HEREDITY, VARIATION AND THE RESULTS OF SELECTION IN THE UNIPARENTAL REPRODUCTION OF *DIFFLUGIA CORONA*[1]

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[1] From the Zoölogical Laboratory of the Johns Hopkins University.

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INTRODUCTION

The problems

Do heritable variations arise in organisms multiplying vegetatively? If so, how frequently and to what extent? Can the inherited characteristics in such an organism become altered as a result of selection? If so, to what extent and at what rate? Does a population consist of diverse strains that are (a) relatively, or (b) completely, permanent in hereditary constitution? What part do such strains play in the observed inheritance and in the results of selection within such a population?

Such are the questions here dealt with, as bearing on the underlying question: Can we see evolution occur if we observe the propagation of a simple organism through many generations? The questions are attacked through an investigation of an organism presenting most favorable conditions for their answer,—the shelled rhizopod, *Difflugia corona* Wallich.

In cross-bred organisms, where each individual arises from a mixture of the substance of two parents, heritable variations appear constantly and selection gives marked results. But this is due largely to the working out of the rules of inheritance in new combinations of germinal material, so that it might occur quite without evolutionary change. Whether any given heritable change is produced in this manner, or is an actual evolutionary change, is in such organisms a question of extreme difficulty.

Where there is no mixing of diverse lines of descent, each individual arising from a piece of a single parent, conditions are infinitely simpler. Many investigations of such uniparental reproduction have yielded the result that there is a marked permanence of hereditary character within any single line of descent, all the progeny being like the parent in hereditary constitution; further that many such lines, diverse in hereditary constitution, may exist in a population, and that the effects of selection consist mainly if not entirely in the isolation of such diverse lines. This permanence of type has appeared so marked as to make it worth while to introduce a term—genotype (JOHANNSEN)—for the hereditary constitution of the line of descent. These results complement those obtained from the study of Mendelian inheritance in cross-bred organisms, the two together seeming to account fully for changes in hereditary characters occurring in biparental reproduction.

The theory of evolution, with all the facts that speak for it, of course requires that actual evolutionary changes, aside from the mere recombination of fixed factors, shall occur. The difficulty of recognizing such changes in the course of biparental reproduction throws much weight upon the study of uniparental reproduction. If, as some maintain, gradual evolutionary changes accompany reproduction, *it must be possible to discover these when there is no mixing of diverse lines at reproduction.* This is the thought that has held investigators to the study of inheritance and selection in uniparental reproduction.

How far are the reported negative results with "pure lines" of general validity? These negative results have been subjected to certain criticisms, notably by PEARSON (1910), HARRIS (1911) and CASTLE (1914 a, b),—criticisms that require serious consideration. As aside from the general desirability of further evidence on the matter, it was these criticisms that inspired the present work, and as the investigation was designed to furnish a precise test of their validity, it will be well to state them briefly. The criticisms that have been or may be made are mainly as follows:

1. The characters studied in the pure line work have not as a rule

been sharply defined and readily determinable; but have been such matters as size, or certain physiological peculiarities, not lending themselves so readily to studies of inheritance as do the absence or the presence and color of pigments, or the existence and number of definite structures. If more definite characters had been studied, possibly inherited variations might have been detected.

2. The characters studied are continually altered during growth, so that many of the so-called variations are mere growth stages.

3. The characters studied are greatly modified by environmental agencies during the life time of the individual, so that many of the supposed variations are merely environmental modifications. The facts set forth in this and the foregoing paragraph are held to account largely for the fact that 'variations' within the 'pure line' were not found to be inherited, that selection was of no effect.

4. PEARSON (1910) has shown that in certain cases of populations propagating by uniparental reproduction, there is a slightly greater correlation between the characters of given individuals and those of their immediate parents, than between those of the individuals and their remote ancestors. This would not be expected on the genotype theory and might seem to indicate a progressive racial change (though in the few cases known it might be due to accidents of the sampling).

5. Furthermore PEARSON (1910) shows that in some of the 'pure line' work there was actually a slight correlation of parent and immediate progeny within the single line,—so that an inheritance of parental peculiarities appears to be indicated; this is shown for the work of JOHANNSEN (1903) and that of HANEL (1908). The facts here have been recently reviewed by LASHLEY (1915).

6. Finally, it is pointed out that in most of the work with 'pure lines', but few selections have been possible, these covering but few generations. If selection could have continued longer (and had not been based largely on growth stages and environmental modifications), it would perhaps have been effective.

To test the validity of these criticisms, it became necessary to find organisms multiplying vegetatively, with definite structural characters that can be counted and measured, these characters being (1) unchanged by growth; (2) unaffected by the environment during the life of the individual; (3) heritable, yet (4) variable. Further the organisms must multiply rapidly, so that a large number of selections may be made, extending over many generations. This unusual combination of favorable conditions is presented in a high degree by *Difflugia corona*.

The investigation of this favorable organism was designed squarely as a test for the validity of the criticisms set forth above. It is part of a general series of investigations on inheritance in uniparental reproduction undertaken by investigators in the ZOÖLOGICAL LABORATORY of the JOHNS HOPKINS UNIVERSITY. It may be remarked that the aim in view in this work has been to *find heritable variations and effects of selection if such occur;* with this in view any clue that seemed to lead in that direction has been eagerly followed. Besides my own earlier papers on Paramecium (JENNINGS 1908, 1913), giving negative results, there have been already published from this series of investigations the papers of LASHLEY (1915, 1916), MIDDLETON (1915) and STOCKING (1915).

The organism: Difflugia corona

The organism studied, *Difflugia corona* Wallich, is an ideal one for determining the course of inheritance and variation in lower animals. It presents six well-marked structural characters, each separately countable or measurable, and none of them modified by growth or environment during the life of the individual. The shell (figure 1), produced at the time of fission and not subsequently changed, has a definite size and structure. We can distinguish the following characters: (1) the diameter of the shell; (2) its dorso-ventral axis ("depth"); (3) the diameter of the mouth on its lower surface; (4) the mouth has about its circumference a definite number of distinct and well formed teeth, which can readily be counted; (5) on the surface of the shell are a varying number of spines which can be counted with ease; (6) the length of the spines can be measured. The number of spines and the number of teeth are at first view the most strikingly favorable characters for work; it was on account of the former that the organism was originally selected. But it turned out later that in many respects the diameter of the shell and the length of the spines furnish most valuable opportunities for work. The diameter of the mouth and the oral-aboral depth of the shell were less studied.

Through the fact that all these characters are produced at the time of fission and are not later altered, there is avoided all such difficulties as are inherent in the study of the size or form in organisms that grow during their life time; or in study of the rate of fission or of other physiological characters. The characters of Difflugia fall thus into the same category as the coat colors and patterns of birds and mammals; if the environment has any effect on them, it acts only at the time of reproduction.

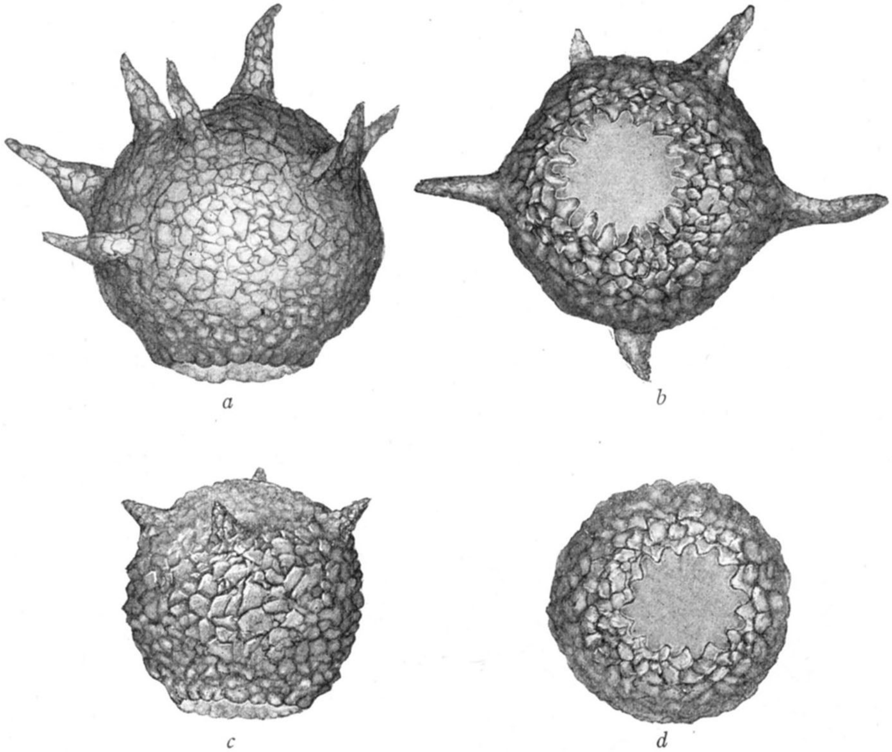


FIGURE 1.—*Difflugia corona,* to show the characters. *a* and *b,* side view and oral view of an individual of the family No. 248, showing the 7 large spines, the mouth with its 16 teeth, etc. *c* and *d,* similar views of an individual of the family No. 314, with 4 small spines, 14 teeth, etc. (× 190).

Furthermore, the shell once formed exists as a permanent record of the characteristics after the death of the animal. As compared with infusoria, it is notable that the new shell formed at fission is a distinct structure, the old one persisting along side of it, so that parent and offspring are in a certain sense distinguishable (see figure 2).

Reproduction in Difflugia corona

To form a clear idea of inheritance and variation in the characters, one must have in mind the method of reproduction in Difflugia (figure 2). The spheroidal shell contains a mass of protoplasm. At the time of reproduction this mass absorbs water, swells, and projects from the mouth. The part projecting attains a volume equal to that of the interior of the parent shell, and assumes a form corresponding to that of the parent. Protoplasmic projections (like pseudopodia) over the surface

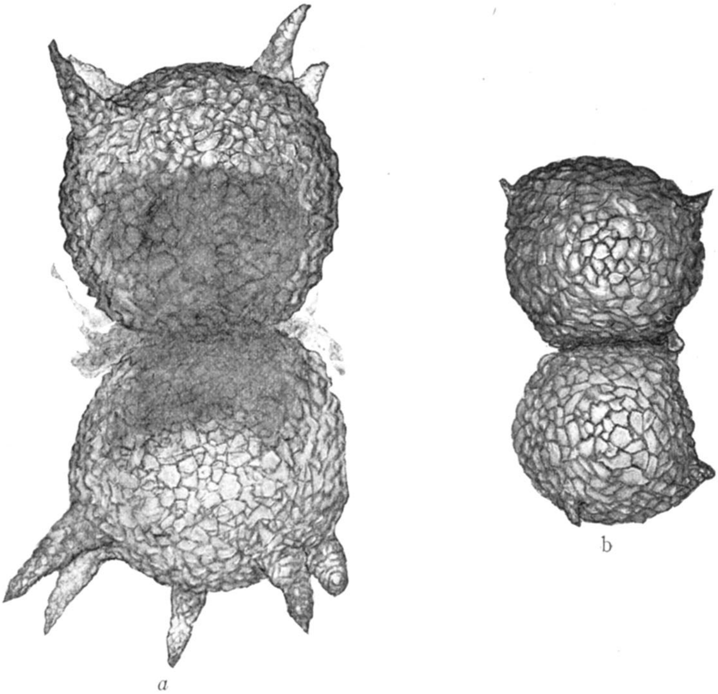


FIGURE 2.—Reproduction in *Difflugia corona*. Note that the newly formed individual (below in each case) is lighter than the parent. *a*, pair from the family 326. *b*, pair from the family 314. (× 190.)

of this mass form the foundation for the spines. Meanwhile there is within the parent a mass of sand-grains that has been collected during its life. This mass passes into the interior of the projecting sphere; the sand grains then come to the surface, and spread themselves over it. They are imbedded in a chitinous secretion which becomes hard, so as to hold the sand grains in place. Thus the new shell forms a mold repeating the form and relief of the protoplasmic mass projecting from the mouth of the parent shell. Meanwhile division of the nucleus (or nuclei) has occurred; the two protoplasmic masses separate; the old and new shells pull apart at the mouths, and the two animals become distinct. The mouth of the new shell, by which it was in contact with that of the mother shell, remains open; and during the reproduction the teeth surrounding the new mouth have been formed. The newly formed shell is always at first somewhat lighter in color than that of the discolored "parent", so that it is possible to identify the two for some time after separation; this difference is shown in figure 2.

As is shown in figure 2, the size and other features of the newly formed shell closely resemble those of the parent,—diverse parents producing diverse progeny. This fact of course furnishes the main basis for this investigation.

Unfortunately, in *Difflugia corona* the animals are, at fission, always imbedded in a mass of detritus, so that the details of the process have not been observed. The modeling of the spines over protoplasmic projections is thus not an observed process, but their formation can hardly occur otherwise. Certain details of reproduction will be brought out in the course of our account.

The animals reproduce at intervals varying from about a day to a month or more. The average interval under good conditions is in the neighborhood of four or five days.

Methods

a. Occurrence

Difflugia corona is not particularly uncommon in quiet ponds or pools on aquatic vegetation. The animals are at times abundant on blue-green algae; also on green algae of various sorts; upon the water net, and the like. At times they occur on Elodea, and though they are not usually abundant here, this plant often forms a very constant and uniform source of supply. The animals feed amid the brown ooze that covers the surface of such water plants. Those I have used came from certain pools about Baltimore; the best of these is a pond at Homewood, on the University grounds.

b. Culture

The animals were cultivated in the concavities of hollow-ground slides, each concavity containing 5-10 drops of water. No cover glass is used, but the slides (each with two concavities) are kept in moist chambers.

The animals thrive and multiply in the ooze washed from the water plants on which they live. This ooze must be freshly collected every three or four days, or for some races, about once a week. The simplest plan is to bring in a handful of the water plant (Elodea for example), together with a little of the pond water. This vegetation is shaken up in a jar (with added water), to remove the ooze. The plant itself is taken out, and the heavier and larger particles are allowed to settle to the bottom. The water with the lighter ooze is then poured off, and this is employed fresh as the culture medium. In the five to ten drops of water used for each individual, enough of the ooze is taken to make a rather thin brown layer over the bottom,—not so thick as to prevent the finding of the animals under the Greenough binocular.

By this method any new specimens of Difflugia occurring in the ooze that is to be used for culture usually sink to the bottom with the heavier particles, so that they are gotten rid of. But of course to avoid contaminating pedigreed stock, it is absolutely necessary to carefully examine each slide for foreign specimens, before the pedigreed individual is removed to it.

Thus when the culture material is to be changed (every 3-7 days), fresh clean slides are prepared with the freshly collected ooze, and examined with the binocular to remove any foreign individuals. It is advisable to remove at the same time any other animals of some size, such as entomostraca, insect larvae, flatworms, etc., as many of these devour Difflugia. Then the individual to be cultivated is transferred with a capillary pipette from the old slide to the new one, and the appropriate label written in lead pencil on the rough-ground surface of the slide. At this time of course 'parents' are separated from 'progeny', so as to keep pedigrees complete and accurate.

An immense amount of time was wasted in attempts to make a culture medium in the laboratory; or to get satisfactory ooze formed on plants growing in aquaria. All such attempts were failures. It is possible that with Elodea growing in large aquaria or basins success might finally be achieved.

c. Pedigree records

For keeping pedigrees, records are kept in card catalogues, a card being devoted to each individual. The system may be illustrated as follows: The original 'wild' individual is given a number—say 21. Its first progeny is called 21.1, its second, 21.2, etc. The first progeny of 21.1 is 21.1.1, its next 21.1.2, etc. Thus in later generations we have cumbrous labels such as 326.1.4.2.2.3.2.1.2.2.2.1.1.2. These labels must be written on the slide and its corresponding card. On the card is written a brief description of the individual, including the number of spines, and any peculiarity that will distinguish it from its progeny. Whenever an individual reproduces, that fact, with its date, and the number of spines of the progeny, is entered on the card of the parent, and a new card is written for the progeny. The long labels become troublesome, but each gives the full pedigree and relationship of the individual, and with the card records of all, the entire history may be reconstructed. It is necessary to give to each specimen the same individual care and attention that one would to rabbits or calves, if satisfactory results are to be attained.

After an individual has reproduced, it may of course be maintained that neither of the resulting individuals is, so far as the protoplasmic mass is concerned, the parent; both have been derived by the division of a single mass. But as one of the new individuals remains in the old shell, it is convenient to call this the parent, the other the progeny, and no later inconvenience or fallacy results.

d. Preservation

When a specimen dies or is no longer to be cultivated, it is preserved in a drop of glycerine, for further study. One places the shell on a slide, withdraws the water with a capillary pipette, and adds a small drop of glycerine. No cover is used (use of a cover usually resulting in crushing the shell), and the specimens in the open drops may be kept in upright boxes for months. The drops, however, unless the glycerine is renewed, finally dry up.

e. Computations

The number of spines was determined in the living individual. The teeth may likewise be counted and the measurements taken while the animal is alive, but these are usually more satisfactorily done on the preserved shells.

Much of the work involved the use of statistical methods; particularly the determination of the coefficient of correlation. The correlations were mostly worked out by the following formula and method, which may be recommended, particularly to persons who desire to obtain the coefficient of correlation without working out first the standard deviation. The formula is:

$$r = \frac{n \,.\, \Sigma xy - \Sigma x \,.\, \Sigma y}{\sqrt{\left(n \,.\, \Sigma x^2 - (\Sigma x)^2\right) \cdot \left(n . \Sigma y^2 - (\Sigma y)^2\right)}}$$

in which x and y represent the *values* of the measurements, not their deviations. The formula gives the same results as the usual formula of the product method, in which the standard deviation is employed, but eliminates a number of unnecessary operations.

For simplification it is well to break the operation into a number of definite steps, as follows:

Find the following five values: Σx, Σx^2, Σy, Σy^2, Σxy. Next find the values a, b, and c, which are the following:

$$n.\Sigma xy - \Sigma x.\ \Sigma y = a$$
$$n.\Sigma x^2 - (\Sigma x)^2 = b$$
$$n.\Sigma y^2 - (\Sigma y)^2 = c$$

Then find the following:

$$R_x = \frac{a}{c}$$

$$R_y = \frac{a}{b}$$

and finally $r = \sqrt{R_x\ .\ R_y}$ (coefficient of correlation).

The quantities R_x and R_y are the two coefficients of regression; their geometrical mean is the coefficient of correlation r. By multiplying R_x by R_y and looking up the square root of the product in Barlow's Tables, one obtains the coefficient of correlation correct to three decimal places.

It may be worth while to observe further that if one is following the above routine, the standard deviations and coefficients of variation are as follows:

$$\sigma_x = \frac{\sqrt{b}}{n} \qquad \sigma_y = \frac{\sqrt{c}}{n}$$

$$\text{C. V. of } x = \frac{100\ \sqrt{b}}{\Sigma x}$$

$$\text{C. V. of } y = \frac{100\ \sqrt{c}}{\Sigma y}$$

A very great number of correlations are presented in the present paper. The problem of publication of the original tables, on which the coefficients are based, becomes therefore a serious one. It appears impracticable to publish all the tables *in extenso;* so that only the more fundamental and illustrative tables will be thus given. The publication of data on inheritance in the form of correlation tables is in any case a most incomplete presentation; only the pedigrees themselves give the data in their proper relations. To a certain extent such pedigrees will be given, but their full presentation for the many thousand individuals dealt with is likewise impracticable.

For much efficient assistance with the counts and measurements, and in the working out of the statistical constants, I am indebted to my assistant, Miss MARY GOVER.

Collections and cultures studied

Four extensive collections of *Difflugia corona* from wild habitats were examined for the determination of characteristics and variations; and six long-continued experimental cultures were followed in the course of the investigation. It will be well to give each of these collections and cultures a designation, and to describe here once for all their origin and history,—reserving details for the later account.

The four wild collections or 'populations' will be designated by the letters A to D; the five laboratory cultures of populations by the letters E to I. The sixth laboratory culture, consisting of a single strain, from one parent, will be called, after its parent, No. 326. The several sets are therefore:

Wild populations

A. A collection of 115 taken by Dr. K. S. LASHLEY from an artificial pond in the BOTANICAL GARDEN at Homewood (University grounds), Baltimore, in July, 1911.

B. Collection of 178 specimens from the same place as A, in March, 1913.

C. A set of 147 specimens from water-net material, from Jones Falls, near Mt. Washington, Md., July 11, 1913.

D. A collection of 217 specimens from a pond at the "Brickyards," Baltimore, in October, 1913.

Laboratory cultures

E. A preliminary culture in the spring of 1913 (March and April) for purposes of orientation, carried out with the aid of my assistant, Mr. FRANCIS M. ROOT. This culture was derived from 64 'wild' parents, and comprised 168 specimens in all (including the parents).

F. Culture from water-net material, Jones Falls, Md., summer of 1913. From 72 'wild' parents that formed a random sample of the population; total number 266.

G. Culture of a population from algae from pools at the "Brickyards," Baltimore, October, 1913, to February, 1914. From 48 original parents; total number 539. One of the single individuals (No. 248) in this group produced 125 progeny.

H. An extensive experiment on the effects of selection within single strains, with specimens from the "Brickyards", April to July, inclusive, 1914. Nineteen original parents; total specimens in the culture, 2521.

I. Cultures for the effects of operations on the number of teeth; 11 parents from a pond on the University grounds, Homewood; October and November, 1914. Total number of individuals, 264.

326. This culture, derived from the single individual designated number 326, from the same place as culture I, continued from October 24, 1914 to July 2, 1915, and comprised 4645 individuals belonging to the single strain.

The total number of individuals examined was thus 9060, of which somewhat more than half formed a family derived from a single parent.

I. POPULATIONS

Constitution, variation, correlation of characters

When one examines a collection of *Difflugia corona* taken at random from some pool, he finds as a rule much variation in size, in number and length of spines, and in other features. Typical variations are shown in figure 3, which presents specimens all drawn to the same scale. The nature, variation and correlation of the measurements obtained are illustrated in table 1, which gives the measurements of the individuals in a typical part of the population G, in such a way as to show the ancestry of each individual, and the combinations of characters found in single specimens. All the data given in table 1 were obtained also for the entire populations C, D, F, G, I, and for a large part of H; to publish the data complete for all would be desirable if it did not appear impracticable. Table 1 will serve as an illustration of many of the relations to be brought out later.

Taking the extremes of variation, including populations from diverse localities and laboratory cultures, the number of spines was found to vary from 0 to 14, the number of teeth from 9 to 21 (with other numbers in certain palpably abnormal individuals), the diameter of the shell from 106 microns to 260 microns; the oral-aboral depth of the shell from 106 to 200 microns; the diameter of the mouth from 56 to 98 microns; the length of the spines from 0 to 149 microns.

EXPLANATION OF TABLE 1

In table 1 are given pedigrees arranged in linear order, yet in such a way that the entire descent of any individual is traceable. As such pedigrees are employed extensively in this paper, the method of presentation will here be explained once for all.

The first row, headed "Family", gives merely a number by which the parent individual was known in my records; this individual was the progenitor of the family made up by all the individuals included between the perpendicular lines. Thus, the first family, No. 159, included but two individuals; family 186 included 21, etc.

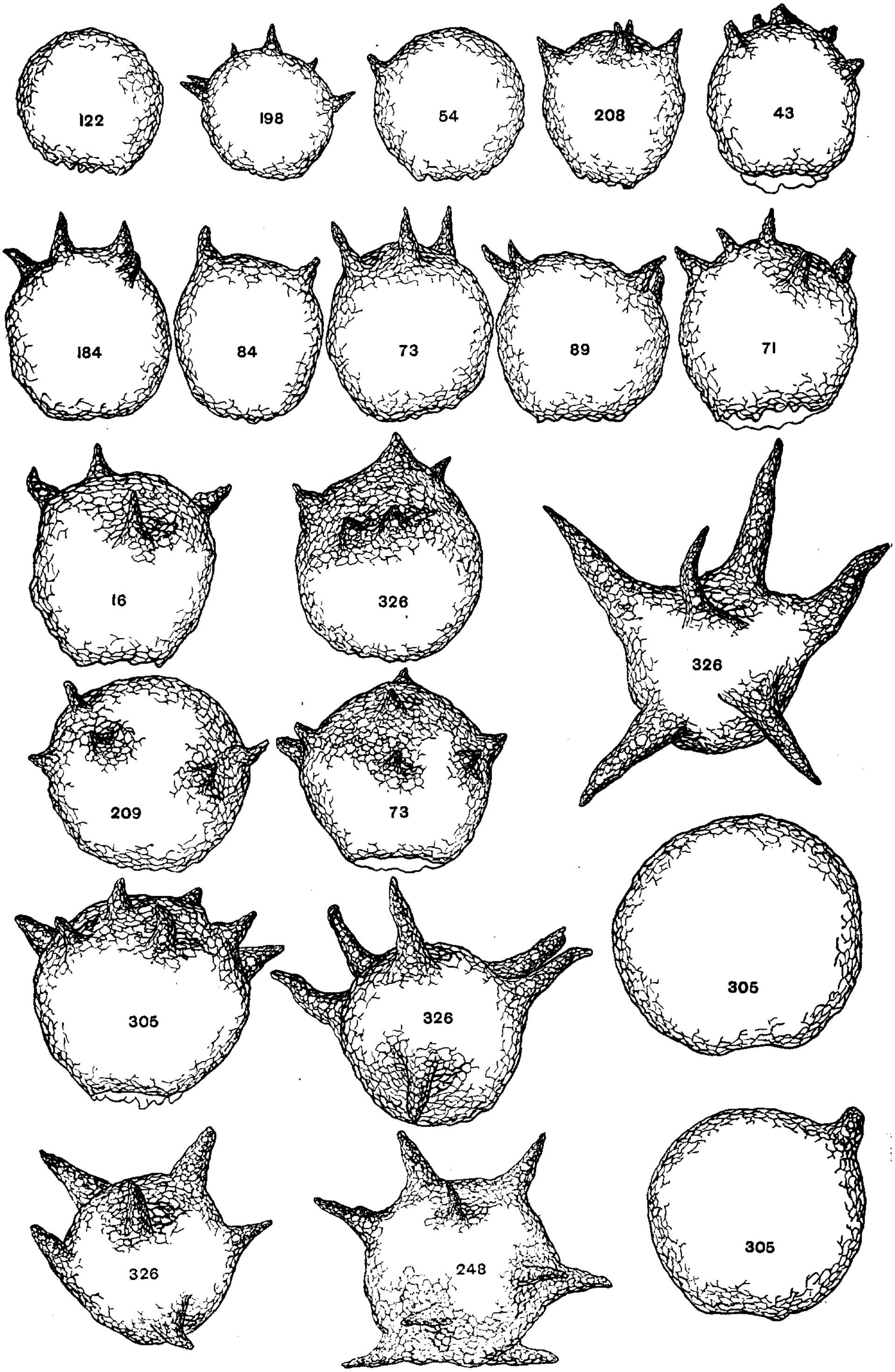

122
198
54
208
43
184
84
73
89
71
16
326
326
209
73
305
326
305
326
248
305

FIGURE 3.

In the second row, headed "Individual", each individual of the family is given a serial number, commencing with the progenitor. Beneath the individual's number are given in six rows the characters of the given individual. Thus, individual 1 in family 159 has 4 spines, a diameter of 30 units (each unit being 4 2/3 microns), a depth of 32 units; the length of its longest spine was 6 units, the number of its teeth 11, and the diameter of its mouth 15 units.

Any individual (or its measurement) not preceded by a dash is the immediate progeny of the one that comes just before it in its row. Thus a series of numbers not separated by dashes represents an unbroken series of descending generations. So in family 195, the individual 2 is the progeny of No. 1; No. 3 is the progeny of No. 2, and so on till we reach individual number 7, which is preceded by a dash.

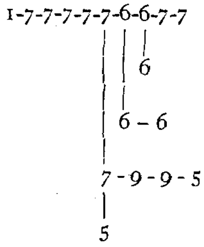
When an individual (or its measurement) is preceded by a dash, its parentage will be found below, in the last row, headed "Parent". Thus, in family 195, the immediate parent of individual No. 7 is individual No. 4; the parent of No. 15 is No. 9, etc.

Thus the complete pedigree of any individual can be at once reconstructed,—with respect to any or all of its characters. Thus, let us suppose that we desire to know the pedigree with respect to the number of spines of the last individual (No. 51) in family 248. It has 8 spines; its parent (just preceding) has 8; its parent (No. 48) has 7; the parent of No. 48 is No. 22, with 8 spines; its parent is No. 19, with 6 spines, etc.,—so that we find the total pedigree of No. 51 with respect to the number of spines to be:

8, 7, 10, 9, 6, 8, 7, 8, 8.

In every case, in each family all the later individuals are descendants of the first one (at the left).

Such linear pedigrees are obtained by merely placing in serial order the successive branches in the ordinary branched pedigree. For example, if we employ only the number of spines as a designation for each individual, the pedigree of the first 19 individuals of family 209 will appear as follows:



Here the progenitor is at the upper left, and the lines show the parentage of the later individuals. The linear pedigree is obtained by placing the branches in series, following each to its end, then taking the next one below or to the left, and placing a dash at the beginning of each new branch.

FIGURE 3.—Collection of individuals of *Difflugia corona*, to show the variations in size and form; in number, length and shape of the spines, etc. The numbers are the designations of the families to which these belonged. (All × 143.)

TABLE 1

Linear pedigrees of several typical families in culture G, showing 6 characters for each individual, and its complete descent. See the explanation in the text.

Family	159	173	181	183
Individual	1 2	1 2- 3 4	1 2- 3 4	1 2 3- 4- 5
No. of spines	4 5	3 5- 2- 5	1 1- 1 5	1 3 4- 6- 5
Diameter	30 30	30 29-28-28	29 28-29 28	30 26 29-28-29
Depth	32 30	30 29-29-28	27 30-30 28	32 28 27-27-29
Length of spine	6 10	5 6- 8- 8	6 8- 6 9	7 5 6- 6- 3
No. of teeth	11 11	11 11-11-10	11 11-11 11	11 11 11-11-11
Diameter mouth	15 14	14 13-13-15	14 13-14 14	13 13 13-13-13
Parent		1 1	1	2 1

Family	184	186
Individual	1 2- 3 4- 5 6 7 8	1 2 3- 4 5 6- 7 8- 9 10 11 12
No. of spines	4 0- 0 2- 0 4 4 1	4 6 3- 4 4 4- 5 5- 4 4 5 4
Diameter	35 37-36 37-35 36 36 37	30 29 26-31 28 28-30 28-28 28 27 29
Depth	35 38-36 37-37 38 36 38	33 26 ?-28 27 28-31 28-28 82 29 29
Length of spine	5 —— 5— 10 8 4	6 3 2-10 6 9-10 6- 7 7 4 8
No. of teeth	12 12-12 12-12 12 12 12	9 9 ?- 9 9 9- 9 9- 9 9 9 9
Diameter mouth	17 16-16 17-16 17 17 17	13 12 b-13 14 12-13 14-14 15 13 14
Parent	1 1	1 4 7

Family	186 (Continued)	195
Individual	13-14-15 16 17 18-19-20-21	1 2 3 4 5 6- 7 8 9 10 11
No. of spines	3- 5- 4 3 4 2- 4- 5- 5	4 3 3 3 5 4- 4 4 4 5 5
Diameter	29-27-29 27 28 28-29-29-29	30 31 32 32 35 33-28 29 31 29 30
Depth	28-27-28 28 27 28-29-28-30	30 29 31 32 33 34-32 30 31 28 30
Length of spine	11- 8- 8 8 8 8-10- 6- 7	6 6 5 4 8 8- 7 8 9 7 10
No. of teeth	9- 9- 9 9 9 9- 9- 9- 9	10 10 11 ? 11 11- 9 9 9 9 9
Diameter mouth	13-13-14 14 14 13-13-14-14	13 12 13 12 13 13-13 13 13 13 14
Parent	11 10 4 1 1	4

Family	195 (Continued)
Individual	12 13 14-15-16-17 18-19 20 21-22 23-24 25 26-27-28-29 30-31 32-33
No. of spines	4 5 5- 5- 5- 5 4- 6 5 5- 4 4- 5 4 5- 4- 6- 4 5- 6 4- 4
Diameter	30 29 28-30-27-28 29-30 29 29-29 ?-28 27 29-28-30-29 30-29 28-31
Depth	30 30 26-30-27-29 29-30 31 29-29 ?-28 28 27-28-28-29 31-30 28-31
Length of spine	9 8 7-10- 7-11 7- 6 10 9- 8 ?- 7 9 6- 6- 7-11 8- 8 8- 9
No. of teeth	10 10 9- 9- 9- 9 9- 9 9 ?- 9 ?- 9 9 b- 9- 9-11 11-11 11-11
Diameter mouth	13 13 13-13-13-13 14-13 13 13-14 ?-14 13 13-13-14-14 14-14 13-13
Parent	9 8 8 7 7 22 22 22- 3 3 3

Family	198	200	207
Individual	1 2 3- 4 5- 6- 7 8- 9-10	1 2 3 4- 5- 6	1 2- 3 4- 5
No. of spines	6 6 6- 6 4- 5- 7 5- 6- 6	2 4 5 4- 4- 4	5 7- 8 10- 9
Diameter	29 29 29-29 29-26-27 30-29-29	34 30 31 29-31-33	42 40-41 43-39
Depth	29 30 29-29 29-24-26 27-28-28	33 32 31 30-28-33	39 37-41 37-38
Length of spine	7 10 9- 8 9- 6-11 8- 6- 8	7 9 13 10-10-10	10 11-13 13-19
No. of teeth	11 10 10-10 10-10-10 10-10-11	12 12 12 12-12-12	15 15-15 b-15
Diameter mouth	14 14 13-14 13-14-14 14-14-13	15 15 15 16-15-15	21 18-20 19-20
Parent	1 4 1 1 1	2 1	1 3

Family	209															
Individual	1	2	3	4	5	6	7	8	9	10-11-12	13-14	15	16	17-18-19-20	21	22-23
No. of spines	1	7	7	7	7	7	6	6	7	7- 6- 6	6- 7	9	9	5- 5- 5- 8	7	7- 7
Diameter	39	38	37	39	37	41	40	38	38	35-40-36	38-39	39	36	37-37-39-37	38	38-37
Depth	37	39	39	37	?	36	37	38	39	36-38-37	37-38	38	36	38-34-38-36	38	39-38
Length of spine	6	12	8	11	?	9	11	10	14	10-11-12	14-11	12	10	13- 8-10-14	11	11-12
No. of teeth	11	11	11	11	?	13	12	12	12	12-12-11	11-13	13	13	13- ?-11-11	12	12-12
Diam. mouth	16	15	16	16	?	16	16	17	16	16-17-15	15-16	18	16	16-16-16-16	17	16-16
Parent										8 7	6			14 5 4		21

Family	209 (Continued)						248				
Individual	-24-25-26-27	28	29-30-31-32-33-34	35	36	37-38-39-40	1	2	3	4- 5	6
No. of spines	-6- 5- 4- 4	5	8- 5- 4- 5- 5- 6	5	4	4- 4- 5- 4	8	7	9	9-10	6
Diameter	-37-38-39-37	38	38-38-39-36-36-38-36	35	35-37-39-35		42	41	?	40- ?	39
Depth	-38-39-35-39	38	37-36-36-37-37-36	37	38	36-35-38-35	42	41	?	43- ?	42
Length of spine	-10-12- 7-14	12	11-12-11-11-13-11	12	13	12-13- 7- 8	22	16	?	15- ?	16
No. of teeth	-11-11-12-11	13	11-12-13-11-12-11	13	13	13-13-11-11	16	16	?	16- ?	16
Diam. mouth	-17-15-16-15	16	15-15-16-15-14-16	16	16	16-16-16-16	18	20	?	19- ?	19
Parent	21 20 4 4		28 28 27 4 3			34 1 1				3	

Family	248 (Continued)														
Individual	7- 8- 9-10	11	12	13-14	15-16-17	18	19	20	21-22	23	24	25	26	27-28-29
No. of spines	6- 6- 5- 7	8	8	9- 9	6- 6-10	9	6	6	9- 8	9	6	8	14	6- 5- 8
Diameter	36-40-40-42	?	43	40-39	43- ?-41	?	41	41	42-40	42	41	41	43	47-41-40
Depth	35-38-39-42	?	40	39-40	39- ?-40	?	39	41	40-41	41	41	41	41	41-41-38
Length of spine	?- ?-16-14	?	24	23-17	15- ?-11	?	12	15	15-16	13	16	18	15	16-14-19
No. of teeth	?- ?-16-16	?	16	16-16	16- ?-16	?	16	16	16- ?	16	15	15	15	16-15-15
Diam. mouth	?- ?-20-19	?	21	21-19	20- ?-19	?	19	19	19-20	18	19	20	20	20-19-19
Parent	5 3 1			11	11 10				19					25 24

Family	248 (Continued)													
Individual	30	31	32-33	34-35	36-37	38	39-40	41	42	43-44-45	46-47-48	49-50	51	etc.
No. of spines	7	8	8- 7	9- 5	6- 7	7	7- 9	9	6	8- 9- 9	7- 9- 7	6- 8	8	
Diameter	40	39	44-43	40-45	39-40	39	40-39	40	42	41-42-41	41-43-40	40-40	41	
Depth	42	39	41-40	37-38	42-39	37	39-38	40	39	42-41-40	37-41-40	40-38	43	
Length of spine	17	10	15-17	16-18	17-19	13	18-21	22	21	23-24-23	32-27-14	24-21	10	
No. of teeth	15	15	16- b	14-15	15-15	15	15-16	16	16	16-16-16	16-16-16	16-16	16	
Diam. mouth	19	18	20-18	19-20	20-19	19	18-19	20	19	21-21-19	20-20-19	20-19	20	
Parent			29	29	24		23			42 23	23 22	48		

Distribution of the variations

The distribution of the variations, with the numerical coefficient of variation, will be presented for a number of the populations listed on page 418, including collections taken in nature and laboratory cultures. As the variations all relate to congenital characteristics, and include no growth changes or environmental modifications, these data appear to be of considerable interest.

Number of spines. The distribution of the various diverse numbers of spines, from 0 to 14, is shown for all the nine populations, in table 2;

TABLE 2

Numbers of individuals having the various different numbers of spines, in wild populations (A *to* D) *and in laboratory cultures* (E *to* I) *with the coefficients of variation* (*C.V.*).

No of spines	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total	C.V.
Wild populations																	
A.	1	2	1	13	49	44	4	1								115	23.18 ± 1.08
B.	17	14	30	54	35	21	7									178	52.30 ± 2.33
C.	19	7	28	37	29	17	4	4	1	1						147	60.13 ± 3.11
D.	3	3	21	61	92	32	5									217	29.10 ± 1.01
Total Wild	40	26	80	165	205	114	20	5	1	1						657	42.97 ± .94
Laboratory Cultures																	
E.		9	14	39	52	41	11	1	1							168	33.63 ± 1.39
F.	31	40	43	54	52	25	14	5	2							266	64.12 ± 2.53
G.	3	15	16	49	130	129	81	51	28	24	11		1		1	539	38.28 ± .89
H.	90	134	290	543	728	438	191	65	24	11	4	2	1			2521	44.38 ± .49
I.		1	8	34	54	113	41	12		1						264	24.82 ± .78
No. 326	3	29	63	286	712	1500	1409	464	129	35	14	1				4645	24.74 ± .19
Grand total	167	254	514	1170	1933	2360	1767	603	185	72	29	3	2	0	1	9060	36.86 ± .21

in order that all specimens examined may be included, the data are given also for the single family No. 326. In figure 4 are shown curves of the

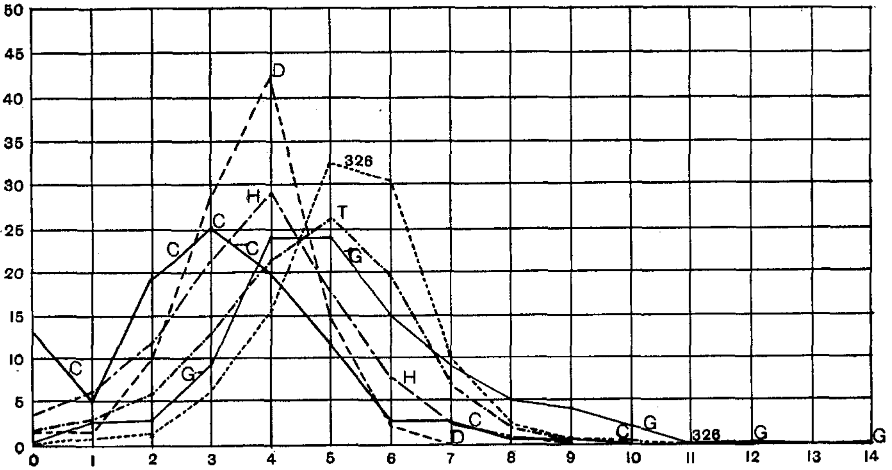


FIGURE 4.—Polygons of variation in number of spines for the two wild populations C and D; the two laboratory populations G and H; the large single family No. 326; and for the total (T) of 9060 individuals examined from all sources.
The ordinates are percentages; the abscissae, numbers of spines.

TABLE 3

Diameter of the shell; distribution in the diverse populations, with the coefficients of variation (C.V.). Each unit is 4 2/3 microns, save in the case of set H, *in which the unit is 4 microns.*

Diameter	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55–60	Total	C.V.
Wild Populations																																			
C.				2	5	8	17	25	25	15	6	7	5	8	13	5	4	1	1															147	10.44 ± .40
D.				2	7	31	71	53	24	13	3	2	2	2	1		2		1	2			1											217	8.42 ± .26
Laboratory Cultures																																			
F.			1		2	5	13	55	39	38	11	10	13	9	11	13	8	14	2	1														245	10.63 ± .34
G.	1			12	40	68	94	62	36	8	4	4	8	11	13	15	20	29	40	18	17	6	2		1									509	16.94 ± .37
H.								7	12	38	28	26	20	22	46	122	240	368	287	190	103	64	54	54	45	32	25	14	3	4	2	1	1	1808	8.83 ± .10
I.														3	16	36	63	60	42	24	8	5		1										258	4.12 ± .12
Single Family No. 326												1	8	28	114	279	406	511	401	261	139	111	50	18	11	11	4	8	6	3	1	2	2	2375	13.65 ± .13

TABLE 4

Depth of shell in populations of Difflugia corona, with coefficients of variation. The measurements are given in units of 4 2/3 microns each.

Depth	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	Total	C.V.
Wild Populations																							
C.				1	5	6	17	21	21	20	17	6	6	6	9	10	2					147	9.54 ± .40
D.				1	12	24	38	61	37	17	6	1	1	3	2		1	1			2	217	7.75 ± .26
Laboratory Cultures																							
F.					1	1	8	40	31	41	32	17	15	8	13	13	10	13				243	9.38 ± .28
G.	1	2	4	14	43	73	81	50	30	20	8	5	5	10	20	28	31	32	34	14	5	510	16.09 ± .35
Totals	1	2	4	16	61	104	154	172	119	98	63	20	27	27	44	51	44	46	34	14	7	1117	13.19 ± .19

variation in spine number for some of these populations, as well as for the largest single family examined, and for all taken together (at T). As will be seen, each population shows a fairly distinct single maximum; there is no trace in the curves, of bimodality, unless the high number at 0 in population C should be considered such. In five populations the maximum number have 4 spines; in three the maximum is at 3, while in one it is at 5; in the single strain 326 it is also at 5. Owing to the great numbers in the single strain the maximum for all taken together is at 5. There is no indication, from the distribution within most of the populations, of the presence of diverse races with respect to spine number, though the differences between the populations may indicate something of the sort.

The coefficients of variation are high; they vary from 23.18 up to 64.12. The former number is approximately that found in the single family No. 326; most of the populations have higher coefficients. These coefficients may be compared with those for certain single families, given in table 21, page 445.

Diameter of the shell. For this we have data from two wild populations, C and D, from the laboratory populations, F, G, H and I, and the large single family No. 326. The number measured is in some of the collections less than the number for which the spines were counted. The measurements are given in table 3, and curves for certain typical populations are shown in figure 5.

The measurements in table 3 are given in units, each of which is 4 2/3 microns, save in the case of population H, in which the unit was 4 microns,—so that in the table the measurements of H are not directly comparable with those of the other sets. But in figure 5, the measurements for H have been brought to the same value as for the rest, so that the curve for H shows the correct relations to the others.

The measurement of the diameter is subject to some slight inaccuracy, owing to the fact that the spines usually project laterally from the broadest part of the shell, and this makes it difficult to determine the limits for the measurements of the shell itself. But this will not alter the general relations. The diameter forms the best measure of the size of the animals.

As table 3 and figure 5 show, there is a tendency for the populations to form two groups, an upper and a lower, with respect to size. This is particularly notable in the wild population C and the laboratory population G (figure 5). In these cases one maximum is at 29 to 31, while the other is at 37 to 41; the region 33 to 35 has very few specimens. In

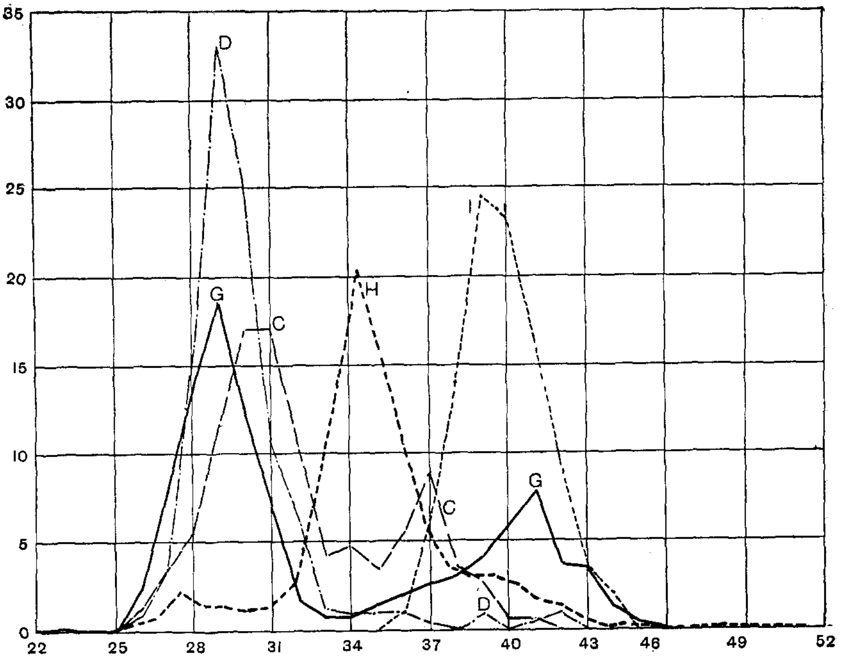


FIGURE 5.—Polygons of variation in diameter of the shell, for the two wild populations C and D, and the three laboratory populations G, H and I.

The ordinates are percentages; the abscissae are diameters in units of 4 2/3 microns each.

the wild population D most of the individuals fall in the lower group, but there are indications of the upper group in the way the curve tails out in the region 33 to 43. In H the maximum, however, corresponds precisely to the region lying between the two maxima of the other curves. This demonstrates that in the species as a whole this minimum is not a necessary characteristic feature. The population I falls entirely in the region of the upper maximum of C and G; it will be recalled that this population I is descended from parents selected for large size.

The coefficient of variation ranges from 4.12 in culture I to 16.94 in culture G; it is small in comparison to that of the number of spines.

Depth of the shell. The depth of the shell, from the mouth to the convexity of the fundus opposite it, was measured in the wild populations C and D, and in the cultures F and G. The measurements are all given in table 4, in units of which each is 4 2/3 microns. In the table the tendency to fall into two groups, of smaller and of larger individuals, is again evident. Curves drawn for depth of the shell would closely resemble those shown in figure 5 for the diameter of the shell. The coefficients of variation run much the same as those for diameter.

Diameter of the mouth. The diameter of the mouth was measured in the same units as the other dimensions, each unit being 4 2/3 microns. The distribution for two wild populations (C and D) and two cultures (F and G) is given in table 5. There is no indication of a separation into two groups in the wild populations C and D, but in the culture G such a separation is marked.

TABLE 5

Diameter of the mouth; distribution of the variations, with the coefficients of variation. The diameters are given in units of 4 2/3 microns each.

Diameter of Mouth	12	13	14	15	16	17	18	19	20	21	Total	C.V.
Wild Populations												
C.		3	15	47	43	21	14	3		1	147	8.37 ± .32
D.	11	71	106	15	6	3	1	1	1	2	217	9.17 ± .29
Cultures												
F.	4	25	59	82	37	20	13				240	8.94 ± .28
G.	20	140	142	38	30	13	14	52	42	14	505	5.39 ± .11
Totals	35	239	322	182	116	57	42	56	43	17	1109	14.00 ± .20

Number of teeth. The teeth are sharply defined, and there is no difficulty in counting them in clean specimens (see figure 1).

(Frequently the mouth is filled with algae or other food material; if the animals are killed in this condition, it may be difficult or impossible to count the teeth. To avoid this difficulty, the animals may be left in a drop of clean water over night or for a few hours, before killing.)

The numbers of teeth, with their variations, are shown for two wild populations, and three laboratory populations, in table 6. Little indication is shown in the wild populations of a division into two groups, but in the laboratory population G such a division is very marked. Only the wild populations C and D and the culture F are to be considered as

TABLE 6

Number of teeth; distribution in the two wild populations, C *and* D, *and in three laboratory populations* F, G and I. *C.V. = coefficients of variation.*

	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Total	C.V.
C.		11	52	33	22	23	5	1							147	12.21 ± .48
D.		32	97	65	14	2	3	2	1	1					217	11.36 ± .36
F.		7	68	56	21	30	12	4							198	12.57 ± .45
G.	1	117	82	100	49	12	1	24	86	1					473	21.91 ± .51
I.			2	2	20	26	20	41	69	52	13	9	2	1	257	12.53 ± .39
Total	1	167	301	256	126	93	41	72	156	54	13	9	2	1	1292	21.68 ± .31

random samples. In the culture I the distribution of the number of teeth has been somewhat modified by operations on the parents of the individuals counted,—as will be described elsewhere.

LEIDY (1879) says that the commonest number of teeth in *Difflugia corona* is 12; this is not confirmed by our statistics of 1292 specimens. It may be observed that one practically never finds a specimen with fewer than 9 teeth, although the number 9 is itself not infrequent. The single specimen recorded with 8 teeth must be considered an abnormality.

Length of the longest spine. The length of the spines varies much. It is not practicable to measure all the spines, so that the plan of measuring the longest one on each individual was adopted. The measurements are subject to some inaccuracy, owing to the difficulty of getting the entire length of the spine in a plane parallel to the plane of the micrometer; and because it is not always clear at just what point the base of the spine begins. But these difficulties are negligible in comparison with the actual lengths and differences in length, of the spines.

Table 7 gives the measurements for two wild populations and two laboratory populations as well as for the single family No. 326. Leaving aside the individuals with no spines (length = 0), in all except G a curve with but one maximum is indicated. In G there is indication of a tendency to separate into two or more groups,—one with a maximum at 8 units; another at 14 to 15 units, and perhaps a third at 19 units.

Correlations between different characters of the individuals

To what extent do the different characters follow one another in their variations? Do specimens of large size have more spines, as a rule? Do specimens with many spines tend to have large spines or small spines? These and similar questions are important in relation to breeding experiments with selection. How far does selection with reference to a certain character influence the other characters?

I have worked out the principal correlations between the six sets of characters for the two wild populations C and D; also for the laboratory culture G, and certain correlations for the laboratory culture I. To publish all the correlation tables is not warranted by the importance of the matter. I shall therefore give merely the correlation coefficients, with the numbers of specimens on which they are based. These are set forth in table 8.

As the table shows, the diverse characters are rather closely corre-

TABLE 7

Length of longest spine in two wild populations, C *and* D; *in three laboratory populations,* F, G *and* I, *and in the single family No. 326. Each unit of measurement is 4 2/3 microns. Those with spine length at* 0 *have no spines. The coefficients of variation are based on the individuals having spines; the totals for these are given in parentheses.*

Length	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	Total		C.V.
Wild																																				
C.	19		3	5	14	26	25	18	18	14	4	1																						147	(128)	30.49 ± 1.43
D.	3		3	4	10	27	43	55	40	23	6	1		1									1											217	(214)	28.48 ± 1.02
Laboratory																																				
F.	30		4	11	26	33	58	38	19	8	5	2	1																					235	(205)	29.68 ± 1.09
G.	3		3	6	12	22	55	68	75	48	39	28	15	13	17	17	15	9	5	10	6	7	5	8	5	2		3					1	497	(494)	49.11 ± 1.77
I.								7	15	21	33	34	44	37	25	18	13	6	2	2	1													258		21.14 ± .47
No. 326			2	3	2	6	10	30	65	105	174	193	221	213	124	82	55	36	45	19	10	6	8	9	3	3	2	3	1	1	1	1		1433		27.41 ± .36
Total	55	0	15	29	64	114	191	216	232	219	261	259	281	264	166	117	83	51	52	31	17	13	14	17	8	5	2	6	1	1	1	1	1	2787	(2732)	38.74 ± .41

TABLE 8

Correlation of the characters in the individuals of Difflugia corona, for two wild populations (C *and* D) *and two laboratory cultures* (G *and* I),

	Population G		Population D		C and D together		Population G		Population I	
	No.	Coef. cor.	No.	Coef. cor.	No.	Coef. cor.	No.	Coef. cor.	No.	Coef. cor.
Diameter with depth	147	.903 ± .010	217	.822 ± .015	364	.881 ± .008	508	.954 ± .003		
“ “ diameter of mouth	“	.691 ± .029	“	.763 ± .019	“	.668 ± .020	505	.923 ± .004		
“ “ number of spines	“	.578 ± .037	“	.121 ± .045	“	.297 ± .032	510	.607 ± .019	251	.115 ± .042
“ “ number of teeth	“	.691 ± .029	“	.713 ± .023	“	.699 ± .018	471	.887 ± .007	251	.243 ± .040
“ “ length of longest spine (all)	“	.505 ± .041	“	.314 ± .041	“	.295 ± .032				
“ “ “ “ “ “ (for all that have spines)	128	.519 ± .044	214	.363 ± .040	342	.337 ± .032	502	.774 ± .012	251	.328 ± .038
Diameter of mouth with number of teeth	147	.620 ± 0.34	217	.696 ± .024	364	.621 ± .022	473	.919 ± .005		
Number of spines with number of teeth	“	.466 ± 0.44	“	.013 ± .046	“	.206 ± .034	471	.604 ± .020	251	.321 ± .038
“ “ “ “ length of longest spine (all)	“	.760 ± .025	“	.275 ± .042	“	.584 ± .023				
“ “ “ “ “ “ “ “ (for all that have spines)	128	.546 ± .042	214	.142 ± .045	342	.331 ± .033	503	.598 ± .019	251	.315 ± .038

lated in most populations. This will indeed become at once evident on examining the typical measurements given in table 1; in general the characters vary together. In some cases the correlations are extremely high; in the population G the lowest coefficient (table 8) is .598, and three of the correlations are above .9. In the population I the coefficients are all low; this population consists of but a few strains, all very similar. Where the variation is small, the correlations between the characters are low. In some of the other populations certain correlations are low; notably is this true of diameter with number of spines, and of number of spines with number of teeth, in D. The great diversity in the correlations of the same pair of characters, for the different populations, is striking; this is very notable in the relation of the diameter to the number of spines; and of the number of spines to the number of teeth.

In all cases the correlation is positive; an increase in number or dimensions of any character is correlated with an increase in the other characters examined. In general, larger specimens have on the average a greater diameter and depth, a wider mouth, longer spines, and a larger number of spines and teeth than smaller specimens. These relations are well illustrated in the measurements in table 1, and are all what might well be expected, save that of course the spines and teeth might be merely increased in size and not in number, in larger specimens.

Thus, in such mixed populations, if we select individuals having a certain character in a higher degree, we shall on the whole obtain specimens having also the other characters in a higher degree. This is of importance in studying the effects of selection in populations. Whether it also holds within single families (progeny of a single individual) remains to be seen.

Inheritance in populations

Are the peculiarities of the individuals in a population inherited by their progeny? How generally or to what degree?

This question may be studied in two ways. (1) One may obtain progeny from a large number of parents, and determine statistically the correlation between parents and offspring; that is, essentially, one obtains the average degree of resemblance of the two. (2) One may isolate individuals, obtain numbers of descendants from each single parent, and compare these progeny with their parents and with each other,—either in a general descriptive way or statistically. That is, one isolates single strains from the population—each derived from a single ancestor

—and compares these, to determine whether particular strains inherit particular characteristics.

The data which form the basis of both these methods of examination are typically illustrated in table 1, for the population G. Both the statistical method and the single strain method of analysis were employed; and in various combinations. We shall take up first the statistical results, then those with single strains.

Statistical study of inheritance in populations

In the preliminary experimental culture E, in the spring of 1913, when the number of spines of each of the offspring was compared with that of its parent, the coefficient of correlation was found to be .402 ± .055, the number of progeny being 104. This indicated that there is inheritance in a population, so that more extensive experiments were undertaken, and other characters were drawn into the field of study.

From July to October in 1913 the culture F, from a random population collected on water-net material, was carried on; 194 offspring were obtained from 72 wild parents. The largest number of descendants from any single progenitor was 13. To determine the inheritance, each offspring was correlated in a table with its immediate parent; such tables were prepared for each of the six sets of characters studied. Two of the tables are here given; that for the numbers of spines in parent and progeny (table 9) and that for numbers of teeth (table 10). The other tables will not be given. The correlations for the six sets of characters are given in table 11.

TABLE 9

Correlation table for the inheritance of the number of spines in the laboratory population F; *parents with their immediate offspring.*

Offspring	Parents 0	1	2	3	4	5	6	7	8	
0	12	3	6		2					23
1	8	9	7	4	1					29
2	1	6	6	12	6	1				32
3	2	7	8	13	6	3	1			40
4			1	11	14	8	1			35
5				1	9	4	4	1		19
6				2	6	1		1	1	11
7							2	2		4
8						1				1
	23	25	28	43	44	18	8	4	1	194

TABLE 10

Correlation table for the inheritance of the number of teeth in the laboratory population F; *parents with their immediate offspring.*

Offspring	Parents 9	10	11	12	13	14	15	
9	4							4
10		26						26
11		1	24					25
12			1	11				12
13					9			9
14						4		4
15							1	1
	4	27	25	11	9	4	1	81

TABLE 11

Correlation between parents and their progeny (f 1), in the culture F, *for the 6 diverse characters.*

Character	No. of progeny	Coef. of Cor.
Number of spines	194	.729 ± .023
Number of teeth	81	.993 ± .001
Diameter of shell	127	.745 ± .027
Depth of shell	127	.756 ± .026
Diameter of mouth	129	.478 ± .047
Length of longest spine	125	.286 ± .055

In preparing the tables, each offspring was tabulated with its immediate parent, so that any given parent appears in the table as many times as it produces offspring (the greatest number of times being six in culture F). As offspring, however, each individual appears but once, the "number of progeny" signifying *diverse* progeny. That is, the fissions are the units of the correlation, each separate fission being entered once (with its parent and progeny). There appears to be no reason why the second and later fissions of a given parent are less significant for correlation and inheritance than the first one.

It will be observed that in table 11 the number of individuals is not the same for all the characters, even for this culture F. The cause of this is as follows: The number of spines was determined in the living specimen, when it was first observed; this character therefore is known for all the specimens. The other characters were determined later, in the preserved specimens. But some specimens were lost before preservation; and in some of those preserved certain characters could not be determined; particularly is this true of the number of teeth. At times the mouth opening is filled with debris, making the counting of the teeth impossible; in other specimens the mouth has been broken, so that neither the diameter of the mouth nor the number of teeth can be determined. If this is the case with a parent, of course all its progeny are unavailable for determining correlation of parent and progeny. The number of progeny actually employed is given for each character.

As table 11 shows, in this population the correlation between parent and progeny is very high for some of the characters, and marked for all. For number of spines, diameter of the shell, depth of shell, and number of teeth, the correlation is above .7; for diameter of the mouth it is about .5, while for the number of teeth the correlation is actually .99. For length of spines the correlation is least, amounting to about .3. It may be remarked that in such a case as the present, where to a large extent the same individuals appear both as parents and as progeny, the coefficient of correlation practically shows what proportion of the parents' peculiarity is *on the average* inherited by the progeny. Thus in this case, if the parent is above the average in number of spines, the

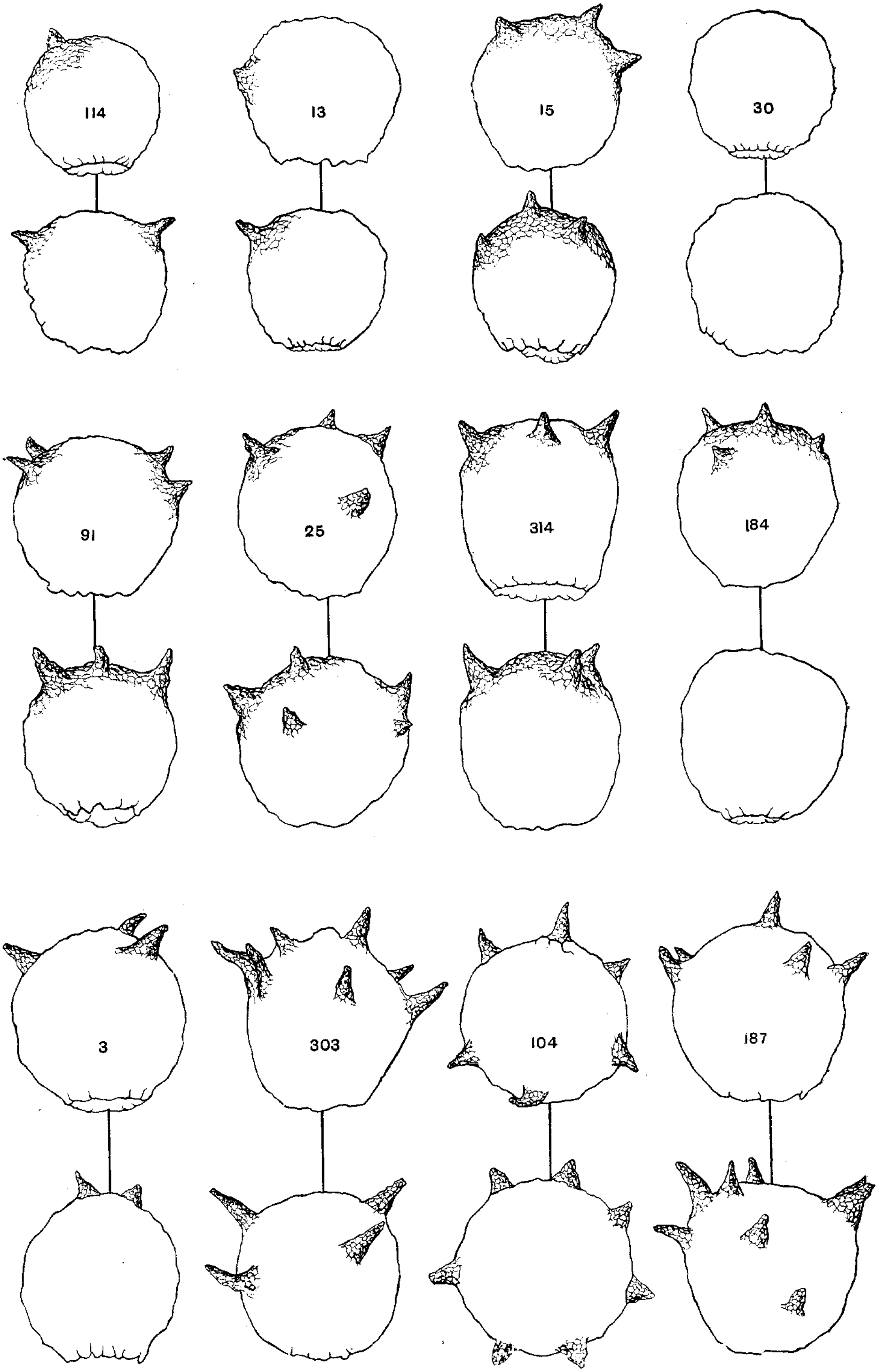


FIGURE 6 A

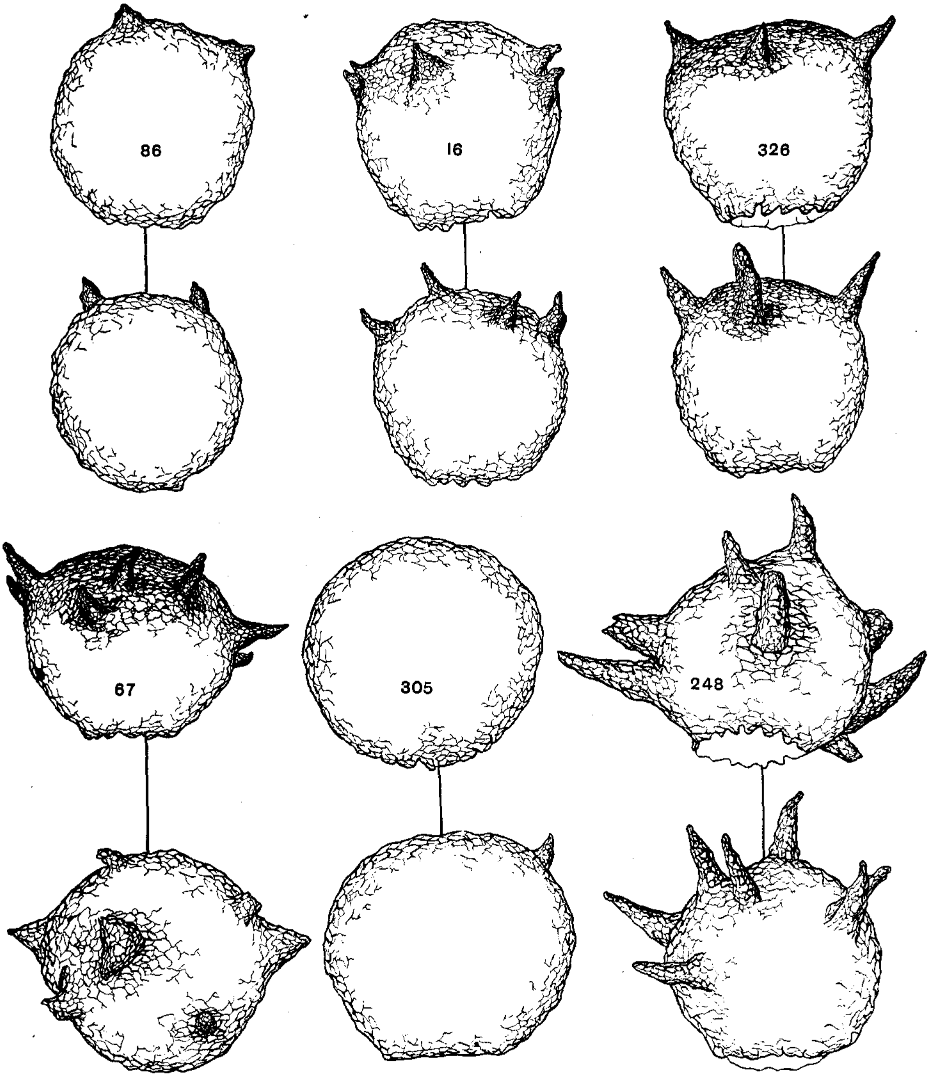


FIGURE 6 B

FIGURE 6 A and B.—Parent and immediate offspring in 18 diverse strains or families, all drawn to the same scale (× 143), to show the variation and the inheritance by the progeny, of the parental diversities. In each pair the parent is above, the progeny below, the two connected by a line. The numbers show the designation of the parent in the author's pedigree cultures. In all but two cases the figures show the 'wild' parent and its first progeny. In the case of family 326 we have the 17th offspring; and in family 305, individuals of the fourth and fifth generation from the original parent are shown.

progeny are above the average likewise, and taken all together the progeny show .7 as much excess as do the selected parents. In the case of the number of teeth, the progeny inherit 99 percent of the parents' peculiarity. This means that the number of teeth is inherited almost absolutely, the number in the progeny being almost identically the same as in the parent. This is well shown in the correlation table for number of teeth (table 10). Here although the number of teeth varies from 9 to 15, out of 81 progeny only two showed a number of teeth diverse from that of the parents, and these differed by but a single tooth. It is extremely rare in biological material to obtain a correlation table like table 10, with correlation practically perfect.

The high degree of correspondence between parent and progeny is likewise directly noticeable in the correlation tables for numbers of spines (table 9).

Figure 6 shows to the eye this correspondence. It gives parent and first progeny for a number of parents differing in size and other characters; these are not all taken from population F. It will be observed that parent and progeny correspond closely in size; less closely but still markedly in number of spines and in size of the spines. The mouth characters are of course not shown.

In this first population cultivated, therefore, the characters studied were inherited in a marked degree. Owing to lack of experience in culture methods, but a small number of progeny were obtained from any single parent, so that the question of the diversity and permanence of the different families, and of inheritance within the lines, could not be thoroughly examined.

A new culture was therefore undertaken; that which I have denominated G (page 418). Forty-eight original parents produced all together 491 progeny. In some cases a considerable number of descendants were obtained from a single ancestor; the eight largest such families contained respectively 18, 21, 25, 33, 40, 43, 65, and 126 individuals. (We shall have occasion to deal with some of these families separately later.) The 'raw' data for a part of this population G are given in table 1 (page 422), which illustrates the combinations of characters, and the ancestry of the individuals.

The three most important tables of correlation for the entire population G, (those for the number of spines, for the diameter of the shell, and for the number of teeth), are given in our tables 12, 13 and 14, while the inheritance correlations for all the six sets of characters are set forth in table 15.

TABLE 12

Correlation table for the inheritance of the number of spines in the laboratory population G. Parents with immediate progeny (f 1).

Offspring \ Parents	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
0				3												3
1		4		1	1											6
2	1	3		1	2			1								8
3		3	6	8	12	4	5	1								39
4	1	7	5	16	39	37	8	4								117
5		6	1	13	37	37	15	8	5	2						124
6			1	4	13	15	18	10	4	7	5		1		1	79
7		1		1	2	5	6	15	12	5	3		1			51
8						3	6	9	8	1						27
9							1	5	7	8	2		1			24
10								4	3	3	1					11
11																0
12								1								1
13																0
14									1							1
	2	24	13	47	106	101	59	58	40	26	11	0	3	0	1	491

TABLE 13

Correlation table for the inheritance of the diameter of the shell in the laboratory population G. *Parents with immediate offspring (f 1). (The diameters are given in units of 4 2/3 microns each.)*

Offspring \ Parents	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	
23		1																			1
24																					0
25																					0
26	3	2	2	3	1																11
27	2	11	11	9	2	1															36
28	1	12	11	22	14	2	1														63
29	1	6	12	28	18	13	5	1													84
30		1	5	12	15	8	2		1												44
31		2	2	4	7	9	4		1												29
32			1	2		1	2														6
33							1		1	1											3
34						2															2
35							1			2	1		2	1							7
36										3	1	1	1	2	1						9
37										2	2		4	4							12
38											2	5	4	1	2	1					15
39												2	1	3	2	4	1	1		1	15
40													1	3	8	7	2	2	1		24
41														1	7	12	8	6	2	1	37
42														1	5	5	2	2		1	16
43														1	4	5	2	3	1		16
44														1		1	1	1	1		5
45																1	1				2
46																					0
47																		1			1
	7	35	44	80	57	36	16	1	3	8	6	8	13	18	29	36	17	16	5	3	438

TABLE 14

Correlation table for the inheritance of the number of teeth in the laboratory population G. Parents with offspring (f 1).

Offspring	Parents 8	9	10	11	12	13	14	15	16	
9	1	97	1	2						101
10		12	40	9						61
11		1	2	72	2	1		1		79
12				5	33	2				40
13				2		7			1	10
14										0
15								18	4	22
16								5	64	69
17									1	1
	1	110	43	90	35	10	0	24	70	383

TABLE 15

Correlations between parents and their immediate progeny (f 1), in the culture G, for the diverse characters studied.

Character	No. of progeny	Coefficient of Correlation
Number of spines	491	.642 ± .018
Number of teeth	383	.989 ± .001
Diameter of shell	438	.949 ± .003
Depth of shell	428	.926 ± .005
Diameter of mouth	432	.936 ± .004
Length of longest spine	435	.770 ± .013

As table 15 shows, this culture gave essentially the same results as the previous one, so far as inheritance in the population is concerned. In all the characters inheritance is marked; in the diameter of the shell, as well as in the number of teeth, the correlation rises to .97, so that inheritance is almost complete.

To complete the statistical data on inheritance in populations, we give in table 16 the coefficients of correlation for such characters as were studied in the populations H and I (page 418). The population H is derived from 19 original parents, which gave 2203 offspring; so that some of the families are very large, four of them containing over 100 progeny,—one including 495, and another 1049. The population I is from 11 parents, giving 253 progeny. This population I was employed primarily for studying the effects of operations on the teeth, and in many cases the teeth of the parents of the progeny on which the coefficients of table 1 are based had been operated on. This work is to be described in a separate paper; the point here is that the operations have

TABLE 16

Correlations between the characters of parents and of the progeny (f 1) in the two populations H *and* I.

Character	Culture H.		Culture I.	
	No. of progeny	Coef. Cor.	No. of progeny	Coef. Cor.
Number of spines	1498	.217 ± .014	253	.141 ± .042
Diameter	2203	.786 ± .007	241	.428 ± .035
Number of teeth			246	.559 ± .030
Length of spines			242	.241 ± .041

resulted in making the correlation of parent and progeny in respect to the number of teeth much smaller than in natural cultures.

Comparing the different inheritance correlations for populations, as given in tables 11, 15 and 16, it will be observed that the inheritance is marked in practically all characters; that in some cases the degree of correlation of parent and offspring is very high (up to .99), but that there is great variation in the degree of correlation,—not only when diverse characters are compared, but also in diverse populations with respect to the same character. The correlation of parent and progeny with respect to number of spines ranges from .143 up to .729; in number of teeth from .559 to .993; in diameter from .428 to .949; in length of the longest spine from .241 to .770. The causes of this great variation will be taken up in a later section (page 461). The general fact is, however, entirely clear, that in populations composed of many lines of descent there is inheritance in a high degree from parent to progeny. This inheritance is clearly illustrated to the eye in figure 6, page 432.

The existence of diverse strains

It remains to examine more closely the nature and method of the inheritance that is revealed in populations by the statistical study. This inheritance might be due to the existence of permanently diverse strains or races in each of which the hereditary constitution remains unchanged, as has seemed to be the case in much of the 'pure line' work; or there might be no diversities of strains, but only a tendency for progeny to reproduce in some degree the peculiarities of their varying parents. Or the condition might be a blending in some degree of these extremes.

We must therefore examine the lines of descent to determine whether there are or are not persistent diversities between them, so that we can speak of diverse strains. Does a set of individuals derived from a single ancestor retain certain peculiarities, as compared with other families?

FIGURE 7.—Series showing linear pedigrees from six diverse families of *Difflugia corona* (× 143). Each row gives members of a single family, all the individuals in the row being descendants of the first one (at the left). The numbers at the beginning (240, etc.) are the designations by which the particular families were known in the records.

The precise descent of each of the individuals is given as follows: The successive individuals of each family are given a serial number. If the number of any individual is not followed by another number in parentheses, then this individual is the offspring of the immediately preceding one; thus, in family 240, No. 2 is the offspring of No. 1. If any individual's serial number is followed by another number in parentheses, this second number shows the parent of the given individual. Thus, the third individual of family 240 we find designated 3 (1); this signifies that it is the offspring of No. 1 of that family; similarly, in family 30, No. 4 is the offspring of No. 1, and No. 7 is the offspring of No. 4.

In presenting the figures the pedigree in the linear form described on page 419 was followed from the original progenitor, and as many individuals are included as could be put into a single row of the plate. There was no selection save in the case of family 248, in which many of the early individuals were destroyed by an accident before they were drawn, so that a later portion of the pedigree is shown. In certain other cases single individuals that were lost had to be omitted. These cases are as follows:

In family 30 an individual is lost that would be designated 11 (1).

In family 303 individual 3 is lost. The figure shows otherwise in this family an uninterrupted series of 12 descending generations.

In family 209, numbers 5 and 8 are lost. The individuals shown are numbers 1-11 (omitting 5 and 8) of family 209 in table 1, page 423.

In family 248 No. 3 is lost; also two individuals are lost before the last one in the row,—so that this last one is the great-grandchild of No. 6. The individuals shown are in series the following numbers from family 248 of table 1 (page 423): 1, 2, 4, 9, 10, 17, and a later one.

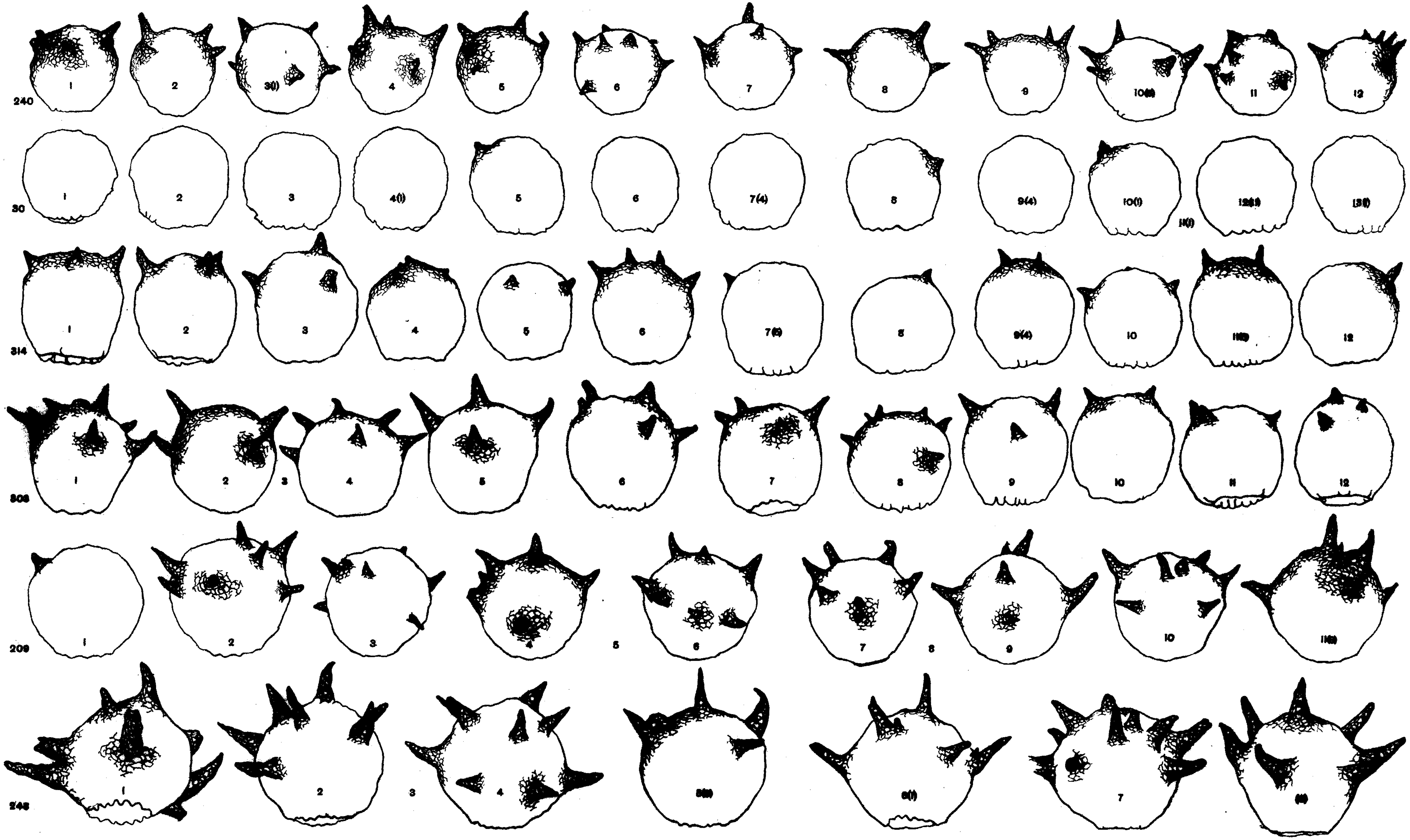

240
1
2
3(1)
4
5
6
7
8
9
10(3)
11
12
30
1
2
3
4(1)
5
6
7(4)
8
9(4)
10(1)
11(1)
12(3)
13(1)
314
1
2
3
4
5
6
7(3)
8
9(4)
10
11(3)
12
308
1
2
3
4
5
6
7
8
9
10
11
12
209
1
2
3
4
5
6
7
8
9
10
11(3)
248
1
2
3
4
5(3)
6(1)
7
(8)

FIGURE 7

Or if we isolate a single family and examine a large number of individuals belonging to it, shall we find the same variations, and the same degree of inheritance of the variations, that we find in a wild population?

Comparison of different families shows that they do, at least to a large extent and for a considerable period, retain their characteristic diversities. This may be illustrated to the eye by the aid of figures.

In figure 6 (page 432) we showed the single parent and its immediate progeny in a number of diverse strains; from this figure little as to the permanence of diversities can be judged. We therefore give in figure 7 the parents and as many as practicable of their descendants for six typical strains; the figures in most cases covering a considerable number of successive descending generations. Comparison of these six strains will give a clear idea of the at least relative permanence of the diversities in the strains. Thus, in the first series (family 240) we have throughout individuals of small size, with usually 4 to 6 spines—the total number of spines in the 12 individuals being 60. In the second series (family 30) we have slightly larger animals, with scarcely any spines, the total number of spines appearing in the entire 11 individuals being 3. In the third strain again (family 314) we have considerably larger individuals with few small spines,—the total number of spines for the 12 individuals being 29. In the fourth row (family 303) we have individuals of about the same size as in 314 (or perhaps slightly larger), with larger numbers of spines,—the total number of spines for the 11 individuals being 49. In the next row (family 209) we have individuals considerably larger than the preceding set, and of a diverse shape; the spines are small and numerous—the total for the 9 individuals being 55. In the lowest row (family 248), finally, we have still larger individuals, with very large and numerous spines,—the total number of spines for the 7 individuals being 53.

It should be remarked that there was no selection of individuals within these strains of figure 7; in each case the series begins with the original wild parent, and the pedigree is followed precisely, being arranged in the 'linear' form described on page 419. The only exception to this is the fact that in several cases certain individuals had to be omitted from the figures, owing to the fact that they were accidentally destroyed before a figure was made. The exact relationships of the individuals shown are given in the description of the figure.

The numbers of individuals shown might be greatly increased for all the strains (except No. 30); thus, family 240 included 43 individuals;

family 314 included 1050; family 303 had 496; family 209 had 40; family 248 had 126. A series taken at random from any part of the pedigree would give much the same picture (the question of whether any hereditary changes do arise within the family is to be dealt with later).

It would be easy to show many other strains diverse from the six presented in figure 7; some such are incidentally shown in figure 13, page 454, figure 14, page 466, and figure 15, page 484. But the distinguishing characteristics of the diverse lines may likewise be illustrated by giving serially the characters of the members of diverse races. These series of characters will show the ways in which the strains differ, as also the variations within the lines. Such series are shown for the diverse characters in tables 17 to 20.

These tables are pedigrees, presented in a linear form. For a full explanation of the arrangement of these pedigrees, page 419 should be consulted. Here we need to understand simply the following: In each series the first individual at the left is the progenitor of all the rest in the series. Then follow a descending series of generations, each individual being the immediate progeny of the one at its left, until we come to a dash. The individual following a dash is the offspring of one of the earlier individuals in the series; of which particular one is not presented in these tables, as being of no special importance for present purposes.

Thus in table 17, the family numbered 70 begins with a series of 4 descending generations (4, 5, 6, 5); then comes an individual (4) derived from one of the first three (which one is not specified); then follows its child and grandchild; then another derived from one of the preceding individuals, etc.

Many of the lines could not be traced in the tables to the end, as some contain hundreds of individuals; a series sufficient to show the typical conditions is given in each case. No selection is made within the pedigrees,—the part presented beginning with the original ancestor and being complete so far as it goes.

We may take first in table 17 a set of the families showing the diverse numbers of spines.

It will be observed that within the single culture (all in existence at the same time and under the same conditions), there are strains diverse for numbers of spines; in culture F, for example, seven strains are distinguishable that are clearly diverse in this respect; the typical number of spines ranging from almost 0 in line 30 to 5-7 in line 88. As a matter of fact, everything shows that no characteristic differences in spine number or other character are due merely to differences of condition in the diverse cultures, but that in each culture all sorts of diverse families may exist, depending on the original progenitors with which the culture began. For these reasons we shall not in the tables for the other char-

TABLE 17

Serial pedigrees by spine numbers, in diverse families. All the individuals of each line are descended from the first one at the left.

Families from culture F.

Family	
No. 30	0 0 0—0 1 0—0 1—0—1—0 0—0—0
" 69	1 2 1 1— 0—1—2
" 32	2 1 2 2— 2—3 2—3
" 24	2 3 3 3 3—3—3 4—1
" 70	4 5 6 5— 4 5 5—4—5
" 75	3 4—3 3 4—4 4
" 88	7 6 5—7 5

Families from culture G.

No. 197	1 2 3—1 4 2 3—2—5
" 245	4 5 5 4 5 4 4 4 4—4—5 5 4 5 4 4— 4—6—6—5 6—5—4—6 etc.
" 198	6 6 6—6 4—5—7 5—6—6
" 209	1 7 7 7 7 7 6 6 7 7—6—6 6—7 9 9 5—5—5—8 7 7—7 6 etc.
" 187	5 8 8 7— 6 8—8 9 6 8—6 7—8 6 6 6 4 5 5 5—6—5 6 5 etc.
" 248	8 7 9 9—10 6 6—6—5—7 8 8 9—9 6—6—10 9 6 6 9—8 9 6 etc.

Families from culture H.

No. 314	3 3 3 4 2 4—1 1—2 3—2 1 3 5—3—3 1—5—1—0 2—3 2 3 etc.
" 303	8 4 3 6 4 5 4 6 3 2 3 3—3 3 3—3— 3—6 4—6—2—3—4—5 etc.
" 304	4 4 6 5— 5 4 5 5 6—4—4—4—5—4 5—4— 3
" 308	4 6 9 9— 8—6 6 6—5

acters (tables 18 to 20) distinguish the cultures to which the lines belong.

Table 18 shows in a similar way the numbers of teeth in certain families. The pedigrees are arranged in the same way as in table 17, but the numbers of teeth take the place of the numbers of spines.

As table 18 shows, the diverse families differ sharply in the number of teeth, and there is high degree of uniformity among the individuals of a given family, although variations do occur (a matter to be dealt with later).

With relation to the diameter of the shell, families differing constantly likewise exist. Table 19 gives serial pedigrees for a number of typical races with respect to this character.

Finally, in table 20 we give a number of typical pedigrees showing hereditary diversities between the different families in length of the longest spine; in depth of the shell from fundus to mouth; and in diameter of the mouth.

TABLE 18

Serial pedigrees by numbers of teeth in certain families. All the individuals are descendants of the one at the left. (The interrogation points represent individuals in which the number of teeth was not determined.)

Family	
No. 186	9 9 ?— 9 9 9— 9 9— 9 9 9 9 9— 9— 9 9 9 9 9— 9— 9— 9
" 30	10 10 10—10 10 ?—10 ?—10—10— ? 10— ?—10
" 208	11 11 11 11 11—11 11— ? 11—11—10—11 11—11 11—11 11— ?—11—11—10 11 etc.
" 184	12 12—12 12—12 12 12—12
" 88	13 ? 13—13—13
" 303	14 14 ? 14 15 15 15 15 15 15 15 15—15 15 15 15— ? 15 15—15—14—15 etc.
" 248	16 16 ? 16— ? 16 ?— ?—16—16 ? 16 16—16 16— ?—16— ?—16 16 16— ? etc.
" 209	11 11 11 11 ? 13 12 12 12 12—12—11 11—13 13 13 13— ?—11—11 12 12 etc.

TABLE 19

Serial pedigrees by diameters of the shell in a number of typical families. The diameters are given in units, each of which is 4 2/3 microns. All individuals of a given line are descendants of the individual at the left.

Family	
No. 186	30 29 26—31 28 28—30 28—28 28 27 29 29—27—29 27 28 28—29—29—29
" 30	29 30 32—29 30 29—30 30—30—30 ? 31— ? 30
" 195	30 31 32 32 35 33—28 29 31 29 30 30 29 28—30—27—28 29—30 29 29—29— ? etc.
" 91	35 31 32—32—30 30—33
" 303	37 37 ? 36 38 38 36 35 35 37—35 35—35 35 35—35 ?—35 38—35—34—34—35 etc.
" 209	39 38 37 39 37 41 40 38 38 35—40—36—38—39 39 36 37—37—39—37 38 38—37 etc.
" 248	42 41 ? 40— ? 39 36—40—40—42 ? 43 40—39 43— ?—41 ? 41 41 42—40 42 etc.

It is indeed extraordinary to see these minute masses of protoplasm reproduce so true to type, yet with such marked diversities between the families. From this point of view the two reproducing pairs in figure 2 should be compared. In the slow progress of an experimental culture it

TABLE 20

Serial pedigrees to show the diversities of families in respect to length of the longest spine, depth of the shell, and diameter of the mouth. The measurements are given in units of 4 2/3 microns each. All the individuals on any line are descendants of the first individual at the left of the line.

Family	1. Length of longest spine
No. 32	5 5 7 6— 5— 8 7— 8
" 195	6 6 5— 4 8 8— 7 8 9 7 10 9 8 7—10— 7—11 7— 6 10 9— 8 7— 7 9 etc.
" 240	7 8— 7 10 9 5 9 12— 9—11 7 7 9— 3— 9 9 7— 8— 8—11—11 6 ? 7— 7 etc.
" 323	10 8 12 10 8 12 11—12—11—10— 8 10 8—11—11 9— 9 12 7 13 12—10 9— 9—12 etc.
" 325	10 14 12 11 14 16—14—14 15—15 16— 8— ? 14 15—17—12— 9
" 248	22 16 ? 15— ? 16 ?— ? 16—14 ? 24 23—17 15— ?—11 ? 12 15 15—16 13 16 18 etc.
	2. Depth of the shell
No. 240	29 29—31 30 29 29 29 29—30—29 27 27 27—25—28 27 29—30—29—31—29 26— ?—26—28 etc.
" 195	30 29 31 32 33 34—32 30 31 28 30 30 30 26—30—27—29 29—30 31 29—29— ? 28 28 etc.
" 209	37 39 39 37 ? 36 37 38 39 36—38—37 37—38 38 36 38—34—38—36 38 39—38—38—39 etc.
" 248	42 41 ? 43— ? 42 35—38—39—42 ? 40 39—40 39— ? 40— ? 39 41 40—41 41 41 41 etc.
	3. Diameter of the mouth
No. 195	13 12 13 12 13 13—13 13 13 13 14 13 13 13—13—13—13 14—13 13 13—14 13—14 13 etc.
" 208	14 15 14 14 14—15 13— ? 14—15—14—14 14—14 13—13 14—13—13—14—14 13 14 14 14
" 209	16 15 16 16 ? 16 16 17 16 16—17—15 15—16 18 16 16—16—16—16 17 16—16—17—15 etc.
" 248	18 20 ? 19— ? 19 ?— ?—20—19 ? 21 21—19 20— ? 19 ? 19 19 19—20 18 19 20 etc.

is most striking to find each new individual that appears reproducing thus the differential characters of its parent, in the way illustrated for example by a comparison of the numbers of spines (table 17) in lines 30 and 32; of line 32 with 75 or 245; of one of the latter with 248.

Equally striking are the differential characters observed in comparing the different families with respect to the features shown in the other tables It is clear that a population of Difflugia consists of large numbers of different strains, each strain remaining in a high degree true to type.

Distribution of characters within the single families

The characters of the individuals of a given family are of course not uniform; each family shows much variation in every set of characters. But when we compare the distribution of the variations in the different families, the hereditary diversities are strongly shown. The variability within the single families is a matter of interest for its own sake, for comparison with the variability of populations; and particularly so in view of the fact that we are here dealing throughout with congenital variations, not complicated by alterations due to growth nor by modifications due to the action of the environment during the life of the individual. We therefore give in tables 21 to 24 the distribution of the variations in the chief characters for the larger families examined, together with, in each case, the mean and the coefficient of variation. In each case we give also the distribution for all the families taken together, with the means and coefficients of variation for these totals. Figures 8 to 12 show curves plotted for the distributions of certain characters in some of the families. Examination of the tables and figures will bring out clearly the diversities of the families.

Table 21 shows the diversities with respect to numbers of spines. Several small families (Nos. 30, 186, 195, etc.), have been included because they show peculiarities of distribution not observed in families that were cultivated more extensively. Figure 8 shows curves plotted for the distributions of spines in certain small families of culture F; six families show maxima at the six diverse numbers from 0 to 5 spines. Figure 9 shows curves plotted for the numbers of spines in five of the large families of table 21; these have maxima ranging from 3 spines in family 314 to 7 in family 248.

The coefficients of variation shown in table 21 vary from 17 percent in family 195 to 45 or 46 percent in families 305 and 314; even indeed to 191 percent in the small family 30. This latter extraordinary coefficient of variation is evidently the result of the fact that the mean number of spines in family 30 is very close to 0, so that although the range of variation is merely from 0 to 1, the coefficient becomes enormous. Such a case raises the question whether the coefficient of variation (obtained

TABLE 21

Distribution of the variations in number of spines within single families, with the coefficients of variation.

Family	Number of spines															Total	Mean	Coef. of Var.
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14			
30	11	3														14	.21	191.48
186			1	3	10	5	1									20	4.10	21.68 ± 3.47
187					20	69	88	51	20	7	3	2	1			261	6.12	22.00 ± .68
195				3	14	13	3									33	4.48	17.46 ± 1.45
209		1			7	10	7	11	2	2						40	5.80	27.04 ± 2.18
240				3	9	21	8	2								43	4.93	18.76 ± 1.43
245				2	29	22	9	3								65	4.72	19.13 ± 1.16
248			1			6	30	31	25	21	10		1		1	126	7.49	21.33 ± .93
302			1	14	25	15	7									62	4.21	23.02 ± 1.46
303	3	13	39	132	186	94	26	2	1							496	3.79	30.51 ± .73
305	5	4	2	9	15	18	10	7			1					71	4.28	46.74 ± 3.19
309			5	14	31	11	7	1	1							70	4.11	28.62 ± 1.79
311			1	10	23	17	5	1	1							58	4.38	24.66 ± 1.66
314	40	107	198	279	273	118	31	3		1						1050	3.08	45.72 ± .81
317	1	8	25	47	57	30	7									175	3.54	34.16 ± 1.36
318	1	2	12	19	42	37	4									117	3.93	29.12 ± 1.38
323		1	3	7	10	21	3	2								47	4.36	28.55 ± 2.18
326	3	29	63	286	712	1500	1409	464	129	35	14	1				4645	5.29	24.74 ± .19
333				6	9	22	9	2								48	4.83	20.83 ± 1.51
Total	64	168	351	834	1472	2029	1664	580	179	66	28	3	2	0	1	7441	4.81	33.73 ± .21

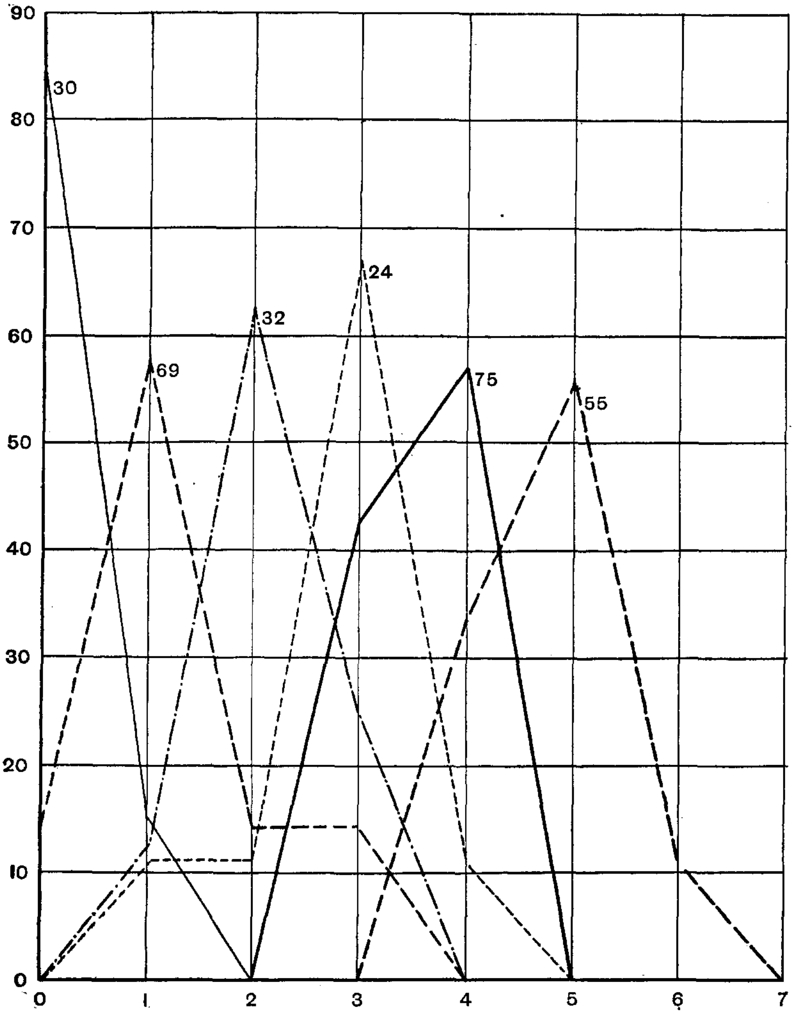


FIGURE 8.—Graphs of the distribution of the variations in spine number in six of the small families of culture F. The number with which each curve is marked is the designation of the family. The numbers of individuals in each of these families are as follows: family 30, 13 individuals; family 69, 7 individuals; family 32, 8 individuals; family 24, 9 individuals; family 75, 7 individuals; family 55, 9 individuals. (For curves from large families see figure 9.) The ordinates are percentages, the abscissae are numbers of spines.

by dividing the standard deviation by the mean), is really a suitable measure of relative variation. It seems somewhat paradoxical to say that family 30, with spines ranging merely from 0 to 1, shows eight times as much variation as family 326, with spines ranging from 0 to 11 in number.

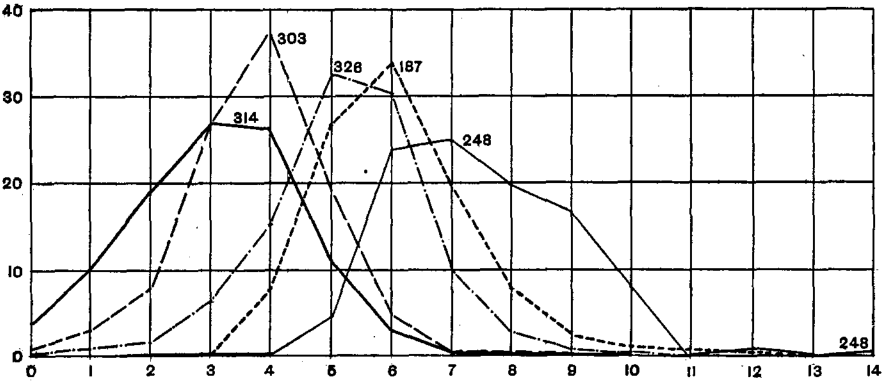


FIGURE 9.—Curves showing the distribution of the variations in number of spines in five large families. The numbers with which the curves are marked are the designations of the families; the number of individuals in each of these families is given in table 21. The ordinates are percentages; the abscissae numbers of spines.

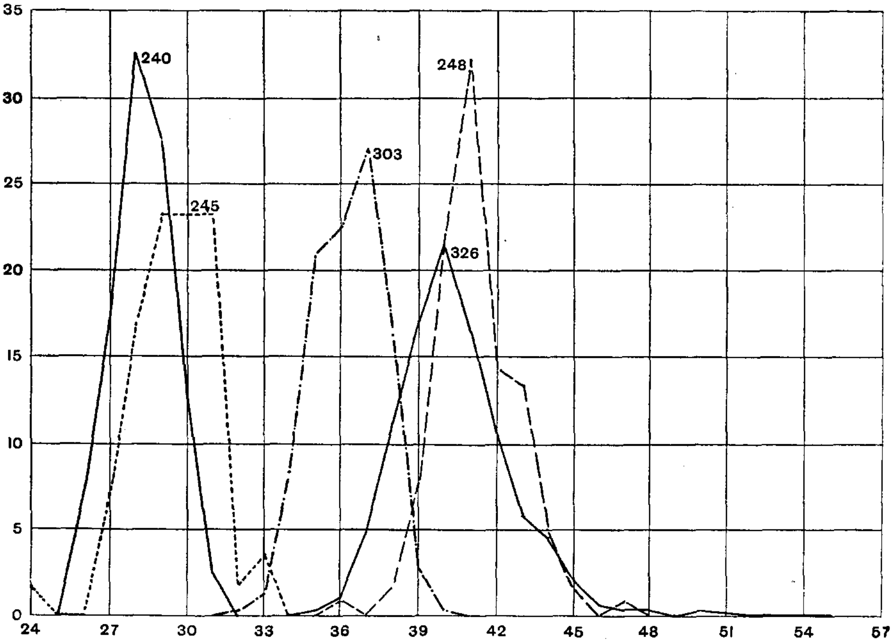


FIGURE 10.—Curves showing the distributions of the variations in diameter, in five of the families of table 22. Each curve bears a number that designates the family which it represents. The numbers of individuals in these families are given in table 22. The ordinates show percentages; the abscissae are diameters in units of 4 2/3 microns each.

On the whole the coefficients of variation in the single families, as shown in table 21, run somewhat lower than those for mixed populations, shown in table 2 (page 424). Yet some of the single families show coefficients higher than most of the populations. It is a peculiar fact that the coefficient of variation (33.73) for the population made up of all the families of table 21 taken together is lower than those for several of the single families taken separately, though it is these families that make up the population.

Table 22 shows the distribution in single families of the variations in diameter, and figure 10 presents graphs of some of these distributions. As appears both from the table and the figures, the different families show completely diverse distributions; families 240 and 248, for example, do not overlap at all, and there are all sorts of intermediate distributions in other families. The coefficients of variation again run smaller than those for populations (table 3, page 425), though the large family 326 (with 2375 individuals) shows a higher coefficient than most of the populations.

TABLE 23

Single families; distribution of the variations in number of teeth, with means and coefficients of variation

	Number of teeth											
Family	9	10	11	12	13	14	15	16	17	Total Number	Mean	Coef. of Var.
186	20									20	9	0
195	17	4	8							29	9.69	9.06 ± .80
208		2	20							22	10.91	2.65 ± .31
209			16	12	10					38	11.84	6.86 ± .54
240	22	10	1							33	9.36	5.74 ± .50
245	45	6	1							52	9.15	4.47 ± .26
248			1		1	1	20	86	1	110	15.74	4.36 ± .18
303				5	29	306	94	18		452	14.20	4.69 ± .11
305				3	5	4	37	4	2	55	14.73	7.00 ± .45
Total	104	22	47	20	45	311	151	108	3	811	13.43	16.22 ± .27

Table 23 and figure 11 show the distribution of the diverse numbers of teeth in the different families. In each family (save 209) the majority of the individuals have a certain definite number of teeth, with relatively few variants a little above or below this number. The proportion of individuals having this typical number of teeth varies from about 40 percent in family 209 to 100 percent in family 180. Different families show completely diverse distributions,—the maxima ranging from 9 to 16 teeth.

In the case of the number of teeth, the coefficient of variation for the population formed by all the families (table 23) is much greater

TABLE 22

Distribution of the variations in diameter, in certain single families, with the coefficients of variation.

	Diameter (in units of 4 2/3 microns each)																																				
Family	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56—60	Total	Mean	Coef. of Var.
186				1	3	7	7	2	1																										21	28.43	4.00 ± .42
195					2	6	10	7	3	2	1		1																						32	29.59	5.74 ± .51
209													4	5	9	11	8	2	1																40	37.60	3.87 ± .30
240				3	7	13	11	5	1																										40	28.28	4.24 ± .30
245	1			4	9	13	13	13	1	2																									56	28.50	5.57 ± .38
248														1		2	9	26	38	17	16	6	2		1										118	41.22	3.87 ± .18
303										1	6	40	101	108	130	80	14	2																	482	36.28	3.74 ± .09
323															3	6	13	14	8	3															47	39.57	3.16 ± .21
326												1	8	28	114	279	406	511	401	261	139	111	50	18	11	11	4	8	6	3	1	2	2		2375	40.48	13.65 ± .13
333																2	17	9	8	6	1	2		1											46	40.35	4.12 ± .28
Total	1			8	21	39	41	27	6	5	7	41	114	142	256	380	467	564	456	287	156	119	52	19	12	11	4	8	6	3	1	2	2		3257	39.29	8.98 ± .07
	(Diameter in units of 4 microns each)																																				
187																			4	8	20	27	42	48	33	24	14	7							227	45.75	4.36 ± .13
302								3	4	12	13	8	9	5	2																				56	33.36	5.20 ± .32
309														1	5	8	11	13	14	9	5	1													67	40.07	4.47 ± .23
311																	4	11	10	8	11	7		2											53	41.79	4.12 ± .26
305																				2	2	7	6	5	6	3	6	4	3	7	6	4	3	1 1	66	48.94	8.19 ± .47
314													2	15	34	96	178	282	222	112	39	13	1		1										995	40.09	3.87 ± .06
317														1	4	9	34	42	27	23	10	3	4		3	3	3	3							169	41.00	6.48 ± .22
318															3	8	11	22	15	21	14	5	1												100	40.88	4.36 ± .19
Total								3	4	12	13	8	11	22	48	121	238	370	292	183	101	63	54	55	43	30	23	14	3	7	6	4	3	1 1	1733	41.13	8.24 ± .09

TABLE 24

Distribution in the single families of the variations in length of the longest spine, with the means and the coefficients of variation. (The measurements are given in units each of which is 4 2/3 microns.)

	Length of the longest spine																																		
Family	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	Total	Mean	Coef. of Var.
186		1	1	1		4	3	6	1	3	1																						21	7.24	31.02 ± 3.52
195				1	1	6	6	8	5	3	2																						32	7.75	21.40 ± 1.85
208				2		2	6	6	4	3																							23	7.65	20.98 ± 2.18
209						1	2	3	1	5	9	9	4	4					1														39	11.21	21.02 ± 1.67
240					1	5	10	8	9	1	4	1																					39	8.10	20.10 ± 1.59
245		1		1	2	8	7	16	10	3	6	2																					56	8.05	24.43 ± 1.62
248										3	2	4	3	13	17	15	9	5	8	6	7	5	8	5	2		3					1	116	17.72	23.56 ± 1.12
303		2	3	19	55	82	110	98	71	22	15	8	2	2	1																		490	7.34	25.85 ± .60
324							2	6	7	10	10	9	2	1																			47	10.28	15.91 ± 1.14
326		2	3	2	6	10	30	65	105	174	193	221	213	124	82	55	36	45	19	10	6	8	9	3	3	2	3	1	1	1	1		1433	12.43	27.41 ± .36
333								2	1	4	4	7	10	5	5	4	3																45	12.96	17.61 ± 1.32
Total		6	7	26	65	118	176	218	214	231	246	261	234	149	105	74	48	50	28	16	13	13	17	8	5	2	6	1	1	1	1	1	2341	11.24	35.86 ± .40

than for any single family. A comparison of table 6 (page 427) and table 23 shows that the coefficients of variation for populations are invariably much greater than those for single families.

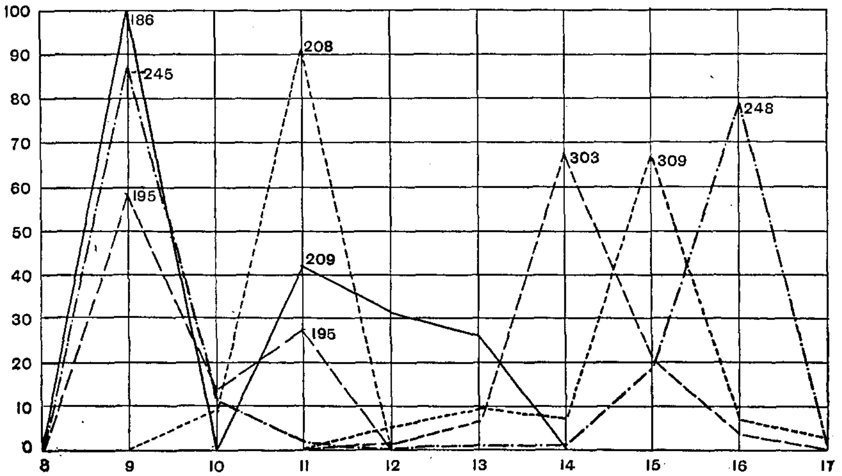


FIGURE 11.—Curves showing the diverse distributions of the numbers of teeth in the different families. The ordinates are percentages, the abscissae numbers of teeth. Each curve bears a number that designates the family to which it belongs; the numbers of individuals in the families are shown in table 23.

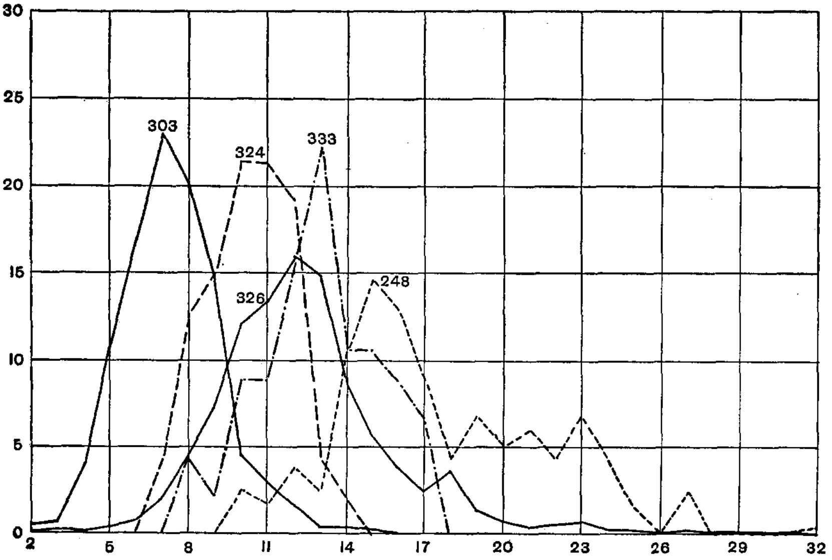


FIGURE 12.—Curves for the distributions of the variations in length of the longest spine, in five families. The ordinates are percentages, the abscissae lengths (in units of 4 2/3 microns each). Each curve bears a number that designates the family to which it belongs; the numbers of individuals in these families are shown in table 24.

Table 24 and figure 12, finally, show the distributions of the variations in length of the longest spine in the different families. Here again the diversities of the families stand out strongly, though the curves are less compact than for the other characters. The maxima for the different families range from a length of 7 units in family 303 to 15 units in family 248. Nearly all the curves show a tendency to tail out toward the upper limits; that is, there are numerous scattering individuals with spines much longer than the mean length. The coefficients of variation for the single families (table 24) are lower than those for populations (table 7, page 428).

In general the examination of the distribution of variations in single families brings out the diversities of the families, and shows that many such diverse families exist, whether we base our examination on the number of the spines, the diameter of the shell, the number of teeth, or the length of the spines. The coefficients of variation are in general smaller for the family than for the population, though with certain exceptions in the case of number of spines and of diameter. The range of variation may be very considerable within a single family. Whether any of these variations within a family represent hereditary differences remains to be determined.

Correlation of the characters of the individuals within single families

We have seen that in mixed populations there is on the whole a positive correlation between all the diverse sets of characters of the individuals (table 8, page 428). Does this hold also for single families taken by themselves? In table 25 are given the coefficients of correlation between the diverse sets of characters in the two families 245 and 248, while in table 26 are given similar coefficients for various pairs of characters in a number of different families.

TABLE 25

Coefficients of correlation between the diverse characters of the individual in the two single families No. 245 and 248.

	Fam. 248		Fam. 245	
	No.	Correlation	No.	Correlation
Diameter and depth	118	.325 ± .055	56	.710 ± .045
" " diameter of mouth	116	.255 ± .059	56	.473 ± .070
" " No. of spines	118	.082 ± .062	56	.302 ± .082
" " No. of teeth	110	.197 ± .062	52	.090 ± .093
" " length of longest spine	116	.139 ± .061	56	.145 ± .088
Diameter of mouth and No. of teeth	110	.348 ± .057	52	.020 ± .093
No. of spines and No. of teeth	110	.103 ± .064	52	.089 ± .092
" " " " length of longest spine	116	.129 ± .065	56	−.135 ± .088

TABLE 26

Correlations between the more important characters of the individual, within single families.

1. Correlation between the size of the individual (diameter of its shell) and the number of its spines, in 12 families.

Family	No. of Individ.	Correlation	Family	No. of Individ.	Correlation
187	248	.153 ± .042	309	43	.042 ± .103
245	56	.302 ± .082	311	39	.282 ± .099
248	118	0.82 ± .062	314	985	.159 ± .021
302	47	.356 ± .086	317	174	—.002 ± .051
303	482	.145 ± .030	318	112	.053 ± .063
305	66	—.368 ± .072	326	2375	.214 ± .013

2. Correlation of diameter of the individual with length of its longest spine, within 4 families.

Family	No.	Correlation
245	56	.145 ± .088
248	116	.139 ± .061
303	493	.212 ± .029
326	1433	—.020 ± .018

3. Correlation of diameter with number of teeth, in 4 families.

Family	No.	Correlation	Family	No.	Correlation
245	52	.090 ± .093	303	451	.017 ± .032
248	110	.197 ± .062	305	55	.348 ± .078

4. Correlation of number of spines with number of teeth.

Family	No.	Correlation	Family	No.	Correlation
245	52	.089 ± .092	303	454	.004 ± .032
248	110	.103 ± .064	305	55	—.188 ± .088

5. Correlation of number of spines with length of the longest spine.

Family	No.	Correlation
303	453	.206 ± .030
326	1435	.208 ± .013

As the tables show, in most cases there is a positive correlation between the diverse characters of the individuals within the single families; larger individuals have on the average more spines, more teeth and longer spines than smaller ones of the same family, and in agreement with this, a larger number of spines goes with longer spines. Only with respect to number of spines and number of teeth is there entire lack of evidence of a positive correlation.

The positive correlations shown in most families are however not present in all. With respect to size (diameter) and number of spines, family

305 (table 26) shows a marked negative correlation in place of the usual positive one; this family will be taken up in detail in a later section. Further, in families 248, 309, 317 and 318 there is no significant correlation between size and number of spines.

Again, with respect to diameter and number of teeth, there is lack of correlation in families 245 and 303. As to diameter and length of spines there is no correlation within the very large family No. 326 (with 1433 individuals).

Thus while in most families there are slight positive correlations between the diverse sets of characters, in any given family this may not be the case, so that for any particular family a special investigation is necessary. The matter is of course of importance with relation to the effects of selecting for any particular character. In most families selection of larger individuals would be on the whole a selection likewise of individuals with more numerous spines and teeth and longer spines. But this would not be the case in all families.

What hereditary combinations of characters may occur in the diverse families?

We have seen on page 428 that there is in mixed populations a statistical positive correlation between the diverse sets of characters, so that larger animals have *on the average* more spines, more teeth, longer spines, a greater depth, and a larger mouth than do smaller animals (see table 8). Do these relations apply to the hereditary diversities of all families? That is, if in any family the hereditary diameter is greater, than in another, will this strain also have the other characters (hereditarily and on the average) likewise in the higher degree indicated by the correlations for populations? Or may we have in different families diverse combinations of hereditary characters,—so that we may find families characterized by large bodies and few spines or few teeth; or families with small bodies and long spines,—as well as the reverse conditions?

The question is an important one, since it bears on the genetic and physiological causation of the various types that occur. If greater number of spines and teeth, longer spines and larger mouth, invariably occur (on the average) in any race of large size, then all the variations of type found in populations may be interpreted as due merely to variations in size, and the genetic problem narrows itself to the question as to how hereditary differences in size are produced. If, however, the hereditary (mean) characters—size, number of spines, number of teeth, length of spines, size of mouth, etc., may vary independently in the diverse races, so that we can find races giving hereditarily different combinations of characters,—then the genetic problem is much less simple. Many diverse factors must then be at work; we must account for the variation of each set of characters independently.

Let us therefore examine some of the lines, to discover whether we may have diverse combinations of hereditary characters in the different lines; combinations not predictable from the positive correlation found in populations. Figure 13 illustrates certain of the relations to be brought out.

Diameter and number of spines. In populations we have found (page 429) that there is a positive correlation between these; larger animals have on the average more spines. But does this relation appear on comparing any two families?

Table 27 shows certain pertinent data from this point of view. Compare the families 198, 195 and 197 from culture G. Nos. 195 and 198 average nearly of the same size, though 195 is a trifle larger (its mean diameter is 29.6 while that of 198 is 28.6). But 198 has distinctly a higher number of spines than 195. Now compare family 197 with both of these. Numbers 198 and 197 are shown in figure 13. No. 197 is much larger (its mean diameter is 37.25) but the number of its spines runs much lower than in either of the other two.

With Nos. 198 and 195 may further be compared family 32 (table 27); the three have approximately the same diameter (that for family 32 being 30.75), yet the number of spines in family 32 is lower than in either of the other two. Again, compare family 30 (which is shown in figure 7, page 438) with all these; the size still remains practically the same (mean diameter of family 30 is 30.00) yet the number of spines now approaches 0. With this family 30 or with 32 compare family 240 (shown in figure 7); the size is still the same, but the number of spines is high. The comparison of family 197 with 240 is likewise instructive.

These points are well brought out to the eye through an examination of figure 7 (page 438) and of figure 13. In figure 7 we have typical lines of descent in different families. The small race 240 is evidently characterized by more numerous spines than race 30, of similar size. In figure 13 the family 198 shows much smaller size and more numerous spines than family 197.

Again, in culture H we may compare families 304 and 314, as next shown in table 27. Here 314 is uniformly much larger than 304, yet

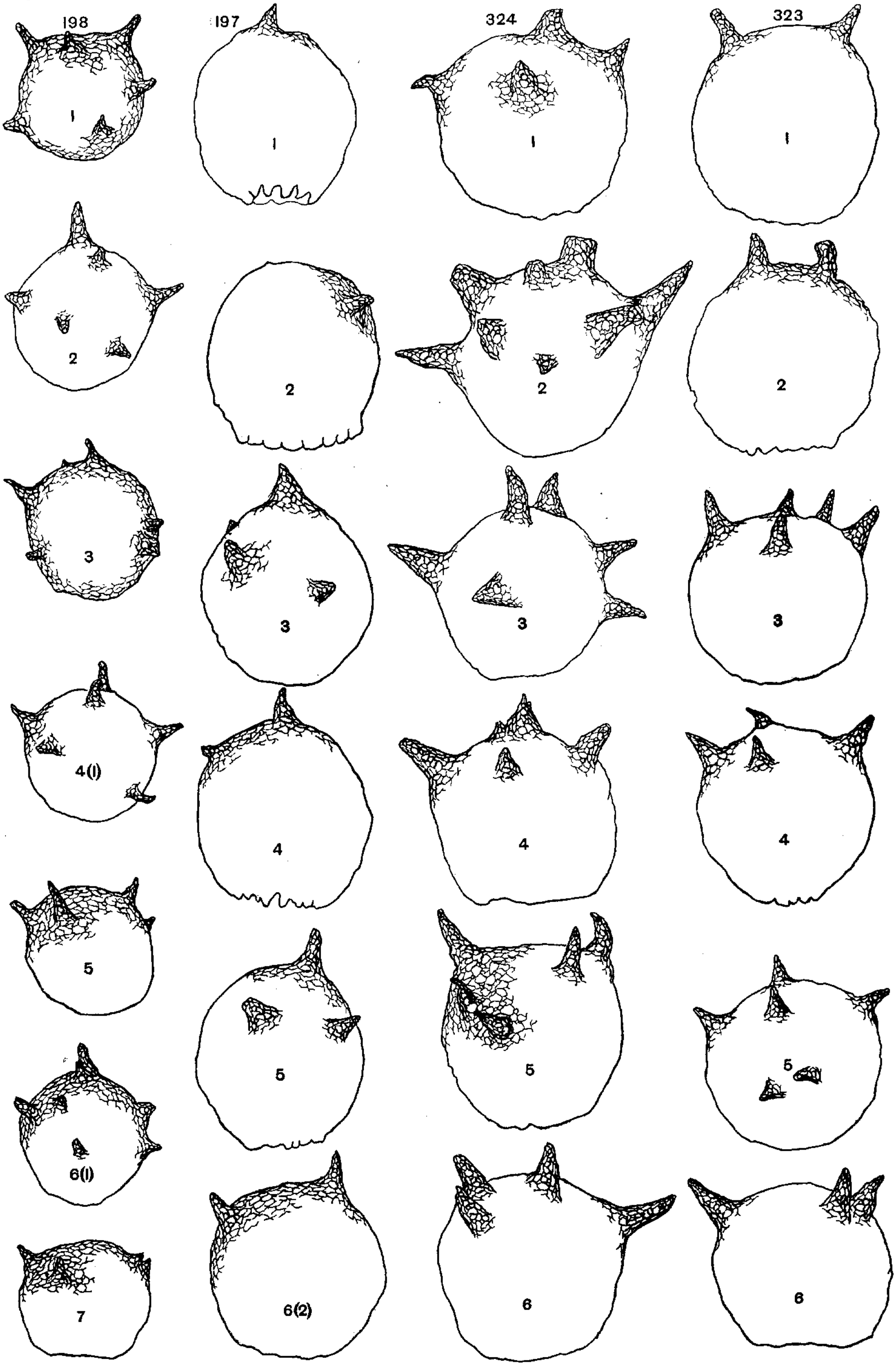


FIGURE 13

TABLE 27

Serial pedigrees for numbers of spines and diameter to show the diverse combinations that occur in different families. In each pedigree the first row shows the number of spines of the individuals, the second row their diameters.

(The diameters are measured in units of 4 2/3 microns each, save in families 304 and 314, in which the unit is 4 microns.)

Fam. 198	6	6	6—6	4—5—7	5—6—6												
	29	29	29—29	29—26—27	30—29—29												
“ 195	4	3	3	3	5	4—4	4	4	5	5	4	5	5—5—5—5	4—6	5	5—4	etc.
	30	31	32	32	35	33—28	29	31	29	30	30	29	28—30—27—28	29—30	29	29—29	“
“ 197	1	2	3—1	4	2	3—2	5										
	36	?	39—37	38	35	36—39	38										
“ 32	2	1	2	2—2—3	2—3												
	28	32	30	30—32—30	33—31												
“ 240	5	4—5	5	5	7	5	3—4—5	6	6	5—3—5	5	5	etc.				
	30	30—29	29	29	29	29	29—28—30	28	26	26—27—29	28	28	“				
“ 30	0	0	0—0	1	0—0	1—0—1—0	0—0										
	29	30	32—29	30	29—30	30—30—30—?	31—30										
“ 304	4	4	6	5—5	4	5	5	6—4—4—4—5—4	5—3								
	32	32	36	33—33	32	30	31	33—34—32—31—32—31	34—30								
“ 314	3	3	3	4	2—1	1—2	3—2	1	3	5—3—3	1—5—1—0	2—3	2	etc.			
	39	42	38	37	38—40	41—40	38—40	38	40	?—40—40	42—37—40—38	39—40	40	“			

FIGURE 13.—Portions of four families to show diversities of combination of characters (all × 143). The figures at the top (197, etc.) show the designation of the families. Each individual is given a number. All individuals of any column are descendants of the one at the top. Any individual is the offspring of the one just above it, unless its number is followed by another number in parentheses; in this case, the number in parentheses indicates the parent (thus No. 4 in family 197 is the offspring of No. 1).

Observe that though the individuals of 197 are much smaller than those of 198, they have more numerous spines. Further, though families 323 and 324 have individuals of the same size, the spines are throughout larger in family 324.

has regularly fewer spines. (These two are not to be compared directly with the others, but only with each other, as they are measured in units slightly smaller than those employed for the others.)

Altogether it is clear from the examples given in table 27 that often hereditarily greater size goes with hereditarily fewer spines; or families with equal diameters may uniformly have diverse numbers of spines. Diameter and number of spines thus show independent hereditary diversities. The positive correlations observed in populations are therefore of a merely average character; they show only the more usual condition. If we should chance upon a population composed exclusively of individuals of families 195, 197 and 198, we should find a marked negative correlation between diameter and number of spines (see page 461). We can not therefore account for diversities of race in respect to spine number through diversities in size, for sometimes larger races have fewer spines, sometimes more spines.

Diameter and number of teeth. In a similar way we compare in table 28 for several lines the relation of diameter to number of teeth. The correlations in populations is, as we have seen, positive; large specimens have usually more teeth. But in table 28 we may observe the following facts:

Families 208 and 240 have individuals of the same size, but family 208 has 11 teeth, line 240 but 9. Family 211, likewise of the same size, has 12 teeth.

Families 230 and 68 have a diameter of about 30, with 11 teeth; family 109 has a diameter of 38-40, also with 11 teeth.

Family 303, with 14-15 teeth, is distinctly smaller than family 209, with 11-13, or than family 109, with 11.

Families 211 and 184 have the same number of teeth (12), but the size of the latter is much greater than that of the former.

Families 303 and 184 are of practically the same size, though the former has 14-15 teeth, the latter but 12.

Family 109 is distinctly larger than 184, but has fewer teeth.

Thus it is clear again that the correlation shown in populations is merely the usual condition, and does not indicate any necessary relation. A family of larger individuals may hereditarily have more teeth than a family of smaller individuals, or it may have less. Decreased size will not account always for hereditarily fewer teeth; the two things may be independent.

Diameter and length of spines. For length of spines in relation to

TABLE 28

Serial pedigrees for certain lines, for comparing the **relations** *of number of teeth to diameter, and showing what sorts of hereditary combinations may occur. (Diameter measured in units of 4 2/3 microns each.)*

Fam.	208	Teeth	11	11	11	11	11—11	11—11—11—10—11	11—11	11—11	11	?—11	11	10	11				etc.
		Diam.	29	32	31	27	29—29	29—29—30—31—29	28—29	28—30	27	29—31	31	29	29				"
"	240	Teeth	9	9—9	9	9	9	9	?	9—9	9	9	?—11—9	9	9—10—?—9	?			"
		Diam.	30	30—29	29	29	29	29	29	28—30	28	26	26—27—29	28	28—31—30—30	29			"
"	230	Teeth	11	11	11	11	11	11	11	11—10—11—11—11	?—?	8	9—10—10						
		Diam.	29	29	27	29	27	28	29	29—30—28—26—27	27—27	27	27—28—28						
"	109	Teeth	11	11	11—11														
		Diam.	40	39	40—38														
"	68	Teeth	11	11	11	11—11—11—11													
		Diam.	28	29	31	30—31—29—31													
"	303	Teeth	14	14—14	15	15	15	15	15	15	15	15—15	15	15—15—15	15—15—14—15—15				etc.
		Diam.	37	37—36	38	38	36	35	35	37	35	35—35	35	35—35—35	38 35—34—34—35				"
"	209	Teeth	11	11	11	11	?	13	12	12	12	12—12—11	11—13	13	13	13—?	11—11	12	"
		Diam.	39	38	37	39	37	41	40	38	38	35—40—36	38—39	39	36	37—34	39—37	38	"
"	211	Teeth	12	12	12	12—12	12—12—12	12											
		Diam.	29	30	30	30—28	28—28—30	29											
"	184	Teeth	12	12—12	12—12	12	12—12												
		Diam.	35	37—36	37—35	36	36—37												

diameter the independence is less noticeable, owing to the great variability of the length of spines within the single family. In table 29 however the following cases are brought together:

TABLE 29

Serial pedigrees for certain families, for comparing the relations of the diameter to the length of the longest spine, with the different combinations that may occur.

In each pedigree the first row gives the length of the longest spine, the second the diameter. Both are measured in units of 4 2/3 microns.

Fam. 197	6	?	4—4	10	8	9—7—6														
	36	?	39—37	38	35	36—39—38														
" 198	7	10	9—8	9—6—11—8—6—8																
	29	29	29—29	29—26—27—30—29—29																
" 209	6	12	8	11	?	9	11	10	14	10—19—12	14	11	12	10	13	8—10—14	11	11	12	etc.
	39	38	37	39	37	41	40	38	38	35—40—36	38	39	39	36	37	37—39—37	38	38	37	"
" 323	10	8	12	10	8	12	11—12—11—10—8	10	8—11—11	9—9	12	7	13	12—10	9	etc.				
	40	39	38	37	37	39	40—38—39—38—38	37	38—39—39	42—41	40	39	40	41 39	41	"				
" 324	10	17	15	13	14	13—15—13	13—13	15	13—12 12	13	15	14—10—9	13—8 18—14	etc.						
	40	41	36	40	39	39—40—39	38—38	39	40—37—42	38	38	38—40—40	40—41—41—40	"						

In family 197 the individuals are about 1/3 larger than in 198, yet in the latter case the spines are longer than in the former.

Family 209 has about the same size as family 197, but the spines average much longer.

Families 323 and 324, cultivated side by side, show the same size, but 324 has constantly longer spines than 323. The first portions of the pedigrees of these two races are shown in figure 13.

There is thus a certain degree of independence in these two characters; a race hereditarily smaller than another may have spines hereditarily longer.

Combinations of other characters. We have dealt thus far with combinations of the diameter with the other characters, since it is these combinations that are of the most interest. With relation to the combinations of other sets of characters, the following may be said:

In my measurements there is no clear indication of diversity of combination in different families, as to diameter with depth of the shell, nor as to diameter with the size of the mouth, though with regard to the latter pair of characters, I believe that a more complete study would be likely to show that diverse combinations do occur.

With relation to diameter of the mouth and number of teeth, different combinations do occur in diverse families. As the diameter of the mouth was little studied, but few lines will be cited to show this diversity of combination. In populations, as we have seen, there is a positive correlation between number of teeth and size of mouth; the two increase together. Compare family 240 with family 195 (table 30); the latter has distinctly a smaller mouth, yet the number of teeth is the same as in 240, or in many individuals one greater. Families 240 and 211 have mouths of the same size, but 211 has one more tooth. Family 209 has a much larger mouth than 211, but has on the average a smaller number of teeth. Thus, not all families show the usual rule of proportional increase of number of teeth with size of mouth.

With respect to the number of spines as compared with the numbers of teeth there is a similar condition of affairs. A family which regularly has more spines than another may have either more teeth or fewer teeth. Thus, in table 30 B, family 69 has more spines than family 30 and fewer than family 240, but has more teeth than either. Family 198 has more spines than family 69, but fewer teeth; it has likewise more spines than family 240, but more teeth. Other combinations of these two sets of characters may be found in table 1 (page 422).

It will not be necessary to take up in detail other sets of characters. Clearly, we find that the different families show, not merely diverse hereditary characters, but diverse hereditary combinations of characters. Families showing a given size may have few spines or many spines; few teeth or many teeth; long spines or short spines. If two families show diverse hereditary sizes, while usually it is the larger that has the greater number of spines, larger teeth and longer spines, in other cases the rela-

TABLE 30

Serial pedigrees for certain families, showing diverse possible combinations of characters.

A. Number of teeth and diameter of the mouth.

Fam. 208	Teeth	11	11	11	11—11	11—11—11—10—11	11—11	11—11	11—11—11—10—11—11							
	Diam. Mouth	14	15	14	14—15	13—14—15—14—14	14—14	13—13	14—13—14—14—13—14							
“ 240	Teeth	9	9—9	9	9	9	9	9	9—9	9	9—11—9	9	9—10—9—9—9			
	Diam. Mouth	14	14—14	13	13	14	13	13	13—15	13	13—14—14	14	13—14—13—14—14			
“ 195	Teeth	10	10	11	?	11	11—9	9	9	9	9	10	10	9—9—9—9	9—9	9
	Diam. Mouth	13	12	13	12	13	13—13	13	13	13	14	13	13	13—13—13—13	14—13	13
“ 211	Teeth	12	12	12	12—12	12—12—12	12									
	Diam. Mouth	14	14	14	14—14	13—14—14	14									
“ 209	Teeth	11	11	11	11	13	12	12	12	12—12—11	11—13	13	13	13—11—11	12	12
	Diam. Mouth	16	15	16	16	16	16	17	16	16—17—15	15—16	16	16	16—16—16	17	16

B. Number of teeth and number of spines.

“ 30	Teeth	10	10	10—10	10	?—10	?—10—10—10					
	Spines	0	0	0—0	1	0—0	1—0—1—0					
“ 240	Teeth	9	9—9	9	9	9—9	?—9—9	9	9	?—11—9	9	9—10—?—9
	Spines	5	4—5	5	5	7—5	3—4—5	6	6	5—3—5	5	5—6—6—5
“ 69	Teeth	11	11	11	11—11—11—11							
	Spines	1	2	1	1—0—1—2							
“ 198	Teeth	11	10	10—10	10—10—10	10—10—11						
	Spines	6	6	6—6	4—5—7	5—6—6						

tion is reversed, the smaller race having more spines or teeth or longer spines. Similar statements can be made with relation to other combinations of characters.

The essential point is that among the different families the diverse hereditary characters *vary independently*, so that the different combinations can not be accounted for as all dependent on some single character such as size.

Correlation of characters in populations composed of diverse sets of families

It results from the facts set forth in the last section that the degree and kind of correlation of characters observed in any population depend upon the kinds of families of which it happens to be composed. As we have seen (table 8, page 428), the correlations between the different characters of the individual are in most populations positive. But it is perfectly possible for populations to occur in which the correlations are negative. Suppose for example a population happened to be made up of a mixture of families 197 and 198 (table 27). The numbers of individuals in these two families are not great; if we throw them all together in a single population the correlation between the number of spines and the diameter is strongly negative and equal to —.760.

Again, suppose that we have a population composed of a mixture of families 303 and 209, and we determine the correlation between the diameter and the number of teeth (see the data for these lines in table 28). Family 209 had 39 individuals in which spines and teeth were both measured; for computation we will mix these with an equal number from family 303 (taking the first 39 in the pedigree of the latter). The population so obtained shows a marked negative correlation (—.490) between diameter of the shell and number of teeth.

Examples of this relation could readily be multiplied. It gives the explanation for the fact shown in table 8, that in different populations we obtain very diverse values for the coefficient of correlation between the same sets of characters of the individuals. What coefficient is obtained,—whether positive or negative, and how great numerically,—depends on the relative numbers of the different sorts of families present.

How many heritably diverse families are distinguishable?

Examination of the data given in the foregoing tables shows that a large number of heritably diverse lines can be distinguished. This is notably true even if we confine our attention to a single character. Thus, with respect to number of teeth, we can certainly distinguish families with each particular number of teeth from 9 to 16 inclusive; this alone gives us eight hereditarily diverse families. A larger number than this could certainly be distinguished on the basis of hereditary shell diameter alone; and at least an equal number on the basis of the hereditary number of spines. Since we find moreover that there are different combinations of the diverse characters in the different families, the number of hereditarily diverse families is evidently greatly increased. Without attempting the difficult task of actually distinguishing and enumerating the hereditarily diverse families that were examined, I believe it must be said that the existing number is in reality indefinitely great. Further ground for this conclusion will appear later.

II. VARIATION AND INHERITANCE WITHIN THE SINGLE FAMILY

Our results thus far show that a wild population of *Difflugia corona* consists of a large number of hereditarily diverse families; families between which the diversity persists for many generations. The next question is: Can such hereditarily diverse groups be derived from a single family, by variation with selection, or otherwise? Does the genotype of the single family remain constant? Or do hereditary variations arise during vegetative reproduction within the family, so that diverse genotypes arise thus from a single one?

These are the fundamental questions with which our investigation deals. Our organism presents us precisely the conditions needed for attacking them: A series of diverse families, hereditarily differentiated. Can we take a single one of these families and produce from it a set of hereditarily diverse families?

This is what in our work on Paramecium (JENNINGS 1908) we were unable to do, and most of the 'pure line' work has agreed in this negative result. In Difflugia we have an organism more favorable for such work perhaps than any thus far investigated, owing to the great variation; the fact that all variations are congenital; and the existence in nature of great numbers of diverse families.

We shall attack the problem (1) first by a quantitative study of the question whether there actually is inheritance of variations within the single family; (2) then we shall determine whether we can by selection or otherwise obtain heritably diverse families from a single family.

Is there inheritance of variations within the single family? A statistical study

In the work of the first six months (culture G, autumn and winter of 1913), seven families were obtained, each containing from 21 to 125 progeny; larger numbers in the family were not obtained, owing to inexperience in methods of culture. To determine whether the variations within the family are inherited, the coefficient of correlation between parent and immediate progeny was determined with relation to the six different characters studied. In such a case as the present, the same individuals may occur in the correlation table both as parent and as progeny; and indeed, a single individual may occur several times as parent, each time of course paired with a diverse offspring. On the other hand, any individual of course occurs in the table as progeny but once. In such a table, where the two classes compared (parents and progeny) are largely the same set of individuals, the coefficient of correlation shows essentially what proportion of the parents' peculiarities are on the average inherited by the progeny (the coefficient of correlation being approximately the same as the coefficient of regression). Thus, if the correlation in number of spines should be .5, this would show that parents who had four spines above the usual number produce progeny likewise with spines above the usual number, though the mean excess for the offspring would be but *two* above the usual number.

Table 31 gives the coefficients of correlation between parents and offspring for six sets of characters in the single families in this culture G.

It will be observed that with respect to diameter of the shell there is a marked positive correlation (up to .5) between parent and progeny in every one of the seven families, and that with respect to the number of teeth the correlation is above .5 in four out of the six families (in family 186 there was no variation in number of teeth, so that correlation was not determinable). With respect to the other characters the correlation varies; sometimes it is slightly negative; in many cases the correlation is not significant in comparison with the probable error. It must be remarked however that in all cases in which the correlation is large enough to be significant in comparison with the probable error, the correlation is positive.

The evidence from this first culture is then, so far as it goes, distinctly in favor of an inheritance of variations within the single family. But the numbers of individuals in the families are too small for drawing positive conclusions. The results evidently call for repetition of the experiment on a larger scale.

In the spring of 1914, therefore, culture H was undertaken for the purpose of obtaining families containing large numbers of individuals; and at the same time for practicing selection within the single family. One family was obtained containing 496 individuals; another with 1050; also a number of smaller families. The number of spines and the diameter were examined in all the families; other characters in certain families. The correlations between parent and offspring are given in table 32

TABLE 31

Coefficients of correlation between parents and offspring (*P* and *f 1*) *within the single families of culture* G, (*October, 1913, to February, 1914*). *The columns of numbers are numbers of progeny in the family; these numbers are given separately for each character, since in some individuals certain of the characters could not be determined.*

Family	Number of Spines		Diam. of Shell		Depth of Shell		Length of longest Spine		Diam. of Mouth		Number of Teeth	
	No.	Correlation	No.	Correlation	No.	Correlation	No.	Correlation	No.	Correlation	No.	Correlation
186	20	−.066 ± .150	20	.398 ± .127	19	.098 ± .153	20	.334 ± .134	19	.027 ± .155		
195	32	.096 ± .118	31	.550 ± .085	31	.522 ± .088	31	.067 ± .121	31	.243 ± .114	26	.923 ± .020
208	24	.194 ± .133	21	.282 ± .135	21	—.214 ± .140	20	.112 ± .149	21	—.007 ± .147	19	—.081 ± .154
209	39	.331 ± .096	36	.280 ± .104	36	—.071 ± .112	36	.152 ± .110	36	.275 ± .104	35	.586 ± .075
240	42	.029 ± .104	38	.452 ± .087	38	.399 ± .092	38	—.051 ± .109	38	.364 ± .095	29	.536 ± .089
245	64	−.029 ± .084	52	.564 ± .064	52	.524 ± .069	52	.129 ± .092	52	.313 ± .084	46	.074 ± .994
248	125	−.010 ± .060	105	.127 ± .065	105	—.037 ± .066	105	.249 ± .062	105	.008 ± .066	91	.510 ± .052

TABLE 32

Correlation between the parents and their immediate progeny, within the single families of culture H (*spring of 1914.*) *Each family derived by fission from a single parent individual. The "No." signifies the number of progeny in the family.*

Family	Number of Spines		Diameter of Shell	
	No.	Correlation	No.	Correlation
187	260	.286 ± .036	226	.342 ± .040
302	61	.075 ± .086	55	.298 ± .083
303	495	.143 ± .030	468	.269 ± .029
305	70	.284 ± .074	61	.725 ± .041
309	69	.172 ± .079	66	.385 ± .071
311	57	.162 ± .087	52	.329 ± .083
314	1049	.153 ± .020	960	.269 ± .020
317	174	.113 ± .051	168.	.658 ± .029
318	116	—.235 ± .059	99	.306 ± .061
319	52	.345 ± .082	50	.089 ± .095
	Number of Teeth		Length of Longest Spine	
303	394	.585 ± .022	467	.235 ± .029
305	44	.690 ± .053		

It will be admitted that the results shown in table 32 are remarkable. In all of the ten families save one there is a marked positive correlation between the number of spines in the parent and that in the progeny. In all the ten there is a positive correlation between the diameter of the parent and that of the offspring; a correlation rising in family 305 to the extraordinary proportion of .725, and in family 317 to .658. In the two families in which the number of teeth was studied the correlation is above .5. In the 467 individuals of family 303, the correlation between length of spine in the parent and progeny was .235 ± .029.

It will be observed that in these cases the numbers of individuals were sufficiently large so that there can be no question regarding the significance of the results. Family 314 contains 1049 progeny, and gives a correlation in spine number of .153 ± .020; in diameter of .269 ± .020. Family 303, with 495 progeny, shows for number of spines a correlation of .143 ± .030; for diameter .269 ± .029; for number of teeth .585 ± .022, and for length of longest spine .235 ± .029. Equally significant figures are given by families 187 and 317.

It is beyond question therefore that in *Difflugia corona* the progeny resemble their parents more closely than they do the more distant members of the same family; and that in some cases this greater resemblance is shown in a high degree. When we consider that all the individuals in the family come finally from the same original individual by fission, it appears almost incredible that within the single family we should find

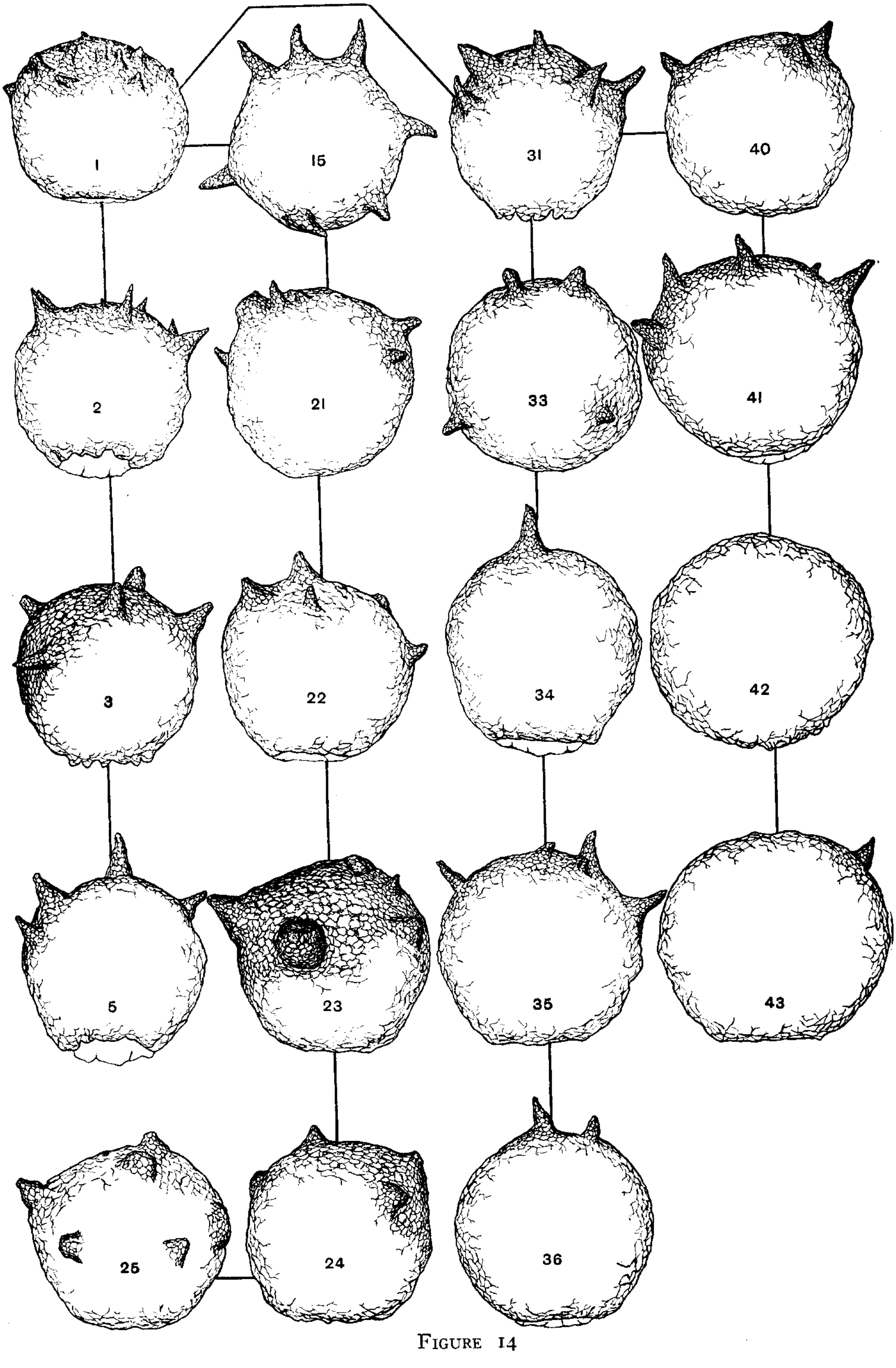


FIGURE 14

for parent and immediate progeny such high correlations as .785, .658, .690, .585, or even such figures as .286, .345, .342, and the like.

Clearly, a *prima facie* case is made out for the inheritance of variations within the single family; for the production of hereditary diversities within the single stock multiplying vegetatively. The matter must be examined further with extreme care, to discover whether the *prima facie* presentations may not be deceptive. There are other relations beside inheritance of variations that may result in an increased resemblance of parent and immediate progeny. In general, the environmental conditions of parent and progeny are more likely to be similar than those of more distant generations, since the latter are separated by wider intervals of time (compare LASHLEY 1915). It is true that in Difflugia the characters are not altered by the environmental conditions during the life of the individual, but it remains possible that the conditions at the time of reproduction affect the characteristics produced. If this be true, and if the conditions be more alike for parent and immediate progeny, than for more distant generations, then the greater resemblance might be brought about without inheritance. The test for this, as for other sources of error, will lie in properly controlled experiments with selection, carried out with adequate numbers. If by selection we can obtain stocks hereditarily diverse for generation after generation, under the same conditions, then the explanation from similarity of environment for parent and progeny will not suffice. Such experiments in selection must therefore be undertaken.

The possibility just suggested appears to be the chief one that might give deceptive results. There are however certain other deceptive possibilities which we shall bring out; all of them can be tested by careful examination of the data and by adequate experiments in selection.

We shall first examine in detail the pedigrees in certain of the families to discover what light these shed on the nature of the variations and their apparent inheritance. We shall find a number of diverse categories of cases.

Family 305: Deceptive parental correlation. As an example of correlation between parent and progeny produced otherwise than by in-

FIGURE 14.—Four branches of the family 305, to illustrate the increase in size in later generations, and the tendency to differentiate into diverse branches. The ancestry of the individuals is shown by the connecting lines; thus No. 1 is the immediate parent of No. 2, of No. 15 and of No. 31. The parent is in each case the individual bearing the lower number. Each individual is given the same number that it bears in table 33. Magnification, 143 diameters.

heritance, we will first examine family 305, which gives the highest parental correlation observed,—a coefficient of .725 with respect to diameter. How is this correlation brought about?

The original parent 305 had a diameter of 44 units (each unit being 4 2/3 microns, so that the diameter was 205 microns); its progeny were cultivated for 48 days, during which time 70 individuals were produced, belonging to six successive filial generations. The original parent with four of its lines of descent is shown in figure 14; and the entire pedigree of the family is given in table 33. The pedigree gives for each individual the number of spines, the diameter and the number of teeth. The entire ancestry of each individual is given, the pedigree being arranged as described on page 419.

TABLE 33

Family 305; linear pedigree, showing the number of spines, diameter of the shell (in units of 4 2/3 microns each), and number of teeth.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
No. of spines	10	7	5	5	4—	5	1—	0—	4	6	4	0	3—	6—	7	7	7
Diameter	44	44	44	?	45—	?	52—	47—	?	45	47	50	50—	46—	42	44	47
No. of teeth	15	15	15	?	15—	?	?—	15—	?	15	15	15	15—	15—	13	13	12
Parent						3		6	2					2	1		

Designation	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
No. of spines	—6	0	0—	5	5	5	4	6—	4—	6	4—	5—	7—	5	5—	4	1
Diameter	—51	55	60—	45	46	49	45	49—	45—	48	45—	44—	43—	43	42—	49	46
No. of teeth	—15	?	15—	?	13	?	12	15—	?—	12	14—	13—	13—	15	15—	15	15
Parent	16			15					22	21		27	15	1		31	

Designation	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
No. of spines	5	2—	1—	4—	3—	3	5	0	1—	6—	3	3	3—	3—	5	5	3
Diameter	49	48—	51—	52—	?—	44	53	54	56—	46—	45	52	52—	47—	44	48	?
No. of teeth	15	15—	15—	15—	?—	15	15	?	?—	15—	15	15	15—	?—	15	15	?
Parent			34	34—	37	31				40	31			45	1		

Designation	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
No. of spines	—6	3—	3—	4	6	4	5—	4	4	5—	6—	7—	2—	4—	5	7	6
Diameter	—49	47—	50—	51	55	55	53—	52	53	53—	52—	52—	54—	54—	54	53	53
No. of teeth	—15	14—	15—	15	15	?	15—	14	16	?—	15—	15—	15—	14—	?	16	17
Parent	50		50	49				56			59	59	56	56	55		

Designation	69	70	71
No. of spines	—4—	4	5
Diameter	—47—	50	49
No. of teeth	—16—	16	16
Parent	67	66	

From the pedigree and from figure 14, it will be observed that on the whole *the diameters increase with later generations.* The first individual has a diameter of 44 units, and its four progeny have diameters of respectively 44, 42, 43, and 44 units. Late in the pedigree we find such series of generations as Nos. 55 to 58, with diameters 51, 55, 55, 53, etc. If we obtain the diameters for the seven successive generations, we find the distributions and means to be those shown in table 34. As will be observed, there is a very great increase in the third filial generation (to 49.2), after which the increase continues less marked. This is well illustrated by figure 14 showing the complete pedigree in a number of branches of the family; the right hand branch shows this particularly well.

TABLE 34

Family 305. Distribution and means of the diameters in the successive generations. The diameter is given for each individual of each generation.

Gen.	Diameters	Mean
p	44	44
f1	44 42 43 44	43.3
f2	44 46 44 46 43 42 49 44 45 48 51	45.6
f3	45 47 51 46 48 46 53 46 52 47 49 50 55 59	49.2
f4	45 32 47 47 55 49 45 45 44 49 51 52 54 52 47 55 52 54 54 53 50	50.1
f5	50 60 45 48 56 53 53 52 52 53 47 49	51.5
f6	50 49 53	50.7

Now, consideration will show that this increase in size with successive generations is sufficient, by itself, to give a high degree of correlation between parent and immediate progeny, even though there be no inheritance of parental peculiarities in any other way; no tendency for the family to differentiate into hereditarily diverse groups. This may be perceived if one will take as a series of successive generations the numbers 1 to 9, then arrange parent and immediate progeny in a correlation table; perfect positive correlation is given.

But is there nothing else involved in the correlation in this family 305? Examination of the pedigree (table 33) and figure 14 indicates that in addition to this increase in size in successive generations, there is likewise a tendency to differentiate branches of the family diverse in size. For example, compare the series of diameters given by the pedigrees of two individuals of the sixth filial generation, No. 25 and No. 61. The former pedigree is 44, 42, 46, 46, 49, 45, 49; the latter is 44, 44, 51, 55, 52, 53, 53. The second series (after it separates from the common ancestor) is throughout higher than the first. Other similarly diverse branches can be traced. The diversities are illustrated in figure 14; the first and second branches (left half of the figure) are small; the third consists of larger individuals; the fourth of still larger ones.

While thus there are indications of a tendency to differentiate into hereditarily diverse groups, the data are perhaps in family 305 insufficient to establish this. What we learn of importance in this family is that we must be on guard against the mere effects of uniform change of size from generation to generation, in giving correlation, and thus the appearance of inherited differentiation. The danger is an insidious one, for examination will show, not only that continued decrease in size would have the same effect in giving correlation as does continued increase, but also that increase followed by decrease, or vice versa; or repeated alternations of increase and decrease, will have the same effect. Thus, consider that the numbers 1 - 2 - 3 - 4 - 3 - 2 - 1 - 2 - 3 - 4 - 5 - 4 - 3 - 2 - 1 represent a series of successive generations. Now correlate each parent with its immediate progeny; a high degree of correlation will be found to result.

Examination of such pedigrees as are given in table 1, tables 17 to 20, tables 27 to 30, etc., indicates that a considerable part in producing the observed correlation of parent and progeny within the family may be due to such increase or decrease as generations pass. For example in family 186 in table 1 (page 422) we find with respect to diameter first a series of three decreasing generations 30, 29, 26; then a similar one of 31, 28, 28, and others of the same sort; these are bound to produce a correlation of parent and progeny even if there be no other ground for it. The reader may readily find other examples in the pedigrees.

To guard against being misled by such changes, the measure necessary is the same as that required for guarding against deceptive correlation due to the environment; experiments in selection form the final test. If from a single family we can isolate diverse strains existing at the same time under the same conditions, hereditary differentiation actually occurs.

This same family No. 305, gives a correlation between parent and progeny in number of spines of .284. Now, we have found that in general greater size is correlated with greater number of spines (see table 8), so that we might suppose that the correlation of parent and progeny in spine number is due to this. If the larger parents have larger numbers of spines, then the steady increase in size would give steady increase in spine number, resulting in positive correlation in this respect also. But most curiously, in this particular family the usual relations are reversed, and there is a negative correlation between number of spines and diameter, amounting to —.386 ± .072. Furthermore, inspection of the pedigree with respect to number of spines (table 33) shows marked indications of actual differentiation of groups with diverse numbers of spines. Thus, compare the series of generations given by the pedigree of individual No. 17 with that given by the pedigree of individual 43. The former is 10, 7, 7, 7; the latter is 10, 5, 3, 5, 0, 1. Other similarly diverse branches exist. The diversity in number of spines in the different branches, as well as the negative correlation of the number of spines with the size is illustrated in figure 14. The two branches of the left have both smaller size and a greater number of spines than the two right hand ones.

The negative correlation of number of spines with the size, taken in connection with the increase in size in later generations, of course gives rise to a positive correlation of parent and offspring with respect to number of spines. For the number of spines must gradually decrease in later generations; and this, as we have seen, gives positive correlation between parent and progeny.

The conditions found, with respect to size and number of spines in this family 305 are far from being usual; throughout its existence the family gave evidence of being in many respects abnormal. Aside from the peculiar size relations, this was shown in the production at fission of many empty shells. This is a rare occurrence in normal Difflugias, but occurred many times in the abnormally large individuals of family 305. The family can not be taken as representing the normal condition of affairs in Difflugia; it is presented as an example of the way in which abnormal conditions give rise to deceptive phenomena. If we compare the pedigree of No. 305 with that of such a normal race as 303 (table 35 and figure 7,) we shall find no such change of size with passage of generations, in the normal race. Such change of size with passage of generations has occurred in several of the families observed (notably in the small family 186) and in such cases may account partially or entirely for the correlation between parent and progeny.

The question in which we are primarily interested is whether, in addition to the correlation due to causes other than the inheritance of parental diversities, there is likewise such inheritance, giving rise to the division of a single strain into hereditarily diverse groups. The direct test for this is by experiments with selection. Can we by continued selection of diverse parents obtain from a single family groups of heritably diverse organisms; groups retaining their diversities under the same conditions?

Experiments in selection within single families

The question just set forth was tested in culture H in the two families designated 303 and 314. On these, selection was practiced with respect to high and low numbers of spines. All parents with low numbers of spines were placed in one set; those with high numbers in another set, while those with intermediate numbers were rejected. In the "low" set, only progeny with low numbers of spines were retained for further propagation; in the 'high' set only progeny with high numbers of spines were retained. The two sets were kept under the same conditions; the 'high' and 'low' individuals being arranged on alternate slides in the same moist chambers. They were kept in the same culture medium, changed at the same time, and treated in all respects alike.

The time of propagation and selection was in each case divided into short periods, each covering about the same time necessary for the production of a single generation; and the results for each of these periods were determined separately. This avoided the production of correlation between parent and progeny through the inclusion in one correlation table of periods of diverse environmental conditions, in which the conditions were more alike for parent and immediate progeny than for more distant generations; and also the difficulty due to possible mere increase or decrease with the passage of generations. In a single period practically but a single generation of each of the selected sets is included, so that any consistent differences between the two can be due only to diversity of inheritance.

Family 303: The progenitor of family 303 was an individual with 8 spines and with a diameter of 37 units (173 microns); it is shown in fig. 7. It was cultivated from May 7 to July 14, 1914, during which time 495 descendants were produced. From May 7 to June 11 all progeny were retained. It was found that the commonest number of spines produced was 4, the range of variation being from 0 to 8. On June 11 selection was begun by rejection of all parents having just 4 spines. (They were preserved for later study.) Parents having 0 to 3 spines were retained for the "low-selected" set; those with 5 to 8 spines for the "high-selected" set. Thenceforth in the "low-selected" group only progeny with 0 to 3 spines were retained for further propagation, all others being killed and preserved for further study. Similarly, in the "high-selected" group, only progeny with 5 to 8 spines were further propagated. Thus in each set we gradually obtain individuals whose parents for a number of successive generations have been either all "low" or all "high."

All progeny not retained for further propagation were preserved in glycerine for later study. Owing to the large numbers of cultures in progress at this time it was found impossible to keep up with the statistics and so to determine whether selection was having an effect. It was only after all the individuals had been preserved and studied at the end that the results were known.

The first one-fourth of the pedigree of No. 303 is given in table 35, in the linear arrangement described on page 419. In this family four characters were determined for each individual—the number of spines,

TABLE 35

Linear pedigree for the first 125 members of the family No. 303, showing four characters for each individual. See the text.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
No. of spines	8	4	3	6	4	5	4	6	3	2	3	3—	3	3	3—	3—	3
Diameter	37	37	?	36	38	38	36	35	35	37	35	35—	35	35	35—	35—	?
Length of spine	12	11	?	12	15	11	11	7	6	7	5	5—	6	9	7—	7—	?
No. of teeth	14	14	?	14	15	15	15	15	15	15	15	15—	15	15	15—	15—	?
Parent													9			9	8

Designation	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
No. of spines	— 6	4—	6—	2—	3—	4—	5	3—	5	4—	3—	4—	5	4—	4—	4—	5
Diameter	— 35	38—	35—	34—	34—	35—	37	36—	35	38—	36—	35—	36	36—	36—	37—	38
Length of spine	— 7	9—	5—	5—	6—	6—	5	8—	7	7—	5—	6—	6	6—	8—	8—	10
No. of teeth	— 15	15—	15—	14—	15—	15—	15	5—	14	15—	15—	15—	15	15—	15—	15—	14
Parent	8		18	18	7	5	5		24		26	26	24		31	24	4

Designation	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
No. of spines	4	3	4	4—	4—	4—	2	4—	3—	3	4—	4—	5	4—	4—	4—	4
Diameter	37	36	36	36—	38—	37—	37	37—	35—	36	35—	36—	35	36—	36—	37—	34
Length of spine	11	6	9	7—	8—	8—	7	5—	5—	8	8—	7—	6	7—	8—	9—	4
No. of teeth	14	14	15	16—	14—	14—	14	14—	14—	14	14—	14—	13	14—	14—	14—	?
Parent					36	36	36		41	36		36	35		47	47	47

Designation	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
No. of spines	— 3—	6—	4—	3—	4—	2—	5	4—	4—	4—	4—	5	3—	5	5	3	4
Diameter	— 35—	36—	36—	37—	38—	39—	35	38—	36—	37—	38—	37	38—	36	36	37	38
Length of spine	— 6—	7—	5—	6—	8—	5—	7	10—	7—	8—	9—	8	4—	8	6	6	7
No. of teeth	— 14—	14—	?—	14—	13—	15—	14	14—	14—	14—	14—	14	15—	15	16	16	15
Parent	35	34	34	34	34	34	4		58	58	58	4		63			

TABLE 35 (continued)

Linear pedigree for the first 125 members of the family No. 303, showing four characters for each individual. See the text.

Designation	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
No. of spines	— 3—	4—	6—	4—	3	2—	1—	3—	4	5	5	4	4—	5	3—	2—	3
Diameter	— 37—	38—	35—	38—	37—	?—	36—	36—	38	38	35	36	36—	35	36—	38—	36
Length of spine	— 6—	6—	6—	9—	10—	?—	5—	5—	14	13	11	9	8—	4	7—	6—	5
No. of teeth	— 16—	15—	15—	16—	?—	?—	15—	14—	14	14	15	15	15—	15	14—	15—	15
Parent	66	65	65	63	63	4	4	4	3					79		82	79

Designation	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102
No. of spines	3	1—	4—	3—	4—	5	5	3—	2—	6—	4	5—	3—	4—	3	5—	4
Diameter	36	36—	?—	32—	39—	38	36	37—	36—	39—	38	38—	40—	37—	36	35—	34
Length of spine	5	6—	?—	2—	7—	14	7	10—	6—	9—	8	10—	9—	8—	12	9—	9
No. of teeth	15	15—	?—	15—	14—	15	15	15—	15—	15—	15	15—	15—	14—	14	14—	14
Parent			79	79	78	77			92	92	91		91	77	3		3

Designation	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119
No. of spines	— 4—	3	3—	4—	6	4	4	5	4	4	3	2	4—	4—	4—	4—	4
Diameter	— 37—	34	35—	36—	38	36	35	37	35	35	37	38	34—	35—	35—	35—	36
Length of spine	— 7—	5	8—	7—	9	8	10	7	11	9	6	8	8—	8—	9—	8—	11
No. of teeth	— 14—	14	14—	14—	14	14	14	4	14	14	14	14	14—	14—	14—	14—	14
Parent	3	3		104	2									114	113	113	110

Designation	120	121	122	123	124	125
No. of spines	— 4—	5	5—	3—	4—	4
Diameter	— 37—	36	35—	36—	35—	36
Length of spine	— 10—	7	7—	6—	5—	11
No. of teeth	— 14—	14	14—	14—	14—	14
Parent	110	110		110	110	109

the diameter, the length of the longest spine, and the number of teeth. All these characters are given for each individual in table 35. The pedigree for No. 303 serves as a type of the propagation of a normal family. In the linear arrangement each branch is of course traced to the end before the next branch is taken up, so that the table gives parts of the pedigree extending from beginning to end.

The first 12 individuals in this pedigree, forming a series of 12 descending generations, are shown in figure 7, save that No. 3 was lost, so that it could not be figured.

The experiment in selection was divided into seven successive periods, and the results for each period was determined separately. Each period except the first included as a rule but one reproduction under uniform conditions. The first period, since it began with a single parent, was necessarily long, since otherwise it would not have included a sufficient number of progeny to be significant; it included in fact nearly half the entire time of the experiment.

Taking up first the number of spines, in each period the coefficient of correlation between parent and progeny was obtained; for this purpose the "high" and "low" sets were thrown together, so that the correlation is based on all parents and all their progeny produced during a given period. Further, the mean number of spines is obtained for the progeny of the two sets separately. That is, the mean number of spines is computed for all the progeny produced by the "low" set (parents having 0 - 3 spines); also for all the progeny produced by the "high" set (parents having 5 - 8 spines.) The results are given in table 36.

TABLE 36

Family 303. Numbers of spines. Results of selection for low (1-3) and high (5-8) numbers of spines, for seven successive periods, in a culture lasting 65 days.

Period	No. of progeny	Correlation	Mean number of spines of progeny from			
			Parents with 1—3 spines		Parents with 5—8 spines	
			No. of prog.	Mean	No. of prog.	Mean
1 (31 days)	91	.078 ± .070	19	3.79	30	4.10
2 (5 ")	72	.146 ± .078	16	3.25	20	4.20
3 (6 ")	65	—.010 ± .084	28	4.03	31	4.06
4 (7 ")	84	.168 ± .071	40	3.65	42	4.00
5 (6 ")	84	.148 ± .072	44	3.36	38	3.61
6 (6 ")	58	.124 ± .087	35	3.14	23	3.48
7 (4 ")	41	.371 ± .091	22	3.23	17	3.83
6 and 7	99	.217 ± .065	57	3.18	40	3.62
Total (65 days)	495	.157 ± .030	204	3.51	201	3.73

As table 36 shows, in every one of the seven periods the parents selected for high numbers of spines produced progeny with a higher average number of spines than did parents selected for low numbers of spines. In every period except one there is a positive correlation between the number of spines of the parent and the number of spines of its progeny The selection of parents gives progeny differing from the mean in the same direction as the parents.

Selection was not practiced in this family with respect to diameter of the shell nor length of the longest spine. But as all individuals were preserved and measured, it is possible to compare the progeny produced by large and small parents respectively; by long-spined and by short-spined parents respectively; and to determine the coefficients of correlation with relation to these characters. The results for each of the seven periods, as well as for the total, are given in tables 37 and 38.

TABLE 37

Family 303. Correspondence between parents and progeny with respect to the diameter of the shell, for the seven successive periods of the culture. (The periods are the same as those defined in table 36.)

Period	No. of progeny	Coefficient of correlation	Mean diameter of progeny			
			From parents with diameter below 36		From parents with diameter above 37	
			No. of prog.	Mean diam.	No. of prog.	Mean diam.
1	81	.124 ± .072	14	35.78	20	36.30
2	68	.206 ± .078	20	36.50	16	37.13
3	60	.332 ± .077	17	35.94	15	37.00
4	79	.241 ± .071	22	36.00	17	38.88
5	81	.191 ± .072	23	36.34	20	36.95
6	58	.277 ± .082	20	35.35	10	36.30
7	41	.463 ± .083	16	34.56	6	36.50
6 and 7	99	.377 ± .060	36	35.00	16	36.38
Total	468	.181 ± .030	132	35.83	104	36.76

As to the diameter the parents are divided into classes, those having diameters below 36, and those above 37. Table 37 shows that in every one of the seven periods the larger parents produced larger progeny. The coefficient of correlation was determined for each period, from *all* progeny; in every period there is a well marked positive correlation between the diameter of the parent and that of the progeny.

With relation to the length of the spines (table 38), the results are less sharply defined. In six of the seven periods the long-spined parents had progeny with longer spines than did the short-spined parents, and there

TABLE 38

Single family No. 303. Correspondence between parents and progeny with respect to the length of the longest spine, for the seven successive periods described in table 36

Period	No. of progeny	Correlation	Mean length of longest spine of progeny			
			From parents with spine less than 7 units long		From parents with spine more than 7 units long	
			No. of prog.	Mean	No. of prog.	Mean
1	80	.176 ± .073	3	9.00	48	9.48
2	68	.145 ± .080	14	6.50	44	7.07
3	60	.020 ± .087	16	6.94	27	7.33
4	79	.036 ± .076	23	7.39	34	7.41
5	81	.150 ± .073	26	6.58	32	7.25
6	58	—.005 ± .088	20	6.55	19	6.26
7	41	.024 ± .105	11	6.00	16	6.13
6 and 7	99	—.021 ± .068	31	6.35	35	6.20
Total	467	.235 ± .029	113	6.79	220	7.57

was a positive correlation between parent and progeny in this respect. But in some of the periods the difference between the two sets was extremely small, and the correlation was too small to be significant.

Thus, for the number of spines and for diameter, and in a less degree for length of the spines, the population was divisible into two sets which at the same time and under the same conditions consistently produced diverse progeny; the two sets were hereditarily diverse.

Is this hereditary diversity due to the appearance of single individuals differing markedly from the rest, and perhaps handing on their diversities in full to their descendants? Careful examination of the records gives no indication of this. To judge of this with relation to the diameter, I give in table 39 for each of the seven periods the actual distribution of the diameters in the progeny of the two diverse sets of parents. Examination of these shows that it is not the presence of a number of extreme individuals that brings about the differences between the two sets, but that rather there is a slight shifting of the mean and the mode, as well as a slightly greater range in one direction in one set, in the other direction in the other set.

TABLE 39

Single family 303. Distribution of the diameters in the progeny of small parents (diameter below 36), and of large parents (diameter above 37), in the seven successive periods of the culture.

Period	Parents	Distribution of diameters in progeny									Total	Mean
		32	33	34	35	36	37	38	39	40		
1	Small			1	5	6	1		1		14	35.78
	Large			1	4	7	4	4			20	36.30
2	Small			2	2	4	8	4			20	36.50
	Large					5	5	5	1		16	37.13
3	Small			3	2	7	3	2			17	35.94
	Large				1	2	9	2	1		15	37.00
4	Small			3	7	3	5	4			22	36.00
	Large			1	3	1	7	3	1	1	17	38.88
5	Small			3	4	5	4	7			23	36.34
	Large				4	2	8	4	1	1	20	36.95
6	Small			4	11	1	2	2			20	35.35
	Large			1	2	1	5	1			10	36.00
7	Small	1	2	5	5	1	2				16	34.56
	Large			1		2	1	2			6	36.50
Total	Small	1	2	21	36	27	25	19	1		132	35.83
	Large			4	14	20	39	21	4	2	104	36.76

With regard to the length of the longest spine, we give in table 40 the general correlation table for parents and progeny. If one compares the distribution of the progeny from the various classes of parents, one finds merely a slight and gradual shifting of mean, mode and range, as one passes from short-spined parents to long-spined ones.

TABLE 40

Family 303. Correlation table for parents and their immediate progeny with respect to the lengths of the longest spine. The unit of measurement is 4 2/3 microns.

	Parents																
Progeny	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
0						1		2									3
1																	0
2								1				1					2
3								1	1								2
4					1	1	3	2	6	2		2	1				18
5	1				4	6	7	15	7	4	4	1	3			1	53
6					3	9	11	18	17	12	4	4	3			1	82
7					4	7	20	25	17	16	8	4	3	1	1		106
8					2	7	14	23	19	16	6	3	3	1	2		96
9							10	19	9	4	3	6	6		1		58
10						1	1	4	7	7	2		1				23
11							2	2	1	3	3	1	1	1		1	15
12								1	1	1		1		1			5
13												1			1		2
14															1		1
15													1				1
	1	0	0	0	14	32	68	113	85	65	30	24	22	4	6	3	467

TABLE 41

Family 303. Correlation table for parent and immediate offspring with respect to the number of teeth. The coefficient of correlation is .598 ± .022.

	Parents					
Offspring	12	13	14	15	16	
12	2	2	1			5
13	5	4	18			27
14	6	27	219	9		261
15		3	32	51	1	87
16			4	3	7	14
	13	36	274	63	8	394

As table 41 shows, the variations in the number of teeth are likewise inherited in a high degree in family 303, the coefficients of correlation for parent and offspring being .598 ± .022. The method of variation and inheritance of the teeth will be dealt with in a special paper on that subject.

Family 314. Selection was likewise practiced in the large family No. 314, in which the original parent, with 3 spines, produced 1049 descendants. The original parent and 11 of its descendants are shown in figure 7, page 438.

With relation to the number of spines selection was carried on in the same manner as in family 303. From April 18 to June 15, all individuals produced were retained. Thereafter all individuals with 4 spines (the modal number) were rejected, and the parents were divided into two sets,—those having less than four spines, and those having more than four spines. The two sets were kept under the same conditions and treated alike. The experiment was divided into seven successive periods, all but the first one covering a short interval; the progeny of the two sets were compared separately in each period. The results are shown in table 42.

TABLE 42

Single family No. 314; effect of selection on number of spines.

			Average No. of spines in progeny of			
			Parents with 1—3 sp.		Parents with 5—9 sp.	
Period	No. of progeny	Correlation	No. of prog.	Mean	No. of prog.	Mean
1 (43 days)	55	.314 ± .082	26	2.96	18	4.22
2 (6 days)	55	.282 ± .084	29	3.62	10	4.00
3 (8 days)	238	.113 ± .043	90	3.64	59	3.88
4 (8 days)	157	.184 ± .052	93	3.40	59	3.95
5 (7 days)	213	.170 ± .045	147	2.67	59	3.32
6 (6 days)	136	.057 ± .058	63	1.87	68	2.01
7 (8 days)	195	.096 ± .048	147	2.40	42	2.74
Total (86 days)	1049	.153 ± .020	595	2.84	315	3.26

In this large family, as in the preceding one, selection was effective. In every one of the seven periods into which the experiment was divided, parents with a greater number of spines produced progeny with a greater number. In every one of the seven periods there is a positive correlation between parents and progeny with respect to the number of spines, though in two of the periods (6 and 7) the coefficient is so small that its significance would be uncertain if these two periods alone were in question. For the entire period the correlation between parent and progeny is .153 ± .020. I give in table 43 the correlation table for the family as a whole.

Similar relations appear as to the diameter of the shell. Selection was not practiced with reference to this, but as all individuals were preserved

TABLE 43

Family 314. Correlation table for parent and immediate progeny with respect to the number of spines. Coefficient, .153 ± .020.

	Parents										
Progeny	0	1	2	3	4	5	6	7	8	9	
0	1	1	10	17	1	6	4				40
1	1	8	20	43	7	20	7			1	107
2	4	14	21	93	9	42	14	1			198
3	2	13	40	115	41	50	13	4			278
4	2	4	30	85	52	72	25	3			273
5		3	14	45	24	20	10	2			118
6		2	1	6	5	12	2	3			31
7						3					3
8											0
9							1				1
	10	45	136	404	139	225	76	13	0	1	1049

and studied, it is possible to examine the relation of parents and progeny with respect to this character. The greatest number of individuals have the diameter 40; I have therefore divided the parents into three classes, those with diameters below 40, those with diameter 40, and those with diameter above 40. The distribution of the diameters of the progeny of these three sets, for each of the seven periods, and for the experiment as a whole, are given in table 44, together with the mean diameters for each lot of progeny, and the coefficient of correlation between the diameters of all parents and all progeny. In every period the progeny of the parents above 40 are larger than those of parents below 40. In every period except two (periods 1 and 5) the progeny of the intermediate parents are intermediate between those of the other two sets. In every period the progeny of the intermediate parents are smaller than the progeny of the larger parents. In every period there is a well marked positive correlation between the parents and progeny.

Here again it is of interest to examine the question whether the inheritance of diversities within the family is due to the sudden appearance of single individuals differing greatly from the type, with inheritance of these marked diversities by the progeny. If this were the case we should in table 44 find marked divergence of type between the progeny of the large parents and those of the small parents. What we find is, as in the case of family 303, merely a slight shifting of the extremes and means in the two sets of progeny—their distributions for the middle region being the same. There is no indication of sudden or great differences between the two sets.

TABLE 44

Single family No. 314. Mean diameters of the progeny of small, intermediate and large parents in seven successive periods; also the correlation between parents and progeny in each period.

Period	Parents' diameter	Diameter of progeny													Total	Mean	Correlation of all parents with all progeny	
		35	36	37	38	39	40	41	42	43	44	45	46	47			No. of progeny	Correlation
1	Below 40		2	1		2	9	3	2		1				20	39.90	50	.200 ± .089
	40					4	7								11	39.64		
	Above 40			1	3	2	4	1	6	1				1	19	40.63		
2	Below 40		1	1	4	2	5	1	1						15	39.07	48	.225 ± .092
	40				4	3	7	4	2						20	39.85		
	Above 40				1	1	6	4	1						13	40.23		
3	Below 40	1	1	5	10	20	13	14	7	1					72	39.54	208	.368 ± .040
	40		3	2	5	14	23	12	5		1				65	39.75		
	Above 40			3	4	12	12	13	15	7	4	1			71	40.79		
4	Below 40			5	7	9	5	4	1						31	38.97	140	.170 ± .055
	40		2	2	1	9	12	10	9						45	40.07		
	Above 40			2		9	17	19	12	4	1				64	40.69		
5	Below 40				4	6	16	15	9	2					52	40.48	197	.197 ± .046
	40	1		4	6	8	18	14	3	2	1				57	39.88		
	Above 40				3	7	19	30	16	9	4				88	41.05		
6	Below 40		1	1	1	7	7	2	1	1	1				22	39.77	125	.159 ± .059
	40			1	2	8	10	9	2	1					33	40.03		
	Above 40			1	8	7	19	24	6	5					70	40.36		
7	Below 40		3	3	16	15	13	3	1						54	38.83	193	.394 ± .040
	40		1	2	10	14	25	9	2	1					64	39.56		
	Above 40			3	7	17	23	16	5	3			1		75	40.01		
Total	Below 40	1	8	16	42	61	68	42	22	4	2				266	39.53	961	.271 ± .020
	40	1	6	11	28	60	102	58	23	4	2				295	39.82		
	Above 40			10	26	55	100	107	61	29	9	1	1	1	400	40.58		

Further evidence on this point will be obtained by examination of the correlation table with respect to size for parent and progeny, given for 961 progeny of this family in table 45. If from this table we determine the mean diameters of the progeny from parents of a given diameter we find the results to be as shown in table 46.

TABLE 45

Family 314. Correlation table for parents and immediate progeny, with respect to diameter. The units of measurement are 4 microns each.

	Parents													
Progeny	35	36	37	38	39	40	41	42	43	44	45	46	47	
35					1	1								2
36		2	1		5	6								14
37	1	1	1	2	6	11	6	3		1				32
38		2	1	10	27	28	14	8	4					94
39	1	4	1	17	36	60	29	20	4	2				174
40		7	3	18	44	102	56	36	3	3	1		1	274
41		6		8	29	58	56	32	10	7	2			208
42		3		7	15	23	25	22	10	4				109
43					5	4	8	12	5	3			1	38
44		1			1	2	5	1		1			2	13
45								1						1
46								1						1
47									1					1
	2	26	7	62	169	295	199	136	37	21	3	0	4	961

TABLE 46

Mean sizes of the progeny from parents of given sizes, in 961 progeny of family 314.

Diameter of parents	Mean diameter of progeny	No. of progeny
35	38.00	2
36	39.88	26
37	38.57	7
38	39.66	62
39	39.67	169
40	39.82	295
41	40.38	199
42	40.60	136
43	41.08	37
44	41.09	21
45	40.66	3
46	——	0
47	42.75	4
	Total	961

In table 46 we see (for all classes containing a sufficient number to be significant) that a single unit's increase in the diameter of the parents is followed consistently by a corresponding (but less) increase in the mean diameter of the progeny. There is no indication of sudden rare mutations inherited fully by the progeny. In the next family dealt with (No. 317) we shall examine a case in which such an isolated mutation has produced high correlation; it will be seen to differ completely in this respect from this family 314, and from the family 303, already dealt with.

Family 317: "Mutation". In family 317 there was, as set forth in table 32, a coefficient of correlation in diameter, between parent and progeny, of .658. A study of the pedigree reveals the conditions on which this unusually high correlation depends. The first part of the pedigree, amounting to a little more than one third of the whole, is given in table 47, while figure 15 illustrates the pertinent conditions.

TABLE 47

Family 317. First part of the pedigree, by numbers of spines and diameter. See text.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
No. of sp.	2	5	5	5	4	3	4	2	4	5—	3—	3—	2	5—	4—	4	3
Diameter	39	41	43	39	39	41	39	40	42	42—	41—	39—	42	39—	40—	42	40
Parent											8	8	7		13	6	

Designation	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
No. of sp.	— 6—	6—	3—	2	0	4	4	3	4	4—	2—	5	2—	1	4—	3—	2
Diameter	—42—	37—	41—	42	48	48	49	45	49	50—	50—	48	45—	47	47—	49—	47
Parent	6	6	5	4							26	25		25		31	24

Designation	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
No. of sp.	3—	3—	1	3	4—	3—	1—	5	3	1	2—	4—	4—	4	5	3—	5
Diameter	50—	44—	42	44	45—	44—	40—	40	40	40	40—	41—	40—	39	43	42—	43
Parent		24	4			37	37	3				42	42	3			49

Designation	52	53	54	55	56	57	58	59	60	61
No. of sp.	— 5—	6	5	5—	5—	4	4	3—	3	3
Diameter	—41—	40	42	43—	41—	39	41	41—	40	40
Parent	49	48			53	3			3	

At the beginning the diameter runs at about 40; this is shown for 10 successive generations in table 47, and 7 of these generations are illustrated in figure 15 (at the left). The second progeny of No. 4 (itself numbered 21) is somewhat larger than usual, and its progeny (No. 22) is much larger. All the descendants of No. 22 (Nos. 22-36 in table 47)

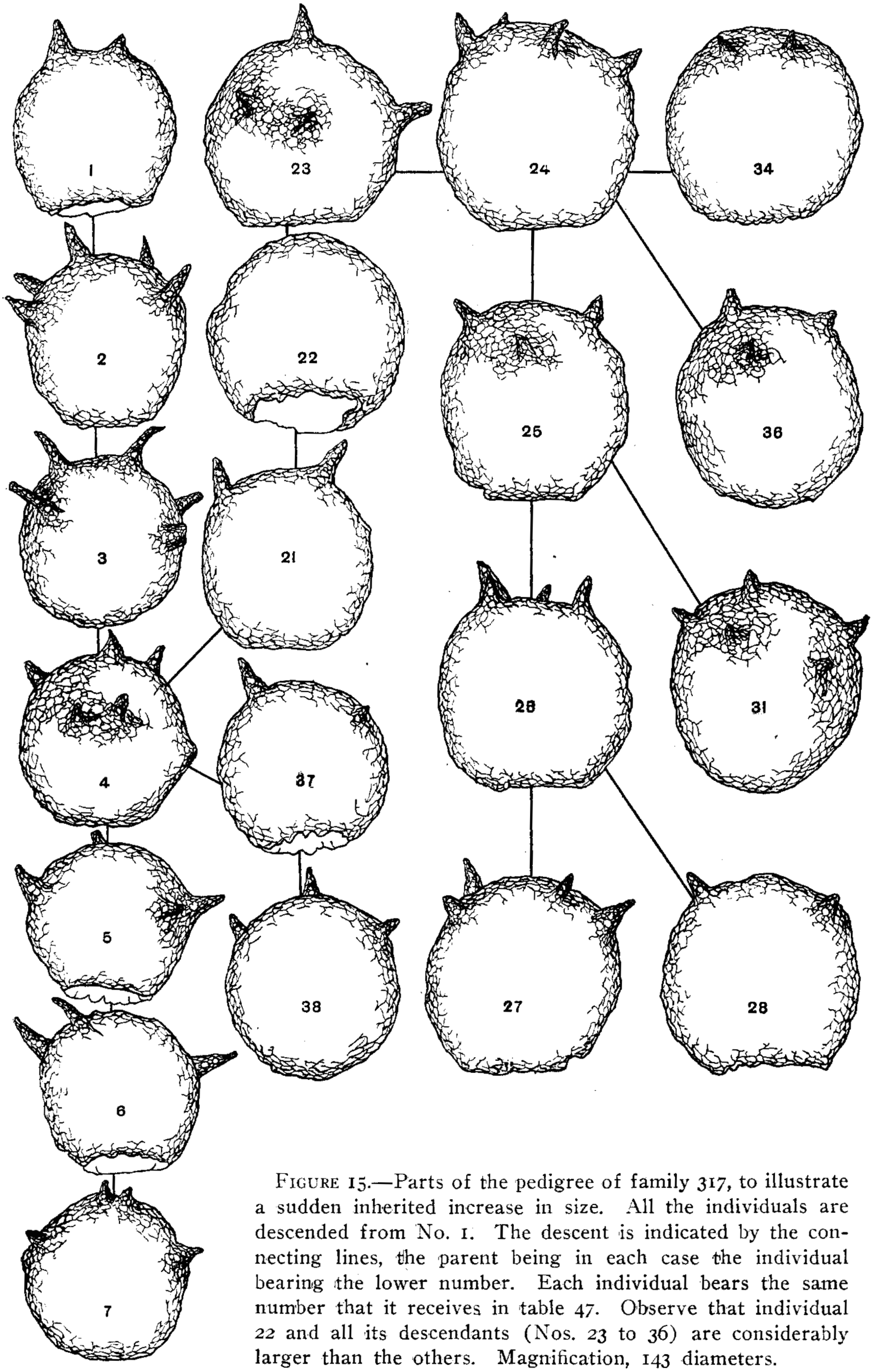


FIGURE 15.—Parts of the pedigree of family 317, to illustrate a sudden inherited increase in size. All the individuals are descended from No. 1. The descent is indicated by the connecting lines, the parent being in each case the individual bearing the lower number. Each individual bears the same number that it receives in table 47. Observe that individual 22 and all its descendants (Nos. 23 to 36) are considerably larger than the others. Magnification, 143 diameters.

inherit this large size. There are thus 14 of these large individuals, ten of which are shown in figure 15. Meanwhile, the remainder of this family continue to show the small size, as shown in Nos. 37 and 38 in figure 15, and in the rest of table 47. The 14 very large individuals of common descent cause the correlation table to take the appearance shown in table 48, giving the high correlation of .658.

TABLE 48

Family 317. Correlation table for parent and immediate progeny with respect to diameter.

Progeny \ Parents	36	37	38	39	40	41	42	43	44	45	46	47	48	49	
36				1											1
37				1		2	1								4
38			3	5		1									9
39		1	3	9	7	4	3	6							33
40	1	3	4	8	10	4	7	5							42
41			1	6	11	4	2	2						1	27
42		2		5	6	5	3	2							23
43				3	1	2	3	1							10
44							2	1							3
45									1	1			1	1	4
46															0
47												2		1	3
48							1			1			1		3
49										1		1	1		3
50												1		2	3
	1	6	11	38	35	22	22	17	1	3	0	4	3	5	168

In this case therefore there is a sudden noticeable variation inherited by the descendants,—something comparable to a "mutation". But the inheritance shown in the case of this rather marked variation occurs also with the small, hardly observable changes in size, that occur frequently. For if in this very family No. 317 we remove this large "mutated" individual (No. 22) and all its descendants, so as to entirely cancel the effect of the "mutation", there still remains a correlation of .205 ± .052 between parent and progeny. Thus in this family, as in others, small variations in size are inherited as well as this large one.

Results of the experiments on inheritance within the family

Thus in our two extensive experiments in selection, with families 303 and 314, it appears clearly that diversities between the parents are inherited within the single family. In each case we have two sets of parents differing in certain characters, but kept under the same conditions. In each case, in the same short intervals of time, under identical conditions, the two sets of parents produce characteristically diverse progeny,—the progeny resembling on the average their own parents more than they resemble other members of the family. In both families this is shown to be true for number of spines and for diameter of the shell. In family 303 it is likewise shown to be true for the length of the spines, and for the number of teeth (the latter to be taken up more fully elsewhere). The same general conditions are shown to hold (though details are not so fully available), in the families 187, 302, 309, 311, 317 and 319 (see table 32).

Further, these results agree throughout with those in the earlier cultures (table 31).

It might perhaps therefore be considered established that parental diversities within the single family are inherited in *Difflugia corona,* and that through selection of diverse parents one can obtain stocks differing hereditarily. This result was, however, so opposed to my own results with Paramecium (JENNINGS 1908) and to those of most other works on uniparental reproduction, that it seemed desirable to test the matter further. I determined therefore to begin anew with a single individual and to follow the results of selection more precisely, keeping in touch with them as the experiment progressed, varying the procedure as the results indicated to be desirable, and obtaining larger numbers of individuals, through a greater number of generations, than had been thus far done. I therefore cultivated the family 326 throughout the school year 1914-15 (October 1914 to July 1915); an account of this experiment is given in the next section.

III. LONG-CONTINUED SELECTION IN THE LARGE SINGLE FAMILY NO. 326.

The individual from which family 326 was derived is shown in figure 6 B (at the right above); it had three short spines, and measured 39 units (182 microns). It was obtained October 24, 1914, from the pond at Homewood; it and its descendants were cultivated from October 24, 1914, to July 2, 1915, a period of eight months and eight days, or a total of 252 days. The original individual (or an animal in the original shell, figure 6 B), lived from October 24, 1914, to March 11, 1915, and produced 19 immediate offspring, the largest number produced by any single individual under my observation. The number of successive generations produced was 34; that is, there were 34 successive fissions in the series from the original parent to the latest descendant. In all 4645 individuals were recorded in this family No. 326.

Selection for diverse numbers of spines

The chief purpose of this culture was, at the beginning, the carrying through of a long series of selections for the diverse numbers of spines. The experiment was divided into successive brief periods, as were the experiments with families 303 and 314; in the case of family 326 there were 21 such periods.

During the first four periods, comprising 59 days (October 24 to December 21) no selection was practiced, but the animals were allowed to multiply freely, in order to obtain large numbers of individuals for later work. The number of spines was found to vary from 1 to 9, the commonest number being 5. The parents may be divided on this basis into three groups; those with fewer than five spines; those with just five spines, and those with more than five spines. The average numbers of spines of the progeny produced by the parents of these three groups for each of these first four periods is given in table 49; also the coefficient of correlation between all parents and all progeny, in these four periods of no selection.

TABLE 49

Family 326. Correspondence of parents and progeny with respect to number of spines, in the first four periods, without selection. Mean numbers of spines of progeny from parents with low, intermediate, and high numbers of spines; also the coefficient of correlation for all parents and all progeny, with respect to the number of spines.

Period	Parents	No. of progeny	Mean spines of progeny	Total progeny	Correlation
1 (38 days)	1—4 spines	21	4.71	50	.027 ± .095
	5 spines	14	4.57		
	6 spines	15	5.06		
2 (4 days)	1—4 sp.	22	4.54	74	—.075 ± .078
	5 sp.	33	4.37		
	6 sp.	19	4.57		
3 (6 days)	1—4 sp.	22	5.00	62	—.190 ± .083
	5 sp.	30	4.90		
	6—7 sp.	10	4.70		
4 (11 days)	1—4 sp.	55	5.13	152	—.069 ± .054
	5 sp.	66	5.41		
	6—9 sp.	31	5.19		

Table 49 shows that during these 59 days there was no correspondence of parents and progeny with respect to number of spines. In no period is there a significant coefficient of correlation. It is true that in three of the four periods the high parents gave progeny with higher numbers of spines than did the low parents, but in view of the irregularities in other respects there is no ground for attaching significance to this.

At this point selection was begun. Parents with five spines were no longer retained for propagation. The two remaining sets—those with fewer than five spines and those with more than five spines,—were cultivated side by side, under the same conditions. In the former—the "low" set—only progeny with 4 spines or less were retained for further propagation; all with five or more than five spines were removed. Similarly, in the "high" set, all progeny with five or fewer than five spines were removed. The result of this method of selection was to bring about, very slowly, a condition in which the surviving progeny in a given set have ancestors for several preceding generations that are of the given selected type—low or high, as the case may be. There will then be a tendency to slowly establish high and low "lines", if such exist or can be produced. This selection for spines below or above five in number was continued for six periods, comprising in all some 36 days (Dec. 22 to Jan. 26). The results are given in table 50.

TABLE 50

Single family No. 326. Selection for number of spines, periods 5-10 (36 days).

			Average number of spines in progeny of			
			Parents with 1—4 spines		Parents with 6—11 spines	
Period	No. of progeny	Correlation	No. of prog.	Mean sp.	No. of prog.	Mean sp.
5 (10 days)	65	—.213 ± 0.80	34	5.24	30	4.73
6 (3 ")	260	.073 ± .041	112	5.10	149	5.20
7 (6 ")	182	.119 ± .049	78	5.15	98	5.40
8 (4 ")	241	.001 ± .043	94	5.53	144	5.56
9 (7 ")	260	.076 ± .042	64	5.83	174	5.90
10 (6 ")	166	—.088 ± .052	48	5.56	91	5.46

In table 50 the progeny of intermediate parents are no longer given, since the intermediate parents were discarded. In some cases the numbers "low" and "high" together do not quite equal the total number of progeny; this is because at times a few of the intermediate parents are allowed to breed, owing to their being of interest in other respects. The coefficients of correlation are based on all parents and all progeny in each period.

Table 50 shows that no progress was made by selection through these six periods. It is true that in four periods out of six the high parents gave slightly higher progeny than the low parents, but significance can hardly be attached to this (a change of one period would leave the result as often negative as positive); furthermore at the end of the six periods—after a total culture period of 95 days—the progeny of the two sets had practically identical mean numbers of spines. There is no indication of the effectiveness of selection.

Change in the basis of selection

During periods 5 to 10 the relative number of progeny having more than five spines showed a marked increase, particularly during the later periods, so that the mean number of spines produced rises. In each of periods 7-10 more progeny were produced with six spines than with five spines. Thus, for whatever cause, the mean number of spines in the family has risen, and 6 has replaced 5 as the modal number. Selection based on the number five had therefore become unsatisfactory, since it retained almost all progeny in the high group and very few in the low group. The basis of selection was therefore changed. In the low group were retained for propagation individuals with 1 to 5 spines; in the high groups individuals with more than 6 spines,—the range being from 7 to 11. It is important to understand that there is no transference from one group to the other; all low progeny of the high group are killed; as are all high progeny of the low group.

Furthermore, after this time selection was based to a considerable extent on past performance. By this time many of the existent individuals had produced several offspring. Where a parent of the low group had been found to bring forth high progeny, that parent was removed. Similarly, if a parent with a high number of spines is found to produce offspring with low numbers, this parent was removed. Thus in the low group we gradually tend to accumulate a set of individuals (1) which in the past have produced progeny with low numbers of spines; (2) whose ancestors for several generations back are individuals with low numbers of spines. In the high group the reverse conditions are fulfilled. It will of course be understood that of the "progeny", given for any period in our tables, there is absolutely no selection *as progeny*. We have merely two selected groups of parents; *all* progeny of each group are included for comparison, in the records. This selection based on past performance was apparently the most efficient procedure in the changed complexion of the results in these next periods.

Selection on the new basis and in the new way was carried on now for six additional periods, comprising in all 63 days (Jan. 27 to March 30, 1915). The results for the successive periods are given in table 51.

TABLE 51

Single family No. 326. Selection for number of spines, on the new basis. Periods 11-16 (63 days).

Period	No. of progeny	Correlation	Average number of spines in progeny of			
			Parents with 1—5 spines		Parents with 7—11 spines	
			No. of prog.	Mean sp.	No. of prog.	Mean sp.
11 (6 days)	132	.169 ± .057	69	5.59	44	6.11
12 (11 ")	133	.218 ± .057	73	5.22	54	5.71
13 (6 ")	111	.261 ± .060	63	5.49	33	6.33
14 (22 ")	110	.132 ± .063	48	5.23	35	5.51
15 (13 ")	146	.160 ± .054	70	5.15	33	5.38
16 (5 ")	86	.242 ± .069	44	4.93	15	5.59

Table 51 shows that throughout these six periods *selection was effective.* In every period the high parents produce progeny with higher numbers of spines than do the low parents, and the difference is in every case considerable. In every one of the six periods there is a marked positive correlation between the number of spines in the parent and the number in the progeny. To further illustrate this, I give the original correlation tables for periods 11-16; these form tables 52 to 57.

TABLES 52-57

Family 326. Correlation tables for parents and immediate progeny with respect to the numbers of spines in the 11th to 16th periods of the experiment in selecting for high and low numbers of spines.

TABLE 52

Eleventh period (Jan. 29-Feb. 1.)

		Parents									
		2	3	4	5	6	7	8	9	10	
Progeny	3			1	1	1					3
	4				3		1				4
	5	1	3	11	13	6	8	1	1		44
	6		3	9	15	7	16	6	1		57
	7	1		2	5	5	4				17
	8						4			1	5
	9						1				1
	10		1								1
		2	7	23	37	19	34	7	2	1	132

TABLE 53

Twelfth period (Feb. 2-12).

Progeny	Parents 2	3	4	5	6	7	8	9	10	11	
2		1	1	1		1					4
3			1	1		1	1				4
4		2	2	9	1	2		1			17
5	2	4	2	17	1	12	6		1		45
6	1	1	4	15	3	8	8	1			41
7		1	4	2	1	5					13
8				1		3	1		1		6
9				1		1				1	3
	3	9	14	47	6	33	16	2	2	1	133

TABLE 54

Thirteenth period (Feb. 13-18).

Progeny	Parents 1	2	3	4	5	6	7	8	9	10	11	
1					2							2
2			1	1	1							3
3					2							2
4		1		1	3		1					6
5		1		2	8	6	1	2		1		21
6	1	1	3	6	16	5	9	4				45
7				4	5	4	3	2	2		1	21
8			1		3		4	1	1			10
9												0
10							1					1
	1	3	5	14	40	15	19	9	3	1	1	111

TABLE 55

Fourteenth period (Feb. 19-March 12).

Progeny	Parents 1	2	3	4	5	6	7	8	9	
2	1									1
3				2	1		1			4
4		1		2	7	3	3			16
5			3	4	7	9	9	6		38
6		1	1	5	5	11	7	4	1	35
7		1			5	2	3		1	12
8			1			2				3
9					1					1
	1	3	5	13	26	27	23	10	2	110

TABLE 56

Fifteenth period (March 13-25).

Progeny \ Parents	1	2	3	4	5	6	7	8	9	
1					1					1
2			1							1
3			2	2	1		1			6
4		1		2	8	7	3	1	1	23
5		1	1	10	17	16	8			53
6	2			4	10	15	10	3	1	45
7				2	4	4	3	1		14
8						1	1			2
9			1							1
	2	2	5	20	41	43	26	5	2	146

TABLE 57

Sixteenth period (March 26-30).

Progeny \ Parents	2	3	4	5	6	7	8	9	
3		1		1	2	1			5
4			4	10	4				18
5	1	1	6	8	6	6			28
6	1		4	5	10	1	2	1	24
7			1		3	2			6
8				1	2	2			5
	2	2	15	25	27	12	2	1	86

It is clear that the family 326 has become differentiated into two sets, which differ in the mean number of spines produced. The next question is as to the permanence of this differentiation. If we cease selection will the two sets remain distinct?

Selection was stopped after March 30, and all the progeny of both sets were retained. The culture was thus continued without selection for five additional periods, from April 1 to June 15, amounting in all to 76 days. In these periods much larger numbers of individuals were obtained, making the tests for inherited differentiation more searching than before. The data for these five periods after the cessation of selection are given in table 58. In each period there are included as "progeny" all descendants of either set *produced within that period.*

Table 58 shows that the inherited differentiation persisted throughout the 76 days of these five periods. Seventy-six days is about eleven generations in *Difflugia corona;* inherited differentiation has therefore lasted for eleven generations without selection. It may well be there-

TABLE 58

Single family 326. Culture to test the permanence of differentiation in spine number, after the cessation of long-continued selection.

			Average number of spines in all descendants of:			
			The low-selected set		The high-selected set	
Period	No. of prog.	Correlation	No. of prog.	Mean sp.	No. of prog.	Mean sp.
17 (13 days)	163	.080 ± .052	83	5.51	80	5.71
18 (20 ")	307	.036 ± .038	164	5.51	143	5.71
19 (22 ")	232	.130 ± .044	121	5.49	111	5.57
20 (8 ")	197	.124 ± .047	91	4.62	106	5.12
21 (14 ")	390	.180 ± .033		4.44	220	4.91
Total of			Parents with 1—5 sp.		Parents with 7—11 sp.	
236 days	3520	.124 ± .011	1830	5.19	634	5.58

fore that the inherited racial differences observed in a wild population of *Difflugia corona* have been similarly produced by differentiation during vegetative reproduction.

It will be noticed in comparing table 51 with table 58 that the difference between the high and low groups becomes somewhat less as cultivation without selection continues. The decreased difference in the later table is probably sufficiently great to be of some real significance. Of course such a lowering of the difference between the high-selected and the low-selected sets after selection ceases is what is to be expected. The two sets have originally been produced through the fact that heritable variations appear during vegetative reproduction and that the effect of these variations has been accumulated through selection. After selection ceases, heritable variations continue to appear, but, in the high group for example, some of these are toward low numbers of spines, and these are no longer removed by selection. The same sort of change occurs within the low group, with the result that the difference between the two groups is no longer so great. It does not appear on logical grounds, however, that in this way the two groups would ever be brought to coincide in heritable characters; and after eleven generations with no selection we find that they do not coincide. Their tendency to approximate is the inevitable result of the same sort of changes through which their hereditary divergence has been produced.

Inheritance of spine number as observed by tracing pedigrees

The number of spines is so variable a character that it is not easy to detect inherited variations save by the use of averages, and by determining the coefficients of correlation of parent and offspring. Nevertheless, a comparative examination of pedigrees of diverse branches of the family No. 326 will show characteristic differences in the number of spines. Table 59 gives pedigrees lineally arranged (as described on page 419) for two branches, one with characteristically low numbers of spines, the other with high numbers. In each case all the individuals of the branch are descendants of the first one at the left.

TABLE 59

Family 326. Linear pedigrees (see page 419) for numbers of spines in two branches of the family.

A. Low numbers of spines; branch beginning with the individual .1.1.2.1.1.3.3.5.1 .1.2.4.1.3 (see page 415).

B. High numbers of spines; branch beginning with the individual .2.1.2.3.1.3.

A	5 4 4 4 2—4—4—3—5 3 4—4—4—4 4—1—4 4—3 3—3—3 4 6 5—5
B	7 6 6 7 6—5—7—6 5—8 6—6 5—7—5 3—7—6 7 7—5 5—5 6—6 7
A	4—3—5—3—4 5—5 5—5 4 4 4—4
B	6—5—4 5—5—4—7—6 6 6 9 5—6

It is at once evident to the eye that the number of spines in branch B runs regularly higher than in A. Of the thirty-nine individuals in each pedigree, if we compare the two that happen to be side by side in the two series, we find that B is greater than A in 35 cases; equal to A in two cases, and less than A in two cases. In branch A there is but a single individual with more than 5 spines; in branch B there are 21. In A, 25 individuals have fewer than 5 spines; in B only 3 have fewer than 5. The two pedigrees show decidedly different hereditary numbers of spines.

In series A the parents have for a long time been selected for low numbers of spines, in series B for high numbers. It must be understood of course that this selection does not affect the number of spines in the pedigrees directly, but only through its indirect effect on inheritance, for in each pedigree are included all the progeny produced, from the first individual to the last.

For more extensive pedigrees with respect to number of spines and other characters, see table 72, page 515.

Summary as to the inheritance of spine number

Our long-continued experiment with family 326 has then with respect to numbers of spines given the same result as the previous experiments with families 303 and 314, and with many smaller families. Heritable variations in number of spines do appear during vegetative reproduction, so that by long-continued selection of two stocks heritably diverse in this respect can be obtained from among the progeny of a single individual.

Inheritance and selection of size in family 326

During the progress of the work on family No. 326, the diameters of large numbers of individuals were measured. It was not possible to measure all the individuals that were studied with reference to other characters. Those measured were mainly individuals that presented themselves at moments when there was time to make the measurements; in addition to these, the 1433 individuals that were studied with reference to length of the spines (see a later section) were likewise measured. Thus those so measured constituted a random sample of the population so far as size was concerned. These included 1728 individuals whose parents were likewise measured, so that they could be employed for the study of inheritance. Further an experiment in selection for large and small diameters was carried on from February 2 to April 18; in this experiment 401 additional progeny were measured, progeny whose parents had likewise been measured.

Thus the total number of measured progeny from measured parents was 2129. The correlated measurements of all parents and the entire 2129 progeny are given in table 61. The measurements are given in units each of which is equal to 4⅔ microns.

The correlation between parents and progeny with respect to size in the 1728 individuals that constituted a random sample was .575 ± .011. The correlation between all parents and the entire 2129 progeny measured (shown in table 61) was .605 ± .009. Thus diversity of size is inherited to a high degree within this family.

On February 2 an experiment in selection with reference to size was begun. The experiment could be carried out only incidentally, in connection with the work on the spines, so that the selection practiced could not be very sharply defined; nevertheless, as we shall see, the results are clear. It was as a rule not practicable to measure the living parents at the time that selection was made; all that could be done was to separate two groups of parents,—one that made the impression of being large, the other appearing small. The parents were of course later measured, so that the accuracy of the experiment does not suffer at all; the only undesirable result was that the two selected groups did not differ very greatly. From February 2 to April 18, only the larger individuals (as judged by appearance) were retained for further propagation in the "large-selected" group; only small individuals in the "small-selected" group.

The experiment was divided, as convenience dictated, into four periods, all progeny from the "large-selected" parents being compared in each period with all progeny from the "small-selected" parents. In table 60 are given for each period the distribution and mean of the parental sizes and the distribution and mean of the sizes of the progeny, for each of the two sets; also for each period the correlation between all parents and all progeny when both sets are thrown together.

Table 60 shows that in all cases the progeny of the larger parents are larger than those of the smaller parents. The difference in size is very marked, amounting to about 2.5 units (of 4⅔ microns each); it persists through the four periods of the experiment. There is a high correlation between parent and progeny, amounting in the experiment as a whole to .670 ± .018—certainly an extraordinarily large figure for parent-offspring correlation within a single strain multiplying vegetatively. The same high coefficient holds also for all of the four periods taken separately. The general result of the experiment on selection for diverse sizes is thus to show that selection is effective quickly and in a marked degree.

Method of inheritance of size

Certain important points as to the method of inheritance of size appear from table 60, and from the general correlation table for parent and progeny with respect to size, given as table 61. In table 60 it is evident that in every case in which the parents are selected as markedly differing from the mean size (which in table 61 is a diameter of 40.43), the progeny deviate in the same direction as the parents, but to a less degree; the progeny are always nearer to the general mean than are the selected parents. It is therefore clear that in fission there is not a mere halving of the parental protoplasm in such a way as to make the progeny of the same size as the parent. On the contrary, the progeny of extreme parents, here as in other organisms, show a marked tendency to regress toward the racial type. But this regression is not complete; the progeny inherit a considerable portion of the parental deviation (about ½, as we shall see).

The same points, with certain others of importance, are illustrated in the general correlation for size (table 61), and in table 62 and figure 16

TABLE 60

Family 326. Results of selection for size (diameter of shell). Four periods, between Feb. 2 and April 18, 1915. Each unit = 4 2/3 microns.

			Diameter of shell																						Difference in favor of progeny of large	All parents with all progeny	
			35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	No.	Mean		No. of progeny	Correlation
1 (Feb. 2-Mar. 11)	Large	Parents						8	10	20	13	11	9	2	5	2	1	2	1	1			85	43.45	2.56	194	.665 ± .027
		Progeny	1		1		8	12	16	21	5	10	1	2		1	1	2	3	1			85	42.31			
	Small	Parents	2	13	15	18	31	20	9				1										109	38.53			
		Progeny		7	13	12	16	23	15	11	8	1	3										109	39.75			
2 (Mar. 12-25)	Large	Parents					1	1	1	8	12	7	6	5	2	1			1				45	43.84	2.40	105	.663 ± .039
		Progeny			1		1	5	5	9	7	6	5	3		2				1			45	43.00			
	Small	Parents		6	8	10	15	14	6	1													60	38.75			
		Progeny			2	3	9	17	17	6	2	2		1		1							60	40.60			
3 (Mar. 26-31)	Large	Parents						1		6	4	3	3										17	43.00	2.59	39	.663 ± .061
		Progeny					1	2	2		6	2	3	1									17	42.82			
	Small	Parents		3	2	7	5	5															22	38.32			
		Progeny			1	1	8	3	4	2	2	1											22	40.23			
4 (Apr. 1-18)	Large	Parents							2	3	9	10	6	3	1	1					1		36	44.19	3.39	63	.740 ± .038
		Progeny					1	1	4	5	6	11	4	1	1				1			1	36	43.69			
	Small	Parents		2	4	3	13	2		2		1											27	38.85			
		Progeny				2	3	11	8	2	1												27	40.30			
Total (Feb. 2-Apr. 18)	Large	Parents					1	10	13	37	38	31	24	10	8	4	1	2	2	1	1		183	43.65	2.70	401	.673 ± .018
		Progeny	1		2		11	20	27	35	24	29	13	7	1	3	1	2	4	2		1	183	42.80			
	Small	Parents	2	24	29	38	64	41	15	3		1	1										218	38.61			
		Progeny		7	16	18	36	54	44	21	13	4	3	1		1							218	40.10			

TABLE 61

Family 326. Correlation table for parents and immediate progeny with respect to diameter, for all that were measured.

Progeny \ Parents	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	
34							1													1
35		1			3	1					1									6
36	1	2	1	4	9	5	1													23
37	1	6	18	31	21	17	10	2	1	1		1								109
38		7	23	60	60	55	26	14	8	1	1	1								256
39		7	22	66	92	81	54	29	12	6	3	1								373
40		6	21	56	90	114	77	44	21	12	7	4	2							454
41		3	9	33	59	77	76	53	24	19	8	2	2							365
42		2	6	9	19	34	47	32	27	39	6	5	2							228
43				1	10	13	25	24	20	15	7	2	3							120
44				1	3	10	11	14	18	22	11	3	3							96
45				1	1	2	5	4	11	9	4	3	2	1						43
46					1		1	1	2		5	1				2				13
47								2			1	1	2			2			1	9
48					1	2			1	1	2					3				10
49											1				1			1		3
50												1	2	1	1	1	1	1		8
51													3	1				1	1	6
52														1			1			2
53												1								1
54														1				1		2
55																		1		1
	2	34	100	262	369	411	334	219	145	125	58	25	21	5	2	8	2	5	2	2129

derived from it. From table 61 we may determine the mean size of the progeny from parents of each given size. The results are shown in table 62, and are indicated graphically in figure 16. The mean size for all progeny is 40.43; parents which deviate from this mean size produce progeny whose mean size deviates in the same direction, but to a less extent. Determining from table 61 the coefficient of regression for the progeny, we find it to be .585; that is, the progeny inherit on the average .585 of the deviation of these parents. In figure 16 if the diameters of the different classes of parents are arranged so that their extremities form the line A-B, the mean diameters of their progeny trace the line C-D, which, as will be observed, follows the same general direction as A-B. In the region *x-y* where this line C-D is traced from adequate numbers of progeny (above 33), it follows nearly a straight course, slightly inclined to A-B. The line G-H shows where this line C-D would fall if it were straightened into what may be called its average position.

Table 62 and figure 16 show further that the inheritance of size is not a

TABLE 62

Single family No. 326. Mean size of progeny from parents of given size, serially arranged, with the deviation of the parents and progeny from the mean size of the progeny (40.43); also the amount of the regression of the progeny toward the mean size, as compared with their parents.

The sizes are given in measurements of the diameter of the shell, in units of 4 2/3 microns each.

Parents		Progeny				
Diameter	Deviation from mean	No.	Mean diameter	Deviation from general mean	Deviation from parental diameter	Regression toward general mean
35	—5.43	2	36.50	—3.93	+1.50	1.50
36	—4.43	34	38.68	—1.73	+2.68	2.68
37	—3.43	100	38.95	—1.48	+1.95	1.95
38	—2.43	262	39.11	—1.32	+1.11	1.11
39	—1.43	369	39.54	—0.89	+0.54	0.54
40	—0.43	411	39.96	—0.47	—0.04	—0.04
41	0.57	334	40.52	0.09	—0.48	0.48
42	1.57	219	41.01	0.58	—0.99	0.99
43	2.57	145	41.75	1.32	—1.25	1.25
44	3.57	125	42.18	1.75	—1.82	1.82
45	4.57	58	42.93	2.50	—2.07	2.07
46	5.57	25	42.48	2.05	—3.52	3.52
47	6.57	21	44.95	4.52	—2.05	2.05
48	7.57	5	50.20	9.77	+2.20	—2.20
49	8.57	2	49.50	9.07	+0.50	—0.50
50	9.57	8	47.50	7.07	—2.50	2.50
51	10.57	2	51.00	10.57	0.00	0.00
52	11.57	5	51.80	11.37	—0.20	0.20
53	12.57	2	49.00	8.57	—4.00	4.00
Total 40.56		2129	40.43	0.00	—0.23	

matter merely of the appearance of individuals differing greatly from the type, which later hand on their marked peculiarities. An increase in the deviation of the parents by a single unit brings about a corresponding (but less) deviation by the progeny. This is well shown in the close way the line C-D (for the progeny) follows the parental line A-B, in the middle region of the two (in figure 16). The numerous slight variations in size show inheritance as do the rare large ones.

Inheritance of size as observed by tracing pedigrees

If we follow separate lines of descent within the family, the inheritance of differences in size is perhaps even more strikingly shown than when

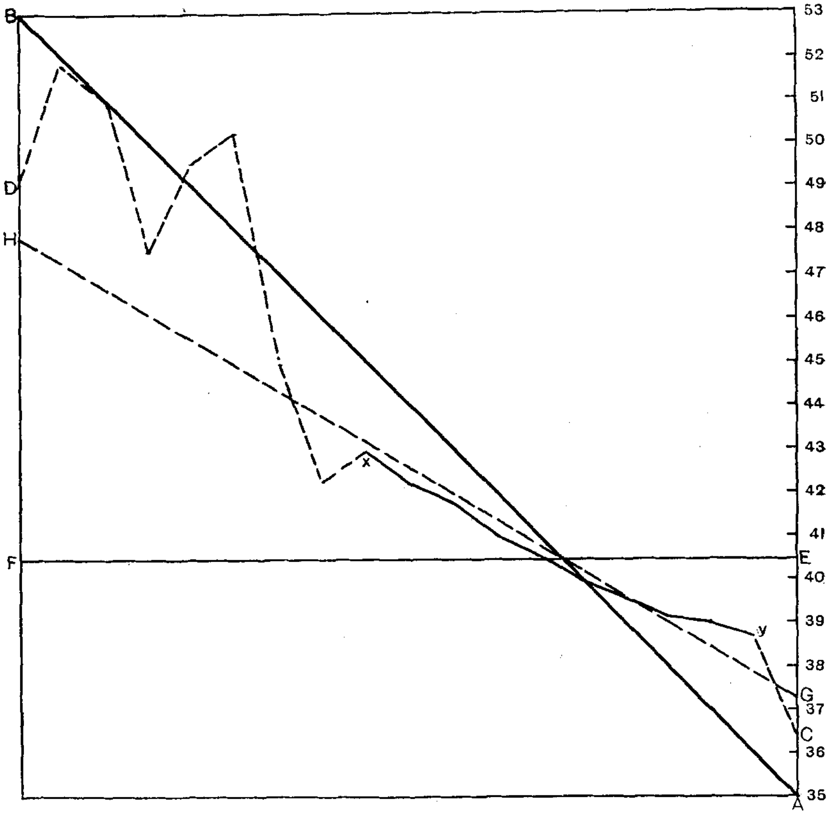


FIGURE 16.—Graph showing the correspondence in size (diameter) between parent and progeny in the 2129 progeny of family 326. A-B, line for the diverse parental diameters; C-D, line for the diameters of the corresponding progeny; E-F, line of no correspondence; G-H, line of regression of the progeny on the parents. The diameters of the parents are to be conceived as arranged in order from smallest to largest, so that their terminations trace the line A-B (the shortest extending 35 units to A, the longest 53 units, to B). Then the irregular line C-D shows the extent of the mean diameters of the progeny of the diverse classes of parents. The horizontal line E-F shows the place to which these diameters would extend if there were no correspondence of progeny with parent (so that all classes of progeny would have the mean diameter, 40.43). Finally the line G-H ('regression line') shows the points along which the diameters of the progeny would be arranged if the line C-D were straightened into its average position.

we employ the correlation method. A series of such diverse lines of descent from family 326 is given with respect to size in table 63. Examination of this table will show the chief facts as to the appearance and inheritance of diversities in size.

TABLE 63

Family No. 326. Linear pedigrees by size (diameters of the shell), of different lines of descent, all derived originally from the single individual No. 326; to show the inherited diversities in size in the different lines.

In each of the series a-o all the individuals are descendants of the individual at the beginning of the series (at the left). Where there are no dashes between the numbers they show a direct unbroken line of descent, each individual being the offspring of the one immediately before it. Where there is a dash, the individual following it is the offspring of some individual farther back (to the left) in the series.

The diameters are given in units of 4 2/3 microns each.

a	39 39 37 37—35 36 37—41—38—35 37 40—38 39 39
b	39 40 40—38 39 38 38 40 39 42—38 40—40—40—37 37 37—37
c	39 38 39 40—40—41—41—39—39 39 40—42—37—40—42—40 42—40 40 40 40 41
d	41 37 39 38 36 37 37—39—36 35—37—42 38 38 40—40—39 40—40—38 37—38—38—41—39 39—40 41—37—41—43 40 37—42—38—39 40—43 38 42 38 38 ——39—44 40—38 40 38—37 39—37—40 40—40—40 41 42—43 39
e	38 39—39—39—39 39 41 42—41 41—42—43 42—38—41—42 41—39 39—42—38
f	39 36 36 39 42—43—40 43—39 41—41—38—36 39 38 41 40—40—39—40—40—40—40—41—40—37 39 46—38 41 41—39 39—41—37—40—39—39 39—40 40
g	42 42 41 39 41 44 41 42—41—45 43—44—39 37 39—40—42—39 38—40 38—41 39—39—40 39 40 39—39—41 41—38—39 40 39 39—40—39 37—39—43 43—40—43
h	41 41—41 41—40 41 40—38—38 38—38—41 40—43—41 40 42 41—40—41 39—41—39 40 40—40—40 41—40—40 44 40 44 40 42—40 38 39 37—38 38—39 41 40—41 39 41 39—41—39—39 40—41—39 40—40 40—41—40 40—39—39 40—40
i	42 42—43 42 44 42 42—43 42—42—42 43 45—42—40 41—44—41—44—38 38 40 41—41—42—41—40 41 42—40—41 41
j	44 42 41 40 39—43 39—39—38 36—40 41—41 40—39 40 40 39—39 38—39—38 36 40—40 39 37—37 41—37—41 38—41—42—43 40 40 40—40—40—39 38
k	40 42 41 40 40 42 44 43—43 41—44—44—40 40 42—39—41 37—41—42—42—41—40—39 41 41 41—43 43 41 40—44 41—46 44—44—42 40—43 43—45—40 41 41—41—39—41 39—44 42 41 40—42 39—40 42—41 42—41 44 42—42 43—42 39 40—39—44 43—44 45—42—39—40 40—44
l	42 40 39—45 43 41 42 39—40—41—43 41—42—43 45—42—46 44—42—42 41 42—42 41—44 42—44 44 42—39—37 40—40—44—46 46 45—45—42 44
m	43 44 44 42—42 41 44 40—41—42—43—41 44—41 38 40—43 41—40—40 39 40 40
n	40 39 47 50 48—47—48 50 48—52 51 52—51—45 48 54 51—47 51 50—45 49 50 50—49 50—44
o	46 ? 44 53 47 47 47—51—51—55—54—48—47—50

Table 63 gives "linear" pedigrees, arranged as described on page 419, but showing only the diameters of the shell. Fuller pedigrees, giving other characters as well, and with precise indication of the descent, will be given later in table 72; here it is worth while to examine the sizes alone.

In table 63 it will be found that the diverse series of descent (*a* to *o*) have been arranged roughly in the order of the inherited sizes, beginning with the smaller. Such order can of course not be perfect, since there are considerable variations within a single series. But in series *a* for example it will be observed that practically all the individuals are below the size 40, while in series *o* all are above 44, most being 47 or more. The intermediate series show on the whole intermediate sizes; thus in series *c* there are considerable numbers of individuals at 40 and 41, the largest being 42; in series *g*, the sizes 41, 42, 43 and 44 are not uncommon; in series *i* such larger sizes are in the majority and size 45 occurs, etc. Thus the single family No. 326 shows clearly a breaking up into groups of diverse hereditary size comparable to the diverse families found in a wild population.

If we follow single pedigrees in table 63, we find illustrated the main facts as to the occurrence and inheritance of variations in size. The following points may be noted:

(1) Small variations, one to three units in extent, occur and are inherited in some degree. Thus, in series *b*, we first have three descending generations of size 39-40. Toward the end of *b*, we find another descending series of three generations, all at 37. In series *c* we have at first a series of 4 generations, 39, 38, 39, 40; later (at the end) there is a series of five, 40, 40, 40, 40, 41. In series *d*, the size seems mainly at 37 to 40; when a small individual at 36 appears, it has small progeny, at 35; later in *d* appears a series 40, 41, 42. In series *i*, we find one descending line 43, 42, 44, 42, 42; another 38, 38, 40, 41. In series *e* we find one descending line of 42, 41, 42; another of 46, 46, 45. In the table many examples can be found of such inheritance of slight diversities among close relatives.

(2) Extensive variations in size at times appear suddenly and are inherited. In series *n* the second individual, with a diameter of 39, produces an offspring with a diameter of 47, and this tremendous increase is then inherited for the rest of the series. In series *f*, a parent at 39 produces offspring at 46. Such cases are much less common than the appearance and inheritance of slight variations.

(3) Heritable increases in size appear to occur more readily and ex-

tensively than heritable decreases. The original progenitor of the family has the diameter 39, and the mean diameter for the race is about 40. The lowest series obtained (*a*) has a mean diameter not lower than 37. On the other side, we have in *n* and *o* series with means in the region of 47 to 48. Selection for increase of size usually produced marked results in a relatively short time, while selection for decrease of size soon met a complete barrier in the region of 37 units.

(4) The very large sizes show a tendency to weakness, particularly at reproduction. It is not rare to find the newly produced progeny of the very large individuals (47 to 55 units) consisting of mere empty shells. On the other hand, individuals up to 44-45 reproduce in a perfectly normal way, and give no indication of weakness.

In figure 19 (page 520) are given figures of successive individuals in certain lines of descent, all drawn to the same scale, in order to give a concrete realization of the differences in size and in other respects between the diverse branches of the family.

Interdependence of number of spines and size

With relation to two characters, the number of the spines, and the diameter of the shell, we have thus far seen that variations are inherited within the family, and that, consequently, selection is effective in isolating stocks hereditarily diverse with respect to these characters. But are these two characters independent? Or does one possibly depend on the other?

To answer this question, the correlation between the diameter and the number of spines was determined for several sets of individuals.

(1) Taking the family No. 326 as a whole, the diameter was measured in 2375 individuals. The correlation between the diameter and number of spines for these is exhibited in table 64. There is a marked positive correlation, amounting to .214 ± .013. From table 64 we may further obtain the mean sizes for the two groups selected for low and high numbers of spines. For the "low" group parents with 1-5 spines were selected; their mean size is 40.123. For the "high" group parents with 7-10 spines were selected; their mean size is 41.415. Parents with greater numbers of spines are therefore on the whole larger than those with few spines.

(2) Furthermore, the correlation between number of spines and diameter was separately determined for the individuals dealt with in the experiment on selection for size; that is (a) for the group selected for

TABLE 64

Family 326. Correlation between number of spines and diameter of the individuals for all measured.

	Number of spines											
Diameter	1	2	3	4	5	6	7	8	9	10	11	
34				1								1
35	2		2		4							8
36		2	5	8	10	2	1					28
37	2	3	9	27	39	24	9	1				114
38	2	3	21	51	110	66	17	9				279
39	2	8	33	76	114	131	29	11	2			406
40	4	8	38	91	144	140	65	18	3			511
41	1	7	18	48	114	131	60	15	5	1	1	401
42	1	1	20	34	83	78	33	6	3	2		261
43		4	7	18	28	49	28	5				139
44			4	11	40	30	20	1	2	3		111
45		1		6	12	16	9	4	1	1		50
46			1		6	6	2	2	1			18
47				2	1	1	3	4				11
48				1	4	1	2	2		1		11
49					1	1	2					4
50					3	4			1			8
51					1	2	1		1	1		6
52					2			1				3
53							1					1
54			1		1							2
55							1	1				2
	14	37	159	374	717	682	283	80	19	9	1	2375

large size (and their progeny); (b) for the group selected for small size (and their progeny); (c) for these two groups together.

(a) Within the group selected for large size (240 individuals) the correlation between the number of spines and the diameter was .221 ± .041. The mean diameter for this group was 41.94, and the mean number of spines was 5.81.

(b) Within the group selected for small size (264 individuals) the correlation between diameter and number of spines was .264 ± .039. The mean diameter for this group was 38.77, and the mean number of spines was 5.55.

Thus there was a marked correlation in each case, and the group of large individuals had a distinctly higher number of spines than the group of small individuals.

(c) When the "large" and "small" groups are thrown together, giving 504 individuals, the correlation is .246 ± .028.

It is therefore clear that in family 326, size and number of spines are not independent. When we select individuals with higher numbers of spines, we at the same time select, on the average, larger individuals. Conversely, when we select large individuals we at the same time select those with higher numbers of spines.

In table 26 (page 451) it is shown that similar relations hold in most other families. Yet, as we have seen on page 453, this correlation does not show a necessary relation between the hereditary conditions, for we found families with hereditarily small size and at the same time hereditarily high number of spines, as well as families with hereditarily large size and low numbers of spines. If such families are derivable from a single one, the union of hereditary large size and high number of spines is, even in the single family, merely the more usual combination,—the reverse combination also occurring at times. To test whether this is the case, it would be necessary to select at the same time for many spines and small size, on the one hand; for few spines and large size and on the other, so as to determine whether stocks could be obtained with these combinations hereditary. It appears to me possible that such selection might be effective in such a family as No. 326, but it was not tried.

So far therefore as our present data go, the mean number of spines may depend entirely on the mean size,—so that our experiment in selection for number of spines might be after all only an indirect selection for diversity of size. (But see further on this point paragraph 4 on page 519).

Inheritance and selection in length of spines

Independence of size and spine length

In view of the possibility just mentioned, that number of spines is dependent on the size, it appeared desirable to work if possible with some other character, that shows hereditary variations which are independent of size. The number of teeth is such a character; it is to be dealt with fully in a later paper. After the work with family 326 had gone far, so that a large number of individuals had been obtained, it could be remarked that some lines of descent showed prevailingly individuals with long spines, others individuals with short spines; and it did not appear that these differences were bound up with diversities in size of the animal. The interrelation of spine length with size was therefore thoroughly tested in the following manner:

(1) The length of the spines was measured in as many as possible

of the individuals for large and small size, in the experiment on selection for size. The spines were measured in 452 individuals, varying in diameter from 35 to 55 units; and in spine length from 2 to 23 units. The coefficient of correlation was —.005 ± .032. That is, there was absolutely no correlation between size and length of spines.

(2) In the sequel an experiment (to be described) was carried out in selecting for diverse lengths of spines; three groups, short-spined, intermediate-spined, and long-spined, were isolated. Of the parents thus selected there were 288, varying in spine length from 2 to 31 units, and in diameter from 34 to 52 units. The correlation between the length of the spines and the diameter was for these selected parents —.109 ± .039. Thus again no correlation is found to exist.

(3) The 288 selected parents just mentioned produced 693 progeny, varying in length of spines from 4 to 30 units, and in diameter from 34 to 49 units. The coefficient of correlation between length of spines and diameter was .079 ± .025; that is, no correlation is present.

All together, therefore, the correlation between the diameter and the length of the spines was determined for 1433 individuals, in the several diverse groups just mentioned. If we throw all these together we obtain table 65. The correlation for the entire 1433 individuals is —.020 ± .018.

Thus it is clear that in this family there is no correlation between length of spines and size; the two characters vary independently. This will be further demonstrated later by comparative pedigrees.

Selection for diverse spine lengths

Since this was the case, an experiment was undertaken as to inheritance of diversities in spine length, and the effects of selection on this character. The experiment was begun June 7, 1915. At this time the family 326 had become very large, and differentiation in its various branches with respect to length of spines was evident to the eye.

Therefore, a large number of the existing parents were divided into three groups; (1) those with long spines; (2) those with spines of intermediate length; and (3) those with short spines. It was not practicable to measure the spines in the living animals, so that the selection had to be carried out merely through estimation with the eye, the measurements being taken later, at the end of the experiment. The data are therefore accurate, but the division into three groups was less precise than would have been attained by measurements. The results are nevertheless sufficiently striking, as will be seen.

TABLE 65

Family No. 326. Correlation table for diameter of the shell and length of the longest spine. (Each unit is 4 2/3 microns). Correlation, —.020 ± .018.

	Diameter of the shell																						
Length of the longest spines	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	
2				1			1																2
3		1		2																			3
4					1	1																	2
5						2		1	3														6
6			1	2	1	1		2		3													10
7					1	1	6	4	4	8	1	1	1		1	1						1	30
8			2	2	6	3	16	8	12	3	8	2	1				1		1				65
9			2	7	4	15	19	14	13	13	7	4	4		1			1			1		105
10		1	2	5	12	19	33	32	21	24	13	6	1		3				2				174
11			5	7	17	20	45	39	20	15	11	5	2	3	1		1	2					193
12			1	5	17	42	42	44	31	13	14	7	3				1			1			221
13			3	5	16	23	45	37	39	15	14	7	3			2	2				1	1	213
14		1		8	7	11	36	19	19	8	9	2	1	1			2						124
15		1	4	2	4	15	15	18	11	4	6	1	1										82
16			1	1	6	10	9	7	6	7	6	2											55
17	1			1	4	4	8	3	5	6	4												36
18				2	5	5	7	6	9	4	4	2	1										45
19				2	2	3	5	3	1	1	1	1											19
20			1		4				1	1		3											10
21				1	1		1	1	2														6
22							1	2	2		1	2											8
23					1	1	3	2		1		1											9
24							1		1		1												3
25										1	1		1										3
26						1					1												2
27					1					2													3
28									1														1
29							1																1
30											1												1
31					1																		1
	1	4	22	53	111	177	294	242	201	129	103	46	19	4	6	3	7	3	3	1	2	2	1433

In the first selection, made June 7-12, 1915, there were 49 parents assigned to the "long-spined" group, with a mean spine length of 17.41 units; 82 to the intermediate group, mean spine length 13.96 units; and 159 to the "short-spined" group, with mean spine length of 10.59 units. (The "units" are each 4⅔ microns).

Now these three sets of parents were allowed to multiply, all under the same favorable conditions. The "long-spined" and "short-spined" were propagated for three periods, these being June 13-18; June 19-24; and June 25 to July 2. In each period all the progeny were retained

TABLE 66

Single family No. 326; results of experiment on the effects of selection for diverse spine lengths. Distribution of the spine lengths for parents and descendants in the three selected groups. The measurements are in units of 4 2/3 microns each.

Length of spines

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Total No.	Mean
1. Long-spined group																																
Selected parents										1	2	4	6	3	4	8	8	2	1	2	4		1	2						1	49	17.41
Progeny, June 13-18								1	1	2	4	6	4	2	2	2	8	1	1	1	1	1		1	1	2		1	1		43	17.20
June 19-24						2	2	1	5	1	8	15	5	5	9	3	4	2	1		1	3					1				68	14.41
June 25-July 2								3	3	5	10	10	9	11	5	5	7	5	3				1		1						78	14.73
Total progeny						2	2	5	9	8	22	31	18	18	16	10	19	8	5	1	2	4	1	1	2	2	1	1	1		189	15.14
2. Medium-spined group																																
Parents								**2**	**4**	**7**	**10**	**19**	**9**	**9**	**7**	**7**	**4**	**3**			**1**										**82**	**13.96**
Total progeny June 13-18							**3**	**3**	**9**	**14**	**21**	**27**	**14**	**10**	**6**	**3**	**1**			**1**		**2**	**1**			**1**					**116**	**13.16**
3. Short-spined group																																
Parents	1			2	4	10	10	22	26	35	20	16	4	4	2		1		1	1											159	10.59
Progeny, June 13-18				1	1	5	12	28	30	29	33	19	14	3	2	3	1		1			1									183	11.15
" June 19-24			1	2	3	3	8	9	17	17	21	10	10	6	1		1		1												110	11.10
" June 25-July 2						3	7	8	15	10	17	17	9	2	1		2	1		1	1	1									95	11.86
Total progeny			1	3	4	11	27	45	62	56	71	46	33	11	4	3	4	1	2	1	1	2									388	11.31
All progeny	1	0	1	3	4	13	32	53	80	78	114	104	65	39	26	16	24	9	7	3	3	8	2	1	2	3	1	1	1		693	12.67

and allowed to become parents in the next period; the progeny produced in each period were later measured separately for each group. The intermediate group was retained for only one period (June 13-18), since it became impossible to care for so many lines of descent. The results of the experiment are given separately for each of the three periods; they will be presented first in a series of tables, followed by a summary and discussion.

In table 66 are given for each of the three selected groups the distribution of the spine lengths in the parents, and their distribution in the progeny of each group for each of the three periods of the culture; also the mean spine length for each lot, and the mean for the total progeny in each group. In figure 17 are plotted graphs for the distribution of the spine lengths in the total progeny of each of the three groups.

In interpreting table 66 and figure 17, it is important to remember that there has been absolutely no selection among the progeny; all progeny produced are included. It is only the parents that have been selected.

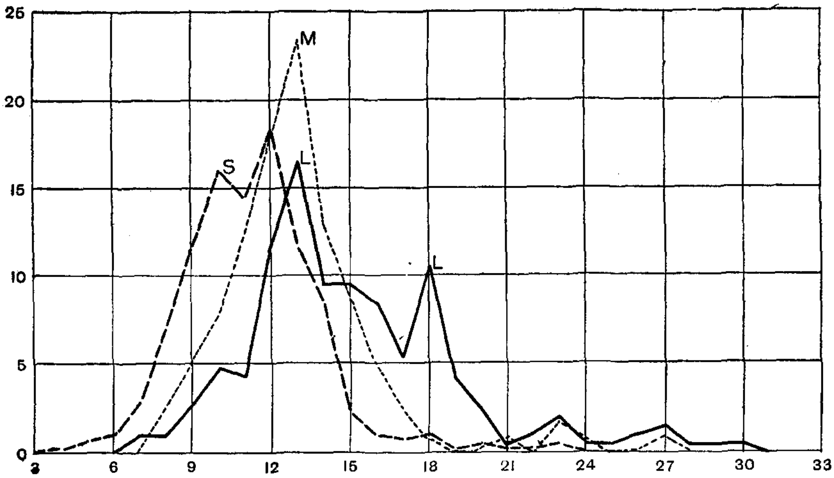


FIGURE 17.—Curves for the distributions of the variations in spine length in the progeny of the long-spined, short-spined and intermediate parents, plotted from the data of table 66. L, curve for progeny from the long-spined parents. S, that from the short-spined parents. M, that from the intermediate parents. The mean for L is at 15.14: for S at 11.31: for M at 13.16.

The ordinates are percentages, the abscissae, lengths of spine, in units of 4 2/3 microns each.

The table and figure show that the diversities of the parents with respect to spine length are inherited in a marked degree. In every period the progeny of the long-spined parents have much longer spines than the progeny of the short-spined parents. From the former the mean spine lengths in the three successive periods are 17.20, 14.41, 14.73; for the latter the corresponding figures are 11.15, 11.10 and 11.86. In the one period in which progeny are obtained from the intermediate group of parents the mean spine length (13.16) of the progeny is intermediate between those of the other two groups.

The mean spine length for all the 693 progeny produced is 12.64 units. It will be observed in table 66 that where the parents diverge in a certain direction from this mean the progeny, although they diverge in the same direction as the parents, show on the average a less deviation from the general mean than do the parents. This regression towards the general mean is however decidedly small in the case of spine length. This point will be illustrated further in connection with tables 68-70, and figure 18.

The relative variability of the progeny from the different groups of parents is of interest, as compared with the variability from all three groups together, as well as with the variability in spine length for the entire family. The coefficients of variation have therefore been worked out from the distributions given in table 66 (that for the entire family 326 coming from the table 65); they are given in table 67.

TABLE 67

Coefficients of variation in spine lengths from the progeny of selected groups of parents within family 326; also for the entire family (so far as measured).

	No.	Coef. of Var.
Progeny from long-spined parents	189	27.46 ± 1.00
Progeny from intermediate parents	116	22.74 ± 1.07
Progeny from short-spined parents	388	23.52 ± 0.58
All progeny in above three groups	693	28.30 ± 0.55
Entire family No. 326	1433	27.41 ± 0.36

In addition to the data already given, the correlations between the spine lengths of parents and progeny were determined for the three groups separately, and all the three together. It did not seem worth while to work out the correlations of parent and progeny for each period separately. Furthermore, since the selections of parents were made without relation to the character of the progeny they had produced be-

TABLE 68

Family 326. Correlation table for parent and immediate progeny, with respect to the length of the longest spine. Units of measurement are each 4 2/3 microns.

Progeny	Parents 4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
2				2																									2
3										1	1																		2
4										1																			1
5		1					2	1																					4
6						4	2			2																			8
7			2		1	2	5	3	3	2	2	1			1														22
8	1		1	1	6	3	6	9	11	7	5	4	2																56
9		2	3	4	8	13	14	12	9	14	2	2	1	1			1									2			88
10			1	2	9	12	17	26	34	21	10	4	1	2	4			1	1										145
11	3		1	12	8	8	15	28	27	26	14	8	6	2	2			3											163
12		1		8	6	19	20	31	26	31	17	9	6	5	4	3					1								187
13	1			2	5	4	19	30	30	34	14	8	11	6	9	2	1	1	2	1		1				1		1	183
14		2	1	5	3	5	8	17	12	24	9	7	4	3	3	1	2		1			2						1	110
15					1	4	3	9	12	15	5	5	4	3	7	2			1	1									72
16					1	1	5	6	5	6	3	5	4	4	5		2	1	1										49
17		1						1	4	5	2	3	4	1	5		1					3							30
18					1		1	5	5	8	4	2		1	5			1	1	2								1	37
19								2	1	2	1	2	1	3	1		1	1		1				1					17
20										5		3		1			1	1											11
21								1		3					1														5
22									2		2			1	2														7
23						2	1		1			1										1	1	2					9
24										1	1		1																3
25																			1										1
26															1				1										2
27											1	1																	2
28																											1		1
29															1														1
30																													0
31											1																		1
	5	7	9	36	49	77	118	181	182	208	94	65	45	33	51	8	9	9	9	5	1	7	1	3	0	3	1	3	1219

fore the selection was made, it appeared desirable to include in the correlation tables all progeny of the individuals in each group, whether produced before or after the beginning of the experiment in selection. Thus the numbers of progeny in the tables is greater than the number produced within the three periods given in table 66, so that the data are made fuller.

The length of spines for parent and progeny was further determined for the groups selected for large and small sizes, and for a number of other individuals taken at random. Measurements for all these individuals,—all not included in the experiments on inheritance of spine length—were gathered into a separate table, comprising 386 individuals whose parents were not selected with reference to spine length; the correlation was determined for these separately. Finally, all the correlation tables on spine length were combined into one with 1219 progeny, and the correlation of parents and progeny in respect to spine length determined for all together.

TABLE 69

Family 326. Correlation between parents and progeny with respect to spine length, in the various groups in which this was determined.

	No. of progeny	Correlation	Mean for parents	Mean for progeny
Long-spined parents	210	.239 ± .044	16.62	15.42
Intermediate parents	167	—.015 ± .052	13.78	13.48
Short-spined parents	456	.224 ± .030	11.01	11.25
Total for parents selected for length of spines	833	.426 ± .019	12.98	12.75
Parents not selected for length of spines	386	—.147 ± .033	11.74	11.92
Total, all groups	1219	.340 ± .017	12.59	12.49

The tables of correlation thus obtained are very large, and the publication of all of them *in extenso* seems scarcely warranted. I therefore give in full only the table that contains all the individuals of all the groups (table 68). The correlations for the different groups taken separately, with other data of importance, are set forth in table 69.

As table 69 shows, there is a marked correlation between parent and progeny with respect to the lengths of the spines. Taking all the descendants of parents selected for spine length, the coefficient is .426. It is a peculiar fact that in the group not selected for spine length, and that with intermediate spine length, there is no correlation between parent and progeny, or even possibly a slight negative correlation. Thus different groups of the family show divergencies as to the inheritance of spine length. But in the family as a whole, with 1219 measured individuals, there is a marked parental correlation of .340 ± .017.

From the correlation table including all parents and progeny in which spine lengths were measured (table 68) we may determine the average spine lengths of the progeny of parents of a given selected length of spines. The results are given in table 70, and a graph of the results is shown in figure 18. It will be observed that the progeny correspond very closely in their order to the order of the parents, in all cases where the number of progeny is large (33 or above); also that the deviation of

TABLE 70

Mean spine lengths of progeny from parents having given lengths of spine, in 1219 progeny of family 326. (The units of measurement are 4 2/3 microns each.)

Spine length of parents	Mean spine length of progeny	Number of progeny
4	10.80	5
5	11.43	7
6	9.33	9
7	10.89	36
8	10.88	49
9	11.15	77
10	11.28	118
11	11.99	181
12	12.09	182
13	12.67	208
14	12.92	94
15	13.61	65
16	13.49	45
17	14.36	33
18	15.20	51
19	13.25	8
20	15.33	9
21	14.33	9
22	16.67	9
23	16.60	5
24	12.00	1
25	16.43	7
26	23.00	1
27	21.67	3
28	——	0
29	10.33	3
30	28.00	1
31	15.00	3
	Total	1219

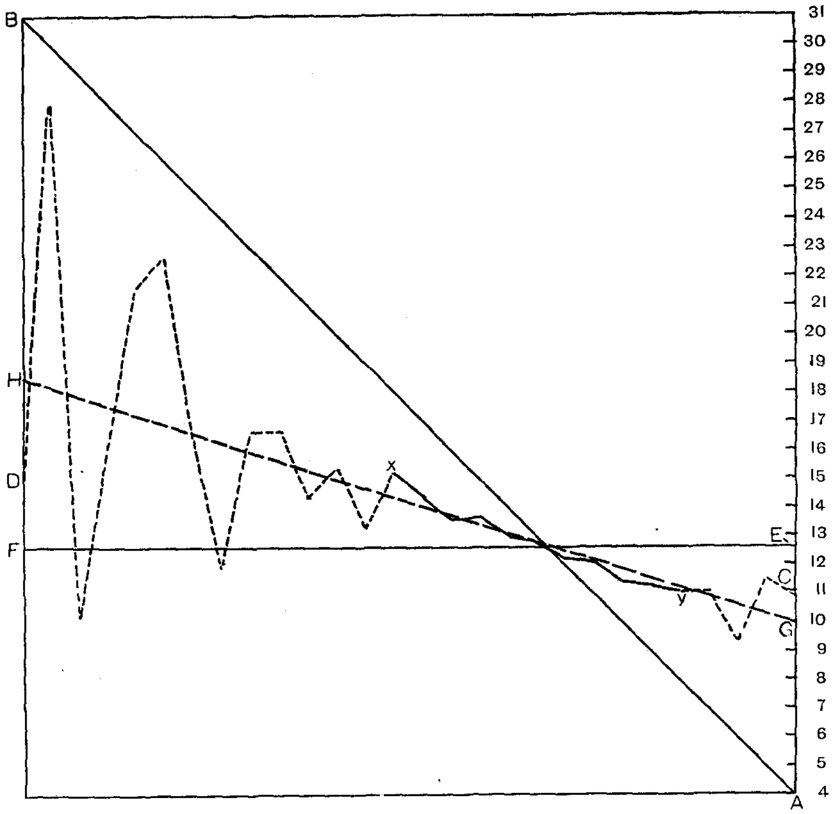


FIGURE 18.—Graph showing the correspondence in length of spine between parent and progeny in the 1219 progeny measured from family 326. A-B, line for the diverse parental spine lengths; C-D, line for the spine lengths of the corresponding progeny; E-F, line of no correspondence; G-H, line of regression of the progeny on the parents.

The spine lengths of the parents are to be conceived as arranged in order from shortest to longest, their terminations tracing the line A-B (the shortest extending to 4 units at A, the longest to 31 units, at B). Then the irregular line C-D shows the mean lengths of the spines of the progeny of the diverse sets of parents. The line E-F shows the place to which the spine lengths of the progeny would extend if there were no correspondence of progeny with parent (so that progeny from all classes of parents would have the mean spine length of 12.50). The regression line G-H shows the points to which the spine lengths of the progeny would extend if the line C-D were straightened into its average position; the progeny inheriting .318 of the parents' deviation from the mean.

In C-D, those parts drawn as an unbroken line are based on groups of progeny in each case above 33; this part of the line will be observed to follow closely the regression line G-H.

the progeny from the mean, while in the same direction as that of the parents, is less than that of the parents (on the average it is .318 of that of the parents). That is, an increase in length of spine in the parents is accompanied by an increase in the average spine length of their progeny, though the increase in the progeny is but ⅓ as great as in the parents.

Thus the statistical analysis and the results of the experiment on selection demonstrate that within the single family multiplying by fission, variations in spine length occur abundantly and are heritable in a high degree, and that selection is effective in isolating lines of descent differing hereditarily in length of spines.

Inheritance of spine length as seen in tracing pedigrees

By following out single lines of descent within the family, the inheritance of spine length appears clearly. Extensive pedigrees of this sort for several characters together will be given in the next section; here I give in table 71 merely certain typical pedigrees, lineally arranged, for spine length alone, to bring out sharply the hereditary diversities. It will be observed that the diverse series have been arranged roughly in the order of their hereditary spine lengths, beginning with the shortest. Comparing the different series it will be observed that in spite of the

TABLE 71

Single family No. 326. Pedigrees arranged lineally (see page 419) to show the hereditary diversities in length of the longest spine, in different branches of the family. The lengths of the spines for the successive individuals are given in units of 4 2/3 microns each. In each pedigree all the individuals are descendants of the first one at the left. Individuals not separated by a dash show directly descending lines of descent, each such individual being the offspring of the one at its left.

a	9 6 10 8 ? 11—10 4 7 ? 10—10 9 9 6—9 6 9—7 14—9—10 11 11—9—8 10—8—8
b	13 11 15 8 9—10—11—13 13—10 9 7—10 12 7 12 8—11 10—10 11—8 9—9—14 12—13—13 10 12—10 12 7—10—7 11—10—10—11—12
c	13 13 15 10 10—13—13—13 15 ? ? 16 8—15—10 12—12—13 17 9—14 11—11 13—10 15 12—16—? 10 ? 14—10 13 13 7—20—10 11
d	8 11 13 12 12—14 10—7—14—11—9 11—11 13—12 12 10 9—8 10—11 11—10—15—12 13 14—10 8—12—9 15—11
e	16 11 18 17 12—11—16—12—15 13—15—14 11—13—22 16 12 19 15—15—15 14—14
f	18 17 ? 17—25 23 18 16—14 15—25 13—14—14 13 11—17 19—16—13 10—17—22—15 18 15 20 20 16 16—13 16 15—19—18 15 17 14—16
g	14 31 ? 21 20 17—18—26 15—18 18 16—14 13—18—13 15—14—22 18 15—16—18

variations within the single series, the different series show marked diversities in their hereditary spine lengths.

All of these series except *e* are given with precise indication of parentage, and the other characters of the individual, in table 72 of our next section.

Hereditarily diverse branches, with diverse combinations of characters, in the single family 326

Toward the end of the experimental culture, when the number of descendants produced by the single individual No. 326 had increased to some thousands, it was evident that the family had differentiated into a number of branches which differed hereditarily in various respects. To show the characteristics of these branches, to show the different existing hereditary combinations of the diverse characters, and to exemplify the method of variation and inheritance of the different characters and their combinations, I give in table 72 extensive pedigrees of diverse branches of the family.

Figure 19 shows typical portions of a number of diverse branches including some of those given in table 72.

EXPLANATION OF TABLE 72

Pedigrees arranged in the linear form described on page 419, of diverse branches of the family 326. For each individual the number of spines, the diameter, and the length of the longest spine are given.

In each pedigree the individuals are designated in the first row by serial numbers; all the individuals of any pedigree are descendants of No. 1 of that pedigree. Any individual whose designation or measurement is not preceded by a dash is the immediate progeny of the one just before it in the series. If the individual is preceded by a dash, then its parentage is shown in the fourth row, headed "parent", the number found in that row is the designation of the parent. Thus, the parent of No. 6 in branch *A* is No. 4.

For example, the pedigree *B* of table 72 is to be read as follows: The ancestor of all individuals in *B* is No. 1; it had 4 spines, a diameter of 37 units, and the length of its longest spine was 13 units. Its first offspring was No. 2; the first offspring of the latter was No. 3, and so on for a series of 8 consecutive descending generations. No. 9 was the offspring of No. 5; No. 10 the offspring of No. 4 and has as its offspring No. 11, etc. Thus the entire descent of any individual can be determined.

The origin of the first individual of each branch, and its place in the entire pedigree of family 326 is given in the title of each branch, in terms of the method of designation described on page 415. For example, the first individual of branch *K* (".3.2.4") is the fourth offspring of the second offspring of the third offspring of the original parent of family 326.

TABLE 72

A. Branch beginning at .14. Small size; spines of intermediate length, rather numerous.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	3	3	5	6	6—	5—	6	7—	6	9—	7—	6—	3	8	5	6	5—	5—	6—	6—	6—
Diameter	39	36	36	39	42—	43—	40	43—	39	41—	41—	38—	36	39	38	41	40—	40—	39—	40—	40—
Length sp.		15	13	12	10—	11—	12	11—	9	14—	15—	10—	8	10	12	15	13—	10—	9—	12	
Parent						4	4		4		4	3	2					3	3	14	14

Designation	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
No. spines	—7—	7	7—	6—	5	4	5—	6	7—	4—	4	6—	6—	5—	7	5—	5	5—	6—	6
Diameter	—40—	40	41—	40—	37	39	43—	38	41—	41—	39	39—	41—	37—	40	39—	39	39—	40—	40
Length sp.		—23	19—	13—	11	9	12—	11	12—	14—	13	12—	14—	11—	11	11—	13	14—	15—	14
Parent	14	14			13			13		29	29		29	13	2		36		36	36

B. Branch beginning at .1.1.1.2.4.3.3.1.1.1.2.1.1.3.2. Small size; spines moderately long, rather few.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	4	4	5	6	6	5	4	5—	4—	6	6—	5—	4	5	4	4—	5—	4—	5	4—	6—
Diameter	37	36	40	41	38	40	40	40—	41—	39	38—	40—	40	40	39	40—	40—	40—	40	39—	41—
Length sp.	13	11	13	21	19	13	10	11—	12—	11	12—	13—	18	17	19	13—	9—	19—	15	12—	16—
Parent									5	4		4	**3**				14	13	3		3

Designation	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
No. spines	—5	6	6	7—	5	4—	5—	3	4	5—	3—	3	6—	4	5—	6	6	6	5—	6—	3
Diameter	—42	41	40	39—	44	44—	40—	41	39	37—	37—	39	37—	41	38		43	40	41—	40—	40
Length sp	—18	16	19	15—	13	9—	13—	18	11	12—	10—	12	17—	7	12		9	13	14—	14—	12
Parent	2				23		23	22			29	22		22		2				38	37

Designation	43	44	45	46	47	48
No. spines	3—	5—	5	3—	6—	6
Diameter	38—	35—	41	36—	39—	40
Length sp.	8—	10—	12	11—	11—	14
Parent		42	2		1	1

C. Branch beginning .1.1.2.1.1.3.3.5.1.1.2.4.1.3. Small size; spines few; rather short.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	5	3	4	6	5—	5	4	3—	5—	3—	4	5—	5	5—	5	4	4	4—	4	4—	4—
Diameter	44	42	41	40	39—	43	39	39—	38—	36—	40	41—	41	40—	39	40	40	39—	39	38—	39—
Length sp.	8	11	13	12	12—	14	10	7—	14—	11—	9	11—	11	13—	12	12	10	9—	8	10—	11—
Parent						3			3	3	2		2		1				16		16

Designation	22	23	24	25	26	27	28	29	30	31	32	33
No. spines	—4	4—	5—	2	5	4—	3	4—	4—	3	4—	4
Diameter	—38	36—	40—	40	39	37—	37	41—	37—	41	38—	41
Length sp.	—11	10—	15—	12	13	14—	10	8—	12—	9	15—	11
Parent	15		15	1			25		25	1		1

D. Branch beginning .1.1.2.1.1.3.3.7.3. Moderate size; spines few, rather short.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	4	5	6	5	6	8—	5	5—	4—	5	6	4—	3	4—	5—	5	4—	5—	6	6	5
Diameter	42				41	41—	41	41—	41—	40	41	40—	38	38—	38—	41	40—	43—	41	40	42
Length sp.					13	9—	12	11—	11—	13	10	13—	12	10—	20—	11	11—	23—	12	11	12
Parent							5		7	6			10		10	6		6	5		

TABLE 72 (continued)

Designation	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
No. spines	4—	4—	4	5—	5—	6	3	5—	3—	3	5—	4—	4	4	5	6	5	4—	6	6	3
Diameter	41—	40—	41	39—	41—	39	40	40—	40—	40	41—	40—	40	49	40	44	40	42—	40	38	39
Length sp.	10—	11—	11	12—	13—	13	11	13—	14—	11	12—	13—	13	9	11	11	12	13—	12	11	12
Parent		20	19		19	5			27	5		5	3						37		

Designation	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
No. spines	4—	4	4—	5	4—	5—	5	3	3	2—	4—	3—	5	5—	5—	4	4—	5	5—	5—	6
Diameter	37—	38	38—	39	41—	40—	41	39	41	39—	41—	39—	39	40—	41—	39	40—	40	40—	41—	40
Length sp.	8—	10	10—	10	10—	12—	15	11	10	5—	13—	11—	9	12—	9—	11	12—	13	14—	13—	15
Parent		40		37		37	36				49	49	36		55	36		35		60	35

Designation	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
No. spines	7—	4—	5	7—	5—	7	3—	5	5	4	4—	3—	4	7—	5	4	4—	3—	4	5—	5
Diameter	40—	39—	39	40—	40—	44		38	43		43—	42—	41	41—	40	39	36—	41—	39	41—	41
Length sp.	10—	11—	12	16—	11—	11		21	11		15—	8—	11	12—	11	15	12—	12—	10	13—	9
Parent		63	35		35	44		69				74	71		69			78	78		69

Designation	85	86	87	88	89	90	91
No. spines	— 4	4—	5	5	3—	5—	4
Diameter	—39	40—	41	41	42—	41—	41
Length sp.	—18	17—	15	11	13—	12—	12
Parent	34		34			87	34

E. Branch beginning .3.1.1.1.2.1.4.1.1.2.3.1.1. Moderate size; spines numerous in first part, few in latter part; intermediate.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	4	6	6	7	5	4	6—	3	7	6—	10—	7	6—	6—	6	8—	5	5	4	5	4
Diameter		41	40	43		38	39—	41	43	43—	44—	44	41—	42—	39	43—	40	41	39	42	40
Length sp.			12	12		11	13—	10	12	17—	18—	16	17—	14—	14	27—	10	12	15	12	13
Parent								4			9	4		4	3		3				

Designation	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
No. spines	— 6—	6—	6—	3—	4—	5—	6—	5	5—	5—	6—	7—	6	6	4	5	6—	6—	6—	6	6
Diameter	—41—	39—	41—	40—	40—	36		38	40—	38—	39—	38		42	41	46	38—	38—	42		
Length sp.	—12—	10—	12—	12—	16—	13		12	11—	18—	10—	13		13	11	14	12—	11—	12		
Parent	19	18	17	17	17	17	3	3		29	3	3	2					36	35	34	

Designation	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
No. spines	— 4	5	5	5—	5—	2	5	5—	3—	4—	7	6	3—	6—	4—	4	4	3	7—	3—	3
Diameter	42	43	38	39—	41—		40	37—	36—	38—	41	40	39—	42—	43—	41	40	39	40—	38—	42
Length sp.	13	13	9	9—	14—		14	11—	10—	9—	15	12	12—	14—	9—	11	14	11	7—	12—	13
Parent	20				44	20			48	20	19				53	1				59	58

Designation	64	65	66	67	68	69
No. spines	6—	4	4—	7—	5—	3
Diameter	42—	38	40—	37—	40—	39
Length sp.	13—	13	14—	19—	13—	14
Parent		59		58	1	1

TABLE 72 (continued)

F. Branch beginning .1.1.1.2.4.3.3.1.2.2. Moderately small size; long spines, rather few in number.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	— 6—	4	5—	3—	5—	6—	6	6	5	5	5	4	6—	5	4—	5—	3	6	5—	5	7
Diameter	41			46	43		41—	43	45	40	39—	41	41—	46	42—	37—	43	43	39—	43	45
Length sp.				18	17		17—	25	23	18	16—	14	15—	25	13—	14—	14	13	11—	17	19
Parent								6				8		6		6	6			6	

Designation	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
No. spines	— 6—	4	5—	3—	5—	6—	6	6	5	5	5	4	3	5	3	4—	4—	3	3—	3—	5
Diameter	—44—	40	38—	39—	42					41	37	39	38	36	37	37—	39—	36	35—	37—	42
Length sp.	—16—	13	10—	17—	22					15	18	15	20	20	16	16—	13—	16	15—	19—	18
Parent	5	5		4	4	3	2										35	34		34	33

Designation	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
No. spines	5	2	5—	3—	4	4—	5—	4	4—	5—	5	7	6—	5	5—	6	3—	3—	6—	6	4
Diameter	39	38	40—	40—	39	40—	40—	38	37—	38		38	41—	39	39—	40	41—	37—	41—	43	40
Length sp.	15	17	14—	16—	13	14—	16—	16	14—	20		27	23—	26	23—	18	18—	15—	19—	27	23
Parent				43	42		42	33		33	32			32		32		32	31	31	

Designation	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
No. spines	4—	5—	5—	5	3—	7	6	4	5	5	4—	5—	5	7—	5	5	5—	4	5—	4—	3
Diameter	37—	42—	38—	39	40—	43	38		42	38	38—	39—	44	40—	38	40	38—	37	39—	37—	40
Length sp.	13—	18—	19—	17	19—	14	31		21	20	17—	18—	26	15—	18	18	16—	14	13—	18—	13
Parent		63	62	31		29						72	71		70			78		78	70

Designation	85	86	87	88	89	90	91
No. spines	4—	5—	5	6	4—	6—	4
Diameter	40—	40—	40	41	42—	43—	39
Length sp.	15—	14—	22	18	15—	16—	18
Parent		70	69			69	69

G. Branch beginning .2.1.2.3.1.3. Rather large size, with numerous spines; these moderately long.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	7	6	6	7	6—	5—	7—	6	5—	8	6—	6	5—	7—	5	3—	7—	6	7	7—	5
Diameter	45	43	41	42	39—	40—	41—	43	41—	42	43—	43	45—	42—	46	44—	42—	42	41	42—	42
Length sp.	13	13	15	10	10—	13—	13—	13	15			16	8—	15—	10	12—	12—	13	17	9—	14
Parent						3	2	2		8		2		2	1		16	16			1

Designation	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
No. spines	5—	5	6—	6	7	6—	5—	4	5—	5—	4—	7—	6	6	6—	9—	5	6
Diameter	41—	44	42—	44	44	42—	39—	37	40		40—	44—	46	46	45—	45—	42	44
Length sp.	11—	11	13—	10	15	12—	16		10		14—	10—	13	13	7—	20—	10	11
Parent		21		21			25	21		29	21	21	1			35	34	

H. Branch beginning .3.1.1.1.2.3.1.1.1.2.1.2. Moderately large; few spines (in most parts); spines short.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	8	5	5	6	5	4	5	4	4—	2—	5—	4	2—	3—	3	5—	7	6	6	5	5
Diameter	46				42	47	45	40	44—	45—	44—	43	43—	43—	43	42		44	44	43	43
Length sp.	9				13	11	15	8	9—	10—	11—	13	13—	10—	9	7		10	12	7	12
Parent										8	6	5		12	5		3				

Table 72 (continued)

Designation	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
No. spines	4—	6	5	3	4—	5	4—	5—	6	5—	4—	4	5	5—	6	4	7—	4—	3	7—	5
Diameter	44—	43	37	40	40—	38	39—	37—	44	42—	42—	43	43	40—	42	41	40—	43—	44	45—	45
Length sp.	8—	11	10	10	11—	8	9—	9—	14	12—	13—	13	10	12—	10	12	7—	10—	7	11—	10
Parent		20				24		24	20		20	19			19			37	36		40

Designation	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
No. spines	— 4—	6	3	5—	3	4—	5—	4	4	5—	4—	5	6	6	4—	4	6	4	4	3—	4
Diameter	—43		42	40—	40	42		—42	42	41—	41—	40	42	41	42—	41	41	40	38	38—	40
Length sp.	—10		11	12—	8	8		— 8	12	13—	12—	11	10	13	14—	6	10	8	9		—11
Parent	19	18			44		18	18			18	2				1					60

Designation	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
No. spines	— 2	2	3—	3	6—	4—	4	3	2—	3	2	4—	2	4—	5—	4	3	4—	3—	3	3
Diameter	—40	38	40		39—	39—	40	39	36—	41	39	38—	41	41—	40—	40	40	38—	40—	41	41
Length sp.	—10	4	7		10—	10—	9	9	6—	9	6	9—	7	14—	9—	10	11	11—	9—	8	10
Parent	59			59		59	58			58			58		1	1			79	1	

Designation	85	86
No. spines	— 2—	4
Diameter	—40—	40
Length sp.	— 8—	8
Parent	83	83

I. Branch beginning .3.1.1.1.2.1.4.1.1.4.2. Moderate size; rather long spines numerous at first, but few in the greater part of the pedigree.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	7	7	5	6	6	5—	6	5—	5	7—	8—	7—	5	5	5	5—	5—	5	5—	3—	5
Diameter	41	45	44	42	41	38—	43	39—	44	42—	45—	42—	40	40	40	41—	42—	42	42—	41—	40
Length sp.	12	22	25	17	13	15—	17	15—	17	22—	20—	17—	14	14	16	16—	13—	18	13—	12—	14
Parent							5		3		9	3	2				14	13		18	13

Designation	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
No. spines	4—	5	4—	5	3	4—	7—	4—	4	4	3	4—	4—	5	4—	3	4	4—	4—	5
Diameter	39		42—	41	40	40—	41—	40—	40	44	39	40—	42—	41	38—	40	41	39—	36—	42
Length sp.	12		18—	15	12	12—	10—	15—	14	17	16	12—	13—	13	14—	17	16	17—	15—	13
Parent		13		2			26	25	1				31	31		1			37	1

J. Branch beginning .1.1.1.2.5.1.3.4.1.2.1.1.5. Size large; spines long, numerous.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	6	5—	7	5	6	4	6—	6	7—	6—	9	6	8—	7—	8	4—	6—	7—	5—	5	6
Diameter	42	42—	43	42	44	42	42—	43	42—	42—	42	43	45—	42—	40	41—	44—	41—	44—	38	39
Length sp.	12	10—	18	15	14	15	17—	16	24—	20—	21	10	13—	16—	29	9—	13—	9—	15—	17	18
Parent			1					4		4	3			11	3		15	15	3	1	

Designation	22	23	24	25	26	27	28	29	30	31	32
No. spines	5	5—	6—	6	5—	4	6	5—	5—	5	8
Diameter	40	41—	41—	42	41—	40	41	42—	40—	41	41
Length sp.	18	12—	13—	14	15—	13	13	13—	12—	16	15
Parent			21	20		1			27	1	

TABLE 72 (continued)

K. Branch beginning .3.2.4. Very large; spines numerous.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
No. spines	6	6	6	7	7	8	8—	10—	6—	8—	5—	7—	6—	7—	6
Diameter	46		44	53	47	47	47—	51—	51—	55—	54—	48		47—	50
Length sp.				12						—13—	9				
Parent								5	5	4	4	3	1	1	1

L. Branch beginning .2.1.2.4. Very large; spines short, rather numerous.

Designation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. spines	4	4	1	4	6	5—	6—	5	5	8—	8	5	5—	6—	6	8	3	7—	5	9	6
Diameter		40	39	47	50	48—	47—	48	50	48—	52	51	52—	51—	45	48	54	51—	47	51	50
Length sp.					14		11		14	10—	10	11	10—	9—	12	10	13	10—	11	11	11
Parent							5	5			8			8	8				5		

Designation	22	23	24	25	26	27	28	29	30
No. spines	— 5	6	5	5—	7—	6—	4—	7—	4
Diameter	—45	49	50	50—	49—	50—	44—	41—	40
Length sp.	—12	13	8	13—	13—	12			
Parent	4				23	4	4	2	1

Comparing the different pedigrees of table 72 and examining figure 19 in connection with these, it will be evident that the family No. 326 has become differentiated into a number of hereditarily diverse branches; and that different branches show different sorts of combinations of the three characters. Specifically, the following important facts appear:

1. Different branches are hereditarily diverse as to their typical numbers of spines. Compare, from this point of view, series C with series G, series H with series G or K, etc.

2. Different branches are hereditarily diverse in diameter. Compare the diameter in A with that in K or L. A considerable number of lines hereditarily diverse with respect to diameter are distinguishable; certainly the following grades are clearly marked, beginning with those having the smaller individuals: A, D, G, H, L.

3. Different branches are hereditarily diverse in length of the longest spine. Several diverse characteristic grades may be distinguished with reference to this. Thus, beginning with shorter spines, compare: H (see particularly that part of the pedigree after the number 57), C, A, B, F.

4. There is some indication in the pedigrees that hereditarily higher numbers of spines need not necessarily go with hereditarily larger size, though they usually do. The series E, with its extremely large individuals, has merely a moderately high number of spines, possibly on the whole not so high as in G, with its much smaller size. Certainly there is no thorough-going proportionality of mean size with mean spine number.

5. Hereditarily diverse combinations of size and length of spines occur in the different branches. Thus series L has a very large size, with short spines; series C has small size with short spines; series H has intermediate size, also with short spines. Again, series D and F are of about the same size, but D has short spines, F has long ones. Series L is larger than J, but has shorter spines; series F is smaller than J, but has likewise shorter spines. Thus we may distinguish:

Long spines with small size (F),
Long spines with rather large size (G),
Short spines with small size (C),
Short spines with rather large size (H),
Short spines with very large size (L),
Intermediate spines with small size (B),
Intermediate spines with large size (E).

Altogether it is clear that hereditary spine length and hereditary size are independent characters. The difference between the different branches of the family in these respects are well brought out in the figures of certain parts of the pedigrees given in figure 19.

FIGURE 19.—Typical portions of the pedigrees of five hereditarily diverse branches of the family 326 (all descended from the same original progenitor). All are drawn to the same scale, at a magnification of 143 diameters.

Each branch is designated by a letter; the three branches F, H and L are parts of the branches so labeled in table 72. In each branch all the individuals figured are descended from the first one figured, save in branch M, in which all are descended from the immediate parent of the first one figured.

The line of descent is indicated as follows: In each branch the successive individuals are given serial numbers; (where an individual is omitted because it was lost before it was drawn, it is nevertheless given one of the serial numbers at its proper place). If the number of any individual is not followed by another number in parentheses, that individual is the immediate offspring of the one that precedes it in the series: thus in branch F, No. 2 is the offspring of No. 1, etc. But if the individual's number is followed by another number in parentheses, the latter is the number of its parent. Thus, in series F, No. 6 (3) is the offspring of No. 3 of the same series.

Branch M. Medium-sized body, small spines. All descended from an individual which is the immediate parent of the first one shown; its designation in the general pedigree was .1.4.2.2.3.2.1.2.2.1.2.1.4 (see page 415).

Branch N. Smaller bodies and longer spines than in M. The first member's place in the family pedigree is given by its designation .5.4.

Branch F. These are numbers 33 to 42 inclusive of the branch F in table 72. Bodies of about the same size as in N, but with still larger spines.

Branch H. These are numbers 5 to 14 of the branch H in table 72. Bodies larger than in M, N or F; spines larger than in M, smaller than in N and F.

Branch L. These are numbers 5, 7, 9, 10, 11, 12, 13, 15 and 16 of branch L in table 72. Very large bodies; small spines.

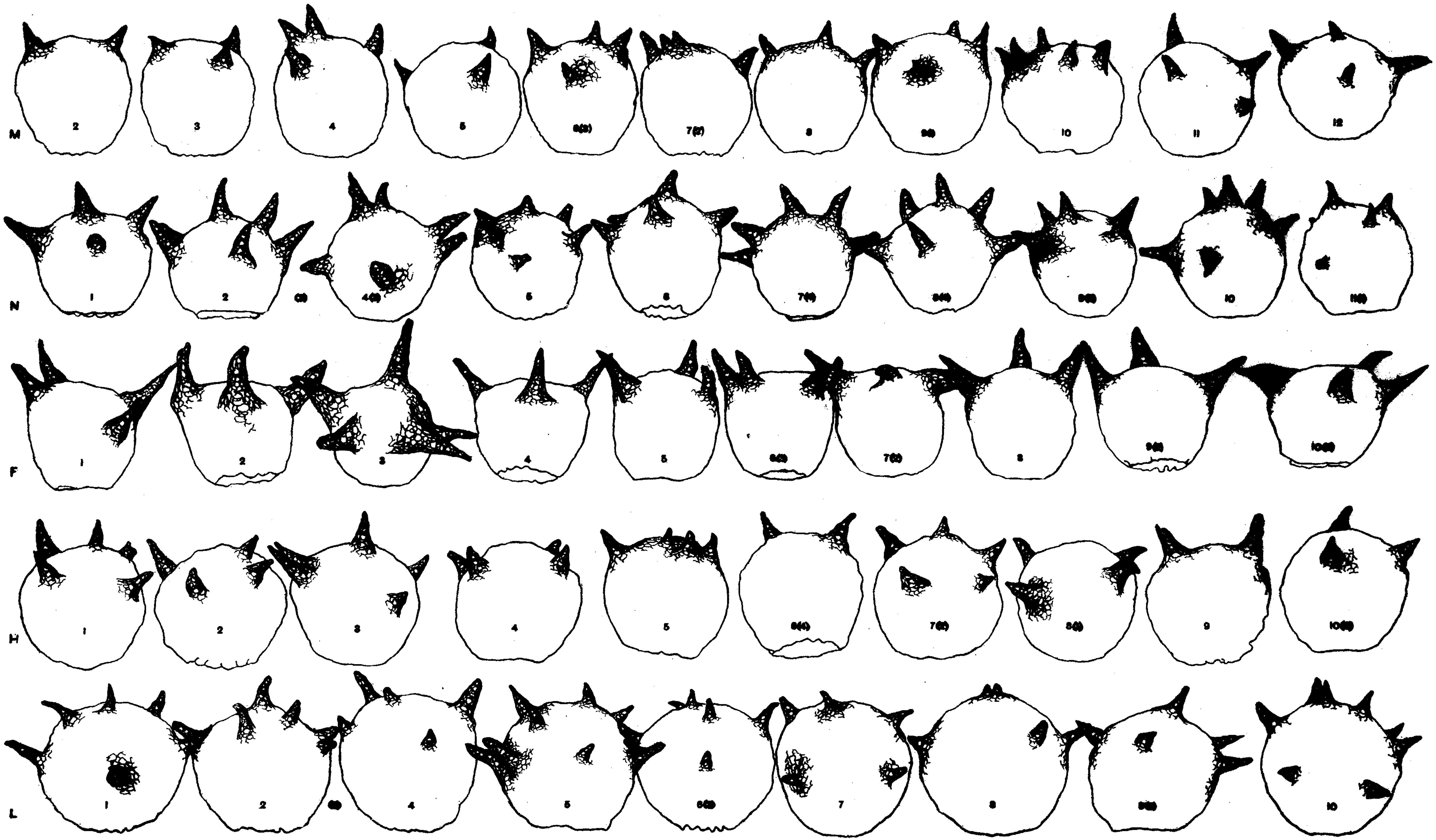

M
2
3
4
5
6(3)
7(2)
8
9(1)
10
11
12
N
1
2
(3)
4(3)
5
6
7(1)
8(1)
9(1)
10
11(1)
F
1
2
3
4
5
6(1)
7(1)
8
9(1)
10(1)
H
1
2
3
4
5
6(1)
7(1)
8(1)
9
10(1)
L
1
2
(3)
4
5
6(1)
7
8
9(1)
10

Figure 19

6. Within the single pedigrees we may observe quantitative changes in the hereditary features.

(a) Thus, in I, the number of spines in the first part of the pedigree (to No. 12) are numerous; in the rest of the pedigree they are few. Similar relations, but less marked, are discoverable in E. Often in short series of generations of a given pedigree marked, apparently hereditary, diversities appear. Thus, in series A we find that No. 14 has 8 spines, and its four progeny with one grandchild show 6-6-7-7-7 spines. On the other hand, No. 13 with its progeny and grandchildren give the series 3-5-4-5-6-7-5, showing consistently smaller numbers. In B we have from No. 13 to 16 a descending series of four generations 4-5-4-4; from Nos. 22 to 25 we have another descending series of four generations, 5-6-6-7. In H we find at the beginning the series 8-5-5-6-5-4-5-4-4; later, we find that No. 58, with its progeny and their descendants give 4-4-3-2-3-2-4-2. In I we find on the one hand the descending series 7-7-5-6-6-5 (at the beginning); later (Nos. 30-34) the descending series 4-4-3-4.

(b) With respect to diameter similar relations are discoverable in the single pedigrees. The matter has been discussed on page 501.

(c) Similar hereditary diversities with respect to spine length are found in different parts of the single pedigree. Thus, in series H, the spine lengths from No. 58 on are distinctly less than before No. 58. In series A the length runs mainly at from 11 to 14; at No. 23 appears an individual with long spines (23 units) and its offspring has likewise long spines (19 units.) In F we find the series of descending generations 18-15-17-14 (Nos. 42-45); elsewhere we find similarly the higher series 27-23-26-23 (Nos. 54-57). In J we find one descending series of 4 generations 13-13-13-12, (Nos. 27-30); another descending series 18-15-14-15-17 (Nos. 3-7). Such instances could be multiplied.

Within each of these branches of the family we find therefore the beginnings of the same sort of hereditary differentiation that has given rise to these hereditarily diverse branches. In each branch we find numerous opportunities for the isolation and propagation by selection of diverse stocks.

Summary of the experimental results with family No. 326

Our very extensive study of the large family No. 326 has demonstrated fully what was strongly indicated if not proved by the earlier studies of smaller families. In *Difflugia corona* the family derived by vegetative reproduction from a single individual gradually differentiates into hereditarily diverse stocks. By selection we can thus isolate diverse strains. Such hereditary diversities appear in all the characters fully studied: in number of spines; in length of spines; in number of teeth; in diameter. These characters are not all bound together; while the number of spines depends at least partly on the diameter, the number of teeth, the length of spines, and the diameter differentiate independently. Thus arise strains characterized by diverse combinations of characters. The hereditary variations are not rare, but arise frequently; in extent they may be either minute, or very considerable.

DISCUSSION

Interpretation of the results with Difflugia

Our study of *Difflugia corona* has thus led to results differing from those that may be called typical for uniparental inheritance. A single strain, descending by fission from a single ancestor, gradually differentiates into strains that are hereditarily diverse; so that through selection within the stock one may isolate many such strains, hereditarily differing in many ways.

How is this result to be interpreted?

As set forth in our introduction, the present work was designed as a test for the adequacy of the results hitherto reached in the study of uniparental inheritance, a test that would meet the criticisms hitherto made, by employing an organism not open to those criticisms. In this favorable organism, as we have seen, the results are the opposite of those commonly reached; gradual hereditary differentiation occurs. The direct, simple and natural conclusion is that the experiments have supplied precisely the test they were designed to supply, and have given clear results. By working with clearly marked characters, by excluding growth stages and environmental modifications; by basing selection entirely on congenital characters, and continuing it through a great number of generations, we have found that in these organisms the genotype is not constant, but changes by slow gradations, such as would not be revealed by imperfect selection for a few generations.

There are of course various possibilities that avoid this logical conclusion. These all amount, in one form or another, to the general proposition that the conditions in Difflugia are in some way exceptional, so that it gives results not typical for other organisms; that it is for this reason that it gives the unusual results; not because its characters are definite and not changed by growth nor by environmental action, so as to be most favorable for such work.

Particular aspects of this general proposition will be taken up below; here I wish to say a word as to it in its general form. In view of the very large body of evidence against the gradual change of the genotype during uniparental reproduction, the contention that our results with Difflugia are not typical seems to have much plausibility; they present after all one positive example against many negative ones.

Yet I am bound to say that after working both with characters that are altered by growth and environment (in Paramecium), and again with congenital characters, not so altered (in Difflugia), I am inclined to give much weight to this difference. The criticisms of negative results as due to the fact that the characters worked with are largely the expression of the particular growth stage of the organism, and its environment up to the time studied, take on much weight when one sees, on the one hand, how long it may require for selection to give an inherited effect even with congenital characters (witness the results with number of spines in our experiment with family 326); on the other how extremely marked the results in time become with such congenital characters (as shown in figure 19 and table 72).

To take up more specifically the possibilities of other explanations of the results in Difflugia, the following points may be set forth. Most of these have been suggested to me orally in discussions of these results.

1. We do not know the mechanism of inheritance in Difflugia. Possibly the characters studied are due to peculiarities of the cytoplasm that are handed on through fission; not to the nucleus, which we have reason to believe in most organisms contains the diversities that result in hereditary diversities. Thus the results in Difflugia may differ in principle from what we find in higher organisms.

This may of course be true, so far as we know. In this case we should have in Difflugia an organism in which the cytoplasm in place of the nucleus is the "organ of inheritance;" i.e., is the seat of the diversities that give rise to diversities in the next generation—at least during vegetative reproduction. It would require us to assume that the nature of the cytoplasm is for many generations independent of that of the nucleus; in view of the known continued interaction of nucleus and cytoplasm this seems rather improbable.

2. The nucleus in the rhizopods is known to be of a somewhat diffuse character, in that large masses or networks of nuclear material are given

off to the cytoplasm, where they may be found distinct from the main nucleus. Such separated portions are known by various names, perhaps most commonly as chromidia. In fission or spore formation the new nuclei may be formed by condensation of parts of these free networks. (A general account of this matter will be found in CALKINS's Protozoölogy, 1909). These matters appear not to have been well worked out for Difflugia, though the work of ZUELZER (1904) shows that such chromidia are prominent features of the structure of *Difflugia urceolata*.

Assuming that these chromidia play the same part in the reproduction of Difflugia that they do in other rhizopods, it appears that we have in these structures a much less definite, less precisely operating apparatus than in the nucleus of higher organisms. It would appear therefore that the substances determining the hereditary characters may be distributed with less accuracy than in higher organisms, so that the two products of fission may often receive parts that are not equivalent. As a result, the two products of fission would differ in hereditary characters; and in time diversities of strains would be brought about such as are described in the present paper. The possibility that this is the state of affairs is entirely open, so far as our present knowledge is concerned.

3. In many lower organisms there occur unions between different nuclear masses existing in the same individual, this process being known as autogamy. So far as we know, such processes may occur in Difflugia. Furthermore, it is possible that such processes are accompanied by a redistribution of the substances or units concerned in heredity, such as we know may occur in self-fertilization in higher organisms. If this is the case, then hereditary diversities might be produced in this way. If, however, the units are definite and exist in certain precise numbers, as in higher organisms, then of course the production of hereditary differentiations in this manner would be strictly limited; by repetition of the process a condition of homozygotism would in time be produced, after which no further hereditary differentiation could be brought about in this way. (For the rate at which homozygotism would be thus produced, see my paper of 1912). If there are no definite units in definite number, the condition of affairs differs so greatly from that in higher organisms that it is hardly worth while to bring in the idea of a possible autogamy to account for the hereditary differentiations observed. Either condition of affairs may exist in Difflugia, so far as our knowledge is concerned.

With relation to all these possible conditions certain considerations are pertinent. First, it must be remembered that they are mere possibilities, having no claim to greater probability than their negatives, so far as our knowledge of the facts is concerned. We are, in Difflugia, as in most organisms, in great need of further knowledge of the cytological processes and of their relation to the external phenomena of heredity and variation.

Secondly, there can be no doubt that any variations which occur, and any inheritance of these variations, have a material basis somewhere in the organism,—either in the nucleus or the cytoplasm, or in both. Such material basis may lie in the changes suggested above, as well as in any other. The question we are studying is whether such inherited variations do arise within a single stock not mixing with others; whether the genotype of such a stock is changeable and what the nature is of any changes that do occur. If the nucleus in Difflugia may vary gradually, it has the properties attributed to organisms in general by old-fashioned Darwinism.

Furthermore, it must be recalled that the concept of the genotype,—the idea of the permanency of the hereditary constitution,—has been based in large degree on observation; on the fact that organisms in uniparental reproduction have been observed to remain constant in hereditary constitution. It is an extension of the observational basis for these ideas that is sought in the present paper. If the observational basis shows itself inadequate or misleading, the foundation of these ideas is to that extent undermined. The genotype is considered constant because it was observed to be so. In Difflugia under the same conditions it is observed not to be so. The latter fact seems to require consideration in any general view equally with the former. In final analysis what we desire is a generalized statement of the observed facts.

At the same time we must of course not assume that the conditions are the same in all organisms. While Difflugia is an organism, and the conditions there found must be recognized in any general theory, it seems not improbable that in more complex organisms the germinal material is more definitely localized, more completely protected from exterior influences, and manipulated in a more precise way, so that inherited changes are less readily brought about. But it is difficult to believe that the difference is anything more than one of degree.

This leads naturally to a consideration of the question of the nature of the hereditary variations observed in Difflugia. The question is asked whether even such slight and seemingly gradual hereditary variations as are here described may not really be essentially discontinuous in nature (and therefore "mutations"), in the sense that they involve chemical change,—since all chemical change is discontinuous. This appears to illustrate the fact that the question of continuity or discontinuity in the nature of hereditary variation is not one of observed fact. There is no change so slight that it might not be chemical in nature. In the immense organic molecule, with its thousands of groups, a simple transfer of one atom, one ion, perhaps one electron, is a chemical change, and perhaps therefore discontinuous, even though its effect is below our perception with the most refined instruments. My observations certainly have no bearing on the question of continuity or discontinuity in this sense. I personally consider it highly probable that any inherited variation does involve a chemical change.

If, however, we are interested in the observational question whether all hereditary variations consist of large or sudden steps that are later inherited in full, then the facts in Difflugia are worthy of notice. In this animal the inherited changes seem as gradual as could well be observed. Large steps do occur, but much more frequent are very slight inherited changes, not fully inherited, and giving a slow alteration of the stock with the passage of generations.

May not the difference in this respect between the large inherited variations commonly observed in higher organisms, and the minute ones of Difflugia be due to the long and complex development through which the former pass? A minute difference produced in the germ cell would affect generation after generation of the differentiating cells of the developing metazoan body, so that in the adult a great mass of cells would be affected, and the variation observed would be a large one. In Difflugia there is no opportunity for such reduplication and reinforcement of the original slight variation of the germinal material; the inherited changes are therefore even in their visible impression minute in extent.

Other work indicating hereditary variations in uniparental reproduction

It is not necessary to again review the work on inheritance in uniparental reproduction; this has been done many times of late. Those not familiar with the situation may consult JOHANNSEN's general text-book (1913). Most of the work on uniparental reproduction, as is well known, has yielded the result that during such reproduction the hereditary constitution (genotype) appears not to change,—all the descendants of a given individual retaining the same hereditary constitution (as determined by the results of further breeding), though they may differ much in their outward characters. Many papers that have appeared since the general summary in JOHANNSEN'S textbook (1913) have strengthened this presentation of the case; notably those of AGAR (1913, 1914), EWING (1914 a, 1914 b), LASHLEY (1915, 1916).

On the other hand, in view of the divergent results given in the present paper, it may be worth while to summarize briefly certain work which appears to be opposed to the constancy of the genotype in uniparental reproduction.

CALKINS and GREGORY (1913) conclude from their experimental cultures of the descendants of ex-conjugants in *Paramecium caudatum* that the four individuals ("quadrants") derived by the first two fissions of an ex-conjugant are often hereditarily diverse; so that the four stocks derived from four such quadrants frequently show hereditary diversities in size, rate of fission, and other characters. This has been hailed by CASTLE (1914 a) as overthrowing my own results (1908) as to the constancy of the hereditary constitution in the uniparental reproduction of Paramecium. The work of CALKINS and GREGORY, taken by itself, seems hardly to warrant all that seems implied by so sweeping a conclusion, as will appear when two points are considered: (1) The first two fissions after conjugation are, as is well known, of a most exceptional character. After conjugation four new macronuclei are formed, from four micronuclei produced in the conjugation processes. In these first two fissions these four macronuclei become separated, one into each of the four quadrants. According to the results of CALKINS and GREGORY, these four macronuclei may be supposed to possess diverse hereditary constitutions, since the stocks derived from them by ordinary fission may be thus diverse. If such hereditary diversities appear only in these first two fissions, when these four macronuclei are separated, and not in the later fissions, it would appear that the diversities are strictly an immediate consequence of conjugation (which I had already shown to give rise to hereditary diversities within a single stock). So far as I can discover, CALKINS and GREGORY *make no claim that they show such hereditary diversities to arise in the later fissions.* Indeed they state expressly that after the diverse lines are once produced, they remain constant in hereditary characters (—"a single ex-conjugant gives rise to varied progeny in the form of pure lines, *each line remaining true to its type for many months at least,*" p. 508). Their results therefore can not be cited as evidence that the hereditary constitution changes during the ordinary vegetative reproductions, independently of the peculiar immediate results of conjugation.

(2) The second point relates to the evidence on the question of fact. In my own work I set forth that slight initial diversities in bacterial content of the culture media of separate stocks were readily perpetuated, causing diversities that simulated hereditary diversities. Diversities due to this cause were, I found, inevitably produced unless one took most elaborate precautions to avoid these environmental diversities. These precautions involved changing the culture material every 1-3 days; washing the animals thoroughly at each change, sterilizing the pipette after every transfer of an individual, and employing elaborate methods for making all drops of the culture medium uniform (see JENNINGS 1913, p. 345). When this was done, no hereditary differentiation could be observed within a single stock, as I showed by extensive statistical records; while if these precautions were omitted, constant diversities between stocks were found.

Now, CALKINS and GREGORY paid no attention to these precautions, so far as their account sets forth[1], and they found between their lines just such differences as were to be expected when these precautions are omitted.

I do not, therefore, feel convinced that they have given any demonstration that the diversities produced were really hereditary (in the sense that differences between progeny are due to preceding diversities between parents and not to diversities of environment in the several lines). Indeed, apparently they are themselves inclined to hold that the differences in size are not really hereditary, ("It is quite evident that the variations in size have little or no value in heredity since all came from the same ancestral cell", p. 513; see also the line of argument in pp. 512, 521, and 523.) It is not clear to me just what is the conception of heredity in the mind of the authors, but they appear to have made out no clearer case for the heredity of other characters than of size, even in case of the four quadrants derived from one ex-conjugant. It

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[1] Indeed it is a remarkable fact that in their discussion of the relative variability in a stock that has conjugated as compared with the same stock that has not, they do not so much as mention my experiment 15 (JENNINGS 1913, pages 343-355), wherein these precautions are set forth, and an extensive and fully worked out experiment is described in detail, giving results which demonstrate that conjugation produces extensive inherited variation within a single stock. The differences between the stock that has conjugated and the same one that has not conjugated are shown to be extraordinarily great; in the former many lines hereditarily diverse in a high degree are found; in the latter none.

is of course quite possible that such hereditary diversities do occur, but it appears that further tests with conditions controlled in the manner I described are necessary to demonstrate these.

In the work of Miss STOCKING (1915) on hereditary abnormalities in Paramecium, it was shown that during vegetative reproduction differentiations occur as to these abnormal characters. A portion of the stock may become quite free of them, while other parts retain the abnormalities in varying degrees. Selection was thus effective in breaking up a single family into hereditarily diverse branches. The characters in this work were so extremely marked (consisting often of complex monstrosities and deformities,) and so nearly independent of the environmental conditions, that no doubt can arise as to the reality of the hereditary differentiations within a stock. On the other hand the fact that the characters were abnormal ones, and the possibility if not probability that they were expressions of abnormal nuclear conditions, lead to the suspicion that the hereditary differentiations may have been due to abnormal nuclear processes. If this be the case, while they would be of great interest in themselves, they could not be used in judging as to what occurs in normal reproduction.

It is otherwise, however, with the results of MIDDLETON (1915); here hereditary differentiation was found to occur in Stylonychia, in what must appear to be precisely the normal course of events in vegetative reproduction. When an individual divides into two, which we may call *a* and *b*, it often happens that *a* divides again before *b* does. By selecting, for long periods, in one set at every fission the individuals that divide first; in another set the individuals that divide latest, MIDDLETON was able to separate the single stock into two that differed characteristically in their rates of fission. The hereditary diversities appeared gradually, and became greater as selection was continued longer; they persisted for long periods after selection had ceased. The work of MIDDLETON was carried on with all the precautions mentioned on page 528 as necessary for securing uniformity of conditions. In the fission rate MIDDLETON has found a character most favorable for study of the effects of diverse procedures on a hereditary feature, and the facts attained thus far are clear. MIDDLETON's work is certainly one of those requiring most careful consideration by upholders of the constancy of the genotype, and of the appearance of hereditary variations only as sudden mutations of considerable extent.

Much work with bacteria has tended to show that in these organisms inherited variations occur frequently during vegetative reproduction.

One of the best of the studies along this line is the paper of WOLF (1909); a review of the entire subject is given by PRINGSHEIM (1910). Biologists outside the field of bacteriology have been inclined to attach less weight to these results than their face value would seem to demand, because of the known very great difficulties in obtaining and keeping a really pure pedigreed stock in such organisms, and the fact that in some cases where this was done (e. g., BARBER 1907), the bacteria showed the same constancy that was observed in other organisms. Possibly the discovery that gradual differentiation does occur within the family in other organisms where pedigrees are readily kept pure may warrant emphasizing more heavily the results obtained with bacteria.

In another group of organisms, the recent most interesting work of STOUT (1915) on Coleus has given striking results. In this variegated plant selection of varying portions of the parent body and the propagation of these parts by vegetative means led to the establishment of great numbers of stocks differing hereditarily in color, pattern, and the form of the leaves. The results are in many respects parallel to those set forth in the present paper for Difflugia; thus the characters dealt with are mainly congenital ones, little affected by growth or environment; selection was effective on a number of diverse characters; and different combinations of these characters could be obtained in the different stocks derived from a single parent.

SUMMARY

1. The rhizopod *Difflugia corona* shows a number of very definite characters that are congenital, not modified by growth, and not affected by the environmental conditions during the life of the individual; these are therefore remarkably favorable for studies of inheritance. These characters are: (1) The number of the spines on the shell; (2) the length of the spines; (3) the diameter of the shell; (4) the depth of the shell; (5) the number of teeth surrounding the mouth; (6) the diameter of the mouth.

A. Populations

2. In a population found in nature the individuals differ among themselves with respect to all these characters.

3. The different sets of characters of the individuals are statistically correlated, in such a way that in large populations an increase in any one of these characters is accompanied on the average by an increase in the others.

4. When a population is allowed to propagate, the characters of the parent are inherited in a high degree by the progeny. Coefficients of correlation between parent and progeny rise even to .9 with respect to some of the characters. The parent-offspring correlation for given characters is diverse in different populations.

B. Diverse strains

5. Following the pedigrees of descendants of given individuals, the populations are found to consist of many hereditarily diverse strains. The heritable characteristics of any given strain or family show a high degree of constancy through many generations, though the individuals within the strain may differ greatly in their personal characters. If two diverse strains are compared, they remain constantly diverse through many generations.

6. The different strains show hereditary diversities with respect to all the six sets of characters enumerated in paragraph 1; also with respect to the way these characters are combined. A strain that shows one of the sets of hereditary characters in a higher degree (for example a large number of spines), may show another one in a low degree (e. g., the measure of the diameter); in other strains the reverse combination may be found. Thus the positive correlation of all characters set forth in paragraph 3 is only the expression of an average condition, which may not hold when particular strains are compared. The combinations of hereditary characters distinctive of particular strains therefore can not be accounted for as due merely to the difference in some one underlying character (as for example the size of the body).

C. Inheritance within the single family

7. When a single family is studied by itself (all the individuals being descended by fission from one original parent), a considerable degree of correlation between parent and offspring is still found to hold for most characters. Thus within the single family the offspring resemble their immediate parents more than they do more distant members of the family. In some characters (e. g., the number of teeth, often also the diameter), the correlation of parent and offspring within the single family is very high (at times .5 or more).

8. In some cases this high correlation is not due to inheritance of parental diversities, but to a mere steady increase in size from generation to generation (family 305, page 467). But in most of the families neither this nor any similar explanation can be given; the correlation is due to the inheritance of parental diversities.

9. Selection for diversities within the single family was carried on in two large families, one (No. 303) including 495 descendants of a single individual; the other (No. 314) including 1049 descendants of the original parent. In both these families selection was effective. To avoid any masking effects due to similarity of environment for parent and immediate progeny, the experiments were divided into short periods, and the progeny for the two diversely selected groups compared for each period. In every period in both families parents with high numbers of spines produced progeny with more spines than those produced by parents with low numbers of spines. Similar relations hold for the inheritance of the diameter of the shell; larger parents produce larger progeny. In family 303 the length of the spines was studied, and similar relations found to hold; longer-spined parents produce longer-spined progeny. Diversities of the parents in number of teeth are inherited by the progeny in a still higher degree than diversities of the other characters.

10. After the results set forth in paragraph 9 had been reached, a much more extensive experiment in selection was carried on with the family No. 326, in which 4644 descendants were studied from a single progenitor. In this family selection was carried on in one set with reference to the number of spines; in another with reference to the size of the animal; in another with reference to the length of the spines. In all these respects selection was effective. With respect to the number of spines selection acts slowly; with respect to the other two characters its action in producing diverse stocks is much more rapid. Number of spines and size were found to be correlated, so that it is not clear that these two characters are acted upon independently in selection. But length of spines is not correlated with the other two, so that hereditary diversities in length of spine are brought about independently of changes in size and number of spines.

11. After many generations of selection the family becomes much diversified with respect to the characters selected, so that the coefficient of correlation between parent and offspring may become almost as high as in populations. Thus in size (diameter of the shell) the coefficient of correlation between parent and offspring rose in family 326 to .605 ± .009, and in length of spines to .340 ± .017. In the case of parents selected for long and short spines, the correlation with the progeny in this respect was .426.

12. In respect to all these characters (number of spines, size of body, length of spines), parents that deviate from the general mean produce

progeny that deviate from the mean in the same direction as the parents, but to a less extent; regression of the progeny toward (but not to) the general mean occurs. Thus it is clear that the inheritance of size is not due to a mere halving of the protoplasmic mass, for the progeny are less divergent from the mean than the parents.

13. The variations which are inherited in later generations are sometimes considerable in extent, so that they may be characterized as saltations (or mutations, if these be defined as marked inherited variations). But most of the inherited variations are very slight; parents which diverge a very little from the general mean transmit their peculiarities as do those that diverge greatly from the general mean. Thus the change of hereditary character in the stocks appears to be gradual.

14. After many generations of descent from a single progenitor, such a single family as No. 326 has differentiated into many hereditarily diverse stocks. These diverse stocks differ hereditarily not only with respect to particular single characters, but also with respect to the combinations of characters. Thus, in some of the stocks the individuals are small with small spines, in others small with large spines, in others large with small spines, etc., so that different sets of characters differentiate independently. Parts of six such diverse stocks, all descended vegetatively from a single progenitor, are shown in figure 19, page 520.

15. Thus in general the investigation shows that in *Difflugia corona* a population consists of many hereditarily diverse stocks; and that a single stock, derived by fission from a single progenitor, gradually differentiates into such hereditarily diverse stocks; so that by selection marked results are produced.

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