicklungsmechanik*, 1904.

[17a] To me, such a viewpoint seems quite reconcilable with the "organismal" conception of Ritter, though Professor Ritter himself (The Unity of the Organism, Vol. I, p. 183) has gone to considerable pains to show the fallacy of Holmes's position.

seem to be closely related to that of Jennings, and indeed Jennings himself views it in this light. It is difficult to gather, however, to what extent Holmes has in mind the principle of "trial and error." His comparison of regeneration with functional hypertrophy does not seem compatible with this principle. "Remove one of a pair of organs," he says, "and its fellow increases in size. Remove a part of one of these organs and the remaining portion grows, forms new tissue, and regenerates the missing part." Furthermore, he believes that these phenomena may be analogous with some of those described under the name of "chemical equilibrium."

> The decomposition of compounds in solution proceeds until there is a definite relation established between the amounts of the old compounds and the new. If the chemical equilibrium thus established is disturbed by the removal of one of these compounds more of that compound will be produced; and the more rapidly the compound is removed, the more rapidly it is formed.

Such an "automatic" restoration of equilibrium as this might seem to be a radically different thing from trial and error. The process by which it is attained would appear to be direct and unhesitating. Holmes says that the solar system, no less than the organism, is a "self-regulating mechanism." Now, in the former, the balance of its opposing forces is effected "automatically" in the sense that any deviation in the movement of one of the parts would result inevitably in a compensating deviation in the others. Is the restoration of an organism to its norm of this direct and automatic type? Are such processes as tend to compensate a disturbance in the normal functioning of an organism the direct and exclusive result of the disturbance itself, or does this disturbance evoke a variety of responses of which the suitable response may finally happen to be one? The first of these alternatives may be admitted as probable in the case of such disturbing factors as have been frequently experienced in the past. But how does it happen that certain cells of the iris of a newt become stimulated to division by the removal of the lens? And why should their metabolism become so affected that they give rise to lens tissue, instead of to iris tissue? Can we believe that the iris cells proceeded unfalteringly to this end as a result of the operation?

The discussion after all hinges upon the word "unfalteringly," and this term has been applied to processes which are beyond the possibility of direct observation. If we grant that a disturbance of growth equilibrium was what led to the reparative processes, and that equilibrium was in the end restored, it does not seem difficult to admit that each minutest step in the direction of restoring this equilibrium was selected from a medley of random reactions. Indeed, Holmes suggests that

> cells which develop in the direction of the missing part receive those advantages which the symbiotic relation afforded the cells whose place they take. Differentiation in any other direction deprives them of these advantages and subjects them to other unfavorable conditions.

Nor need it be assumed that these responses are wholly random. Although it is incredible that each type of possible injury has been provided for in advance by a specific mechanism, it seems more than possible that certain reactions have been acquired which are of service in *any* emergency—a sort of "first aid to the injured," as we might say. After these preliminary steps of a general character—which are, as a matter of fact, the common precursors of regeneration[18]—the more special processes may be supposed to proceed in a tentative fashion.

All that is meant by "growth equilibrium," in this discussion, is such a normal state of metabolic balance that the growth of each part is checked through its organic relations with the rest. Attainment of this goal would bring the organism into a condition of "no stimulation," like that of the protozoan which has escaped from an unfavorable environment.

Since we commonly are able to observe only the final outcome of such a process, and overlook the minute steps

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[18] These steps are frequently retrogressive ones and include the loss of specialized structures.

by which it comes to pass, we are wont to believe that the reparative activities move directly toward the end which we observe to be ultimately attained. Thus Driesch tells us that

> the process of restitution, perfect the very first time it occurs, . . . is the classical instance against this new sort of contingency. . . . Here we see with our own eyes that the organism can do more than simply perpetuate variations which have occurred at random.

What we see with our own eyes, as I have already said, is only a series of visible stages in the process of restitution. We *do not see* the inmost morphogenetic processes, physical and chemical, by which this end is attained.

Perhaps it may seem that the foregoing explanation merely resorts to the familiar expedient of throwing our difficulties back into an invisible realm where they are safely beyond the reach of scientific investigation. I would say first of all that even this type of explanation, which at least speaks in the language of known facts, is preferable to one which frankly abandons scientific principles altogether. And secondly, I would point out once more the possibility that this hypothesis is one which may in reality be put to experimental test. For any indication of a profiting by "experience," *i. e.*, of a shortening of the time required to effect a given regulative response, would harmonize well with the hypothesis that the response was at first effected through tentative steps. Indeed, such evidence, even now, is not wholly lacking.

It may be well to remind ourselves at this point that the perfect regeneration of missing parts, or the complete reconstruction of a mutilated embryo is after all an exceptional phenomenon. Many animals almost entirely lack the power of regeneration, while most injured eggs either die or give rise to abnormal embryos. These facts harmonize best with the view that regenerative processes are causally produced in the same sense as inorganic phenomena, and that they are not determined, in any direct way, by needs or ends to be realized. The formation of misplaced, supernumerary and other useless structures, and the occurrence of anaphylaxis, instead of immunization, certainly do not argue for the existence of a "primary teleology" in nature, though, of course, they do not wholly refute it.

On the other hand, the occurrence of these non-adaptive responses to growth stimuli is no more inconsistent with an intra-selection hypothesis, such as that here advocated, than is the occurrence of multitudes of non-adaptive structures or colors in nature inconsistent with the theory of natural selection. There must be rigid limitations to the operation of both processes. The task which I have undertaken here is not to explain structures and function in general, but the more modest one of trying to explain why certain among these are directed toward the conservation of the individual or the species. If various other vital phenomena are found to be non-adaptive, our difficulties ought not to be increased.

There are cases, it is true, in which some simple physical factor, such as gravity, or the plane of section, may determine whether the actual missing part is restored or a misplaced organ is the result. It certainly seems arbitrary to offer fundamentally different explanations in the two cases. Now, I have nowhere made the contention that the processes involved in regeneration are wholly random, in the sense of being unrelated to one another and to the past history of the individual. In normal development the processes are doubtless so concatenated that growth and differentiation proceed in a direct way with little or no "lost motion." And every detached portion of such an organism must receive its share of this established developmental machinery. The tendency to reconstruct the whole, to attain the normal specific form, is therefore opposed by another set of tendencies, urging it to develop as if it were still part of the undivided organism. As is well known, the outcome of this conflict of forces varies, depending upon the species of animal and the time of operation. We may have either total or fractional development as a result. It does not seem unlikely, therefore, that in every case of regeneration the control of the "organism as a whole" is opposed, more or less successfully, by the specific growth tendencies of the various cells and tissues from which restitution proceeds. These might, in consequence, bring about the "autonomous" production of a wholly misplaced part.[19] Thus the phenomena of "heteromorphosis" should seem to offer no insuperable obstacle to the views herein set forth.

Applied to the ordinary phenomena of regeneration, say to the restoration of an amputated limb, or even the lens of an eye, this hypothesis of achievement through experimentation would seem to make no impossible demands upon our imagination. We need only suppose that the absence of the missing part serves as a stimulus to varied and undirected metabolic activities, that such of these as serve to restore the normal condition tend to be continued and that growth equilibrium (absence of stimulus to growth) is not normally attained until the missing part is restored. The case would seem to be not very different from that of an animal finding its way out of an unfavorable environment. In both instances we may suppose the organism to be in a condition of "unrest" until the end is achieved. This condition may or may not be conceived in psychical terms. If so conceived, the notion would be philosophically legitimate, though scientifically unnecessary.[20]

When, however, we consider Driesch's crucial case of the development of an entire organism from an embryonic fragment, the matter is admittedly far less conceivable. For this fragment has retained nearly or quite the same potentialities as the entire egg or embryo, in that its career of multiplication and growth is brought

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[19] This explanation of heteromorphosis is, I think, quite in harmony with that offered by Holmes (*op. cit.*, pp. 302–303).

[20] Cf. Baldwin's statement ("Mental Development," p. 177): "*the life-history of organisms involves from the start the presence of the organic analogue of the hedonic consciousness.*"

to a close only through the attainment of the form which is typical for the species in question. Why should this ultimate condition of equilibrium be the same whether we start from an isolated blastomere, an irregular fragment of a blastula or a normal egg? Does it not seem as if the only constant feature in this case were the end itself? In considering the behavior of a protozoan, the stimuli may vary and the method of escape may vary, but the organism itself is the same. The "equi-finality" of the result—to use an expression of Driesch's—may be attributed to this fact that we are dealing with the same physico-chemical system, and one of the self-regulating type. But what of our various embryonic fragments? Are they not obviously different physico-chemical systems?

Now, after all, the difference between this case and that of a regenerating limb or lens appears to me to be only one of degree. The distinctions relate (1) to the stage in development at which the injury is inflicted, and (2) to the proportional part of the organism which is left to reconstruct the remainder.

1. As regards the first point, we must suppose that at each stage of ontogeny such a state of physiological balance is normally maintained as is appropriate to that particular stage. That the multiplication and differentiation of certain cells is profoundly influenced by the presence or absence of other cells is one of the assured results of experimental embryology. One need only cite the difference between the development undergone by an amphibian blastomere which is totally detached at the two-celled stage, and that of the blastomere whose partner has been injured by a needle-prick and left in position.

Thus we have as much right to assume for the blastula as for the adult animal that any disturbance of metabolic balance will be followed by varied responses, some of which will tend to restore the balance normal to that period. The fact that these responses are known to differ radically, following the same type of operation, and that the result is often a very imperfect reconstruction of the whole, lends support to the view that the cells of the injured embryo "feel their way"—so to speak—back into a condition of mutual equilibrium. In some cases this equilibrium appears to be of a simple physical sort, as for instance, that which is brought about by the folding together of the edges of a blastula fragment so as to reconstruct the spherical form. But in most cases the factors are doubtless vastly more complex.

Once the reconstruction of the normal embryonic form is attained, the difficulties in understanding the further stages of ontogeny are no greater than we meet with in the case of an uninjured embryo—that is, unless we are encumbered by a preformation theory of development.

2. As regards the second point above raised, there is theoretically no greater difficulty in understanding how one tenth of an organism may restore the remaining nine tenths than in understanding how the nine tenths may restore the one tenth. As a matter of fact, in dealing with certain organisms, the size or shape of the piece, or the region of the body from which it is taken count for little in the outcome. But they do count for something, and that something is significant. It has been found in some cases, for example, that there are lower limits to the side of the pieces which may carry out development or regeneration. And in other cases, the position of the plane of section may determine whether a useful structure is formed or one which is wholly useless.

But whether or not the size or shape of the fragment count for anything in the reparation of a given organism, we find that the *species* from which it is taken counts for everything. There must, therefore, be something that is common to all detached portions of an organism which are capable of reconstructing the same whole. The portion in question may be an asexual spore or a fertilized egg, or it may be an isolated blastomere or other artificially detached fragment of either an embryo or adult organism. What is this greatest common divisor? Is it a unit of structure or is it a chemical substance?

There would seem to be no third possibility, as long as we keep within the bounds of scientific explanation. But a unit of structure may none the less be itself a chemical individual. Modern speculative physics refers all qualitative differences in the last resort to differences of structure, even in the case of the elements. And it has been suggested that the various specific protoplasms, which are responsible for the slightly different metabolic products of different species, owe their differences to stereoisomers, *i. e.,* substances which agree quantitatively in their composition, but whose enormously complex molecules differ as the result of some slight transposition of atoms or radicals.[21]

To the majority of present-day geneticists there is doubtless a ready answer to the question: what is this something that is common to all detached portions of an organism which are capable of reconstructing the same whole? It is likely that to most of them a completely satisfactory answer would be: *the cell nucleus.* Thus Jennings,[21a] in discussing specifically certain of the questions raised by Driesch, assures us that "the recent study of genetics has shown that this [the chromosomal] apparatus is the system on which the peculiarities of development mainly depend. This system is not equipotential; the fate of its parts is not a function of their position; it has a complex structure with a corresponding complexity of action; altering any of its parts alters correspondingly the action of the system; irregular removal or disarrangement of the parts destroys the action."

Whether or not this aggregate chromatin matter of the nucleus constitutes the *minimum divisible* of the organism, as recent students of heredity are disposed to believe, is still quite undecided. For protozoa we are definitely able to state that this is not true. Experiments in regen-

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[21] Reichert, *Science,* November 6, 1914. This article contains much interesting evidence for the chemical distinctness of genera and species, and even of individual organisms.

[21a] *Philosophical Review,* Nov., 1918, p. 586.

eration show that there must be smaller bodies within the nucleus, each containing the potentialities of the entire organism. Ritter[21b] has recently insisted that the concept of *heredity* must be applied unreservedly to these one-celled organisms, many of which are quite complex in structure and undergo a true ontogeny. Indeed, the experimental studies of Jennings and his students have demonstrated the transmission of individual peculiarities, both of structure and function. As for the metazoa, despite the considerable evidence for chromosomal "individuality" and for the localization of genetic "factors," it seems to be entirely premature for us to assume the existence of a mosaic of parts, rigidly predetermined and incapable of making good a loss. One should recall what happened to an earlier "mosaic theory" of development.

To go to the other extreme, it might be supposed that for each form of organism there was at least one substance, or molecular structure, which was typical for it, and which determined its specific physical and chemical characteristics. The other constituents of the adult body would be modifications of this typical substance, which had lost certain of its original components or acquired new ones. This specific protoplasm would have some points in common with the "germ plasm" of Weismann. It might be credited with the power of indefinite growth and self-division, so long as these were not checked by counterbalancing forces. When completely checked, a growth equilibrium would be established which would represent the normal form of the species in question.

The rather vague and indefinite point of view here suggested would avoid, however, the tangle of unverified assumptions that are involved in the hypothesis of a "germ-plasm," conceived as an aggregation either of Weismannian "determinants" or twentieth-century "genes." The admitted possibility that certain material particles of the nucleus are functionally related to separately heritable adult characters does not constitute

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[21b] The Unity of the Organism, Chapt. XII, XIII.

a proof that the entire organism develops through the combined activities of such particles. Moreover, even if such a complete germinal representation of adult characters were shown to exist, only a part—and a minor part—of our difficulties would be solved. We should still have to explain how the elementary parts of the body came to arrange themselves in proper spatial order and in proper chronological sequence during development. Blocks do not build themselves into houses. Driesch points out that historically vitalism and epigenesis have always been closely related, while the mechanistic school has commonly adopted some form of preformationism. Such a connection is far from being logically necessary, however. To me it would seem that preformation lent itself most readily to vitalism—to the notion of a builder who put the blocks together. In our particulate theories of organic differentiation, we commonly leave out of account the spatial and chronological relationships of the parts, or rather we take them for granted. We assume that somehow our "organismules" will find their way to their proper places at the proper moments, just as in a laboratory experiment the experimenter himself sees to it that everything is at each moment just where it belongs.

Let us return to an illustrative case, already considered, and ask why no one has ever seriously proposed a preformation theory of the earth's origin. Most moderns (M. Bergson is an exception) believe that our present world was the inevitable outcome of forces that were inherent in a fairly homogeneous molten mass, interacting with those of its cosmic environment. It has never been thought necessary to invoke the aid of special "determinants" to account for the various geographic and geologic features of our planet's structure. In dealing with inorganic things we are content to let our analysis rest, in the lack of more detailed information, with the acceptance of such general principles as "creative synthesis" or the "multiplication of effects." We simply have to admit that differentiation means just this fact of *de novo* formation. Otherwise it means nothing at all.

We must, however, recognize certain essential differences between the development of a sea-urchin from an egg and that of our world from the structureless spore which was long ago liberated by its nebular parent. Let us suppose that some experimental cosmogonist, using the refined technique of a Morgan, Roux or Driesch, had skilfully removed about three quarters of our newly formed globe, leaving the remainder to reconstruct itself as best it could. The spherical shape would doubtless have been quickly restored, but is it likely that there would have formed in the ensuing ages just that same arrangement of Europe, Asia, Africa, America and the Islands of the Sea that we now find upon our maps? Unfortunately it is too late to perform this experiment, but I think that most geologists would expect a much modified world as the result. Indeed, if the excision had been made after the mixture of molten substances had begun to separate we should be perfectly certain that a quite "abnormal" world would have been the outcome. All this may be granted.

Let us ask another question. Why is it that no modern thinker[22] has set forth a preformation theory of *racial* evolution? It is only in accounting for individual development that this has been thought necessary. Yet the same paradox of *de novo* formation would seem to confront us in both cases, while other essential points of resemblance between phylogeny and ontogeny have often been pointed out.

One difference, doubtless, is that every process of phylogeny is regarded as a unique thing, while ontogeny is merely the *n*th reduplication of a known type, the character of which can be stated in advance. Hence it is that we are satisfied to resign the former process to the realm of "chance," while the latter we come to look on as determined in advance. Another difference seems to be that we look upon racial evolution as largely swayed by exter-

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[22] We must except Bateson.

nal factors, of the haphazard sort which operate in the realms of geography and meteorology; while individual development appears to be swayed chiefly by internal factors, and to pursue its preordained course in a high degree independent of the outside world.

But where in all this is the necessity for preformation? That two specific types of protoplasm, under identical conditions of environment, will give rise to widely different organisms implies, of course, considerable difference in the protoplasms. It does not, however, compel us to believe in the existence of correspondingly numerous differences in the two cases. A single initial difference between two physico-chemical systems may determine a multitude of differences at the end. For example, the presence or absence of a certain amount of annual rainfall on a given area of the earth's surface would determine the nature of an indefinite number of other characteristics, both geographical and biological. We do not in this case endeavor to pick out a particular element of the cause to account for each particular element in the effect. Driesch's assumption that any "mechanical" (*i. e.,* non-vitalistic) conception of the developing organism must be based on a preformation of parts may once more be dismissed as untenable.

Some preformation there is to be sure. Recent Mendelian studies, particularly the investigations of sex determination, make it highly probable that certain adult characters, though perhaps in no case single anatomical structures, are represented by spatially separated particles in the nucleus. Furthermore, a certain amount of "promorphology" has been demonstrated in the cytoplasm of the unfertilized egg, though this is perhaps to be regarded as representing merely an early stage in individual development. I feel bound to express the belief, however, that many recent students of Mendelian inheritance have carried their factorial speculations far beyond the evidence, and that their detailed localization of representative particles may prove in the future to have more interest for psychology than for genetics. We are dealing with a field in which ever more minute differences are being distinguished—many of them by purely subjective tests—and one in which the ratio of inference to observed fact is ever lengthening. May it not be that we have here hitherto unsuspected possibilities of self-deception on the part of even our most competent investigators? The subject is one which seems to me to deserve more attention than it has received.

On the whole, we are not compelled to assume the existence of any more preformation than can be experimentally demonstrated. And it may be regarded as settled that we have no parcelling out of "determinants" to appropriate cells during ontogeny, such as Weismann imagined. The "sex chromosomes," which seem to be the best authenticated instances of material bearers of hereditary traits, do not pass into definite body cells in the course of development and thus give rise to the primary and secondary organs of sex. Rather are they to be found distributed in every cell of the body. The assumption that they set free their characteristic determinants only in particular cells has no experimental or observational foundation.

Now, I am quite aware that any such "intra-selection" hypothesis of organic regulation as has here been advocated will be rejected by a large proportion of biologists on the ground that it is entirely superfluous. Various types of self-regulating mechanisms have been found in the non-living world, and the phenomena of growth and regeneration have long been known to be duplicated in crystals. Przibram has gone to considerable lengths in pointing out analogies between the behavior of the so-called "fluid crystals" and that of a regenerating organism.[23] And these analogies are reinforced by further ones, based upon the regeneration of crystals of hemoglobin. Many characteristically "vital" phenomena were

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[23] (*Archiv für Entwicklungsmechanik*, October 16, 1906.) Likewise Torrey (*Scientific Monthly*, December, 1915) has discussed some interesting analogies between certain inorganic phenomena and the processes of "acclimatization" and "regulation."

observed by him in these studies, among which the most impressive was doubtless the making over of a softened hemoglobin crystal by a process of "morphallaxis," *i. e.*, the readjustment of the matter already contained in the fragment. There must thus be recognized in these nonliving masses of matter a tendency toward the attainment of a specific form. And it seems plain that this tendency may realize itself in more than one way. Yet we should never, in this case, think of proposing any hypothesis of "trial and error," nor speak of the choice by the crystal of "means" to an "end."

Now, I will hasten to express my own belief that the phenomena in the two cases do not differ in any very fundamental way. *I am disposed to regard the regeneration of a crystal, the reconstruction of a mutilated organism, and the solving of a problem by a mathematician as members of a single series of increasing complexity. They have in common the reattainment of a condition of equilibrium which has been overthrown.* The fact that the organism is possessed of life, or that the mathematician has a conscious end in view do not alter the situation.

Such a "regulative" tendency in the inorganic world is recognized by physical chemists as the "principle of mobile equilibrium," or the "theorem of Le Chatelier." As stated by Lewis,[23a] this law asserts that "when a factor determining the equilibrium of the system is altered, the system tends to change in such a way as to oppose and partially annul the alteration in the factor. The same idea is conveyed by saying that every system in equilibrium is conservative, or tends to remain unchanged." Bancroft[23b] has given to this principle the dignity of a "universal law," pointing out analogies in the realms of biology, sociology and economics. More recently, its importance in ecology has been urged by Adams.[32c]

[23a] "A System of Physical Chemistry," Vol. II, 1916, pp. 140–141.

[23b] *Science*, Feb. 3, 1911.

[23c] American Naturalist, Oct.–Nov., 1918; Jan.–Feb., 1919.

In the regeneration of the more familiar type of crystal, the latter doubtless goes about its task "unhesitatingly," we may believe. But this is not true of every inorganic system. "In a stream [of water]," says Jennings, "opposing actions of all sorts are combatted in ways almost as varied as in organisms: a hole is filled up, a dam overflowed, an obstacle circumvented, another obstacle floated away, a bank of earth undermined or cut through; and the stream finally reaches the sea."[24] Must we not recognize important points of resemblance between such behavior and that of a penned-up cat, scratching wildly at the objects in its cage until finally a way out is found?

But if we admit this essential unity between the living and the non-living in respect to their method of correcting a disturbed equilibrium, why should we have resort in one case more than the other to a theory of "contingency" as regards the relation of means to end? Why may we not suppose the regulative processes of protoplasm to proceed as directly toward a goal as those of a crystal?

Answering the first question, I would say that the conception of contingency has been introduced into this discussion merely in the sense of a denial of teleology. Such a denial has been deemed necessary only in the case of organic phenomena. For inorganic events are seldom thought of as governed by "ends," and the question of "means" does not therefore arise. But in this respect there is really no difference between the living and the non-living.

The reason why the regulative processes of protoplasm probably do not proceed as directly toward a goal as those of a crystal lies, I believe, in the vastly greater complexity of the former. But it does not seem likely that any rigid distinction can be drawn. If it is really true that a damaged crystal of hemoglobin can restore its original form without the taking on of new material, it seems hardly likely that this rearrangement is effected

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[24] *Johns Hopkins University Circular*, 1914, No. 10, p. 16.

by the simple transfer of material from one point to another along the straightest possible paths. There is doubtless much random molecular movement which serves only to retard the consummation of the process.

The more complex the system with which we are dealing, the more of these "fortuitous" steps will intervene between overthrow and recovery of equilibrium. The chances that an entirely new disturbing factor will directly call forth the means to its own removal will correspondingly decrease. The more plainly, therefore, will the adjustment proceed in an "experimental" fashion.[25] Processes which favor the restoration of equilibrium (*i. e.*, which satisfy the need) will be accelerated; those which work in a contrary direction will be retarded.

At this point it may be profitable to cite certain closely related utterances of Jennings:[26]

> The condition which results in . . . regulative action is the presence, in a system, of a constant force, or stream of energy having a uniform tendency or direction (or set of such forces), together with intermittent forces having varied tendencies; whenever this condition exists, regulative action appears. . . . When the constant stream of energy is restrained for some time from producing its usual effects, it overflows in various directions, depending on the distribution of the resistance and amount and intensity of the free energy. It thus produces one effect after another. Often, at the end, one of these effects is of such a nature as to overcome or avoid the restraint; the stream of energy may then continue in the channel thus opened.

Has our prolonged discussion now led us, after all, merely to a denial of the scientific validity of the adaptation concept? I think not. The concept of adaptation stands upon the same footing as those of life, organization, function, food, enemy, offspring, environment, stimulus, heredity and the scores of other indubitable facts with which biology deals. By the use of pedantic circumlocutions, all of these various expressions could doubtless be avoided, and our ideas thus squared with the most rigid demands of "mechanistic" philosophy.

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[25] Of course, such expressions as "experiment" and "trial and error" must be used in a strictly objective sense, so far as they are given any explanatory value.

[26] *Johns Hopkins University Circular*, 1914, No. 10.

But would such a renunciation bring us any nearer to the truth? Only if we are ready to regard the whole science of biology as a provisional one, a mere temporary resting place on the way to the more "exact" knowledge which constitutes mathematical physics. How many of us are prepared to make this admission?

Before passing on to the next subdivision of our field, a few words are desirable in answer to another general criticism which may be raised against the line of argument here followed. Exception may be taken to the apparent assumption that the responses to a new situation, whether physiological or psychological, are wholly random. Many responses are so obviously direct and unvarying as to appear "fatally" determined.[27]

Again, even where "experimentation" or "trial and error" is admittedly concerned in the process, the tentative efforts frequently lie within a quite restricted range of possible movements, and from the first approximate the goal to be reached much more nearly than if they were wholly undirected. Thus the experiments of Hobhouse[28] upon various mammals suggest to him "that recent writers have overestimated the effect of pure accident." Furthermore, he concludes that "the more a success was accidental the less likely were the animals to take advantage of it." So, too, in learning to throw at a mark, we do not commence by casting our missiles indifferently in every direction, but from the outset we throw them in the general direction of the target. And the same is palpably true when we attempt the solution of a mental problem. The trains of thought are doubtless "spontaneous," as pointed out above, but certain more or less relevant trains are favored in advance. It is from these that our selections are made.

Now, all these difficulties seem to me more apparent than real. After the first dawn of conscious experience, no situation is wholly new. Every problem which arises contains elements in common with earlier ones which we

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[27] It is these which Loeb seems to regard as the more typical ones.

[28] "Mind in Evolution," 1915, pp. 236–237.

have already solved. This is the more true the more complex our problem. The "newness" of the latter may relate to a very few features, the residue consisting of elements which, in the last analysis, have been solved in an entirely empirical fashion. And the same may doubtless be said of those adaptive physiological responses which are generally assumed to be unconscious. As regards the fixed reactions known as "tropisms," I have already pointed out the probability that the predominantly adaptive character of these has been the outcome of racial history and therefore of some form of selection.

V. Evolution and "Contingency"

In the two preceding sections of this paper stress has been laid upon manifestations of the power of self-adaptation in the individual organism. Very little has been said regarding those fixed structural and functional mechanisms by which the more usual needs of life are provided for. The origin of such structures and functions—"adaptations," as they are familiarly called—must be accounted for in any adequate theory of evolution. Now, I have already argued that no theory of evolution, so far as it is scientific, can admit the possibility that the needs of the organism may call forth in any direct way the initiation of those processes by which these needs come to be satisfied. Let us look somewhat further into this question.

The field of organic evolution is one which has lent itself in a high degree to vitalistic and quasi-vitalistic exploitation. From the time of the establishment of the doctrine of descent, there were always persons who, in spirit, still clung to the creation principle, while accepting in form the newer ideas. Indeed, among biologists themselves, there have always been those who have seen in organic evolution the working out of a "perfecting principle," in a large degree independent of environment. Even Lamarck, who propounded one of the chief naturalistic accounts of this process, admitted that life "tends by its very nature to a higher organization."[29] The botanist Naegeli is one of the best known exponents of such a view. With some, like St. George Mivart, the question has been closely interwoven with special theological beliefs.

This writer believed in an "innate tendency to deviate at certain times and under certain conditions," which tendency he held to be "an harmonious one, calculated to simultaneously adjust the various parts of the organism to their new relations." And this guiding hand seems to have been exercised not only in the direction of satisfying the needs of the organism itself, but in adapting the latter to the needs of man. Speaking of the evolution of the horse, he tells us:

> The series is an admirable example of successive modification in one special direction along one beneficial line, and the teleologist must here be allowed to consider that one motive of this modification (among probably an indefinite number of motives inconceivable to us) was the relationship in which the horse was to stand to the human inhabitants of this planet.[30]

Others, like Wallace, have had recourse to such a guiding principle only in accounting for the origin of man.

In recent years, the philosopher Bergson has adopted a vitalistic theory of evolution, weaving it into a metaphysical system of which an important feature is the essentially creative character of time or "duration." We see the world of living things moving grandly on through the ages, impelled by a mysterious force, the "*élan vital,*" and flowering out spontaneously into a never-ending succession of living wonders. Such a conception may stir the imagination, but it does not add to our knowledge.

Now, curiously enough, this "teleological" factor has been introduced by various writers to explain two exactly opposite classes of cases: (1) the origin of adaptive char-

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[29] Philosophie Zoologique (Elliot's translation), p. 239, and elsewhere. Lamarck's statements are not wholly consistent, however, and I cannot feel quite sure that he had in view any principle distinct from the one with which his name is commonly associated.

[30] "Genesis of Species," p. 151.

acters (Paley's argument), and (2) the origin of highly perfected structures and functions which are not believed to be adaptive in the biological sense, at least to the extent of influencing survival. The musical and artistic faculties of man belong to this second class.

Natural selection, as is well known, provides us with at least a formal explanation of the first class of characters, but not of the second. Lamarckism, with a varying degree of plausibility, accounts for the origin of characters belonging to either class. That both of these theories are, in last analysis, theories of selection has been pointed out in section II.

But the claim is to-day heard on various sides that both natural selection and Lamarckism have broken down completely, and that no other existing evolutionary theories merit serious attention. So impossible is it for some biologists to square the widespread appearance of adaptation in nature with their own special theories of life that they seek to escape the dilemma by declaring this appearance to be largely illusory. Thus Loeb[31] tells us:

> While it is possible for forms with moderate disharmonies to survive, those with gross disharmonies can not exist and we are not reminded of their possible existence. As a consequence the cases of apparent adaptation prevail in nature.

In much the same vein, Davenport[32] writes:

> Strictly, we may say adaptation is not the thing that is brought about, but rather absence of non-adaptedness. Such adjustment as we find is, doubtless, only such a residuum of variants as has not proved incompatible with conditions of existence.

One might profitably compare such conclusions as the foregoing with the findings of Cannon,[33] based upon the detailed study of certain adaptive mechanisms in man. To most of us the conviction is doubtless irresistible, not that such mechanisms now exist because of their *harmlessness*, but that they came into existence, step by step, *on account of their utility*.

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[31] "The Organism as a Whole," p. 344.

[32] AMERICAN NATURALIST, August, 1916.

[33] "Bodily Changes in Pain, Hunger, Fear and Rage," 1916.

Taking heart from this skepticism among the biologists themselves, reactionaries are boldly coming forward with the assertion that the evolution principle has been discredited. It is certain that the spread of such ideas is not calculated to further the advancement of knowledge. Lack of an adequate hypothesis is not disproof of any possible hypothesis.

Moreover, it would now seem that some of these admissions of inadequacy have been premature. Much of the recent abandonment of the natural selection theory has been due to neo-Mendelian dogmatism. Selection, it is claimed, can only separate strains having different mean characters. It can not change the mean characters of a pure strain. But the experiments of Castle and some other breeders may be cited as evidence that such a contention is far from being established. And even those who reject Castle's interpretation of these results have been forced to concede that in some cases selection may bring about the indefinite modification of our stock —call the process "sorting" if we will.

So, too, the Lamarckian principle occupies the curious position of being dogmatically denied or wholly ignored by a large and influential class of writers, at the same time that others are able to adduce apparently convincing arguments for its reality. We certainly have a vast array of indirect or circumstantial evidence for this principle, derived from an inspection of the actual products of evolution as we find them. And we have a certain amount of direct, experimental evidence which can not be thrown aside as irrelevant or untrustworthy. While, therefore, sweeping conclusions regarding the Lamarckian factor are doubtless premature, the dogmatic denial of this factor very nearly amounts to self-stultification.

Thus, if we may read the signs of the times, the two chief naturalistic explanations of evolution may survive the fire of destructive criticism and again play an important part in our interpretation of life. By this, I do not wish to be understood as arguing that either or both of these theories constitute an adequate explanation (even in the sense of a description) of how evolution has come to pass. For many years past, I have been endeavoring to weigh the evidence for and against both of these hypotheses and I have reached the same verdict with respect to the two: *each is both proved and disproved.* It is not that adequate evidence is lacking, as some assume. Rather, in each case, is the evidence well-nigh overwhelming—*on both sides.*

Now, obviously, no single proposition can be both true and untrue at the same time. What is meant here is this. I believe the selection of virtually continuous variations and the inheritance of functional and environmental modifications to have both played *some* part in evolution. And I do not hesitate to say that the evidence in favor of such a view is of the same general character as the evidence for the evolution theory itself, and nearly as convincing.

On the other hand, it seems no less probable that the operation of each of these factors is strictly limited. Indeed, it would appear likely that much of the adaptiveness in nature is not adequately accounted for by either process or by both taken together. There may well be other factors the existence of which is as little suspected to-day as was that of natural selection before the time of Darwin and Wallace.

But will our explanations remain purely naturalistic, or will they find room for extra-natural directive agents, by whatever name called? Will they, like the two chief historic theories, base themselves on the contingency of every adaptive variation in structure or function, antecedent to the test of experience, or will they be forced to concede a primary adaptiveness inherent in living matter.

Many of those who admit the widespread occurrence of natural selection as a process, are wont to deny to it any *explanatory* value. To quote a now familiar saying, it is said that the survival of the fittest does not account for the origin of fitness. The real cause of modification, these writers insist, is to be sought in the process by which variations are produced and not in the fact that many of these variations fail to maintain themselves.

This argument is so plausible that it seems self-evident. And indeed in a sense it is. But there is another sense in which it is quite specious. Truly enough, no individual can survive which is not first born or hatched, or in some way brought into being by its parents. And those peculiarities which distinguish one individual from another are largely ushered into life along with it. They exist prior to selection. But fitness is a *relation,* not an absolute property of the organism. The word denotes merely a certain measure of adjustment to specific conditions of life, and the degree of this adjustment we know to vary almost indefinitely. To say that the conditions of life, acting through the selective process, can not be the cause of an increasing degree of fitness is like denying that a sculptor produces a statue, on the ground that he does not create the stone. It is well to note that even the sculptor's function is wholly selective. He eliminates certain portions of an unshaped mass of material.[34]

The foregoing analogy admittedly fails in one important respect. It implies that the possibilities of selection in a given race are wholly unlimited. We know this to be very wide of the truth. The question to be answered here is merely whether or not they are completely *random* in the sense which has been employed throughout this article.

Now, some selectionists are wont to deny the completely random character of variation. So far as this is simply a denial of the infinite variability of any species, it is a mere truism. We may perhaps admit the possibility that a given strain might, through rigid selection, acquire the "habit" of varying preponderantly in certain definite directions, thus limiting the possibilities of further evolution within that group. And we might even grant that such definitely directed variations might ac-

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[34] I do not recall the previous use of this analogy, but it is such an obvious one that it has doubtless occurred to many.

cumulate without the influence of selection at all (orthogenesis). But can we, without departing from naturalistic grounds, conceive of the production in this way of a structure in anticipation of a need? May we even conceive how appropriate variations could be called forth by an already existing need.

Of course, much obscurity of thought may be concealed beneath this innocent-looking word "need." What is a need? It is notorious that what is a luxury to some of us is a necessity to others. Our needs grow with our incomes. And this line of reasoning is directly applicable to sub-human realms. What an animal has, if this adjusts it to certain conditions of the environment, may be regarded retrospectively as the fulfilment of a need. Thus eyes fulfil the need of seeing. But can we say that such a need existed before the appearance of visual organs? There are beyond doubt still many forms of wave-motion or molecular vibration for which we have no organs of perception. Thus, in a large measure the organism creates its own needs, even in an unchanging environment. The word "need," like the word "end," is one which has a distinctly teleological implication. The more factors of the environmental complex an organism is brought into relation with, the better is it adjusted to its life conditions, and—other things equal—the higher position it holds in the scale of life. But these adjustments are only thought of as satisfying needs when we come to look back on what has actually happened.[35]

There is a more limited sense, however, in which the use of this expression involves us in no such obscurities. All those fundamental requirements, such as food, oxygen, protection from enemies, etc., may be termed *needs*, without there resulting any confusion of thought. Now, anything which led to the removal of one or more of these fundamental requirements—say the drying up of a lake—might bring about the extermination of an entire species, unless some adaptive response were made.

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[35] They may all, however, be properly termed *adaptations*, as has already been said.

Here, likewise, we may legitimately speak of the *need* for some sort of readjustment. Let us, then, restrict the word to anything without which a species would become extinct.

With this limitation of meaning understood, let us return to certain questions which I have left unanswered. Can we, on naturalistic grounds, conceive how an appropriate trend of variation could anticipate a given need; or can we even conceive how it could be called forth by an existing need? The former possibility certainly can not be admitted without frankly taking refuge in principles which lie beyond the range of scientific analysis. The latter possibility has, however, been vaguely implied by some writers on evolution.

So far as the "need" might be the result of some marked change in the environment or in the functional activities of the organism, it is credible that new variations might be offered to selection as a consequence of disturbances in the germinal material. But how could these occur preponderatingly in the direction of meeting the particular need in question? *Only in one way, so far as I can see, and that way is by the previous adaptive modification of the parent body.* For the latter may adapt itself experimentally, according to principles already discussed. The germ-cells could not adapt themselves experimentally, since the need is commonly one which does not as such affect them at all. Thus, the imperative demand for *directed* germinal variations—or at least ones of a useful sort—can be met, so far as now appears, only by assuming the transmission to the germ-cell of adaptive responses of the parent body.

The Lamarckian principle has the added advantage of being able to account for many of the "luxuries" of organization—adaptations, in the sense of fitting their possessors for a fuller and more varied life, but not of any conceivable survival value. Our own race, as has often been pointed out, is endowed with multitudes of such faculties. But we are sadly in need of direct experimental evidence along these lines.

Biologists of the future may recognize the importance of determining experimentally whether the germinal variations of a species ever respond to changed life conditions in such a way as to shift the mode of any character in the direction of greater adaptation. If such a general tendency as this were revealed, and if, at the same time, the transmission of somatic modifications were rigidly excluded, we should be brought to a crisis in the history of our science. The question at issue would not be merely the adequacy or this or that hypothesis. It would be the adequacy of our recognized scientific methods to deal with such problems. Despite the lengthy arguments with which I have sought to defend a purely naturalistic position, I should not, in advance, be supremely confident as to the outcome of such experiments. It might, after all, turn out that there was just such an "immanent teleology" in living things as the vitalists claim. If this should prove to be true, science would have to re-survey its territory and set itself new boundaries well within the old ones.

Such an undertaking, like that of settling once for all the "acquired characters" question, would doubtless be beset by great technical difficulties. But these difficulties should not be insuperable. So long, however, as "genetics" is held to be nearly or quite synonymous with Mendelism, evolution along dynamic lines is likely to languish. We must grant the enormous strides which have been made in our knowledge of the inheritance of certain types of variations, but the much more fundamental question of the causes of these variations is almost as far from solution as in the days of Darwin.

In conclusion, I would say a few further words in regard to my use of the expressions "contingency" and "chance" throughout these pages. It is needless to say that I have not used these words as synonymous with uncaused. I have spoken of an event as contingent, merely in the sense of its being causally unrelated to something else: for example, a variation in relation to a need to be fulfilled. Whether or not, in the last analysis, all things are causally related in an Absolute, or whether the Universe is pluralistic in its nature, need not concern us here. That there may be some measure of pre-established harmony among its various parts is possible. It has recently been ably argued—and by a chemist, not a theologian—that there exists such a pre-established harmony between the organic and the inorganic worlds as a whole.[36]

But even granting such very problematic relationships as this, we can not deny that much happens in a purely "accidental" way. No degree of fitness on the part of the environment for life in general can avail to prevent the wholesale destruction of organisms which "happen" into unfavorable surroundings. That all of the special adjustments between organism and environment arose primarily through contingency or chance in the sense here indicated is the main thesis which I have defended in these pages. There may be little of an original nature, either in the views proposed or the arguments used in support of them. But I believe that this essay may serve a useful purpose in bringing together a number of apparently distinct problems under a common viewpoint.

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[36] L. J. Henderson: "The Fitness of the Environment" (1913), "The Order of Nature" (1917).

SHORTER ARTICLES AND DISCUSSION

PIEBALD RATS AND SELECTION, A CORRECTION

In a recent important publication Dr. Sturtevant makes "an analysis of the effects of selection" in which he ably maintains the current view that the single gene is not changed by processes of systematic selection. His argument rests on a careful experimental study of the behavior of the character "dichaet" in *Drosophila,* followed by a general discussion of other work, my own in particular. I am represented as completely opposed to his view, and so I have been at times, but such is not the case at present. I agree so fully with his general conclusion that I want to obviate needless discussion based on the misapprehension.

I thought two years ago that I had evidence that a single gene had changed in the course of a selection experiment, this gene being concerned in producing the hooded pattern of rats. I now find this view rendered untenable by further experiments, the results of which are in course of publication. These results show that the supposed changes in a single gene are more probably due to changed residual heredity, which very likely may consist wholly of other "modifying" genes.

The crucial experiment was one suggested by Dr. Sewall Wright. The divergent hooded races, "plus" and "minus," resulting from selection, were to be crossed repeatedly with a third race, the hooded character being recovered as a recessive in F_2 following each cross and its variability compared with that of the uncrossed race. It was believed that if multiple modifying genes were involved, repeated crossing with a pure third race would tend to remove these, in which case the extracted hooded character being deprived of its plus modifiers would be substantially identical with the hooded character deprived of its minus modifiers, as seen respectively in hooded recessives derived from the plus and from the minus crosses. Well, they *are* substantially identical, but it has taken some time and a good deal of trouble to establish the fact. First we had to secure a satisfactory third race to use in the crosses, one free from contamination of any sort by crosses. This we sought in a wild race. But ordinary wild rats will not breed under laboratory conditions. So we resorted to trapping immature wild rats from a single locality and using these as a foundation stock. Crosses with the plus race were then started successfully, but the corresponding experiment with the minus race was hard to get going and so has lagged behind the plus crosses. A report on the result of the plus crosses was made in 1916 (Castle and Wright). The crosses with the minus race were not then sufficiently advanced to show what their outcome would be and this was still true when reply was made to the criticism of MacDowell, as it had been previously when reply was made to Muller and to Pearl, and subsequently when I addressed the Washington Academy of Science on the rôle of selection in evolution (1917). But since then the minus crosses have given what seems to be conclusive evidence that the single gene had not been altered by selection, although the inherited complex responsible for the hooded character had steadily been altered in opposite directions and these alterations were permanent in the sense that they represented racial modes, stable so long as the race was not outcrossed.

I still have on hand a few representatives of the plus and of the minus races which because of their low fecundity it has been impossible to select further for several generations. The two races are very different in appearance. The plus race shows no white except on the under side and sometimes along the flank. The minus race shows no black except a short hood lying anterior to the shoulders, and in an occasional individual a small black spot or two in the middle of the back or on the tail. Yet the variability of each race is still considerable; as measured by our "grades" it has not appreciably diminished in recent generations. The somatic differences entailed by the selection experiments with the hooded character of rats are seemingly greater than those secured by Sturtevant or by MacDowell in regard to bristle number in *Drosophila*, yet I doubt not they may be explained on similar grounds.

Crossing with a wild race affects very differently the plus and the minus selected races. See Tables I and II. The plus race was much less affected than the minus race. Its mean grade was lowered, by three successive crosses with the wild race, not over three quarters of a grade. The standard deviation was about doubled by the first cross. That is the variability of the hooded character, when extracted in F_2 from the first wild cross, was about twice as great as the variability of the hooded character in the uncrossed plus selected race. In the second and third crosses the variability declined somewhat, but was still considerably greater than that of the uncrossed race. It was indeed very similar to that of the plus race in the first seven generations of the plus selection experiment. (See Castle and Wright, p. 186.)

TABLE I

RESULTS OF REPEATEDLY CROSSING THE PLUS SELECTED RACE WITH A WILD RACE

	Mean Grade	Standard Deviation	Number of Hooded Young
Control, uncrossed plus race, generation 10......	+ 3.73	.36	776
Once extracted hooded F_2 young...............	+ 3.17	.73	73
Twice extracted hooded F_2 young..............	+ 3.34	.50	256
Thrice extracted hooded F_2 young..............	+ 3.04	.64	19

TABLE II

RESULTS OF REPEATEDLY CROSSING THE MINUS SELECTED RACE WITH A WILD RACE

	Mean Grade	Standard Deviation	Number of Hooded Young
Control, uncrossed minus race, generation 16....	− 2.63	.27	1,980
Once extracted hooded F_2 young...............	− .38	1.25	121
Twice extracted hooded F_2 young..............	+ 1.01	.92	49
Thrice extracted hooded F_2 young..............	+ 2.55	.66	104

The crosses of the minus race were started six generations later in the course of the selection experiments, with animals of generation 16, minus selection series. They show effects much more striking than those of the plus crosses. See Table II. The minus selected race had now attained a mean of —2.63. A single cross, with the same wild race used in the crosses of the plus series, lower the grade to —.38, extinguishing all the changes in mean grade made by sixteen generations of selection, and leaving the extracted hooded character in a highly variable state (standard deviation 1.25, nearly five times what it had been before). A second cross with the same wild race converted the extracted hooded individuals for the most part into a plus group, mean + 1.01, but with variability somewhat decreased, standard deviation .92. A third cross with the wild race has given extracted hooded individuals *exclusively plus in character,* range from + 1.00 to + 3.50, mean + 2.55. The variability has simultaneously fallen to .66, which is only about one third greater than that of the minus race in the first five generations of the selection experiment. (See Castle and Wright.) One family containing fourteen thrice extracted hooded individuals has a mean grade for the hooded individuals of + 3.05, which is practically identical with the grade of the thrice extracted hooded individuals resulting from the plus crosses (Table I).

It thus appears that three or at most four crosses with a wild race suffice to obliterate all the racial differences which had been induced by ten generations of selection in the case of the plus race and sixteen generations in the case of the minus race. The plus race was changed almost immediately by a single cross, but the change was small (a fact which misled me until the results of the minus crosses were secured). The changes with the minus race were so great that they could not be fully secured by less than three or possibly four successive crosses (eight generations of offspring). The wild race, which we used in our crosses, evidently had a residual heredity much more like that of our plus-selected than like that of our minus-selected race. When the hooded gene from either race was introduced by repeated crosses into this residual heredity, the result was to produce hooded races of very similar grade, a little lower in grade than the plus selected race, but very much higher in grade than the minus selected race.

It thus becomes clear that the changes which had occurred in the hooded character as a result of selection were *detachable* changes and are probably in nature independently inherited modifying factors. This is a view which Phillips and I gave as one of two possible interpretations of the results which we published in 1914. Morgan, Muller, MacDowell and others have insisted that this was the only reasonable interpretation which could be given, but I have not been satisfied with this conclusion in advance of a really crucial experiment, such as I believe has now been performed. Meanwhile the probability that the theory of multiple modifying factors is correct as a general explanation of similar cases has been greatly strengthened by the work of Muller, Bridges, Sturtevant and others, showing that genetic factors, having a definite demonstrable position in linkage systems, influence in a particular way the somatic manifestation of characters varying quantitatively or qualitatively. I accept their interpretations as correct in the light of our present knowledge.

I should feel like apologizing for my own obtuseness in not reaching a similar conclusion sooner, did I not recall with satisfaction how much clearer the rôle of selection now stands revealed than it did when these experiments were begun, and to the clearing up of the situation I shall at least hope that this rat work has contributed something, if only by provoking investigation.

The "Mutation Theory" of DeVries gave us a picture of selection as an agency temporarily effective in producing racial changes, but with those changes gradually vanishing as soon as the selection ceased. Johannsen denied within "pure lines" even temporary effectiveness of selection. A strictly logical use of Johannsen's conclusions would have limited their application to such organisms as he studied, self-fertilizing ones completely homozygous for all genetic factors and subject apparently to no new changes in such factors. But the doctrine was straightway extended in the views of most geneticists to selection of every sort and he was treated as a traitor to Mendelism who saw any utility in selection or advocated its use as a means of improving the inherited characters of animals or plants.

The situation is wholly different to-day. Through the investigations of Jennings and his pupils on protozoa, of Stout on *Coleus,* and of Shammel on citrous fruits, the fact is clear that even within clones genetic changes may and do frequently occur and that systematic selection will serve to isolate these and thus lead to racial improvement. Those who have tried systematic selection in the case of cross fertilizing organisms have in some cases noted the occurrence of "mutations" with such frequency as to make progressive change under selection easily obtainable. Emerson and Hayes, in the case of certain pericarp color patterns of maize, find "mutations" so common that a wide range of variability results and selection is able to isolate, from such material, types "relatively stable," but very diverse in appearance. Modifying factors are not involved in Emerson's explanation of his results, but rather such instability of a single gene as leads to frequent mutation. Selection experiments with the variegated coat-patterns of mammals seem to involve less abrupt but otherwise similar changes, but modifying factors rather than repeated mutation seems to be the explanation required in view of the results of crosses reported in this paper.

That selection by one means or another is an effective agency in producing racial changes is not questioned to-day, as it was ten years ago.[1] The only question now at issue is whether the single gene is changeable. I am inclined to think, with Sturtevant, that while single genes do occasionally change producing multiple allelomorphs, a much more common occurrence is change in visible characters through modifying factors. Whether the direction of genetic variation is controllable, other than by the manipulation of modifying genes or the discovery of multiple allelomorphs remains to be determined. The evidence at present is largely negative. It is undeniable that liability to genetic variation is much greater in some organisms than others, much greater as regards some kinds of character than as regards others, but whether we can produce variability of a genetic character is quite a different question. We certainly at present have to follow nature's lead rather than to lead nature, as regards the course of evolutionary change.

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[1] Sturtevant's presentation of my views is a bit unfair in that it seems to imply that whenever I have spoken of "variation in a unit character," I have consistently meant variation in a single gene, whereas in discussing the case of the English rabbit, I have expressly reserved judgment on this point. In a large part of my experimental work, the question under investigation has been—do the visible characters which conform with Mendel's law in transmission suffer modification in crosses or as a result of selection? The present generation of geneticists has apparently forgotten that this was ever a debatable question. We all admit now that contamination occurs in crosses and that modification may be effected by selection, and we seek only to explain *how* the contamination is brought about (as by modifying factors) or *how* the modification is produced in the course of systematic selection (as by the isolation of modifiers in homozygous state). But in the days when the doctrine of gametic purity was under discussion, such "contamination" or "modification" was not admitted.

When Sturtevant denies the occurrence of "contamination," he uses the term in a very restricted sense, not as I have used it in the foregoing sentence, nor as it was formerly used in Mendelian discussions. What he means is not change in the visible character, as the hooded character of rats, but change in a single gene which is known absolutely to limit the manifestation of the hooded character in any form. I agree with his view that there is no conclusive evidence that this single gene had changed in the course of selection experiments, except in the case of our "mutant" race.

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EGG-WEIGHT AS A CRITERION OF NUMERICAL PRODUCTION IN THE DOMESTIC FOWL[1]

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I

WHEN one surveys the field of literature dedicated to the subject of egg-production in the domestic fowl he may well be astonished at the vast number of ways and means by which a poultryman can detect the best layers of his flock. Indeed one exaggerates only slightly to say that there is scarcely an incident in the hen's daily program, nor an event in her life, that has not been interpreted by some unusually keen observer as a sign of producing ability—good or poor. Was the hen seen to rise early and dispatch a one-hundred-calory portion of mash, together with nine bugs and three worms, before her sisters were off the roost? Then put her down unqualifiedly as an industrious hen and enthusiastic layer—a credit to any poultry house. Was the hen observed to work after hours gleaning the last fragment of grain from the litter, or perchance chasing lightning bugs through the twilight grass, when other union-members of the flock had ceased work for the day and retired to roost? Then register her as one that has her master's interests at heart, and one that should be vigorously encouraged to reproduce her like. Did the hen lose the yellow glamour of her shanks and beak (doubtless the equivalent of good complexion in a hen)? Did she molt in July or August? Was her comb

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[1] Contribution 250 from the Agricultural Experiment Station of the Rhode Island State College.

a ruddy red in September? Was her pelvis broad and flexible in April? Did she start laying in October? Did she lay thirty or more eggs before the first day of March? Did she lay 200 eggs in her pullet year, or 500 eggs in three years? Did she lay small eggs or large eggs? By all these signs one may (it is alleged) detect the hen that is (or has been) the good producer. But the curious part of the matter is that, notwithstanding these many signs and evidences of producing ability, the hens of the average poultryman continue to deliver the same number of eggs per year—estimated at about 120.

Among this variety of criteria, however, it must in fairness be said that some of the tests are of practical significance. It can scarcely be doubted that, as a rule, hens that lay the largest number of eggs during the "winter period" (November 1 to March 1), as first stated by Pearl, are the best layers for the entire year. On the other hand, it has been shown by Goodale that the production during the winter period may be strongly influenced by the time of hatching: the early-hatched hens make the highest winter records—at least they lay the greater number of eggs between the beginning of the laying period (sometimes as early as August) and March 1.[2]

If a hen is entitled to be called a good producer only on condition that she makes a creditable record for two or more years successively—then there is point to the recent contention of other investigators that hens that make a low first year's record usually "make up" during the second year, so that a three-year production record appears to them as representing the fairest measure of producing ability. This is of course the equivalent of saying that the number of eggs that a hen lays is a good criterion of her egg-producing ability—a circumstance which no one can deny. But it frequently happens that, for practical purposes, one desires such a criterion as will indi-

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[2] It may be a question, however, whether the "winter period" of Goodale's early-hatched pullets may not in reality represent a combining of *two* laying cycles. His data on production seem to make possible this interpretation.

cate a hen's producing ability before she has attained that stage in life when economic production ceases; and when, even as a breeder, her further producing days are few.

II

To the casual reader it will no doubt appear preposterous that a biologist should attempt to measure the numerical egg-production of a hen by *weighing* her eggs, rather than by counting them. But the author freely admits that this ridiculous thing has actually been done in his laboratories; and, what is more, that the method appears to work: a flock of hens can be divided into groups, each characterized by a different mean producing ability, as a result of weighing a certain number of eggs at a certain time in the laying year, and subsequently by making certain computations therefrom. The results depend upon *the relation existing between egg-weight and egg-production at different periods of the laying year.* These points may be considered separately.

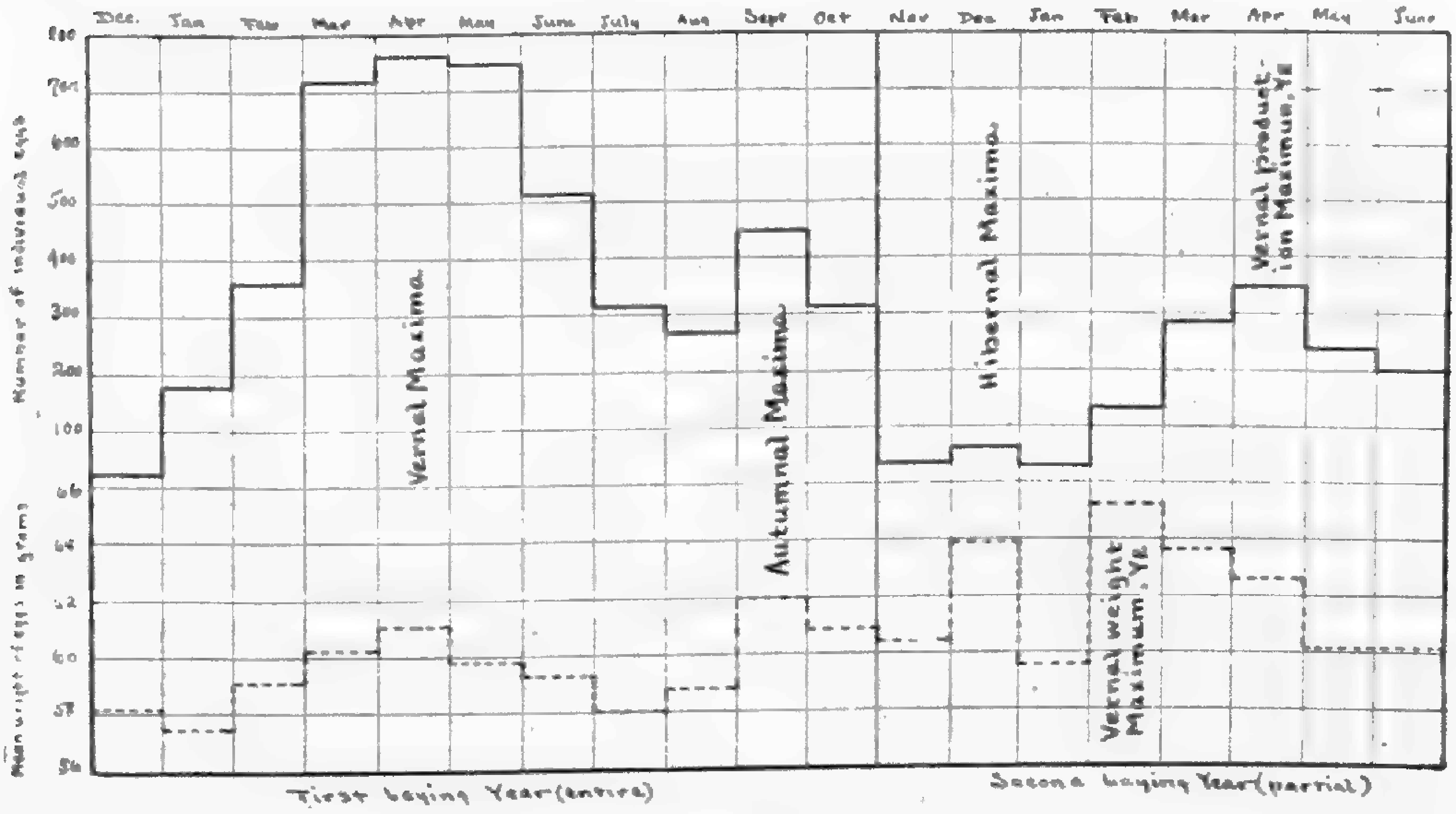

FIG. 1.

When the first yearly production of a flock of hens of equal age and condition is plotted on monthly ordinates one frequently obtains a curve such as indicated by the full line in Fig. 1. It is observed that the production curve for the year ending October 31 is of the bimodal type.[3]

One of these modes, appearing on the spring of the year (in April), may be termed the *vernal production maximum.* The second mode, falling in September, may be called the *autumnal production maximum.* Of these two maxima for the first laying year the vernal maximum manifests the higher peak, in keeping with the heavy April production which is the highest of the year. Between any two successive maxima lies a fundus whose minimum is attained either in July or August, or in November of each year. The late summer depression may be termed the *æstival production minimum,* and the November depression, the *autumnal production minimum.* In the month of December of the second laying year it will be noted that the curve rises slightly. This represents the increased production of the "winter cycle" or, as it may be called, the *hibernal production maximum.* Between this and the vernal production maximum of the second laying year is another depression in the curve, following the period of winter production and indicating the *hibernal production minimum.* This is followed in turn by the vernal maximum of the second year.

The presence of these two maxima in the curve of production for the first laying year indicates that at least twice during this year (closing October 31), once in the spring and once in the autumn, the egg production of a hen rises from its lower limits and expresses itself by laying a larger number of eggs than at any other season. These periods of increased production represent the spring and the autumn cycles respectively. There exists also the winter cycle which is usually manifested with clearness only in those flocks which show a fairly high mean production. It is a significant productive period, but will not receive further consideration at this time. It may be added, however, that in birds that are fairly high producers and which are hatched sufficiently early

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[3] These hens were poor winter producers and the expected mode for December-January of the pullet year does not appear.

in the year, the winter production maximum may make its appearance as the first cycle of production of the first laying year.

We have considered some of the more obvious variations in the curve of numerical production and come now to the curve of variations in egg-weight. Such variations may be considered with reference to the clutch, the litter, the cycle or the year.[4]

For present convenience, however, we shall consider the variation by months—purely arbitrary divisions in the life of the hen, which cut in on, and interrupt clutches, litters and cycles in such a way as frequently to obscure many of the problems involved. For our present purpose, however, division by months offers a rough and ready division of the year into short periods of time in which the productions may be compared.

When all the eggs laid by a flock of hens are weighed and recorded, and the monthly means computed and plotted on monthly ordinates, such a curve of mean monthly variation in egg-weight is obtained as that shown by the broken line in Fig. 1. Such a curve shows that all the eggs that a hen lays are by no means of equal weight. The first eggs laid are relatively small, but the weight increases gradually until a maximum weight for the first year is attained in the month of April. This is termed the *vernal weight maximum* and may represent mean increase of five grams over the mean weight of eggs for the first laying-month of the year. This maximum forms the first mode of the frequency curve of variation in egg weight as shown in the figure.

After April, the curve of variation in egg-weight drops for May, again for June, and reaches the lowest point in July, at which time the mean weight of the eggs of the flock may be scarcely greater than for the first month of production. Having struck this low point, however, the

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[4] A *clutch* may be regarded as the group of eggs laid on successive days without an interruption. A *litter* is the group of eggs laid immediately preceding the onset of a broody period. A *cycle* is the larger group of eggs laid during any one of the seasonal periods of increased production.

mean egg-weight begins to rise again and reaches a second mode or maximum in September, at which peak the mean egg weight is slightly higher than for the period of the vernal maximum (April). This September peak may be called the *autumnal weight maximum.* The mean difference between the vernal maximum and the autumnal maximum is usually about one or two grams. Having attained this peak of weight, the curve drops again through October to strike its fundus in November (the first month of the second laying-year).[5] From this point it rises in December to the first weight maximum (*hibernal weight maximum*) of the second laying year, and then drops again in January to form the *hibernal weight minimum* immediately preceding the vernal maximum of the second year.

It will now be clear to the reader that there exists a noteworthy circumstance with reference to these curves of numerical production and of egg-weight: they parallel one another to a remarkable degree. The vernal maxima of production and of weight fall together in April; and the autumnal maxima of production and of weight fall together in September. The only departure from coincidence lies in the circumstance that the summer production minimum arrives in August, while the summer weight minimum is found in July. It should be said, however, that the plotting of the curves on ten or five-day ordinates might show a closer correspondence of these minima in point of time. The difference observed is scarcely significant. The definite agreements in the trends of the respective curves are taken to indicate that, on the average, increased production is accompanied by increased mean weight of the eggs produced; and that, *vice versa,* a decrease in production is, on the average, accompanied by decreased mean weight in the eggs produced. Whatever, therefore, may be the biological significance of the two production maxima for the hen's first

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[5] It has become common to consider the laying year of a hen as extending from November 1 of the pullet year to and including October 31 of the year following.

laying year, the weight maxima would appear to possess a similar significance. Since the two are so closely correlated it would seem possible to measure a hen's innate egg-producing ability by the one phenomenon as well as by the other. This constitutes the hypothesis which we will now attempt to verify.

III

If we take a cross-section of the April production as nearly as possible to the absolute mode[6] of the weight curve, we learn that, although the egg-weight of most of the individuals of the flock has increased at this time, there are a few in which it has not increased significantly; and a still smaller number in which there has occurred a loss in egg-weight. The same is true for a cross-section of production taken at or near the absolute mode of the autumnal weight maximum. The following question therefore arises: *Does there exist any significant correlation between a tendency to manifest an increase in egg-weight at the period of the vernal weight maximum (or autumnal weight maximum) and the number of eggs produced for the entire first laying year (November 1 to October 31 following)?*

In order to demonstrate such a correlation one must first define more exactly the nature of the second variable, namely, the "tendency to manifest increased egg-weight" as referred to above. There must be a fixed point from which one can calculate, for each individual hen, the amount or the extent of increase in egg-weight manifested at the weight maxima. For certain reasons

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[6] In explanation of this point it may be added that by plotting the frequency distribution of variation in April egg-weight on daily ordinates one may approximate more closely the absolute mode. This has been found to lie (for the flock in question) between April 11 and 15. For the autumnal weight maximum it lies between September 21 and 25. The absolute vernal production maximum lies between April 16 and 20, while the absolute autumnal production maximum appears between September 11 and 15. It is of course to be expected that these dates are only relative; that they would vary with different flocks, depending upon the climate, the date of hatching, the method of housing and presumably upon still other varying, environmental factors.

it was decided to compute all increase or decrease in egg-weight, for each individual, from the mean weight of the first ten eggs laid at the beginning of the first laying year of that particular bird. And, in order to translate the differences into comparable terms, the increase or decrease was calculated as a percentage increase or as a percentage decrease above or below the mean weight of those first ten eggs. Consequently, the percentage of increase or decrease in mean weight for all April eggs, over or under the mean weight of the first ten eggs laid, was ascertained in the case of each bird in the flock; and the same data were derived for the September production. It is upon the analysis of these raw data[7] that the appended computations rest. In the succeeding paragraphs it is therefore the aim of the writer to demonstrate the following point: that the higher percentages of increase in mean egg-weight, reckoned at the periods of the weight maxima, are so closely correlated with higher production for the first laying year, that, by the method to be presented, a flock of hens may be divided into groups characterized respectively by higher, medium and lower producing ability; and that this method is effective, whether the computations are based upon the vernal or the autumnal weight maxima.

IV

We may first concern ourselves with computations based upon the mean weight of the April eggs, including the eggs of the entire month; and it is scarcely necessary to resort to formal correlation tables to demonstrate the point involved. The simpler methods may be employed: (1) Dividing the birds on the basis of annual production above or below the flock-mean and then computing the percentage of net increase or decrease in mean egg-weight; (2) dividing the birds into groups based upon percentages of net increase or decrease in mean egg-

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[7] It would be impossible to present these raw data in an article of this scope. They will be published, however, at the close of the investigation which is still in progress.

weight and then ascertaining the mean annual production for each percentage-group. To make the matter more clear both methods will now be applied—first to a differentiation of the flock on the basis of production groups.

For the purposes of the present inquiry the flock[8] may be divided into two groups on the basis of the mean annual production which was 120 eggs. One group was made up of individuals whose production was above the mean, and the other group included birds whose production was below. The mean production of the plus group was found to be 143 eggs, while the mean production of the minus group was 99. After these production-groups had been established the mean net increase or decrease of egg-weight for each group was computed. The mean increase for the plus group was 5.4 per cent., and for the minus group 2.6 per cent. These results appear to indicate that, on the average, birds which manifest a greater percentage of increase in the weight of April eggs are likely to be the better producers of the flock.

TABLE I

SHOWING THE PRODUCTION OF THE FIRST LAYING YEAR OF GROUPS OF BIRDS SELECTED FOR DIFFERENT PERCENTAGES OF INCREASE OR DECREASE IN MEAN EGG WEIGHT, MEASURED AT THE PERIOD OF THE VERNAL (APRIL) WEIGHT MAXIMUM

PERCENTAGE-CLASS: Birds Selected for Increase in Egg Weight as Indicated Below	Number of Individuals Making the Record	Mean Production for the First Laying Year	PERCENTAGE-CLASS: Birds Selected for Increase in Egg Weight as Indicated Below	Number of Individuals Making the Record	Mean Production for the First Laying Year
> 10 per cent.	2	147	> 4 per cent.	17	132
> 9 " "	3	142	> 3 " "	21	122
> 8 " "	4	141	> 0 " "	31	122
> 7 " "	6	140	< 0 " "	6	111
> 6 " "	9	137	< 6 " "	28	112
> 5 " "	16	134			
			Total flock...	37[9]	120

In utilizing the second method mentioned above, the

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[8] The flock in question consisted of 38 white Plymouth Rocks hatched in April, 1909. Some of the birds have now completed their seventh laying year.

[9] One hen, showing no increase and no decrease in mean egg-weight, and a production of 91 eggs, was omitted from the records.

birds of the original flock were divided into groups according to the percentage of net increase (or decrease) in the mean weight of eggs laid during the period of the vernal maximum (April). The percentage-groups were based on the scale indicated in the accompanying table.

From the data presented in Table I it is apparent that, on the average, the birds that showed the higher percentages of increase in the weight of the April eggs were also characterized by the higher productions. Those characterized by a weight-increase of 10 per cent. or more showed a mean production of 147 eggs, while those characterized by a weight-increase of more than 3 per cent. only, showed a mean production of only 122 eggs. The mean production of the group characterized by a *decrease* in egg-weight was the lowest of all—111 eggs, this being below the mean production of the entire flock.

If the birds are divided into two groups only, one having an increase of 6 per cent. or more, the other showing an increase of less than 6 per cent. or an actual decrease in egg-weight, it is found that the high-percentage group gives a mean production of 137 eggs, while the low-percentage group gives a production of only 112. In this instance the portion of the flock falling in the high-percentage class was approximately 24 per cent.; and this small group gave an average production that was 23 per cent. in excess of the production of the low-percentage group. The fact is thus brought out that, although a certain small proportion of high-producing individuals that are also characterized as manifesting only a slight percentage of increase in egg-weight at the period of the vernal weight maximum, will usually be found, the higher producers are, on the average, characterized by the larger percentages of increase (6 per cent. or above); and the selection of hens on this basis results in the separation of those individuals possessing the highest producing value.

V

In view of this correlation between numerical production and percentage of increase in egg-weight when measured at the period of the vernal maximum, it appeared desirable to ascertain whether a similar correlation existed between production and increase in egg-weight manifested at the *autumnal* (September) maximum. The same two demonstrational methods used in the previous instance may be applied.

The data on production were first re-distributed in such a manner as to group the percentages of increase or of decrease in egg-weight under two headings: (1) hens having an individual annual production greater than the mean (120 eggs), and (2) hens having an individual annual proportion of less than the mean production of the entire flock. In this way it was brought out that the plus group, with a mean production of 151 eggs, showed a mean net increase in egg-weight for September of 5.8 per cent., while the minus group with a mean production of 105 eggs showed a mean net increase of only one per cent.

TABLE II

Showing the Production of the First Laying Year or Groups of Birds Selected for Different Percentages of Increase or Decrease in Mean Egg-Weight, Measured at the Period of the Autumnal (September) Weight Maximum.

Percentage-class Birds Selected for Increase in Weight Indicated Below	Number of Individuals Making the Record	Mean Production for the First Laying Year	Percentage-class Birds Selected for Increase in Weight Indicated Below	Number of Individuals Making the Record	Mean Production for the First Laying Year
> 10 per cent.	8	143	> 4 per cent.	—	—
> 9 " "	9	141	> 3 " "	18	131
> 8 " "	10	140	> 0 " "	25	127
> 7 " "	11	142	< 0 " "	8	108
> 6 " "	12	141	< 6 " "	21	111
> 5 " "	14	137			
			Total flock...	33[10]	120

When the second method was applied, and the data redistributed so as to give the percentage-classes, the results shown in Table II were obtained.

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[10] Four hens included in Table I were not employed in the present computations, because they failed to lay during September.

From the data presented in Table II it appears that, on the average, the birds that manifested the higher percentages of increase in the weight of the September eggs were characterized by higher annual production. Those showing a weight-increase of 10 per cent. or more gave a mean annual production of 143 eggs, while those birds characterized by a decrease in mean egg-weight showed an annual production of only 108 eggs. When the flock was divided into two groups according as the egg-weight had increased by more than 6 per cent. or less, the high-percentage group gave a production of 141 eggs as opposed to 111 eggs laid by the low-percentage group. Thus, dividing the flock on the basis of a 6 per cent. increase in the mean weight of all the September eggs, gave a group of 12 hens (out of 33) which showed a mean production 17.5 per cent. higher than the flock average (120), about 27 per cent. higher than the mean production of the low-percentage group, and 30 per cent. higher than the mean production of the small group of eight hens which manifested a decrease in mean egg-weight at the period considered.

It will hardly be necessary to call the attention of the reader to the circumstance that this method of demonstrating the correlation involved in the frequency distribution of these two variables (increase in egg-weight and numerical production) is, by its very nature, such as to constitute a practical application of the means involved.

The correlations between weight-increase and production, considered in the foregoing paragraphs, were so obvious that the question arose as to whether satisfactory correlations could not be demonstrated between these two variables under conditions in which a smaller amount of statistical data was employed. For instance, if the method should prove of value to poultrymen in affording a means for the detection of the higher producers of the flock, it would be desirable to reduce the machinery of computation to the lowest point consistent with valid results. It thus appeared pertinent to inquire whether computations based upon the weight of only ten eggs, laid as closely as possible to the periods of the absolute vernal and autumnal maxima, respectively, would afford a satisfactory basis for establishing the weight-production correlations.

To this end, therefore, the mean weight of ten eggs laid by each member of the flock between the eleventh and twenty-fifth days of April[11] was computed, and the difference between the mean weight of these ten eggs and the mean weight of the first ten eggs laid by that hen at the beginning of her laying performance calculated as a percentage-increase or as a percentage-decrease. It should be added that the production during April was conducted at so rapid a rate that, in the case of 28 individuals out of 37, it was possible to obtain the record of ten eggs within the dates mentioned. In the remainder of individuals it was necessary to transcend these limits slightly. In no instance, however, was it necessary to take eggs from a date earlier than April 8, nor later than April 29. The data thus acquired were redistributed according to the percentage groups, and the results summarized in Table III.

TABLE III

SHOWING THE MEAN ANNUAL PRODUCTION FOR THE FIRST LAYING YEAR OF GROUPS OF INDIVIDUALS SELECTED FOR VARYING PERCENTAGES OF INCREASE OR DECREASE IN EGG-WEIGHT, COMPUTED ON THE BASIS OF THE WEIGHT OF TEN EGGS LAID AT THE PERIOD OF THE VERNAL WEIGHT MAXIMUM

PERCENTAGE-CLASS: Birds Selected for Increase in Weight Indicated Below	Number of Individuals Making the Record	Mean Production for the First Laying Year	PERCENTAGE-CLASS: Birds Selected for Increase in Weight Indicated Below	Number of Individuals Making the Record	Mean Production for the First Laying Year
> 10 per cent.	3	142	> 2 per cent.	27	123
> 8 " "	7	141	> 1 " "	29	122
> 7 " "	9	140	> 0 " "	31	120
> 6 " "	13	138	< 0 " "	16	106
> 5 " "	19	127	< 6 " "	24	114
> 4 " "	22	126			
> 3 " "	23	125	Total flock. . .	37	120

From the data presented in Table III it is clear that the small group of hens characterized by a percentage-increase on egg-weight of more than 10 gave a higher mean production (142 eggs) than any group manifesting a smaller percentage of increase in egg-weight. Each suc-

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[11] See footnote on page 383.

ceeding group, characterized on a smaller percentage-increase, gave a correspondingly smaller annual production, until, when we reach "< 0 per cent.," the group manifesting a decrease in mean egg-weight, we find a mean annual production of only 106 eggs. When the flock is divided according as the mean percentage of increase is more than 6, or less than 6, we find that in the high-percentage group there are 13 hens with a mean annual production of 138 eggs, while in the low-percentage group there are 24 hens with a mean production of 114 eggs. In other words, upon the division point of 6 per cent. increase, one may separate about one third of the flock whose annual production is 15 per cent. higher than the flock average and 21 per cent. higher than the mean production of the remainder of the birds.

If the reader will now make a comparison of the results reported in Tables I and III, it will be seen that the correlation demonstrated through the employment of the "ten-egg method" is as clearly established, and as valuable from the practical point of view, as the correlation demonstrated through the use of a full month's production.

VII

In view, therefore, of these results obtained from the weighing of ten eggs at the period of the vernal weight maximum, it seemed desirable to ascertain whether the same "ten-egg method" at the period of the autumnal weight maximum would also serve to distinguish a group of hens characterized by the possession of higher producing ability. Accordingly the production data for September were analyzed from this point of view.

In explanation of the September results, however, several points should be noted. In the first place, although September production represents a definite mode in the annual production curve when plotted on monthly ordinates, in the case of the flock studied the month's production falls considerably short of the April production. In April all members of the flock, without an exception, were laying. In September there were four hens that did not lay at all; and three hens laid only three eggs or less.

In the redistribution of the data for the present purpose the records of no hens are included that did not lay at least five eggs in September. Two hens laid nine eggs five eggs. So that, in reality, the results of this case are based upon the mean weight of somewhat less than ten eggs from each hen.

In the second place it should be noted that the September production was scattered when compared with the April production; and although an attempt was made to secure eggs laid during the latter half of the month, it frequently happened that it was necessary to include eggs laid in the earlier part. The results of this redistribution of data and the attendant computations are presented in Table V.

TABLE IV

SHOWING THE MEAN ANNUAL PRODUCTION FOR THE FIRST LAYING YEAR OF GROUPS OF INDIVIDUALS SELECTED FOR VARYING PERCENTAGES OF INCREASE OR DECREASE IN MEAN EGG-WEIGHT, COMPUTED ON THE BASIS OF THE WEIGHT OF TEN EGGS OR LESS, LAID AT THE PERIOD OF THE AUTUMNAL WEIGHT MAXIMUM.

PERCENTAGE-CLASS: Birds Selected for Increase in Weight Indicated Below	Number of Individuals Making the Record	Mean Production for the First Laying Year	PERCENTAGE-CLASS: Birds Selected for Increase in Weight Indicated Below	Number of Individuals Making the Record	Mean Production for the First Laying Year
> 13 per cent.	3	147	> 2 per cent.	21	125
> 11 " "	6	145	> 1 " "	23	125
> 10 " "	7	143	> 0 " "	26	124
> 9 " "	8	144	< 0 " "	5	108
> 8 " "	10	144	< 6 " "	19	112
> 7 " "	12	139			
> 6 " "	12	139	September production 3 eggs or less..	7	96
> 5 " "	14	135			
> 4 " "	16	134	Ditto, plus hens showing decrease in wgt.	12	101
> 3 " "	19	131	Total flock........	31	120

From the data presented in Table IV it appears, as in the former case, that higher production is correlated with the higher percentages of increase in egg-weight. The maximum group-production (147) occurred in those hens whose mean increase in weight was above 13 per cent. Selecting above 10 per cent. gave seven birds whose mean production was 143 eggs. Selecting above 6 per cent. gave twelve hens whose mean production was 139 eggs. On the other hand, selecting *below* 0 per cent. (*i. e.*, birds showing a decrease in egg-weight) gave five hens with a mean production of only 108. When we add to these the hens that laid three eggs or less in September, we obtain a group whose mean production was only 96; and when we consider the hens that (1) gave a September production of 3 eggs or less, and (2) gave a decrease in egg weight, we obtain a combined group of 12 whose mean annual production was only 101 eggs for the first laying year.

A comparison of Tables I, II, III and IV thus shows that the last case presents the clearest evidence yet obtained for the positive correlation existing between percentage of increase in egg-weight and total annual production. The results are more definite than those obtained for the "ten-egg test" at the vernal weight maximum, or for the "month test" at either the vernal or the autumnal weight maxima. In other words a test based upon a smaller number of eggs, laid nearer to the absolute mode, gives a clearer indication of innate producing ability than does a test based upon a larger number of eggs laid in a "scatter grouping" about the approximate mode. This conclusion is in harmony with the views expressed by Gavin[12] and by Wilson[13] to the effect that the best unit of time for measuring a cow's milk-producing ability is not the year test, nor the thirty-day test, nor even the seven-day test, but the one-day test conducted when the production reaches its maximum. Apparently the measurement of egg-production in the domestic fowl, considered as a quantitative performance, rests upon a similar basis.

VIII

In bringing this paper to a close the writer wishes to have it distinctly understood that nowhere in these pages has it been stated that there exists in the domestic fowl a

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[12] *Jour. Royal Agricultural Society,* 1913, 73. *Jour. Agricultural Society,* 1913, 5, 309–319. *Ibid.,* 1913, 5, 377–390 (on authority of Pearl).

[13] *Proc. Royal Dublin Society,* 1911, 13, 89–113. Jour. Dept. Agriculture, Ireland, 1913, 13, (4) (on authority of Pearl).

correlation between egg-production and egg-weight. Most poultrymen believe that, if a hen produces smaller eggs, she consequently produces more eggs; and, conversely, that if a hen produces larger eggs, she produces fewer eggs. This matter has not been considered in the present paper; it will be dealt with at a later time. The point may again be stated, that the significant correlation exists between numerical production and *the ability on the part of the hen to manifest an increase in egg-weight* at those seasons of the laying year when both production and egg-weight attain their respective maxima. A higher percentage of increase and absolute mean egg weight for the entire year has not yet been attempted. Many points like this remain to be worked out and the author does not wish to present his results dogmatically, but only with the hope that the problem will be attacked by other investigators. It is not improbable that the results may be found to vary with the breed of fowl, the date of hatching, the housing, the feeding and with other factors.

With these points openly in mind, and only with the purpose of stimulating further investigation and discussion, the author presents the following brief summary as expressing a biological fact which, if later proved to be of general application, may take its place as a fundamental law of production in the domestic fowl:

The innate egg-producing ability of a hen is manifested, not only by the number of eggs laid within a year, or within some shorter or longer period of time, but also by the degree of increase or decrease in the mean weight of her eggs, when this increase or decrease (calculated as a percentage-increase or as a percentage-decrease) is measured at those periods of laying (the vernal and autumnal maxima) characterized by the markedly increased production of the flock; and on this basis, groups of hens characterized by higher producing ability can be differentiated as accurately as, and more easily than by any other known means.

SOME HABITAT RESPONSES OF THE LARGE WATER-STRIDER, GERRIS REMIGIS SAY

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CONTENTS

I. Introduction

The large water-strider, *Gerris remigis* Say (Fig. 1), is one of our most interesting and familiar aquatic bugs. During the years 1911–1913 inclusive, I made a somewhat intensive study of the responses of this species to the physical conditions of its environment, in the vicinity of Urbana, Illinois. This study has been continued, intermittently, up to the present time. The present publication forms only a part of the entire investigations. Part of this paper treats of observations made near Urbana, Illinois, and part treats of observations made near Syracuse, New York.

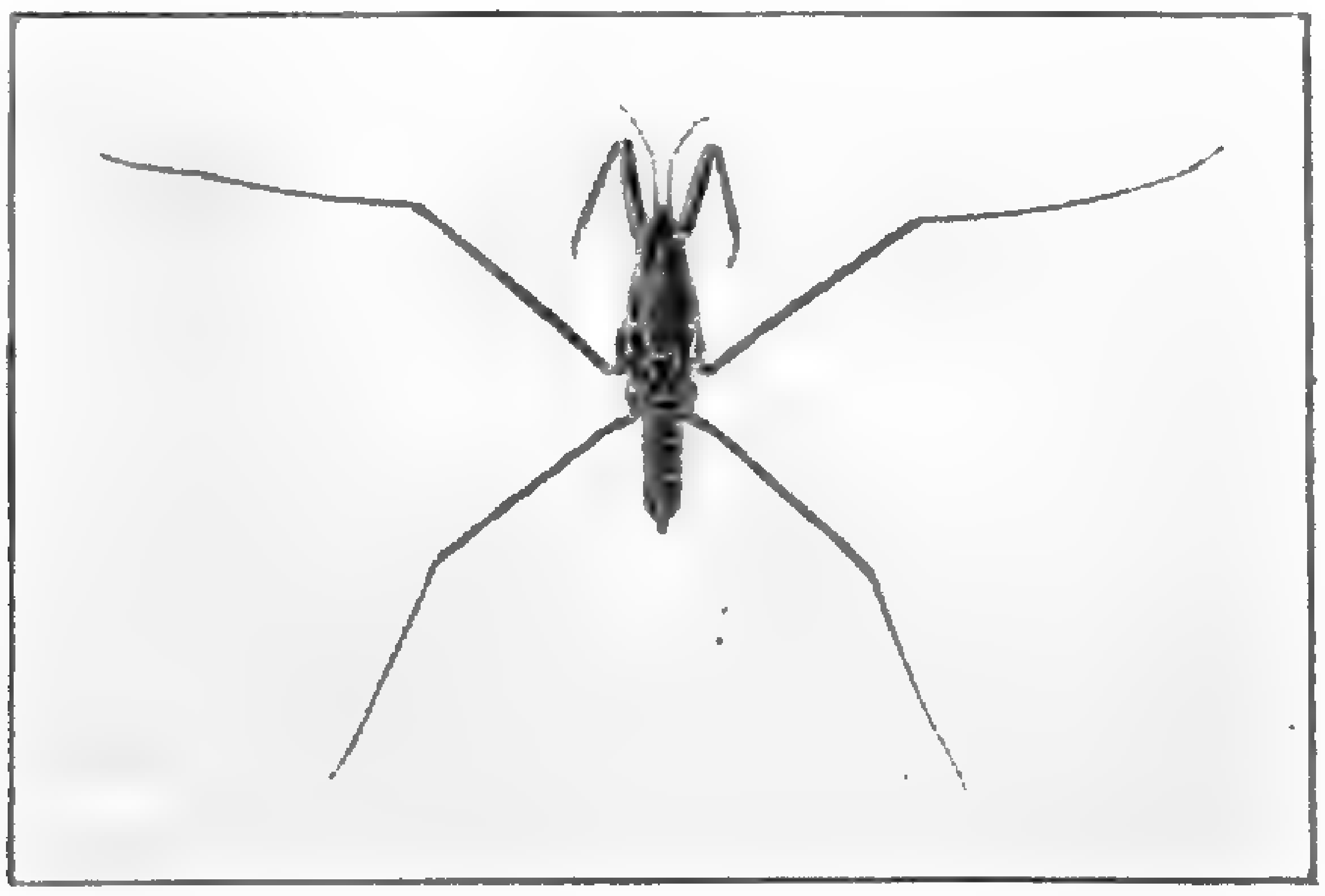

Fig. 1. The large water-strider, *Gerris remigis* Say, natural size. (Folsom.)

In the summer of 1911, a severe drought occurred in the vicinity of Urbana. In fact so extended was the period of dry weather, that many streams in the region, that usually were to be classed as permanent, became absolutely dry, and others were reduced to a few isolated pools. Water-striders, *Gerris remigis,* were trapped in many of these pools. As the gerrids belonging to this species are *mainly* apterous insects, they were unable to migrate by flight to some other body of water. Because of this, serious results might accrue to those individuals that were isolated in such situations when the pools became dry. It was a matter of interest to know what would become of these hemipterons when the water entirely disappeared. Therefore, a number of observations were recorded in connection with this subject.

II. PHYSICAL CONDITIONS OF AND BEHAVIOR IN BROOK HABITAT DURING SEVERE DROUGHT AT WHITE HEATH

1. Description of Physical Conditions.—Frequently certain physical conditions were found to exist in brook habitats in the early stages of droughts that had a direct bearing upon the very existence of the water-striders, *Gerris remigis,* but which will be mentioned here only very briefly. I wish to refer particularly to a brook, flowing partly through a forested region, near White Heath. This brook is situated about eighteen miles southwest of Urbana, and the physical conditions to be considered are such as existed during a drought, in the summer of 1911. During the earlier periods of this drought, I often found, in the drying brook bed, small pools of water not entirely isolated from each other. (In Figs. 2 and 3 are shown drought stages in the bed of the brook near White Heath that are very similar to those under consideration. The only difference here, of importance, is that the pools are in somewhat earlier drought stages than are those to which I have referred.) Such pools were connected by means of riffles not more than 6–12 inches wide (Figs. 2, 3). When food became scarce in pools of this character, or when a scum, often due to bacterial growth (Fig. 3), formed on their surfaces, I have observed that the water-striders made their way from one pool to another, by means of these small riffles of water, until such connecting links disappeared and the majority of the pools became dry. Eventually the gerrids were concentrated on the surfaces of the few isolated pools that remained. Sometimes, the bacterial growth, which was of a gray color, caused the death of hundreds of water-striders.

Such pools as have been mentioned persisted longer in that part of the brook's course that extended through the wooded region. In such a region the pools were larger, with a greater volume of water, than frequently was the case in more exposed situations. These conditions were due primarily to the protection afforded to the

FIG. 2. Detail of brook near White Heath, along margin of forested region, showing conditions during early stage of drought (July). Arrow indicates direction of current. *a*, pools on surface of which water striders, *Gerris remigis*, live; *b*, small riffle connecting two pools; water striders pass from one pool to another by means of such riffles. *c*, dry bed of brook exposed during early and late stages of drought. (Original.)

water by the surrounding trees. There, undoubtedly, is less evaporation in a region of this character than is true in those parts of the brook which are situated in regions lacking both trees and shade and are thus exposed to a high temperature and to the full effects of the summer sun. Very similar facts were observed near Charleston, Illinois, by Adams (1915, pp. 65, 66) in connection with a small stream in a forested area. He makes the following statement:

> This small temporary stream in a ravine formed the southern boundary of the area examined. . . . At the season of our examination it was a series of small disconnected pools. . . . On the surface of the pools were numerous specimens of a water-strider, *Gerris remigis*. The forest cover is undoubtedly an important factor in the preservation of such pools, as it controls the evaporating power of the air.

In this connection I wish to state that the water-striders were found in far greater numbers, in the late spring, summer, and early fall, on those portions of the stream that flowed through the forested area. After several years of observation, I have come to the conclusion that the shade and lower temperature are the important factors in influencing the gerrids to remain in such situations. De la Torre Bueno (1911, p. 246) has observed somewhat similar facts, as is indicated in the quotation:

> It [*Gerris remigis*] is to be found most frequently on running waters, although it also frequents still, but to a less extent. . . . They congregate in groups in shady, slow-moving parts of streams, at the tree roots projecting from banks into the water, in the shadow of bridges, and in general in almost any place where they have some shelter from the burning rays of the summer sun.

This observer (1917, p. 201), again writing of *Gerris remigis*, states that:

> These beasties are common and familiar sights to the lover of the quiet flowing waters running to the distant seas. In these haunts, in some still little bay or moveless backwater, under a bridge, or in the shadow of a tree, or in the cool recesses of an overhanging bank, you may see *remigis* gathered in numbers, rowing silently about. . . . Here they rear large families and spend at ease the sultry dog-days.

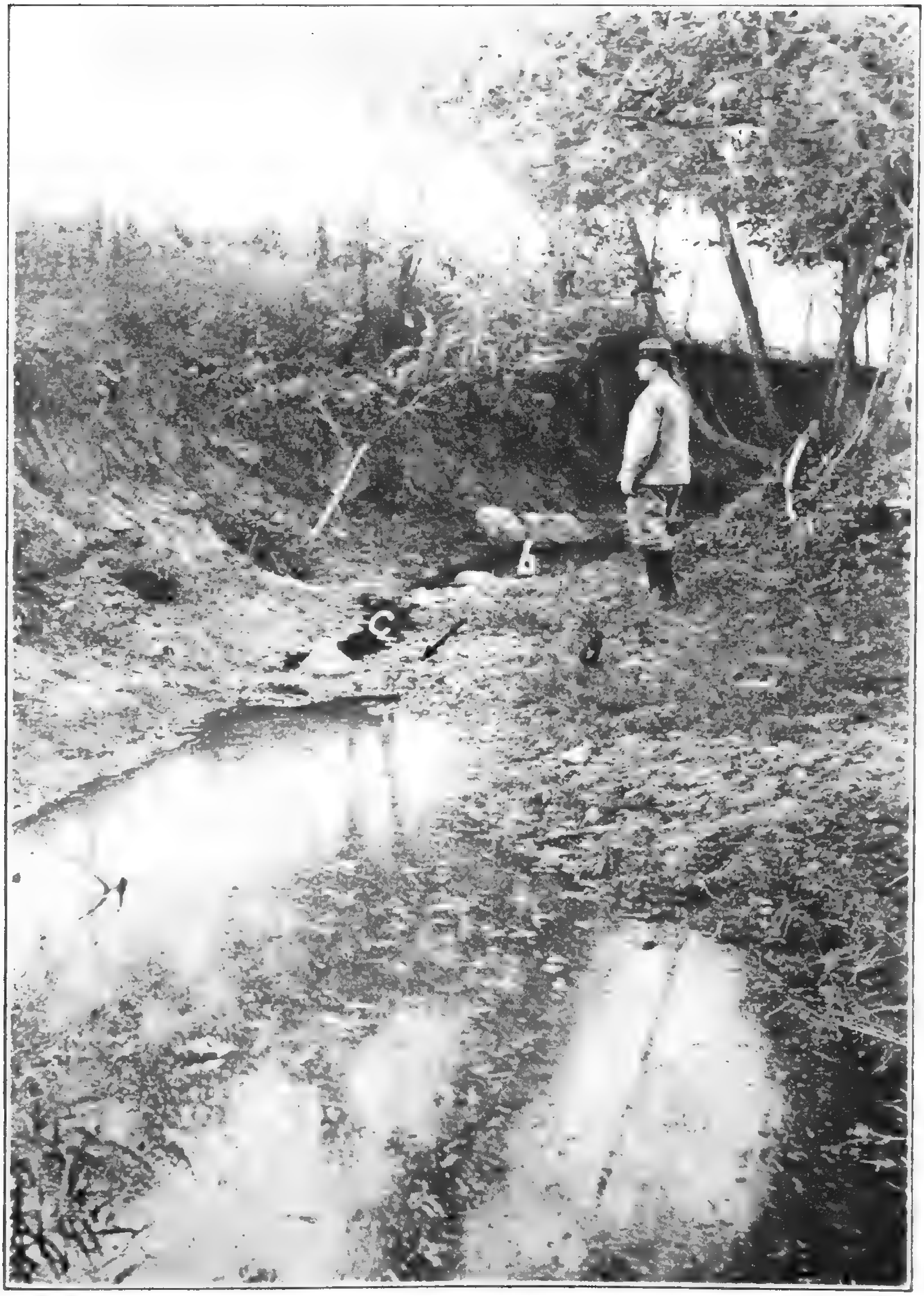

FIG. 3. Detail of brook near White Heath, along margin of forested region, showing conditions during a later stage of drought than indicated in Fig. 2 (August). Arrow indicates direction of current. *a*, pool showing scum on surface, formed by bacterial growth, which frequently kills water striders in large numbers; *b*, pool on surface of which water-striders, *Gerris remigis*, live, surface being free from scum; *c*, small riffle connecting two pools; water-striders pass from one pool to another by means of such riffles. *d*, dry bed of brook exposed during early and late stages of drought. (Original.)

Attention has been directed to some of the physical conditions that existed in a brook water-strider habitat in the early stages of a drought. Certain features of such a habitat in the later drought stages, will now be considered. So far as I am aware, there are no records in the literature on aquatic Hemiptera, that describe the responses of these gerrids, *Gerris remigis,* after the water in their habitat actually disappears. The statements given here are very condensed records taken, chiefly, from my extensive field notes of the summer of 1911.

Late in the summer a trip was made to White Heath for the purpose of examining a number of isolated pools, on the surface of which water-striders were trapped, in the bed of the brook near that place. Particular attention was directed to one pool in which the water had evaporated rapidly during the previous week. It was examined about 8:00 A.M. and at that time the dimensions of the pool were approximately $12 \times 5 \times \frac{1}{2}$ inches. It was evident that the pool would be completely dry before night. Evaporation was taking place rapidly, as the atmosphere had been very dry for several days. The heat had been intense for a number of weeks, a temperature of 90°–100° F. not being uncommon.

2. Behavior in a Drying Pool.—There were twenty gerrids trapped on the surface of the pool, already mentioned. The insects did not move about very much on the water-film. They were very quiet, frequently remaining, practically, motionless for several consecutive minutes. There was no behavior on the part of the hemipterons that indicated any attempt to escape from the unfavorable surroundings. The members of this species being *largely* apterous forms and their optimum habitat being permanent brooks and streams of moderate size, with a current of medium velocity, it was, perhaps, not strange that they evinced no responses that showed definitely adapted behavior of a character suitable to cope with such abnormal conditions and unusual habitat changes. At 2:00 P.M. the pool was almost dry, and by 3:30 P.M.

there was little to indicate its location except a small area of rapidly drying mud.

3. Hibernation and Æstivation.—A number of writers —among others Uhler (1888, pp. 268, 275), McCook (1907, p. 265), and Kellogg (1908, p. 198)—on water-striders have stated that during hibernation these gerrids burrowed into the mud, under the banks of streams, at the bottom of water under stones and roots of trees, and at the bottom of the pool under roots or stones; and as some investigators, Tower (1906, p. 245), for example, consider hibernation and æstivation to be "fundamentally one and the same process," I was interested to observe whether the gerrids would burrow into the mud, or into some moist, sheltered spot under the banks of the brook, and remain there in a quiescent condition, a state of æstivation, until the rains came. However, there were no definite responses of such a character. I doubt whether water-striders do æstivate in the true sense of that term during periods of drought, although more evidence is necessary before a definite statement can be made.

As will be noticed later, the gerrids do respond to contact stimuli. Generally such a stimulus resulted in inhibiting locomotor activity and the insects remained motionless with their bodies closely applied to some solid object in the bed of the brook. This might prove to be a piece of dry mud, a stick of driftwool, a stone, or a clump of dead leaves. As a result of contact stimuli, sometimes they would crawl under such objects as have been enumerated and remain there for a considerable length of time. I have recorded observations which prove that they stayed in such situations from a few seconds to thirty minutes. The gerrids might remain in places of this character for even a longer time, as I have noticed, on a few occasions, that they were still there when I discontinued my observations for the day. However, I was not able to find them in the same situation the next day, even after most carefully marking the place. On several other occasions, I have made similar observations, but never was I able to discover the water-striders the following day.

It is possible that there was a trifle of moisture in such situations, and that it was this, acting as a stimulus, which kept the gerrids there. But during these periods of drought—accompanied, as they are, in the prairie regions of Illinois with excessive temperature and glaring sunlight—I have failed, positively, to find moisture in such places, except under large objects, which were not present in the bed of the brook. Frequently, however, I have noticed that under these objects, in the brook bed, the temperature was slightly lower and of course there also was the shade. It is probable, also, that evaporation is reduced in such protected places. That certain arthropods are sensitive to the evaporating power of air is known from the work of Shelford (1913, pp. 85–102), who has demonstrated that the yellow-margined millipede, *Fontaria corrugate* Wood, and the ground beetles, *Pterostichus adoxus* and *Pterostichus pennsylvanicus,* respond negatively to the increased evaporating power of air. Therefore, lower temperature, shaded surroundings and reduced evaporation may be the three factors that accounted for the water-striders remaining in situations of the character that have been mentioned. Of course if it was proved that they stayed there day after day, this would indicate the possibility of their tiding over a short drought in such protected places. I have noticed on a few occasions, at least, that the gerrids have died, if away from water, when exposed to glaring sunshine and high temperature, during a drought. I also have observed, when the water in my laboratory aquaria was allowed to evaporate gradually, until it entirely disappeared, that, sometimes in a few hours and at other times in a few days, the gerrids died. This occurred, not infrequently, when the temperature was only 85° F.

During hibernation, there is no question about water-striders remaining quietly in one place for a long period of time. But it must be recalled that the temperature is low at such times, and that they frequently seek dry situations. The subject of hibernation will be discussed at greater length in another paper. I may say, however, that these water-striders do not hibernate in any of the situations mentioned by the writers quoted, except under the banks of streams, and then away from the water. The positive thigmotactic responses of these gerrids have been observed frequently during periods of hibernation. At such times they formed tangled masses, which were due to the water-striders crowding closely together. These facts were recorded in my field notes as early as the winter of 1912–1913. It is interesting to recall that Essenberg (1915; pp. 397, 400) has observed similar responses in the case of *Gerris orba* Stål.

4. Initial Responses in Dry Bed of Brook.—With reference to the water-striders in the dry bed of the brook at White Heath, it appeared as if the gerrids might die right where they were, for no movements occurred for approximately ten minutes after the water had disappeared. Soon they began to move away. I can not state absolutely what was the stimulus that caused the initial locomotor responses, although it probably was the total disappearance of all moisture, as this was the only evident change in the external conditions. Singly and in small groups they jumped and walked in an ungainly fashion from the site of the former pool. While it was evident that the water-striders were less accustomed to locomotion on the land than they were to locomotion on the water, yet they made fairly good progress along the bed of the stream.

The evidence that the initial locomotor responses of the gerrids, away from the pool in which they had been living, were due to the drying up of the water is further supported by the following facts: Very frequently, I have observed that when water-striders were removed from the surface of a pool in a stream, or from an aquarium, where they had been kept in captivity, and placed on the ground or on some other solid surface that they at once became active. This was true even if the gerrids previously had been inactive. They would start to jump and walk in a very agile, if ungainly, fashion, and made rapid progress, especially if they were on a smooth and level surface. It seemed that the transference from the water-film to a solid surface—for all other conditions were as before—was a sufficient stimulus to cause internal changes in the insects, that set free energy in the form of locomotor activity. To induce this result there was but one change in the conditions. In this connection I wish to direct attention to a statement by Jennings (1906, p. 285):

> Often, of course, stimulation does rouse an organism to increased activity. But even in this case the activity is due to the release of internal energy. It may, therefore, continue long after the stimulation which inaugurated the release has ceased to act. Such continuance thus does not necessarily imply continued action of the stimulus. In many cases the specific stimulus to action is only the *change* of conditions.

At this point, it may not be out of place to refer to certain observations which, possibly, may have a bearing on the locomotor responses of the gerrids, after the drying up of the pool of water. Abbott (1918, p. 234), in connection with some responses of land isopods, *Oniscus asellus* Linn., *Porcellio rathkei* Brandt, and *Porcellio scaber* Latreille, to humidity and evaporation makes the following statement:

> So far as observation shows, the effect on land isopods of exposure to a dry atmosphere, including the first effect in desiccation experiments, is an increase of activity. This is a useful adaptation, provided the activity carries them to other regions where moisture conditions approach more nearly the optimum.

5. *Behavior in Dry Bed of Brook.*—About ten yards farther downstream there was another much larger pool. Its dimensions were approximately 3 yds. × 2 yds. × 5 in. I was interested to observe how many, indeed if any, of the gerrids would reach it, and thus tide over the period of drought. Of the twenty water-striders present, eight of them went in the direction of the large pool, and wandered in an aimless, awkward manner down the dry

channel of the brook. They first tried one path and then another. These trials resulted in bringing some of the gerrids to the pool, but with reference to other water-striders the trials were not so successful. I found that it was a rather strenuous task to watch all the gerrids, although some of them frequently would come to rest. Without giving too many details, it may be stated that all of the eight individuals, already mentioned, made their way in a blundering fashion to the large pool of water. The first one reached the pool in 5 minutes and 30 seconds, and at once moved on to the surface-film. The time required by the others to reach the water varied to a considerable extent, the average being 14 minutes and 30 seconds. The last individual, of the group of eight, to reach the pool was fifteen minutes in making the journey. Three gerrids out of the eight traversed the distance to the pool with only a limited number of stops and deviations from the straight path. However, this is not to say that the journey was free from erratic movements, on the part of these insects, for such was not the case. The stops usually occurred when the gerrids came in contact with some obstacle in their path. It was not at all uncommon, when the insects moved away from their stopping place, for the direction of locomotion to be changed. The five other water-striders frequently came to rest against stones and pieces of dry mud. Such contact pauses were evidences of the thigmotactic propensities of the gerrids. They also wandered from side to side of the stream bed, trying one direction for a certain length of time, and then, through the influence of some stimulus, trying another. However, they made only a very few turns, directly away from the down-stream pool during their entire journey. One water-strider crawled under a piece of dried mud and remained there for three minutes.

There were twelve other water-striders that have not yet been accounted for. Four of these wandered up-stream and from one bank of the brook to the other, first in one direction and then in another. Sometimes they stopped with their bodies in contact with some obstacle in their path. Frequently the direction was changed when they renewed the journey. The gerrids did not turn downstream for any considerable distance during any of their movements. After having observed them at intervals for two hours, I decided that they were unlikely to reach the water unless they eventually should wander to a pool somewhere upstream. The gerrids had moved away from the site of the former pool to such a distance that the water-strider farthest upstream was twenty yards distant from the starting point. One individual crawled under a piece of driftwood and had been in that situation for twenty-five minutes, when the observations were discontinued. Another water-strider crawled among some dead leaves and was there for twenty minutes previous to the time when I left that place for observations elsewhere.

Of the eight gerrids that have not yet been mentioned, three of them stumbled toward the left bank and five of them wandered toward the right bank of the brook. There were various obstacles in their paths, such as small rocks, pieces of dry mud, dead leaves and driftwood. The water-striders frequently came to rest in close contact with these objects—response to contact being a prominent feature in the behavior of these gerrids—and at length two of those, that had moved toward the left bank of the stream, jumped into a large crack formed in the baked mud of the bed of the brook. I observed these individuals from time to time—for at least three hours—until I left for Urbana, at about 8:00 P.M., and they were still in the same situation. I should state here that I searched for these two gerrids the next day and was unable to find them; nor was I able to discover the other four water-striders—to which I already have referred—that had moved upstream. The responses of one of the three gerrids, that in the first instance had moved toward the left bank of the brook, have not yet been described completely. After reaching the bank, it began to jump downstream. This continued for a distance of two yards, when it turned, facing the right bank of the stream, and jumped in that direction for one yard until it reached the middle of the brook channel. The gerrid again turned to the left, this position directing its head downstream, in which general direction it continued to travel, until after a number of stops, it eventually reached the large pool. In passing over its entire route, this water-strider consumed fifteen minutes.

It has been stated that five gerrids wandered toward the right bank of the brook, on first leaving the site of the former pool. Three of these turned toward the middle of the stream channel and jumped upstream for two yards, turning to the left, they moved toward the bank of the brook. On reaching it, first one and then the others jumped downstream. After a number of pauses and deviations to the right and left, two of them again turned with their heads directed upstream and continued to jump and walk in that general direction. After several erratic movements and two stops, the third gerrid turned upstream. The insect jumped in this direction for three yards and then stopped with its body in contact with a small rock. It remained in that position for five minutes. In the meantime, the two other water-striders had worked still farther upstream. On going back to observe the gerrid that had been resting against the rock, it was discovered that this insect had moved away and was walking upstream. These three water-striders were observed for 1 hour and 50 minutes and as there appeared to be less and less possibility of their reaching the large pool downstream, the observations were discontinued. When the insects were noticed last, they had traveled eighteen yards upstream away from the site of the former pool, from which they originally came. One of them had crawled under a piece of driftwood and had been there for thirty minutes when I discontinued my observations. These gerrids were sought carefully the following day, but I was unable to find them.

The wanderings of two water-striders, out of the group of five, have not yet been traced. Attention already has been directed to the fact that, when they first left the site of the former pool, they wandered toward the right bank of the brook. After reaching this point, they turned downstream. I lost sight of one of them, while observing some of the other gerrids, and I was not able to find it again. The other water-strider proceeded downstream, but frequently deviated from a straight path, and often paused with its body in contact with various obstacles. After wandering downstream for three yards, it made a complete turn and its head thus pointed upstream. This occurred as the insect was making a jump, it appearing to lose control of the orientation of its body. The water-strider moved upstream for two feet and then turned to the left, walking in that direction for four feet. The gerrid made a wide turn to the left, so that its head was directed downstream. After much erratic wandering, it eventually blundered upon the large pool of water, having consumed forty minutes in completing the journey. It was a task of considerable difficulty to keep all the gerrids under observation, because, being almost the color of the background, they were very inconspicuous.

I have records of a number of other instances, treating of my observations on the responses of water-striders after the drying up of several other stream pools, at different times and during different seasons. Some of these pools were at distances of less than ten yards, while others were eleven, twelve, and fourteen yards distant from the original pool on which the water-striders lived. It is true that, on the particular occasion to which attention has been directed and which has been described in some detail, half of the gerrids entrapped on the surface of the pool escaped—when it became dry—to another and larger body of water by making their way overland. But in all the other instances that were recorded in my field notes of similar phenomena, a very much smaller percentage of the entrapped gerrids was successful in reaching other bodies of water, after their own pool became dry. I will give a few examples: In one instance, only two of the trapped water-striders out of eight reached the surface of another pool, situated about eleven yards upstream. This was not accomplished until the gerrids had consumed much time in random movements, stops and deviations from the straight path. At another time, fifteen gerrids were trapped in a pool along the bed of a brook that had become almost dry, owing to a prolonged drought. Five water-striders out of the fifteen, or one third of the total number, only, were able to find another pool of water seven yards upstream from the point where they had been isolated. These gerrids made many trials, errors, delays, and turnings before they reached the surface-film. On still another occasion forty water-striders were entrapped on the surface of a stream pool. After the water had disappeared entirely, the hemipterons left their haunts, and stumbled along the dry bed of the stream. After much wandering about, first in one direction and then in another, six of the gerrids found a pool fourteen yards downstream from their former abode. The method of reaching the water seemed to be due to a crude form of trial and error.

I am inclined to believe that in periods of severe drought, large numbers of apterous individuals die. If the drought is a short one, and there is a certain minimum of dampness under logs, stones, and clumps of dead leaves, some of the water-striders may survive in such situations. In regard to physical conditions of a somewhat comparable character, Kirkaldy (1899, pp. 109, 110) makes the following statement with reference to *Gerris lacustris* Linné:

> In small wayside pools or streamlets which dry up periodically, it is obvious that the apterous inhabitants will die out unless their habitat is sufficiently near to a larger stream or pond; a severe drought occurring over a fairly large area, prolonged sufficiently to dry up all the water within that area, would cause all the species represented in that year by apterous individuals only to become extinct.

After having observed the erratic, aimless character of the responses of these insects, *Gerris remigis,* their ability to reach some other distant body of water appeared doubtful, and very largely dependent upon chance. If a larger body of water should be very near to the haunts of the gerrids, then there would be, through their random journeys, a greater possibility of reaching such a situation. In any case, their responses appear to be responses of repeated trial and failure, until through many repetitions, some gerrids eventually reach the water.

III. EXPERIMENTS IN CONNECTION WITH BROOK HABITAT AT WHITE HEATH

1. Methods.—I now wish to record certain other observations, on the responses of *Gerris remigis,* of a somewhat different character from those that already have been discussed. Many times when out in the field collecting *Gerris remigis,* some water-striders escaped while I was picking them out of the net as it lay on the ground near the margin of the stream. I noticed that these individuals generally found their way back on to the surface of the water. Several times it occurred to me to undertake a series of experiments with these water-striders for the purpose of discovering their ability to return to their own habitat after having been removed from it. The plan was to place them on the ground at various distances away from the stream and observe whether or not they returned to the water, and if so to record the readiness with which this was done. Up to the present, the experimental work has not yet been carried out as extensively as was desired, but the results that have been obtained may be of interest. The experiments were undertaken at the brook near White Heath, that has been mentioned previously. The site selected was at a place where the bank was flat, with its surface raised only a few inches above that of the water.

2. Responses When Facing Brook.—Twenty gerrids with their heads turned directly toward the stream, were placed on the ground one yard away from the water. All those that got back to the water succeeded in reaching the surface-film in less than one minute. Similar experiments were repeated for four successive times, using different individuals. There was no experiment in which more than two gerrids failed to reach the water. Other experiments were carried out in which the water-striders were placed two, three, and four yards away from the stream. The majority of the gerrids found their way back to the water. All those that were taken two and three yards away from the stream were back on the surface-film within 2 minutes and 30 seconds. Gerrids that were placed on the ground four yards away from the brook evinced a few more random movements than was the case of those nearer to the water. A slightly smaller percentage of the gerrids found the way back to the stream from this distance. Those water-striders that reached the surface of the brook did so within four minutes from the time each experiment began.

3. Responses When Parallel with Brook.—A series of experiments were performed identical to those already described, except that the water-striders were placed on a line with the long axis of their bodies parallel with the bank of the stream. It was observed that the majority of the gerrids were successful in reaching the water. In the case of some individuals, a longer time elapsed than was true in the first series of experiments. But most of the water-striders either turned at once toward the brook, or else they did so a few seconds after the first locomotor movements began. In some instances the gerrids jumped, for one yard or more, in the direction in which their heads were directed, before turning toward the brook. Some gerrids were placed on the ground four yards distant from the water. Certain individuals of these evinced some hesitancy in jumping directly toward the brook and there were a number of random movements.

4. Responses When Facing Away from Brook.—Other experiments, of a character similar to those that already have been described, were carried out, in which the heads of the water-striders were directed away from the stream. As before, a majority of the gerrids were successful in reaching the water. The same distances were used as in the former experiments, but in all cases there was less promptness in moving toward the brook. It also was evident that there were more random movements than was true in the former experiments. Of the water-striders placed four yards away from the stream, a greater percentage, than in any of the other experiments, failed to reach the water.

These hemipterons employed two methods of locomotion on land, walking and jumping. The more rapid progress was made by jumping. The individual jumps averaged about one inch in length, although frequently they were greater than this. Sometimes when jumping, the gerrids made a complete turn, as if they were not able, fully, to control the orientation of the body, and this frequently resulted in changing their direction of progress. In this connection, I wish to direct attention to the fact that Essenberg (1915, p. 399) has observed a somewhat similar response on the part of *Gerris orba* Stål and makes the following statement:

> It runs with a jerking motion, making from four to six jumps in succession and then making a short stop. Very often it turns a somersault and continues running without interrupting its course until it reaches a place of safety. There it lies quietly for from fifteen to twenty-five minutes, then suddenly begins its race again.

Often during one of these jumping movements, the water-striders struck against some obstacle and when this occurred, their direction of progression was changed. There was some tendency for the gerrids to continue to move in the direction which they already had taken, without regard to the position of the stream. In the three series of experiments it is of interest to notice that the water-striders reached the brook with a fair degree of directness. It was only in the series of experiments, in which the heads of the gerrids were turned away from the water, that there was much evidence of lack of promptness in turning toward the brook and of random movements.

5. *Experiments with Barrier.*—In the experiments that have been described, I felt that the sense of sight was the important factor in directing the water-striders to the brook. However, there was always the possibility that moisture, as a stimulus, might influence the responses of the gerrids. Therefore, I planned a number of experiments for the purpose of obtaining more definite information on this subject. My idea was to arrange a sort of barrier, along a limited section of the bank of the brook, which was to be of such construction as to permit diffusing moisture to pass through it readily, but on the other hand, the barrier was to be so opaque that the reflection from the water of either sunlight or diffuse daylight could not be seen through it. The barrier first employed was made of roughly interwoven leafy branches of trees. This was held in position by wooden stakes. It was four feet high and extended along the bank of the stream for a distance of approximately fifteen yards. There were two reasons for employing a barrier of this character: first, the readiness with which the materials could be obtained; and second, the fact that its appearance was in harmony with the general environment. However, it was found to be practically impossible to make it sufficiently tight so as to prevent reflections from the surface of the water from passing through it.

A number of series of experiments were tried with water-striders placed on the ground one yard and also three yards away from the brook. While the experiments were not sufficiently satisfactory, as a basis for definite conclusions, it may be stated that the gerrids displayed somewhat less promptness in reaching the water than was the case when such a barrier was absent. However, in general it was evident that the water-striders jumped toward the brook with considerable expedition and definiteness. If the barrier had proved to be light-tight, I should have been inclined to explain such a measure of promptness in moving to the water as due, perhaps, to the effect of moisture from the stream.

Of course if the means of finding the brook was mainly through vision, it was to be expected that the gerrids would be a little less prompt in reaching the water, because less reflection from the surface of the brook could be seen than was true with the barrier removed. Unfortunately the movements of the leaves by the wind permitted many bright reflections to pass through the barrier. Lying flat on the ground, with my eyes as close to it as practicable, in order to take a position as nearly the same as possible to that of the water-striders, I found that I was still able to see the bright sunlight of the hot summer day, reflected from the surface of the water. I planned to use another form of barrier and test this matter fully, when, because of the character of the season, I was compelled to take up certain other observations, and I have not yet had the opportunity to supplement this work with additional experiments.

(To be continued)

ONCHIDIUM AND THE QUESTION OF ADAPTIVE COLORATION[1]

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I. As the result of his extensive study of the phenomena of coloration in the tropical reef-fishes, Longley (1917) comes to the conclusion that the colors of these animals are "correlated with their habits in such a way that their conspicuousness is thereby reduced. There is no correlation of bright colors with special modes of defence, and no evidence that bright-colored types enjoy immunity greater than that of their fellows." The general tendency of this, the most recent, and in many ways the most thorough, observational study of the question of adaptation in animal coloration that has yet appeared, favors adherence to the view that as a whole the coloration of animals is of a concealing, hence adaptively protective kind. There are instances among invertebrates which seem fundamentally inconsistent with this interpretation, because the organisms in question are not colored like their habitual background and because they are for this, and for other independent reasons not inconspicuous. It is also a fact that in specific instances of this sort special repugnatorial systems are frequently encountered. Because of its importance for the theory of adaptation, this matter is deserving of careful scrutiny. The natural history of the littoral pulmonate *Onchidium floridanum* Dall affords a case in point.

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[1] Contributions from the Bermuda Biological Station for Research and from the Anatomical Laboratory of the Northwestern University Medical School.

In his notes on the fauna of Bermuda, Heilprin (1889, p. 187) described as new the form "Onchidium (Onchidiella) trans-Atlanticum," saying of its pigmentation: "smoke color or dark olive," in dorsal view. Some years later Pilsbry (1900, p. 503), reporting on Verrill's collections at Bermuda, listed this species under the designation by which it is now known, *Onchidium floridanum* Dall, adding, "Its dark olive green color agrees so well with the stains on the rocks that it is very inconspicuous. —(A.E.V.)"

It is possible, though not certain, from these brief descriptions, that Heilprin and Verrill had respectively collected representatives of the two differently colored types of *Onchidium* which occur at Bermuda. No constant morphological differences have been detected upon which to base a separation of these types, one of which is in nature blue-black in general aspect, the other characteristically of a light ("smoky") olivaceous hue. Some intermediate shades do occur, but in the field a rather sharp separation of the two groups is always possible. The very dark form is much the more numerous. So far as pigmentation is concerned, it is probable that the blue-black types contain merely a heavier deposit of a subepidermal pigment, which is chemically alike in both kinds of Onchidia. Nevertheless, we are inclined to believe that the difference in pigmentation may be representative of a real genetic difference between the two types, for reasons which may briefly be stated as follows: The two modes of colorization are in many places exemplified side by side; young and adults of maximal size are found belonging to either group; the occurrence of the pale form is independent of the seasons, and is found year after year in the same spots; in other places, where blue-black individuals may be very numerous, no lightly pigmented individuals have ever been encountered. Therefore we are probably dealing, not with a temporary fluctuation in color, determined by some metabolic cycle, but with constitutionally diverse races of *Onchidium;*

whether they be "species" or not is immaterial. A similar phenomenon seems to occur in other genera of this family, for v. Wissel (1898) notes that Plate (cf. Plate, 1893, 1894) collected two differently colored forms of *Onchidiella coquimbensis* Plate; in this instance the color difference between the two types, found in nature under the same stones, was not so pronounced as we find it in *O. floridanum.* In an *Onchidiella* which is very abundant at Bermuda one of us has observed a corresponding sort of color difference. The variation in question cannot be in any way a sexual one, for reasons already given and because the animals are hermaphroditic.

II. *Onchidium floridanum* lives between tide levels. It is never seen when the intertidal shore-zone is covered by the sea; during this period it inhabits deep crevices and cavities within the eroded rock. A dozen or more Onchidia live together in this way. Their "nest" opens to the exterior by means of a small opening, usually further obstructed by the growth of *Modiolus,* which is almost invariably quite inconspicuous, although the densely packed small black "mussels" within and around the entrance itself may form a very definite patch standing out clearly amid the olive-brown algæ covering the surface of the rock. When the tide falls so far as to have left the level of the *Onchidium* nest about an hour before, the occupants of that nest emerge, successively and in a steady stream, wander some little distance over the rock, feed, and then, before the tide has risen again, the members of each group synchronously begin to creep back to the respective nests from which they originated. The remarkable character of this "homing" behavior we have separately studied with considerable care, and have discussed in another place (Arey and Crozier, 1918). Here we would emphasize simply the fact that *O. floridanum* appears in the open, on the intertidal rocks, only during the period of low water.[2]

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[2] The experimental observations from which some of these statements are derived will be found described in a report, by Arey and Crozier, on the general behavior of *Onchidium,* now in course of preparation.

The nature of the background provided on this rock surface is by no means constant in different localities. Commonly, as in the case of rocks in sheltered places, completely submerged at high water, or on lee-shores generally, the limestone is covered by a feltwork of matted Enteromorpha and associated plants, sun-bleached to an olivaceous yellow tint. This is the usual condition within the sounds (Great Sound, Castle Harbor), and along the shores of bays protected from the surf. In places not so sheltered the rock may be colored by minute green algæ, or by the growth of calcareous green or reddish algæ, with which, as in the former case, many serpulas are intermingled; barnacles (*Tetraclita porosa*) also sometimes extend into the *Onchidium* zone, but the prevailing hue, and the color of any particular spot of small area, is largely determined by algæ.

Onchidium also occurs, though more sparingly, on surfaces of a still different type. In some places the layer of red earth (clay) underlying superficial æolian limestone is exposed at the water's edge, usually in a small cove containing loose rocks left bare by the tide. This earth provides a muddy layer of reddish brown, over which Onchidia are occasionally found to be creeping. From such tiny coves the direct rays of the sun are largely excluded, so that the in-shore surfaces of the stones are overgrown by algæ, green or red-brown, unbleached; on these surfaces also *Onchidium* may be found.

The zone inhabited by *Onchidium* is also that in which great numbers of the common *Modiolus* occur. These mussels, as already stated, almost invariably line the approaches to the *Onchidium* nest, and grow within the entering passageway itself. Except where the mussels have settled thickly in more or less horizontal fissures between the wind-formed strata of the limestone, they occur conspicuously in little groups, frequently not more than 3–4 cm. in diameter, occupying every slight depression in the surface; this is usually the case in situations where *Onchidium* abounds. A typical instance is that of a low-lying islet such as "Little Agar's," in Great Sound. The leeward (eastern) side of this island, well protected by the mass of the larger Agar's Island, exposes at low water a considerable extent of almost horizontal rock-surfaces, whereon occur sparingly clumps of *Modiolus*, which are, however, much more abundant around the vertical edges of these slabs. Within the clumps of *Modiolus* lie many *Onchidium* nests, from which the mollusks at appropriate times creep out and wander over the flat, yellowish, sunlit beach-rock. It is in situations of this general type that *Onchidium* is most abundant; in less freely illuminated places it occurs more sparingly.

It is a remarkable fact that, in addition to frequenting characteristically, though not exclusively, habitats which during most of the day receive the direct rays of the sun, *Onchidium* comes out into the open only during daylight hours, and never (in our experience) at night;[3] the circumstance which makes this condition particularly curious is that *O. floridanum is at all times negatively phototropic,* and in a very precise manner, when tested apart from its usual environment. No more striking instance is known to us of apparent contradiction between the findings of analytical experimentation regarding the behavior of an animal and the actual life of the same creature, for the snails when on the intertidal rocks move toward or away from the horizontal rays of the sun with perfect indifference. The cloudiness or brightness of the day, however, has but an unimportant influence, if any, on the numbers of Onchidia which appear upon the rocks.

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[3] That the wandering of *Onchidium* into the open is determined by immediate physical circumstances in the environment is shown by two facts: No rhythmic periods of migration persist when the snails are removed to the laboratory; on days when strong winds and accompanying ocean currents prevent the escape of the tidal water from the partially enclosed Great Sound, so that there is no occurrence of "low water," the Onchidia remain within their nests. *O. floridanum* can remain below water for 6–7 days without much impairment; a small amount of air is sometimes trapped within the rock cavities which they utilize as nests and this may in some cases help during prolonged submersion.

III. The coloration of an *Onchidium* is the result of its intensity of pigmentation, the texture of its mantle, and the activity of its mantle glands. An adult measures, on the average, 17 mm. long by 12 mm. broad by 6 mm. high when resting undisturbed, being then oval in outline; but it becomes more elongated during creeping, measuring then about 24 by 8 mm., and also less strongly arched, being about 4 mm. high. When first observed creeping out of its nest for an "airing," it usually happens that the *Onchidium* bears upon its dorsal surface a thin pellicle of slime completely investing the mantle. This slime-layer is tough, somewhat thickened about the periphery, and can be peeled off intact. Frequently it is so removed, mechanically, during the snail's efforts to creep out of its nest, for the passage-way is commonly so obstructed by the growth of *Modiolus* that the Onchidia must slowly insinuate themselves through slit-like apertures not more than 2 mm. wide. Occasionally Onchidia are seen creeping about with their slime-coat but partially removed.

The slime-pellicle is encrusted with the muddy fecal matter which the Onchidia deposit. This calcareous mud is swallowed when feeding on the algæ over which they creep in the open; it represents the ordinary silt of the shore-line, and may in part be chemically abstracted from the thin layer of sea-water covering the algæ as the tide recedes, owing to photosynthetic removal of CO_2, especially as accelerated by increasing temperature and by isolation as the sea-weeds become more exposed.

When the slime-coat is removed, an ordinary *O. floridanum* seems at first sight jet black; the mantle is wet and shiny; closer examination shows that the color is really a very dark and smoky olive. The mantle-glands continue their slime secretion, however, and by the action of wind and sun the surface of the mollusk quickly assumes a dry blue-black aspect, its numerous papillæ glistening in the light; the appearance of the mantle, with a slight "bloom" on it, then resembles that of the tiny thysanurans so common on the beach sands and also on the rocks where *Onchidium* lives.

Typical Onchidia of the lighter colored variety appear at all times light olive or greenish yellow. The coloration is not "solid," for the dark-hued internal organs usually show through as one or more dull blackish patches. The edge of the mantle is quite pale.

It has not been possible to convert one variety into the other by laboratory experimentation. The dark Onchidia are still dark after six weeks complete starvation.

Onchidia of either type are found, frequently side by side, in all the varieties of habitat which we have described. To mention some specific localities, we may list the following: Bailey's Bay; Flatt's Inlet; the east side of the channel entrance to Hungry Bay, at its inner end; an island at the entrance to Fairyland Creek; a small cove on Burgess Point. These situations are widely separated, and cover the different sorts of backgrounds to which allusion has been made.

Not only in a general way, merely, but also in any given place where they occur, the lightly pigmented Onchidia fail to indicate by any peculiarity of behavior that they differ essentially from the dark ones. That they are easily overlooked is quite true; they are homochromically colored in practically all the instances that have been observed. But it should be noted that in one such place the homochromically colored individuals were found in the proportion of but one to nearly 190 of the dark black ones. This was on a greenish rock surface of northern exposure where a color-changing form like the isopod Ligia was pale-greenish, like the pale Onchidia. In other places more or less isolated colonies of fifty or more pale specimens were encountered. In some cases the coloration was decidedly greenish, rather than olivaceous yellow.

IV. The numerous dorsal papillæ of *Onchidium* were said by Semper (1877, 1881) to indicate the location of mantle-eyes; since, however, no sensory nerve-terminals were at that time demonstrated within the "eyes," some writers followed Joyeux-Laffuie (1882) in the opinion that the "dorsal eyes" of Semper were in reality mantle glands, corresponding to those undoubted glands found in the related genus *Oncidiella* (cf. v. Wissel, 1898). The more complete analysis of the histology of the mantle in *Onchidium* by Stantschinsky (1908), nevertheless, proved that the "dorsal eyes" do possess nervous structures appropriate for photoreception, the retinulæ being, in addition, of the inverted ("vertebrate") type. *O. floridanum* possesses, however, repugnatorial mantle glands as well, which are not associated with the dorsal papillæ, these last being relatively minute.

The glands are comparatively large, but are easily overlooked in an undisturbed *Onchidium*. The periphery of the mantle has a frilled appearance, numerous tiny projecting papillæ giving it a serrated outline. If the animal be disturbed, the tissues surrounding each of the glands become erected, and 14 stout conical papillæ, 7 on either side and each with a terminal pore, become evident.

If the animal is suddenly removed from the rock by grasping its dorsum, the glands all become turgid, point upward and inward, and quickly discharge by the contraction of their muscular investments. The secretion is a viscid fluid, milk-white, non-miscible with sea-water, and decidedly acid in reaction. Discharge is more easily elicited in air than when the animal is submerged. Under water the secretion is expelled in long threads, but in air the stream as it leaves the gland breaks up into a fine spray, which may be shot to a distance of 12–15 cm. With vigorous stimulation, as when the back of the *Onchidium* is pinched with forceps, the discharge appears from every gland as a stream about 0.2 mm. in diameter, which is often too stout to form fine droplets. In nature, however, the initial repugnatorial discharge is less copious; it then takes the form of a fine spray, almost invisible, which may be thrown for as much as 15 cm., or about ten times the length of the *Onchidium*.

As discharged, the secretion is found to contain at least three elements visible under the microscope: a clear fluid, apparently water; clear droplets of oily appearance; and a finely granular material. The relative proportions of these three elements vary in different glands. An individual tested in the field, without previous disturbance, usually secretes a densely granular mass containing a fair proportion of globules; in the activation, a good deal of the secretion usually adheres to, or falls back upon, the mantle of the snail itself—the dryness of the mantle, and the fact that in nature violent discharges of secretion seem seldom to be invoked are important for the freedom of the mantle from being itself sprayed. On the other hand, the fluids ejected from one or more glands of starved Onchidia are almost always clear and watery, sometimes with no trace of the granular or droplet constituents. Variation in the composition of the corresponding glands of *Oncidiella* was recognized by v. Wissel (1898), who also discovered the secretion droplets (globules) which previous workers had overlooked.

When the secretion adheres to the mantle of an *Onchidium,* it can be seen that considerable stimulation of the skin is thus produced. The secretion is quite acid to litmus and to a number of other indicators. The acid is found in the dense granular material, and does not occur, save in relatively slight amount, when this material is absent. The white masses may be caught on a clean slide and studied under the microscope. The granular material is insoluble in 90 per cent. alcohol, or in water. If indicators are added to a drop of the secretion under a coverslip, it can be seen that the acid slowly diffuses out into the water from the granular mass.

The white substance, if received on the tongue, is found to sting with considerable persistence, like wild mustard. It does not taste sour. Plate, testing the secretion of the mantle-glands of an *Oncidiella,* found "dass das Secret dieser Drüsen auf der Zunge ein deutlich wahrnehmbares

Brennen hervorruft" (according to v. Wissel, 1898, p. 597).

Stimuli initiated in several different ways may serve to elicit discharge of the repugnatorial glands, as: stroking the mantle with a blunt point; pinching it with forceps; applying solutions (5/8 M) of NaCl or (less effectively) LiCl, or of methyl or ethyl alcohol (5 M). Touching or pinching the *periphery* of the mantle itself does not lead to discharge, but on the contrary leads to localized retractive puckering; when a gland is erected, preparatory to discharge, stimulation of that gland causes it to collapse, or "wilt," a process similar to that following normal discharge. If the dorsum be scratched until erection of the glands occurs, and then NaCl solution be applied to one of them, it is found, as also with mild faradization, that two or even three successive discharges are possible; but the later out-pourings of secretion are very meager as compared with the first explosive ejection. About twenty-four hours is required for the regeneration of a new supply of repugnatorial substance.

Before the glands discharge, the edge of the mantle curls upward, forming around the *Onchidium* an encircling saucer-edge bearing the now prominent glands; thus, depending upon the intensity of excitation, the glands come to point more and more dorsal, and in this position release their contents. Not only so, but the individual gland papillæ are themselves further directed in a general way toward the irritated spot, so that if a slip of glass be held horizontally 1 or 2 cm. above an *Onchidium* the back of which is at one point subjected to mild faradic excitation, the contents of all the discharging glands are found to impinge upon very nearly the same point; sometimes all the discharges converge to an area of less than 3 × 3 mm., immediately above the spot irritated. The gland or glands nearest the site of stimulation are the first discharged, and the implication of more distant ones depends on the degree of stimulation.

Semper (1881, p. 372 *et seq.*) considered that the dorsal eyes of *Onchidium* were employed in sensing the approach of animals which might attack it. He had in mind the attacks of the Philippine *Periopthalmus,* a blenny which, leaping along the intertidal beach-zone on its ventral fins, feeds upon *Onchidium* and on arthropods. Semper thought that the eyes of the Onchidia rendered them sensitive to the shadow of an approaching fish, whereupon a fluid spray was discharged from the skin glands, driving off the fish. Whether Semper regarded the secretion as repugnant to the fish in a chemical way, or whether it was to act in a mechanical fashion merely, is not altogether clear. Semper endeavored to make out a correlation, illustrative of evolutionary principles, between the geographical distribution, on the one hand, of the species of Onchidia possessing dorsal eyes, and, on the other, of the genus *Periopthalmus.*

There are at Bermuda no *Periopthalmus,* nor any other fishes of similar habits. *Onchidium floridanum* is, however, quite reactive to shading. The dorsal surface of the mantle is the part sensitive to decrease of light intensity. In a moving *Onchidium* the ensuing reaction involves a momentary cessation of creeping, retraction of the tentacles, and a depression of the periphery of the mantle to the surface of the rock. The tentacles themselves, which in air are much further protruded than when under water, are not photosensitive. An *Onchidium* shaded when not creeping, but at rest or feeding, exhibits the same type of response, but the mantle is more decidedly humped. But, in our experience at least, no discharge of the repugnatorial glands is induced by shading. This does not mean that Semper's observations were not correct. In *O. floridanum* the type of excitation which is preeminently and characteristically effective for gland discharge is of a mechanical nature, namely, a rubbing or pinching of the apex of the dorsum or a dislodging thrust upon the ventral surface of the girdle. Although when tested by faradic excitation it is found that gland discharge *may* be elicited when even the sole of the foot is irritated, or almost any other region (with difficulty in the case of the tentacles), a greater intensity of stimulus is necessary than when applied on the back of the animal. Mechanical stimulation is in general more effective than chemical. Of the chemical excitants tried, only NaCl, LiCl, methyl and ethyl alcohols were successful, whereas such substances as pure amyl alcohol, numerous acids, alkalies and salts, in concentrations corresponding to those used in the case of the successful stimulating agents, as well as a series of alkaloids, were without effect when small volumes (a half or one c.c.) were applied to the mantle.

The designation of the mantle glands as repugnatorial is justified by observations in nature. Isopods (*Ligia*) and grapsoid crabs (*Sesarma,* and in some places, *Pachygrapsus*) abound in certain spots where the Onchidia take their airing. By prolonged watching, unequivocal instances have been noted in which these arthropods have come into direct contact with Onchidia, and in every case the glandular discharge took place, followed immediately by the retreat of the crab or isopod; it is not implied that the crabs were endeavoring to eat the snails, but it seemed rather that it was important for *Onchidium* to avoid being accidentally pushed off the rock into the water; it does not adhere to the rock with any great firmness, particularly under water, is easily dislodged, and if purposely pushed over the edge of the stone on which it may be creeping into the water, the animal finds it difficult if not impossible to return to its own nest.

Tests upon a number of animals (*e. g., Fundulus* from the land-locked brackish ponds at Bermuda) which could not by any possibility have ever come into contact with the *Onchidium* secretion, have invariably demonstrated the powerfully repugnant character of gland contents.

Finally, it is important to note that *Onchidia of whatever degree of pigmentation possess these repugnatorial glands, and in an equivalent state of development.* The behavior of the differently pigmented individuals, with reference to the use of the glands, is identical throughout the whole series.

V. Without entering upon a lengthy setting-forth of the several alternative possibilities which might readily be suggested in partial explanation of the foregoing series of facts, we may state our belief that an attempt at such explanation in terms of color-adaptation is confronted by serious, and indeed fatal, obstacles. From such a standpoint we are required to consider only the period during which the *Onchidium* is emerging from its nest and creeping about in the open. In the case of a dark *Onchidium* it is quite true that the animal is often very easily overlooked while in process of creeping over the *Modiolus* at the entrance of its nest; the color-match of the snail and the mussel is a fairly exact one. But an *Onchidium* does not resemble *Modiolus*, although of about the same size, when creeping upon algæ at the rate of 5 cm. per minute or faster. The paler kinds of *Onchidium* are, in almost every instance noted, a very precise match for their background, and sometimes careful search is necessary in order to detect them.

. The non-homochromic pigmentation of the dark Onchidia would, in view of the presence and behavior of the poison glands, be of special interest in connection with the idea of warning coloration. But this view is rendered unintelligible in the face of the paler, concealingly-colored types. Moreover, the Bermudian Oncidiellas to which we have already alluded are very inconspicuous indeed, and they also possess poison-glands; their mode of life is quite different from that of *Onchidium*, since, although likewise inhabiting the intertidal zone, they retreat during low water to tiny holes,—dead serpula tubes and the like,—coming forth again only when covered by the water. These Oncidiellas are small, not more than 3 mm. long, and both light and dark individuals are in the highest degree difficult to detect when on their natural background; a delicate mottling of brownish pigment, in various shades, has a pronounced concealing effect in these places. Perhaps this accounts for the fact that *Oncidiella* has not previously been reported from the Bermuda area.

Not only does the idea of "warning" coloration become untenable for *Onchidium,* but the idea of adaptive concealing pigmentation is likewise without adequate support. The dark Onchidia are not concealingly colored, except during the transitory interval of their actual emergence from the nest, and even there they are easily seen, if looked for. The slime-coating, which would undoubtedly be of assistance in making them look like the background (for the silt it contains is formed on rocks where the pale bleached yellow algæ grow, and in other places where *Onchidium* lives), is almost invariably removed before the snail begins its promenade in the open. The relatively meager proportion of the Onchidia found pigmented in a truly homochromic manner is not explained by the idea of adaptive coloration, although the variation in the hues of differently tinted individuals would seem to provide favorable ground for the operation of selection. In this connection it might be suggested that *Onchidium floridanum* represents a comparatively recent addition to the fauna of Bermuda, and that the dark pigmentation common to this species and its immediate relatives throughout the world is even now in process of modification; but the fact that in the neighboring genus *Oncidiella* two more or less distinct general modes may be of widespread occurrence forbids the placing of any special emphasis upon this possibility, and even then, if correct, it would have no final significance for the conception of selective color-modification. If nutritive conditions, and temperature or light, or all three, do operate in a manner favorable to Onchidia of one or the other type in different places, the habit of living together in colonies might lead to a measurable degree of inbreeding, tending to prevent the general distribution of one variety of pigmentation, but at the same time a paler coloration, probably recessive in genetic behavior, would to that extent achieve a greater opportunity for perpetuation.

SUMMARY

VI. *Onchidium floridanum* Dall exhibits at Bermuda two chief types of pigmentation, a pale type tending to dull olive yellow, which tends to be concealingly colored, and a much more abundant type of dark blue-black appearance.

No correlation can be established between the pigmentation of an *Onchidium*—which there is some reason to consider the result of genetic factors primarily—and the hue of the substratum over which the snail creeps in the open at low tide.

O. floridanum possesses repugnatorial mantle-glands of an effective type, secreting a granular emulsion of substances having a strongly acid reaction and producing on moist surfaces of the human mouth a pronounced stinging sensation. Touch and pressure stimuli on the dorsal surface of the mantle are characteristically involved in releasing the discharge of these glands, which shoot their contents, in the form of a fine spray, to a distance about ten times the length of the *Onchidium* and with conspicuous accuracy of direction toward the source of excitation.

These facts are incompatible with the view that the coloration of *Onchidium* is determined or controlled by selection in the direction of homochromicity or concealment. Nor can they be understood in terms of ''warning'' coloration.

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THE CONTRIBUTION OF CARL FRIEDRICH VON GÄRTNER TO THE HISTORY OF PLANT HYBRIDIZATION

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IN the beginning of the nineteenth century, the question of the sexuality of plants was still undergoing a certain amount of disputation, despite Koelreuter's investigations; the history of which episode is sufficiently traceable through the writings of Schelver and Henschel. In order to assist in the settlement of the matter, the Royal Prussian Academy of the Sciences at Berlin, made public announcement in 1819 of an offer of a prize for the solution of the question—"Does hybrid fertilization exist in the plant kingdom." No response having been evoked, the Academy extended the competition period, and doubled the amount of the prize offered. On July 3, 1826, the prize was awarded, although not in its entirety, since the Academy did not consider the solution adequate, to Dr. A. F. Wiegmann, of Braunschweig.

In January, 1830, the question was propounded anew by the Dutch Academy of the Sciences at Haarlem, in the following language:

> What does experience teach regarding the production of new species and varieties, through the artificial fertilization of flowers of the one with the pollen of the others, and what economic and ornamental plants can be produced and multiplied in this way.

Since, by the termination of the contest period, January 1, 1834, no response had been received, the period was extended to January 1, 1836. In October, 1835, Carl Friedrich von Gärtner of Calw, son of a distinguished botanist, Joseph Gärtner, formerly professor at the universities of Tübingen and St. Petersburg, and who for a considerable period of years had been conducting experiments of his own in hybridization, became aware of the offer of the Dutch Academy. Thus far, only brief reports of his work had appeared at Tübingen and Paris.

On account of the shortness of the time available, Gärtner sent to the academy merely a preliminary report of his experiments, accompanied by one hundred and fifty mounted specimen sheets of his different plant hybrids, which elicited a favorable response, and induced the academy to grant an extension of the time for sending in the completed work to December 30, 1836. The interesting resolution of the committee runs in part as follows:

> That, in view of the number of new results, which could only have been obtained through very manifold investigations over many years, the service of the author be acknowledged.

The requirements of the committee having been compiled with, the award was formally conferred on May 20, 1837. The thesis appeared in Dutch translation, as a document of 202 pages, in the *Proceedings* of the Academy for 1838. In 1849, a revised and greatly enlarged edition, "the fruit of unbroken, zealous, almost twenty-five years' work," was published in German at Stuttgart.

The writer has found nowhere in current literature any adequate presentation of this seldom read, and little referred-to work, and yet it contains not only much interesting information of a concrete nature, but a great deal of speculative philosophical insight in dealing with problems in hybridization, that shows a scientific mind of distinct value.

Sachs says of the writings of Gärtner (3), "The two works together, are the most thorough and complete account of experimental investigation into sexual relations in plants which had yet been written. They are a brilliant termination of the period of doubt with respect to sexuality in plants, which succeeded to the age of Koelreuter." "And thus it was," says Sachs further,—"in two small cities of Württemberg, that the foundations of the sexual theory were laid, and the theory itself perfected, so far as it could be, by experiment only, by three of the most eminent of observers, Camerarius of Tübingen, Koelreuter and K. F.

> Gärtner of Calw, who contributed so largely to the empirical establishment of the theory, that all that was done by others would seem of small importance" (p. 427).
>
> As Focke says ((1) p. 437), "In numbers of experiments, he has probably been surpassed by no other hybridizer."

An idea of the sheer laborious work which Gärtner's operations involved, may be obtained from the mere statement that he performed close to ten thousand separate experiments in crossing, involving nearly seven hundred different species belonging to eighty different genera, and from which some two hundred and fifty hybrid plants were produced.

From such a large mass of detail as Gärtner's memoir involves, it is difficult to derive a concise series of statements of the experimental results. In endeavoring to group the phenomena of hybridization upon a scientific basis, Gärtner undertook to classify hybrids into three divisions, according to their external habit: (1) "intermediate types," (2) "commingled types," and (3) "decided types," although, as he says (p. 277):

> There exists no exact delimitation among them, but they go variously over into one another, so that it is not seldom very doubtful to which of these forms, this or that hybrid should, with the greater right be assigned.

In regard to the intermediate types, Gärtner follows Koelreuter's view

> that, as in the fertilization of pure species, so also with hybrid breeding in the case of simple hybrids, a complete balance occurred of both fertilizing materials, either in respect to mass or activity. In this assumption he was still further strengthened through the similarity of types from reciprocal crossing. He believed further, that in the later generations of simple hybrids, and in the further grades of hybridization, where no such regular process of hybridization occurs, the inclination of types either toward the father or the mother, proceeded from the not quite complete balance, or the slight overbalance of the one or the other fertilization materials (p. 277).

Regarding the so-called "commingled" types, Gärtner says as follows (p. 282):

> The second kind of types, frequently occurring among hybrids, is that with commingled parental characters, insofar as now this, now that part of the hybrid, approaches more to the maternal or to the paternal form, whereby, however, the characters of the parents in their transference to the new organism, never go over pure, but in which the parental characters always suffer a certain modification.

Under the third class of hybrid types, Gärtner considers those—

> Among which the resemblance of a hybrid to one of its parents, either to the father or to the mother, is so marked and preponderating that the agreement with the one or with the other is unquestioned, and strikes one at once (p. 285).

Regarding the behavior of plant hybrids in the first hybrid or F_1 generation, as compared with their behavior in the second generation, Gärtner's remarks are interesting, although not based on numerical data.

> Among plants, by far the greater number of the normal and regular types of the hybrids from the first cross, as compared with the exceptions and varieties, testifies against the operation of . . . external influences, and proves rather the inner necessity of a regular formative development according to law on the part of pure species in general as well as of hybrids (p. 275).

Regarding this supposed formative force (Bildungskraft), Gärtner arrived at a conception of the inner nature of the phenomenon occurring in hybridization, which is scientifically interesting, although amounting to a theory, and not to a conclusion directly derived from experiment.

> The foundation and the determination of the types of hybrids, might therefore be discoverable, not so much in the mass and the relationship of the germinal materials, as in a vital modification of the formative force of the one or the other fertilization material (p. 270).

As we now know from Mendel's experiments, however, it is this modification of the "sexual material" itself which pre-determines the direction in which the formative force may run. In Gärtner's day, the abstract conception of a relative potency of the one or the other parent in hybridization, was a prevalent one, and this statement above is a philosophical conception, which

Mendel's data made it possible to precipitate into a definite morphological theory. Gärtner went so far, however, as to attempt to measure this "potency" in a definite manner, by means of the number of viable seeds produced in reciprocal crosses.

> That this relation of the factors of the fertilization forces in the case of species of plants capable of hybridization, is definite and according to law, we assume from the fact that from such a hybrid combination come more or fewer good seeds to be sure, according to the favorableness or otherwise of the incidental circumstance, but that, however, in the case of every such hybrid combination, it is never able to produce over a certain maximum of viable seeds, which maximum is peculiar to each combination of that kind (p. 206).

Gärtner goes so far as to say:

> The inequality in the strength of sexual affinity (Wahlverwandtschaft), in the case of the reciprocal combination of species, is a general phenomenon occurring in plants, and will therefore lead in time to the disclosure of the relations, and to a closer determination of the value in respect to magnitude of the individual factors of sexual affinity. This inequality establishes a scale of sexual affinity peculiar to each species, which lies in the difference in the relationship of the strength of the two factors. In this singular characteristic of plants, the peculiar nature of the species is most plainly recognized,—much more, in fact than in its external form (p. 200).

Those species which are able in crossing, to exert a preponderating influence upon other species, Gärtner calls "generic types."

> Just as such generic types in hybrid breeding, are able, as it were, to gain the upper hand over the type of other species, so is the strength and form of these species broken and overmastered by others (p. 290).
>
> This manifestation of generic types, according to which one species acts in a predominant manner over several other species in hybrid breeding, is a further uncontradictable proof, that the relationship of the forces, through which the union of two pure species takes place, must be unlike, and that there can be no question there of any balance of factors. To be sure in mixed hybrids, the relationship of the formative forces of the two sexual substrata appears to be tolerably alike; however, in them likewise, in this or that part of the hybrid, now the character of the one, now that of the other factor is more plainly expressed (p. 290).

Gärtner seems to see in this dominance of type in species, a way of evolution which leads to the establishment of dominant family types.

> The generic types appear to have their analogue in the natural family types, and, since the origin of family types has occurred according to certain laws, so will type-formation of hybrids, since it is not at random, but is constant, follow the same laws, according to which plant forms in general are formed and have developed (p. 291).

This brings Gärtner to a further statement regarding the possibility of recreating ancestral types, which is especially interesting as a pre-Darwinian view upon evolution. Referring to species of *Lobelia, Lychnis, Dianthus*, etc., he says:

> If these nearly related species had once come from a common ancestral type, or had become separated from one another through the subsequent development of the one or the other individual, then it appears to be highly improbable that they would not again unite in their ancestral form through reciprocal crossing, or prove themselves to be analogous types in hybrid breeding (p. 163).

Gärtner then arrives at one of the most striking conclusions in the older literature on the then so much mooted species question, and which is the more interesting because it takes the physiological rather than the morphological point of view. He says:

> The essential nature of a species, therefore, consists in the definite relation of its sexual forces to other species, which relationship, taken together with the specific form, is a characteristic, individual and constant one; for every species, form and essence in this regard are one (p. 163).

Gärtner frequently returns to a philosophical contemplation of the nature of the fertilization process in hybridization, characteristically as follows:

> Not external resemblance in form and habit of species, but the harmony of the inner nature, gives the capacity for hybrid fertilization; both are not always harmoniously bound together (p. 186).
>
> For an actual hybrid combination, a certain harmony in both sexual elements is, however, necessary, and precisely in this harmony lies the capacity for the union of two otherwise heterogeneous species (p. 110).
>
> Only a harmony of the inner nature, on which the relationship of the germinal materials rests, which indeed is ordinarily accustomed to be associated with the external generic characters, but is not necessarily

bound up with concordance in external structure, determines the presence of the capacity for hybrid fertilization (p. 142).

In the following discussion, more or less in the same manner, Gärtner shows an intellectual freedom from the fetish of morphological species, and clearly demonstrates the possession of a physiological temper and attitude of mind.

> Our investigation concerning harmony of forms in families and genera, have shown that we have to consider two different kinds of relationship among plants, an external and an internal: the former rests upon conformity in habit, *i. e.,* in growth, in the shape and form of the leaves, and in the harmony of the flowers and the organs of pollination: these, however, in their greater or lesser inclination to sexual combination of species in hybrid fertilization. The former might be identified with the morphological, the latter closely with the physical relationship. Now, since both are not infrequently met with in combination, for that reason, our predecessors have not clearly distinguished both kinds of relationship from one another, but have held both as identical, or rather, have regarded the inner relationship as an immediate consequence of the external, and assumed this as a law, so that the agreement of species in habit, not only favored, not merely the existence, but also the strength of the sexual attraction, and indeed likewise conditioned it (p. 166).
>
> From the agreement of the external form and habit of species of plants it may not therefore be inferred, that the sexual powers and relationships must also agree therewith, as experience indeed teaches, that many plants, however congruent they otherwise are in form, and even in organs of fertilization, nevertheless possess little or no inclination to unite in hybrid fertilization. One of the best-known examples of this is *Pyrus* and *Malus,* which, despite their near relationship in habit and sex organs, from the testimony of other observers also, do not admit of fertilization on the one side or the other (p. 167).

In the following passage, the morphological and the physiological points of view are well contrasted:

> The systematic genera are artificial syntheses, which are not united according to absolute laws, but according to arbitrary external characters, which indeed often harmonize with the inner nature of the species, but likewise not seldom differ from this, if indeed it is not to be questioned, that even these characters proceed from the inner organism, and are determined through it (p. 139).

Gärtner, no more than any other investigator in the field of hybridization of his day, with the possible exception of Sageret, had any conception of the idea of unit characters operating as such, and capable of being analyzed separately. The then prevalent idea was one of "potency" and "pre-potency," in the case of the hybrid types that Gärtner called "decided," *i. e.*, in which the dominance of the one or the other parent was plainly evident. A species in a cross was supposed to function as a whole as such. An idea of this older point of view is obtained from the following:

> Thus, just as there are species in a natural genus, which possess a prepotent fertilizing power upon several other species of their genus, so there are also species, which exert upon several others such a typical predominating effect, not to an equal extent, to be sure, but still of such a nature that their operation in all combinations is to be recognized by a character in common. Both of these forces, are, however of different kinds, and follow different laws (p. 289).

Gärtner did not regard Sageret's case of segregation of characters to be the normal result of hybrid fertilization. While it is true that Gärtner recognized in a certain sense the fact that parental characters often behave in a more or less unitary manner, he was led by the nature of his mind, as well as by the results of his observations, to take a synthetic rather than an analytical view of the hybrid organism.

> The explanation of the origin and development of the forms of the hybrids from the elements and characters of the parents, is as important for plant physiology as for systematic botany (p. 25), and further,—
>
> The laws of hybrid types orient themselves not toward the individual organs of plants,—do not apply to a single part, *e. g.*, stems, leaves, etc., but are applicable rather to the inner nature of species. The organs which determine the types of hybrids, must therefore be investigated and compared in their totality, and in their mutual interrelationship. For the most part, the individuality of a hybrid expresses itself in its entire habit, but in this respect, the flower above other parts of the plant, is most frequently and plainly distinguished (p. 251).

However, Gärtner's most fundamental view upon the question whether the plant as a whole, or its individual characters considered as such, determine the nature of the hybrid offspring, is expressed in the following clear manner.

> In the formation of simple hybrids, as in sexual propagation in general, two factors are functional; this inequality of activity flowing out of the specific difference of species, expresses itself in the more marked or the more feeble emergence of the individual paternal characters in the different parts of the hybrid. Whether the species nature in its entirety and its formative impetus, determines the direction and form of the type, *or whether also the individual parts of plants have a special influence upon modifications, can only be determined through further investigations* (p. 257).

In the absence of what he deemed sufficient evidence to the contrary, Gärtner conservatively adhered to the view that the parent organism entered into the cross as a whole, rather than as a congeries of character-units, behaving in a manner separately, although often linked together.

Regarding the recognized instability of hybrids, Gärtner simply says, without distinguishing as to the generation:

> Variability in the progeny of hybrids is a principal character of hybridity (p. 518).

So far as any distinction as between the first and second generation is concerned, Gärtner merely says:

> The general laws of development of the parts of plants, hence appear to undergo through hybridization no change perceptible to the senses, but all the developments and changes of the hybrid plant body appear to follow the same laws as in pure species, the organs of reproduction, and the material ground materials of the cross alone excepted.
>
> The latter behaves differently in the second generation and in the succeeding stages of hybrid fertilization, where, on account of the different nature of the two factors of the hybrid in the succeeding zygoses, an altered, shifting, variable direction in type-formation enters into the varieties thus originating (p. 572).

Concerning variability in hybrids of the second and succeeding generations, he says:

> Other hybrids, and in fact the most of them which are fertile, present from the seeds of the second and further generations, different forms, *i. e.*, varieties, varying from the normal type, which in part are unlike the original hybrid mother, or deviate from the same, now more, now less (p. 422).

Perhaps the most definite allusion describing the condition in general terms, of what we term segregation in the second generation, is the following:

> Among many fertile hybrids, this change in the second and succeeding generations, affects not only the flowers, but also the entire habit, even to the exclusion of the flowers, whereby the majority of the individuals from a single cross ordinarily retain the form of the hybrid mother, a few others have become more like the original mother parent, and finally here and there an individual more nearly reverted to the original father (p. 422).

Regarding the matter of unusual vigor in hybrids, Gärtner remarks, giving examples, although again without referring to any particular generation—

> The marked increase in the size of the flowers, is a phenomenon not seldom occurring among hybrids (p. 295), and—
>
> One of the most marked and general characters of plant hybrids, is the luxuriance of all their parts, since among very many of them, an exuberance of growth and development of roots, branches, leaves and flowers manifests itself, which is not encountered among the parents, even under careful cultivation (p. 526).

Gärtner did not omit to apprehend the possible value of this fact to agriculture, although, of course, he did not recognize the first hybrid generation as a special phenomenon.

> Among the characters of hybrids worthy of recommendation for agriculture, their tendency toward luxuriance in stalks and leaves, and their extraordinary capacity for tillering is related above. With respect to the raising of forage, agriculture could, without doubt, make great use of this characteristic (p. 634).

So far as genetics from the present technical standpoint is concerned, Gärtner's data of course are not of special interest, because his crossing was made upon species as units, and not upon the character-unit basis, and no records were made of the numbers of the different types secured from his crosses. It is of interest to note, however, that Gärtner's methods in his hybridization operations partially anticipated the rigorous methods of to-day, regarding the purity of parental types.

> In order to judge with certainty concerning the nature of the types which have arisen, and in order to obtain entirely reliable results, it is

> above all necessary that one be in advance in complete certainty concerning the species with which the experiments shall have been instituted, that they be specifically correctly determined, and that no doubt prevail concerning their purity (p. 252).

Finally, Gärtner's investigations upon color inheritance, which cover thirty pages of text, while not of genetic value from the modern standpoint, are interesting and valuable as a summary of the then existing knowledge on the subject. One observation upon intensification of color deserves mention:

> Red with red, not seldom gives a heightened brilliancy of color, as is especially plainly shown in the flame-colored flowers of *Lobelia cardinalis, fulgens* and *splendens* (p. 315).

One of the matters of genetic interest is the fact that Gärtner experimented in the crossing of corn, with a view to determining the matter of change of color in the seeds due to crossing, as reported by Sageret. Unfortunately for Gärtner's experiment, however, he crossed a dwarf yellow corn without pericarp color, with corn having colored pericarp ("of red, gray and striped color"), instead of with colored endosperm. In consequence, of course, the seeds borne the first year, "differed neither in size nor in color in the least from the natural seeds of *Zea Mays nana* of the earlier sowings" (p. 322).

The following year, however, instead of getting complete color dominance, he obtained from one ear a ratio of 224 with non-colored pericarp, to 64 with pericarp colored. The other ear gave 104 seeds without pericarp color to 39 colored. He carried the seeds through to the next generation, but gives no numbers for them. Gärtner also crossed *Lychnis diurna* with reddish or dark-brown seeds, and *Lychnis vespertina* with ashy-gray seeds, finding no change occurring as the result of crossing, but obtaining what we should call dominance of ashy-gray in the first hybrid generation. From Gärtner's observations, therefore, he felt justified in stating as a law—

> That the influence of the foreign pollen in hybrid fertilization, alters nothing in the forms and external characters of the fruits and seeds

> peculiar to the mother plant, but produces in the embryo only, the capacity of bringing forth a mixed product from both concurrent factors, through the germination and the further development of the new plant (p. 327).

In an earlier paper of Gärtner's (2b), he cites Mauz's case of modifications in the character of different fruits on a pear tree, through pollination from various varieties of pears, whereby he was said to have obtained, "a great number of fruits different in form and colors" (p. 138). His interest aroused by the phenomenon reported in maize, he undertook a series of crossing experiments to determine "whether foreign pollen exercises or does not exercise an immediate influence on the external character of the fruits and seeds which are the result of these fertilizations," but with entirely negative results. No change whatsoever was observed in the color or external characteristics of the fruits arising from crossing.

> The influence of the foreign pollen does not then change anything in the external forms peculiar to the mother plant, or in the external qualities of the fruits, the seeds and even the embryo. This influence only gives to the latter the faculty of producing, through germination and through the ulterior development of the new plant, an intimate combination of the form of the members of the two species which have united in its production (p. 139).

One of the most interesting matters, of course, is that which concerns the alteration in the character of hybrid seeds or fruits due to the immediate effect of foreign pollen. Gärtner reviews in detail the previous work of Knight, Goss and Seton with peas. In 1829, he started a selfed and a crossed series of peas, using four varieties (pp. 81–85).

1. Paris Wax (yellow seeds).
2. Dwarf Creeping (white flowers, yellow seeds).
3. Sugar peas (red flowers, wrinkled greenish-yellow seeds).
4. Early Green Brockel (white flowers, green seeds).

The results as to the immediate effect of the cross on the seeds were as follows:

Parents.	*Hybrid Seeds.*
Paris Wax (yellow) × Sugar Peas (greenish yellow)	yellow.
Paris Wax (yellow) × Early Green Brockel (green)	greenish-yellow.
Sugar Pea (greenish yellow) × Dwarf Creeping (yellow)	dirty-yellow.
Sugar Pea (greenish yellow) × Early Green Brockel (green)	no change.
Dwarf Creeping (yellow) × Early Green Brockel (green)	greenish-yellow.
Early Green Brockel (green) × Paris Wax (yellow)	dirty-yellow.
Early Green Brockel (green) × Sugar Pea (greenish yellow)	yellow.
Early Green Brockel (green) × Dwarf Creeping (yellow)	yellow.

As the above results show, the same dominance of yellow over green in the hybrid seed appears as in the experience of Knight, Goss and Seton.

Respecting identical results obtained as the result of reciprocal crosses, Gärtner makes the following unqualified statement:

> The most important and the most interesting phenomenon in the crossing of plants in hybrid breeding, is the complete similarity of the two products; since the seeds produced from the one as from the other fertilization, give rise to plants of the most complete similarity, so that their different origin and derivation, upon the most careful investigation of both kinds of hybrids, does not show the least difference in respect to their form and type; and even the most practiced specialist with a hybrid species, is not in position to distinguish the origin of the hybrid with respect to the sex of the parents (p. 223).

Gärtner's work is not only noteworthy for its remarkable extent with respect to the number of species experimented upon, but with regard to the care which he exercised in his operations, he says:

> For complete assurance of the purity and reliability of the products of hybrid breeding, and for testing the conclusions derived therefrom, we have repeated most of the experiments, especially the doubtful cases, not once only, but several times, and put them to the test through crossing of the same species, using different individuals of that species, for even with the most scrupulous foresight and precision, individual rare instances have still occurred in these tedious and wearisome investigations, where the suspicion had made itself felt, of a mistake or error having crept in, either in pollination or emasculation, since such results stood in direct contradiction to the usual experiences, and on a repetition of the experiments, made itself incontrovertibly evident as an error. We believed it possible to attain no higher degree of certainty in this branch of natural science, and to be able to bring the conclusions derived therefrom to no higher proof, than through the precise coincidence of

> the forms of the products, by repetition under the same conditions with the same species, but with different individuals, and at different times (p. 675).

Again, in another place, he makes substantially the same statement with respect to testing what he refers to as "selective affinity."

> In order to gradually get as close as possible to the true selective affinity relation among the species of plants, it is necessary not only that a greater number of experiments be instituted with the same species of plants, but also that the same experiments be repeated with different individuals and at different times, because as well in the female organs of a plant, as in the pollen of another species, a basis for different results may be concealed (p. 214).

Gärtner was not behind in realizing the practical utility of hybridization in agriculture and horticulture. The following somewhat extended extract shows his keen sense of interest to the possibilities latent therein, although his own scientific efforts did not lead him into economic experiments.

> The heightened fruiting capacity of hybrids and variety crosses, deserves the most marked attention in respect to orchard, vineyard, and the whole of garden culture. The striking fertility of several orchard and vineyard varieties may find its explanation herein. It is, to be sure, to be surmised that this capacity does not reside in an equal degree in all variety crosses, and that this character would incline toward the peculiarity of the species; nevertheless it is to be expected with tolerable certainty, that with many valuable orchard and vineyard varieties, an increased yield might be able to be attained through crossing with other varieties. Improved sorts with weak or weakened vegetative power, united with other species of more vigorous growth, would promise an improved product with a longer life duration and a stronger structure of the plant body. As already many admirable stone, pome and vineyard varieties have been raised from seeds which had originated through chance crossing, so, through intentional artificial crossing of varieties, still many other sorts might be very easily produced. But to get definite results, and to be able to determine the outcome exactly, for the advantage of science as a whole, fertilization should not be committed to mere chance, but an exact and scrupulous procedure must be observed, with careful records of the varieties combined.
>
> Of still more extended utility is hybrid breeding for æsthetic botany; for the latter, artificial fertilization opens a wide field for activity, enjoyment and achievement. For the fancier of ornamental plants, the

ease with which many hybrids are able to be produced, is an inexhaustible source of satisfaction and profit. He recognizes that he is in possession of materials with which he can busy himself, and he deliberates over the way and manner he can best and most profitably combine them; in that, he gives attention to the characters wherein each species characterizes itself, whether in the splendor of the colors of the flowers, the fineness of their delineation; fragrance, growth, form, quantity of flowers; whether endurance of the severity of our climate in this or that combination is to be taken into special consideration;—he will attempt to calculate provisorily with some probability the possible appearance of the hybrids, and he will finally be surprised at getting a plant which had never before existed in nature (pp. 638–639).

This concludes the matter of general interest in Gärtner's memoir. The writer believes that it should be carefully read by every plant breeder, not only for the details of practical and historical value therein contained, but because of the philosophical spirit underlying Gärtner's scientific attitude upon the nature of the hybrid organism.

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ON THE USE OF THE SUCKING-FISH FOR CATCHING FISH AND TURTLES: STUDIES IN ECHENEIS OR REMORA, II.

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II

In 1507, there was published at Venice by Franconzio another collection of travels, entitled "Paesi Nouamente Retrouati Et Nous Mondo da Alberico Vesputio Florentino Intitulato" [Countries Newly Found and the New World of Albericus Vesputius Called the Florentine]. Chapters LXXXIIII to CXIIII faithfully reproduce the Libretto of 1504, are in fact a second edition of the Libretto, and need not detain us.[14]

All this however simply pushes the question back one step further and it now becomes "What or who is the source of Peter Martyr's information?" The answer is that these sources are identical with those for the "Life of Christopher Columbus" by his son Ferdinand, for Las Casas's history of the West Indies, and for Bernaldez's "Reyes Catalicos." In addition Dr. Eastman has skilfully worked out certain internal evidence which points directly to the one person who gave to Peter Martyr the data incorporated in Chapter XV of the Libretto.

Let us first of all consider the account which Ferdinand gives of the fisherman-fish incident, which seems to

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[14] The "Paesi" was also reprinted at Milan in 1508 by Arcangelo Madrignano, and later at both Basle and Paris by Simon Gryneo. Martyr says that this plagiarism was the work of Alvico de Cadamosto and denounces him in Decade II, book 7. Martyr's "First Decade" was published in 1511, and the first edition of the "Decades" appeared in 1516 under the editorship of the author's friend, Antonio de Nebrija. The publisher seems to have been Alcala de Henores.

have occurred on or about May 19, 1494. This is found in his "Historie" as follows:

> The nearer they sailed to Cuba, the higher and pleasanter the little islands appeared which were all over that sea, and it being a matter of difficulty and to no purpose to give every one of them a name, the Admiral called them all in general Jardin de la Reina, the Queen's Garden. . . . In these islands they saw crows and cranes like those of Spain, and sea-crows [gulls], and infinite numbers of little birds that sung sweetly, and the air was sweet as if they had been among roses, and the finest perfumes in the world; yet the danger was very great, there being such abundance of channels, that much time was spent in finding the way out.
>
> In one of these channels they spy'd a canoe of Indian fishermen, who very quietly, without the least concern, awaited the boat which was making towards them, and being come near, made a sign to them in it to attend till they had done fishing.
>
> Their manner of fishing was so strange and new to our men, that they were willing to comply with them. It was thus: they had ty'd some small fishes they call *Reverso* by the tail, which run themselves against other fish, and with a certain roughness they have from the head to the middle of the back they stick fast to the next fish they meet; and when the Indians perceive it, drawing their line they hand them both in together. And it was a tortoise our men saw so taken by those fishermen, that fish (the *Reverso*) clinging about the neck of it, where they generally fasten, being by that means safe from the other fish biting them; and we have seen them fasten upon vast sharks.
>
> When the Indians in the canoe had taken their tortoise, and two other fishes they had before, they presently came very friendly to the boat, to know what our men would have, and by their directions went along aboard the ships, where the Admiral treated them very courteously. . . .

The close similarity between the accounts of Ferdinand and Martyr will already have occurred to the reader. Before going further it is but fair to say that Ferdinand's original copy is not known, the printed text being from Ulloa's Italian translation. However, Ferdinand was the heir of the admiral, and, since all his father's papers which were preserved seem to have fallen into his hands, may be considered as his father's literary executor. Winsor says (pages 9–10) that "Ferdinand, or the writer of the 'Historie,' . . . it seems clear, had Columbus's journal before him." Columbus kept a journal of his second voyage until he was stricken down by sickness, and this is attested to by both the Historie and by Las Casas.

Ferdinand himself on this point says (Churchill's Voyages, II, p. 560) that, after the fishing scene above described, the Admiral held on his course though worn out with fatigue, neither having had his clothes off nor lain in a bed since leaving Spain "till the 19th of May (1494) when he writ this," *i.e.*, the account of the fishing scene in Queen's Garden. Windsor states (page 39) that the "Historie" was up to 1871 believed to be a biography of Columbus by his son Ferdinand, and that though doubted by some, is still firmly held to by many authorities. With the above conclusions, Dr. Eastman and I, after a careful study of all the available data, found ourselves in full accord.

Las Casas, the great apostle to the Indians, left at his death a manuscript history of the West Indies. This had been long in the writing, from 1527 possibly, or more positively from 1552, to 1561 (Las Casas died 1566), but was longer in getting published (1875). However, in its manuscript form, it was available from the time of his death for all later historians.

Las Casas's account of the fishing scene need not detain us here since it is essentially like that in the "Historie" by Ferdinand, and like that in the "Libretto" of 1504 and the "Decades" of 1511. Much more important is the query as to the source of Las Casas's data. Winsor (pp. 39 and 47) quotes Harrisse that he thinks that both Ferdinand, or the author of the "Historie," and Las Casas had access to common documents or may be a manuscript prototype of their writings. And later (p. 56) Winsor speaks of "the journal of Columbus as preserved by Las Casas."

One further source of information needs to be set forth, and then after a brief consideration of Peter Martyr's sources, this part of our study will be finished. About the middle of April, 1915, Dr. Eastman got word of a manuscript copy in the Harvard Library of a manuscript document in the Royal Library at Madrid of Columbus's time written by a personal friend of the great navigator and narrating the events of the second voyage. A few days later he wrote me as follows:

> Everything run down thus far is overshadowed in importance by the new find, ante 1500, which I take to be the *ipsissima verba* of *Columbus* himself. The MS. . . . now in the Harvard College Library formerly belonged to Mr. Prescott, who had it transcribed from a MS. work in the Royal Library of Madrid. A part of it was translated, rather poorly, in the Massachusetts Historical Collection before 1850, and some years later the Madrid MS. was printed (1856 at Seville and 1870 at Madrid). Irving and Humboldt both consulted the original MS. or copies of it, and historians agree that the author, Bernaldez, an Archbishop of Andalusia, not only entertained Columbus at his house on his return from his second voyage, but received the journals and other papers then in Columbus's possession. Prescott makes this statement and it is repeated by others. Now Bernaldez, in his work written before 1500 embodies practically all of Dr. Chanca's[15] letter, and hence we may suppose that what he takes from Columbus's papers and journals was copied nearly verbatim. I regard this as one of the most important authentic sources for the second voyage . . . coming as it does nearest to the fountain head.

Let us now consider Bernaldez's account, which as just shown seems to be a transcription of Columbus's own words.

> The Admiral set sail [from Jamaica] with his three caravels, and sailed 24 leagues towards the west, as far as the gulf Buen Tiemps. . . . On Whitsunday, 1494, they stopped at a place which was uninhabited—but not from the inclemency of the sky, or the barrenness of the soil,—in the midst of a large grove of pam-trees, which seemed to reach from the sea-shore to the very heavens. . . . Here they all rested themselves upon the grass about these fountains, enjoying the charming fragrance of the flowers, and the melody of the song of birds, so many and so sweet, and the shade of the palm trees, so tall and so beautiful, that the whole was a wonder. . . . As the number of islands in this region was so great that he could not give to each a separate name, the Admiral called them all by the common name of the Queen's Garden.
>
> On the day following, the Admiral being very desirous to fall in with

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[15] Dr. Chanca was a physician who accompanied Columbus on his second voyage, and who wrote back a long letter describing various natural objects in the New World, but saying nothing of the Remora.

> some natives with whom he might parley, there came a canoe to hunt for fish:—for they call it hunting, and they hunt for one fish with others of a particular kind. They have certain fishes which they hold by a line fastened to their tails, and which are like conger-eels in shape, and have a large mouth [*i. e.,* head] completely covered with suckers, like the octopus. They are very fierce, like our ferrets, and when they are thrown into the water they fly to fasten themselves upon whatsoever fish they may espy, and sooner die than let go their hold till they are drawn out of the water.
>
> The hunting fish is very light, and as soon as he has taken hold, the Indians draw him by the long cord attached to his body, and in this manner they take a fish each time on drawing both to the surface of the water.
>
> As these hunters were at a distance from the caravel, the Admiral sent his boats to them with armed men, contriving it so that they should not escape to the land. As the boats came up to them, these hunters called out to the men in mildest manner and as unconcernedly as if they had known them all their lives, to hold off, because one of the fishes had fastened upon the under side of a large turtle and they must wait till they got it into the canoe. This our men did, and afterwards they took the canoe, and those in it, together with four turtles each of which was three feet in length, and brought them to the ships of the Admiral; and there they gave some account of these islands, and of their cacique who was close at hand, and had sent them to hunt. They asked the Admiral to go on shore, and they would make for him a great feast and would give him all of the four turtles they had caught.

Now for a short consideration of Peter Martyr's sources, which seem to be in common with those of Ferdinand Columbus, Las Casas and Bernaldez, if we may judge by the marked similarity of the accounts. There can be no doubt that Martyr, who during all the years of Columbus's voyages, was an attendant at the Spanish court, knew Columbus personally and held converse with him about his voyages and the wonders seen thereon. Winsor says (page 34) that "Peter Martyr knew Columbus," and adds that "Las Casas tells us how Peter Martyr got his accounts of the first discoveries directly from the lips of Columbus himself and from those who accompanied him." And on the next page (35) we read "Martyr . . . composed a special treatise on the discoveries in the New World . . . under the title 'De Orbe Novo' . . .

(which) occupied his attention . . . till the day of his death. For the earlier years he had . . . not a little help from Columbus himself.''

Let us now see what Thacher, the latest and most profound of the biographers of Columbus, has to say as to Peter Martyr's sources, and we have done with this part of this paper. On p. 215 of volume II (1903), he says: ''The Admiral and some of his followers wrote to Peter Martyr, and Peter Martyr thereupon wrote [a series of letters] to an Italian Duke and to a few Cardinals.'' On p. 218 ''. . . Peter Martyr, who not only had access to all public documents, but who himself corresponded with Columbus.'' On p. 440 Thacher referring to Peter Martyr speaks again of ''. . . Personal correspondence with the Admiral.''

Confirmatory of all the preceding it may be noted that the Spanish Jesuit, Nieremberg, professor of physiology in the Royal Academy of Madrid, in writing of the Reversus, quotes Christopher Columbus. It seems not unlikely that he had in his day (his book was published in 1635) access to some of the Columbus manuscripts, may be to the journal of the second voyage. And earlier than Nieremberg, Gesner (1558) on page 483 refers to ''Christ. Colūbus'' as his authority for the story of the hunting fish. Furthermore Humboldt (1826) quotes Columbus on the activities of the *Reves.*

From a consideration of all this testimony, no other conclusion can be reached than that Peter Martyr had from Columbus's own lips or from his manuscript journal of the second voyage (see reference to Ferdinand's ''Historie'' on p. 447), or from both, the account of the use of the fisherman fish at the Queen's Gardens on May 19, 1494. Consequently the first man to see and describe the use of the sucking-fish as a living fish-hook was no other than Christopher Columbus, the great admiral of the ocean.

Long before this the reader has probably asked, ''What belief is to be given these accounts of a matter apparently so incredible?" In answer first let us consider the innate probability of these accounts coming from such diverse sources. It hardly seems probable that such an extraordinary phenomenon, reported separately by Dampier, by Commerson, by Salt, by Holmwood and by Wills for one general locality, and by Columbus and his chroniclers for a part of the world nearly 5,000 miles away, could be other than an actuality. Indeed Humboldt, knowing only of Commerson's and the Spanish accounts, gave them full credence (1826 and 1833). He quotes Captains Rogers and Dampier, and Columbus, and then comments on the manner in which distant and alien peoples achieve the same ends by diverse means, the Americans having a fisherman-fish and the Chinese a fisherman-bird (the cormorant), both serving the same purpose. He thinks that the particular fish is not the small *Remora* but the large *Echeneis naucrates*.

P. H. Gosse (1851) in the volume on "Fishes" in his "Natural History," refers briefly to the old use of Remora as a fisherman at "Hispaniola and Jamaica" and concludes as follows:

> From some observations of our own on the habits of a large West Indian[16] species, we are inclined to believe this account, though we do not know that the device is at present employed.

The distinguished Cuban ichthyologist, Felipe Poey (1856), refers to the Reversus story in a general way, does not seem to think it improbable, but is silent as to any such use in Cuban waters in his time, hence we may safely conclude that the Jardinellas de la Reina no longer witness the exploits of the fisherman fish.

But the reader may object that these stories, especially the Columbus accounts, date back into the far past, and may wish to know if there are any present-day statements to be adduced confirmatory of those already given. It may be answered that there is quite a number equally as

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[16] Acting on this hint, Gosse's "A Naturalist's Sojourn in Jamaica" (1851) was carefully worked over, but with negative results.

circumstantial as those quoted above. These will be taken up chronologically for the localities involved.

And just at this point I am happy at being able to give what is almost an eye witness account of an almost present day use of the Remora as a living fish-hook in the very waters in which Columbus sailed. Lady Annie Brassey tells us that, while the "Sunbeam" lay at anchor in the roadstead of La Guayra, Venezuela in 1885:

> . . . in one of the Indian canoes which we passed we noticed a sort of sucking-fish (*Echeneis remora*), which is used in catching other fish. Arrived at the field of operations, the fisherman lets go an anchor and puts the sucking-fish, attached to a long line with a buoy at the end of it, overboard. It sees other fish at a great distance, darts after them, and attaches itself to them by means of the sucker on top of its head. The Indian easily raises his little anchor, paddles leisurely after the remora, removes the captured fish into his canoe, and repeats the operation until he has caught as many fish as he wants. Thus, one of the ugliest and most incapable-looking of creatures is made by savage instinct to become of some use in procuring food for the superior animal.

C. F. Holder, who knew the fishes of the Florida Reef as no other scientific man ever has, refers to Holmwood's accounts, makes mention of Columbus, notes that the fish is easily tamed and goes on to say (1905):

> It is this Remora of which the story is told that fishermen employ it in the Caribbean Sea to catch turtles. The Remora is kept, so runs the story, in a pail; a ring is placed about its tail and to this a line. When the men sight a turtle the Remora is slipped overboard and it is supposed darts at the turtle, seizes it, and holds on with such firmness and vigor that the animal can be hauled in.

It is interesting to note that in the first paragraph, Holder uses the present tense. Since he refers to them, he certainly had knowledge of the Columbus Guiacan stories in all of which the fish has no ring affixed to its tail, and is carried to the fishing grounds not in a pail but adhering to the outside of the canoe. The same account in almost the same words is found in one of the stories in his charming little book "Stories of Animal Life" (1899). In this the account of this curious fishing is somewhat amplified, and is accompanied by a drawing, Fig. 8, Plate III, of this paper in a photographic reproduction of Holder's illustration and being a very spirited one is of interest and value. It is of course not a picture of an actual occurrence.[17]

In the paper previously referred to (1905) Holder tells of trying to catch turtles and sharks by means of a living fish-hook, in which effort, however, he was unsuccessful. He says:

> I experimented with the Remora but the fish invariably refused to dart after the turtle, preferring to find shelter under the boat. One tossed to a shark was seized by the latter, that doubtless thought it a votive offering. Possibly something was wrong: our remoras may have been stale: they surely were not ship or turtle slayers.

In this connection the only other modern figures of fishing with the living fish-hook may be given. Fig. 9, Plate III, is a reproduction of one of the illustrations from Hudson's "Curious Bread Winners of the Deep" (1893). It was made to illustrate the story copied from Ogilby's "America," and is reproduced here for the sake of completeness. The other figure number 10, Plate III, is from Frederic Ober's "Crusoe's Island" (1901). He gives the Columbus story and has had this figure drawn to illustrate it. The same data without the figure is found in an earlier book by Ober—"Travel Tales of the West Indies," 1888.

THE LIVING FISH-HOOK IN CHINESE WATERS

From the Caribbean we will go half way round the world to find the same story in all its essentials told of the fishermen along the southern coast of the Celestial Empire. Our reference here is to Frank T. Bullen, who in his delightful book "Denizens of the Deep" (1904) gives the following interesting account:

> Turtles are many on the Chinese Coast, and the guileful Chinese fisherman has developed a splendid plan for securing them with little

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[17] The same figure and essentially the same data are to be found in Holder's "Half Hours with Fishes, Reptiles, and Birds." New York, 1906, page 80 and figure 49.

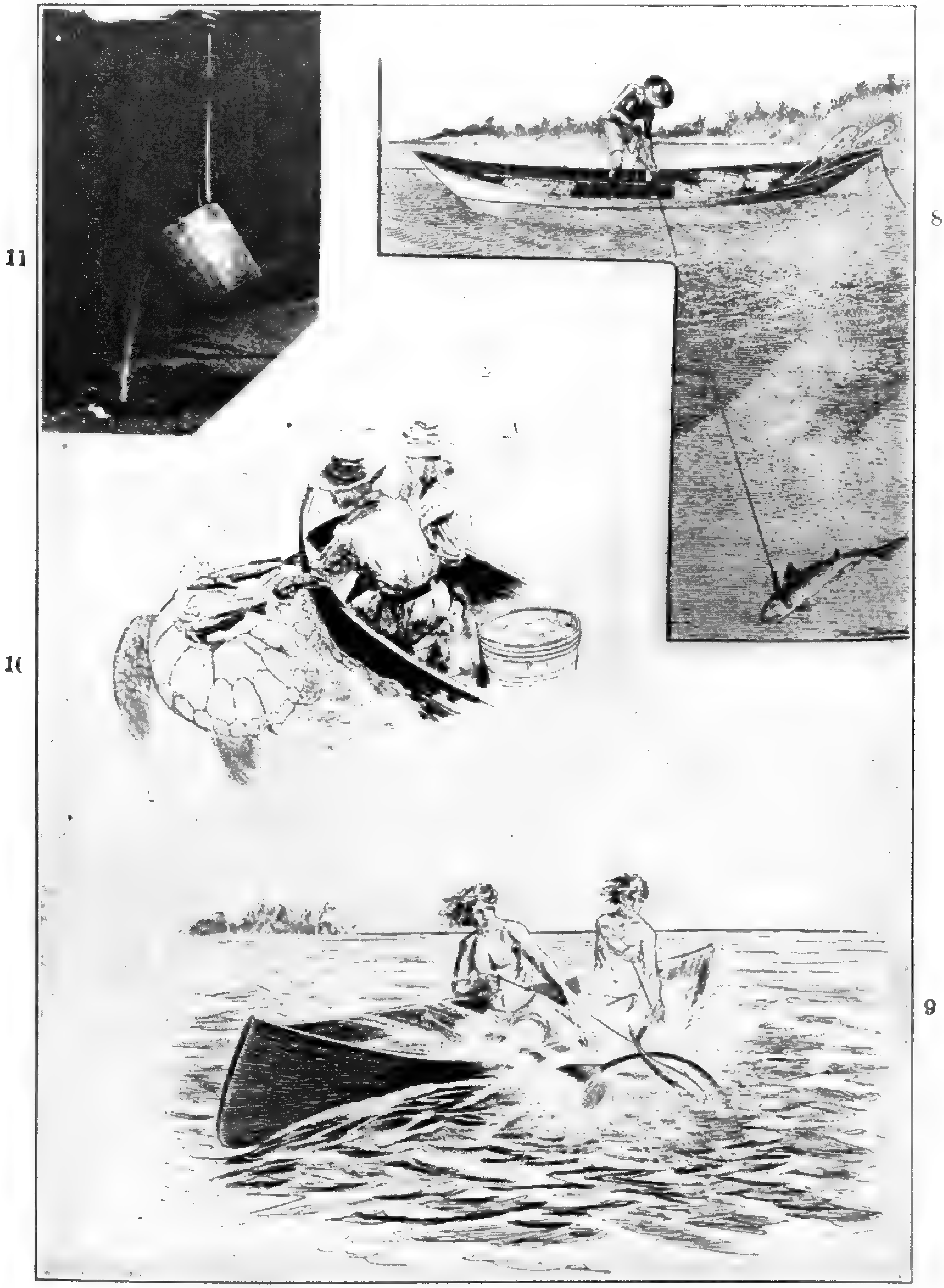

PLATE III

FIG. 8. Fishing with the living fish-hook. After Ober, 1901.
FIG. 9. Fishing with *Echeneis.* After Hudson, 1893.
FIG. 10. Fishing with the Remora. After Holder, 1899.
FIG. 11. An *Echeneis*, twenty-six and one half inches long, having a disk five and one half inches long, lifting a bucket of water weighing twenty-four pounds. After Townsend, 1915.

> trouble to himself. He captures some *Remoræ,* those little sharks [?] that are so lazy that they have developed a sucking arrangement on the top of their heads, whereby they may, and do, attach themselves to anything that is likely to float them into the vicinity of food to be obtained without effort. Carefully he welds [?] a ring round their tails in such wise that it cannot be pulled off, and to it he attaches a thin, strong line; then, putting out to sea with six or seven of his unwilling helpers attached to the bottom of his sampan, he gets a good offing and waits patiently for the appearance of a turtle asleep upon the sea. As soon as his keen eyes have detected one, he paddles noiselessly in that direction until, getting near enough, he ships his paddle and, with a long bamboo, pushes off one or two or more of his *Remoræ.* Now all he needs to do is to keep them from fastening on to the canoe again, for they speedily discover the turtle and attach themselves to him. When they have done so, the quaint yellow fisherman in the boat needs but to haul in, for you may, by pulling upon a *Remora* from aft, tear him in two pieces, but you cannot make him let go his hold. And so despite his struggles the poor turtle must come [in]. . . .

In corroboration of this account, Dr. Alfred G. Mayor tells me that he has read in Singapore newspapers that the fishermen of that city commonly make use of the sucking-fish in the manner just described.

FISHING WITH THE REMORA IN TORRES STRAITS

There are now to be given a number of very circumstantial accounts of this mode of fishing in yet another part of the world—Torres Straits between Australia and New Guinea. The first is from the pen of John MacGillivray. In his "Narrative of the Voyage of the Rattlesnake" (1852), volume I, page 300, he tells of the rescue of a white woman, Barbara Thompson by name, who had been held captive for some years by the natives of Muralug or Western Prince of Wales Island in Torres Straits and had been named by them Giom or Gi(a)om.

In Volume II, pages 21–22, MacGillivray says:

> This last (an unnamed species of turtle), I was informed by Gi'om, is fished for in the following extraordinary manner. A live sucking-fish (*Echeneis remora*), having previously been secured by a line passed round the tail, is thrown into the water in certain places known to be suitable for the purpose; the fish while swimming about makes fast by

its sucker to any turtle of this small kind which it may chance to encounter, and both are hauled in together.

Our next account is an eye witness one dated but a few years after MacGillivray's. John Jardine was for some years police magistrate at Somerset, Cape York, where his duties brought him into close contact with the natives. As a result of his experiences, in 1866 he published the following account of fishing with the sucking-fish at Cape York:

> A singular mode of taking the hawkbill turtle is followed by the natives here. This custom, though said to be known so long back as the time of the discovery of America by Columbus, is so strangely interesting that I will give a short account of it as I have seen it practised. A species of sucking-fish (Remora) is used. On the occasion to which I allude, two of these were caught by the blacks in the small pools in a coral reef, care being taken not to injure them. They were laid in the bottom of a canoe, and covered over with sea-weed—a strong fishing-line having been previously fastened to the tail of each. Four men went in the canoe; one steering with a paddle in the stern, one paddling on either side, and one in the fore-part, looking out for the turtle and attending to the fishing lines; while I sat on a sort of stage fixed midship, supported by the outrigger-poles. The day was very calm and warm, and the canoe was allowed to drift with the current, which runs very strong on these shores. A small turtle was seen, and the sucking-fish was put into the water. At first it swam lazily about, apparently recovering the strength which it had lost by removal from its native element; but presently it swam slowly in the direction of the turtle, till out of sight; in a very short time the line was rapidly carried out, there was a jerk, and the turtle was fast. The line was handled gently for two or three minutes, the steersman causing the canoe to follow the course of the turtle with great dexerity. It was soon exhausted and hauled up to the canoe. It was a small turtle, weighing a little under 40 lbs., but the sucking-fish adhered so tenaciously to it, as to raise it from the ground, when held up by the tail, and this some time after being taken out of the water. A strong breeze coming on, the canoe had to seek the shore without any more sport. I have seen turtles weighing more than 100 lbs., which have been taken in the manner described.

We next hear of this fish in Gill's "Life in the Southern Isles" (1876), wherein he corroborates MacGillivray and Jardine in the following citation:

> Another mode of turtling is to call in the aid of the *Echeneis remora,* or sucking-fish, which is about three feet in length, and is easily caught by a line. When caught the Straits Islanders pierce the tail, in order to insert a strong cord, which is also wound round it for the sake of security. Generally captive sucking-fish are kept swimming after the canoe until a turtle is seen, when three or four of them are thrown as near the sleeper as possible. These sucking-fishes at once attach themselves to the turtle, which awakes to find itself a prisoner. The cords are now cautiously hauled in, bringing the sucking-fishes and the turtle. This ingenious device is used only with the smaller turtle. Sucking-fishes are sometimes kept two or three days in a lagoon or in a boat half-filled with sea-water, until turtles are seen.

In 1888, Professor A. C. Haddon was a member of an expedition to Torres Straits to study corals, and while there (some eight months) he made notes of the use of Echeneis as a turtle-catcher and of its supernatural powers. Brief accounts of this remarkable use of the fish were published in 1889, 1890 and 1890a (see in bibliography under Haddon), but as a much fuller account by him will be given later the above need not be quoted here.

Stirred up by Haddon's note of 1889, Sclater later in the same year in *Nature* called attention to Holmwood's article. And, stirred by Sclater, H. Ling Roth in the same volume of the same journal cited the account by Ferdinand Columbus given in Churchill's Voyages as quoted on page 448.

Saville Kent in his book, "The Great Barrier Reef of Australia" (1893), has the following to say anent our subject:

> A method frequently employed by the natives of Torres Straits to capture turtles is remarkable. The large sucking-fish, *Echeneis naucrates,* which grows to a length of three or four feet, and is distinguished by the natives by the title of "Gapu," is pressed into service. The fish is kept alive in water in the bottom of the native canoe, a thin line being fastened round its tail and through its gills. On a turtle being sighted in the vicinity of the canoe, the sucking-fish is thrown towards it, and immediately swims to and fastens on its carapace. If the turtle is of small or medium size, it is hauled in by the line, the fish retaining its tenacious hold; but if it be a large one, a native jumps overboard with a stronger line, and, following the smaller one down, secures the reptile.

Corroboratory of the foregoing is the following account extracted from Semon's book "In the Australian Bush" (1899). In describing the catching of the turtle, *Chelone midas,* by divers who jump on its back, or by fishermen who harpoon it, Semon adds:

> . . . but a third very peculiar method of capture is adopted in Torres Straits. In clear weather and a tranquil sea, the sharp eye of the native is able to discern any turtle reposing on the bottom of the sea in the neighborhood of the coral reefs. Now a sucking-fish, or Echeneis, to the hind fin of which a long string has been fixed, is thrown into the water above the place where the turtle has been seen. It will immediately descend into the depth and attach itself to the shell of the reposing Chelonian, and as a communication is thus established between the boat and the turtle, a native following the leading string, dives and winds a rope round the beast, as the sucking-fish does not attach itself quite firmly enough for the fisherman to draw the heavy weight up by it.[18]

This last statement must not be interpreted as contradictory of the foregoing accounts of catching turtles *on the surface* with the sucking fish. Bringing boat and turtle together on the surface by pulling on the line is one thing, hauling a turtle up from the bottom is quite another; as any reader knows who has ever endeavored to land a ray or other large flat fish which insisted on clinging to the bottom. This latter is purely a problem in hydrostatics.

Entirely independent of any of the foregoing accounts is that of the Australian ethnologist, W. E. Roth. Here the location (Tulley River) is different, as is the final manner of taking the fish, turtle, or dugong. Roth's statement follows:

> On the coast-line in the neighborhood of the Tulley River, the sucker-fish, *Remora,* is utilised as a guide for spearing or harpooning fish, as well as turtle and dugong. This sucker-fish, known to the Mallanpara blacks as *kamai,* is found usually on the rocks at the outlying islands, and sometimes stuck on their own canoes. It is removed, kept in a canoe, bark-trough, etc., with a little water, and left there for a few days. Then, going out to sea, the native ties a fine twine round the Remora's tail, and as soon as he sights any big fish, turtle or dugong,

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[18] This account is also found in the German edition of Semon's book published at Leipzig in 1903.

> advances his canoe as far as possible, and drops the sucker-fish overboard. In all probability, the sucker will go straight for the object and attach itself: it acts only as a guide, and tells the hunter the next move of his prey. The aboriginal now plays the line out very guardedly, draws it in with equal care and caution, and as soon as the length submerged reaches a point on the line, previously marked, he knows that he is within striking distance, and as his quarry comes to the surface, uses the spear or harpoon accordingly. It must be borne in mind that in no sense does the sucker-fish pull the prey into the hands of the hunter: it only indicates the direction in which the harpoon, etc., can be advantageously thrown.

The account given by N. W. Thomas in his book "Natives of Australia" (1906) is taken almost verbatim from the above and beyond this mere citation no notice will be taken of it here.

We now come to another account of the peculiar use of *Echeneis* under discussion, and I am able to offer no less an authority than the "Encyclopædia Britannica," in the eleventh edition of which, in Volume XXII (1911), in the article on Queensland, Australia, Mr. T. A. Coghlan writes:

> In Torres Strait and the northern coast the hawksbill turtle . . . is said to be captured in a peculiar manner, the sucking-fish or remora (*Echeneis naucrates*) being utilized by the islanders for that purpose. The remora is carried alive in the bottom of the canoe, a long thin line being attached to the fish's tail and another usually to the gills. On a turtle being sighted and approached to within the length of the line, the sucking-fish is thrown towards it, and immediately swims to and attaches itself by its singular head sucker to the under surface of the turtle which if of moderate size is easily pulled into the canoe.

During the year 1898, Professor A. C. Haddon was leader of the Cambridge University Anthropological Expedition to Torres Straits. On this expedition he made an extensive study of the use of the fisherman fish. Professor Haddon's data is so complete that he has effectually settled the matter of the present-day actual use of the fish for taking other fish, and since his reports are of the highest value, putting as they do the imprimatur of truth on the whole matter, they will be referred to in some detail.

Professor Haddon's first account based on the data of his second expedition is to be found in his "Head Hunters: Black, White and Brown" (1901). This gives essentially the same data as that contained in the short article in *Folklore,* 1890, but for fuller accounts we must turn to the various reports of the Cambridge Anthropological Expedition to Torres Straits.

Taking up these reports chronologically fits in well with the scheme of this paper, as will be seen presently. Volume V (1904) deals with the "Sociology, Magic and Religion of the Western Islanders." Here Haddon gives three folk tales, one of which has to do with the origin of the use of the *Gapu* (the native name of the sucking-fish), and two with its use. Later in the same volume Dr. Rivers gives a very detailed account of the method of procedure in fishing with the *Gapu.* This data will be found later in Haddon's final account of the use of this fish. Further along in Volume V Haddon and Rivers give accounts of the *Gapu* as a totem.

Volume VI of the Reports bearing date 1908 has for its title the "Sociology, Magic and Relation of the Eastern Islanders." These peoples do not seem to have so many tales of the *Gapu* as their western brethren since Haddon records but two. It seems apart from the purpose of this paper to insert any of these folk tales here, but it is my purpose later with Professor Haddon's kind permission to collect them and publish them in a short article.

We now come to the latest, most detailed, and most valuable of all the accounts of the use of the living fish hook in Torres Straits. In Volume IV of the Reports issued in 1912, Professor Haddon gives a very circumstantial account and this will be quoted in full. In this volume, dealing with arts and crafts, fishing with the sucking-fish is frequently referred to. The fish is well known to the natives as their myths and legends show and it is a common motif in their ornaments and ornamentation. Haddon's account of its use now follows:

> The most interesting method of catching turtle is that in which the sucking fish (called *gapu* in the western part of the straits, and *gep* in

> the eastern) is employed. . . . The sucker-fish is not used to haul in the large green turtles; I was repeatedly assured that it would be pulled off, as the turtle was too heavy; but small ones are caught in this manner. . . .
>
> According to one of the folk tales, there was a time when the people of Badu did not know how to catch turtle by means of the sucker-fish, and they used to employ a black toothless "dog-fish," *Kumsar,* when they went for turtle. The story goes on to tell how Bia taught his fellow islanders how to employ the sucker-fish. In the Bomai-malu legend of the Miriam, it is stated that Barat of Moa, according to the fashion of olden times, tied a rope around the tail of a *kamosar,* then he made a sucker-fish, and instructed the Western Islanders who were with him how to catch turtle with it. I do not understand how turtle could be caught by a "dog-fish," but as the identity of this fish, which is said to live in the crevices of the rock in deep water, is unknown, nothing further can be said, except to hazard the suggestion that it may be an unidentified kind of lamprey; but against this it must be stated that no member of the Cyclostomata is known from Queensland waters, though *Mordacia mordax* occurs in Tasmania and species of *Geotria* are found in southern Australian waters.
>
> I was informed that in leashing a sucker-fish, a hole is made at the base of the tail-fin by means of a turtle-bone and one end of a very long piece of string inserted through the hole and made fast to the tail, the other end being permanently retained. A short piece of string is passed through the mouth and out at the gills, thus securing the head end. By means of these two strings the fish is retained, while slung over the sides of the canoe, in the water. The short piece is pulled out of the mouth of the fish when the turtle is sighted and the *gapu* is free to attach itself to the turtle.

According to Professor Haddon there is a certain ceremonial or set rule of procedure always definitely followed in fishing with the *gapu.* This he describes as follows, his data being chiefly taken from Rivers as noted above:

> When starting on a trip to fish for turtle by means of the sucker-fish, the owner (or captain) of the canoe gives the order where to go and when to let go the anchor, having arrived at their destination.
>
> The *buai-garka* (mate, also brother-in-law of the owner or captain) makes a fire on which he places some turtle-bone which the owner has brought with him. When the bone is charred the *buai-garka* breaks it up and throws it into the water so as to attract the sucker-fish. When one is caught it is the duty of the *buai-garka* to attach to the fish the leashing which he had previously made.
>
> The direction of affairs is now assumed by the *buai-garka,* who gives the word to move to another place, and the directions where to go.

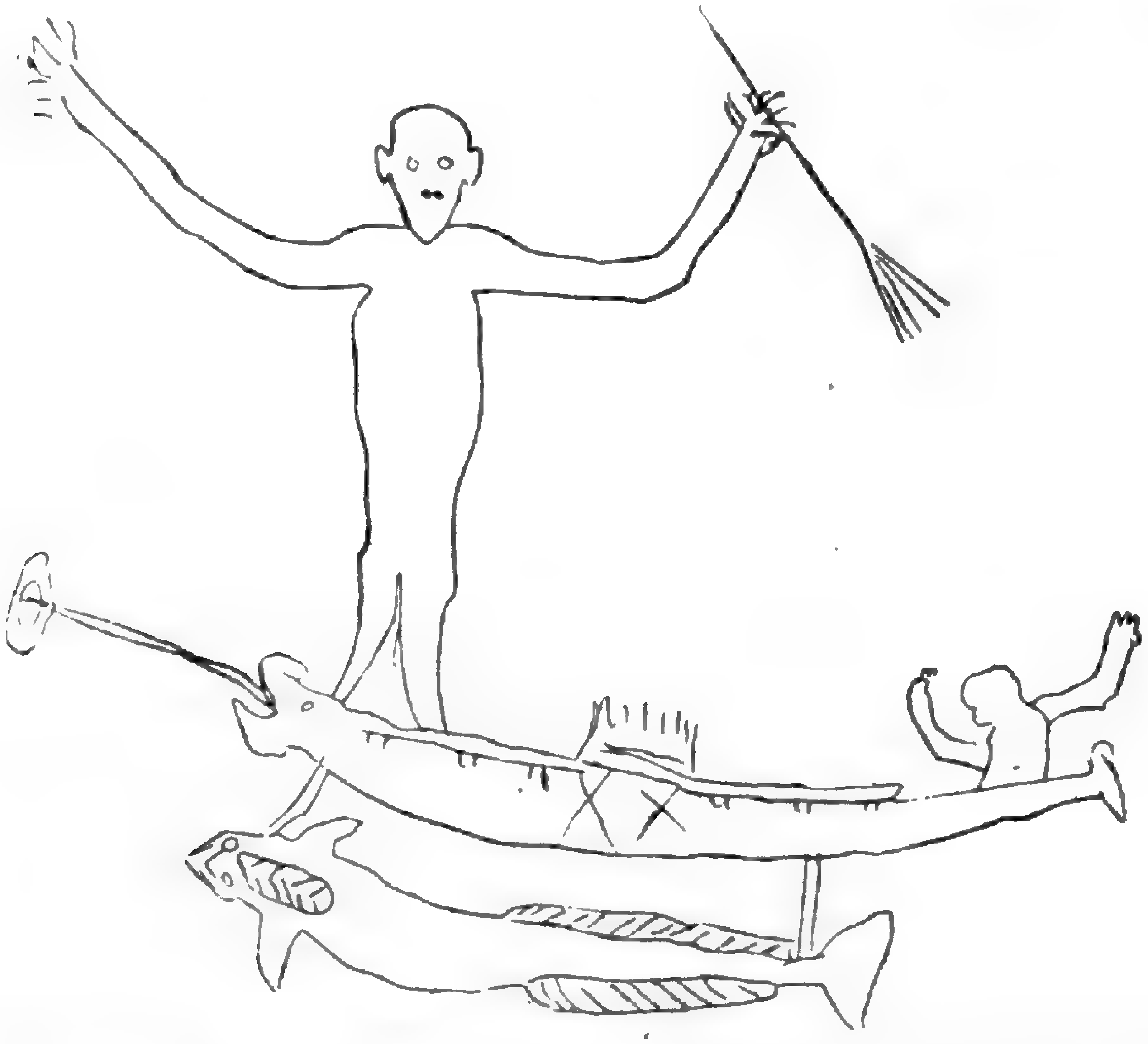
When he gives the order to stop, the mat sail is rolled up by the other men (or at the present time the sail is lowered), he not taking any part. He gives the order to paddle till he sees the turtle, then gives the word to stop, and the anchor is let go by the owner, having been previously shifted to the stern of the canoe. When the *buai-garka* sights a turtle swimming deep down in the water, he removes the mouth string from the sucker-fish and throws the fish overboard with the tail-line attached and plenty of slack is thrown with it, he then hauls in the superfluous slack and as far as possible indicates the direction of the turtle by pressure on the line. The sucker-fish on perceiving the turtle immediately swims towards it, and attaches itself to the reptile's carapace. When this is accomplished, the *buai-garka* gives the order to heave up the anchor and move the boat up to the position of the turtle.

One of the crew (but not the *buai-garka*), with a long rope attached to the right upper arm, dives into the water, and is guided to the turtle by the line fastened to the fish's tail. On reaching the turtle, the man gets on to its back and passes his arms behind and below the fore flappers and his legs in front of and below the hind flappers, or secures it in some other way. The man is then rapidly drawn up to the surface of the water bearing the turtle with him. On the arrival of the diver the sucker-fish usually shifts its position from the upper to the under surface of the turtle. As soon as enough turtle have been obtained, the owner of the canoe gives the order to go home, and the *buai-garka* resumes his subordinate functions, and resigns into the hands of his brother-in-law the direction of affairs which had been his part during the actual process of fishing. The *buai-garka* knows whether the fish has attached itself to a turtle or to a shark by the nature of the motion of the string. If the pull is intermittent it means that the fish has adhered to a shark, but if steady, then a turtle has been secured.

In a footnote Professor Haddon tells us that the sucker-fish is eaten at the end of the day's fishing. This seems like a very wasteful course of action, but it may have arisen because of the difficulty in keeping the fish alive until the next time it would be needed. In text-figure 5, we have a native drawing showing how the "Gapu" is attached to the canoe during the trip to the fishing grounds.

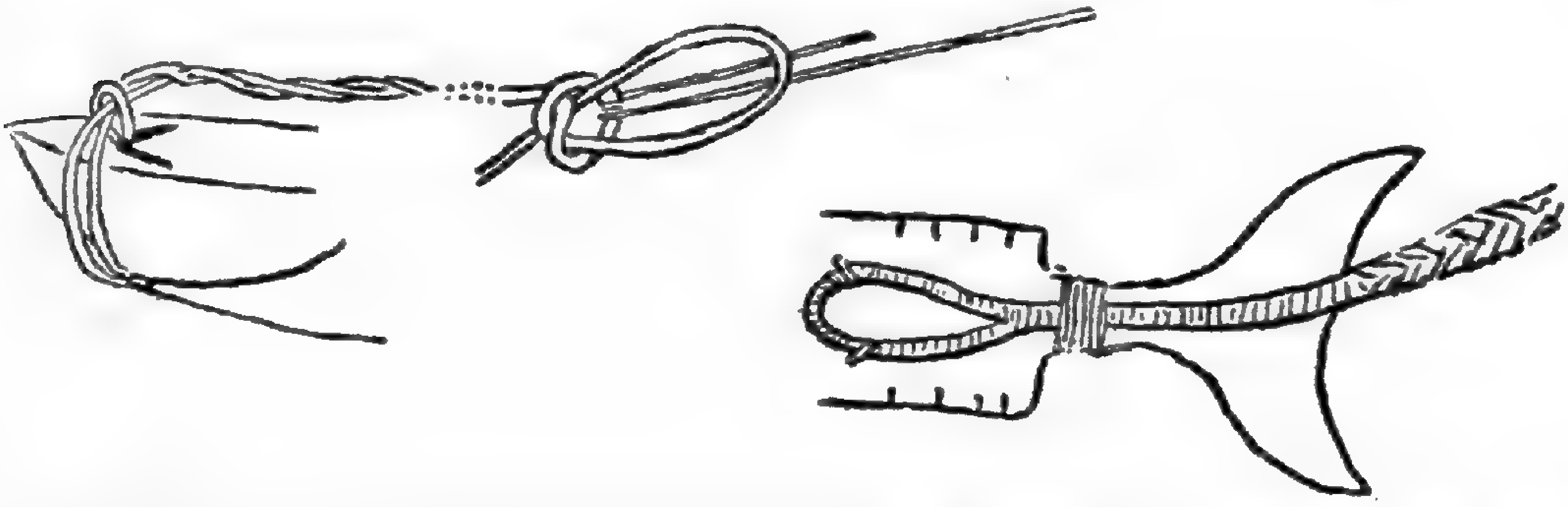
We have in Holmwood's account a description with figures of how the leashing is accomplished, and Haddon also is too good a scientist to leave us in doubt as to how the Torres Straits natives manage this matter. In addition to what has already been given as to the manner of making the leashings fast, his detailed account is as follows:

In order to understand the method of leashing a sucker-fish, I induced a native to make a model of a *gapu* for me. Fig. 173 [present text-figure 5] indicates diagrammatically the arrangements. A loop is inserted by means of a wooden arrow point through the gills and out at the mouth, the ends are passed through the loop, and one of the strands is threaded through the other, the two are then twisted into a string. The mouth string is called *gudaz* and is made of the inner bark of the root of the *wali* tree. The other end of the *gudaz* is tied into a slip knot, *kaza wiaikab,* the end of a long piece of twine is simply bent twice round the string at the knot; when the free end of the *gudaz* is pulled the knot runs out, and the twine (one end of which is still held, by the fisherman) slips off the *gudaz.* The main fishing string is a very long and strong cord of twisted coco-nut fibre, *igal;* this is fastened to a braid of plaited string, *dan,* the other end of which is bent round on itself so as to form a loop; the end of the *dan* and the loop are bound round with *wali.* The loop is furnished with two strings of *wali;* it looks as if these were threaded through the tail of the fish above and below the vertebral column and tied together on the other side. Another lashing binds the cord close to the side of the narrow portion of the tail.



TEXT-FIGURE 5. Showing how the sucker-fish is leashed by the natives of Torres Straits. Drawing of Tagai and Kareg in their canoe by Gizu of Mabuiag, reduced by one half. In this drawing, the canoe, Kareg and the sucker-fish are represented the wrong way round. After Haddon, 1912.

The sucker-fish is so well known to the natives as to give rise to a decorative motive in their decorative art. Haddon gives numerous figures of this. It is also a subsidiary totem of one of the clans in the western islands and Haddon thinks may once have been a chief totem of a larger but now extinct clan. The natives moreover ascribe to it considerable intelligence. Haddon thus concludes his interesting account:



TEXT-FIGURE 6. Native drawing illustrating the method of attachment of the sucker-fish to the canoe in Torres Straits.

> The natives have great respect for the sucker-fish and firmly believe it to possess ominous powers. For example: when the fish does not take a good hold on the turtle and then swims off it indicates that some part of the canoe is not secure; when there is something the matter with the bow of the canoe, the fish is said to attach itself to the neck of the turtle, but should the stern of the canoe be weak, the fish adheres to the extreme hinder end of the carapace; when it fixes itself firmly to the front part of the carapace, the canoe is strong; when it goes to one side of the carapace or keeps moving about, it shows that the leashings of the float to the outrigger on that particular side are insecure. More than once I was told, *Gapu* savey all same man. I think him half devil (*i. e.,* spirit).[19]

One other account is now to follow and all the known data will have been fully presented to the reader. E. J. Banfield, the well-known Australian, lived for a number of years on Dunk Island, off the coast of tropical Queensland, in about latitude 18° S. His experiences there are

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[19] After Haddon's full and very detailed accounts, Meek's brief reference (1913) that the ingenious natives of Thursday Island and the adjacent parts of Torres Straits use one fish to catch another—*i. e.,* the sucking-fish with a string fastened to itstail—needs no fuller statement than that given in this footnote.

recounted in a charming book, "The Confessions of a Beachcomber." This was first published in 1908, and reprinted in 1910, and again in 1913. The following quotations are from the 1913 reprint:

> Generally unprogressive and uninventive, the aboriginals of the coast of North Queensland apply practically the result of the observation of a certain fact in the life history of a fish to obtain food. By them the sucker (remora) is not regarded as an interesting example of a fish . . . , but as a ready means of effecting the capture of . . . two . . . animals (turtle and dugong), always eagerly hunted for their flesh.
>
> Other countries have sucker-fish of different form; but it remained for the benighted Australian blacks, among a few other savage races, to make practical use of the creature, which, as a means of locomotion, forms strong attachments to the dugong, turtle, shark and porpoise. It can hardly be called domesticated, yet it is employed after the manner of the falcon in hawking, save that the sucker is fastened to a light line when the game is revealed.

Having located the haunts of a remora the blacks feed it from day to day until its shyness is worn off, and then catch it with a hook.

> Having secured the sucker, the blacks farm it in their haphazard fashion. They fasten a line above the forked tail so securely that it cannot slip, nor be likely to readily cut through the skin, and tether it in shallow water, when it usually attaches itself to the bottom of the canoe. When as the result of frequent use and heavy strain, the tail of the sucker is so deeply cut by the line that it is in danger of being completely severed, a hole is callously bored right through the body beside the backbone, and the line passed through it for additional security.

When ready to hunt for turtle, the natives armed with spears go out in their bark canoe to the bottom of which one of the sucking fish is attached by its sucker. When they reach a locality where turtle abound, they soon get into action.

> In sight of the game the sucker which has been adhering to the bottom of the canoe is tugged off and thrown in its direction. As a preliminary the disc and shoulders of the sucker are rigorously scrubbed with dry sand or the palm of the hand, to remove the slime and to excite the ruling passion of the fish. It makes a dash for a more congenial companionship than an insipid canoe. The line by which it is secured is made from the bark of the "Boo-bah" (*Ficus fasciculata*) and is of

two strands, so light as not to seriously encumber the sucker, and yet strong enough to withstand a considerable strain. Two small loops are made in the line at intervals of two fathoms from the sucker, to act as indicators.

As soon as the sucker has attached itself to the turtle, a slight pull is given and the startled turtle makes a rush, the line being eased out smartly. Then sport of the kind that a salmon-fisher enjoys when he has hooked a 40-pounder begins. The turtle goes as he please; but when he begins to tire, he finds that there is a certain check upon him—slow, steady, never-ceasing. After ten minutes or so a critical phase of the sport occurs. The turtle bobs up to the surface for a gulp of air, and should he catch sight of the occupants of the canoe, his start and sudden descent may result in such a severe tug that the sucker may be divorced. But the blacks watch, and in their experience judge to a nicety when and where the turtle may rise; telegrams along the line from the sucker give precise information. They crouch low on their knees in the canoe, as the game emerges with half-shut eyes and dives again without having ascertained the cause of the trifling annoyance to which he is being subjected. The line is shortened up. Perhaps the turtle sulks among the rocks and coral, and endeavors to free himself from the sucker by rubbing against the boulders. Knowing all the wiles and manœuvres, the blacks play the game accordingly, and hour after hour may pass, they giving and taking line with fine skill and the utmost patience. The turtle has become accustomed to the incumbrance and visits the surface oftener for air. One of the harpoons is raised, and as the turtle gleams grey, a couple of fathoms or so under the water, the canoe is smartly paddled towards the spot whence it will emerge, and before it can get a mouthful of air the barbed point, with a strong line attached, is sticking a couple of inches deep in its shoulder.

From the foregoing interesting accounts it is clear first that in Torres Straits at the present time the aborigines use the sucking fish as a living fish-hook just as fishermen in other regions use a veritable fish-hook, *i. e.*, to bring the fish or turtle to the gaff. The gaff is, in the last account quoted, a harpoon or spear, according to others a native who dives down, guided to the turtle by the line attached to the Echeneis, and who then ties a line to a flipper of the turtle.

THE ENGLISH SPARROW HAS ARRIVED IN DEATH VALLEY: AN EXPERIMENT IN NATURE[1]

THE English sparrow first became well established in the United States in 1860–1864 in the vicinity of New York City. Several small plants had been made in other Atlantic cities within the few years preceding, but practically all of these are definitely known to have failed. The original stock is in nearly all the cases of importation known to have been obtained in England. Its spread through the eastern United States after once established was phenomenal; its rate of invasion towards the west only slowed up at about the 100th meridian, and this, significantly enough, is about at the line limiting a great many species of native eastern birds toward the west and of native western birds toward the east. Nevertheless, the English sparrow ultimately crossed this barrier, constituted by change in humidity, and it has continued expanding its range until it exists now in nearly every part of every state in the Union. It has also extended throughout southern Canada and has become well settled in the Hawaiian Islands.

In California the English sparrow was first noticed in 1871 or 1872, in San Francisco, and it quickly thereafter appeared in many of the towns in the west-central part of the state. But it was very slow to enter southern California. It did not reach Los Angeles for nearly thirty-five years, in 1907; and San Diego was not reached until 1913. To-day it is familiar in practically every town "south of Tehachapi." Among the places in California now inhabited by the English sparrow, to designate some of those showing extremes of climate as regards temperature and humidity, are Brawley, Imperial County, and Sisson, Siskiyou County; Needles, San Bernardino County, and Eureka, Humboldt County.

In 1917 the California Museum of Vertebrate Zoology undertook as field work for that year a study of the vertebrate animal life of the Inyo region of southeastern California. In connection with this work it was the writer's not unpleasant fortune to spend the month of April in Death Valley. What was his sur-

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[1] Contribution from the Museum of Vertebrate Zoology of the University of California.

prise to find there a thriving colony of English sparrows. These were established on the Greenland Ranch (otherwise known as Furnace Creek Ranch), elevation 178 feet *below* sea level. Specimens were collected, both as alcoholics and as dry study skins, but not to an extent to threaten the persistence of the colony. For here, it occurred to the writer, we had at hand a particularly convincing "experiment" already under way, of just the sort called for by certain critics of the work of the systematist and distributionist, which in time would test the question of the evanescence versus the relative permanence of characters of the category commonly viewed as subspecific.

The sparrows of Furnace Creek Ranch, which were estimated to number about fifty, had their main headquarters in the tops of the several tall Washington Palms which overshadow the ranch house; also several nests were seen in the Fremont cottonwoods which line the irrigation ditches along the alfalfa fields for a quarter of a mile down toward the glistening borax flats. The traveller on entering Death Valley is impressed by Greenland Ranch as a wonderfully rich oasis surrounded by a desert of surpassing barrenness. The English sparrow colony there is, then, isolated under a climate that is probably of the greatest extreme in the direction of high temperature combined with low relative humidity, of any place in North America.

Greenland Ranch is owned by the Pacific Coast Borax Company, who value it for its output of alfalfa hay and for certain appurtenant water rights, there being a constant flow of forty inches from the warm springs nearby. Fortunately for our present problem, the company has for years required its managers to keep a daily record of weather conditions. There is a standard instrument shelter, and the records are kept in available form, and furthermore have been transmitted regularly to the United States Weather Bureau. Without going into details here, it is of interest to note that the highest recorded temperature for any place in the United States was observed there on July 10, 1913, when an afternoon temperature of 134° Fahrenheit in the shade was reached.

As to the time of appearance of the sparrows in Death Valley I have good reason to rely on the statements of Mr. Oscar Denton, who is the present manager of the Greenland Ranch. He says that he first saw them in the ranch yard five years ago (1914). That was about the time the Death Valley spur of the Tonopah and Tidewater Railroad was run to the present location of Ryan. Ryan, by the way, is the terminus of the narrow-gauge line, wherever that terminus happens to be, and this shifts about as determined by the extent of the different ledges of borax ore mined. The borax deposits on the floor of Death Valley are no longer gathered. The day of the 20-mule-team borax wagons is gone except on the labels. It is cheaper to handle the richer borax ore high on the mountain sides and to reach these ledges by railroad. The present Ryan, the nearest the railroad has so far gotten to Death Valley, is 17 miles from Greenland Ranch and 3,000 feet altitudinally above it. I saw English sparrows there repeatedly in April and May, 1917, as also at Death Valley Junction, 40 miles farther away, on the Tonopah and Tidewater Railway. Mr. Denton believes, and I think he is likely right, that the sparrows followed the construction camps along the route of the T. & T. R. R. from Ludlow to Death Valley Junction and thence along the narrow-gauge to Ryan. It may be further suggested that since hauling is done from time to time down the 17 miles of Furnace Creek Wash from Ryan to Greenland Ranch this is the route probably travelled by those sparrows which reached Death Valley. It is less probable to my mind that the birds simply started out overland, from some more distant point, and a pair or more just happened to reach this remote and forbidding valley. It is true, however, that the green of the ranch shines out conspicuously for miles round about and would surely attract to it any vagrant sparrow coming within sight.

We here in America have been accustomed to think of the English sparrow as a full *species, Passer domesticus.* The bird was originally named by Linnaeus, and thus has seemed from all standpoints to constitute a truly "Linnaean species." However, recent developments in the geographic knowledge of birds in the Old World has brought out the fact of geographic variation within the species *Passer domesticus* as previously understood, and also that a number of forms once considered specifically distinct are really connected with the *domesticus* stock through ordinary geographic intergradation. Hartert (1910, pp. 147–151) after a study of the group came to recognize no less than eight subspecies occupying different areas in Europe, western Asia and northern Africa. Subsequently, at least two more races have been named. And now, a German, Kleinschmidt, has discovered that the sparrows of England are distinguishable from those on the continent. The latter, having been the basis of Linnaeus's name, becomes *Passer domesticus domesticus,* and the sparrow of England Kleinschmidt names (cited under date 1915, though I have not seen the original description myself) *Passer domesticus hostilis.* As pointed out by Oberholser (1917, p. 329), since the American stock came from England our bird must also be known under this name. And furthermore, the vernacular term, European house sparrow, which some people have preferred because of a fancied unpleasant association in the name English sparrow, can not be used properly for the American bird.

The point I wish to make now is that the English sparrow, which is spread all over the United States, is itself a subspecies of a wide ranging and decidedly variable species which is thus, geographically speaking, quite like our American song sparrow, or the horned lark. In the Old World, each race "stays put" as regards aggregate of population, each in its own faunal area just as do our own song sparrows. All of these races are nonmigratory. *Passer domesticus hostilis* Kleinschmidt is also nonmigratory, as far as I have been able to learn, wherever it now occurs, north and south, in America. But here, by reason of its marvellous powers of accommodation, and finding no competitor in exactly its own ecologic niche, it has gradually advanced its frontiers and overleaped all the faunal boundaries which hem in the habitats of our native bird races; and we find flourishing representations of it under the most diverse conditions of environment, as for example those shown in contrast by Death Valley and Boston.

Possibly our critics have been merely baiting us when they asked us to transplant a desert song sparrow to the humid coast belt and "see what would happen." But is not this demand met exactly in the case of the English sparrow, only in reverse direction? I have carefully compared the seven skins taken in Death Valley with others taken in Berkeley, and also with examples taken in the eastern United States, without finding any peculiarities of color tone, extent of markings, or dimensions. And I think my eyes are pretty well trained to find small subspecific distinctions, at least of such magnitude as characterize the currently recognized subspecies of song sparrows, Savannah sparrows, and horned larks. The Death Valley birds, it is true, stand out rather sharply from most of the material taken elsewhere, but only in that they are fresh and clean, and lack the sooty overcast of the majority of town birds. To repeat, no differences are now discernible from place to place in North America, in so far as perfectly comparable material is at hand. This accords with the findings of Phillips (1915), which also were practically negative.

Are we not to infer, then, that there has not as yet been sufficient time (up to three years and as many possible generations in Death Valley and up to sixty years elsewhere in North America) for the impress of diverse environments in the different parts of the territory newly occupied by *Passer domesticus hostilis* to bring physical changes in the birds of sufficient magnitude for the modern systematist to detect? Is there not here a demonstration of the relative permanence of subspecific characters far beyond what many naturalists have supposed? Are not such characters in general far more likely to be germinal than somatic?

How intensely interesting it will be to watch the course of this "experiment," now under way, irrespective of human effort, in Death Valley, with "controls" vigorously maintaining themselves (against man's wish!) in San Diego, Berkeley and Boston.

But perhaps it will be urged that the conditions of an orthodox experiment are not here properly met. The "factors" of the environment are not sorted out, and none is under any kind of regulation. Moreover, rigid control has not been secured, in that there is no way in which any of the naturally established colonies of English sparrows can be strictly isolated and kept from genetic contamination by new influxes of birds from elsewhere.

In reply, I would say that we are not expecting more from our natural experiment than the demonstration of what we set out to prove, namely, the length of time necessary for the development, in a stock under natural conditions some of which are known, of characters of subspecific value. In the breeding cage there are always "unknown" factors; so let us admit the existence of those in the wild as not invalidating the "experiment" as such. In nature, subspecies *have* differentiated under just the conditions self-imposed by the English sparrows through their powers of invasion. *Individual* song sparrows and horned larks are continually overstepping the bounds of the habitats of the races to which they belong and have doubtless done so since the initiation of their respective descent lines. But differentiation of the mass *has taken place, under just these conditions.*

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INHERITANCE OF WHITE-SPOTTING AND OTHER COLOR CHARACTERS IN CATS

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IN a previous paper[1] I have presented data bearing on the general subject of the inheritance of coat-color in cats. The experiments at the University of Pennsylvania were still in progress when the paper was published and further results have since been obtained. Unfortunately an eczema infected the stock and the investigations were brought to an end by the death of several animals. It is thought advisable therefore to present the rest of the data in the present paper and to summarize results thus far obtained.

Numbers denoting individuals or matings are inserted as in the previous paper for the purpose of cross reference. In the genetic formulæ A' denotes much-ticked; A, little-ticked; a, non-ticked; B' denotes lined; B, striped; b, blotched; M, denotes intensely pigmented; m, maltese dilution; W denotes dominant solid white; w, color; Y denotes yellow; y, black; Yy, tortoiseshell. Symbols are omitted when character was for any reason undetermined.

A cream male (24) (b.m.w.Y) was crossed (48) to a solid-white yellow-eyed half sister (29) (W) from mating 43 (a white male by an "anomalous" (Yy) cream female (23) mentioned below). There were produced one orange male (b.M.w.Y), and one cream female (b.m.w.Y). Both

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[1] Whiting, P. W., "Inheritance of Coat-Color in Cats," *The Journal of Experimental Zoology*, Vol. 25, No. 2, April, 1918.

had an extreme amount of white-spotting. The same male (24), when crossed (51) to his "anomalous" (Yy) cream mother, (23) (b.m.w.Yy), sired two cream females (b.m.w.Y). He was also crossed (53) to a black female, (32) (a.B.M), and sired one maltese male, (a.B.m.w.y) and four tortoiseshell females, (one a.B.M, one b.m, and two a.M).

The progeny from the "anomalous" (Yy) cream female (23) by her cream son (24) now consists of four litters (41, 46, 50, and 51) containing two maltese males (yX —), one cream male (YX —) and four cream females (YX ?X).

There are now in all eight matings of "yellow" male (YX —) by "black" female (yX yX) giving sixteen "black" males (yX —) and seventeen "tortoiseshell" females (YX yX).

Dr. Charles Penrose, of Philadelphia, very kindly loaned his Caffer cat for crossing, a much-ticked lined male (21) (A′.B′.M.y) mentioned in the previous paper. A cross (52) made with an orange striped female (31) (B.M.Y), from mating 37 produced three tortoiseshell females,—a much-ticked lined (A′.B′.M.Yy), a lined with ticking present but with so much yellow that the exact degree was uncertain, (B′.M.Yy), a ticked of uncertain degree in which the banding was also uncertain on account of admixture of black and yellow, (M.Yy).

The same male (21), crossed (55) to an orange striped sister (33) (B.M.Y) of female 31, sired five orange lined males (B′.M.Y).

The same male (21) crossed (54) to a tortoiseshell (28) (a.B.M.Yy) sired four lined non-yellow kittens,—two little-ticked males (A.B′.M.y), and two much-ticked females (A′.B′.M.y).

The same male (21) crossed (56) to a blotched maltese tortoiseshell (13) (A.b.m.Yy) sired four lined orange males (B′.M.Y) and two lined tortoiseshell females (B′.M.Yy).

When he was crossed (57) to a dilute tortoiseshell (34) (a.b.m.yY), there were produced a lined orange male (B′M.Y) and a lined tortoiseshell female (B′.M.Yy).

When he was crossed (58) to a tortoiseshell female (30) (a.B.M.Yy) he sired two orange lined males (B′.M.Y), one little-ticked, lined male (A.B′.M.y), and two lined females,—one tortoiseshell with so much yellow that degree of ticking could not be made out (B′.M.Yy), and one non-yellow with so much white that degree of ticking could not be made out (B′.M.y).

The crosses of this Caffer cat are reciprocal to those summarized above, crosses of "yellow" males (YX —) by "black" (yX yX) and by "tortoiseshell" (YX yX) females. Here we have a "black" male (yX —) by "yellow" females (YX YX) giving five "yellow" males (YX —) and three "tortoiseshell" females (YX yX) and a "black" male (yX —) by "tortoiseshell" females (YX yX) giving three "black" males (yX —) and seven "yellow" males (YX —) and four "tortoiseshell" females (YX yX) and three "black" females (yX yX). It may be seen, therefore, that the principle of sex-linkage applies in all these cases.

The progeny of the Caffer cat (21) are of interest also from the point of view of ticking and banding. The essential characteristic of Caffer is the narrow banded or "lined" condition. Banding of intermediate width, "striping," acts as a recessive as previously shown and the widest bands, "blotches," are recessive to both "lines" and "stripes." The parents (18, 19) of this cat were both lined, but produced blotched offspring as well as lined. Evidently this cat (21) is the homozygous segregate, for twenty-four of his twenty-five offspring are certainly lined and in the other (52.3) there is so much white-spotting and so much intermixture of yellow and black in the pigmented areas that the condition of banding is uncertain. It is probable, however, that even in this case a wider type of bands,—stripes or blotches, would have been more easily seen. Of the females to which cat 21 was crossed, two (13, 34) were blotched, and the other four (28, 30, 31, 33) were striped but known to be carrying blotched. Lined is therefore dominant to both striped and blotched as previously stated. The results thus far obtained do not demonstrate the allelomorphism of the three types of banding. In order to do that it would be necessary to cross one of the offspring carrying striped (B′B) to blotched cats (bb). All kittens should be lined (B′b) or striped (Bb). If blotched occurred it would demonstrate that two loci were involved, Ll and Ss. Blotched would then be ll.ss, and the nomenclature would have to be changed.

The production of orange and tortoiseshell lined cats is of interest. They are as expected in every way comparable to other oranges and tortoiseshells except for the narrower bands.

Results in regard to ticking may now be considered. In the previous paper a was used to denote lack of ticking; A, little-ticked or dark tabby; and A', much-ticked or light tabby. It now appears that there are two hereditary grades of ticking previously grouped under A' between which there is a fairly wide difference. Comparison of kittens at birth or of adult cats makes the distinction clear. During growth intergradations appear for ticking increases with age as in rodents. A' should therefore be divided into A^e, extreme-ticking, and A^m, much-ticking. Fully as much difference exists between A^e and A^m as between A^m and A.

A blotched male (11) crossed (14) with a black female (15) sired four blotched kittens, and a blotched female (14) crossed (31) with a lined little-ticked male (18) produced one lined and three blotched offspring. The two blotched cats (11 and 14) were extremely-ticked, A^e, as were also the eight kittens. A much-ticked, A^m, Caffer female (19) when crossed (19) to the little-ticked, A, Caffer male (18) produced one much-ticked (21) and three little-ticked. The much-ticked mother (19) and son (21) are very similar and contrast strongly with the extremely-ticked cats mentioned as well as with little-ticked. With the exception of five kittens, the offspring of the much-ticked male (21) are useless for determining degree of ticking on account of the presence of yellow. Three kittens (58.2, 54.3, and 54.4) are little-ticked like their grandfather (18). Two kittens (54.1, 54.2) were much-ticked like their father and grandmother. The mothers of all of these kittens were non-ticked. The same degrees of ticking, A^m and A, have been possessed by three generations.

Skins illustrating the three types of ticking A^c, A^m, and A are preserved for reference.

The crosses summarized in the preceding paper and above may now be considered from the point of view of white-spotting. Solid-white acts as a complete dominant to other colors as shown in the previous paper. White-spotting as seen among cats in general grades all the way from solid-white to self. In individual fraternities, however, it may show wide and clean segregation as the crosses below demonstrate. A "self" cat may have a *minute* white spot on breast of belly or a few sparsely scattered white hairs. In this case it might be called near-self. Restricted spotting denotes white on nose, breast, belly, or feet. It segregates widely from near-self in the crosses here considered, but grades into moderate spotting, which denotes the further extension of white to sides of body as well. Moderate spotting in turn grades into considerable, which denotes more white than color. Extreme spotting denotes that pigment is limited to small spots on head, back, or tail.

Crosses involving only self, restricted and moderate spotting, and solid-white may be considered first.

A self male (18) crossed (19, 31) to two self females (19, 14) sired eight self. One of these self offspring (21) crossed (55) to a self female (33) sired five self. Self *may* therefore breed true.

The first mentioned self male (18) crossed (28, 29) with two restricted spot females (10, 2) sired three self and four restricted spot. The other self male (21) crossed (54, 56) to two restricted spot females (28, 13) sired five self and five restricted spot. A restricted spot male (8) crossed twice (9, 30) to a self female (20) sired three self and seven restricted spot. A restricted spot female (3) crossed (16) to a self male (6) produced six self. Self by restricted spot therefore has produced seventeen self and sixteen restricted spot, the expectation if restricted spot is heterozygous.

The restricted spot male (8) crossed (12, 33) to two restricted spot females (25, 3) sired one self, three restricted, and one moderate. This is in line with expectation if spotting is dominant, the moderate in this case possibly representing the homozygote.

The same restricted spot male (8) crossed (32) to a solid-white (22) sired two solid-white and two completely self. This is in line with the assumption that the white female was homozygous for self, ss, and heterozygous for color, Ww, or that spotting and white are both allelomorphic with self and that she was carrying self. The male would then be w^1w, w^1 standing for restricted or moderate spotting.

Crosses involving greater amounts of spotting may now be considered.

The self male (21) crossed (52) to a considerable spot female (31) sired one self and two considerable. When crossed (58) to a moderate spot (30) he sired three self and two considerable. These results show that considerable segregates from self and that a greater degree of spotting may be produced from a less by crossing to self. Modifiers are indicated.

The same male was also crossed (57) to a considerable (34) and sired two restricted. In this case modifiers may have been assorted to produce restriction, but the female (34) was derived from a cross (34) of a considerable (24) by a restricted (3) each of which was known to carry self. She may therefore have been of composition w^mw^1; w^m, much spotting, being derived from her considerable parent and w^1, little spotting, from her restricted parent. She could then produce restricted offspring, w^1w, when crossed to self.

Offspring of self by spotted known to carry self are therefore twenty-one self and twenty spotted.

The considerable spot male (24) was crossed to various spotted females known by these or other crosses to produce self. With a restricted (3) he sired (34, 49) two self, one restricted, three moderate, and three considerable. With a moderate (32) he sired (53) two self, one restricted, one moderate and one extreme. With a restricted (28) he sired (44) one self, one restricted, one moderate, and one considerable. With a moderate (30) he sired (45) two considerable and one extreme. With a restricted (13) he sired (47) two self, two considerable (one of which graded toward extreme), and one very extreme. This last cross is interesting for the offspring vary far in both directions from the parental types.

Crosses of spotted by spotted when both carry self have produced twenty-three spotted to eight self which is very close to the three-to-one expectation.

The considerable spot male (24) above mentioned when crossed (41, 46, 50, 51) to his considerable spot mother (23) sired five considerable and two restricted, the segregation being striking through failure of any moderates to appear. This is in line with the supposition that the mother (23) was carrying little spotting and was therefore of composition w^mw^1. The cross might therefore be $w^mw \times w^mw^1 = 5(w^mw^m, w^mw \text{ or } w^mw^1) + 2(w^1w)$.

The same male (24) (w^mw) was crossed (48) to a solid-white half sister (29) from the same mother (23) (w^mw^1) by a white male (W?). There were produced two extreme spot. The white female (29) may therefore have been Ww^m and the extreme spot offspring w^mw^m.

The failure of anything higher than restricted spotting to occur among the offspring of restricted by self, although cats with considerable may carry self, indicates that there may be allelomorphic factors determining different degrees of spotting. In any case it appears that self is recessive to spotting and that color is recessive to solid-white. The principle is suggested that there is a quadruple allelomorphic series:—W, solid-white; w^m, much spotted; w^1, little spotted; and w, self, with dominance in the degree of decreasing pigmentation. Crosses of white to self and of spotted to self would be of value in checking this principle. Any one white cat might throw besides white *either* much spotted, little spotted, *or* self; a much spotted might throw besides much, *either* little *or* self, and little should throw little or little and self. If three distinct types were produced from any one white or spotted cat crossed to numerous self cats, this would demonstrate modifiers of considerable importance or disprove the hypothesis of allelomorphism suggested.

Attention should be called to an interesting but unexplained relation that exists between yellow- and white-spotting. "Self" tortoiseshells have yellow hairs closely intermixed with non-yellow. This makes it very difficult to determine degree of ticking in such animals. Tortoiseshells with restricted white-spotting tend to have yellow separated into patches, while further extension of white separates yellow and non-yellow areas still more. Separation of yellow into patches appears not to be correlated with amount of yellow.

GENERAL SUMMARY OF INHERITANCE OF COAT-COLOR IN CATS

It may be of interest to summarize very briefly the genetic data thus far collected on coat-color in cats. Ratios are not significant since fraternities from homozygous dominants and heterozygotes are included together.

Maltese dilution, m, is presumably a simple recessive to intensity, M. Intense by intense have produced 41 intense. Intense by dilute have produced 37 intense and 23 dilute. Dilute by dilute have produced 18 dilute.

Solid-white, W, evidently acts as a simple dominant over color, *w*. It is true-breeding in the hands of fanciers. White by color (amount of white-spotting undetermined) have produced 3 white and 4 colored (one near-self). Table I shows summaries for white and white-spotting of determined degree. It is obvious that although extensively pigmented animals appear among the offspring of cats showing much white there is little tendency for a kitten to show more white than appears in either parent.

TABLE I

Parents.	Offspring					
	Solid White, *W*	Extreme Spotting, *E*	Considerable Spotting, *C*	Moderate Spotting *M*	Restricted Spotting, *R*	Self or Near-Self, *S*
W×W	3					1
W×C	1	2				
W×R	7					2
C×C			5		2	
C×M		2	2	1	1	2
C×R		1	6	4	2	5
R×R				1	3	1
Spotted×spotted		3	13	6	8	8
C×S			2		2	1
M×S			2			3
R×S					16	17
Spotted× self			4		18	21
S×S						13

Table II gives a summary of the results thus far col-

TABLE II

Parents	Offspring					
	Black		Yellow		Tortoiseshell	
	♂	♀	♂	♀	♂	♀
Yellow ♂ × black ♀ Doncaster	51	*13*			*1*	51
Whiting	16					17
Total	67	*13*			*1*	68
Black ♂ × yellow ♀ Doncaster			20			16
Whiting			5			3
Total			25			19
Yellow ♂ × tortoiseshell ♀ Doncaster	45	*6*	58	53	*1*	45
Whiting	3		3	4		4
Total	48	*6*	61	57	*1*	49
Black ♂ × tortoiseshell ♀ Doncaster	32	15	37		*1*	21
Whiting	3	3	7			4
Total	35	18	44		*1*	25
Yellow ♂ × yellow ♀ Doncaster			48	40		*3* from one pair
Yellow ♂ × yellow ♀ no. 23	*3*		1	4		*1*
Black ♂ × yellow ♀ no. 23	*2*	*1*	2			2

lected in reference to the inheritance of yellow. Doncaster's[2] summaries from fancy breeders and from Little's data are given, kittens of undetermined sex being omitted. The three tortoiseshell females from one pair of Doncaster's yellow by yellow may be readily explained if it be supposed that the mother was an extreme yellow variant of the heterozygote *Yy*, comparable with my cream female number 23. Anomalous black females may be similarly heterozygous. Anomalous blacks and tortoiseshells are to be expected from anomalous yellow females. Anomalous offspring are recorded in italics in Table II.

As regards banding, certain creams and blacks could not be classified and are consequently omitted from the summaries. Lined by lined have given 2 lined and 2 blotched. Lined by striped have given 17 lined and 2 striped. Lined by blotched have given 12 lined and 4 blotched. Striped by blotched have given 19 striped and 8 blotched. Blotched by blotched have given 4 blotched.

As regards ticking, it is necessary to omit all yellows and many tortoiseshells, as well as some with much white. Extremely-ticked by little-ticked have given 4 extremely-ticked. Extremely-ticked by black have given 4 extremely-ticked. Much-ticked by little-ticked have given 1 much-ticked and 3 little-ticked. Much-ticked by black have given 2 much-ticked and 3 little-ticked. Little-ticked by little-ticked have given 5 little-ticked and 1 black. Little-ticked by black have given 7 little-ticked.

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[2] Doncaster, L., "On Sex-limited Inheritance in Cats, and Its Bearing on the Sex-limited Transmission of Certain Human Abnormalities," *Journal of Genetics*, June, 1913.

SOME HABITAT RESPONSES OF THE LARGE WATER-STRIDER, GERRIS REMIGIS SAY. II

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IV. Description of and Experiments in Connection with Brook Habitat at Syracuse

1. Description of Habitat.—Some further experimental work, much like that which previously has been considered, was done near a small, rapid stream (Figs. 4, 5), approximately 4.5 miles southwest of Syracuse, New York, in the late summer of 1918. The stream flows in an easterly direction, into Onondaga Creek, its source being a spring in the hills, forming the western side of Onondaga Valley. Water-striders, *Gerris remigis,* are common in certain situations on the surface of this brook (Figs. 4, 5). The water in the stream is clear, and its channel contains silt, gravel, small and large rocks. There is little rooted aquatic vegetation growing along the greater part of its course. At certain places the current is quite rapid, but even at those points where it is swiftest, there are small areas of quieter water, protected by rocks, or points of land jutting out into the stream. In such situations (Fig. 4) are found water-striders, singly and in small groups of two, three, or four individuals. Occasionally there is a short reach of quieter water, sometimes protected by trees (Fig. 5), on the surface of which water-striders are found in small numbers. Near the headwaters there is a large pool, formed mainly by an artificial dam, and this is separated into two parts by the decaying trunk of a large fallen tree. *Chara* grows rankly and in great mats in the pool. On its surface water-striders live in large numbers (Fig.

6). At this place, I have captured gerrids by the hundreds. I have examined this pool and the immediate vicinity for two successive seasons and I am convinced that they breed here from year to year. They undoubtedly hibernate, in large numbers, along the shores of this pool. In fact I have found a few of them hibernating in interstices where the shore slightly overhangs the water, and also among dead leaves and other vegetation at points from a few inches to three yards away from the pool (Fig. 6).

FIG. 4. Detail of small, rapid brook near Syracuse, showing spring conditions (May). Arrow indicates direction of current. *a*, areas of quieter water, formed by points of land, jutting out into the stream. Water-striders, *Gerris remigis*, are found, in small numbers, in such situations. (Original. Whitney.)

2. *Methods.*—The experiments were performed on the shore of the pool, which is a large one for such a small brook. The dimensions of this body of water are approximately 55 × 17 × 2.5 feet. The shore, where the experimental work was done, is flat and its surface is only a few inches higher than that of the water (Fig. 6). Back of this flat area, a little more than three yards away from the pool, there is a hill with a moderate slope. Only those experiments will be considered here that were carried far enough to evince fairly definite results. The water-striders used in these experiments were taken directly from the surface of the pool. Different individuals were used in each experiment. All these experi-

ments were carried on at Syracuse in the afternoon, at which time there was considerable reflection of the rays of the sun from the surface of the water.

3. Responses When Facing Away from Pool.—The first set of experiments deals with gerrids that were placed on the ground one yard away from the margin of the water. The heads of the gerrids were pointed directly away from the pool. In general, the responses of the water-striders, in those experiments performed under like conditions, showed much similarity. Therefore, I give a condensed account of several typical experiments.

Fig. 5. Detail of small, rapid brook near Syracuse, showing spring conditions (May). *a*, reach of quieter water, protected by trees; water-striders, *Gerris remigis*, are found in small numbers in such situations. (Original. Whitney.)

Experiment VI.—The water-strider is placed on the ground. It immediately turns and faces the pool, and at once begins to jump toward the water. While the gerrid does not turn away from the pool, it jumps toward it slowly. Thirty seconds after being placed on the ground, the insect is back on the surface of the pool.

Experiment VII.—After being placed on the ground, the gerrid turns toward the pool, and jumps in the direction of the water for a distance of one foot. During one of the jumps, the body is so oriented that the head is turned away from the pool. The water-strider continues to jump, but is now moving away from the water. It proceeds in the same direction until it reaches a point four yards away from the pool and part way up the side of the slope. This gerrid is observed for ten minutes and is still jumping away from the water.

Experiment VIII.—This water-strider jumps away from the water for a distance of five inches. It now turns directly to the right, which position places the long axis of the body parallel with the margin of the pool. I am not sure whether this turn is due to the body striking against some object during a jump, or whether the water-strider makes the turn as a result of some other stimulus. The gerrid jumps and walks parallel with the margin of the pool for a distance of two yards. In a few seconds it turns a little more to the right, so that it is now jumping obliquely toward the water. The insect continues to move in the same direction until it reaches the pool. This gerrid is back on the surface-film of the water in twenty-five seconds after the experiment began.

FIG. 6. Detail of large pool at headwaters of small, rapid brook near Syracuse, showing spring conditions (May). *Chara* grows in great abundance in this pool. *a*, surface of pool on which water-striders, *Gerris remigis*, are found in large numbers; *b*, vegetation and dead leaves among which water-striders hibernate; *c*, overhanging shore of pool in interstices of which water-striders hibernate; *d*, shore of pool where experiments were performed; *e*, artificial dam built of concrete. (Original. Whitney.)

Experiment IX.—The water-strider is placed on the ground and it immediately turns to the left, thus placing the long axis of the body parallel with the margin of the pool. The creature jumps straight ahead for a few inches, and then turns obliquely toward the water. It moves along rapidly and soon attains the surface-film. This gerrid reaches the pool in twenty-five seconds from the time it first was placed on the ground.

Experiment X.—This water-strider at once turns in such a manner that the longitudinal axis of the body is placed parallel with the margin of the pool. The gerrid walks for five inches in a path parallel with the shore of the pool. It now turns so that its head points away from the water, and jumps in that direction for two feet. The insect again turns, this time the head being directed toward the water, but it walks in that direction for two inches only. It turns to the left, thus again placing the body parallel with the margin of the pool. The gerrid jumps straight ahead for four feet, and again turns directly toward the water, jumping rapidly along a practically straight path until it reaches the pool. The creature is back again on the surface of the pool in forty seconds after the experiment began. This water-strider was active from the time it was placed on the ground until it reached the water.

Experiment XI.—The gerrid walks away from the water for a distance of two inches. It then turns to the left and jumps along a path parallel with the margin of the water for four inches. The insect now makes a turn of ninety degrees, so that its head is directed toward the pool, and jumps rapidly to the water. In fourteen seconds after being placed on the ground, the gerrid is striding back and forth on the surface of the pool.

In these experiments I have condensed the statements in such a manner as to give prominence to the factors of time and direction. With reference to these particular elements, the experiments are typical of many others recorded in my field notes. It is evident that a large majority of the gerrids get back safely to the water, only one out of the six failing to do so. This was the individual used in Experiment VII. A large number of experiments furnish similar results. Although there were a number of random and trial movements, the water-striders returned to the pool with a fair degree of promptness. The total amount of time consumed by all the gerrids was 12 minutes and 14 seconds. The average time taken to reach the water was 2 minutes and 2⅓ seconds. Omitting Experiment VII, the total amount of time necessary for all the gerrids to get back into the pool was 2 minutes and 14 seconds. With this experiment omitted, the average time consumed in reaching the water was 26⅘ seconds. These results are indicated in Table I. The results of two other sets of experiments are indicated in Table II and Table III. Attention is directed to the similarity in the records of the three series of experiments as expressed in the tables.

TABLE I

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Away from Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
VI	0	30	+	..
VII	10	0	..	—
VIII	0	25	+	..
IX	0	25	+	..
X	0	40	+	..
XI	0	14	+	..
Totals 6	12	14	5	1
Averages	2	$2\frac{1}{3}$	$0\frac{5}{6}$	$0\frac{1}{6}$
Totals, omitting experiment VII	2	14	5	0
Averages, omitting experiment VII	0	$26\frac{4}{5}$	1	0

TABLE II

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Away from Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
XVIII	0	18	+	..
XIX	0	20	+	..
XX	0	25	+	..
XXI	0	28	+	..
XXII	0	35	+	..
XXIII	1	0	+	..
Totals 6	3	6	6	..
Averages	0	31	1	..

4. *Responses When Facing Pool.*—A condensed statement will be given now of experiments in which the heads of the water-striders were turned toward the pool. As before, the gerrids were placed one yard away from the water. Special attention again was directed to the factors of time and direction.

Experiment XXX.—The water-strider jumps three inches directly toward the water. It then turns to the right, jumping parallel with the margin of the pool for one foot. The gerrid again turns slightly to the right, being now in a position oblique to the pool, and continues jumping away from the water for two feet. The insect turns to the left, so that its head points obliquely toward the pool, and jumps in a

TABLE III

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Away from Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
XXIV	0	20	+	..
XXV	0	30	+	..
XXVI	15	25	..	—
XXVII	0	32	+	..
XXVIII	0	50	+	..
XXIX	0	18	+	..
Totals 6	17	55	5	1
Averages	2	$55\frac{5}{12}$	$0\frac{5}{6}$	$0\frac{1}{6}$
Totals, omitting experiment XXVI	2	30	5	0
Averages, omitting experiment XXVI	0	30	1	0

straight path until it reaches the water. This water-strider consumed twenty-five seconds in making the journey to the pool.

Experiment XXXI.—This gerrid jumps in a zigzag course toward the water, arriving on the surface-film of the pool in ten seconds from the time it was first placed on the ground.

Experiment XXXII.—The water-strider moves toward the pool, jumping in a direction slightly oblique to its margin and gaining the water-film in twelve seconds.

Experiment XXXIII.—The path taken at first, by this water-strider, is toward the pool, but after jumping for a distance of four inches in that direction, it turns obliquely to the right, still jumping toward the water. The gerrid is back on the surface of the pool in eleven seconds from the time it was placed on the ground.

Experiment XXXIV.—This hemipteron takes a position so that the body is slightly oblique with reference to the margin of the pool. The gerrid jumps along a straight path toward the water for two feet. It now turns so that the long axis of the body is parallel with the margin of the pool. It jumps straight ahead for one yard, when it turns toward the water, arriving at the pool in ninety seconds.

Experiment XXXV.—This gerrid turns to the right, as soon as it is placed on the ground, and jumps for a distance of two feet in a direction parallel with the margin of the pool. It then makes a turn of ninety degrees to the left, thus pointing its head directly toward the water. The creature jumps in this direction until it reaches the pool, twelve seconds after the experiment began.

The results evinced in these experiments are typical of the results obtained in many others not recorded here, except a few which are indicated by tables. It is noticed that the water-striders reached the pool much more promptly than was the case when they were placed on the ground with their heads directed away from the water. All the gerrids reached the water—as was generally the case in many other experiments of a similar character—with but a limited number of random movements. The only prominent exception to this was the gerrid used in Experiment XXXIV. Usually, there were one or two individuals that displayed this lack of promptness. All the gerrids employed in the six experiments consumed a total amount of time of 2 minutes and 40 seconds. The average amount of time necessary to return to the pool was 26⅔ seconds. If Experiment XXXIV should be omitted, it is evident that the total amount of time consumed by five water-striders in reaching the pool was 1 minute and 10 seconds. The omission of this experiment reduces the average time, consumed in reaching the water, to fourteen seconds. These results are shown in Table IV. The results of other experiments of a similar character are indicated in Table V and Table VI.

TABLE IV

Time Consumed by Water-Striders in Reaching Water from Distance of 1 Yard

Experiments				
Heads Directed Toward Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
XXX	0	25	+	..
XXXI	0	10	+	..
XXXII	0	12	+	..
XXXIII	0	11	+	..
XXXIV	0	90	+	..
XXXV	0	12	+	..
Totals 6	2	40	6	..
Averages	0	26⅔	1	..
Totals, omitting experiment XXXIV	1	10	5	..
Averages, omitting experiment XXXIV	0	14	1	..

5. *Responses When Parallel With Pool.*—Some experiments were performed with water-striders having the long axis of the body parallel with the margin of the pool. In all other respects, the conditions were similar

TABLE V

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Toward Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
XXXVI	0	20	+	..
XXXVII	0	15	+	..
XXXVIII	0	17	+	..
XXXIX	0	22	+	..
XL	0	20	+	..
XLI	0	18	+	..
Totals 6	1	52	6	..
Averages	0	$18\frac{2}{3}$	1	..

TABLE VI

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Toward Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
LI	0	13	+	..
LII	0	17	+	..
LIII	0	12	+	..
LIV	0	14	+	..
LV	0	12	+	..
LVI	0	16	+	..
Totals 6	1	24	6	..
Averages	0	14	1	..

to those when the heads were directed toward and when they were directed away from the pool. The results were much like those evinced in Table II, except that the time consumed in reaching the water was slightly greater in the majority of cases. There was a little less promptness, perhaps, in moving toward the water and a greater number of trial directions. Occasionally a gerrid did not reach the pool at all.

6. Responses When Not Oriented with Reference to Pool.—A number of other simple experiments were carried out near the large pool in the brook previously mentioned (Fig. 6). In these the water-striders were not oriented with reference to the position of the pool at the beginning of each experiment. Forty gerrids just captured from the surface-film were put into a small wooden box. This was taken to the place where the other experiments were performed (Fig. 6). It was then inverted and all the water-striders carefully shaken out on to the ground one yard away from the water. It was of course impossible to watch in detail every gerrid, but it was possible to observe how many of the hemipterons reached the water. The majority of them were back on the surface-film within fifteen seconds after being placed on the ground. All but two individuals had reached the water within thirty-five seconds after the experiment began. At the end of one minute of time all the gerrids were on the surface of the pool. Sometimes a water-strider was not successful in reaching the pool. These statements are fairly typical of the results of many other similar experiments.

A series of experiments of a similar character was undertaken in which the gerrids were placed on the ground three yards away from the pool. As in the experiments one yard away from the water, the hemipterons found the surface of the pool with reasonable promptness and directness. The greater number reached the water within forty seconds from the time that they touched the surface of the ground. In the majority of these experiments, all the water-striders were back on the surface of the pool, 2 minutes and 5 seconds later. In each of two different trials, out of a total of six, there were two gerrids that jumped away from the pool and had not reached the water at the time my observations were discontinued. I believe that vision was the chief factor employed in directing the gerrids to the water in the experiments when forty individuals were used at each trial.

I have not yet observed the results of placing the water-striders on the ground in large numbers farther away from the pool than three yards. Nor have I made any trials, either in the vicinity of Urbana or Syracuse, with the gerrids for a greater distance from the water than four yards.

V. Discussion of Observations at White Heath

1. Initial Locomotor Responses.—It is an interesting fact that, just previous to the drying up of the pool, in which the water-striders were living, there were no responses on the part of the gerrids which indicated any attempt to escape from the unfavorable surroundings. Not until the water had disappeared entirely was there any tendency to leave the place. Soon after it became dry the water-striders began to move away from the site of the former pool. What the immediate stimulus was, it is difficult to say. A change in the physiological condition of the body, which might have been induced by the drying up of the pool, would be sufficient to account for the locomotor responses. Whatever the stimulus was, the gerrids began to walk and jump away in different directions. But as Jennings (1906, pp. 284, 285) has pointed out:

> Often . . . movement in a certain direction is due only to the release of inhibition. The organism moves in the given direction because it is moving from internal impulse, and because movement in this direction is not prevented. This possibility must be considered in all cases.

Therefore, it is not always necessary to assume that movement is due to some very recent external stimulation. Whatever the explanation may be, the water-striders moved off in the direction in which their heads were pointed. They continued along the same line of progress until they arrived at some obstacle in their pathway. Such an obstacle might be a lump of dried mud, a stone, or a piece of driftwood. Then they usually turned to the right or left, as the case might be, thus being deflected from their former direction of movement. They continued along the new path until they were deflected again, in a new direction.

2. Rôle of Trial and Error.—Such responses as previously have been described occurred again and again. The various objects in the path of the water-striders served as stimuli to turn the gerrids aside and swerve them in another direction. First they tried one line of progression and then they tried another. As Holmes (1916, pp. 157, 158) has said:

> Where there is "error," the organism tries again, and keeps on doing so until it attains ultimate success.

This statement does not mean that all achieve success, nor does it necessarily mean that the organism possesses any conscious appreciation of means to an end. Certainly, I do not consider that water-striders have such an appreciation. Frequently, on coming in contact with such obstacles, as have been mentioned, the gerrids came to rest with the side or sides of the body closely applied to the object. This was due to their thigmotactic proclivities. They remained in such positions for varying lengths of time and then moved forward again, but usually the direction of progression was changed. Occasionally, they remained motionless in such situations until the time set for me to discontinue my field observations for that particular day. Sometimes individuals crawled under lumps of dried mud, under pieces of driftwood, or among dead leaves. On a few occasions, a few gerrids jumped into large cracks in the baked mud of the stream bed. Water-striders getting into such places, occasionally remained there, but I never have been able to find them the day following the observation.

It already has been stated that some of the gerrids reached the larger pool of water some distance downstream, and attention also has been directed to the fact that on several other occasions, when water-striders had been trapped in stream pools, some of their number were successful in reaching other bodies of water in the immediate vicinity. I have not observed that gerrids ever were succesful in finding another body of water that was situated farther away than fourteen yards. In none of these cases that have come under my observation, have I been able to see that there was any definite response, on the part of the gerrids, to another body of water *per se*. In many instances, the locomotor movements of the water-striders, in so far as their final goal was concerned, have proved to be lacking in definiteness, precision, and in direction of response. Their locomotor movements were very awkward and they stumbled along the route in a very blundering fashion. Their method, if it can be called such, of reaching the water seemed to be entirely one of chance. They might blunder on to a pool of water in the vicinity or they might not. They frequently took the wrong direction and made many mistakes. A better way, perhaps, to express my thought, is to state that these gerrids pass from the site of a former pool to another body of water by a blundering method of trial and error. As Holmes (1916, p. 158) well has said:

> The method is round about and expensive, but it is better than nothing. It is Nature's way of blundering into success.

It is not improbable that the method of trial and error forms a large part of the habitat responses of arthropods. It is certainly true that a number of writers have been impressed with the prevalence of behavior of such a character among the members of this group. Among others, this is evident from the work of Bohn (1903) in connection with hermit crabs. Holmes (1905, p. 106) in describing the behavior of the blow-fly larva, with reference to light, makes the following statement:

> It may be said to be a form of the trial and error method minus the element of learning by experience.

Writing of the trial and error method in the conduct of lower animals, Holmes (1905, p. 108) states that:

> The lives of most insects, crustaceans, . . . and hosts of lower invertebrate forms, . . . show an amount of busy exploration that in many cases far exceeds that made by any higher animal.

In this connection the following general statements are of great interest, as they show the importance that is now attached to such a method of conduct among invertebrates: Holmes (1905, pp. 107, 108) points out that:

> The rôle played by the trial and error method in the behavior of the lower organisms has, as yet, elicited but little comment, owing probably to the fact that attention has been centered more upon other features of their behavior. It may have been considered by some investigators as

too obvious for remark since any one who attentively observes the conduct of almost any of the lower animals for ten minutes can scarcely fail to see the method exemplified.

Jennings (1906, pp. 246, 247), also, directs attention to this form of behavior in the following words:

> In most if not all other invertebrates there occur many "trial movements" similar to those already described. In many recent accounts of the behavior of other invertebrates little mention, it is true, will be found of such movements. This is apparently because attention has been directed by current theories to other features of the behavior, and the trial movements have been considered of no consequence. Often an attentive reading of papers on "tropisms," etc., will reveal parenthetical mention of various "disordered" movements, turnings to one side and the other, and other irregularities, which disturb the even tenor of the "tropism," and are looked upon for some reason as without significance and not requiring explanation. Further, one often finds in such papers accounts of movements which are clearly of the "trial" character, yet are not recognized as such by the author, on the watch only for "tropisms." In the earlier literature of animal behavior, before the prevalence of the recent hard-and-fast theories, one finds the trial movements fully recognized and described in detail. . . .
>
> Unprejudiced observation of most invertebrates will show that they perform many movements which have no fixed relation to sources of external stimuli, but which do serve to test the surroundings and thus to guide the animal. . . . As Holmes (1905) has recently pointed out, in a most excellent paper, this is really a matter of common observation on all sorts of animals. The fact that such movements are not emphasized by writers on animal behavior is evidently due to their being considered without significance.
>
> In a number of recent papers the importance of trial movements in behavior has been more explicitly recognized. . . .

I have made a statement about a final goal, but I do not intend to convey the idea, in any way, that these insects are endowed with even the smallest amount of prevision, nor do I wish to be understood as assuming that because of certain perception, on the part of the water-striders, of the exigencies of the case, they therefore responded with a special form of behavior suitable to meet the difficulties of the situation. But, on the other hand, I wish to present the thought that these gerrids, in moving away from their former haunts, may or may not come upon another body of water, if there is one in the vicinity, and that this happens not because of any direct or definite response or responses to the body of water *per se,* but rather is due more to the fact that many of their locomotor responses are spontaneous ones, modified frequently as to direction and speed, mainly, by contact stimulus, many of these movements probably being due not to some very recent stimulus or stimuli which have any direct relation to the body of water, but that they, more probably, are due, as Jennings (1906, p. 285) suggests,

> to the simple outflow of the stored-up energy of the organism through the channels provided by its structure.

3. *Rôle of Moisture.*—Undoubtedly it is true that water-striders, *Gerris remigis,* are sensitive and responsive to moisture. The fact that the greater portion of their lives is passed on the surface-film of brooks and streams would seem to be sufficiently indicative of this. Then, also, the ability to find their way back to the stream in the spring, having left it in the fall, frequently from distances of three and four yards, and sometimes from greater distances, after passing several months in hibernation, is further indication that they are sensitive to some stimulus or stimuli, the response to which results in bringing them back to the water.

That the migration of these gerrids from the site of a former pool to another body of water is mainly an expression of hydrotropism, according to the manner in which that form of response is usually interpreted, I believe to be extremely doubtful. However, it is not my intention to assert that moisture does not play an important rôle in the economy of these water-striders. But I do not believe that the movements of the gerrids in the dry bed of the brook afford any definite indication that they are direct responses to moisture. It is very improbable that, during severe droughts and high temperatures, moisture, diffusing through the atmosphere, from such comparatively small bodies of water (dimensions 3 yds. × 2 yds. × 5 in. and in several instances smaller than this) as already have been indicated, impinged on the bodies of the hemipterons in any manner that would be effective in producing definite responses to the source of this moisture, as for example positive responses, resulting in the water-striders wandering toward the pool. This is the more improbable when it is recalled that the gerrids were ten yards away from the water, and in other instances, not recorded in detail in this paper, they were even farther away than this, eleven, twelve and fourteen yards distant. I also have observed their responses in the dry bed of a stream, when there were pools of water at a less distance than ten yards apart.

In this connection it may be of interest to quote a statement from Weiss (1914, p. 33):

> Wingless forms of *Gerris marginatus,* which is quite common throughout New Jersey, when removed from a pond containing some three thousand square feet of water and liberated at distances of one, two, three, four, five, six, seven, eight, and nine yards from the water, immediately made their way back to the water without hesitancy. Of course their movements, which consisted of a series of jumps, were more or less clumsy, but all started in the right direction even though purposely headed the wrong way.
>
> When liberated at a distance of ten yards, they had some slight trouble in getting their bearings, but after making several false starts, finally wound up by going in the direction of the water. At a distance of fifteen yards, a longer time and more moving around were required before the right direction was located. At thirty and forty yards away, they seemed to lose their bearings completely and moved aimlessly about in all directions. Even at the end of an hour they were no nearer the water.

The observations of Weiss were of responses of water-striders under experimental conditions and not observations of their responses under the natural conditions of their own environment undisturbed by any extraneous stimulus, as was the case of my observations. However, it is pertinent to direct attention to certain facts in connection with his experiments. It is evident that the responses of *Gerris marginatus,* especially those individuals that were placed on the ground seven, eight, and nine yards away from the water, differ from those of *Gerris remigis.* Members of this species do not make their way to water, from such distances, with the promptness and definiteness recorded in the experiments of Weiss with individuals of *Gerris marginatus.* I infer from the little description recorded, that the responses of individuals of the same species, when placed on the ground ten yards away from the water, were more of the character of those of *Gerris remigis* at such a distance from a pool of water. While I have not observed gerrids of this species make their way to a body of water quite so far away as fifteen yards distant, as did Weiss in some of his experiments with *Gerris marginatus,* yet I am not prepared to state that they can not do so. However, if they are able to find water at such a distance, I believe that the achievement is one purely of chance, or the result of a blundering sort of trial and error. On one occasion, I observed individuals of *Gerris remigis* leave the site of a former pool in the bed of a stream and although I watched them for an entire afternoon, only one, out of a group of thirty, had reached an isolated pool fourteen yards distant, when I discontinued my observations at dusk. On another occasion, six water-striders only, out of a group of forty individuals, were successful in finding a body of water fourteen yards from the site of the pool in which they formerly had lived. I would expect, from my own observations of *Gerris remigis,* the responses of apterous *Gerris marginatus,* at distances of thirty and forty yards, to be much as described by Weiss, although I have recorded no observations of the responses of gerrids at such distances from water.

I believe that alate individuals of *Gerris marginatus,* during migration by flight, find bodies of water mainly through the sense of vision, as is probably true in the case of many different species of aquatic Hemiptera, a subject to which Kirkaldy (1899, p. 110) and other writers have directed attention. Recent work on phototaxis—(Holmes, 1905a), (Holmes, 1907, pp. 160, 161), (Cole, 1907, pp. 382–388), (Essenberg, 1915, p. 400), and (Riley, MS.)—has demonstrated that many species of aquatic bugs respond positively to light. *Benacus* and *Belostoma* respond to light during migration. In the fall of 1908, at

Mankato, Minnesota, a few hundred yards from a large swamp, near the confines of the city, I observed them for several nights, as they flew in great swarms, around the globes of the street arc lights. On the ground, within a radius of thirty to fifty feet of certain of the lights, were thousands of these aquatic bugs, both alive and dead. On several occasions, it was possible, in thirty minutes of time, to fill a half bushel measure with the insects. In the fall of 1915, at Milwaukee, Wisconsin, in the vicinity of Lake Park, between the Milwaukee River and the west shore of Lake Michigan, I observed several occurrences similar to those just described. In these instances, the aquatic bugs were not present in quite such large numbers as in the former cases. The point of importance here is, of course, the fact that members of the two groups, *Benacus* and *Belostoma,* respond positively to light during migration. Comstock and Comstock (1895, p. 132) refer to somewhat similar responses. All these facts add still more emphasis to the probability that alate gerrids, when migrating, locate streams and standing water by means of vision. It should be recalled that such bodies of water are effective reflecting surfaces. However, it is quite possible that both alate and apterous individuals of *Gerris marginatus* are responsive to moisture at greater distances than is the case with apterous members of *Gerris remigis.* If this should prove to be the case, it would be of assistance to the gerrids in finding bodies of water. Further, it must be recalled that the pond to which Weiss directs attention covered an area of 3,000 square feet, while the pools of water to which I refer were very small in size.

It is probably true that many arthropods respond readily to moisture. But there is not a great deal of experimental evidence recorded in the literature, treating of the behavior of members of the group, that presents definite information bearing on the particular phase of the subject under discussion. The experimental work that proved to be most nearly related to the form of behavior under consideration was found in a paper by Drzewina (1908) on the hydrotropism of crabs, *Carcinus mænas*. Because of the character of this work, I shall refer to it and quote from it at some length. This writer makes a careful analysis of the responses of these crustaceans to the sea. She noticed that when one of the crabs was placed on the beach that it oriented itself and moved toward the sea, even at a distance of 100 meters. Her statement (1908, pp. 1009–1010) follows:

> Parmi les réactions du *Carcinus maenas* que j'ai eu l'occasion d'étudier pendant mon séjour au laboratoire maritime de Tatihou et à la station biologique d'Arcachon, une des plus frappantes est l'orientation du Crabe dans son habitat naturel. C'est un fait d'observation banal qu'un *Carcinus* déposé sur la plage se dirige aussitôt du côté de la mer, celle-ci pouvant être distante de plus de 100 mètres. Il m'a paru intéressant de déterminer les facteurs qui influencent cette orientation particulière.

Her observations seem to prove that both orientation to and direction of movement toward the sea were not due to responses to light, to the sight of the sea, to the wind, or to gravity, but on the other hand were due to the moisture given off by the sea. Observations were made every day for more than a month, at different times of the day, both in bright sunlight and also in cloudy weather. These facts are brought out in the following quotation (1908, p. 1010):

> J'ai pu montrer que ni la lumière, ni la "vue" de la mer, ni la direction du vent n'interviennent dans ce phénomène. J'ai fait des expériences, et j'ai obtenu des résultats identiques, aux différentes heures de la matinée et de l'après-midi, avec un soleil vif ou sous un ceil couvert; les *Carcinus* dont les yeux ont été noircis ou sectionnés se comportaient à ce point de vue comme des Crabes normaux. Comme mes expériences ont été faites tous les jours pendant plus d'un mois, j'ai eu le vent venant soit de la terre, soit de la mer, soufflant dans diverses directions, vent très fort, ou faible, ou nul, ce qui ne modifiait pas sensiblement le sens de l'orientation des animaux; bien entendu, quand se vent était fort, il pouvait accélérer ou arrêter les mouvements des Crabes.
>
> En ce qui concerne l'inclinaison de la plage, celle-ci exerce bien une influence sur les mouvements du *Carcinus*, qui, souvent, se laisse entraîner par elle et suit, dans la descente, la ligne de la plus grande pente; mais ce n'est pas elle qui le guide dans son orientation par rap-

> port à la mer. J'ai pu en effet montrer, en faisant marcher des Crabes sur des pentes creusées artificiellement et diversement inclinées, que ces animaux peuvent tout aussi bien descendre que monter les pentes dans leur "fuite" vers la mer.
>
> Après avoir éliminé successivement divers facteurs, je me suis arrêtée à cette hypothèse: les Crabes se dirigent du côté de la mer attirés par l'humidité dégagée par celle-ci; il y aurait *hydrotropisme*.

Drzewina noticed the character of the behavior of the crabs after a heavy rain. The peculiarity of this behavior seemed to present additional evidence that the movements of the crustaceans, previously mentioned were responses to the moisture from the sea. At such a time the ground was very moist. Therefore there was no longer a sharp contrast between the land and the sea, with respect to the amount of water vapor given off by each. The crabs did not go directly toward the sea; but some of them moved obliquely to the right and to the left; others followed a zigzag course, parallel to the sea; while still others climbed a slope and proceeded in a direction opposite from the sea. I will record these very interesting observations in her own words (1908, p. 1010):

> Plusieurs faits que j'ai observés viennent á l'appui de cette hypothèse. Après une pluie abondante, le sol étant humide, quand on dépose les Crabes sur da pente sableuse, ils ne se dirigent pas directement vers la mer, comme ils le font d'habitude, mais ils vont d'une façon quelconque: les uns obliquent à droite ou à gauche, d'autres vont en zigzaguant parallèlement à la mer, d'autres enfin remontent la pente, dans le sens opposé à la mer. Il est évident que dans le cas présent, comme il n'y a plus de contraste assez net entre la mer et la terre, celle-ci dégageant également de la vapeur d'eau, l'orientation des Crabes se fait d'une façon de la quelconque.

This observer found that, when a crab was placed in front of a kind of dyke, which at low tide separated two bodies of water, the animal did not respond by moving toward either body of water, but, instead, it took an intermediate direction, and walked toward the dyke. She recorded these facts as follows (1908, pp. 1010, 1011):

> Voici un autre fait intéressant au point de vue de l'hydrotropisme: Je dépose un Crabe en face d'une sorte de digue qui, à mer basse, sépare deux masses d'eau s'éntendant à droite et à gauche. Le Crabe est attiré

> à la fois par l'une et par l'autre; il prend une direction intermediaire et va vers la digue au lieu d'aller vers une des bandes d'eau.

The responses of crabs living in shallow water differed from the responses of those living in deeper water. When the former were placed on the beach, they displayed a very definite hydrotropism, but the latter, under similar experimental conditions, evinced no such definiteness of response. Drzewina considered such responses to be adaptive in character. She seems to infer that the character of the behavior, already acquired, must be taken into consideration in the interpretation of their present responses. These observations are described by her as follows (1908, p. 1011):

> Quand on prend le même Crabe dans divers habitats, on s'aperçoit que son orientation est adaptée aux conditions dans lesquelles il vit et qu'elle correspond aux habitudes qu'il a pu acquérir dans le cours de son développement. Les Crabes de hauts niveaux, ayant à subir de courtes périodes de submersion alternant avec les périodes d'émersion, c'est-à-dire de dessiccation relative, sont très sensibles aux contrastes de l'humidité et de la secheresse et, déposés sur la plage, manifestent un hydrotropisme très net. Mais les *Carcinus* des niveaux plus bas, pris sur fond vaseux se comportent autrement: déposés sur la plage, ils se dispersent dans toutes les directions, devient facilement, et, surtout, se terrent constamment; d'une manière générale ils sont lents, peu sensibles aux contrastes de l'ombre et de la lumière.

4. *Rôle of Vision.*—On the several occasions that I have observed the drying up of isolated stream pools, having on their surfaces trapped *Gerris remigis,* I have watched carefully in order to detect whether the sense of sight was the principal factor in aiding these aquatic bugs to find other bodies of water. The rôle played, directly, by vision, is probably not of immediate importance during their responses in this connection, except in those instances when the ground is flat and level and the gerrids are comparatively close to the water. There are various obstacles that modify the possibilities of such an explanation. If there are two or more bodies of water in the immediate vicinity, it has been observed that the gerrids are just as likely to move toward the farthest one, as they

are to move toward the nearest one. If vision were the main factor in assisting the hemipterons in finding pools of water, they would be expected to go to the nearest one first. Another fact against the idea of vision being the chief influence in guiding these insects to water is that the dry channels of the streams, where I have made my observations, frequently have very rough and uneven surfaces, with small boulders, stones, lumps of baked mud, pieces of driftwood, and clumps of dead leaves scattered along them. When the small size of these insects and the nearness of their eyes to the surface of the ground are both taken into consideration, it becomes very evident that the various objects that have been enumerated must obstruct the view of the water-striders in a very serious fashion. Then again, sometimes the nearest pool was around a bend in the stream, away from the gerrids, thus making it impossible to be seen by them at a distance.

With reference to the experiments of Weiss (1914, p. 33) it is probable that sight was an important factor in directing the gerrids to the water, especially over the shorter distances, one to six yards inclusive. On a bright, sunny day, it is evident that the glistening and reflective qualities of a body of water must be factors of importance in attracting these aquatic hemipterons. It must be recalled that the pond to which Weiss refers was a body of water extending over an area of 3,000 square feet in extent while the pools to which I have referred were proportionately insignificant in size. If there was a gradual slope to the shore of this pond and if the ground, where the experiments of Weiss were performed, had a smooth surface free of obstructions to the view, all this should be in favor of the idea that vision was the important factor in directing the water-striders back again to the pond. However, the local physical conditions are not described.

Certain experiments of Drzewina (1908) are, perhaps, worthy of mention in this general connection. This writer found, in her observations on the hydrotropism of crabs, that these animals responded positively, and with considerable precision, to the moisture given off from the sea. However, in other experiments with crabs she considered that the past life of the crustaceans and the character of the behavior, already acquired, must be taken into consideration, in the interpretation of their present responses. Crabs, living in deep water, among rocks covered with algæ and beaten by the waves, when placed on the sand, in the vicinity of the sea, did not evince definite hydrotropic movements, but, on the other hand, their responses were of a very different character. The factor, in these responses, of importance to the present discussion is that of sight. Vision, apparently, played a prominent rôle in determining the direction of movement of the crabs. Drzewina (1908, p. 1011) has given a rather full statement concerning these facts:

> Les *Carcinus* de la zone basse de *Fucus serratus,* pris à une pointe rocheuse (Gatteville), où ils vivent cramponnés parmi les rochers couverts d'algues et battus par les flots, se comportent encore autrement: lâches sur du sable, au voisinage de la mer, au lieu de descendre vers celle-ci, ils se dirigent immédiatement, en ligne droite, vers des rochers couverts d'algues, ces rochers pouvant etre sitúes a plusieurs mètres de distance latéralement à droite, à gauche, ou à la limite d'eau, ou même dans le sens opposé à la mer. Et ceci, quelle que soit la direction du vent et du soleil. Ces mêmes Crabes, déposés sur du sable clair, légèrement humide, où, par places, se trouvent disséminées des taches sombres de *Fucus,* se dirigent vers ces taches. Jamais je n'ai pu constater, avec ces Crabes, d'orientation directe par rapport à la mer, mais toujours une attraction très prononcée exercée soit par des rochers, soit par des touffes d'algues, par des surfaces d'ombre, en un mot.
>
> Ces quelques faits montrent combien il est important, dans l'interprétation des réactions, de tenir compte du passé de l'animal et des "habitudes" que celui-ci a pu créer. Dans l'hydrotropisme du *Carcinus maenas,* l'intervention des habitudes est des plus manifestes.

(*To be concluded*)

BEHAVIOR AND ASSIMILATION

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I

In a discussion of Liebig's law of the minimum (Hooker, '17), proof was given of the existence of an integrating principle which, as Adams ('18, p. 481) points out, is equivalent to Bancroft's law, so called because Bancroft ('11) was the first to indicate the application of Le Chatelier's theorem to biology. In fact, if it be admitted that organisms are systems in equilibrium, it follows that they obey the theorem of Le Chatelier. Bancroft's formulation of the law is "that a system tends to change so as to minimize an external disturbance." But this statement is so broad that it fails to convey the full significance of the theorem and apparently has led to some confusion. It therefore seems advisable to give a detailed discussion of the theorem of Le Chatelier in its application to biology and more particularly to point out its relation to other biological principles.

"It will be perceived," says Troland ('17, p. 325), "that the demand . . . is not for new biological facts, but for physico-chemical conceptions in terms of which a chaos of biological facts, already at hand, can be explained or systematized."

Findlay ('04, p. 56) defines the theorem of Le Chatelier as follows:

> *If a system in equilibrium is subjected to a constraint by which the equilibrium is shifted, a reaction takes place which opposes the constraint, i. e., one by which its effect is partially annulled.* . . . In all cases, whenever changes in the external condition of a system in equilibrium are produced, processes also occur within the system which tend to counteract the effect of the external changes.

Let us consider, by way of example, a simple case of a system of three phases, namely, ice, water and water-vapor, in equilibrium with respect to temperature and pressure. This system can exist only at 0° C. and at atmospheric pressure. If heat is withdrawn from the system and the pressure and volume are kept constant, a part of the water freezes to ice and the temperature is maintained by the latent heat of fusion. Since the formation of ice would increase the volume and therefore raise the pressure, a certain amount of vapor condenses to water. If heat is added to the system, changes take place in the reverse direction. Similar changes occur when the pressure is altered at constant temperature. In general (Findley, '04, pp. 56, 57), "so long as the three phases are present, no change in the temperature or pressure of the system can occur, but *only changes in the relative amounts of the phases;* that is to say, the effect on the system of change in the external conditions is opposed by the reactions or changes which take place within the system (p. 60). If the specific volumes of the phases are known and the sign of the heat effects which accompany the transformation of one phase into the other, it is possible to predict (by means of the theorem of Le Chatelier) the changes which will be produced in the system by alterations of the pressure and temperature. . . . It should be noted that *all three phases are involved in the change.*"

It is evident that these remarks apply in detail to the behavior of living organisms. The system in equilibrium is the organism. The external condition of the system is the environment. The constraint by which the equilibrium is shifted is the stimulus. The reaction that opposes the constraint and partially annuls its effect is the response of the irritable mechanism.

A stimulus is generally considered to be any change in the relation between the organism and a factor of its environment, but no response occurs unless the change be one by which the equilibrium is shifted, to effect which it must be, (*a*) of a magnitude sufficient to overcome the inertia of the system, that is it must be a liminal stimulus and (*b*) it must relate to a limiting factor of assimilation) cf. Hooker, '17, p. 204). Furthermore, the change in the relation between the organism and a factor of its environment may be produced either by a change in the environment, *i. e.*, it is heterotrophic, or by a change in the organism, *i. e.*, it is autotrophic, or by changes in both.

The response is characterized by the facts that (*a*) its nature and direction are determined by the stimulus but (*b*) the energy is supplied by processes that occur within the system; in other words the stimulus releases the response. Thus in the ice-water-vapor system when heat is withdrawn, this is supplied by the latent heat of fusion of ice. In this simple system there is a direct relation between the amount of heat withdrawn and the amount supplied. Such a relation does not exist in the behavior of organisms, nor should we expect it in such complicated systems. A wealth of examples illustrating the application of the theorem of Le Chatelier to the behavior of plants and animals will be found in Bancroft's article ('17). A brief discussion of the integrating character of development, evolution and biotic succession has been made elsewhere (Hooker, '17) and supplies illustrations of these principles. It will be sufficient to reiterate here that cells, organs and groups of organisms form systems as well as the single organism. Correlations and morphogenic responses are therefore conditioned in accordance with the theorem of Le Chatelier, and it is unnecessary to postulate the existence of hypothetical inhibiting substances to account for the normal behavior of parts.

Inasmuch as the reaction of a system is directed according to the theorem of Le Chatelier, every system in equilibrium is teleological. The means that produce the reaction are directed to a definite end, to overcome the constraint, and the reaction might be said to take place in order that the system may be preserved. This is evidently the source of the "purposefulness," that has occasioned endless biological discussion. The living organism, however, is teleological only to the same extent as the ice-water-vapor system.

These being the facts, the essential problem that confronts us is a study of the physical and chemical aspects of the equilibrium under the influence of a complex of environmental factors. There must exist some degree of correspondence between this equilibrium and the environment. Comparative morphological structure is evidence of this and the same must obtain of chemical composition. The task before us is not so much to ascertain the "function" of any particular substance or element, as to acquire a knowledge of the equilibrium as a whole, for it is only in relation to the other constituents that the function of any one compound can be understood. The need is consequently for a more detailed knowledge of the interrelationships of the chemical constituents and for determinations of how these relationships are altered by changes in the organism itself. This can probably be carried out more readily with plants, but the problem demands more comprehensive analyses than any that have hitherto been made. Investigations with these points in view are now under way and the remarks in this paper will serve as an introduction to them. A knowledge of the conditions governing the change from one phase to another within the organic system is a necessary prerequisite to a more complete understanding of organic equilibria. For the discussion of Le Chatelier's theorem has shown, that in any reaction all the phases are involved, and if the changes, such as the sign of the heat effects, etc., accompanying the transformation of one phase into another are known, it will be possible to predict by means of the theorem of Le Chatelier the effects that will be produced within the system by altering any of its relations with the environment.

Adams ('19, p. 74) says: "Irritability may not be causally explained, but it seems to obey these general laws in the same measure as causal changes.'' A complete description is the only adequate explanation. Although it is impossible to give a complete description of the physical and chemical processes involved in the irritable mechanism, it should be evident that organisms are irritable because they are systems in equilibrium and as such obey the theorem of Le Chatelier.

II

When Adams ('18, p. 474) says, referring to Bancroft's law: ''In other words this is a perpetuating tendency, a method of assimilation, of which reproduction may be considered but a special phase,'' he makes a serious error. That some other principle is involved is hinted at in the following passages (Adams, '18, p. 474, 475):

> In addition to influences which interfere with systems as expressed by Bancroft, there are those which reinforce or accelerate (tend to continue or hasten activity) and do not change its character, but only the intensity of the response (temperature, enzymes, repetition, etc.). By this method also systems tend to be perpetuated and organisms in "favorable" (non-interfering) conditions, tend to continue their normal activities.
>
> Thorndike in summarizing the laws of "acquired behavior or learning" formulates two laws. The first is essentially a statement of Bancroft's law of response to interference (discomfort or satisfaction) and the second (exercise or repetition) is that of reinforcement.

But when Adams ('18, p. 475) states: ''This law appears to be a corollary of Bancroft's law which is concerned with interference or retardation,'' he is dodging the question.

The second principle which Adams calls the law of reinforcement is the basis of assimilation and the related processes of growth, reproduction and inheritance. That the assimilation of an organism may take place, three conditions are essential: (*a*) available materials to construct the organism; (*b*) a supply of energy; and (*c*) the presence of the living organism. There are also certain formal conditions of temperature, pressure, etc., which need not concern us at present. In short, assimilation is an autocatalytic process; because the end products of assimilation act as catalytic agents for their own synthesis. In green plants and the independent bacteria it is also an endothermic process, because the end products of assimilation have a higher energy content than the compounds from which they are constructed. As an illustration of an autocatalytic reaction between inorganic compounds, the formation of Millon's reagent may be cited. When mercury is dissolved in nitric acid, a certain amount of nitrous acid is formed. Nitrous acid is a catalytic agent for the solution of mercury in nitric acid, and therefore for its own production. To quote from Troland ('17, p. 337), who has discussed the theory of autocatalysis:

> The suggestion that the fundamental life-process of *growth* is the expression of an autocatalytic chemical reaction has been made independently by a number of investigators. It will be perceived that on the basis of the foregoing theory of autocatalysis, this suggestion becomes closely allied to the familiar and ancient comparison of vital growth to the growth of the crystal. The customary objection to this comparison, viz., that a crystal grows by accretion whereas protoplasm increases by intussusception, loses its force as soon as we regard living matter as a complex mixture of substances suspended by colloidal subdivision in water, since there is no evidence that the individual colloidal particles do not grow by accretion. On the contrary, it is almost inconceivable that these bodies, which are the real chemical units in protoplasm, should grow in any other way. The growth of a system like a cell could be regarded as the resultant effect of a very large number of component growths, each governed by its specific autocatalytic mechanism. It has been shown by T. B. Robertson that growth curves, with respect to time, actually do coincide in general form with the curve characteristic of an autocatalytic reaction.

In other words, the process of assimilation is like crystallization from a supersaturated solution by seeding with a crystal. The following quotation from Findlay ('04, pp. 67–68) throws light on this process:

> In general, then, we may say that a *new phase will not necessarily be formed immediately the system passes into such a condition that the existence of the phase is possible;* but rather, instead of the system undergoing transformation so as to pass into the more stable condition

> under the existing pressure and temperature, this transformation will be "suspended" or delayed, and the system will become metastable (that is temporarily stable as long as it is not brought in contact with the new phase). Only in the case of the formation of the liquid from the solid phase, in a one-component system, has this reluctance to form a new phase not been observed.
>
> *To ensure the formation of the new phase, it is necessary to have that phase present.* The presence of the solid phase will prevent the supercooling of the liquid.
>
> As to the amount of the new phase required to bring about the transformation of the metastable phase, quantitative measurements have been carried out only in the case of the initiation of crystallization in a supercooled liquid. As the result of these investigations, it was found that, in the case of superfused salol, the very small amount of 1×10^{-1} gm. of the solid phase was sufficient to induce crystallization. Crystallization of the supercooled liquid, however, can be initiated only by a "nucleus" of the same substance in the solid state; . . . it is not brought about by the presence of any chance solid.

The following illustration is of interest in this connection. From a saturated solution of anhydrous sodium sulphate, Na_2SO_4, at 24° C. different compounds may be obtained by seeding with different crystals. If a crystal of the heptahydrate, $Na_2SO_4 \cdot 7H_2O$, is added, this salt crystallizes out; if a crystal of the decahydrate known as Glauber's salt, $Na_2SO_4 \cdot 10H_2O$, is added, Glauber's salt crystallizes out. In this case both the solution and the heptahydrate are metastable. It should be noted that the seeding accomplishes two things: (*a*) it induces crystallization and (*b*) determines the nature of the crystals. Moreover since the crystals produced are hydrates, they represent products of synthesis.

III

Living organisms accordingly perform two processes, behavior and assimilation, and depending on whether the one or the other process is considered, they present fundamentally different aspects. If we make a cross-section (to borrow an expression of E. B. Holt) through the organism in one direction, it appears as a system in equilibrium obeying the theorem of Le Chatelier. If we make a cross-section at right angles, as it were, it appears as part of an autocatalytic reaction. Behavior and assimilation work in different planes. The theory of autocatalysis does not explain all biological enigmas as Troland ('17) intimates, nor does the theorem of Le Chatelier account for assimilation.

However, these planes intersect; the two processes are interrelated in the following four respects.

1. The factors of the environment that constitute the external conditions of the behaving system are the possible limiting factors of assimilation.
2. Assimilation is an endothermic process that supplies the energy expended by the responses of behavior.
3. Behavior overcomes the effects of the limiting factors of assimilation and so places the organism in what is, under the circumstances, the most favorable situation for assimilation.
4. Assimilation and growth eventually change the relations between the organism and the factors of its environment, consequently producing stimuli to behavior.

Behavior is the process by which the organism is able to cope with its environment, it renders its condition as "favorable" as the situation permits, but contributes nothing to its increase. It is the progressive element to which change and variability are due. It is the "guide of life." Assimilation is the autocatalytic process by which the organism increases and multiplies, but which would soon be brought to a standstill according to the law of the minimum, were it not for behavior. It is the conservative element that determines that like shall beget like; it is the principle of heredity. An organism may be defined as a system that perpetuates itself by autocatalysis and reacts according to the theorem of Le Chatelier.

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ON THE USE OF THE SUCKING-FISH FOR CATCHING FISH AND TURTLES: STUDIES IN ECHENEIS OR REMORA, III

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Are These Accounts Credible?

Even with the cumulative evidence of all the foregoing accounts, the matter seems almost incredible. Dr. Eastman, when working up the data for his Reversus paper, wrote Dr. David Starr Jordan, and I also have written him. Dr. Jordan, without having had laid before him the later accounts found in this paper, doubts the Columbus stories and kindly gives some data from his own wide experience. He notes that the Remora rarely grows over sixteen inches long, and, although it holds so tightly that it may be drawn out of water, is so small that it could hardly be used as a hunting fish. He further adds that Echeneis though it grows to a length of three feet doesn't "sit tight" but drops off the minute "the shark to which it is fastened is drawn out of the water." This observation of Dr. Jordan's is in full accord, it may be noted, with the records left by Columbus and his chroniclers that the fish cannot stand access to the air, and hence they affirm that, while it cannot by pulling be dislodged from its prey, it may easily be disengaged by lifting both hunter and hunted up into the air when the former at once drops off.

In this connection it is pertinent to give here an observation which I made at Beaufort, N. C., a number of years ago. A shark was hooked off the laboratory wharf and when pulled in was found to have an Echeneis attendant about a foot long. As shark and Echeneis were both drawn up, whenever the latter was elevated above the water it would let go, drop down into the water, and take a fresh hold. This was repeated several times, but at last the sucking-fish dropped off and swam away into deeper water.

A shark, which I hooked at Tortugas, had two Echeneises and one Remora on it. Being rapidly dragged up on the beach, the attendants did not let go until the shark was high and dry. One Echeneis was captured but the other two "suckers" got back in the water, and in many other cases I have been unable to bring the fish out with the shark. Dr. Townsend, however, writes (1915) that he has taken many sharks while on the United States Fisheries Steamer *Albatross,* and that nearly all of them came aboard with one or more Echeneises attached. Thus it would seem that in some cases the Echeneis holds fast and that in others it lets go. The causes of these different actions are not clear.

However, it is after all not a question of whether the sucking-fish lets go when brought into the air, but whether it can stand the strain of hauling in a heavy turtle or large fish. Hence the question is one to be settled by experiment and if possible by mathematics.

Holder (1905) has been quoted as having tried the experiment but without results since his "suckers" would not leave the sides of his boat to lay hold of the turtles and sharks. No record has been found of any similar experiments. In the same paper Holder speaks of lifting a bucket of water by a Remora which gripped the bottom with its disk.

Dr. C. H. Townsend, in an article in the *Bulletin* of the New York Zoological Society (1915), describes experiments to test the holding powers of sucking-fish in the New York Aquarium. A two-foot specimen (size of disk not noted) held by the tail lifted a pail half full of water—total weight 21 pounds. A second, 26.5 inches long and having a disk 5.5 inches in length, supported a pail and water weighing 24.25 pounds. Had a deeper bucket been used so that the water would not spill out, Dr. Townsend thinks that the fish could have lifted an even greater weight. Fig. 11, Plate III, is reproduced from the article in question.

Dr. Townsend made another and even more pertinent experiment which we will let him describe in his own words:

> By way of testing its fish-catching capacity, a shark-sucker sixteen inches long was liberated in one of the tanks of the Aquarium containing fishes. It took hold at once, and by hauling on the cord fastened to its tail a good-sized grouper was brought to the surface of the water, although it could not be lifted out of the tank. When the fish began to struggle the shark-sucker let go. When tried on a fifteen pound sea turtle, the latter could easily be drawn to the surface.
>
> There can be no doubt that with a line attached to a large remora [Echeneis?] a much larger sea turtle could be hauled in without difficulty.

My opportunities for making such experiments have unfortunately been very few. At Tortugas in 1914, I pulled on the tail of a sucking-fish, stuck fast to the glass wall of the aquarium, so hard that its muscles could be heard to crack, and I had to desist for fear of pulling the tail off. In 1913 in the Bight of Cape Lookout, N. C., we caught a 27.25 inch Echeneis having a sucking disk 6 inches long by 2.13 wide. When stuck to the wet deck, I pulled on this fish so hard that I feared that I would tear it in two, but it resisted all efforts to pull it off backwards—a pull of possibly 50 pounds. On pulling upwards on it, it held fast until the disk began to tear loose from the head.

Another fish 33 inches long, with a sucker 7.25 x 2.63 inches, caught on the same day, was also experimented on but it was not in good condition and did not have the "grip" of its predecessor. A spring balance was attached to its tail, and the fish was found to resist a pull of 14 pounds lengthwise and 17 at an upward angle of 45 degrees. The other fish would undoubtedly have shown better results. In both the popping of the muscles was noted. The literature is found to be filled with statements that the fish holds tight so strongly that it will suffer itself to be torn in two rather than let go.

In ascertaining the "pull" that an Echeneis might withstand when used as a fisherman-fish, the problem may be attacked from two standpoints. One might first ascertain how much adhesion the sucker would develop or secondly work out the "pull" necessary to land a turtle or large fish. This has never before been attempted, but it is worth while trying.

My largest Echeneis had a sucking disk whose longest diameter measured 7.25 × 2.63 inches. Assuming that it was an ellipse in shape let us proceed to get its area. The formula for the area of an ellipse whose longest diameters are a and b is as follows: Area $= \pi \times a \times b/4$. Substituting and performing the operations indicated we get 14.98 square inches for the area. This is of course too large, for no allowance has been made for the longitudinal raphe or for the lamellæ arranged like the slats of a Venetian blind. This cannot be ascertained but we will allow 1.48 square inches for this and thus reduce the available sucking area to 13.5 square inches. It is understood that the fish adheres to its host by raising its disk through muscular action and thus creating a partial vacuum. If this vacuum were perfect the adhesion would be 13.5 × 14.7 pounds or 198.45 pounds, or in round numbers 198 pounds would be the measure of the adhesion of the disk to the host fish, shark or turtle.

But it is objected that the disk can not develop a perfect vacuum, and as this is true our figures must be reduced. Let the reduction be 50 per cent. and the adhesion is still 99 pounds, or if it be cut by three fourths the adhesion will still be 49.5 pounds. The latter is probably too low just as the first is undoubtedly too high. For one thing there has not been and can not be figured out the additional adhesion developed by the backwardly directed teeth of the lamellæ, which were formerly thought to do all the holding. Assuming that the holding force is 99 pounds, it will be seen that when I pulled on this fish's tail with a pull estimated at 50 pounds the limits of its adhesion had not nearly been reached. And yet at the time it was noted that the muscles of the fish snapped and cracked until it looked as if its tail would be pulled off. Furthermore, scores of observers have noted that the fish would allow itself to be pulled in two rather than let go. In Dr. Townsend's article, Mr. L. L. Mowbray, of the New York Aquarium, is quoted as believing that the fish under strain while under the weight of a considerable column of water *can not* relax the grip of its disk. With a backward pull on its tail the teeth setting in the epidermis of its host would tend to keep the lamellæ vertical, for the lamellæ can only come to rest, relaxing the grasp of the disk, by describing an arc backward and downward. Whether or not Mr. Mowbray's suggestion is tenable, it is certain that with a strong pull backward on its tail the Echeneis would find it hard, perhaps impossible, to flatten the disk and let go its hold.

The data offered above ought to convince any one that Echeneis can hold on tightly enough to enable the fisherman to haul in the prey thus laid hold of by the fish, but whether the fish, without being literally torn in two can stand the strain of this hauling in is a question that must be met. The answer here is an unhesitating "Yes"!

Dr. Townsend pulled on his 26.5-inch sucking-fish having a 5.5-inch disk with a measured force of 24.25 pounds. Let us see what a pull so great as this will do in landing a large fish. Dr. Charles Frederick Holder has done more than any man in America to popularize the taking of big game fishes with light tackle. In his "Big Game Fishes of the United States" (1903) to face page 80 he has a photograph of a 251-pound tuna (*Thynnus thynnus*) caught on a 21-thread line tested to break at 42 pounds dead pull. On page 115 he tells of the capture of a 419-pound black sea bass (*Stereolepis gigas*), and to face page 116 gives a photograph of it. The size of the line is not given but it is elsewhere specifically stated that it was not over 24-thread having a breaking strength of 48 pounds. In his "Big Game at Sea" (1908) on page 129 Holder gives a table of nine tunas ranging from 94 to 251 pounds in weight and none caught on lines of more than 24 threads and many on 15- and 18-thread lines. On the following page (130) he tabulates the weights of eight black sea bass ranging from 327 to 436 pounds caught on number 24 lines. Again on page 109 he states that Edwin vom Hofe took a 600-pound sawfish on a 15-thread line breaking at 30 pounds dead pull. On pages 166–167 of his "Recreations of a Sportsman on the Pacific Coast" (1910) Holder describes the catching of an 8- or 9-foot shark with a 9-thread line, and on page 169 he describes the taking of a 12-foot, 310-pound shark with a tuna rod and reel, the line of which was not heavier than 24 threads. Examples might be still further multiplied, but enough have been given to establish the facts.

Now the tuna is probably the hardest fighting game fish in the world taken on a light line, while the black sea bass and the sharks are undoubtedly the heaviest dead weights of any fishes taken with rod and reel. Thus the argument is that if these fishes can be taken on lines breaking at dead weight pulls of from 18 to 48 pounds, then an Echeneis, which, suspended by a cord around its tail, supports a dead weight of 24.25 pounds, could easily be used to draw in fish and turtles of the sizes noted throughout this paper. And this without any danger of tearing its tail off.

To the present writer, all the evidence at hand sustains and confirms the stories of the living fishhook from the time of Columbus to the present day.

POSTSCRIPT

Since this paper was written I have chanced upon an article by F. Tamborini, bearing the title "Jagd- und Kunstschafterdienst im Meere," published in "Die Natur," 1900, Vol. 49, pp. 234–235. Examination of this shows that it contains nothing new, but note is made of it here that this may be understood and for the sake of completeness.

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VARIABILITY IN FLOWER-NUMBER IN VERNONIA MISSURICA RAF.

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IN studying the species of *Vernonia* in the western states, the writer was impressed as early as 1903 by the constancy with which the number of flowers in each head of certain species agrees with the numbers of the Fibonacci series. This appeared at the time to be particularly true of *Vernonia fasciculata,* which normally presents 18 to 21 flowers. Extending his studies later to the species of tropical America, he found a still closer agreement with the Fibonacci series in the species with fewer-flowered heads, where the numbers 8 and 13 are repeated with little or no variation in several species. Inspired by the more recent studies of Stout and Boas,[1] who reported a steady seasonal decrease in flower-number in the heads of *Cichorium Intybus,* he again examined in 1918 a series of specimens of *Vernonia missurica,* the only species native in the vicinity of Ann Arbor, Mich., and made careful determinations of the number of flowers in every head of several plants, chosen from different localities and habitats. The results of these studies are presented here.

In the western part of its range, from Kansas to Illinois, *Vernonia missurica* is essentially a prairie species and is seldom or never found in woods or swamps. In Indiana it is excessively common on rolling hills in clay soil, preferring land formerly wooded but now used for pasture, where it is apparently avoided by live-stock. In the extreme eastern end of its range, in southeastern

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[1] Stout, A. B., and Boas, H. M., "Statistical Studies of Flower Number per Head in *Cichorium Intybus;* Kinds of Variability, Heredity and Effects of Selection," *Mem. Torrey Club,* 17, 334–458, *pl. 10–13 + f. 1,* 1918.

Michigan and adjacent Ontario, it is typically a species of moist, cleared, uncultivated bottom-lands along the rivers and lakes and occasionally is found in low woods as well, where it is taller and more slender, with relatively lax, irregular, few-headed inflorescences. Judged from herbarium evidence from all parts of its range, the mode of its flower-number seems to be 34. Since flower-numbers deviate more freely from the Fibonacci series in the higher numbers and since the species has such a wide range and such a wide variation in its habitat, it may naturally be expected that it will present a wider variation in flower-number than many other species of restricted range and habitat and with smaller heads.

The inflorescence of the species may be described in some detail. It is strictly cymose. The main axis of the plant is unbranched and rises to a height of one to two meters. The lower nodes bear full-sized foliage leaves and are separated by internodes of fairly uniform length, while the upper internodes are abbreviated and bear reduced or bracteal leaves only. The main axis terminates in a single head on a short peduncle, and this head is the first, or among the first, to bloom. From the axils of the uppermost leaves branches appear which are in turn terminated by a single head on a longer peduncle, which therefore overtops the primary head. The next nodes, subtended by larger leaves, bear short simple leafless cymes of 2–5 heads. Below these, leafy branches appear from the lower nodes, and these bear single primary terminal heads, axillary heads on longer peduncles, and simple cymes in the same order in which they appear at the summit of the main axis. The uppermost of these leafy branches, since they arise relatively near the summit of the plant, also overtop the main axis and with it produce a more or less flattened or depressed corymbiform cluster. The lower lateral leafy branches are successively shorter, bear fewer heads which bloom later, and tend to produce in conjunction with the upper ones a more or less cylindrical cluster. Finally, the lowest nodes bear short and frequently undeveloped lateral branches, which usually appear so late in the season that none of their heads, or only a part of them, open their flowers before frost. In many plants only the uppermost nodes bear branches at all, and in such cases the inflorescence is flattened or depressed. Every plant normally bears the primary terminal head and few or several subterminal heads and simple cymes from the uppermost axils. The number of heads is at a minimum in shady situations. The middle nodes bear floriferous branches only on large plants of favorable situations, where there is sufficient light and the plants are not crowded for space.

A single cyme consists of two or more heads on peduncles 1–3 cm. long with subulate bracts. Each peduncle is usually accurately curved and leaves the straight axis at a prominent angle, so that the true terminal heads are easily recognized. The usual number of heads in each cyme is two to five and the maximum number observed is nine. A cyme of two heads consists of a terminal head and an inferior lateral head. A cyme of three heads consists of the terminal and (*a*) two inferior lateral heads or (*b*) an inferior two-headed cluster. A cyme of four heads presents the usual terminal head and (*a*) three inferior lateral ones on separate peduncles or (*b*) one lateral head and one two-headed cluster. One of five heads has the true terminal and (*a*) a single inferior lateral head and a three-headed cyme of either of the types mentioned above or (*b*) two two-headed clusters. Cymes of greater numbers of heads have the same general structure, of a single terminal head with various combinations of single inferior heads, two-headed clusters and three-headed clusters.

Three types of variation were looked for in examining the species: (1) a variation between the heads of each cyme, possibly correlated with their position, whether terminal or inferior; (2) a variation between different floriferous branches of the same plant, possibly correlated with the amount of available nourishment; and (3) a general variation between different individuals, possibly correlated with the size and vigor of the plant and therefore indirectly with the habitat.

1. Within a single cyme of 2–6 heads, the terminal head is usually the largest. In larger cymes of 7–9 heads some of the secondary terminal heads, ending the lower lateral branches of the leafless cluster, are frequently larger than the primary terminal head.

Table I exhibits the number of flowers in the terminal head and the average number in the other heads on each of 25 floriferous branches from the same plant, the numbers beginning at the base. On 4 branches, numbers 2, 5, 7 and 23, the terminal head was defective or worm-eaten, and these have been omitted in the table. On 22 branches of the 25, the primary terminal head is larger than the average of the other heads and the difference may be as

TABLE I

RELATION OF FLOWER-NUMBER TO POSITION ON THE BRANCH

Branch	Primary Terminal	All Other Heads		
		Number	Largest	Average
1	46	1	46	46
3	59	5	53	49.6
4	56	5	53	51.0
6	57	8	55	51.4
8	54	4	50	48.5
9	53	5	51	49.2
10	57	12	54	51.1
11	55	13	55	49.5
12	57	10	55	49.3
13	57	8	54	50.4
14	58	9	56	52.6
15	56	18	58	53.1
16	52	14	57	52.9
17	55	14	59	52.1
18	50	21	58	52.9
19	54	22	60	53.4
20	54	16	56	52.4
21	54	14	56	51.7
22	52	15	60	52.9
24	59	8	62	53.0
25	57	5	55	53.8
26	53	2	50	48.5
27	50	3	52	49.7
28	53	2	53	50.0
29	52	1	50	50.0

much as 9.4. On 15 branches the primary terminal is actually the largest head on the branch. In 3 cases the primary terminal is smaller than the average, and in 10 cases it is exceeded in size by one or more of the lateral heads. It will be noticed that these conditions occur only on branches with numerous heads, where the terminal heads of certain individual cymes tend to raise the average. In fact, on those branches which bear a total of less than ten heads, and in which there are accordingly fewer chances for large secondary terminal heads, the average sizes of the two classes are 55 and 50.8 and with two exceptions (branches nos. 24 and 27) the primary terminal is actually the largest head on the branch. On branches with a total of 10–20 heads the averages are 55 and 51.9 and the primary terminal is actually the largest in only two fifths of the branches. In the two cases with over 20 heads the averages are 52 and 53.2 and the primary terminals are conspicuously exceeded in size by some of the other heads. Since the heads of each cyme differ but little in age, the variation in their size may possibly be due to difference in the amount of food-stuff or water available, by which the terminal heads at the end of a continuous axis are favored.

2. It has already been stated that the solitary heads and the floriferous branches appear in basipetal order and that those from the lowest nodes may not be sufficiently developed to bloom before frost stops all further growth. Table II shows the variation in flower-number correlated with the position of the branch.

The table indicates a steady increase in the number of abortive heads from the older branches at the summit to the younger ones at the base. The greatest number of heads are found near the middle of the series on the longest lateral branches, which rise from the middle internodes to a height equal to or surpassing the summit of the stem. But the average number of flowers is remarkably constant throughout, varying only from 50.7 to 52.9 for each set and, in general, reaching the maximum among the larger branches. It is obvious that there is very little relation between position and flower-number and the same conclusion is supported by the data from other plants.

TABLE II

RELATION OF FLOWER-NUMBER TO POSITION OF BRANCH

Branch	Number of Heads				Number of Flowers			Average by Groups
	Defective	Abortive	Fertile	Total	High	Low	Average	
1	0	10	2	12	46	46	46.0	
2	0	11	0	11				Fertile heads 3.2
3	1	16	6	23	59	47	51.2	Abortive heads 10
4	1	10	6	17	56	47	51.8	Flower-number 50.7
5	0	3	0	3				
6	0	10	9	19	57	47	52.0	
7	1	8	6	15	53	47	49.5	Fertile heads 8.6
8	0	5	5	10	54	47	49.6	Abortive heads 7.8
9	3	7	6	16	53	48	49.8	Flower-number 50.8
10	0	9	13	22	57	48	51.5	
11	0	6	14	20	55	45	49.9	
12	0	9	11	20	57	45	50.0	Fertile heads 13.4
13	3	5	9	17	57	47	51.1	Abortive heads 6.2
14	1	4	10	15	58	48	53.1	Flower-number 51.6
15	0	7	19	26	58	47	53.3	
16	0	1	15	16	57	49	52.9	
17	0	4	15	19	59	47	52.3	Fertile heads 18.8
18	1	5	22	28	58	46	52.8	Abortive heads 3.8
19	0	7	23	30	60	47	53.4	Flower-number 52.8
20	1	2	17	20	57	47	52.5	
21	2	2	15	19	56	48	51.9	
22	3	1	16	20	60	49	52.8	Fertile heads 12.4
23	3	0	8	11	58	47	53.0	Abortive heads 1.2
24	0	1	9	10	62	48	53.7	Flower-number 52.9
25	0	2	6	8	57	52	54.3	
26	1	0	3	4	53	47	50.0	
27	0	0	4	4	52	46	49.8	
28	0	0	3	3	53	47	51.0	
29	0	0	2	2	52	50	51.0	Fertile heads 2.1
30	0	0	1	1			55	Abortive heads 0
31	0	0	1	1			52	Flower-number 51.0
32	0	0	1	1			49	
33	0	0	1	1			56	
Total ...	21	145	278	444	62	45	52.1	

3. The number of maturing heads and the minimum, maximum, and average number of flowers per head in 22 plants is exhibited in Table III. Of these plants, numbers 1–18 inclusive were collected from a variety of

habitats and stations, in shade and sun, and in relatively wet and relatively dry soils. They show in every case a small variation within each plant, but a great variation between different plants, the averages ranging from 29.3 to 52.1. It happens that the plant with the largest number of heads also presents the highest flower-number, but in general there is no correlation between them, and the third highest average is presented by the plant with the smallest number of heads.

TABLE III

Variation in Flower-number on Different Plants

Plant	Number Heads	Number of Flowers		
		High	Low	Average
1	278	62	45	52.1
2	26	43	37	40.0
3	26	41	34	37.3
4	15	38	29	31.9
5	14	36	27	31.9
6	31	40	31	36.4
7	19	45	37	42.2
8	25	39	32	35.4
9	95	37	22	29.3
10	62	35	26	29.7
11	43	39	28	34.2
12	15	51	45	47.7
13	7	36	32	34.0
14	11	45	36	40.5
15	3	46	44	45.0
16	19	38	34	35.5
17	3	39	35	37.0
18	33	34	26	29.4
19	126	38	26	32.5
20	98	37	26	32.2
21	61	38	27	32.0
22	74	36	25	32.7

The last four plants, numbers 19–22, were collected from the same station and grew under similar environmental conditions in the usual (and for the region probably also the optimum) habitat of the species. They also present very similar averages in their flower-number. Others of the same station were also examined and demonstrated that essentially the same averages were repeated throughout the group.

From an examination of this table and from additional experience with the plants, the writer is led to the tentative idea that two sets of factors, which may be environmental, or hereditary, or both, act on the plants independently, one determining the number of heads produced and the other the average number of flowers in each, so that there may result plants with many large heads (as no. 1), many small heads (no. 10), few large heads (no. 15), or few small heads (nos. 5, 18).

Table 4 shows the distribution of flower-numbers for all the heads of five plants. In each case the curves show a close relation to the main or secondary numbers of the Fibonacci series, 55, 29, 29, 34 and 34 respectively, although in only two cases do the modes fall precisely on these figures. Plant 1 shows a rather close grouping of heads just short of 55, plant 9 has over half of the heads grouped at 28–30, and plant 11 has almost half grouped at 33–35. It is scarcely to be expected that the series will be followed closely with such large numbers of flowers; in fact, Stout has demonstrated that there is no relation whatever to the Fibonacci series in the heads of *Cichorium Intybus.* Since the numbers were determined in every case by counting the mature achenes, the numbers should fall somewhat below the Fibonacci series, rather than above them, because of the possibility of some flowers not setting seed.

The plants used for these five tabulations were selected merely because of their large number of heads, which offer better data for developing a representative curve. Plants 20–22, with large numbers of heads also, agree closely with plant 19. A moment's inspection of the averages for the other plants, as shown in Table III, shows that in many cases, such as plants 2 and 3, they could not agree closely with the Fibonacci series, or that an apparent agreement might be fictitious if based on plants with a few heads only, as numbers 12 and 13.

TABLE IV

Distribution of Flower-numbers

Plant 1

No. of heads..	3	7	15	16	26	23	30	31	38	24	24	13	15	7	3	2	0	1
No. of flowers.	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62

Plant 9

No. of heads..	1	0	1	3	5	10	15	16	18	11	6	4	2	1	1	1
No. of flowers.	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37

Plant 10

No. of heads..	2	1	15	16	9	9	6	1	2	1
No. of flowers.	26	27	28	29	30	31	32	33	34	35

Plant 11

No. of heads..	1	0	1	1	8	7	4	10	3	4	2	2
No. of flowers.	28	29	30	31	32	33	34	35	36	37	38	39

Plant 19

No. of heads..	3	5	4	11	8	12	6	16	37	11	9	3	1
No. of flowers.	26	27	28	29	30	31	32	33	34	35	36	37	38

Summary

1. The number of flowers in each head is greatest for the terminal heads of each cyme.
2. Otherwise the number of flowers in each head is relatively constant for each individual plant.
3. There is a great variation between individuals but, in those plants with numerous heads, the mode falls on or near one of the main or secondary numbers of the Fibonacci series.

DARWIN'S CONTRIBUTION TO THE KNOWLEDGE OF HYBRIDIZATION

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THE period from 1859 until the re-discovery of Mendel's papers in 1900 was so strongly colored by the views of Charles Darwin, and so dominated by the magnitude of his work, that it sometimes seems as though originality and initiative had been abandoned, and as though, so far as evolution were concerned, the scientific world had remained content simply to quote Darwin.

It is the purpose of the present paper to present the contributions of Darwin to the knowledge of hybrids. To this end it seems desirable, so far as possible, to let Darwin's words speak for themselves, and hence, although the paper may seem burdened with extracts, yet, for those interested in tracing the history of ideas in genetics, it will perhaps be of service to assemble such a résumé of Darwin's work and thought in the field of hybridization. Brought together in such a way, an author's contribution may be more successfully valuated at leisure by those who may be interested. The writer has, therefore, sought to bring together, in somewhat connected and coherent form, the various views, conclusions and experimental data on the subject of hybrids and hybridization, found in Darwin's different writings.

It is also the purpose of the writer to bring into relief certain fields of investigation opened by him, but in which, so far as appears, there has been little or no research since his time.

On November 24, 1859, appeared the first edition of "The Origin of Species (1), antedating by seven years, the appearance of the papers of Mendel.

One of the primary questions concerning crossing that interested Darwin was the matter of sterility and fertility in hybrids. Investigators before Darwin's time had been to a considerable extent obsessed by the species question, which crossing was supposed to solve. If a cross succeeded, or produced fertile offspring, it argued that the parent forms were "varieties." If the cross failed, or if its offspring were sterile, it demonstrated that they were "species." With the sole exception of Sageret (2), none of the earlier hybridists seems to have formed anything like the unit-character conception, and with the sole exception of Naudin and Darwin, no scientific theory was conceived of which might explain the *modus operandi* of amphimixis in the case of hybrids.

By Darwin, the question of hybridization, while indeed for the most part, taken up more or less conventionally, received, nevertheless, broader treatment. To begin with, Darwin held that the inability of species to cross "is often completely independent of their systematic affinity, that is, of any difference in their structure or constitution, excepting their reproductive systems" (1a, 2:14).

So that, even as early as the writing of the "Origin of Species," Darwin is seen to maintain that the susceptibility of plants to crossing stood in no relation to the degree of their resemblance to either parent, and that "the facility of making a first cross between any two species is not always governed by their systematic affinity or degree of resemblance to each other" (1a, 2:16).

This fact, he adds, is demonstrated by the case of reciprocal crosses, alluding here to the relative facility of making the cross, according as the one or the other species is used as the male or the female.

Occasionally he says there is "the widest possible difference in the facility of effecting a union. The hybrids, moreover, produced from reciprocal crosses, often differ in fertility" (*ibid.*).

Darwin again later in "Animals and Plants under Domestication," refers to the matter as follows:

> Why should some species cross with facility, and yet produce very sterile hybrids, and other species cross with extreme difficulty, and yet produce fairly fertile hybrids? Why should there often be so great a difference in the result of a reciprocal cross between the same two species? (1a, 2:17).

Darwin comments frequently in the "Origin of Species," upon the fact that the hybrids produced from reciprocal crosses often differ in fertility, and that while two species may be difficult to cross, there is no strict parallelism between the difficulty of effecting the cross and the degree of sterility of the hybrids resulting therefrom.

As Darwin observes, differences in the results in respect to the relative ease of making reciprocal crosses had been previously noted by Koelreuter, who found, after two hundred trials, continued for eight years, that while *Mirabilis jalapa* could easily be fertilized by *M. longiflora*, the reverse cross could not be effected.

With regard to the difference in the facility with which reciprocal crosses can be made, there may be some fundamental resemblance between this fact and the ease with which reciprocal grafts can be made, wherein Darwin instances the fact that the currant can, although with difficulty, be grafted upon the gooseberry, while the reciprocal graft can not be made. Certainly the well-established facts of somatic segregation followed by germinal "mutation"—so-called, should sufficiently indicate that the behavior of the somatic and of the reproductive cells should not be regarded as being so sharply separated as is usually done in genetic studies. At all events, the problem as to the reason for the relative differences in the respective facility of making reciprocal crosses, as well as the further one of the differences as in the case of mule and hinny, between the respective products of reciprocal crosses, are questions that have been but very little investigated since Darwin's time, and demand thorough exploration.

Since the advent of Mendelian studies in 1900, it has been rather conventionally and very loosely assumed that reciprocal crosses are invariably identical in type. That such is not necessarily the case, Darwin's early observations should suffice to indicate.

The problem of the fertility of selfed and crossed plants engaged Darwin's close interest in forty-one cases belonging to twenty-three species. The ratio of the fertility of the crossed to that of the self-fertilized plants was found to be as 100:60. In another experiment to determine the relative fertility of flowers when crossed or selfed, the ratio in thirty cases belonging to twenty-seven species was as 100:55.

> There is no evidence, Darwin finds, That the fertility of plants goes on diminishing in successive self-fertilized generations, and no close correspondence, either in the parent plants or in the successive generations, between the relative number of seeds produced by the crossed and self-fertilized flowers, and the relative powers of growth of the seedlings raised from such seeds (1b, 327).

Darwin's investigations were directed quite extensively to the question of self-fertility in plants, a field which bears strongly upon our knowledge of heredity, but in which likewise comparatively little experimental work has been done since his time. As the result of his own studies, supplemented by those of Hildebrand and Fritz Müller, he was able to say:

> We may therefore confidently assert, that a self-sterile plant can be fertilized by the pollen out of any one out of a thousand or ten thousand individuals of the same species, but not by its own (*ibid.*, 347).

Regarding the cause of sterility or inability to accept fertilization, we are as greatly at a loss for an explanation to-day as was Darwin. As Darwin well states it:

> The veil of secrecy is as yet far from lifted; nor will it be, until we can say why it is beneficial that the sexual elements should be differentiated to a certain extent, and why, if the differentiation be carried still further, inquiry follows. It is an extraordinary fact that with many species, flowers fertilized with their pollen are either absolutely

> or in some degree sterile; if fertilized with pollen from another flower on the same plant, they are sometimes, though rarely, a little more fertile; if fertilized with pollen from another individual or variety of the same species they are fully fertile; but if with pollen from a distant species they are sterile in all possible degrees, until utter sterility is reached. We thus have a long series with absolute sterility at the two ends; at one end due to the sexual elements not having been differentiated, and at the other end to their having been differentiated in too great a degree, or in some peculiar manner (*ibid.*, 455).

The questions which Darwin raises in this connection are as follows (p. 458):

1. Why the individuals of some species profit greatly, others very little by being crossed.
2. Why the advantages from crossing now seem to accrue exclusively to the vegetative and now to the reproductive system, although generally to both.
3. Why some members of a species should be sterile, while others are entirely fertile with their own pollen.
4. Why a change of environment or of climate should affect the sterility of self-sterile species.
5. Why the members of some species should be more fertile with the pollen from another species than with that of their own.

Regarding the general matter of sterility in hybrids, Darwin comments as follows:

> It is notorious that when distinct species of plants are crossed they produce with the rarest exceptions, fewer seeds than the normal number. This unproductiveness varies in different species up to sterility so complete that not even an empty capsule is formed (1b, 463).
>
> It is also notorious that not only the parent species, but the hybrids raised from them are more or less sterile, and that their pollen is in a more or less aborted condition. The degree of sterility of various hybrids does not always strictly correspond with the degree of difficulty in uniting the parent forms. When hybrids are capable of breeding *inter se,* their descendants are more or less sterile, and they often become still more sterile in the later generations (*ibid.*).
>
> With the majority of species, flowers fertilized with their own pollen yield fewer, sometimes much fewer seeds, than those fertilized from another individual or variety (*ibid.*, 464).

As the result of his investigations regarding sterility to pollen, Darwin was able to render at least one service, that of removing the obsession which had so long afflicted the study of the hybrid question, viz., the variety-species discussion. He says:

> It can thus be shown that neither sterility nor fertility affords any certain distinction between species and varieties. The evidence from this source graduates away, and is doubtful in the same degree as is the evidence derived from other constitutional and structural differences (1a, 2:4).

The question of the chemical and cytological basis for sterility or non-receptivity to pollen, remains still in part an open field for the investigator.

One of the most important questions from our present-day point of view which Darwin investigated was the relative vigor of first-generation hybrids as compared with that of their parents. The following allusions occur in the "Origin of Species."

Darwin comments on the fact that crosses between individuals of the same species, where they differ to a certain extent, give increased vigor and fertility, while close fertilization, long continued, almost always leads to physical degeneracy, and remarks:

> We know also that a cross between the distinct individuals of the same variety, and between distinct varieties, increases the number of the offspring, and certainly gives to them increased size and vigor (1a, 2:296).

Darwin thoroughly investigated, as is well known, the comparative relation of the offspring of crossed to those of selfed plants with respect to vigor.

> I have made so many experiments, and collected so many facts, showing on the one hand that an occasional cross with a distinct individual or variety increases the vigor and fertility of the offspring, and on the other hand that very close interbreeding lessens their vigor and fertility, that I can not doubt the correctness of this conclusion (2a, 2:5).

> Again, from both plants and animals, there is the clearest evidence that a cross between individuals of the same species, which differs to a certain extent, gives vigor and fertility to the offspring, and that close interbreeding, continued during several generations between the nearest relations, if these be kept under the same conditions of life, almost always leads to decreased size, weakness or sterility (1a, 2: 27).

In "Cross and Self Fertilization," Darwin again discusses the effects of crossing as follows, expressing the view:

> Firstly, that the advantages of cross-fertilization do not follow from some mysterious virtue in the mere union of two distinct individuals, but from such individuals having been subjected during previous generations to different conditions, or to their having varied in a manner commonly called spontaneous, so that in either case their sexual elements have been in some degree differentiated; and secondly from the want of such differentiation in the sexual elements (1b, 443).
>
> A cross with a fresh stock or with another variety seems to be always beneficial, whether or not the mother plants have been intercrossed or self-fertilized for several previous generations (1b, 444).

Darwin also remarks upon the greater power of the cross-fertilized plants in his experiment to stand exposure, the crossed plants enduring sudden removal from greenhouse to out-of-door conditions better than did the self-fertilized, and also resisting cold and intemperate weather conditions more successfully. This was the case with morning glory and with *Mimulus*.

> The offspring of plants of the eight self-fertilized generations of *Mimulus* crossed by a fresh stock, survived a frost which killed every single self-fertilized and intercrossed plant of the old stock.
>
> Independently of any external cause which could be detected, the self-fertilized plants were more liable to premature death than the crossed (*ibid.*, 290).

Out of several hundred plants in all involved in the experiment, only seven of the crossed plants died, while at least twenty-nine of the self-fertilized were thus lost.

With regard to time of flowering, in four out of fifty-eight cases, a crossed plant, in nine cases a selfed plant, flowered first.

Darwin broached the view that the increased vigor of first-generation hybrids was chiefly due to the forms used in the cross having been exposed to somewhat different conditions of life. He also contended that his experiments proved that

> If all the individuals of the same variety be subjected during several generations to the same conditions, the good derived from crossing is often much diminished or wholly disappears (1a, 2:270).

This statement appears to be an *obiter dictum* of Darwin's to the support of which he does not adduce direct experimental evidence.

Again he says:

> Anyhow my experiments indicate that crossing plants which have been long subjected to almost though not quite the same conditions, is the most powerful of all the means for retaining some degree of differentiation in the sexual elements, as shown by the superiority in the later generations, of the intercrossed over the self-fertilized seedlings (1b, 450).
>
> We know, he says, that a plant propagated for some generations in another garden in the same district serves as a first stock, and has high fertilization powers (*ibid.*).

The importance of this view has yet, so far as the writer knows, to be thoroughly re-investigated under completely controlled conditions.

It was Darwin's view, as the result of his experiments, that the increased vigor of intercrossed plants is due to the constitution or nature of the sexual elements, which condition he took to be of the general nature of differentiation due to the action of environment.

> It is certain, he says, that the differences are not of an external nature, for two plants which resemble each other as closely as the individuals of the same species ever do, profit in the plainest manner when intercrossed, if their progenitors have been exposed during several generations to different conditions (1b, 270).

Darwin asserts that there is not a single case in his experiments,

> Which affords decisive evidence against the rule, that a cross between plants, the progenitors of which have been subjected to somewhat diversified conditions, is beneficial to the offspring (*ibid.,* 281).

The fact that increased vegetative vigor in first generation hybrids was also sometimes accompanied by diminished fertility was likewise observed by Darwin,

> For it deserves especial attention that mongrel animals and plants, which are so far from being sterile, that their fertility is often actually augmented, have, as previously shown, their size, hardiness and constitutional vigor generally increased. It is not a little remarkable that an accession of vigor and size should thus arise under the opposite contingencies of increased and diminished fertility (1c, 2:108).

In the case of Darwin's experiments to determine the relative effects upon vigor of selfing and crossing, respectively, the data were determined chiefly with respect to height and weight of the plants, which were grown on opposite sides of the same pot in all instances.

Regarding the relative heights and weights of 292 plants, derived from a cross with a fresh stock, and of 305 plants either selfed or intercrossed, between plants of the same stock and belonging to thirteen species and twelve genera, Darwin says:

> Considering all the cases . . . there can be no doubt that plants profit immensely, though in different ways, by a cross with a fresh stock, or with a distinct sub-variety. He emphasizes further, It can not be maintained that the benefit thus derived is due merely to the plants of the fresh stock being perfectly healthy, whilst those which had been long intercrossed or self-fertilized had become unhealthy; for in most cases there was no appearance of such unhealthiness (1b, 269).

Experiments were also made with plants belonging to five genera in four different families. One of the most interesting cases was that of a plant of marjoram (*Origanum vulgare*). The height of the crossed was to that of the selfed plants as 100:86.

> They differed also to a wonderful degree in constitutional vigor. The crossed plants flowered first, and produced twice as many flower-stems; and they afterward increased by stolons to such an extent as almost to overwhelm the self-fertilized plants (1b, 302).

Darwin holds that the inferiority of the selfed seedlings in height can have been in no way due to any morbidity or disease in the mother plants; certainly, he maintains, no such theory of a diseased condition would in any wise hold, in the case of

> intercrossing the individuals of the same variety or of distinct varieties, if these have been subjected during some generations to different conditions (1b, 445).

In four out of the five cases experimented with, the intercrossing of flowers upon the same plant did not differ in effect from the strictest self-fertilization. Concluding, he says:

> On the whole the results here arrived at . . . agree well with our general conclusion, that the advantage of a cross depends on the progenitors of the crossed plants possessing somewhat different constitutions, either from having been exposed to different conditions, or to their having varied from unknown causes in a manner which we in our ignorance are forced to speak of as spontaneous (1b, 302).

Darwin's experiments indicated as in the case of heartsease and sweet pea, that

> the advantage derived from a cross between two plants was not confined to the offspring of the first generation (1b, 305).

Laxton's varieties of sweet peas produced by crossing, as Darwin says:

> have retained their astonishing vigor and luxuriance for a considerable number of generations (*ibid.*).

Darwin concludes:

> As the advantage from a cross depends on the plants which are crossed differing somewhat in constitution, it may be inferred as prob-

> able that under similar conditions, a cross between the nearest relations would not benefit the offspring so much as one between non-related plants (*ibid.*).

Darwin finally also remarks in general:

> It is interesting to observe . . . the graduated series from plants which, when fertilized by their own pollen, yield the full number of seeds, but with the seedlings a little dwarfed in stature, to plants which, when self-fertilized, yield few seeds, to those which yield none, but have their ovaria somewhat developed,—and, lastly, to those in which the plant's own pollen and stigma mutually act on one another like poison (1c, 2: 119).

The relative weight and germinative energy of seeds from crossed and from self-fertilized plants, was investigated by Darwin in the case of sixteen species, with the result that the weight of the seeds of the former to that of the latter was found on the average to be as 100:96. In ten out of the sixteen cases the self-fertilized seeds were either equal or superior to the crossed in weight, but in six out of these ten, the plants raised from these selfed seeds were greatly superior in height and in other respects to those from the crossed seeds. In the matter of germination of selfed and crossed seeds, the results were conflicting. Darwin, however, discovered that, in general, seedlings of greater constitutional vigor are obtained when crossed by other individuals of the same stock, than when pollinated by their own pollen.

In the cases of plants of fifty-seven different species, belonging in all to fifty-two genera and thirty different families, Darwin carried out the most extensive experiment yet recorded, conducted for the purpose of determining the differences in size, between the offspring of cross-fertilized and of close-fertilized plants.

The total number of the crossed plants amounted to 1101, and of the selfed plants to 1076. As a result, Darwin found that the plants derived from crosses between different strains of the same species, were taller on the average, than plants derived from crosses within the same strain, and taller in the latter case than in the case of the offspring of self-fertilized plants. The average ratio of 620 crossed to 607 selfed plants in height, derived from Darwin's tables, was as 100:86.

From the fact that flower buds are in a sense distinct individual plant units, which sometimes vary and differ widely from one another, and yet, when on the same plant, owing to the fact that the plant has come from the same fertilized cell, rarely are widely differentiated, Darwin reasons that the effects of intercrossing can be explained. He says:

> The fact that a cross between two flowers on the same plant does no good or very little good, is likewise a strong corroboration of our conclusion; for the sexual elements in the flowers on the same plant can rarely have been differentiated, though this is possible, as flower buds are in one sense distinct individuals, sometimes varying and differing from one another in structure or constitution (1b, 444).

Hence, he concludes:

> Thus the proposition that the benefit from cross-fertilization depends on the plants which are crossed having been subjected to somewhat different conditions, or to their having varied from some unknown cause as if they had been thus subjected, is securely fortified from all sides (1b, 444).

Darwin comments also on the reversed situation, where changes in the external condition result in sterility, for which he seeks to find a logical connection with the condition induced by crossing.

> On the one hand, slight changes in the conditions of life are favorable to plants and animals, and the crossing of varieties adds to the size, vigor, and fertility of their offspring, so on the other hand, certain other changes in the conditions of life cause sterility; and as this likewise ensues from crossing much modified forms or species, we have a parallel and a double series of facts, which apparently stand in close relation to each other (1c, 2:126).

Darwin's view as to the reason for the good effects of crossing was based upon the long prevalent opinion that, since animals, and hence presumably plants, profit from changes in their conditions, that probably such changes operate to affect the germ cells, or that in some way the germ cells receive an extra stimulation on that account, which redounds to the benefit of the offspring (1c, 2:155).

Darwin appears to hold the ill effects of close fertilization to be due to the fact that the sexual elements in the different flowers on the same plant have not differentiated, while in his conclusion he appears to consider the benefits of cross-fertilization to be due to the individuals involved in the cross having differentiated through having been exposed to different conditions.

Darwin frequently emphasizes the same view regarding the differentiating effects of a new environment.

> But hardly any cases afford more striking evidence how powerfully a change in the conditions of life acts on the sexual elements, than those already given, of plants which are completely self-sterile in one country, and when brought to another, yield even in the first generation, a fair supply of self-fertilized seeds (1b, 477), and again, . . . we know that a plant propagated for some generations in another garden in the same district scores as a fresh stock and has high fertilizing powers. The curious cases of plants which can fertilize and be fertilized by any other individual of the same species but are altogether sterile with their own pollen, become intelligible, if the view here propounded is correct, namely, that the individuals of the same species, growing in a state of Nature near, have not really been subjected during several previous generations to quite the same conditions (1b, 450).

> When two varieties which present well-marked differences are crossed, their descendants in the later generations differ greatly from one another in external characters; and this is due to the augmentation or obliteration of some of these characters, and to the reappearance of former ones through reversion; and so it will be, as we may feel almost sure, with any slight differences in the constitution of their sexual elements (1b, 449).

With regard to the ill effects derived from self-fertilization, Darwin says:

> Whether the evil from self-fertilization goes on increasing during successive generations is not as yet known, but we may infer from my

> experiments that the increase, if any, is far from rapid. *After plants have been propagated by self-fertilization for several generations, a single cross with a fresh stock restores their pristine vigor,* and we have a strictly analogous result with our domestic animals. The good effects of cross fertilization are transmitted by plants to the next generation, and judging from the varieties of the common pea, to many succeeding generations. But this may merely be that crossed plants of the first generation are extremely vigorous, and transmit their vigor like any other character to their successors (1b, 438).

In this paragraph Darwin calls attention to a fact that attracted little attention for a generation,—viz., the immediate improvement due to a cross. Darwin was thus if not the first to call sharply to attention, the matter of the relatively increased size and vigor of first generation hybrids, at least the first to subject the question to experimental analysis.

So far as plant hybrids are concerned, Darwin's mind was chiefly occupied, as we have seen, not so much with the fundamental theory of hybrids, as with the question of sterility in hybrids and its inheritance. The general question of what is the essential nature of hybridity, and how and in what manner the characters are distributed in the hybrid offspring, seems not to have come to an issue with him.

However, among the matters of interest to modern students of genetics are his recognition of the general fact of the intermediacy of F_1 hybrids, and of the occasional complete dominance of one or the other set of parental characters, together with the phenomena which he terms "reversion." Regarding the former matter he remarks:

> There are certain hybrids which, instead of having, as is usual, an intermediate character between their two parents, always closely resemble one of them (1, 2:15).

In regard to the behavior of characters in crosses, while admitting that, in the majority of cases, the hybrid offspring are intermediate between their parents, he recognized that certain characters are incapable of fusion.

> When two breeds are crossed, their characters usually become intimately fused together, but some characters refuse to blend, and are transmitted in an unmodified state, either from both parents or from one (1c, 2:67).

As cases in point, Darwin cites the crossing of gray and white mice, the offspring being pure white or gray, but not intermediate, and the crossing of white, black and fawn-colored Angora rabbits, in which the colors are separately inherited, and not combined in the same animal. The non-intermediate character of the inheritance in the case of turnspit dogs and ancon sheep is referred to, as is also the inheritance in the case of tail-less, horn-less breeds. Similar results in the case of stocks, toad-flax and sweet peas are cited (1b, p. 68).

Darwin (1c, 44–45), in discussing what he called "prepotency," was dealing in very many cases with that which we now recognize as simple dominance. For example, in the crossing of snap-dragons, Darwin found that when the normal or irregular-flowered type was crossed with the abnormal or regular-flowered type, the former prevails in the first generation to the exclusion of the latter. These 127 hybrid plants self-fertilized, yielded in the second generation irregular to regular plants in the ratio of 88 to 37. This is very close to the exact 3:1 ratio which would be represented by the numbers 85:42. Darwin, however, simply regards it as a

> good instance of the wide difference between the inheritance of a character and the power of transmitting it to the crossed offspring (1b, 45).

Darwin was thus quite unable, with the information then available, to frame a satisfactory explanation for the various phenomena passing under the name of "prepotency."

He makes one remark relative to prepotency, however, that slightly grazes the present-day presence and absence theory of Mendelian inheritance.

> We can seldom tell what makes one race or species prepotent over another; but it sometimes depends on the same character being present and visible in one parent, and latent or potentially present in the other (1c, 2:58).

The matter of sex-linked characters did not escape Darwin's observation, alluding to cases where a son does not inherit a character directly from his father, or transmit it directly to his son, but receives it by transmission from a mother who does not show it, and transmits it through his non-affected daughter. Darwin observes:

> We thus learn that transmission and development are distinct powers (*ibid.*).

Respecting the matter of reversion, or what we should now call recombination after segregation, Darwin's utterances are remarkable, especially in "Animals and Plants under Domestication." In most cases he regards "reversion" as the coming to light of a "latent" character, as, e. g.,

> hornless breeds of cattle possess a latent capacity to reproduce horns, yet when crossed with horned breeds they do not invariably produce offspring bearing horns (1c, 2:44).

Darwin deserves credit for strictly contesting the point of view then widely current, that the longer a character is handed down by a breed, the more fully it will be continued in transmission. Discussing some of the cases, he says (1c, 2:37):

> In none of these nor in the following cases, does there appear to be any relation between the force with which a character is transmitted and the length of time during which it has been transmitted.

The basis for such a view, that the longer a breed is handled and the more it is selected, the more homozygous it becomes, was not scientifically known in Darwin's time, but Darwin actually perceived that the mere repeated act of selection itself, whatever else might be involved, would not increase the potency of transmission, or eliminate beyond question the liability to reversion.

Darwin considered it doubtful whether, as was then popularly supposed, the length of time during which a character had been inherited, had any influence on its fixedness, and concluded from the fact that when wild species which have remained so for ages, are brought into cultivation, they immediately begin to vary, that no character by long inheritance can be considered as absolutely fixed (1c, 2:56).

In this work, more than elsewhere, Darwin devoted himself particularly to the question of the meaning of inheritance in hybrids. The question always demanding explanation was the reason for the reappearance after the first generation of a hybrid of a parental, or even of an ancestral form, a phenomenon then called "reversion," including, as Darwin says:

> all cases in which an individual with some distinguishable character, a race or species, has, at some former period been crossed, and a character derived from his cross, after having disappeared during one or several generations, suddenly reappears (1c, 2:2).

Darwin, at the outset, merely comments on the result of crossing as follows:

> In considering the final result of the commingling of two or more breeds, we must not forget that the act of crossing in itself tends to bring back long-lost characters not proper to the immediate parent form (1c, 2:64).

It was noticed that from three to eight generations were usually required before a breed derived from a cross comes to be considered free from danger of reversion. What constituted the machinery to bring about reversion remained, but for Mendel's as yet undiscovered researches, absolutely unknown. The state of knowledge in that regard is well exemplified by Darwin's remark,

> That the act of crossing in itself gives an impulse towards reversion, as shown by the reappearance of long-lost characters, has never, I believe been hitherto proved (1c, 2:13).

Darwin recognized, as did most of the breeders before Mendel, that

> As a general rule, crossed offspring in the first generation are nearly intermediate between their parents, but the grandchildren and succeeding generations continually revert in a greater or lesser degree, to one or both of their progenitors (1c, 2:22).

From cases of intermediacy, Darwin proceeds to discuss what we should call cases of dominance, and finally cases in which the offspring in the first generation are neither intermediate nor uni-parental in type, but in which there is vegetative splitting, or somatic segregation:

> In which differently colored flowers borne on the same root resemble both parents, . . . and those in which the same flower or fruit is striped or blotched with the two parental colors, or bears a single stripe of the color or other characteristic quality of one of the parent forms (1c, 2:69).

It is interesting to see how Darwin now undertook, in the absence of experimental evidence, to devise a scientific solution for the reappearance of parental characters in the second generation of the offspring. Taking Naudin's idea of segregation or "disjunction" of the elements of the species, he concludes as follows:

> If . . . pollen which included the elements of one species happened to unite with ovules including the elements of the other species, the *intermediate or hybrid state would still be retained, and there would be no reversion.* But it would, as I suspect, be more *correct to say that the elements of both parent species exist in every hybrid in a double* state, namely, blended together and completely separated (1c, 2:23).

The above paragraph comes more nearly being a statement of the true nature of the hybrid or heterozygote condition as Mendel's analysis has revealed it, than any other account hitherto published.

Combining this with the following statements, we have very nearly the same idea which Mendel's theory involves, based, however, upon Darwin's theory of pangenesis, whereby each cell was supposed to throw off "gemmules" which carried the characters to the reproductive cells. He says:

> The tendency to reversion is often induced by a change of conditions, and in the plainest manner by crossing. Crossed forms of the first generation are generally nearly intermediate in character between their two parents, but in the next generation the offspring commonly revert to one or both of their grandparents, and occasionally to more remote ancestors (1c, 2: 383).

Darwin then assumes that in the hybrid there exist two kinds of "gemmules" or character-carriers; viz., pure gemmules from each of the two parent forms, and combined or hybridized gemmules as well, and proceeds in the following statement, to give about as clear an account as we have to-day, of the cause for the reappearance of the parental or homozygote forms.

> . . . *when two hybrids pair, the combination of pure gemmules derived from the one hybrid with the pure gemmules of the same parts derived from the other would necessarily lead to complete reversion of character*, and it is perhaps not too bold a supposition that unmodified and undeteriorated gemmules of the same nature would be especially apt to combine.
>
> Pure gemmules in combination with hybridized gemmules would lead to partial reversion, and lastly, *hybridized gemmules derived from both parent-hybrids, would simply reproduce the original hybrid form.* All these cases and degrees of reversion incessantly occur (1c, 2: 383).

The latter statement is virtually a statement of the condition of things in heterozygosis, in principle as we have it to-day. If we assume the "hybridized" gemmules to represent the "*Dr.*" combination, we have the necessary substitution.

Darwin's theory was a natural corrollary to his doctrine of pangenesis. It seems strange that with Naudin's idea of disjunction in hand, and with the phenomenon of segregation in peas, noticed by five observers, all of whose experiments Darwin remarks upon, that Darwin did not himself perform Mendel's experiment. However, it is a manner of special interest that *à priori,* in the absence of experimental data, he should have come as near the principle of the Mendelian explanation as the above passages indicate.

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SHORTER ARTICLES AND DISCUSSION

DOES EVOLUTION OCCUR EXCLUSIVELY BY LOSS OF GENETIC FACTORS?

In an extremely interesting article, Professor Duerden[1] has recently discussed certain aspects of evolution in the light of observations on ostrich farming. He shows that as regards most characters the germ plasm of the ostrich is remarkably stable and yet that quantitative variation as regards wing and toe characters is occurring and is being utilized, in particular for a gradual amelioration of the valued plume characters. He believes that the quantitative variation in question has a factorial genetic basis, a view which I see no reason to question. He holds that repeated selection may probably extend the existing range of variation *downward,* but not *upward.* In this last conclusion I can not concur. It rests, I believe, on too close adherence to the "presence-absence hypothesis." It assumes that minus variation occurs only by loss of factors and further that factors once lost can not be recovered. I do not think that either of these assumptions will bear critical examination. Morgan has recorded, in *Drosophila,* the occurrence of a reversed mutation by which colored eyes were recovered in a white-eyed race, and on this ground has questioned the validity of the entire presence-absence hypothesis. I have found that in the piebald patterns of rats and rabbits steady progress may be made by repeated selection in changing the racial average *either* in a plus or in a minus direction. Genetic changes affecting the extent of the pigmented areas are clearly of frequent occurrence in such cases, precisely as they are in the case of number of remiges in the ostrich wing, but there is no indication that the changes are exclusively in a minus direction, as Duerden assumes them to be in the ostrich. He has observed variation in the number of plumes on the ostrich wing ranging from 33 to 42. He assumes that the variation can probably be carried below 33 by selection, through cumulation of loss variations by dropping out of factors, but that variation in the opposite direction is not to be expected because 42 is the present maximum and factors for a higher number having once been lost can not be recovered. Of course, the thing to do in order to test the validity of this view is to give it an experimental trial,

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[1] Duerden, J. E., "The Germ Plasm of the Ostrich," AMER. NAT., 53, p. 312.

and this, no doubt, Duerden is already doing. If the 42-plumed cock has descendants with a higher plume number than 42, the theory will have been disproved, which would undoubtly be highly pleasing to Duerden because it would give him a more hopeful basis for economic work. Now my own experimental work with loss-variations leads me strongly to hold the more hopeful view, that genetic changes are plus as well as minus, even in the case of structures which are in course of phylogenetic degeneration.

The degenerating lateral digits of the guinea-pig's foot[2] present a case parallel with those of the degenerating wing and the degenerating fourth toe of the ostrich. The guinea-pig, like all wild species of the genus, *Cavia,* has lost altogether the first of the five typical digits, and has lost the fifth digit from its hind foot, but not from the front foot. Some years ago I discovered a guinea-pig which had an imperfectly developed fifth digit on one hind foot. Neither of its parents had a fifth digit on either hind foot. This fact alone shows the possibility of *plus fluctuation* in a degenerate organ. The polydactylous individual, a male, was mated both with related and with unrelated females. By the former, he had 13 polydactylous and 32 normal individuals; by the latter he had 2 polydactylous and 30 normal individuals. This result showed that normal females related to the polydactyl male, even though themselves normal, transmitted a factor or factors favorable to the production of the fifth toe, since more of their offspring were polydactyl than of the offspring of ordinary females, when both sorts were mated to the same polydactyl male. Breeding the polydactyl offspring together and continuing the race by selecting those individuals which had the best developed toes (purely somatic selection), a race was secured within four generations which produced regularly 90 to 100 per cent. of polydactylous young. The race was continued for several years and showed no signs during this period of returning deterioration.

In this case we have an example of plus fluctuation in a character supposed to have been completely lost from the genus, *Cavia,* yet which, having shown itself sporadically and feebly in a single individual, was recovered and fully established as a racial character by the practise of inbreeding and selection on a purely somatic basis.

The first digit has, so far as I know, never been observed to

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[2] Castle, W. E., "The Origin of a Polydactylous Race of Guinea-pigs," Publication No. 49, Carnegie Inst., Washington, 1906.

occur in the genus, *Cavia,* except in the case of a single individual born in one of our experiments. As this individual was stillborn we had no chance to experiment further in the case, but the occurrence shows that degenerating characters are not of necessity lost for all time when they have ceased to have somatic expression in the race. I am therefore hopeful that Duerden will live to see not only other 42-plumed ostriches but also those which are 45-plumed or possibly even better, if selection for high number of plumes and inbreeding are persistently practised.

One point is worth noticing, which Duerden does not especially emphasize, though it is highly suggestive. He notes the advanced state of degeneration of the ostrich foot (presumably through irrecoverable loss of factors) as seen in the complete disappearance of digits 1, 2 and 5, and the greatly reduced size of digit 4, which leaves the ostrich with practically a single functional toe (digit 3), this being among birds an unparalleled amount of digital reduction. He concludes "Should the loss of plumage continue to a much further degree and marked degenerative changes be set up in the big middle toe, natural selection may then be expected to bring about extinction." This, it seems to me, is a needlessly gloomy view of the case. The fact that the middle toe is "big" contradicts the idea that it will soon degenerate as the other digits have done. If evolution occurred only by loss and never by gain, the middle toe could never have grown "big." But in reality it has probably *grown* as the other digits have disappeared. If so, factors must have been *added* to the genetic complex, or plus factorial changes must have occurred by some other means. Reduction in number of digits does not necessarily mean degeneration. Note the parallel evolution of the horse. Does any one consider it degenerate? Yet in the horse digital reduction has gone even farther than in the ostrich and for a like reason, increasing perfection of a cursorial type, for which one *good* toe is better than three or five ordinary toes. Increase in body size has occurred in both horse and ostrich concurrently with digital reduction. It too has doubtless improved the cursorial type, increasing its swiftness. Thus in the horse and in the ostrich we have the culmination of cursorial types among mammals and birds respectively. Each is highly specialized, but not on that account degenerate or verging on extinction. Extinction will come for each when man says the word but not sooner, so far as we can foresee. Great specialization or great phylogenetic age does not of necessity mean early extinction, if we may judge by the geological history of brachiopods, echinoderms and mollusks. If a suitable environment continues, the specialized organism may continue indefinitely. The idea that genetic variation occurs only in one direction and is irreversible is widespread, but needs substantiation before we accept it into a category of fixed ideas. The world indeed may wait long to see again a four-toed horse, but the reason probably is that we already have a *better* type in the one-toed horse, which replaced the former because it *was* better, not because it was degenerate. If selection, natural or artificial, saw at the present time a distinct advantage in a polydactylous horse, it is quite possible that the type might once again be produced. The animal breeder would ask only such a start as was seen in Cæsar's three-toed steed, to produce a race of polydactyl horses.

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ANOMALOUS RATIOS IN A FAMILY OF YELLOW MICE SUGGESTING LINKAGE BETWEEN THE GENES FOR YELLOW AND FOR BLACK

DURING the course of an experiment involving the breeding of yellow and non-yellow varieties of mice certain anomalous ratios were produced by a family of yellow mice. Since an explanation of these facts brings out considerations regarding yellows which have not been treated in the literature of the subject, it seems well to put the case on record.

The peculiar family originated in a cross of black-and-tan (a very dark form of yellow) with brown. F_1 consisted of blacks and yellows. The blacks when tested proved to be heterozygous for brown and showed in their subsequent generations no peculiarities of inheritance. The F_1 yellows should theoretically have been heterozygous for both black and brown for,

Let YyBB = black-and-tan parent (yellow carrying black) and yybb = brown parent;

Then F_1 should consist of yellows, YybB, and blacks, yyBb.

These F_1 yellows were back-crossed to pure browns.

The progeny distribution to be expected would be as follows:

The F_1 yellow parent, YybB, would form gametes, YB, Yb, yB and yb.

The brown parent, yybb, would form only one type of gamete, *viz.*, yb. The expected zygotic combinations would be

The yellow young obtained from this back-cross should be of two genotypes, YyBb (carrying both black and brown) and

(1)

	YyBb, Yybb	yyBb	yybb
Somatic ratio	2 yellows	1 black	1 brown
Percentage expected	50	25	25
Percentage observed	53.6	28.6	17.7
Number observed	88	47	29

Yybb (carrying brown only). Two were selected for breeding to determine in which genetic class each belonged. If both mice were YyBb we should expect

(2)	2 YyBB 2 Yybb 4 YybB	1 yyBB 2 yyBb	1 yybb
	8 yellow	3 black	1 brown

If both mice were Yybb, we should expect

(3)	2 Yybb	1 yybb
	2 yellow	1 brown

If one mouse were YyBb and the other Yybb, we should expect

(4)	2 YyBb 2 Yybb	1 yyBB	1 yybb
	4 yellow	1 black	1 brown

The actual figures from this mating were (616 × 766) 14 yellow, 4 brown. This result resembles most closely that to be expected if both parents were Yybb. If such were the case, all of the yellows should carry brown only, never black. To test them, two of the 14 yellows were mated with each other (2160 × 2162). They produced 18 yellow, 1 black and 10 brown young. To account for the black young, we must suppose one or both parents (2160 and 2162) to have been heterozygous for black and hence that one of the yellow grandparents (616 or 766) carried black. Black young should have resulted from their mating with each other but failed to do so. Black young were also deficient in the mating of their descendants, 2160 and 2162. The ratio observed among the progeny of 2160 and 2162 indicates that one of them carried black rather than that both of them did, for the expectation if both parents carried black, as in (2), fits even more poorly than the expectation if only one parent carried black, as in (4). The deficiency of black young in the mating of 2162 and 2160 is shown by the percentage of various young observed and expected:

	Yellow	Black	Brown
Per Cent. expected	66.6	16.6	16.6
Per Cent. observed	62.0	3.4	34.5

Of the yellows resulting from this mating six when tested proved to be heterozygous for black as well as brown, while four carried brown only; and of the yellow young resulting from these tests four were shown to carry black and brown, while three carried brown only. Equality of yellows carrying both black and brown and of yellow carrying brown only was expected in contrast with the observed ratio of 10 carrying black and brown to 7 carrying brown only.

CONCLUSIONS

In the case reported the occurrence of black and brown recessives out of crosses between yellows carrying both black and brown is the reverse of that expected because brown (normally recessive to black) has appeared in a frequency more than double the expected, and black has appeared in a frequency less than one third of the expected.

There are three theories which might explain these facts. (1) Reversal of dominance resulting in the dominance of brown over black. This may be discarded because the brown young in this experiment were found not to carry black. (2) Selective fertilization by means of which brown gametes united with brown gametes in more than normal frequency. There is known at present no mechanism for such a type of fertilization nor have any cases of it been shown to occur. (3) Linkage of the genes for yellow and black so that YB and yb gametes are formed more often than yB and Yb gametes. Since in the above matings black animals could only result from a combination of yB with yB or yb the result of a linkage of Y and B would reduce the number of blacks produced. This is substantially the result obtained.

Of the three theories the last is favored because it affords a satisfactory explanation of the observed facts in harmony with other cases of linkage, and because it is more readily susceptible of proof or disproof. It encounters the difficulty of positing a linkage between two genes, one of which (yellow) is either identical with or closely linked to a lethal gene and the other of which has hitherto shown no evidence of being related to the lethal.

It is hoped that more data on the subject will be forthcoming which will show whether the foregoing case is exceptional and due to random sampling or whether the genes for yellow and for black are commonly linked in the gametes of mice.

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GENETICS AND EVOLUTION IN LEPTINOTARSA

In considering work of the kind presented by Professor Tower in his latest partial report on Evolution in *Leptinotarsa* (Tower, 1918) it is necessary, in justice to the author, that we distinguish carefully between three different things: the actual experimental work, the author's interpretation of its results, and his general speculations. Professor Tower had secured an unusually favorable opportunity for attacking his problem, by a fortunate selection of material. The "lineata" group of the genus *Leptinotarsa* comprises a large number of forms generally recognized as "good species," highly variable, crossing freely, often inhabiting markedly different environmental complexes, and easily bred in the laboratory. His work represents a prodigious amount of painstaking labor, covering many years, under most favorable conditions. It will be a matter of regret to many that so large a proportion of this volume has been devoted to very general speculation, rather than a more complete presentation of the large mass of interesting data which he has accumulated.

Considered as a contribution to genetics, there is ample confirmation, but nothing added, to what we already know, though much that was unknown at the time this work was started. The results of his extensive breeding experiments—including selection, intraspecific and interspecific crossing—show nothing, as the author clearly points out, that is not perfectly Mendelian and in accord with the factorial hypothesis. This portion of the work is valuable, at least, as added refutation to the idea that there is anything different involved in species crosses than in intraspecific crosses.

One or two of the experiments, however, give results that seem somewhat anomalous; and it is on these that the author has attempted to build far-reaching hypotheses considerably at variance with those held by other geneticists. The most striking case, perhaps, is in connection with the crosses *L. signaticollis* × *diversa* and *L. signaticollis* × *undecemlineata*. These crosses, when made with material which had been bred in the laboratory for several generations, gave normal Mendelian ratios (monohybrid in the one case, trihybrid in the other). Certain strains of *signaticollis* "fresh from nature" gave, however, in these crosses, very complex and variable arrays. Crossed with *diversa*, for example, there appeared in F_1, besides the ordinary heterozygote, breaking up normally in F_2, a varying number (0–100 per cent.) of forms apparently pure *signaticollis*, which *bred true in all subsequent generations.*

These experiments, to this point, had been previously published by the author (Tower, 1910). Further work on this apparently true-breeding race, however, has served to modify the earlier conclusions as to its composition and behavior. Careful measurements showed that this apparently pure *signaticollis* race behaved normally as regards the form-index (relation of width to length), a specific character never dissociated, in other experiments, from the conspicuous pattern difference involved. Numerous experiments with this peculiarly behaving hybrid failed, with one exception, to find any evidence of the *diversa* pattern factor present. Individuals of this race having the *diversa* (broad) form, crossed with *one particular strain of signaticollis,* gave in F_2 four homozygous forms: pure *signaticollis,* the peculiar true-breeding hybrid (*diversa* form with *signaticollis* pattern), pure *diversa,* and a new form, with a different pattern. These appeared in the ratio of 4:2:1:1 (actual numbers not given), with the corresponding array of heterozygotes.

At first sight, all this seems easy to account for: one or both of the parents in the original cross were heterozygous for one or more factors. The actual results, however, can not be accounted for, according to any known genetic principles, on the basis of the facts given. There are many things at every stage of this work, which we should like to know, about which we are told nothing. The author states that the original parents were "not heterozygous," but no evidence of any genetic analysis is given. In fact, the author declares more than once that he is not interested in ordinary Mendelian analysis, implying that it is unimportant. We do know that one, at least, of these parents was "fresh from nature," that is, genetically an unknown quantity. The author himself shows very completely, in later chapters, that these species, as found in nature, are genetically very heterogeneous. He also emphasizes that the results here obtained can probably not be repeated with material from other locations or even from the same location at other times. Again, we know nothing of the genetic constitution of the *signaticollis* strain used in the "test reaction" where typical *diversa* is recovered; except that only this particular strain will give these results. The F_2 array in this case shows that there are at least two factor-differences involved, while there is only one in the ordinary cross *L. signaticollis* × *diversa.* Other crosses, which will immediately suggest themselves as bearing on the problem, have not been made or are, at least, not mentioned.

Above all, it is to be regretted that in none of these experiments have any definite pedigrees been given, nor the methods of mating in the various stocks. The tables, moreover, are in most cases merely summaries, the original and complete data not being presented. It may well be that the full data and pedigrees of all the author's extensive experiments would be too bulky for publication; but in view of the fact that on this particular series only is based any claim of modification or addition to genetic theory, the raw data and pedigrees might profitably have been included, even to the possible exclusion of a part of the discussion.

Under these circumstances, no attempt can be made at an analysis by ordinary genetic conceptions. This whole experiment illustrates perfectly the real basis of the familiar distinction (implied also by the author in this volume) between results obtained "in the laboratory" and "in nature." The real difference, as well shown in this case, is merely one between working with known materials under controlled conditions and uncontrolled operations with unknown things.

This particular experiment has been reviewed at length, because it is, apparently, solely upon it that the author bases a large amount of rather far-fetched speculation on the "architecture of the germinal material," and the influences of the "surrounding medium" and the effects of crossing upon it. His interpretation of the results involves at least four independent, and distinctly undemonstrated, assumptions: (1) that the observed results are due, immediately, to a (reversible) change in the *relations of the genetic factors to each other;* (2) that these changes are the *direct result of the crosses;* (3) that these particular strains of *signaticollis* owe this peculiar behavior to the direct effect of (cumulative) environmental influence *on the rate of ontogeny;* and (4) that the results are profoundly and permanently modified by the environmental conditions surrounding the parents of the original cross during the maturation of the particular gametes involved.

It is needless to state that none of these hypotheses derives any support from the experience of other geneticists; the only evidence adduced by the author is that above described. The first of these hypotheses is entirely inconsistent with all that we know of the phenomena of linkage; if there is anything certain about genetic factors, it is that they do *not* change their relations to each other. The second hypothesis is evidently reminiscent of the pre-Mendelian conception that something new is produced by the act of hybridization.

In his third hypothesis, the most characteristic and the most involved of this group, there seems to be some confusion in the mind of the author himself as to whether the environment has produced its effect directly upon the gametes, or through its modification of the rate of ontogeny. The latter, however, is clearly implied in several places. But, beyond speaking of hypothetical and rather vague "cytoplasmic determiners," he makes no attempt to even postulate a mechanism by which the *rate of ontogeny*—in this case clearly, on the evidence, a somatic modification, directly dependent on temperature and moisture—can effect genetic changes in the germ-plasm. In regard to the direct effects (immediate or cumulative) of environmental conditions upon the gametes, of which the author makes much throughout his work, it can only be said that, however inherently probable this hypothesis may be, there is no evidence for it in the present work that will be acceptable to most geneticists. For the attempts to distinguish between genetic and environmental factors are, in this case, invalidated by an entirely inadequate analysis of the former. The author assumes, throughout the work, that he is dealing with materials of known genetic constitution; but this is obviously, on his own evidence, not the case. In the absence of a more complete genetic analysis of the materials, there is no valid reason to assume that there is anything involved beyond the ordinary recombination of factors originally present.

Another anomalous result is found in the cross of *L. decemlineata* × *diversa*. These species cross with difficulty; in only 2 cases out of 200 attempts was the cross successful. In both these cases (*decemlineata* ♀ × *diversa* ♂) the F_1 beetles showed all the external characters of the mother, but the food choice and development rate of the father. This hybrid *bred true indefinitely*, showing no splitting up in F_2 or subsequent generations. This kind of "stable hybrid" is familiar to us, from pre-Mendelian literature, but has never withstood the test of rigorous Mendelian and cytological investigation. Such a result can be produced deliberately, where the gametic constitution of our materials has been thoroughly analyzed, by means of "balanced lethals." Should the present case be confirmed, and the numerous sources of error eliminated, this explanation will undoubtedly be found to cover it also. The possibilities of contamination or parthenogenesis should, however, not be overlooked in such cases.

In connection with his selection experiments, the author has unfortunately adopted the theory of "germinal variations" (*i. e.*, modifiability of the genes) since abandoned by its principal proponent. Tower's evidence, like all the other evidence for this theory, is based on a very evident confusion of biotypes with phenotypes, and an apparent failure to recognize *the vital importance of rigid brother-sister mating* in such experiments. In the same experiments, the author finds a very complete refutation (in this case, at least) of his own favorite theory of the direct influence of the environment. In contrast to these indecisive or negative results, there is at least one very beautiful and unquestionable demonstration of the effect of modifying factors (here called "genetic impurities"). Of the three methods by which he attempted to limit the range of variation in the form-index of a certain "biotype" (as he calls it) of *L. multitæniata*—namely, control of the environmental complex, ordinary selection of extremes, and selection of an obvious modifying factor—only the latter gave definite and permanent results. When certain individuals, showing a peculiar variation in pronotal pattern, were selected and bred for this character, *there was an immediate and permanent reduction of the form-index variation to less than half its former range.*

The most interesting and startling contribution made in the author's earlier report (Tower, 1906)—the production of mutations in *L. decemlineata* by temperature and humidity, combined with selection—is not again referred to in the present paper. In regard to the supposed effects of these external conditions in the present work—granting, in the absence of the details of his technique, that the author has been more successful than any other worker in the exact control of humidity and evaporation-rate, there is no evidence, which will be satisfactory to most geneticists, that these factors had anything to do with the results observed.

The results of the author's extended observations and experiments with these same materials "in nature," while generally inconclusive, like all such experiments, are in complete harmony with the general conception of the processes of evolution held by the modern adherents of the factorial hypothesis. The picture we get of the conditions in this group of organisms is one of complex genetic constitution, differing greatly in different localities, resolvable entirely into simple Mendelian factor-differences, a probable selective effect of environmental complexes, with a direct modifying effect of temperature and moisture actually demonstrated only as regards the rate of ontogeny.

With regard to the general philosophic speculations of the author, which occupy a large portion of this volume, little need be said, as this sort of thing is largely a matter of taste. The author states very unmistakeably that his viewpoint is purely mechanistic, but there is much that will scarcely be accepted as such by most mechanists. For instance, his list (p. 6) of the "Categories of Organic Characteristics"—(1) "Specific Properties or Qualities," (2) "Attributes" and (3) "Conditions"—will be regarded with suspicion by those to whom metaphysics is the bête noir of biology. The same may be said of his aversion to "particularistic" theories of heredity. His objections, like most other recent ones, are based on a supposed identification of the gene with a somatic "unit character." Yet he is himself guilty, to an extraordinary degree, of such a confusion in his "scheme of classification of the agents of the germ plasm" (p. 86), where his hypothetical factors are classified entirely according to their apparent somatic effects. This scheme is also dominated by the "organism as a whole" dogma—that the "basic" characteristics of the race are transmitted through the cytoplasm, only trivial characters through the chromosomes and capable of dissociation from the "species complex."

On the whole, it may be said that Professor Tower has convincingly demonstrated the truth of his fundamental premise, that "the general philosophical conceptions from which we interpret nature will largely determine the logical, philosophical, and experimental methods used in investigation and the hypotheses created."

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