issued, 160 pp. Most of the articles treat of insects injurious to man or animals.

SOME years ago Dr. O. M. Reuter published a system of classification of the hemipterous family Capsidæ. Now he has issued a new arrangement.[8] He has modified his previous classification in various details and made nine subfamilies. He gives a list of the genera, placing most of them in the proper subfamily. The article also includes a review of the classifications of the Heteroptera, and a new one, in which he arranges the 40 families in 12 superfamilies. There are tables to these families and to the groups of the Capsidæ. One of the new features is the elevation of *Piesma* to family rank.

NATHAN BANKS

[8] "Neue Beiträge zur Phylogenie und Systematik der Miriden," *Acta Soc. Sci. Fenn.*, XXXVII., No. 3, 1910, pp. 171.

SPECIAL ARTICLES

THE SELECTIVE ELIMINATION OF ORGANS

ONE of the monuments erected to Charles Darwin on the hundredth anniversary of his birth might have been a bibliographic index to the literature of organic evolution. But it is very much easier to pen a series of addresses on Darwin's method, Darwin's real opinion, Darwin's influence, than it is to compile a comprehensive bibliography and analyze it with the thoroughness and detail and wisdom necessary to make it a really useful aid to the investigator; it would have taken a very plucky librarian (with wealthy friends and a genius for interesting them in his undertakings) to carry it through.

As his card manuscript for the subject index approached completion he would have found that several drawers in his cabinet were required for the cards bearing the caption *natural selection*. These cards would have been a key to everything that can be said in a theoretical way about natural selection. The student who would take these cards and attempt conscientiously to cover the field would be ready, after a year's floundering about in the morass of rhetoric, to believe that all the arguments—for and against—have been presented in all their possible permutations.

That no solid foundation for a scientific superstructure is to be found in this polemic quagmire has often been recognized; at present natural selection is out of fashion among biologists. Other problems are in the searchlight.

It is quite natural that a theory which has been so much talked about but as little investigated should cease to be attractive at a time when concrete experimental proof is so much in demand. But can not such proof be adduced for natural selection? Is it not possible that the biologist of to-day with the powerful tools of statistical analysis at his service may be able to demonstrate the existence of natural selection, just as by the use of these tools he has been able to measure the strength of heredity?

Fortunately a beginning has already been made, for if the index were brought well up to date probably over a dozen of the cards in the drawers devoted to natural selection would bear titles of papers embodying the results of serious attempts to measure the intensity of the selective death rate in some organism.

In the selection theory of evolution—the pure Darwinian theory as popularly conceived—there are three factors which must be not only existent, but coexistent, if there is to be any shift in the characteristics of succeeding generations of any organism. These factors are variation, inheritance and selective elimination. If any one of these be absent or its force counterbalanced by some other factor, Darwinian evolution in that species can not be taking place at the moment in question.

Now a great mistake of most of the men who have written on organic evolution has been that they have tried to solve the whole problem. Lacking data (or having only a modicum of data), they have invoked assumptions and logic, and, having proved their assumptions by their logic, have proceeded to generalizations. In dealing with a problem of so great complexity we should keep constantly in mind the fact that it is idle to attempt to untangle the whole snarl at once. Rather we should try to study each factor intensively, isolating it when possible from others and measuring its force. If in doing this we find that variations do occur and in abundance, we have demonstrated an important physiological fact, but a fact without significance in Darwinian evolution unless the variations be both heritable and some of them of such superior utility that they have an advantage over others in the struggle for existence. Again the demonstration of the inheritance of any character does not yield conclusive evidence on Darwinian evolution unless accompanied by a proof of its selective value. Finally it is quite conceivable that a stringent selection should recur every generation without effecting any change in a species—such being necessary to maintain the type in its present condition or without significance because acting upon characters not inherited.

In the face of these difficulties only one course is open to the naturalist: to spend much time in the potting shed and the breeding pen, to be strenuous in the use of the eye piece micrometer, the calipers, the color scale, the statistical tables and the calculating machine; to believe that ten times the conventional number of observations are desirable; to repeat his experiments and to make new series of measurements; and to believe that a few gourds full of statistical constants with tabulated data from which they may be verified are more to be desired than an artesian well of personal opinion based on non-quantitative observations.

The results outlined in this essay are drawn from recent contributions to these gourds full of quantitative data. The tabulated observations and the detailed analysis from which others may verify these statements if they choose are to appear in a forthcoming number of *Biometrika*.

By a selective elimination one understands that the members of a population do not die at random, but that some individuals are, because of innate physical, physiological or psychical peculiarities, much more likely to die[1] than others.

Theories may be spun concerning the relationships of any character whatever to natural selection, but for purposes of scientific investigation one must limit his attention to those which are directly or indirectly measurable. Illustrations of the directly measurable characters are to be found in Bumpus's sparrows, Weldon's crabs, Crampton's moths and Weldon's and di Cesnola's snails.

The characteristics of an individual are the sum of the characteristics of several organs: probably it is the fitness of these organs which largely determines whether the individual shall be able to survive and leave the average number of offspring or more. But suppose that each individual produces a great number of organs, only a small fraction of which become matured and functional. Might it not be possible to determine from some measurable character of such organs whether failure to develop to maturity is due to any characteristic of the organ—in short, whether there is a selective elimination of organs? Ideal material for such investigation is found in some of the flowering plants. A large number of ovaries are formed, of which only a small per cent. develop to maturity. There is a large elimination: to determine whether this is a selective elimination, whether those which survive to maturity differ in any measure from those which die and fall from the plant, is our problem.

The American bladder nut, *Staphylea trifolia,* has a fruit with three cells in each of which from four to a dozen ovules are formed. The number of the ovules can be counted in the ovary of the opened flower and in the matured fruit. Only a small proportion of the ovaries formed reach maturity and by com-

[1] In sexual selection the elimination would occur as a failure to mate. In reproductive selection it would occur as a relatively lower capacity for producing offspring. Here only elimination involving death—in our present material the death of an organ—is taken into account.

paring samples of those which fall from the tree with those which ripen, one can judge whether elimination has been in any degree dependent upon the number or arrangement of ovules in the locules. Naturally conclusions to be valid must be based upon a very large series of countings, and to be quite sure that the differences are not obscured by heterogeneity of material, the ovaries of each individual should be treated separately. In the spring and summer of 1908, about 7,000 ovaries (involving the opening and counting of 21,000 locules) were taken from twenty-eight individuals in the North American tract of the Missouri Botanical Garden. These were in three series; a sample of flowers which fell from the tree when it was shaken gently and which had therefore ceased to develop and were ready to fall from the tree, a sample of those which remained, and, finally, a collection of the matured fruits later in the summer.

The second collection represents probably most nearly the condition in the original population of pods; it contains some which would have developed to maturity and some which would have fallen from the tree later. The most critical comparison for the detection of selective elimination is that of the eliminated with the matured ovaries. This is the comparison which will be chiefly employed in these pages.[2]

The conviction that there must be a selective elimination of ovaries came to me through an extensive biometric study of fertility in various kinds of fruits. The immediate suggestion for the detailed investigation begun in 1908 was furnished by a small series of developing ovaries of *Staphylea* collected for quite a different purpose in the spring of 1906. These fell into three length groups, 5–10, 11–15 and 16–20 mm. If selective elimination really occurs one would expect the third series, which has most nearly reached maturity, to differ sensibly from the second and especially from the first. The results from this series are in general agreement with those for the 1908 collections, although the method in which they were made prevents their being strictly comparable. The difference in method emphasizes the soundness of the conclusions drawn.

Changes in Mean due to Selective Elimination.—In any investigation of natural selection the first step is to ascertain whether a difference in the size of organs or in the number of parts can be demonstrated between those individuals which are eliminated and those which survive. Concretely, for our present problem, are ovaries with many or ovaries with few ovules best fitted to become functional?

Diagram 1 makes very clear the differences in the average number of ovules per locule for the 1908 series. The arrows show that in 27 out of the 28 individuals the result of the elimination has been to raise the average number of ovules per locule by the elimination of those with lower numbers. The amount of difference in the mean of eliminated and matured ovaries is shown by the length of the shaft for the individual shrubs and by the two transverse lines for the combined collections. The broken line shows the mean for all the eliminated, and the solid line the mean for all the matured, ovaries. The difference between the two is pronounced. Arithmetically it is

Average for eliminated ovaries	$= 7.2355 \pm .0092$
Average for matured ovaries	$= 7.7474 \pm .0080$
Difference	$= .5119 \pm .0121$

Absolutely the difference is only half an ovule, but the number of observations on which this average is calculated is so large that the probable error of the difference is small and its trustworthiness very great. Relatively the difference represents an increase of no less than seven per cent. in the number of ovules per fruit.

Looking at the diagram again, we note that individuals differ widely among themselves in the lengths of the arrow shafts—the amount of the difference between the eliminated and

[2] All comparisons are worked out in the original memoir, which must be consulted for details.

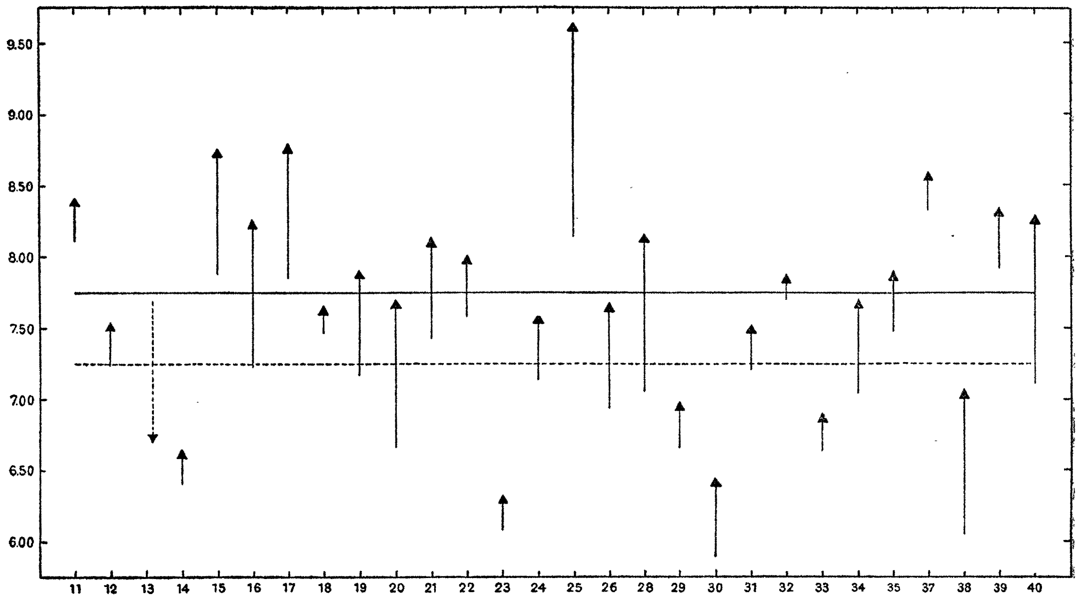

DIAGRAM 1. Showing change in mean number of ovules due to selective elimination for each of twenty-eight individuals.

the matured ovaries. There are probably two reasons for this. The first is that there is a real difference between individuals in this respect. The second is that a part of the variation is due to the probable errors of the constants.

Both constants, based as they are upon random samples—and in the case of the individuals, not very large samples—are subject to the limitations of a probable error of random sampling.[3]

It is interesting to inquire how many of the differences for individual trees may be regarded as trustworthy. Following the conventional standard, we find one significantly negative difference, two which are positive and probably significant, and twenty-five which are positive and unquestionably significant.

From the 1906 series in which the ovaries were taken in different stages of development, we find confirmatory evidence. We have for average ovules per locule:

Series A = 6–10 mm. ovaries,	Av. =	7.232 ± .029
Series C = 16–20 mm. ovaries,	Av. =	7.821 ± .016
Difference	=	.589 ± .033

Here the difference is nearly eighteen times its probable error, and represents an increase in mean number of locules of over eight per cent. of the mean for the youngest fruits.

From the foregoing facts only one conclusion can be drawn. In *Staphylea* the failure of ovaries to develop to maturity is not random but selective. Ovaries with lower number of ovules have smaller chances of becoming fruits than those with higher numbers. The intensity of selection is such that there is a difference of about seven per cent. in the mean number of eliminated and matured ovaries.

Changes in Variability due to Selective Elimination.—The comparisons for variabil-

[3] This is the plus or minus quantity attached to the means given above. Conventionally a difference between constants is considered trustworthy if it is two and a half times its probable error. The difference of the two general-series means given above is over forty times its probable error.

ity in the number of ovules per locule and per fruit are somewhat more complicated than those for mean number, so the reader need not be burdened with details.

On the whole it seems that the variability of the matured fruits is less than that of the original series of ovaries before elimination has taken place. In the 1906 series, where we are working with ovaries in different stages of development, there seems to be a steady decrease in the variability as we pass from the youngest to the oldest.

In the 1908 collections the eliminated organs also seem to be less variable than the original series. Probably this means that those which develop to maturity came largely from the upper end of the original range of variation, while those which fail came chiefly from the lower end. Obviously the variability of a part of a population selected towards a particular mean or type can not equal that of the whole population.

Changes in Mean Radial Asymmetry due to Selective Elimination.—In a fruit of *Staphylea* the numbers of ovules may be the same in all three cells or differ from locule to locule. Opening the compartments quite at random—there being no external characteristic to indicate any difference in them—one may find such numbers of ovules as

11—11—11
10—11—10
8—10—9
9—9—11
9—7—10

and so on.

Now we may consider a fruit in which the ovules are distributed equally among the three locules as radially symmetrical with respect to number of ovules per locule; such are fruits of the type 8–8–8, 9–9–9, 11–11–11. Ovaries with one locule differing from the others by a single ovule, *e. g.*, 9–8–9, are somewhat radially asymmetrical, while those with all three locules with different numbers of ovules, for instance 9–8–7, are more so.

As a measure of this radial asymmetry we may take the mean square deviation of the number of ovules per locule from the mean number in the whole fruit. For a fruit of the type

$$\begin{matrix} (a) & (b) & (c) \\ 7 & -\;8\; - & 6 \end{matrix}$$

the mean number per locule is 7 and we have:

$$(A-a)^2=0$$
$$(A-b)^2=1 \qquad \text{Coefficient of asymmetry}$$
$$(A-c)^2=1 \qquad \sqrt{2/3}=.8165$$

For an ovary of the formula 7–8–7, $A=7.333$, $(A-a)=+.3333$, $(A-b)=-.6666$, $(A-c)=+.3333$, and the coefficient of asymmetry is

$$\sqrt{\frac{.3333^2+.6666^2+.3333^2}{3}}=.4714.$$

The asymmetries of the fruits studied in 1908 ranged from .0000 to 2.1602. To determine whether there is a selective elimination depending upon the radial asymmetry of the fruit as just defined, we obtain the coefficient for each individual ovary and compare the means of those in the eliminated series with those which develop to maturity. Diagram 2 constructed in the same manner as that for the means shows the result for the individual trees. The arrows show that in seven cases the mean asymmetry is greater after elimination has taken place, while in twenty-one cases it is less. The two transverse lines show that for the grand totals there is a very decided reduction in asymmetry as we pass from the eliminated to the matured ovaries. Statistically the differences are:

Mean asymmetry of eliminated ovaries
$=.4515 \pm .0051$
Mean asymmetry of matured ovaries
$=.3724 \pm .0045$
Reduction in asymmetry by selective elimination
$=.0791 \pm .0068$

Absolutely the difference is not large, but relatively it appears that there has been a reduction of $(.0791 \times .100)/.4515=17.5$ per cent. The difference is more than ten times its probable error and highly reliable.

For the developing ovaries taken in 1906

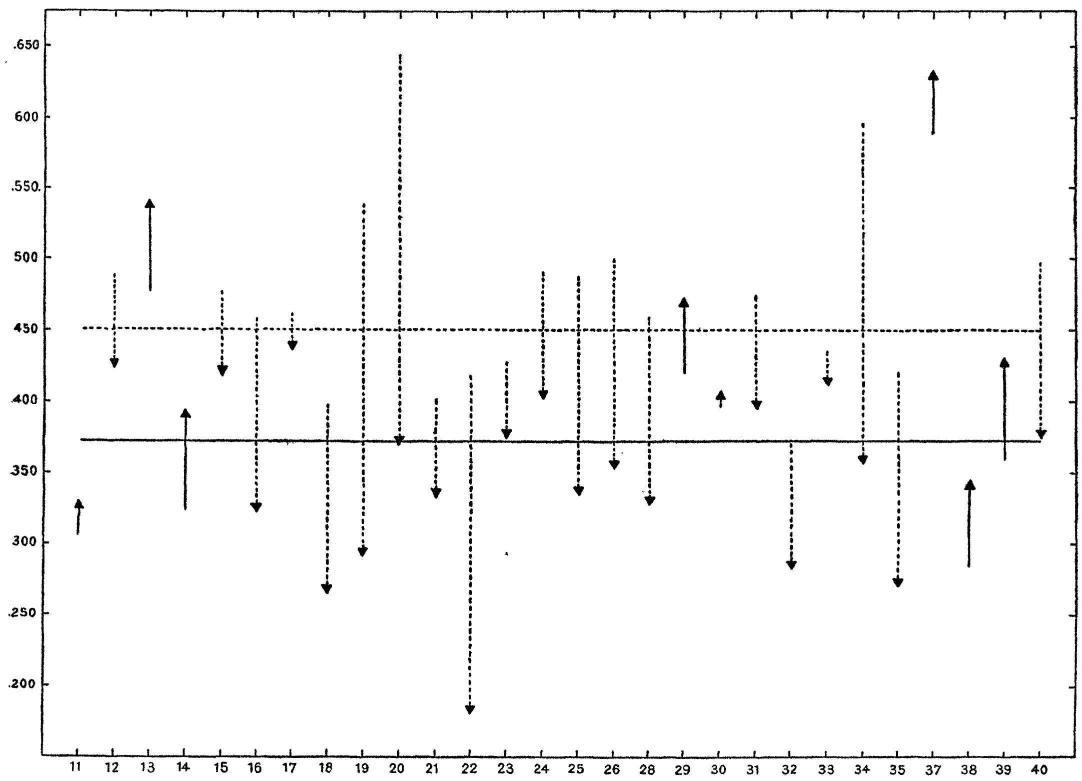

Diagram 2. Showing change in radial asymmetry due to selective elimination for each of twenty-eight individuals.

the differences in asymmetry between largest and smallest are:

Average asymmetry of 6–10 mm. ovaries
$= .382 \pm .016$

Average asymmetry of 16–20 mm. ovaries
$= .302 \pm .013$

Reduction in asymmetry by selective elimination
$= .080 \pm .020$

This result, a decrease of 20.9 per cent. in asymmetry, agrees with the preceding, but owing to the smallness of the series the probable errors are relatively large.

The differences in the eliminated and matured ovaries appear in the frequencies of the individual asymmetry classes. Grouping together the relatively few asymmetries of 1.2472 and over, reducing the frequencies of both eliminated and matured ovaries to a percentage basis, we obtain diagrams 3 and 4. Here the areas with horizontal shading represent the frequency of eliminated ovaries or of the youngest ovaries, while the vertical shading shows the frequency of matured fruits or of the most mature fruits for each of the five asymmetry classes.

The conclusions to be drawn are as obvious as in the case of the mean number of ovules. The failure of pods to complete their development is not a matter of chance, but there is a selective elimination in which the proportion of radially asymmetrical fruits is very greatly reduced. The ovaries which survive to maturity are much more symmetrical than those which are unable to complete their development.

Changes in Locular Composition due to Selective Elimination.—The number of ovules in *Staphylea* varies from about four to about thirteen. Locules with numbers such

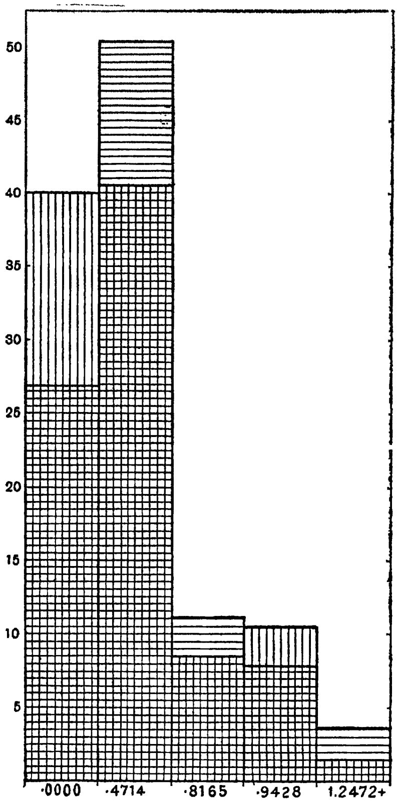

DIAGRAM 3.

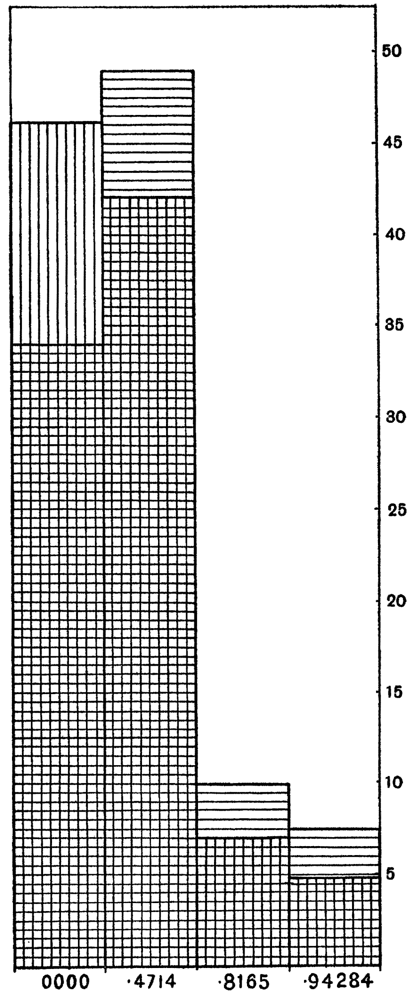

DIAGRAM 4.

as 4, 6 and 8 are conveniently designated as "even" while those with the numbers 5, 7, 9 and so on are tersely described as "odd."

The suggestion that these two types of locules may differ in their capacity of developing to maturity is not the product of the mathematician's fancy, but the working hypothesis sequent upon a large mass of biological observations. The biological reasons for determining whether there is a selective elimination of fruits with a preponderance of "odd" locules are two.

First: I knew from large and numerous series of statistical data that there are in some species of plants differences in the relative numbers of "odd" and "even" locules in the matured fruits.

Second: The ovules in the flowering plants are generally borne on the two margins of a carpellary plate. The ovary is formed by the fusing of the two margins of the embryonic plates, either with each other or with the margin of the adjoining plate. So far as I am aware the development of the ovary of *Staphylea* has not been investigated, but judging by analogy with other forms, it would seem that each locule represents a single carpel with two ovule-bearing margins fused together.

If this be true it is clear that a carpel with an odd number of ovules,[4] say seven, must have a different number on the two margins, while one with an even number of ovules quite generally, though not invariably, has them equally divided between the two sides. In short, a locule with an even number of ovules more generally represents a bilaterally symmetrical plate of carpellary tissue.

Let us hope that there is no mistake in regard to these two suggestions. They are not advanced as proofs of, or arguments for, a selective elimination, but merely as the reasons which led me to look for elimination on the basis of this character.

The actual results secured are now to be considered.

With respect to the character of their locules, the fruits may be classified:

3 "even"
2 "even" + 1 "odd"
1 "even" + 2 "odd"
3 "odd"

One test may be made in either of two ways: we may either compare the percentage of "odd" locules in eliminated ovaries with the percentage in matured ovaries, or by studying the percentage of each of the four classes in the two series.

Using the first method we find for the 1908 series:

"Odd" locules in eliminated series
$= 37.407 \pm .412$ per cent.
"Odd" locules in matured series
$= 25.185 \pm .325$ per cent.
Decrease in "odd" locules by selective elimination
$= 12.222 \pm .524$ per cent.

And for the 1906 collections:

"Odd" locules in youngest series
$= 33.91 \pm 1.40$ per cent.
"Odd" locules in oldest series
$= 27.23 \pm 1.05$ per cent.
Decrease in "odd" locules by selective elimination
$= 6.68 \pm 1.75$ per cent.

There can be no reasonable doubt that these differences are significant, and that there is some biological reason why locules with "odd" numbers of ovules are less capable of completing their development than those with "even" numbers.

Naturally one locule can not fail to develop without two others falling at the same time. The final test of our theory is to determine whether ovaries with one to three "odd" locules are more likely to be eliminated than those with all three locules with "even" numbers. The results are obtained at once by reducing the frequencies for the 2,095 eliminated ovaries and the 2,707 matured fruits of the 1908 series and the frequencies for the 174 youngest and the 273 oldest ovaries in the 1906 collections to percentages. Tables I. and II. show the figures.

TABLE I

1908 Series. Elimination of Ovaries with a Preponderance of "Odd" Locules

Locular Composition.	Percentage in Eliminated Series.	Percentage in Matured Series.	Difference Due to Selective Elimination.
3 "even"	28.40	46.78	+18.38
2 "even" + 1 "odd"	37.61	34.32	— 3.29
1 "even" + 2 "odd"	27.35	15.46	—11.89
3 "odd"	6.64	3.44	— 3.20

TABLE II

1906 Series. Elimination of Ovaries with a Preponderance of "Odd" Locules

Locular Composition.	Percentage in Youngest Ovaries (6–10 mm.).	Percentage in Oldest Ovaries (16–20 mm.).	Difference Due to Selective Elimination.
3 "even"	33.33	45.78	+12.45
2 "even" + 1 "odd"	39.08	31.14	— 7.94
1 "even" + 2 "odd"	20.12	18.68	— 1.44
3 "odd"	7.47	4.40	— 3.07

Two things are very prominent in these tables. The first is the fact that in all four series the formulæ with a preponderance of "even" are greatly in excess of those with a preponderance of "odd" locules. For 1908 these are 66 per cent. of the eliminated and 81 per cent. of the matured ovaries. In 1906 they are 72 per cent. of the youngest and 87 per cent. of the most mature ovaries.

No less marked is the fact that all classes of ovaries except those with only "even" locules have become relatively less frequent

[4] I see no reason to doubt it, but of course a working out of the problem on *Staphylea* itself by some embryologist is highly desirable.

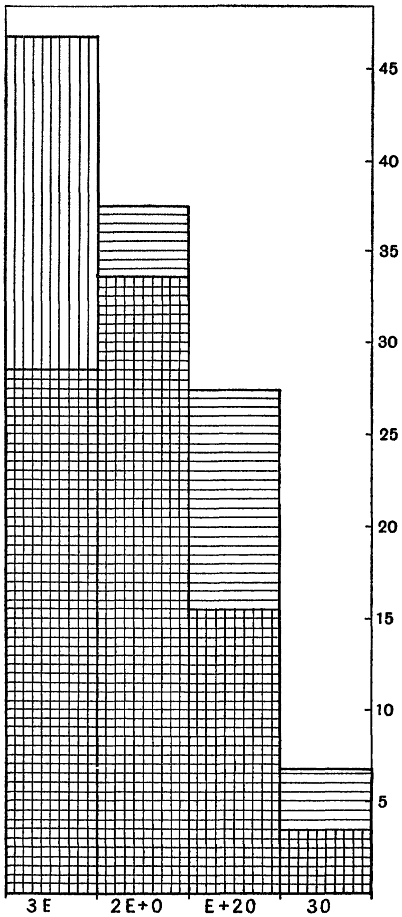

DIAGRAM 5.

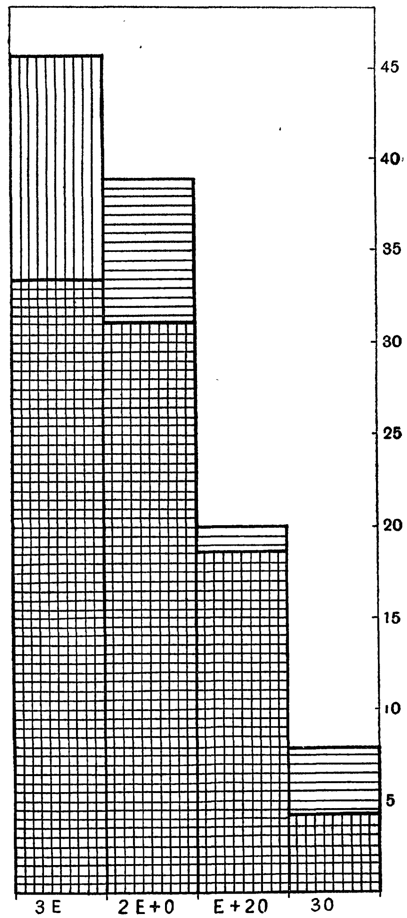

DIAGRAM 6.

by the elimination. Diagrams 5 for 1908 and 6 for 1906 constructed on the same plan as diagrams 3 and 4 make this perfectly clear.

The two characters, radial asymmetry and locular composition, are not independent. The more asymmetrical fruits are, in the long run, somewhat more likely to have more "odd" locules than the average. The intensity of the relationship is shown by a correlation of about .300. In consequence of this condition it is not possible to say without further analysis whether both characters are of selective value, or whether the elimination of ovaries with one of the characters—either the presence of "odd" locules or radial asymmetry—is due merely to the fact that they also possess, in some degree, the other.

If we divide our material up into groups according to both asymmetry and locular composition, and then determine whether within these groups there is a change in the mean value of the other character as we pass from the eliminated ovaries to those which have developed to maturity, we shall, I believe, be

TABLE III

1908 Series. Selective Elimination of "Odd" Locules within the Chief Asymmetry Classes

Radial Asymmetry	Difference in Number of Odd Locules in Eliminated and Matured Ovaries.
.0000	—.335
.4714	—.106
.8165	—.115
.9428	—.454
1.2472	—.157

able to ascertain whether one or both of the characters are of some selective value.

Tables III. and IV. show the results for the 1908 material. The differences are not large, but they are consistent throughout. This indicates, I think, that both characters are of some independent selective value.

TABLE IV

1908 Series. Selective Elimination for Radial Asymmetry within the four Locular Composition Types

Character of Ovary.	Difference in Radial Asymmetry in Elimination and Matured Ovaries.
3 "even"	—.017
2 "even" + 1 "odd"	—.019
1 "even" + 2 "odd"	—.034
3 "odd"	—.077

Change in Number of Locules per Ovary due to Selective Elimination.—Normally in *Staphylea* the fruit is three-celled, but not infrequently (in some individuals especially) those with two and those with four cells occur.

To determine finally whether either of these types has better chances of surviving than the others would require very large series of observations.

So far as the results from 2,000 eliminated and 3,000 matured ovaries are trustworthy

TABLE V

1908 Series. Showing Elimination of Dimerous Ovaries

Description of Ovaries.	Actual Frequencies.		Percentage Frequencies.	
	Eliminated.	Matured.	Eliminated.	Matured.
2-celled ovaries	54	52	2.48	1.49
3-celled ovaries	2,095	3,355	96.14	96.05
4-celled ovaries	30	86	1.38	2.46
Total ovaries	2,179	3,493	100.00	100.00

Table V. shows that dimerous ovaries are more liable to elimination than tetramerous ones.

Summary.—From the constants in the foregoing sections there can be little doubt concerning the fact of a selective elimination of the ovaries of *Staphylea* during their development from flowering time to the maturing of the fruit. By this selective elimination the mean number of ovules is increased, the mean radial asymmetry is lowered, the proportion of ovaries with odd numbers of ovules in one or more locules is very stringently cut down, and perhaps the mean number of locules per fruit slightly raised.

These results are, I am inclined to think, of considerable importance from the standpoint of morphology and physiology. They show that a physiological unfitness—an incapacity for developing to maturity—is coupled with certain definite morphological characters. Personally I take it that we are not to assume that low numbers of ovules, high radial asymmetry and the presence of "odd" locules are fundamental causes of the incapacity for development, but rather that both morphological and physiological peculiarities are dependent upon some inherent abnormality of the growing point which morphologically finds its expression in the structural features of the fruit and physiologically in its relative capacity for development. These interrelationships between slight aberrations of structure and the capacity of organs for performing their functions offer a most attractive field for research.

In their bearing on the problem of organic evolution the results outlined in this paper are of interest in showing that natural selection may act upon the organs of an individual as well as upon the individual organisms of a population. Without knowing whether the characters we have investigated are inherited it is impossible to say that this elimination is a factor in maintaining the present type of the species.[5] And to argue that this kind of natural selection has been of significance in evolving the considerable degree of radial symmetry found in the fruits of many species of plants with compound ovaries would be stepping too far from a secure pier of facts into the uncertain bog of speculation.

J. ARTHUR HARRIS

COLD SPRING HARBOR, N. Y.,

September 8, 1910

[5] It seems to me unlikely that we shall ever be so fortunate as to find many cases of Darwinian evolution going on in nature. That a constant selection may maintain a type already secured, and that one may be able to observe and measure the intensity of this factor, seems much more probable.