XI. *Experiments on Inheritance in Parthenogenesis.*

By W. E. Agar, *University of Glasgow.*

Communicated by Prof. J. Graham Kerr.

(Received June 2,—Read June 25, 1914.)

Contents.

Introduction and Terminology.

Johannsen's work on inheritance within "populations" of beans, extended as it has been by subsequent workers, forms a fitting complement to the Mendelian hypothesis, and the two conceptions together have enabled our knowledge of genetics to increase by leaps and bounds. The object of the present work, which was begun some years ago and which has extended beyond the limits at first planned, was to

[Published separately, October 23, 1914.

investigate inheritance within parthenogenetic animal populations from the point of view of JOHANNSEN'S well-known work. The terminology adopted is accordingly in agreement with that introduced by him, in spite of the fact that some objections have been raised to the use of the word genotype in JOHANNSEN'S sense, on the grounds of its prior usage with a different meaning by systematists.

Where it is necessary to express the group of individuals descended asexually (in our case parthenogenetically) from a single ancestor, the word *clone* has been used, following SHULL. As this author points out, the extension of JOHANNSEN'S term pure line to include groups of individuals related in this way is not legitimate. It must be distinctly understood that a genotype, and hence the individuals forming a biotype,* need not be homozygous as long as they all have the same factorial composition. In sexual reproduction such heterozygous biotypes are easily recognised on breeding, but in asexual reproduction where Mendelian segregation is not taking place, they cannot be distinguished in this way from homozygous ones.

When a population is known to have been descended asexually from a single common ancestor, it consists of a single clone and may be described as *monoclonal.* When on the other hand it is composed of a number of clones each descended from an original ancestor not asexually connected with the original ancestors of the other clones, the population may be called *polyclonal.*

HISTORICAL.

Although they do not deal with asexual inheritance, and although they have become almost as classical as MENDEL'S own, it will be convenient to begin with a brief review of certain of the evidence on which JOHANNSEN'S conclusions were based. This is presented in his publication 'Ueber Erblichkeit in Populationen und in reinen Linien,' 1903, and elaborated in his text-book of 1909. Confining ourselves to his experiments on *Phaseolus vulgaris*, the original material for his experiments was a sample of beans bought in 1900. From these was descended his "population," consisting, since the bean is self-fertilising, of as many pure lines as there were ancestral beans. Two characters were measured—weight of the bean and the ratio between its width and length. The experiments on the former were the most extensive, and (1) he found that, treating the population as a whole, the distribution of the variants followed closely the normal curve and that inheritance was of the usual type for such characters, the deviations of the parents being partially inherited by the offspring with regression to the population mean. The correlation between parent and offspring was given in 1909 as $0{\cdot}336 \pm 0{\cdot}012$. (2) On the other hand, when single pure lines were considered separately he found, that though the distribution of the variants round the mean also followed the normal curve, the inheritance was of quite a different type, the correlation between parent and offspring

* A biotype being a group of individuals of the same genotype.

being in fact *nil.* This is to say, considering a pure line as a population by itself, the deviations of the parents from the population mean were not inherited at all. In 1909 he gives the correlation between parent and offspring for such a population of 712 beans, all descended from a single ancestor, as $-0{\cdot}018 \pm 0{\cdot}038$, *i.e.* of no significance; (3) he also showed the non-inheritance of variation within the pure line by selection. In his 1903 paper he gives the effects of selection for one generation, in 19 pure lines. The results are summarised in his "Übersichstabelle 4," in which are included 574 parent seeds belonging altogether to 19 pure lines, together with their 5494 offspring. The parent seeds are divided into two classes, plus and minus variants from the means of their respective pure lines, and it is shown that the mean weight of the offspring of all the plus variants is to that of the offspring of the minus variants as 98·5 : 100·9. That is, in the total the plus variants had actually rather smaller offspring than the minus variants. In his book of 1909, chapter X, he gives the results of several selection experiments within pure lines, carried on on a sufficiently large scale for six generations, with the same negative results.

JOHANNSEN'S original paper was subjected to severe criticism by WELDON and PEARSON (1903). The most important point which they establish by re-treatment of JOHANNSEN'S own data is a diminution of the correlation coefficients as we pass back from parent to grandparent in the mixed population. They found the values as follows for the weights of the beans:—

Parental correlation . . .	$0{\cdot}3481 \pm 0{\cdot}0080$
Grandparental correlation . .	$0{\cdot}2428 \pm 0{\cdot}0086$

Now, in the case of a population reproducing itself sexually, a diminution of the correlation as we rise in the scale of ancestry is quite in consonance with JOHANNSEN'S theory when the correlations are found for complex somatic characters. For these are dependent upon the interaction of several different factors or genes, and consequently the shuffling of these which takes place at each conjugation of gametes must result in a diminution of the intensity of resemblance between individuals and their more remote ancestors, even though the genes themselves do not vary.

WELDON and PEARSON, however, rightly insisted that to find a similar diminishing of the coefficients in a population such as JOHANNSEN'S was contrary to the expectations from his conclusions. For if variations within a pure line are not inherited at all, but the genetic constitution of the offspring in any line is determined solely by the type of that line and not by the characters of any particular ancestor, it follows that the correlations between any two generations, whatever their remoteness from each other, should be approximately the same, being determined by the same factor, namely the degree to which the type of the line is obscured by impressed modifications. (If there were no such modifications the correlation would of course be unity, whatever the remoteness of the ancestry.)

However, the significance of the relative values of a single pair of correlation

coefficients is small, since as we shall see later the apparent intensity of inheritance may vary greatly from generation to generation according to variation in the amount of disturbance caused by environmental modification.

In 1899 WARREN published an account of some experiments on parthenogenetic inheritance in *Daphnia magna*, the character used being the ratio

$$\frac{\text{length of protopodite of antenna}}{\text{length of body}}.$$

The research was of a preliminary nature only, and only very small numbers were used. He obtained the results—

Parental correlation . . .	$0{\cdot}466 \pm 0{\cdot}054$	(founded on 23 parents and 96 offspring).
Grandparental correlation .	$0{\cdot}27 \pm 0{\cdot}12$	(founded on 7 grandparents and 26 offspring).

In view of the very small numbers employed for the grandparental coefficient WARREN himself gives this value with all reserve, but so far as it goes it shows a diminution of the correlation coefficient as we pass back from parent to grandparent.

Very similar results were obtained by him in his investigation into variation and inheritance in the parthenogenetic reproduction of the Aphid, *Hyalopterus trirhodus*. The origin of his material was a number of the Aphids from some Aquilegia plants. It is most unfortunate that no information is given about the mutual relationships of these individuals. These specimens, 60 in number, were isolated in separate cages and bred for two further generations, and the parental and grandparental correlation coefficients were calculated for three characters: (1) the distance between the eyes, (2) the length of the right antenna, and (3) the ratio between (1) and (2). The three characters gave very similar results, the values for the ratio, which WARREN thought the most reliable, being—

Parental correlation . . .	$0{\cdot}4392 \pm 0{\cdot}0284$	(60 parents, 368 offspring).
Grandparental correlation. .	$0{\cdot}2305 \pm 0{\cdot}0374$	(30 grandparents, 291 offspring).

The existence of a significant correlation at all, if indeed not due to non-genetic factors as we shall discuss presently, must mean, granting the generality of JOHANNSEN'S conclusions, that the 60 original ancestors comprised two or more biotypes. But again we meet with the diminishing value of the coefficient as we ascend the scale of ancestry, the significance of which point as evidence against the genotype hypothesis was again emphasised by PEARSON in 1910.

The next work to be considered is JENNINGS' experiments with *Paramecium* (1908). These extensive experiments led to the same conclusions as those of

JOHANNSEN. We may select a few representative illustrations from the wealth of material presented by JENNINGS. A "wild" culture of *Paramecium* was brought into the laboratory, and from it were isolated six conjugating pairs and two ex-conjugates. Each of these gave rise to a clone cultured synchronously under as far as possible identical conditions. Eight clones were cultivated from these parents, and after a few days 100 individuals from each were measured. Three weeks later similar measurements were made, and he concludes from the results, summarised in his Table XXV, that these eight clones included at least six separate biotypes, which had retained their characteristics (size) for the considerable number of generations which had elapsed between the two sets of measurements. To find six biotypes represented among a sample of eight parents is a most suggestive hint of the enormous genetic diversity existing in natural populations, and this we shall meet with again in my own experiments.

Again, other clones maintained their characteristics without selection for 90 or 100 generations, measurements being taken of representative samples at intervals.

Thus the size differences among the individuals of a natural population of *Paramecium* are inheritable, and there is no doubt that, if a correlation table had been constructed, we should have found typical inheritance with regression to the population mean brought about in the same way as in JOHANNSEN'S population.

When, however, we turn to the conditions obtaining within a clone, we find things very different, and again corresponding with JOHANNSEN'S experience. The variations within the clone appear to be non-inheritable modifications only, as shown by the negative effects of selection. JENNINGS (5) records several such experiments on pp. 505–511, some showing the result of a single, some of repeated selection, but with an average negative result, in sharp contrast to the results of selection within the mixed population.

ELISE HANEL, 1908, investigated the inheritance of the number of tentacles in *Hydra grisea* in asexual reproduction. The number, which changes with age, was taken as the number present when the Hydra liberated its first bud. The experiment dealt with a population composed of 26 clones, which, however, were not cultivated synchronously, but we are told that they were bred at intervals over a period of two years, the population evidently being synthesised by massing together the records at the end. While this experiment must be considered less satisfactory than those recorded above, the conclusions which the author draws are in accordance with those of JOHANNSEN. Considering the population as a whole, the number of tentacles is inherited to a small degree, but considering each clone by itself, not at all. This latter point was tested by selecting within each clone the individuals with the greatest and least number of tentacles, the results being negative.

PEARSON, in 1910, published a trenchant criticism of the work on which the genotype hypothesis was founded at that date, subjecting HANEL'S work to a specially detailed examination. The part of this criticism which concerns us chiefly

flows from his subjection of HANEL'S data to statistical treatment. He finds that, dealing with the whole population, the correlation coefficients are as follows :—

Parent and offspring	$0{\cdot}230 \pm 0{\cdot}011$
Grandparent and offspring.	$0{\cdot}030 \pm 0{\cdot}016$
Great-grandparent and offspring . .	$0{\cdot}059$

Thus the parental correlation is much higher than that for the more remote ancestry, though, indeed, the coefficients do not form a progressively diminishing series. As PEARSON points out, however, the absolute values of the coefficients are not very reliable, the experiment not having been planned with a view to providing material for determining the correlation coefficients. Still, it is enough to show that the individual characteristics of the parents have more influence in determining those of the offspring than have those of the more remote ancestry.

Thus, as PEARSON pointed out, in all the four works at that date bearing on the genotype hypothesis presenting data which could be treated statistically (*Phaseolus*, *Daphnia*, *Hyalopterus*, *Hydra*) we find the same thing, namely, that inheritance is stronger from the parent than from the grandparent, and therefore that the individual characteristics of the parent, and not exclusively those of the clone or pure line, do seem to determine to some extent the characteristics of the offspring.

WOLTERECK (especially 1909, 1911) has carried out extensive experiments dealing with the genetics of Cladocera under parthenogenetic reproduction, but by somewhat different methods. The records of his prolonged experiments contain many interesting and important results, but I confess that I am unable to appreciate the argument which he draws from them in favour of the change of one genotype into another by a gradual continuous process. He finds that certain "elementary species," which are scarcely distinguishable under some conditions, are very distinct under others, and considers that this is proof that they arose from one another by a continuous process of change, and not by a mutation.

MATERIAL.

The material used in my own investigations consists of four species which commonly reproduce parthenogenetically, namely, the three Cladocera, *Simocephalus exspinosus*, *S. vetulus*, and *Daphnia obtusa*, and the Aphid *Macrosiphum antherinii*. The Cladocera were chosen because I had already become well acquainted with the bionomics of these species in captivity, and the Aphid was selected in order to test WARREN'S *Hyalopterus* results. The case of *S. exspinosus* was the most thoroughly worked out, and therefore I will present it first, though the work was actually done after that on the other two Cladoceran species.

In order not to interrupt the description of the experiments unduly, the tables in the text have been limited to the summaries needed for the argument. The full tables on which these summaries are based appear in Appendix II.

The labour of reducing the large bulk of data dealt with in the various experiments has been greatly lessened by the use of a Layton's Arithmometer, lent for the purpose by the Trustees of the Carnegie Trust for the Universities of Scotland.

Experiments with Simocephalus.

Breeding Methods.

The methods of breeding were the same as those used for the experiments with *S. vetulus* described by the author in 1913–14. The animals were kept throughout in cylindrical glass tubes, 10 × 3 cm., when corked containing about 50 c.c. of water and 15 c.c. of air. One individual only was kept in each tube, and when a mature specimen produced a brood of young, this was removed and measured within 24 hours (with insignificant exceptions). The culture medium used was, as before, the water from a heated tank containing living *Lepidosiren paradoxa* fed daily with *Anodonta*. The water in this tank, which is changed weekly, contains a large amount of organic matter and infusoria, and has proved an excellent medium for cultivating Cladocera of various species. A large jar of water was taken from this tank on alternate days and strained through linen to avoid all chance of infection with foreign strains of *Simocephalus* (though, as a matter of fact, none were ever observed in the tank). The jar of tank-water was then brought into the room in which the breeding tubes were kept, in order to bring it to the same temperature, and on the day following it was used to renew the water in the breeding tubes. The Simocephalus was picked out of the tube with a pipette, the water poured away, and then the animal returned and fresh water added. The vessel containing the tank-water was well shaken up before filling each tube, so that every Simocephalus was provided on the same day with approximately the same amount of a practically identical medium. Before using an old tube for a new specimen it was always well sponged out and sterilised by heat in order to remove bacterial growth from the sides. By these means it was hoped to keep the conditions under which the animals were living as nearly identical as possible for them all, and to insure that should any slight differences develop among the tubes, these should be equalised the next time the water was changed, that is, every other day. The tubes were kept in a rack in the laboratory, and their relative positions changed daily in order to distribute equally any slight differences in light intensity, etc.

Some Points in the Biology of Simocephalus bearing on the Experiments.

In my paper of 1913, certain points in the biology of *S. vetulus* were discussed, which have some bearing on these experiments. They need only be briefly recalled here. The eggs are produced in batches or broods, containing from one to about thirty eggs, all laid within the space of a very few minutes at most. The oviducts open into a brood pouch, where the development of the young takes place. About four

days after oviposition (at room temperature) the young emerge. At first they are enclosed in an embryonic cuticle, but this is cast off within a few minutes of birth, and the young assume at once a form which in all but details is simply that of a small adult. This condition is called the first free-living instar, or, simply, the first instar. After two ecdyses the "adolescent instar" is reached, in which the first batch of eggs undergo their ovarian growth (yolk deposition). Immediately after the next moult, which introduces the "first adult instar," the eggs are laid. All increase in size takes place immediately after ecdysis. Once the new cuticle has hardened, the dimensions of the animal are fixed for that instar—at least, no further growth detectable by the micrometer takes place.

The supposed dependence of the developing embryo on a nutritive fluid secreted by the mother into the brood pouch was shown not to be a fact.

Characters used in the Experiments.

The character employed in the case of both species of *Simocephalus* was the length of the body measured along its longest line, from the postero-dorsal angle of the carapace to the front of the head. Measurements were made at two points in the life-history, viz., in the first instar, referred to hereafter as the *Birth Measurements*, and in the first adult instar, referred to as the *Adult Measurements*. The measurements were made with an eyepiece micrometer, with combinations of lenses making the unit of measurement in the case of the birth measurements 0·015 mm., and in the case of the adult measurements, 0·042 mm. The experiments required, of course, that all the measurements should be made on the living animal, which for this purpose was put on a slide in a minimum amount of water, so that it was compelled to lie on its side, almost incapable of movement.

Other things being equal, the length varies with the temperature.* At a higher temperature the animal is smaller at all instars than at a lower one. This factor is not of any great importance in these experiments, however, as whatever changes in temperature may have taken place they must have affected all individuals of any group simultaneously. Moreover, variations in temperature were, as a rule, not great, the laboratory being heated day and night by a system controlled by thermostats.

Three characters are closely correlated—size of adult animal, the number of eggs produced by it (first broods only considered), and size of the young produced from these eggs. The latter value is practically the same as the size of the eggs themselves, since the first instar is assumed before the animal has begun to feed. By this is meant an organic, not a genetic, correlation. If we compare individuals of identical genetic constitution, such as those of a monoclonal population (see below), we find that when the size of the adult parent is constant the size of the eggs, as estimated from the size of the young developing from them, varies inversely as

* 'Phil. Trans.,' 1913.

their number. Given the number of eggs to be the same, their size varies directly as the size of the animal which laid them. Given the size of eggs constant, their number varies directly as the size of the animal which laid them.

Table I gives the relation between these three characters as shown by the correlation coefficient (r) between them found for three separate groups of *S. exspinosus* (Generations 2, 4, and 5 of the monoclonal population to be described shortly). The last three columns show the partial correlation coefficients, ${}_a r_{ny}$ being the correlation between the number of eggs in the brood and size of the young developing from them when the size of the adult parent is constant. The partial correlations are naturally higher and more constant than the total correlations. The coefficients for r_{ny} and ${}_a r_{ny}$ are negative because the two things vary inversely, the higher the value of n the lower being that of y.

TABLE I.—Correlation (r) between Adult Measurement of Parent (a), the Number of Eggs laid by it in its First Brood (n), and the Birth Measurement of the Young developing from those Eggs (y), for Three Generations of the Monoclonal Population of *S. exspinosus*.

	No. of broods.	$r_{ny.}$	$r_{ya.}$	$r_{an.}$	${}_a r_{ny.}$	${}_n r_{ya.}$	${}_y r_{an.}$
Generation 2	135	$-0{\cdot}628 \pm 0{\cdot}035$	$0{\cdot}544 \pm 0{\cdot}041$	$-0{\cdot}071 \pm 0{\cdot}058$	$-0{\cdot}70$	$0{\cdot}64$	$0{\cdot}41$
Generation 4	130	$-0{\cdot}345 \pm 0{\cdot}052$	$0{\cdot}368 \pm 0{\cdot}051$	$0{\cdot}298 \pm 0{\cdot}054$	$-0{\cdot}51$	$0{\cdot}53$	$0{\cdot}49$
Generation 5	135	$-0{\cdot}329 \pm 0{\cdot}052$	$0{\cdot}205 \pm 0{\cdot}056$	$0{\cdot}449 \pm 0{\cdot}046$	$-0{\cdot}48$	$0{\cdot}42$	$0{\cdot}56$
Mean . .	—	$-0{\cdot}434$	$0{\cdot}372$	$0{\cdot}273$	$-0{\cdot}56$	$0{\cdot}53$	$0{\cdot}49$

Another important feature about the birth measurements is that they tend to be nearly of the same value for all the members of a single brood. There is much more resemblance between these members than there is between members of the population taken at random. This is found highly marked even in the monoclonal population, where, as we shall see, it cannot be due to a greater genetic resemblance between members of a brood than between any members of the clone, but where it is plainly due to the very similar conditions under which the eggs of any one brood have developed specially during their ovarian growth, but also during embryonic development in the brood pouch. Worked out for a monoclonal population of *S. vetulus*, the correlation between birth measurements of members of the same brood gave the high figure $0{\cdot}822 \pm 0{\cdot}007$.

Experiments with *S. exspinosus*.

General Course of Experiments.

A large number of the fertilised winter eggs or ephippia were collected in January within a few yards of one another in a backwater of the Forth and Clyde Canal in Glasgow. They were dried and placed in this condition on the roof of the laboratory, where they were left for a fortnight. For several days during this period they were subjected to a severe frost. At the end of the fortnight they were put in water again and kept at room temperature. Four days later several of the eggs had hatched, and by the fifth day some hundreds had done so; 84 of the young which had hatched during the night of the fourth to fifth day were taken at random without measurement and placed separately in breeding tubes. Six of them died before reaching maturity, and one was lost in the process of changing the water in the tubes. Of the remaining 77 two were rejected, because at the time that the others produced young they were still immature. Five of the 75 which laid eggs produced no living young, the eggs degenerating in the brood pouch. This is a phenomenon which I have observed occasionally throughout this experiment, but never again in such a large percentage of cases; 70 individuals were thus left, and eight of these failed, owing to death or accident, to leave more than four generations of offspring. These eight are omitted from consideration, except where the contrary is stated, leaving therefore 62 individuals to build up the required population. These 62 constituted the *original ancestors* in the experiment. It should be remembered that the ephippium of *Simocephalus* bears only one egg, so that each of the ancestors came from a separate ephippium.

In due time each of these 62 original ancestors produced its first brood—parthenogenetically—and these young constituted *Generation* 1, and their birth measurements were determined as described above. From each family two individuals were chosen to become the parents of the next generation. Thus two lines of each clone were initiated, which we may call the *a* and *b* lines, 124 lines in all. The two individuals selected to become parents were chosen as being, as nearly as could be determined by a rough mental calculation, the nearest to the mean birth measurement for the whole brood. In the case of broods with more than 10 young, only 10 chosen at random were measured.

Besides being measured in their first instar, those individuals chosen to become parents were again measured in their first adult instar, giving the adult measurements.

This process was repeated in each succeeding generation, with the difference that in future only one specimen from each family was chosen to become a parent of the next generation, except where the individual selected in the previous generation from either the *a* or the *b* line in the clone had died. In this case two members were taken from the surviving line in order to maintain the two parallel lines from each

clone. The specimen selected for parentage was always chosen as having a birth measurement near to the average for the brood to which it belonged.

After the first generation a maximum of five, instead of ten, members of each brood were measured.

In every case, throughout the whole experiment, parents were allowed to produce one brood only, and therefore all specimens recorded belong to the first broods of their parents.

Altogether six generations of this polyclonal population were bred in this way—all of course exclusively by parthenogenesis. That is counting the females which hatched out of the ephippia as the original ancestors, Generations 1, 2, 3, 4, and 5 were bred from them. In Generation 5 one clone was chosen for the second part of the experiment—inheritance within a monoclonal population, and the other 61 clones were brought to an end. In Generation 6 two members of the selected clone were kept as parents, one of which produced eight and the other nine young in Generation 7. These 17 were all kept, and from their first broods (constituting Generation 8) 70 individuals were measured and kept. These 70 are counted as the *original ancestors* of the monoclonal population, which was now bred for five more generations (Generations 1–5), and treated in exactly the same manner as the polyclonal population.

The following is a key to the relationship of the different parts of the experiment :—

62 original ancestors = ex-ephippio females.

Generation 1, „ 2, „ 3, „ 4, „ 5 } of the polyclonal population.

All clones brought to an end except one, which was continued as—

Generation 6.
„ 7.
„ 8 = 70 original ancestors of the monoclonal population.
„ 9 = Generation 1
„ 10 = „ 2
„ 11 = „ 3 } of the monoclonal population.
„ 12 = „ 4
„ 13 = „ 5

Throughout the experiment of course every individual, except the 62 original ancestors of the polyclonal population, was descended from its parent by partheno-

genesis. In the six generations covered by the monoclonal population no sexual forms of any kind were observed, and this clone did not produce any observed sexual forms in any of the preceding seven generations either. In the six generations covered by the polyclonal population, however, eight out of the 62 clones produced one or more males. No sexual females were observed at all during the experiment. The first males to appear were in Generation 2, therefore among the grandchildren of the original ex-ephippio ancestors.

Preparation of the Data for Statistical Treatment.

The methods and units of measurement have already been detailed. So also have the precautions taken to insure the conditions being similar for all individuals. On coming to work out the results, however, it was found that either the conditions had fluctuated more than had seemed likely at the time or that *S. exspinosus* was more sensitive to changes than had been realised. This was shown by the following facts concerning the monoclonal population.

The 70 original ancestors of this population were all born within a period of about 20 hours. As the generations succeeded one another, however, the interval between the birth of the first and last members of each generation lengthened out, so that in Generation 5 this interval had reached the length of four days. It soon became obvious that this was too long a period for the conditions to remain constant enough to avoid serious disturbances. This was shown by the parental correlation coefficients, which for the birth measurements fluctuated round zero but ranged from $+0{\cdot}303$ to $-0{\cdot}356$. It became quite clear that this was due to conditions changing in the interval between the births of the first and last members of each generation. When two generations happened both to be born at a period of improving or deteriorating conditions, then a positive correlation resulted. For the early births of the one generation naturally provided the parents for the early births of the next generation, and therefore both were submitted to similar conditions, while the later members of the first generation became the parents of the later members of the second, and therefore both were subjected to conditions changed in a similar direction from those acting on the early members of the two generations. When, on the other hand, the births of one generation occurred through a period of improving conditions, and the next through a time of deteriorating environment, then for similar reasons a negative parental correlation resulted.

It was therefore necessary to employ shorter periods of time than those covered by the births of a whole generation.

During the experiment, at those times when births were expected, the breeding tubes were examined at intervals of a few hours and all births recorded. The births of each generation were thus divided into a number of groups. The mean birth measurement of each group was determined and a central group containing a large number of

births was selected as a *standard*, and all the birth measurements of the other groups reduced to this standard by multiplying them by the factor

$$\frac{\text{Mean birth measure of standard}}{\text{Mean birth measure of group in question.}}$$

The following example (Generation 2, monoclonal population) will illustrate this :—

	Group 1.	Group 2.	Group 3.
Time of birth	9 A.M.–1 P.M., May 23	1 P.M.–9 P.M., May 23	9 P.M., May 23–9 A.M., May 24
Number of broods	14	32	39
Mean brood mean	48·735	48·955	49·167
Correction factor	1·0089	1·0043	Standard
	Group 4.	**Group 5.**	**Group 6.**
Time of birth	9 A.M.–1 P.M., May 24	1 P.M.–4.30 P.M., May 24	4.30 P.M., May 24–11 A.M., May 25
Number of broods	14	22	14
Mean brood mean	46·093	45·958	47·509
Correction factor	1·0667	1·0698	1·0349

It will be seen that the conditions became more and more favourable for increasing size up to Group 3 and then dropped again. Within the limits of each group, however, the fluctuation due to changing environment is comparatively slight and, as the result will show, has no seriously disturbing effect.

The absolute dimensions obtained in this way have, of course, a somewhat artificial value, but the relative values remain little altered. Any clone or line which tends to produce young above the average size of young produced by other clones or lines under the same conditions will be above the average for the group in which it is found, and after correction in the way described will be proportionately above the mean for the whole generation.

[*Added July* 21.—This process is in fact the same in principle as that adopted when dealing with the inheritance of stature in man. The mean height of females bears to that of males about the proportion 100 : 108, and the heights of all females were therefore multiplied by GALTON by 108 and then treated as male measurements. In the present case we find that the conditions prevailing for Group 1 were such as to make the mean size of the young bear to the mean size of the standard group the proportion 48·735 : 49·167, and therefore the sizes of all the individuals in Group 1 are multiplied by 1·0089 and they are then treated as having been born under the same conditions as the standard group.

Of course the assumption is here made that the difference between the groups is due to environmental conditions and not to genetic differences between the lines or clones composing the different groups. This assumption is justified by the fact that in different generations the successive groups—arranged in order of time of birth—do not bear the same relations to one another as regards the size of the individuals, though the same clones or lines appear in the main in the same grouping in each generation. Thus for example the groups in the polyclonal population, numbered in order of time of birth, when arranged in order of the mean size of the individuals in each group give in Generation 2—4, 5, 3, 6, 2, 1, and in Generation 5—7, 5, 1, 2, 6, 3, 4, and in the monoclonal population in Generation 4—1, 2, 5, 7, 4, 6, 3, and in Generation 5—7, 3, 6, 2, 5, 4, 1. (The increase, in the later generations, of the period between the first and last births of each generation accounts for the greater number of groups in the later generations.)

Finally it must be emphasised that any process which may slightly affect the absolute values of the correlation coefficients may be disregarded for our purposes, for here we are chiefly concerned with (1) the relative magnitudes of the coefficients between offspring and more and more remote ancestry, each generation having been treated in the same way, and (2) the comparison of the coefficients of the monoclonal with those of the polyclonal populations, each population having been treated in the same way.]

Each generation, therefore, both of the polyclonal and monoclonal populations was treated in this way (with the slight modification in the case of the small strain of the polyclonal population, to be referred to later on) both for birth and adult measurements. The measurements thus treated will be referred to hereafter as *corrected* in distinction to the actual or *uncorrected* measurements.

Inheritance within the Polyclonal Population.

Preliminary Analysis of the Population.—We have seen that the original ancestors of this population consisted of 62 ex-ephippio females, each of which was the ancestor of a clone, two parallel lines of which were bred for five more generations.

The death-rate among those individuals selected to become parents, *i.e.* the number dying before laying eggs, was

Generation	1	. . .	0·82 per cent.
,,	2	. . .	2·50 ,,
,,	3	. . .	1·67 ,,
,,	4	. . .	12·50 ,,

The death-rate for Generation 5 cannot be given, as the young were not allowed to grow up. The high death-rate in Generation 4 must not by any means be put down to the number of parthenogenetic generations which had preceded it, but to unknown factors of the environment. This is shown by the fact that the death-rate in the

monoclonal population, which had a much longer parthenogenetic ancestry, was much smaller.

Before beginning the detailed consideration of inheritance within this population it is necessary to inquire into its "homogeneity." It is of course heterogeneous in the sense that it is composed of 62 clones, but is the population as a whole homogeneous in the statistical sense, consisting of a mass of individuals distributed round the mean roughly in a normal curve of distribution, or can it be divided into two or more groups which must be considered separately? After a few generations it became apparent that it consisted of two sharply defined groups, one containing 57 and the other the remaining 5 clones. These will be referred to as the *large strain* (the 57 clones) and the *small strain*, as the former was characterised by the larger size of the individuals. The characters separating the two groups are very insignificant from a systematic point of view, and indeed without statistical methods extending over a number of generations the existence of the two strains would not have been noticed. I sent a few specimens of both strains to Mr. D. J. S. SCOURFIELD, who very kindly undertook to examine them from the systematist's point of view. He communicated the results of his examination as follows: "So far as I can make out there is no marked morphological difference between the larger and the smaller strains, but I think I have detected very slight differences in the armature of the claws and post-abdomen. So far as the few specimens at my disposal are concerned, the slight differences run fairly constant, allowing of course for individual variations. . . . In regard to the question whether the two strains can be regarded as distinct species or varieties, I scarcely think that they can claim even varietal rank. The differences mentioned above, even if confirmed by the examination of large numbers of individuals, are still very minute, and would not, in the ordinary way, be sufficient to found a named variety upon."

The features which make it necessary to separate the two strains for statistical treatment are: Birth measurements, adult measurements, number of eggs per brood, and time taken to reach maturity. The first three of these being correlated, it is natural that they should all differ if one does.

The relation between the two strains for the two characters specially dealt with in this investigation are shown in fig. 1.

It will be seen that the differences in birth measurements alone would not be enough to separate the two strains, but when the adult measurements are considered the two groups prove very distinct. The curves only just meet, the class containing the smallest specimen of the large strain also containing the two largest ones of the small strain. Of course, there is no difficulty in relegating these three individuals to their respective strains, as the line which produced the extreme small specimen of the large strain produced in other generations typical large strain individuals, the same principle applying to the extreme large specimens of the small strain.

Quite as striking as the difference in adult sizes is the difference in the number of

eggs laid. The mean number of eggs per (first) brood for the large strain was 6·6, with a maximum of 16, and for the small strain 3·6, with a maximum of 8.

At room temperature the members of the small strain took about $11\frac{1}{2}$ days to

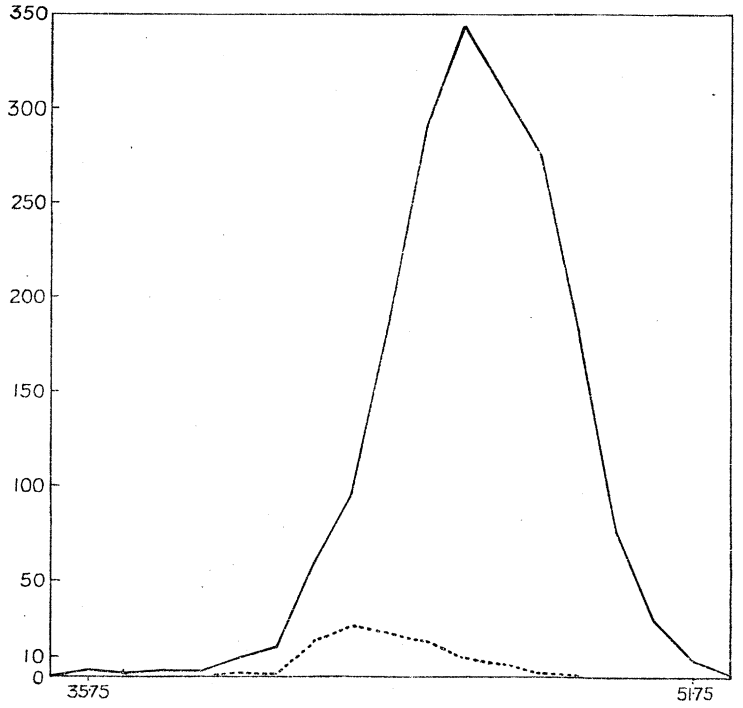

FIG. 1A.

Birth Measurements.
Continuous line = Large strain. Mean = 46·048 ± 0·034. No. of individuals = 1915.
Dotted line = Small strain. Mean = 43·642 ± 0·101. No. of individuals = 102.

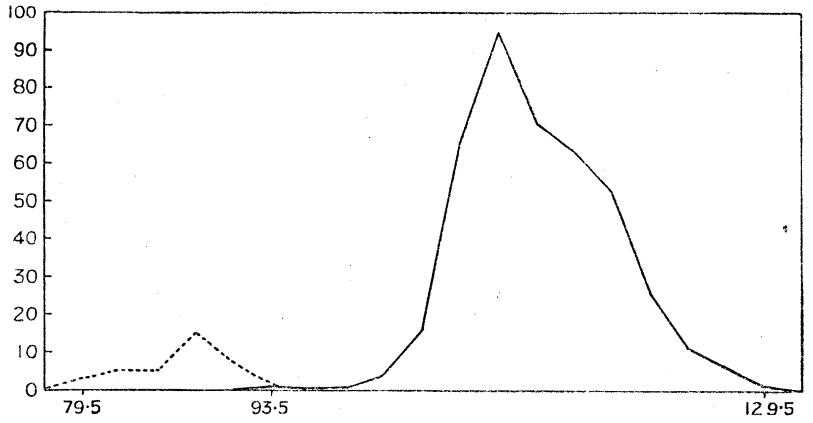

FIG. 1B.

Adult Measurements.
Continuous line = Large strain. Mean = 113·074 ± 0·175. No. of individuals = 411.
Dotted line = Small strain. Mean = 86·975 ± 0·399. No. of individuals = 37.

complete their life-history, those of the large strain about $10\frac{1}{2}$. This, acting in a cumulative fashion through a number of generations, became a striking difference by the time Generation 5 was reached, so that though they started level at the

beginning, in the last generation the small strain was four or five days behind the large one.

Inheritance within the Large Strain.

The large strain, then, consisted of 57 clones, each clone descended parthenogenetically from a separate ex-ephippio female and represented in each generation by two lines *a* and *b*. The original ancestors were not measured, so we are left with five generations measured for birth lengths. From this data it is, therefore, possible to calculate 10 coefficients of correlation between ancestor and offspring for the character birth measurement—viz. four parental, three grandparental, two great-grandparental, and one great-great-grandparental correlation. These coefficients are given in Table II. In the case of the adult measurements we have only four available generations, as Generation 5 was not allowed to become adult. The six possible correlation coefficients are given in Table III. (For full tables, see Appendix II, Tables XXII–XXXVII.)

In reading these tables three points must be borne in mind. (1) In Table II the correlations are not between ancestors and their individual offspring. The mean measurement for each family, consisting of up to five individuals, was found, and each ancestor was correlated with its mean offspring and not with each of its five offspring separately. Moreover, the measurement of each ancestor was not its individual measurement, but was taken as the mean of the brood of which it was a member. This, however, will have little influence on the result, for, as stated above, each individual selected for parentage was chosen as being, so far as could be judged by a rough mental calculation, the most nearly average member of its brood. When therefore the measurements come to be grouped into classes, as is necessary before they can be statistically treated, in the majority of cases of course the actual measurement of the selected individual will fall into the same class as will the mean of the family it was taken from—and if not into that class, then in the next one to it. Therefore, for all practical purposes this table gives the correlation coefficient between ancestors and offspring, but if greater accuracy of definition be required it is the correlation between the mean of a brood in one generation and the mean of the brood produced by its most nearly average member in the other generation. On the other hand, Table III gives the correlation between individual ancestors and their individual offspring. (2) The "number of individuals per family" is the number measured, not the number produced. (3) The "number of ancestors" becomes less in proportion to the number of families of offspring (Table II), or number of individual offspring (Table III), as we rise in the scale of ancestry, owing to the fact, already mentioned, that when in any generation the individual selected for parentage in the *a* or *b* line failed by death or accident to leave a family, two individuals were chosen from the surviving line in the next generation. There is, therefore, a slight convergence of ancestry within a few of the clones.

TABLE II.—Polyclonal Population, Large Strain. Ancestral Correlations for Birth Measurements (corrected).

	Number of ancestors.	Number of families of offspring.	Mean number of individuals per family of offspring.	Correlation coefficient.
Parental correlations—				
Between Generations 1 and 2 . . .	110	110	3·9	0·640 ± 0·038
,, ,, 2 ,, 3 . . .	107	107	4·9	0·339 ± 0·058
,, ,, 3 ,, 4 . . .	105	105	3·9	0·298 ± 0·060
,, ,, 4 ,, 5 . . .	91	91	4·9	0·365 ± 0·061
Grandparental correlations—				
Between Generations 1 and 3 . . .	104	107	4·9	0·447 ± 0·052
,, ,, 2 ,, 4 . . .	100	105	3·9	0·349 ± 0·058
,, ,, 3 ,, 5 . . .	87	92	4·9	0·379 ± 0·060
Great-grandparental correlations—				
Between Generations 1 and 4 . . .	99	105	3·9	0·492 ± 0·050
,, ,, 2 ,, 5 . . .	83	92	4·9	0·323 ± 0·063
Great-great-grandparental correlation—				
Between Generations 1 and 5 . . .	82	92	4·9	0·430 ± 0·057

TABLE III.—Polyclonal Population, Large Strain. Ancestral Correlations for Adult Measurements (corrected).

	Number of ancestors.	Number of offspring.	Correlation coefficient.
Parental correlations—			
Between Generations 1 and 2	104	107	0·423 ± 0·054
,, ,, 2 ,, 3	100	105	0·348 ± 0·058
,, ,, 3 ,, 4	86	91	0·412 ± 0·059
Grandparental correlations—			
Between Generations 1 and 3	99	105	0·436 ± 0·053
,, ,, 2 ,, 4	83	92	0·409 ± 0·059
Great-grandparental correlation—			
Between Generations 1 and 4	82	92	0·505 ± 0·052

TABLE IV.—Polyclonal Population, Large Strain. Summary of Tables II and III, showing Mean Correlation Coefficients.

	Birth measurement.	Adult measurement.
Parental	0·410	0·395
Grandparental	0·392	0·413
Great-grandparental	0·408	0·505
Great-great-grandparental . . .	0·430	—

The general conclusion to be drawn from the two tables is quite plain. There is a very decided correlation between ancestor and offspring, which fluctuates, according as the relative genetic constitutions of the clones are more or less obscured by environmental modifications, but which *shows no diminution as the scale of ancestry is ascended.* This is specially well brought out by the summary Table IV, giving the mean coefficients for the different orders.

It is clear, therefore, that the 57 original ancestors belonged to a number of different biotypes which have reproduced their characteristics generation after generation, so far as they were not obscured by environmental modifications (if these had been absent the correlation must have been unity in each generation). Genetic variation has not been detectable, as is shown by the fact that individuals do not resemble their parents any more closely than they do their great-great-grandparents. The characteristics of the individuals of each generation are determined, apart from environment, solely by the characteristics of the genotype of their clone, and not in any way by the individual characteristics of the parent or any other particular ancestor. The results are therefore in complete accord with the views of inheritance in mixed populations upheld by JOHANNSEN.

There is another method by which we can determine whether there was any inheritance of intraclonal variation. The material for this is provided by the fact that two lines were bred from each clone, so that in each generation a pair of members of each clone was selected for parentage. We can see therefore whether the large members of these pairs had larger offspring than the small members or not.

The number of individuals available for this investigation is less than for the previous one, owing to the fact that of course all those pairs of which the two members were of equal size, or of which one died, had to be rejected. The number left, however, is quite large enough for our purposes. Altogether 135 such pairs could be utilised for birth measurements and 100 for adult measurements. The results are given in Table V.

In reading this table, the following points must be kept in mind :—

(1) The measurements here used are the actual not the corrected ones. Correction was unnecessary owing to the fact that the two lines of a single clone naturally kept nearly synchronous in their development from generation to generation, so that an allowance for conditions changing between corresponding points in their life-history was not so urgent ;

(2) The differences between the large and small parents gives an exaggerated idea of the extent of intraclonal (environmental) variation, owing to the fact that all those pairs of which the members were equal had to be omitted. If they were included, the mean difference between the large and small members of pairs would be much reduced ; 54 pairs had to be omitted from the birth measurements and 28 from the adult measurements because the members were equal ;

TABLE V.—Polyclonal Population, Large Strain. Comparison of Offspring of Large and Small Members of the Pairs of Parents. Uncorrected Measurements.

	No. of pairs of parents.	Mean measurement of large parents.	Mean measurement of small parents.
Birth measurements	135	46·922	45·407
Adult measurements	100	114·675	111·548

	No. of offspring of large parents.	Mean measurement of offspring of large parents.	No. of offspring of small parents.	Mean measurement of offspring of small parents.	Mean of offspring of large parents *minus* Mean of offspring of small parents.
Birth measurements . .	587	46·140	596	46·244	−0·104 ± 0·118
Adult measurements . .	100	113·584	100	113·584	0·000 ± 0·280

(3) The number of offspring is the number measured, not the whole number produced;

(4) Both birth and adult measurements are given in terms of the same unit of measurement, 0·015 mm. (p. 428);

(5) This table included the available pairs from those four clones which are not included in Tables II–IV because they did not survive to Generation 5 (p. 428).

The result of this test is in perfect accord with the conclusions from the ancestral correlation coefficients. Variation within the clones is not inherited. In the case of the adult measurements the average of the offspring produced by the large and small parents was actually the same, while for the birth measurements the large parents had rather smaller offspring than the small parents, but as seen by the magnitude of its probable error, the difference is quite insignificant—that is to say, the offspring of the two sets of parents are to be taken as equal.

It would be very interesting to determine the number of biotypes represented among these 57 clones, but the data are not sufficient for deciding this question satisfactorily. If the clones are drawn up in order of magnitude, it is of course quite easy to separate off those at one end of the scale from those at the other, but they are connected up with such a complete series of intermediates, and transgressive environmental variation is so great, that it is quite impossible to decide where to draw the lines separating clones of the same genotype from those of the next one. Far more than two families of each clone would have to be bred in each generation, or else far more than six generations would be necessary to separate off satisfactorily the various genotypes. The number of biotypes can, however, as we shall see immediately, be estimated to a certain extent in the small strain.

Inheritance within the Small Strain.

As this strain consisted of only five clones, and was therefore represented by at most 10 lines in each generation, the numbers are too small to be treated in the same way as was used for the large strain, and a modification was introduced. Generations 1–4 were taken together (Generation 5 was not measured in this strain), the measurements in each generation being corrected in the same way as in the large strain, with the exception that a whole generation corresponded to a single group on p. 423.

Thus it is only possible to find one correlation coefficient for each degree of ancestry for each measurement, and the numbers were too small to justify the calculation of the coefficient beyond the grandparental for the birth measurements and the parental for the adult measurements.

The three available coefficients are given in Table VI (founded on Tables XXXVIII–XL, Appendix II).

TABLE VI.—Polyclonal Population, Small Strain. Ancestral Correlations. Corrected Measurements.

	Number of ancestors.	Number of offspring.	Correlation coefficient.
Birth measurements—			
Parental	26	76	$0\cdot472 \pm 0\cdot060$
Grandparental	17	48	$0\cdot425 \pm 0\cdot080$
Adult measurements—			
Parental	24	26	$0\cdot598 \pm 0\cdot085$

It will be noticed, on comparing the first two columns of this Table with the first three of Table II, that here parents (or grandparents) are not correlated with the mean of their respective families of offspring, but with each of their offspring separately. Whereas the coefficient in the first line of Table II is founded on the 110 families of 110 parents, in Table VI it is founded on only 76 separate offspring of 26 parents.

The numbers, especially of ancestors, is too small to allow of any value being attached to the precise magnitude of the coefficients. This applies with greatest force to the grandparental coefficient, which is founded on the 48 grandchildren of only 17 grandparents. The slight diminution in the grandparental coefficient, as compared with the parental, is therefore quite without significance, especially when compared with the fluctuations shown in Tables II and III.

The object of Table VI, then, is not to compare the correlation coefficients as we rise in the scale of ancestry, but rather to show that there is a significant ancestral correlation within the small strain. For since, as we have seen and shall still further demonstrate in the next section, intraclonal (intra-biotypical) variation is not inherited, the presence of this correlation shows that the small strain, though composed of only five clones, embraced more than one biotype.

It is possible to estimate the minimum number of biotypes present. On inspecting the records for the small strain throughout the whole experiment it became clear that one clone differed from the remaining four much more markedly than these could be differentiated from each other. This clone stood in a position somewhat intermediate between the large and small strains, though very much nearer the latter, so that there was no doubt about the propriety of including it in that group. There could be no question that this clone was of a different genotype to the other four, so it was removed and the parental correlations recalculated for the remainder. The result showed for birth measurements a correlation of $0{\cdot}244 \pm 0{\cdot}081$ and for adult measurements $0{\cdot}598 \pm 0{\cdot}097$. The numbers of individuals on which these coefficients are founded are, of course, very small, but their significant values—especially of the second—suffice to make it highly probable that the remaining four clones were still not included in a single biotype. Beyond this it is not safe to go, as the numbers were too small and transgressive fluctuation too great to justify an attempt to decide whether indeed each clone had not a distinct genotypical constitution. We can, however, say with some confidence that *at least three genotypes were represented among the five clones of the small strain.*

This is very suggestive of the enormous genetic diversity existing not only within a single species but within a given population of a species inhabiting a restricted and continuous area. The fact, however, must not be lost sight of that, in the absence of segregation, heterozygous genotypes retain their individuality, and therefore a greater diversity may be expected to reveal itself here than in a self-fertilising or closely inbred sexual population.

Comparison with the Monoclonal Population.

As we have seen, the monoclonal population was descended from 70 original ancestors, themselves all descended parthenogenetically from a single known female. One of these 70 failed to leave offspring beyond Generation 1 and is left out of consideration, leaving 69 original ancestors of the population. Each of these became the ancestor of a separate line, of which two sub-lines *a* and *b* were bred, giving in Generations 1–5 138 sub-lines in all (except where temporarily reduced by death or accident).

The death-rate during these five generations, corresponding to the list on p. 434, was—

Generation	1 . . .	0·72 per cent.
,,	2 . . .	1·45 ,,
,,	3 . . .	2·19 ,,
,,	4 . . .	0·00 ,,

As before, Generation 5 was not allowed to grow up, so its mortality cannot be given.

It was at once clear that there was much less diversity among the population for the characters which we are specially considering. Indeed, it was so much less that in grouping the measurements for statistical reduction it was necessary to make the class intervals a half unit of measurement instead of the full unit which was used in the case of the polyclonal population.

Tables VII, VIII, and IX correspond to Tables II, III, and IV, giving the ancestral correlations for birth and adult measurements. They were constructed in precisely the same way as the polyclonal Tables, the full Tables on which they are based being Nos. XLI–LVI in Appendix II.

The three points mentioned on p. 427 in connection with Tables II and III apply with equal force to Tables VII and VIII.

TABLE VII.—Monoclonal Population. Ancestral Correlations for Birth Measurements (corrected).

	Number of ancestors.	Number of families of offspring.	Mean number of individuals per family of offspring.	Correlation coefficient.
Parental correlations—				
Between Generations 1 and 2 . . .	135	135	4·7	0·101 ± 0·057
,, ,, 2 ,, 3 . . .	135	135	5·0	−0·111 ± 0·057
,, ,, 3 ,, 4 . . .	130	130	5·0	0·048 ± 0·059
,, ,, 4 ,, 5 . . .	135	135	5·0	−0·139 ± 0·057
Grandparental correlations—				
Between Generations 1 and 3 . . .	132	135	5·0	−0·058 ± 0·058
,, ,, 2 ,, 4 . . .	128	130	5·0	0·142 ± 0·058
,, ,, 3 ,, 5 . . .	128	135	5·0	−0·041 ± 0·058
Great-grandparental correlations—				
Between Generations 1 and 4 . . .	126	130	5·0	−0·077 ± 0·059
,, ,, 2 ,, 5 . . .	125	135	5·0	−0·119 ± 0·057
Great-great-grandparental correlation—				
Between Generations 1 and 5 . . .	125	135	5·0	0·066 ± 0·058

The testimony of these tables is striking, and again in complete accord with the genotype hypothesis. The correlation coefficients fluctuate round zero, some (as it

TABLE VIII.—Monoclonal Population. Ancestral Correlations for Adult Measurements (corrected).

	Number of ancestors.	Number of offspring.	Correlation coefficient.
Parental correlations—			
Between Generations 1 and 2	131	135	$0\cdot039\pm0\cdot058$
„ „ 2 „ 3	128	130	$0\cdot022\pm0\cdot059$
„ „ 3 „ 4	128	134	$-0\cdot040\pm0\cdot058$
Grandparental correlations—			
Between Generations 1 and 3	126	130	$-0\cdot036\pm0\cdot059$
„ „ 2 „ 4	126	134	$-0\cdot087\pm0\cdot058$
Great-grandparental correlation—			
Between Generations 1 and 4	124	134	$-0\cdot113\pm0\cdot058$

TABLE IX.—Monoclonal Population. Summary of Tables VII and VIII, showing Mean Correlation Coefficients.

	Birth measurements.	Adult measurements.
Parental	−0·025	−0·007
Grandparental	0·014	−0·062
Great-grandparental	−0·098	−0·113
Great-great-grandparental . . .	0·066	—

happens the majority) being negative and some positive. None of them fulfil the accepted criterion of significance—namely, being at least three times as large as their probable errors.

It is plain, therefore, that the ancestral correlation coefficients in the monoclonal population are to be taken as zero—the fluctuations round the zero point being due to chance influence of environment, which also accounted for the fluctuations of the polyclonal coefficients. In other words, *no inheritable variation could be detected within the monoclonal population.*

In the case of the polyclonal population we further tested the possibility of the inheritance of intraclonal variation by comparing the offspring of the large and small members of the pairs chosen for parentage in each clone in each generation. It is possible to treat the 69 lines of the monoclonal population as we treated the 57 clones of the polyclonal population, and taking the pair of individuals chosen for parentage in each line, examine whether the large members have larger offspring than the smaller members. In view of the correlation coefficients just presented it is, of course, practically a foregone conclusion that no inheritance will be disclosed in this way, but Table X was calculated in order to make the comparison between the two populations complete.

TABLE X.—Monoclonal Population. Comparison of Offspring of Large and Small Members of the Pairs of Parents. Uncorrected Measurements.

	No. of pairs of parents.	Mean measurement of large parents.	Mean measurement of small parents.
Birth measurements	196	48·156	46·980
Adult measurements	138	124·528	121·789

	No. of offspring of large parents.	Mean measurement of offspring of large parents.	No. of offspring of small parents.	Mean measurement of offspring of small parents.	Mean of offspring of large parents *minus* Mean of offspring of small parents.
Birth measurements . .	963	47·941	968	47·958	$-0·017 \pm 0·079$
Adult measurements . .	138	123·246	138	122·894	$+0·352 \pm 0·208$

The first four points mentioned on p. 439 apply to this table with equal force as to Table V, with the exception that the number of pairs rejected because of the equality of the members was 65 in the case of the birth measurements and 46 for the adult measurements.

From this table we see again that there is no significant difference between the offspring of the large and small parents. For one dimension the large parents have on the average smaller offspring, and in the other larger ones than do the small parents. In neither case, however, does the difference approach the criterion of significance by being three times its probable error.

Mendelian Segregation and Parthenogenesis.

These results add indirectly to our evidence that Mendelian segregation does not normally take place in parthenogenesis. For the 62 clones of the polyclonal population comprised a number—probably a large number—of different biotypes, and hence it is very probable that a considerable proportion of them was heterozygous. Hence if Mendelian segregation were taking place, the parental correlations should increase from generation to generation since heterozygotes could split into homozygotes, but these could not recombine into heterozygotes. A glance at the four parental correlations in Table II, and the three in Table III shows no evidence for such an increase. It is also plain that no segregation was detectable in the monoclonal population.

On p. 365 HANEL (4) gives a table showing the same thing for *Hydra* for propagation by budding. It must be remembered, however, that the 26 original animals of that experiment were of unknown ancestry, and may have been descended through many asexual generations, in which case if vegetative segregation were taking place they would probably all have become homozygous before the experiment began.

These results then are in accord with the direct evidence of the absence of segregation in asexual reproduction in plants obtained by MENDEL, OSTENFELD and ROSENBERG for *Hieracium*. The apparent segregation in a single parthenogenetic brood of a Phasmid bred by FRYER may prove explicable on quite other grounds or may be established as an exceptional case, but the evidence at present is very strong that segregation does not normally take place in parthenogenesis. This fact is also indirect evidence that it normally takes place in the reduction division, as appears so probable on purely cytological grounds.

EXPERIMENTS WITH *Simocephalus vetulus*.

Selection Experiment.

The experiments with this species were carried out in a different manner, inheritance within a monoclonal population being tested by a selection experiment carried over 15 generations. The character selected was birth measurement, the results being summarised in Table XI.

The experiment was carried out on the clone that furnished the material for my papers of 1913 and 1914. Its origin was an adult parthenogenetic female taken from one of the laboratory aquaria on September 27, 1911. No sexual forms appeared in the generations to be dealt with below.

The common ancestor of the individuals included in the experiment to be described immediately was a member of the eighth generation from this female. The eight great-granddaughters of this individual produced collectively in their first broods 32 + offspring, all born within 48 hours of each other. The smallest and largest members of the first broods produced by these 32 individuals were selected, forming two groups of 32 each, the group containing the largest member of each brood averaging 44·172 units, and that containing the smallest averaging 42·672. These head Table XI, as "Parents of Generation 2," and are the first progenitors of the two parallel sections selected for 15 generations for largeness and smallness respectively.

Three broods were taken from each of these 64 individuals, the first, second, and third broods of Generation 2 in the table. The parents of Generation 3 were selected from the first broods of Generation 2 as follows:—From 15 of the broods of the section undergoing selection for largeness the largest individual was selected, and from 15 of the broods of the other section the smallest individual was chosen. This method of selection was carried on up to and including Generation 7, except that sometimes the two largest or smallest specimens of a brood were selected instead of one.

The parents of Generation 8 were chosen in a different way. After the first broods of Generation 7 had been produced a review was made of the effects of the selection experiment so far. As can be seen, the result of six successive selections has been negative.

Owing to the method of selecting one or two members of several broods in each generation, both the sections consisted of a number of lines which could trace their

pedigrees separately back to the beginning of the experiment. Now although the results of the experiment were in the mass negative at this point, nevertheless it was naturally possible to pick out of each group a few lines in which the results appeared to be more promising than in the others. The three lines which had been most consistently the largest were picked out of the section undergoing selection for increase of size, and the three consistently smallest lines out of the other section. The parents for Generation 8 were chosen from the second broods of these six lines—the 16 largest individuals being chosen from the three large lines and the 13 smallest from the three small lines.

In the subsequent selections, instead of choosing the largest or smallest from each brood, the population in each section was treated as a whole and the appropriate individuals selected. In Generation 8, for example, there were in the section selected for largeness 125 individuals altogether, comprising 16 families, and the 18 largest of these were selected instead of the largest member of each of the 16 families as hitherto.

Table XI thus shows the result of selecting the largest specimens for parentage for 15 successive generations, compared with the result of a similar selection of smallest individuals.

The following are the chief points to be noted in regard to the table :—

(1) *No positive result of the selection can be observed.* Out of the 15 generations from selected parents, in nine cases the offspring of the large parents are smaller than those of the small parents. Nor is there any evidence of a cumulative effect, as the + differences in the last column do not occur more frequently towards the end than towards the beginning of the experiment.

(2) Except where otherwise shown, only one brood was taken from each parent. Where more than one was taken, the broods of different orders are treated separately. This is advisable for the reason that, as can be gathered from the table, the birth measurements increase in successive broods of the same parent. The parents of Generations 8 and 14 were selected from the second broods of their generation. In all the other cases the parents were selected from the first broods.

(3) The mean birth measurement for each group fluctuates from generation to generation from environmental causes. The only useful method by which the results of the selection can be estimated is the method adopted in the table, namely, by comparing the same generations of the two sections which lived at the same time under the same conditions.

(4) The synchronism between the corresponding generations of the two sections is, however, not complete, chiefly owing to a tendency of small individuals to mature more quickly than large ones, so that the large section gradually lagged behind the small one. In Generation 15 the last brood of the small section was born 24 hours before the first of the large one. (The duration of the life-cycle from birth of parent to birth of its first young is about 13 days).

TABLE XI.—Selection Experiment.

	Selected for largeness.		Selected for smallness.		Difference. Mean of individuals selected for largeness *minus* Mean of individuals selected for smallness.
	Number of individuals.	Mean birth measurement.	Number of individuals.	Mean birth measurement.	
Parents of Generation 2 . .	*32*	*44·17*	*32*	*42·67*	
Generation 2 { 1st broods .	320	41·67	319	41·81	−0·14
Generation 2 { 2nd broods .	319	41·85	318	41·81	+0·04
Generation 2 { 3rd broods .	316	45·97	305	46·21	−0·24
Parents of Generation 3 . .	*15*	*43·07*	*15*	*38·43*	
Generation 3, 1st broods .	120	41·95	105	42·54	−0·59
Parents of Generation 4 . .	*13*	*42·85*	*15*	*41·63*	
Generation 4, 1st broods .	93	45·09	110	44·73	+0·36
Parents of Generation 5 . .	*12*	*45·87*	*12*	*44·04*	
Generation 5, 1st broods .	110	44·66	108	44·12	+0·54
Parents of Generation 6 . .	*20*	*45·50*	*18*	*43·58*	
Generation 6, 1st broods .	117	43·23	95	43·68	−0·45
Parents of Generation 7 . .	*18*	*44·31*	*20*	*41·12*	
Generation 7 { 1st broods .	130	43·52	142	42·99	+0·53
Generation 7 { 2nd broods .	175	44·47	189	44·08	+0·39
Parents of Generation 8 . .	*16*	*45·56*	*13*	*43·00*	
Generation 8, 1st broods .	125	41·31	98	41·82	−0·51
Parents of Generation 9 . .	*18*	*43·67*	*18*	*40·31*	
Generation 9, 1st broods .	99	41·12	74	41·45	−0·33
Parents of Generation 10 . .	*4*	*42·75*	*4*	*38·87*	
Generation 10, 1st broods .	22	44·34	26	43·73	+0·61
Parents of Generation 11 . .	*2*	*46·75*	*2*	*42·00*	
Generation 11, 1st broods .	9	46·33	11	42·73	+3·61
Parents of Generation 12 . .	*2*	*47·25*	*2*	*41·25*	
Generation 12 { 1st broods	18	42·33	12	45·67	−3·33
Generation 12 { 2nd broods	13	44·23	15	46·10	−1·87
Parents of Generation 13 . .	*1*	*46·00*	*2*	*45·00*	
Generation 13 { 1st broods	1	45·50	12	44·58	+0·92
Generation 13 { 2nd broods	6	44·33	16	47·31	−2·98
Parents of Generation 14 . .	*6*	*44·33*	*6*	*46·67*	
Generation 14, 1st broods .	34	42·75	42	44·93	−2·18
Parents of Generation 15 . .	*12*	*44·96*	*11*	*43·73*	
Generation 15, 1st broods .	87	45·78	108	44·88	+0·90
Parents of Generation 16 . .	*5*	*47·10*	*6*	*41·58*	
Generation 16, 1st broods .	38	43·80	20	46·20	−2·40

(5) This increasing dischronism will doubtless account for a large part of the irregularities especially noticeable towards the end of the table, but these are also partly accounted for by the small numbers of individuals, especially of parents, employed in the later part of the experiment. There is a high fraternal correlation (0·822) between members of a brood, so that a dozen offspring have not nearly the same value when derived from one parent as when derived each from one of a dozen parents. Moreover, during Generations 10–13 the water in the breeding-tubes was not changed regularly every second day as during the rest of the experiment, but at longer intervals. There was, therefore, more opportunity for different conditions to develop within the tubes.

(6) When a character is subject to much environmental fluctuation like the character dealt with here, the selection of only small numbers of parents is likely to have very slow results, even granting the presence of inheritable variations, as these may often be rejected in favour of more marked environmental modifications. In the first part of the experiment, however, when the smallest or largest member of each brood was selected, germinal variations of birth measurements would be much less liable to escape selection owing to the very similar environmental conditions to which members of the same brood have been subjected. (This similarity of environment is of course reflected in the high fraternal correlation for members of the same brood noticed above.)

(7) For several reasons, therefore, the latter part of the experiment is less important than the first part, though, so far as it is worth, it confirms the negative results obtained in the first portion.

Existence of Distinct Biotypes in S. vetulus.

The negative result of this selection experiment is in agreement with the *S. exspinosus* results, but a possible criticism remains to be answered, namely, that perhaps the birth measurement in *S. vetulus* is a character which is peculiarly free from genetic diversity in any circumstances. Improbable as this is in view of the great number of biotypes discovered in *S. exspinosus*, it is of interest to find evidence of distinct biotypes in *S. vetulus* also. That such do occur is shown by Table XII, in which the clone we have just been dealing with (designated the Glasgow clone) is compared with two others, bred synchronously with it under identical conditions. The Cambridge clone was derived from a parthenogenetic female kindly sent to me from that place by Mr. F. A. Potts, and the ancestor of the third clone was a parthenogenetic female sent by Mr. John Ritchie from Beith, about 16 miles from Glasgow.

It is plain that the Glasgow clone is a smaller biotype than the other two, being the smallest of the three on 16 out of the 18 occasions. It is probable that the other two must also be separated genotypically, the Beith clone being larger than the Cambridge one on 11 out of 17 occasions.

Experiments with *Daphnia obtusa*.

The experiments with this species have little independent value, but they add cumulative evidence to that already obtained. The character used was the ratio between the posterior spine of the carapace and the body length, in the first instar. The numbers are small and the dimensions very sensitive to environmental influences. The disturbance caused by the latter, however, was minimised by taking contemporary individuals for comparison.

All the specimens belonged to the same clone. The experiment was not designed

TABLE XII.—Birth Measurements of Three Clones of *S. vetulus*.

Generation.	Glasgow Clone.				Cambridge Clone.				Beith Clone.			
	Date of birth.	Number of families.	Number of individuals.	Mean birth measurement.	Date of birth.	Number of families.	Number of individuals.	Mean birth measurement.	Date of birth.	Number of families.	Number of individuals.	Mean birth measurement.
1. 1st broods	June 22–23	38	212	43·43	June 22–23	3	14	44·89	June 23–24	2	12	44·25
2. 1st „	July 4–6	38	272	43·24	July 5–6	3	20	44·02	July 6	3	18	45·78
2nd „	„ 9–10	37	364	44·26	„ 9–10	3	28	45·77	„ 10	1	8	48·25
3. 1st „	„ 21–23	29	223	41·53	„ 22–23	2	10	45·10	„ 23	1	4	46·50
4. 1st „	Aug. 1–2	36	173	41·26	Aug. 2–3	3	13	43·61	Aug. 2–3	3	13	44·38
5. 1st „	„ 14–16	8	47	44·00	„ 16	1	2	46·75	„ 16	1	4	45·87
6. 1st „	„ 30–31	4	20	44·35	„ 30–31	2	10	46·95	„ 31	1	5	48·60
7. 1st „	Sept. 13–15	4	30	43·67	Sept. 14–15	1	8	43·81	Sept. 14–15	1	9	43·06
2nd „	„ 17–20	4	28	45·23	„ 19–20	1	5	45·70	„ 19–20	1	6	46·17
8. 2nd „	Oct. 7–10	3	22	46·50	—	—	—	—	Oct. 9–10	2	17	47·41
9. 1st „	„ 21–25	12	76	43·95	Oct. 21–25	9	51	45·52	„ 22–23	5	32	46·34
10. 1st „	Nov. 3–7	23	195	45·28	Nov. 3–8	12	89	45·59	Nov. 5–6	11	85	45·08
11. 1st „	„ 15–19	11	58	44·63	„ 16–20	5	20	46·45	„ 17–18	5	31	47·10
12. 2nd „	Dec. 3–4	3	14	46·68	Dec. 3–4	3	9	49·17	Dec. 4–5	3	12	46·91
13. 1st „	„ 26–27	3	15	45·13	„ 27	1	4	45·87	„ 26–27	1	6	46·67
14. 1st „	Jan. 7–8	2	4	46·50	Jan. 7–8	2	7	46·71	Jan. 7–8	3	10	47·20
15. 1st „	„ 17–18	3	28	43·71	„ 17–19	3	23	44·93	„ 18–19	3	23	43·80
16. 1st „	„ 30–31	3	14	42·07	„ 30–31	2	7	45·64	„ 30–31	2	6	45·75

in relation to the problem before us, but from the records it was possible to pick out 13 pairs of parents, the members of each pair being born on the same day, and to compare their offspring, with the following result:—

Mean ratio of the high-ratioed member of the 13 pairs . .	3·126
Mean ratio of their 57 offspring	2·809±0·217
Mean ratio of the low-ratioed member of the 13 pairs . .	2·741
Mean ratio of their 69 offspring	2·899±0·193

Again, there is no evidence of inheritance of intraclonal variation.

Experiments with *Macrosiphum antherinii*.

The experiments with this insect, one of the Aphidæ, were undertaken to see if the results would be similar to those obtained by Warren for the Aphid, *Hyalopterus trirhodus*, namely correlation coefficients diminishing as the scale of ancestry is ascended from parent to grandparent. For this purpose advantage was taken of the presence of *Macrosiphum antherinii* Macch.* on plants of *Antirrhinum majus* growing in pots.

Technique of Breeding Methods and Characters used in the Experiments.

As in the other experiments described in this paper, the characters dealt with were measurable dimensions, and in this case the same as those used by Warren. These are (1) the frontal breadth or distance between the eyes (AB, fig. 2), (2) the length of the antenna (CD, fig. 2), and (3) the ratio of the second of these to the first.

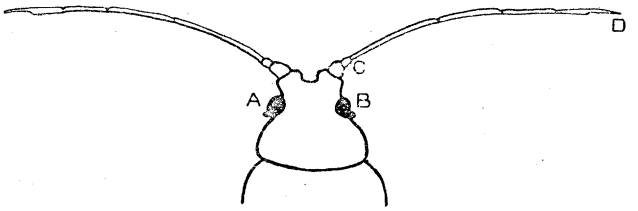

Fig. 2.

(1) *Frontal Breadth.*—The animals (preserved in alcohol) were placed in a well slide and covered with a cover-glass, and the distance between the eyes read off by an eyepiece micrometer, the unit of measurement being 0·0095 mm. Care was taken to get the line AB horizontal. As a rule this was managed with but little manipulation, but in some cases it was necessary to dissect off the legs first. It will be noticed from the figure that the surface of the eye is produced at one point into a projecting knob, and this makes it very easy to determine whether the line AB is horizontal or not. For when these knobs are sharply in focus at the same time AB must be at right angles to the axis of the microscope.

* I am indebted to Prof. F. V. Theobald for kindly identifying the species.

(2) *Length of Antenna.*—This measurement presented some troublesome features. I was unable to measure the antennæ directly, as WARREN found possible for *Hyalopterus*, owing to the fact that they have a curvature both in the horizontal and vertical planes. The vertical curve was flattened out by dissecting off the head, with the antennæ attached, and placing it on a flat slide and covering with a cover-slip. The weight of this was sufficient to flatten out the antenna without crushing it. The curvature in the horizontal plane still prevented direct measurement, so the antenna was now drawn under the camera lucida, and the curved line so obtained measured with an ordinary map measurer. The unit of measurement worked out at 0·02 mm.

Finding that greater accuracy could be obtained by omitting the first two segments, I did this, and by "antennar length" must be understood throughout, the total length without these two joints (see fig. 2).

252 specimens in all were preserved during the course of the experiment, but four of these were accidentally injured, and could not be measured, and one had both antennæ so short that it was rejected as abnormal though there was no evidence that the antennæ had been broken.

Of the remaining 247 animals, 241 had their right antenna measured. In the other six the left antenna was measured as the one on the other side had been injured.

(3) *Ratio.*—The ratio between the two dimensions was found by dividing the frontal breadth into the antennar length, first multiplying the latter by 2·1 as the unit of measurement of the antennæ (0·02 mm.) was 2·1 times that of the frontal breadth (0·0095 mm.).

The magnitudes of the frontal breadth and antennar length are of course highly correlated, the value of the coefficient being $0{\cdot}805 \pm 0{\cdot}016$ (Table LVII, Appendix II).

The general course of the experiment was as follows. Early in May, 1913, a single parthenogenetic female was isolated on an Antirrhinum leaf which was enclosed in a cage, and all the individuals dealt with in the experiment were descended by parthenogenesis from this specimen. Thus we are dealing with a monoclonal population. Throughout the whole experiment only parthenogenetic, viviparous, wingless females appeared.

The cages in which the great majority of the individuals were enclosed consisted of cylinders of glass just wide and long enough to contain an Antirrhinum leaf. The free end of the cage was closed with muslin gummed on to the cylinder, and the other end of the glass fitted into a paper collar to which was gummed a sleeve of muslin which was tied firmly round the petiole of the leaf. This type of cage proved to be very convenient. The paper collar at the end of the muslin sleeve, into which the glass cylinder fitted, was made to fit tightly round the cylinder without being actually attached to it, so that when a close examination of the enclosed Aphid was desired, the cage was easily opened by withdrawing the cylinder from this collar. The weight of the cages would have been sufficient to tear the leaves off the stem, and so they were supported by wires.

A few cages were made of muslin and paper only, but the great majority of them were of the type described.

One of the most difficult sources of environmental dissimilarity to be guarded against in an experiment of this kind lasting over several weeks is changes of temperature. The Antirrhinum plants were growing in pots, kept in an artificially heated greenhouse. In a house of this kind it is comparatively easy to keep the lower limit of the temperature constant by means of a thermostat, but it is impossible to prevent a rise at noon on a sunny day. The readings of the thermometer were noted several times a day, but it is not worth publishing the records, because the sole interest we have at present in the environmental changes from time to time is their effect upon the dimensions with which we are dealing. The degree to which the animals were influenced by the sum total of the environmental changes, of which temperature was probably the most important, is shown in Table XIII. Here the mean values for the two dimensions and for the ratio between them is shown for the five weeks of the experiment, each week taken separately. It will be seen that the efforts to keep the conditions constant were not entirely successful, there being a significant difference between the means for certain weeks. How far this may have influenced the result is put to the test later on.

TABLE XIII.—Comparison of the Dimensions for the Five Weeks of the Experiment.

	June 4–10.		June 11–17.		June 18–24.	
	Number of individuals.	Mean.	Number of individuals.	Mean.	Number of individuals.	Mean.
Antenna	31	163·22 ± 1·22	47	166·27 ± 0·81	56	171·69 ± 0·90
Frontal breadth . . .	31	38·32 ± 0·15	47	38·29 ± 0·10	56	38·96 ± 0·10
Ratio	31	4·26 ± 0·02	47	4·34 ± 0·02	56	4·41 ± 0·01

	June 25–July 1.		July 2–8.	
	Number of individuals.	Mean.	Number of individuals.	Mean.
Antenna	41	171·07 ± 1·13	46	167·28 ± 0·75
Frontal breadth	41	39·54 ± 0·16	46	39·04 ± 0·11
Ratio	41	4·33 ± 0·02	46	4·29 ± 0·01

The number of cages in use at one time was far too great to be accommodated on a single plant. In order to avoid as far as possible the diverse influence of dissimilar food plants, all the animals included in the experiment were distributed on the leaves

of six plants which had all grown from vegetative cuttings of the same parent plant and were therefore presumably closely similar in constitution.

In spite of all precautions, however, minute differences in the nature of food supply, etc., available to each insect are sure to exist, as the leaves even of the same plant are certain to vary slightly in their food contents, etc. These differences were probably very small, as all the leaves enclosed by cages remained healthy throughout the experiment. The only possible counterstroke to this local dissimilarity of conditions is to take care that these differences are distributed impartially, that is to say, at random, among the various individuals. This was attempted as follows:

As more fully described below, each individual was removed from its cage at maturity, and its offspring left in the cage. Every third day the catalogue numbers of all the cages which contained individuals from five to seven days old were each written down on two slips of paper, and then these slips were drawn at random in pairs. When any number was drawn with its own number, the individual in that cage was left where it was, but in the other cases an exchange was made between the individuals in the pairs of cages of which the numbers were drawn together. Thus, whether or not any young one should mature in the same cage as its parent was left to chance.

Out of the 124 pairs of parents and offspring of Table XIV, 15 offspring matured in their parents' cages, and the other 109 were exchanged when 5–7 days old into another.

Influence of Growth upon the Dimensions.—The most important factor which influences the dimensions is, of course, the growth of the animal, and consequently it is of the greatest importance to make the measurements on animals of the same age, or, rather, at the same stage of development. This is not so easily done in an Aphid as in a Cladoceran, owing to the fact that the former grows continuously, and not only at each ecdysis.

This is shown by the following record of measurements and observations on a living specimen. This is only one example of several such records, all of which are closely similar to this one. The measurement is of body length, not of the dimensions dealt with in the rest of the experiment, which are scarcely capable of measurement in the living animal:—

Individual born 10 A.M.–3 P.M., May 27.

At 3 P.M.,	May 27,	measured 17·5 units.		
„ 4.30 „	„ 28,	„ 20	„	
„ 9 A.M.,	„ 29,	„ 23	„	
„ 3 P.M.,	„ 30,	„ 24	„	Cuticle cast since last measurement.
„ 6.30 P.M.,	„ 31,	„ 26·5	„	
„ 1 „	June 1,	„ 29	„	Cuticle cast since last measurement.
„ 5 „	„ 2,	„ 32·5	„	
„ 6 „	„ 3,	„ 33	„	Cuticle cast since last measurement.
„ 5.30 „	„ 4,	„ 39	„	
„ 3 „	„ 5,	„ 40·5	„	
„ 9 A.M.	„ 6,	„ 42	„	Cuticle cast since last measurement. End of abdomen assumed adult condition.
„ 9 A.M.	„ 7,	„ 46	„	
„ 1 P.M.	„ 8,	First two young born.		

This growth between, as well as at each of the ecdyses, makes it impermissible to measure the animals after the 1st, 2nd, or *n*th moult as we did with the Cladocera. Some more precise point in the life-history has to be taken, and the moment at which to preserve the animals for measurement finally selected was the interval between the production of the fifth and sixth young ones. The young are produced singly at considerably varying intervals, but roughly at the rate of two or three a day at the temperature employed. A day or two before the time that any individual was expected to produce its first young one its cage was examined daily, and as soon as it was seen to have produced at least two young it was removed to an observation cage consisting of a corked glass tube containing a freshly picked Antirrhinum leaf. The Macrosiphum was now examined every few hours, night and day, until its fifth young one had been produced, and then it was preserved in alcohol. The average time which the insects spent in the observation cages was under 24 hours—and it may be mentioned that tests showed that a large number of the insects could live together in perfect health in such a cage containing a single leaf for considerably over a week.

In spite of careful examination at frequent intervals, a number of parents produced six young before they were preserved—either owing to the overlooking of a young one at a previous examination or to the fifth and sixth young being produced very quickly one after the other. Altogether 26 individuals produced six young in this way, and these are excluded from all the tables and discussions which follow, reducing, therefore, the number of available specimens, especially for the determination of the parental and grandparental correlation coefficients, since the exclusion of these individuals involved the exclusion of their ancestors or offspring.

We have mentioned above that the parents were removed to the observation cages after they had produced two young. These two were left in their parent's cage till 5–7 days old, then one was killed and the other either left in the cage or exchanged into another according to the scheme already detailed. Thus only one young one from each parent was kept, except in a very small percentage of cases, where two young were allowed to mature (never in the same cage) to make up for losses due to accident, etc. The number of deaths not due to accident was quite negligible.

Inheritance in the Population.

The monoclonal population of *S. exspinosus* was started from 69 contemporary ancestors, so that all the births of each generation took place comparatively close to each other with long intervals between each two generations. The *Macrosiphum* population did not start in this way from a number of contemporary ancestors, but was bred up from offspring produced at short intervals by the original ancestor. Consequently the births were distributed irregularly over the period of the experiment, several a day, and at the end all the available parents and grandparents were extracted out of the records.

The parental and grandparental correlation for the two dimensions and for the ratio are given in Table XIV, in which WARREN'S figures for *Hyalopterus* are added for comparison. It is plain that the inheritance here appears at first sight to be of the same type as usually found for measurable characters in heterogeneous sexual populations. In spite of its being a monoclonal population, the ancestral—or, at any rate, the parental—correlations are significant, and, in spite of the absence of sexual intermixture, the correlations diminish in intensity as we pass back from the parental to the grandparental relation.

TABLE XIV.—Ancestral Correlation Coefficients for *M. antherinii* and *H. trirhodus.*

	Macrosiphum antherinii.		*Hyalopterus trirhodus.*	
	Parental. 117 parents and 124 offspring.	Grandparental. 54 grandparents and 60 offspring.	Parental. 60 parents and 368 offspring.	Grandparental. 30 grandparents and 291 offspring.
Antenna . . .	0·482 ± 0·046	0·165 ± 0·085	0·427 ± 0·029	0·177 ± 0·038
Frontal breadth	0·433 ± 0·049	0·231 ± 0·082	0·335 ± 0·031	0·321 ± 0·035
Ratio	0·235 ± 0·057	−0·002 ± 0·087	0·439 ± 0·028	0·230 ± 0·037

Note.—WARREN'S figures for Hyalopterus are given in the original to four places of decimals.

The values for *Hyalopterus* are on the whole higher than those for *Macrosiphum*, especially for the grandparental coefficients. In the latter genus these are, indeed, doubtfully significant for the two absolute dimensions, and certainly not significant

for the ratio. It must be remembered that the antennar length and the frontal breadth are closely correlated, so that the ancestral correlations for the two dimensions do not constitute independent mutually corroborative evidence.

The similarity of the results of the experiments with these two species affords a certain presumption that the coefficients are due to the physiological relationship between grandparent, parent, and offspring, and not the accidental result of extrinsic causes. In addition, independent evidence for this can be adduced in the case of *Macrosiphum*.

There are specially two extrinsic factors which might account for significant positive correlations of this kind. Firstly, a progressive change of the sum total environment in the same direction throughout. This would cause a progressive increase or decrease of the dimensions employed. This would result, if the change were in the direction of increase, in the earliest and hence smallest parents being taken with the earliest and hence smallest offspring, the next smallest parents with the next smallest offspring, and so on, and so a positive correlation between parent and offspring would be produced. Table XIII shows, however, that the change from week to week was not regularly progressive. Besides, it is possible to establish the fact that the larger parents really do have larger offspring by a method which practically excludes the influence of changing environment. For this purpose the mean antennar length and frontal breadth were found for all the parents preserved on the same day for each of the 22 days of the experiment on which parents were preserved. All the parents below the mean for their day were placed on one side (small parents) and all the parents above the mean on the other side (large parents). The mean for the offspring of both these groups was then found, with the result shown in Table XV.

TABLE XV.—Comparison of the Offspring of Large and Small Parents.

	No. of large parents and offspring.	No. of small parents and offspring.	Mean of large parents.	Mean of small parents.	Mean of offspring of large parents.	Mean of offspring of small parents.	Mean of offspring of large parents *minus* Mean of offspring of small parents.
Antenna.	66	49	174·848	159·796	173·182 ± 0·665	164·388 ± 0·863	+8·794 ± 1·089
Frontal breadth	62	52	39·371	37·558	39·476 ± 0·090	38·577 ± 0·112	+0·899 ± 0·144

The number of available parents, and consequently of offspring, is reduced by the fact that those which happened to fall on the mean for their day had to be rejected. It will also be noticed that the number of large parents is greater than the number of small ones. This is because the curve of distribution is skew, the number of

+ variants from the mean being greater than the number of — variants. Half-a-dozen parents had two offspring each and are counted twice over, once for each offspring. Hence in the table the number of parents and offspring appears the same.

It will be seen from the table that for both dimensions the mean size of the offspring of the large parents is significantly greater than that of the offspring of the small ones, thus confirming the positive parental correlation coefficients while practically excluding the disturbing influence of changing environment.

TABLE XVI.—Comparison of Grandchildren of Large and Small Grandparents.

	No. of large grand-parents and grand-children.	No. of small grand-parents and grand-children.	Mean of large grand-parents.	Mean of small grand-parents.	Mean of grand-children of large grandparents.	Mean of grand-children of small grandparents.	Mean offspring of large grand-parents *minus* Mean offspring of small grand-parents.
Antenna.	32	23	170·156	158·043	171·095 ± 1·092	168·478 ± 1·066	+2·617 ± 1·526
Frontal breadth	29	24	39·052	37·312	39·603 ± 0·161	39·021 ± 0·145	+0·582 ± 0·217

Table XVI was prepared in precisely the same way as Table XV, but deals with grandparents and grandchildren. The results are much less conclusive than for parents and offspring. In both dimensions the grandchildren of the large grand-parents are indeed larger than those of the small grandparents, but the difference is less than twice its probable error in the case of the antennar length and less than three times in the case of frontal breadth. Taken by itself, therefore, this test does not give reliable evidence that the grandchildren of larger grandparents are larger than those of smaller ones when the possible effects of environment are excluded.

The test just described was not made by WARREN for *Hyalopterus*.

The second extrinsic factor which might cause a significant positive correlation of the kind we have found is a greater similarity of local environment for parent and offspring than for pairs of individuals taken at random. I have already described the precautions that were taken to minimise this source of error by random exchanges among the cages. It is true that the exchanges were not made till the animals were 5–7 days old, so that the first part of each individual's life was spent on the same leaf as the latter part of its parent's, though the corresponding portions of their lives, when similar environments might be expected to have the greatest similarity of effect, were passed in different cages, with the exception of the 15 offspring already mentioned who remained in their parent's cage till maturity. In order to find whether the parental correlation were increased when parent and offspring both matured in the

same cage, I found the coefficients for the two absolute dimensions for the 109 pairs left after excluding these 15. The result was: for the antenna, $0{\cdot}461 \pm 0{\cdot}051$ instead of $0{\cdot}482 \pm 0{\cdot}046$; and for the frontal breadth, $0{\cdot}406 \pm 0{\cdot}056$ instead of $0{\cdot}433 \pm 0{\cdot}049$.

It is difficult to estimate how much significance is to be attached to this slight lowering of the correlation coefficient caused by the withdrawal of so small a number of individuals, but so far as it goes it shows that there was a greater resemblance between these 15 pairs of parents and offspring than between the rest. It is therefore probable that when nearly the whole life-history (*i.e.* except for the final hours passed in the observation cages) is passed on the same leaf, the parental correlation is increased.

It is obviously impossible to avoid all overlapping of local environments, of parent and offspring, since the animals are viviparous, and so even if the young were removed to a different cage immediately after birth, still they would have undergone an important part of their life-history in an environment identical with their mothers.

Whatever influence the sojourn of the offspring in their parent's cage may have had upon the parental correlation coefficient, it is scarcely relevant to the grandparental coefficient, as the grandchildren were never, except by chance, on the same leaf as their grandparents at any time of their lives. It is precisely here, however, as Table XVI shows, that the results are dubious when periodic changes of environment are excluded, and even the grandparental correlation coefficients themselves are none of them three times their probable errors. It must therefore be left open whether there is really any grandparental correlation at all in the population.

In WARREN'S *Hyalopterus* experiment the offspring spent their whole lives on the leaf on which their parents had matured, and in many cases the grandchildren also lived on the same leaf.

Discussion of the Results of the Macrosiphum Experiment.

If then we grant that the parental and perhaps also the grandparental correlation coefficients in *Macrosiphum* and *Hyalopterus* are not explicable by the extrinsic factors which we have discussed (and if they are explicable there is no special problem here, and they fall into line with the Cladoceran experiments) it is important to see what bearing they have on theories of genetics.

In comparing the results of the two experiments it must be borne in mind that we do not know whether WARREN'S animals composed a monoclonal or a polyclonal population. But while if the latter were the case positive ancestral correlation coefficients were to be expected, the fact that the grandparental coefficient is lower than the parental is still left unexplained. The problems at present before us are therefore:—

(1) The existence of a significant ancestral correlation in the monoclonal parthenogenetic population of *Macrosiphum*.

(2) The diminution of the correlation coefficient as we rise in the scale of ancestry from parent to grandparent in the parthenogenetic populations of both *Macrosiphum* and *Hyalopterus*, whether mono- or polyclonal.

Some will doubtless see the answer to these problems in the supposed continual genetic variation of living organisms round their mean, with the tendency of these newly arisen variations to be unstable—that is, only partially inherited and hence in the absence of selection fading out in succeeding generations. Such an explanation is, however, by no means the only possible one, and in the light of recent genetic research and of the Cladoceran experiments detailed in this paper, another hypothesis seems much more probable.

It is significant that all these cases in which we get correlation coefficients in asexual reproduction diminishing as we pass from parent to grandparent are viviparous, and most of them have short life-histories—that is, there is a comparatively short time in which to level out bias produced by the effects of maternal nutrition. Moreover, in every case the characters used were dimensions or, in the case of *Hydra*, a feature known to be influenced by nutrition. These cases* are *Hyalopterus*, *Macrosiphum*, *Hydra*, and *Phaseolus* (the last according to WELDON and PEARSON). To these might be added DE VRIES' case of polycephalic poppies, though the actual coefficients of inheritance are not given here. This last case is specially instructive, as DE VRIES showed that the number of supplementary carpels developed by the mature plant was influenced by the amount or character of the nutrition which it had as an embryo received from the mother plant. Moreover, the character of parents may reappear in the offspring through a process of "parallel induction."

It is therefore very dangerous to ascribe the parental correlations of the cases just mentioned entirely to inheritance, and the diminution of the intensity of correlation with the grandparents as evidence of an instability or partial inheritance of variations.

GENERAL THEORETICAL DISCUSSION.

In general, the results of the Cladoceran experiments are in complete accord with those of JOHANNSEN. In *Macrosiphum* alone did there seem any evidence in favour of the "partial inheritance" of variations, and the probability that we were here dealing with causes of resemblance other than inheritance proper has just been indicated.

In the absence of bisexual reproduction with its consequent shuffling of the individual genes, the resemblance between the somatic characters of ancestor and offspring depends solely, except for probably rare mutations, on the degree to which identical genetic constitutions are masked by environmental modifications. In *S. exspinosus* these modifications are potent enough to lower the intensity of inheritance as measured by the correlation coefficients between the somatic characters

* The evidence for *Daphnia magna* is so slight (p. 424) that it may be omitted from consideration.

of individuals and their ancestors to about 0·4 to 0·5. That this is not a partial inheritance of genetic constitution, but a partial obscuring (by environmental modification) of identical genetic constitutions is indicated by the fact that the correlation between individuals and their immediate parents is no higher than between them and their more remote ancestors, while the opposite would be expected if the genetic constitution were not inherited intact.

The diminution in the intensity of resemblance between individuals and their more and more remote ancestry, for certain complex somatic characters in sexual populations, receives a perfectly satisfactory explanation in the shuffling, at each successive conjugation, of the factors on whose interaction the character depends. And since, when this shuffling is absent, as in parthenogenesis, this diminishing of the degree of resemblance to more remote ancestors does not take place, we are bound to accept it as the most probable explanation.

In the case of "eversporting" varieties it is true that it is possible to speak of inheritance as being partial, but if this is done the expression is used in a different sense. The character is indeed inherited by only some of the offspring, but that is quite another thing to individuals inheriting it in different degrees. The most useful working hypothesis in the present state of our knowledge of genetics seems to be that the only grades of inheritance, when a single gene or Mendelian factor is concerned, are unity and zero.

Since the species *S. exspinosus* consists of an enormous number of pure-breeding biotypes, and since intraclonal fluctuations do not provide material from which a genetic diversity of this kind could be brought about, it is to be concluded that this diversity was produced by small mutations, that is to say, by genetic variations of a specific nature, which do not need a course of selection to become "fixed," but display at once that degree (generally an extremely high degree) of constancy in reproduction which is characteristic of that particular mutation.

I have never been able to observe a mutation in several years' experience of breeding Cladocera. Not only were none detectable in the experiments described in the present paper, but conspicuous variations have been constantly looked for and tested by breeding. Such variations were invariably found to show no trace of inheritance, and must therefore be supposed to be of a purely somatic nature. Variations tested in this way include absence and duplicity of the simple eye, abnormalities of the compound eye, pseudo-hermaphroditism affecting antenna 1, abnormalities of antenna 2, notching of both valves of the carapace, reduction of the carapace so that the abdomen projected freely behind it, etc. Mutations seem therefore to be rare, at any rate during the parthenogenetic reproduction of the Cladocera. It must be remembered, however, that even a comparatively small number of mutations gives rise to a possibility of a much greater amount of genetic diversity by crossing, as has recently been specially brought to notice by the crosses between species of *Antirrhinum* by Baur and Lotsy.

The greatest opposition to modern views of genetics has come from those who consider that they have taken away the philosophical basis of the theory of evolution, and especially of the evolution of adaptation. For while mutation could quickly bring about specific diversity, the evolution of complex adaptive structures is undoubtedly most easily grasped when the inheritable variations presented to natural selection are minute and abundant. This difficulty, though real, would probably have assumed smaller proportions had it not been for the natural fact that the earliest mutations studied were large morphological ones, and consequently that these have become fixed in many minds as types of mutational change. *S. exspinosus* shows us that very small mutations are more typical. The genetic diversity in this species is expressed in the most minute external differences, so that it is plain that the small differences required for adaptive evolution are there in abundance, and the fittest biotypes could be isolated by selection. That isolation once accomplished, however, further selection would have only non-inheritable environmental modifications to work upon, and so would be powerless until new genotypical differences were produced by mutation or crossing. These differences apparently occur very rarely compared with the universality of fluctuating variations, but this is to some extent compensated for by their constancy once they have appeared.

Throughout this paper the terminology accepted by the majority of contemporary workers on genetics has been adopted (because the author believes it to be justified), but it may be worth while pointing out to those to whom the idea of "units" in the constitution of an organism is repugnant, that the general finding of these experiments is quite independent of the Mendelian interpretation of the constitution of living beings. This general conclusion is, of course, that by far the greater part of variation (excluding environmental modification) is due, not to the tendency of living matter to vary its composition, but to recombinations of living substances in amphimixis —a question which was, of course, keenly discussed long before the re-discovery of MENDEL.

SUMMARY OF CHIEF RESULTS.

A. The genetic identity between parent and offspring in parthenogenesis is indicated by the following facts :—

(1) In a polyclonal population of *S. exspinosus* the correlation coefficients between individuals and their ancestors do not diminish as the scale of ancestry is ascended (Table IV).

(2) In a monoclonal population the ancestral correlation coefficients for all degrees tested are insignificant and fluctuate on both sides of zero (Table IX).

(3) The offspring of a large number of pairs of parents, each pair belonging to one clone, were compared, and it was found that the offspring of the larger members of the pairs did not differ significantly from those of the smaller members of the pairs (Tables V and X).

(4) An intraclonal selection experiment on *S. vetulus* had negative results (Table XI).

B. An experiment with *Macrosiphum* gave possible evidence of a partial inheritance of individual variations in parthenogenesis (Tables XIV and XV), contrary to the conclusions of the much more extensive *Simocephalus* experiments. A closer analysis, however, showed the danger of attributing this to true inheritance.

C. An estimation of the number of biotypes living together in a single natural population of *S. exspinosus* was attempted (p. 444).

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APPENDIX I.

INCREASED VARIABILITY UNDER ABNORMAL CONDITIONS.

Many investigators have noticed the increased variability or diversity of organisms in abnormal environments. It has been measured by VERNON in Echinoderms, by JENKINSON in *Rana* and *Salmo*, by PETER in Echinoderms and *Phallusia*, by COVENTRY in *Bufo*, and by KLEBS in Phanerogams, and has been observed by numerous other investigators in many organisms.

In these cases it is impossible to say whether the material was genotypically uniform or not, and consequently it is impossible to decide whether the increased variability was purely somatic, or due to different powers of resistance to the abnormal conditions possessed by genotypes indistinguishable from one another under more favourable conditions. In the absence of heredity tests there are, of course, no grounds for ascribing it to genetic variation.

Some evidence provided by *S. vetulus* is of interest here, because we know that we are dealing with genetically homogeneous material. The clone of this species used for the selection experiment was also employed for certain experiments on the effects of abnormal conditions (1913). Two conditions used were (1) high temperature, which has the effect of reducing the size of the animals, and (2) feeding with a protophyte culture grown in the Chlamydomonas medium, recommended by KLEBS. The chief abnormality produced by this is the rolling back of the valves of the carapace, so as to expose the abdominal appendages.

The variability (standard deviation and coefficient of variation) of each separate brood which contained four members and upwards was calculated for the characters birth measurement and distance between the ventral edges of the carapace, as seen when the animal is lying on its back, in a watch-glass under the microscope (intervalvular width). The results are given in Tables XVII and XVIII :—

TABLE XVII.—*S. vetulus*. Variability of Birth Measurements under different Conditions.

	Number of broods.	Mean number in each brood.	Mean birth measurement.	Mean standard deviation.	Coefficient of variation.
Controls	157	6·93	43·52 ± 0·09	0·543 ± 0·018	1·248
At high temperature . . .	54	5·98	35·84 ± 0·16	0·735 ± 0·026	2·051
In Klebs' culture medium .	8	7·12	45·01	1·428	3·152

TABLE XVIII.—*S. vetulus.* Variability of Intervalvular Width under different Conditions.

	Number of broods.	Mean number in each brood.	Mean intervalvular width.	Mean standard deviation.	Coefficient of variation.
Controls	41	5·80	9·63 ± 0·12	0·541 ± 0·026	5·618
In Klebs' culture medium .	7	8·71	29·93	5·042	16·846

The diversity, even among members of the same brood, is greatly increased by abnormal environments, but, in the light of the experience gained from the main part of this paper, it must be ascribed to purely somatic fluctuation, and not to genetic variation. Nor can it be ascribed to the different reactions by different genotypes, since, as we have seen, the material was throughout genotypically uniform.

The fact that purely somatic fluctuation is increased when a biotype is subjected to abnormal conditions must be reckoned with when discussing the increased variability observed under such conditions from the point of view of its evolutionary significance.

APPENDIX II.

TABLES.

Tables XIX–LVI.—*Simocephalus exspinosus.*

For purposes of statistical treatment the measurements have to be grouped into classes. The class interval in the case of the polyclonal population was one unit of measurement, but in the monoclonal population only a half unit. This difference was necessitated by the greater variability of the polyclonal population. The mean of each class was counted as its middle point.

Thus, in the polyclonal population, Class 45·25 includes all measurements between 44·750 and 45·749 inclusive, and, in the monoclonal population, Class 45·5 includes all measurements between 45·250 and 45·749 inclusive.

The unit of measurement for the birth measurements was 0·015 mm., and for the adult measurements 0·042. To bring the tables for adult measurements to the same units as those for birth measurements, the value of each class must therefore be multiplied by 2·77.

In a few tables the lowest class is given as "below 42·25," etc. In these cases there was one measurement separated from the next smallest measurement by more than one class interval. In these cases the lowest class was, nevertheless, treated as being consecutive with the lowest but one, in order to avoid unduly influencing the correlation coefficient by a single outlying observation.

As explained in the text, the ancestral correlation for birth measurements (except in the small strain) are not between individual ancestors and their individual offspring, but between the mean of the brood to which the ancestor belonged and the mean of its brood of offspring. The actual number of individual measurements is therefore much greater than the number of entries in the correlation tables. In the case of the adult measurements, the correlations are between individual ancestors and their individual offspring.

Tables XIX–XXI.—Correlations between adult measurement of parent, the number of eggs laid by it in its first brood, and the birth measurement of the young developing from those eggs. This last is the mean of the five young measured in each brood.

Only the tables for Generation 4 of the monoclonal population are given, these being sufficient to illustrate the connection between the three features. The measurements are the actual or uncorrected ones (p. 433).

Tables XXII–XXXI.—Ancestral correlations for birth measurements (corrected), polyclonal population, large strain.

In compiling these tables from the original records, one line of one clone was omitted altogether, as it fell out of synchronism with the rest of the population, so that the method of correction described on p. 433 could not be applied to it. In addition, one brood from each of two other clones was omitted, one because the new-born young were so small as to fall into the category of pathological deformities, and the other because all the young were born dead or dying.

Tables XXXII–XXXVII.—Ancestral correlations for adult measurements (corrected), polyclonal population, large strain.

With the same omissions as for birth measurements.

Tables XXXVIII–XL.—Ancestral correlations for the corrected measurements, polyclonal population, small strain.

In compiling these tables, one brood was omitted owing to the extreme pathological smallness of the new-born young. It must also be recorded that in one generation one line of each of two clones was kept for a few days under slightly different conditions from those described in the text as the general conditions. This fact is, however, only recorded for the purely formal reason that it constituted an exception to these conditions.* It certainly had no significant influence on the correlation coefficient.

As stated in the text, four generations were combined to construct these tables. Hence a number of individuals appear in them twice, both as offspring of their ancestors and ancestors of their own offspring. Also each ancestor was taken over again with each of its separate offspring. The total numbers of separate individuals dealt

* The only other exception in the whole *S. exspinosus* experiment was that on one occasion during the life-time of Generation 4 three days instead of two elapsed between the changing of the water in the breeding tubes.

with are 86 (instead of $76 \times 2 = 152$) in Table XXXVIII, 69 in Table XXXIX, and 37 in Table XL.

Tables XXXVIII and XXXIX are for birth measurements, Table XL for adult measurements.

Tables XLI–L.—Ancestral correlations for birth measurements (corrected) in the monoclonal population.

Tables LI–LVI.—Ancestral correlations for adult measurements (corrected) in the monoclonal population. In compiling these tables from the original records, one individual was omitted, as being pathologically small.

Tables LVII–LXIII.—*Macrosiphum antherinii.*

Table LVII.—Organic correlation between antennar length and frontal breadth.

Tables LVIII–LX.—Correlations between parent and offspring for antennar length, frontal breadth and ratio. In these tables 50 individuals appear twice, once as offspring and once as parents. All the parents had one offspring only, except seven which had two each. These parents are counted twice over, once with each offspring, in the usual way. The total number of separate individuals comprised in each of these tables is therefore not 248 but 191.

Tables LXI–LXIII.—Correlations between grandparent and offspring for the same three characters. The actual number of grandparents in each table is 54, and of offspring 60, six of the grandparents having two offspring each.

TABLE XIX.

Birth measurements of young.	Number of eggs in the brood.								Total.
	7.	8.	9.	10.	11.	12.	13.	14.	
44·5	—	—	—	—	1	—	—	—	1
45	—	—	—	—	—	1	—	—	1
45·5	—	—	1	2	1	—	—	—	4
46	—	—	—	3	6	1	—	1	11
46·5	—	1	1	9	5	1	1	—	18
47	—	—	6	8	2	—	—	—	16
47·5	—	1	10	4	1	—	—	—	16
48	2	4	1	4	2	—	—	—	13
48·5	—	1	3	5	3	—	—	—	12
49	2	1	3	6	2	—	—	—	14
49·5	—	1	4	6	2	—	—	—	13
50	—	1	2	5	1	—	—	—	9
50·5	—	1	1	—	—	—	—	—	2
Total . . .	4	11	32	52	26	3	1	1	130

$r = -0{\cdot}345 \pm 0{\cdot}052.$

TABLE XX.

Birth measurements of young.	Adult measurement of parent.											Total.
	42.	42·5.	43.	43·5.	44.	44·5.	45.	45·5.	46.	46·5.	47.	
44·5	—	—	—	—	—	1	—	—	—	—	—	1
45	—	—	—	—	—	—	—	1	—	—	—	1
45·5	—	—	—	1	—	1	1	1	—	—	—	4
46	—	—	1	1	4	2	1	2	—	—	—	11
46·5	—	—	1	3	3	6	5	—	—	—	—	18
47	—	—	1	3	3	5	2	—	2	—	—	16
47·5	—	—	2	1	4	2	5	2	—	—	—	16
48	1	—	2	—	3	3	2	2	—	—	—	13
48·5	—	—	—	2	1	2	5	1	—	1	—	12
49	—	—	1	—	1	6	3	2	1	—	—	14
49·5	—	—	—	—	1	2	4	3	2	1	—	13
50	—	—	—	—	—	—	2	4	2	—	1	9
50·5	—	—	—	—	—	—	1	—	1	—	—	2
Total . .	1	0	8	11	20	30	31	18	8	2	1	130

$r = 0{\cdot}368 \pm 0{\cdot}051$.

TABLE XXI.

Adult measurement of parent.	Number of eggs in the brood.								Total.
	7.	8.	9.	10.	11.	12.	13.	14.	
42	1	—	—	—	—	—	—	—	1
42·5	—	—	—	—	—	—	—	—	0
43	2	1	3	2	—	—	—	—	8
43·5	—	1	3	5	2	—	—	—	11
44	—	1	8	5	4	2	—	—	20
44·5	1	4	7	15	3	—	—	—	30
45	—	1	7	12	10	—	1	—	31
45·5	—	2	3	9	2	1	—	1	18
46	—	—	1	4	3	—	—	—	8
46·5	—	1	—	—	1	—	—	—	2
47	—	—	—	—	1	—	—	—	1
Total . .	4	11	32	52	26	3	1	1	130

$r = 0{\cdot}298 \pm 0{\cdot}054$.

TABLE XXII.—Generations 1 and 2.

Offspring.	Parents.							Total.
	42·25.	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	
42·25	1	1	1	—	—	—	—	3
43·25	—	—	4	—	3	—	—	7
44·25	1	2	5	5	10	—	—	23
45·25	—	1	2	5	6	1	2	17
46·25	—	2	2	4	7	6	2	23
47·25	—	—	—	2	9	8	8	27
48·25	—	—	—	—	2	3	2	7
49·25	—	—	—	—	—	1	1	2
50·25	—	—	—	—	—	—	1	1
Total. . .	2	6	14	16	37	19	16	110

$r = 0{\cdot}640 \pm 0{\cdot}038.$

TABLE XXIII.—Generations 2 and 3.

Offspring.	Parents.									Total.
	42·25.	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	49·25.	50·25	
41·25	1	—	—	—	—	—	—	—	—	1
42·25	—	—	1	—	—	—	—	—	—	1
43·25	—	—	1	1	2	1	1	—	—	6
44·25	1	1	5	—	—	2	—	—	—	9
45·25	1	1	5	5	6	4	—	—	—	22
46·25	—	4	8	5	8	5	4	—	—	34
47·25	—	—	1	4	4	5	1	2	1	18
48·25	—	1	2	1	2	8	—	—	—	14
49·25	—	—	—	—	—	1	1	—	—	2
Total . .	3	7	23	16	22	26	7	2	1	107

$r = 0{\cdot}339 \pm 0{\cdot}058.$

TABLE XXIV.—Generations 3 and 4.

Offspring.	Parents.									Total.
	41·25.	42·25.	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	49·25.	
Below 42·25	—	—	—	—	—	—	1	—	—	1
42·25	—	—	1	—	—	—	—	—	—	1
43·25	—	—	—	1	1	1	1	—	—	4
44·25	1	1	3	2	3	2	2	1	—	15
45·25	—	—	1	4	6	14	3	4	—	32
46·25	—	—	—	1	8	8	5	4	—	26
47·25	—	—	—	—	4	8	2	1	1	16
48·25	—	—	1	—	1	2	2	2	—	8
49·25	—	—	—	—	—	—	2	—	—	2
Total . .	1	1	6	8	23	35	18	12	1	105

$r = 0{\cdot}298 \pm 0{\cdot}060.$

TABLE XXV.—Generations 4 and 5.

Offspring.	Parents.								Total.
	Below 43·25.	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	49·25.	
42·25	—	—	—	1	—	—	—	—	1
43·25	—	1	4	2	1	—	—	—	8
44·25	1	—	3	6	3	5	1	—	19
45·25	—	1	4	14	11	3	1	1	35
46·25	—	—	2	5	4	4	4	2	21
47·25	—	—	—	1	1	1	1	—	4
48·25	—	—	—	—	2	—	—	—	2
49·25	—	—	—	—	—	1	—	—	1
Total . .	1	2	13	29	22	14	7	3	91

$r = 0{\cdot}365 \pm 0{\cdot}061.$

TABLE XXVI.—Generations 1 and 3.

Offspring.	Grandparents.							Total.
	42·25.	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	
41·25	1	—	—	—	—	—	—	1
42·25	1	—	—	—	—	—	—	1
43·25	—	2	—	—	2	1	1	6
44·25	—	—	5	1	3	—	—	9
45·25	—	2	5	3	10	1	1	22
46·25	—	1	1	9	13	7	3	34
47·25	—	1	2	2	5	2	6	18
48·25	—	—	1	2	4	4	3	14
49·25	—	—	—	—	—	1	1	2
Total . .	2	6	14	17	37	16	15	107

$r = 0{\cdot}447 \pm 0{\cdot}052.$

TABLE XXVII.—Generations 2 and 4.

Offspring.	Grandparents.									Total.
	42·25.	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	49·25.	50·25.	
Below 42·25	—	—	—	1	—	—	—	—	—	1
42·25	—	—	1	—	—	—	—	—	—	1
43·25	—	1	1	—	1	1	—	—	—	4
44·25	1	1	6	1	4	1	1	—	—	15
45·25	1	4	7	4	6	7	3	—	—	32
46·25	1	—	5	5	7	5	2	—	1	26
47·25	—	—	2	3	5	3	2	1	—	16
48·25	—	—	—	2	—	6	—	—	—	8
49·25	—	—	—	—	—	1	—	1	—	2
Total . .	3	6	22	16	23	24	8	2	1	105

$r = 0{\cdot}349 \pm 0{\cdot}058.$

TABLE XXVIII.—Generations 3 and 5.

Offspring.	Grandparents.							Total.
	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	49·25.	
42·25	—	—	—	1	—	—	—	1
43·25	1	2	1	2	2	—	—	8
44·25	2	2	6	7	2	—	—	19
45·25	1	3	8	14	3	6	—	35
46·25	—	1	3	6	7	4	1	22
47·25	—	—	—	1	1	2	—	4
48·25	—	—	—	—	2	—	—	2
49·25	—	—	—	1	—	—	—	1
Total. . .	4	8	18	32	17	12	1	92

$r = 0{\cdot}379 \pm 0{\cdot}060$.

TABLE XXIX.—Generations 1 and 4.

Offspring.	Great-grandparents.							Total.
	42·25.	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	
Below 42·25	—	—	1	—	—	—	—	1
42·25	—	—	—	—	1	—	—	1
43·25	—	—	1	2	1	—	—	4
44·25	2	3	4	1	4	—	1	15
45·25	—	1	5	6	14	5	1	32
46·25	—	2	2	7	8	3	4	26
47·25	—	—	—	1	4	6	5	16
48·25	—	—	—	—	4	2	2	8
49·25	—	—	—	—	—	1	1	2
Total. . .	2	6	13	17	36	17	14	105

$r = 0{\cdot}492 \pm 0{\cdot}050$.

TABLE XXX.—Generations 2 and 5.

Offspring.	Great-grandparents.									Total.
	42·25.	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	49·25.	50·25.	
42·25	—	—	1	—	—	—	—	—	—	1
43·25	—	2	2	—	2	2	—	—	—	8
44·25	—	—	7	3	6	3	—	—	—	19
45·25	2	2	5	7	9	5	5	—	—	35
46·25	—	1	3	3	2	11	1	1	—	22
47·25	—	—	1	—	—	2	1	—	—	4
48·25	—	—	—	—	1	—	—	—	1	2
49·25	—	—	—	—	1	—	—	—	—	1
Total . .	2	5	19	13	21	23	7	1	1	92

$r = 0 \cdot 323 \pm 0 \cdot 063$.

TABLE XXXI.—Generations 1 and 5.

Offspring	Great-great-grandparents.						Total.
	43·25.	44·25.	45·25.	46·25.	47·25.	48·25.	
42·25	—	—	—	1	—	—	1
43·25	—	2	1	5	—	—	8
44·25	4	2	3	7	3	—	19
45·25	1	3	8	15	6	2	35
46·25	—	3	2	3	3	11	22
47·25	—	—	—	1	2	1	4
48·25	—	—	—	1	—	1	2
49·25	—	—	—	—	1	—	1
Total . . .	5	10	14	33	15	15	92

$r = 0 \cdot 430 \pm 0 \cdot 057$.

TABLE XXXII.—Generations 1 and 2.

Offspring.	Parents.								Total.
	Below 36·25.	36·25.	37·25.	38·25.	39·25.	40·25.	41·25.	42·25.	
38·25	—	—	—	1	1	—	—	—	2
39·25	—	—	—	—	2	1	—	—	3
40·25	1	—	—	1	2	—	—	—	4
41·25	—	—	2	7	2	—	—	—	11
42·25	—	—	1	8	16	7	—	1	33
43·25	—	—	—	5	15	10	5	2	37
44·25	—	1	—	—	1	4	6	—	12
45·25	—	—	—	—	2	2	—	1	5
Total . . .	1	1	3	22	41	24	11	4	107

$r = 0{\cdot}423 \pm 0{\cdot}054.$

TABLE XXXIII.—Generations 2 and 3.

Offspring.	Parents.								Total.
	38·25.	39·25.	40·25.	41·25.	42·25.	43·25.	44·25.	45·25.	
37·25	—	—	—	—	2	2	—	—	4
38·25	1	—	2	4	9	3	—	—	19
39·25	—	1	2	5	8	15	2	—	33
40·25	1	2	—	2	11	11	6	2	35
41·25	—	—	—	—	2	5	3	2	12
42·25	—	—	—	—	—	1	—	1	2
Total . . .	2	3	4	11	32	37	11	5	105

$r = 0{\cdot}348 \pm 0{\cdot}058.$

TABLE XXXIV.—Generations 3 and 4.

Offspring.	Parents.						Total.
	37·25.	38·25.	39·25.	40·25.	41·25.	42·25.	
37·25	—	—	—	1	—	—	1
38·25	1	—	3	1	—	—	5
39·25	2	9	9	6	1	—	27
40·25	1	7	11	10	2	—	31
41·25	—	2	5	6	6	—	19
42·25	—	—	1	4	—	—	5
43·25	—	—	—	1	1	1	3
Total . . .	4	18	29	29	10	1	91

$r = 0{\cdot}412 \pm 0{\cdot}059.$

TABLE XXXV.—Generations 1 and 3.

Offspring.	Grandparents.								Total.
	Below 36·25.	36·25.	37·25.	38·25.	39·25.	40·25.	41·25.	42·25.	
37·25	—	—	—	1	2	1	—	—	4
38·25	—	—	1	6	9	3	—	—	19
39·25	1	1	1	9	14	6	1	—	33
40·25	—	—	1	4	14	9	5	2	35
41·25	—	—	—	—	1	5	5	1	12
42·25	—	—	—	—	1	—	—	1	2
Total. . .	1	1	3	20	41	24	11	4	105

$r = 0{\cdot}436 \pm 0{\cdot}053.$

TABLE XXXVI.—Generations 2 and 4.

Offspring.	Grandparents.								Total.
	38·25.	39·25.	40·25.	41·25.	42·25.	43·25.	44·25.	45·25.	
37·25	—	—	—	—	—	1	—	—	1
38·25	—	1	—	1	2	1	—	—	5
39·25	1	1	2	5	7	10	2	—	28
40·25	1	—	2	2	11	12	3	—	31
41·25	—	—	—	1	6	6	5	1	19
42·25	—	—	—	—	—	3	2	—	5
43·25	—	—	—	—	—	1	—	2	3
Total. . .	2	2	4	9	26	34	12	3	92

$r = 0 \cdot 409 \pm 0 \cdot 059$.

TABLE XXXVII.—Generations 1 and 4.

Offspring.	Great-grandparents.								Total.
	Below 36·25.	36·25.	37·25.	38·25.	39·25.	40·25.	41·25.	42·25.	
37·25	—	—	—	1	—	—	—	—	1
38·25	—	—	—	2	2	1	—	—	5
39·25	1	1	1	7	15	3	—	—	28
40·25	—	—	1	4	15	6	4	1	31
41·25	—	—	—	4	1	9	5	—	19
42·25	—	—	—	—	—	3	2	—	5
43·25	—	—	—	—	1	—	—	2	3
Total. . .	1	1	2	18	34	22	11	3	92

$r = 0 \cdot 505 \pm 0 \cdot 052$.

Table XXXVIII.

Offspring.	Parents.						Total.
	40·75.	41·75.	42·75.	43·75.	44·75.	45·75.	
39·75	—	2	—	—	—	—	2
40·75	—	—	1	2	—	—	3
41·75	—	3	5	6	—	—	14
42·75	2	5	7	5	2	—	21
43·75	—	2	7	2	3	—	14
44·75	—	1	—	6	3	3	13
45·75	—	—	2	1	4	—	7
46·75	—	—	—	—	1	—	1
47·75	—	—	—	—	1	—	1
Total . . .	2	13	22	22	14	3	76

$r = 0 \cdot 472 \pm 0 \cdot 060.$

Table XXXIX.

Offspring.	Grandparents.						Total.
	40·75.	41·75.	42·75.	43·75.	44·75.	45·75.	
39·75	—	—	—	1	—	—	1
40·75	—	—	—	—	—	—	—
41·75	3	3	2	2	—	—	10
42·75	1	4	2	7	1	—	15
43·75	—	7	—	1	1	1	10
44·75	—	3	3	1	—	—	7
45·75	—	—	—	—	1	2	3
46·75	—	—	—	—	—	1	1
47·75	—	—	—	—	—	1	1
Total . . .	4	17	7	12	3	5	48

$r = 0 \cdot 425 \pm 0 \cdot 080.$

TABLE XL.

Offspring.	Parents.						Total.
	28·75.	29·75.	30·75.	31·75.	32·75.	33·75.	
28·75	—	1	—	1	—	—	2
29·75	2	1	—	—	—	—	3
30·75	—	3	—	1	—	—	4
31·75	—	—	2	2	5	1	10
32·75	—	—	1	2	3	—	6
33·75	—	—	—	1	—	—	1
Total . . .	2	5	3	7	8	1	26

$r = 0{\cdot}598 \pm 0{\cdot}085.$

TABLE XLI.—Generations 1 and 2.

Offspring.	Parents.						Total.
	46.	46·5.	47.	47·5.	48.	48·5.	
Below 46·5	—	—	—	—	—	1	1
46·5	1	—	—	—	—	—	1
47	1	—	1	—	—	—	2
47·5	1	1	4	1	—	—	7
48	2	3	4	3	—	—	12
48·5	2	6	3	3	—	4	18
49	3	3	8	5	4	2	25
49·5	7	2	9	9	4	1	32
50	5	5	6	3	4	1	24
50·5	—	1	2	1	2	1	7
51	—	1	2	1	1	—	5
51·5	—	—	—	1	—	—	1
Total . . .	22	22	39	27	15	10	135

$r = 0{\cdot}101 \pm 0{\cdot}057.$

TABLE XLII.—Generations 2 and 3.

Offspring.	Parents.												Total.
	Below 46·5.	46·5.	47.	47·5.	48.	48·5.	49.	49·5.	50.	50·5.	51.	51·5.	
46	—	—	—	—	—	—	1	—	—	—	—	—	1
46·5	—	—	—	—	3	1	1	1	4	—	—	—	10
47	—	—	—	—	—	2	—	4	1	—	—	—	7
47·5	—	—	1	—	1	2	4	5	3	1	2	—	19
48	—	—	—	—	2	6	4	9	3	1	2	1	28
48·5	1	1	—	1	4	—	6	5	7	3	1	—	29
49	—	—	—	2	1	4	8	6	4	1	—	—	26
49·5	—	—	1	4	—	2	1	3	2	1	—	—	14
50	—	—	—	—	—	—	—	1	—	—	—	—	1
Total . .	1	1	2	7	11	17	25	34	24	7	5	1	135

$r = -0{\cdot}111 \pm 0{\cdot}057.$

TABLE XLIII.—Generations 3 and 4.

Offspring.	Parents.								Total.
	46.	46·5.	47.	47·5.	48.	48·5.	49.	49·5.	
44·5	—	—	—	—	—	1	—	—	1
45	—	1	—	—	—	1	—	—	2
45·5	—	1	—	1	1	2	2	1	8
46	—	1	—	3	1	4	4	4	17
46·5	1	2	3	5	7	8	5	1	32
47	—	3	2	5	8	4	4	3	29
47·5	—	3	2	3	7	6	9	2	32
48	—	—	—	—	3	2	1	2	8
48·5	—	—	—	—	—	—	—	1	1
Total . . .	1	11	7	17	27	28	25	14	130

$r = 0{\cdot}048 \pm 0{\cdot}059.$

TABLE XLIV.—Generations 4 and 5.

Offspring.	Parents.									Total.
	44·5.	45.	45·5.	46.	46·5.	47.	47·5.	48.	48·5.	
46	—	—	—	—	—	—	1	—	—	1
46·5	—	—	—	—	2	—	—	—	—	2
47	—	—	1	—	—	—	2	—	—	3
47·5	—	—	—	—	1	—	1	1	—	3
48	—	—	1	—	4	3	4	1	—	13
48·5	—	1	1	6	4	11	7	2	—	32
49	1	—	3	9	15	10	9	4	1	52
49·5	—	1	3	2	4	5	5	—	—	20
50	—	—	—	1	3	1	2	—	—	7
50·5	—	—	—	1	1	—	—	—	—	2
Total. .	1	2	9	19	34	30	31	8	1	135

$r = -0{\cdot}139 \pm 0{\cdot}057.$

TABLE XLV.—Generations 1 and 3.

Offspring.	Grandparents.						Total.
	46.	46·5.	47.	47·5.	48.	48·5.	
46	—	—	1	—	—	—	1
46·5	2	2	4	1	1	—	10
47	1	—	2	2	—	2	7
47·5	1	4	5	6	2	1	19
48	1	6	6	10	4	1	28
48·5	8	1	6	6	6	2	29
49	6	3	11	2	2	2	26
49·5	2	3	5	1	1	2	14
50	—	1	—	—	—	—	1
Total . .	21	20	40	28	16	10	135

$r = -0{\cdot}058 \pm 0{\cdot}058.$

TABLE XLVI.—Generations 2 and 4.

Offspring.	Grandparents.												Total.
	Below 46·5.	46·5.	47.	47·5.	48.	48·5.	49.	49·5.	50.	50·5.	51.	51·5.	
44·5	—	1	—	—	—	—	—	—	—	—	—	—	1
45	—	—	—	—	1	—	—	1	—	—	—	—	2
45·5	—	—	—	1	1	1	1	2	1	1	—	—	8
46	—	—	—	3	1	1	5	2	4	1	—	—	17
46·5	1	—	2	—	2	3	6	10	4	2	2	—	32
47	—	—	—	1	2	5	4	7	8	1	1	—	29
47·5	—	—	—	1	2	6	7	6	7	—	2	1	32
48	—	—	—	—	1	2	—	3	—	2	—	—	8
48·5	—	—	—	1	—	—	—	—	—	—	—	—	1
Total . .	1	1	2	7	10	18	23	31	24	7	5	1	130

$r = 0 \cdot 142 \pm 0 \cdot 058$.

TABLE XLVII.—Generations 3 and 5.

Offspring.	Grandparents.								Total.
	46.	46·5.	47.	47·5.	48.	48·5.	49.	49·5.	
46	—	—	—	—	—	—	1	—	1
46·5	1	—	—	—	—	—	1	—	2
47	—	—	—	—	—	1	2	—	3
47·5	—	—	—	—	2	1	—	—	3
48	—	—	1	1	4	4	2	1	13
48·5	—	3	1	6	5	8	7	2	32
49	—	6	2	8	10	10	9	7	52
49·5	—	2	2	4	4	2	3	3	20
50	—	—	1	—	3	3	—	—	7
50·5	—	—	—	—	—	1	—	1	2
Total . .	1	11	7	19	28	30	25	14	135

$r = -0 \cdot 041 \pm 0 \cdot 058$.

TABLE XLVIII.—Generations 1 and 4.

Offspring.	Great-grandparents.						Total.
	46.	46·5.	47.	47·5.	48.	48·5.	
44·5	1	—	—	—	—	—	1
45	—	—	—	1	1	—	2
45·5	2	1	3	2	—	—	8
46	1	2	5	5	2	2	17
46·5	5	3	10	6	4	4	32
47	3	6	9	3	6	2	29
47·5	8	6	7	7	2	2	32
48	1	1	5	—	1	—	8
48·5	—	—	—	1	—	—	1
Total . . .	21	19	39	25	16	10	130

$r = -0{\cdot}077 \pm 0{\cdot}059.$

TABLE XLIX.—Generations 2 and 5.

Offspring.	Great-grandparents.											Total.
	Below 46·5.	46·5.	47.	47·5.	48.	48·5.	49.	49·5.	50.	50·5.	51.	
46	—	—	—	—	—	—	—	1	—	—	—	1
46·5	—	—	—	—	—	—	1	—	1	—	—	2
47	—	—	—	1	—	1	1	—	—	—	—	3
47·5	—	—	—	—	1	—	—	1	1	—	—	3
48	—	—	—	2	—	2	1	3	1	2	2	13
48·5	—	—	—	2	2	9	5	4	6	3	1	32
49	—	1	2	2	4	4	8	16	11	2	2	52
49·5	—	—	—	—	1	3	6	5	5	—	—	20
50	1	—	—	—	2	1	2	1	—	—	—	7
50·5	—	—	—	1	1	—	—	—	—	—	—	2
Total .	1	1	2	8	11	20	24	31	25	7	5	135

$r = -0{\cdot}119 \pm 0{\cdot}057.$

TABLE L.—Generations 1 and 5.

Offspring.	Great-great-grandparents.						Total.
	46.	46·5.	47.	47·5.	48.	48·5.	
46	—	—	1	—	—	—	1
46·5	—	—	2	—	—	—	2
47	2	—	1	—	—	—	3
47·5	—	1	2	—	—	—	3
48	1	1	6	3	2	—	13
48·5	6	9	6	4	4	3	32
49	7	3	15	14	9	4	52
49·5	3	6	6	2	1	2	20
50	2	1	1	2	—	1	7
50·5	—	1	—	1	—	—	2
Total . . .	21	22	40	26	16	10	135

$r = 0{\cdot}066 \pm 0{\cdot}058$.

TABLE LI.—Generations 1 and 2.

Offspring.	Parents.							Total.
	43.	43·5.	44.	44·5.	45.	45·5.	46.	
42	—	—	1	—	—	—	—	1
42·5	—	—	1	—	—	1	1	3
43	—	1	1	1	1	1	—	5
43·5	2	2	2	1	1	—	1	9
44	—	2	3	4	3	—	1	13
44·5	—	2	7	10	8	5	1	33
45	3	3	8	9	7	9	1	40
45·5	—	—	3	3	7	3	—	16
46	1	1	6	2	3	2	—	15
Total . . .	6	11	32	30	30	21	5	135

$r = 0{\cdot}039 \pm 0{\cdot}058$.

TABLE LII.—Generations 2 and 3.

Offspring.	Parents.									Total.
	42.	42·5.	43.	43·5.	44.	44·5.	45.	45·5.	46.	
42	—	—	—	—	—	1	—	—	—	1
42·5	—	—	—	—	—	1	—	—	—	1
43	—	1	—	—	—	3	3	1	1	9
43·5	—	1	1	2	1	—	3	3	—	11
44	—	—	1	1	3	5	7	3	4	24
44·5	1	—	—	6	3	9	12	2	5	38
45	—	—	1	—	2	8	9	4	2	26
45·5	—	1	2	—	3	2	4	1	2	15
46	—	—	—	—	1	1	2	—	—	4
46·5	—	—	—	—	—	—	—	1	—	1
Total . . .	1	3	5	9	13	30	40	15	14	130

$r = 0 \cdot 022 \pm 0 \cdot 059.$

TABLE LIII.—Generations 3 and 4.

Offspring.	Parents.										Total.
	42.	42·5.	43.	43·5.	44.	44·5.	45.	45·5.	46.	46·5.	
40·5	—	—	—	—	—	—	1	—	—	—	1
41	—	—	1	—	—	—	1	—	—	—	2
41·5	—	—	—	—	3	3	3	—	1	—	10
42	—	—	1	3	2	7	3	1	—	—	17
42·5	1	—	3	1	3	8	9	4	1	—	30
43	—	—	1	3	6	12	8	4	1	—	35
43·5	—	1	2	2	3	6	3	4	—	—	21
44	—	—	—	—	5	3	1	1	1	1	12
44·5	—	—	—	2	1	1	—	1	—	—	5
45	—	—	1	—	—	—	—	—	—	—	1
Total .	1	1	9	11	23	40	29	15	4	1	134

$r = -0 \cdot 040 \pm 0 \cdot 058.$

TABLE LIV.—Generations 1 and 3.

Offspring.	Grandparents.							Total.
	43.	43·5.	44.	44·5.	45.	45·5.	46.	
42	—	—	—	1	—	—	—	1
42·5	—	—	—	1	—	—	—	1
43	—	—	2	2	3	2	—	9
43·5	1	—	2	1	2	3	2	11
44	—	3	7	6	6	2	—	24
44·5	5	2	10	7	7	6	1	38
45	—	3	6	5	8	4	—	26
45·5	—	4	2	4	3	1	1	15
46	—	—	1	—	—	2	1	4
46·5	—	—	—	1	—	—	—	1
Total . .	6	12	30	28	29	20	5	130

$r = -0{\cdot}036 \pm 0{\cdot}059.$

TABLE LV.—Generations 2 and 4.

Offspring.	Grandparents.									Total.
	42.	42·5.	43.	43·5.	44.	44·5.	45.	45·5.	46.	
40·5	—	—	—	—	—	—	1	—	—	1
41	—	—	—	—	—	2	—	—	—	2
41·5	—	—	2	—	2	3	2	—	1	10
42	—	—	—	2	1	3	6	2	3	17
42·5	—	1	1	2	3	6	9	4	4	30
43	—	1	—	4	2	10	10	4	4	35
43·5	1	1	1	—	4	7	5	1	1	21
44	—	—	2	2	—	1	3	4	—	12
44·5	—	1	—	—	1	—	3	—	—	5
45	—	—	—	—	—	—	1	—	—	1
Total . .	1	4	6	10	13	32	40	15	13	134

$r = -0{\cdot}087 \pm 0{\cdot}058.$

TABLE LVI.—Generations 1 and 4.

Offspring.	Great-grandparents.							Total.
	43.	43·5.	44.	44·5.	45.	45·5.	46.	
40·5	—	1	—	—	—	—	—	1
41	—	—	—	2	—	—	—	2
41·5	—	—	2	3	3	1	1	10
42	1	1	4	4	1	4	2	17
42·5	2	2	5	6	9	6	—	30
43	2	1	14	6	6	5	1	35
43·5	1	2	4	6	5	2	1	21
44	—	3	2	3	3	1	—	12
44·5	—	2	2	—	—	1	—	5
45	—	—	—	—	1	—	—	1
Total . .	6	12	33	30	28	20	5	134

$r = -0{\cdot}113 \pm 0{\cdot}058.$

TABLE LVII.

Frontal breadth.	Length of antenna.											Total.
	145.	150.	155.	160.	165.	170.	175.	180.	185.	190.	195.	
35·5	1	—	—	—	—	—	—	—	—	—	—	1
36	1	—	1	1	—	—	—	—	—	—	—	3
36·5	4	1	2	1	—	—	—	—	—	—	—	8
37	1	—	7	5	3	—	—	1	—	—	—	17
37·5	—	2	2	6	2	—	—	—	—	—	—	12
38	1	—	4	14	7	5	—	—	—	—	—	31
38·5	—	1	—	2	5	13	1	—	—	—	—	22
39	—	—	—	2	12	21	7	4	—	—	—	46
39·5	—	—	—	1	4	14	6	4	2	—	—	31
40	—	—	—	—	1	4	5	5	4	2	—	21
40·5	—	—	—	—	—	1	5	5	—	—	—	11
41	—	—	—	—	—	3	1	3	3	1	—	11
41·5	—	—	—	—	—	—	—	2	2	—	1	5
42	—	—	—	—	—	—	—	1	1	—	—	2
Total . .	8	4	16	32	34	61	25	25	12	3	1	221

$r = 0{\cdot}805 \pm 0{\cdot}016.$

TABLE LVIII.—Length of Antenna.

Offspring.	Parents.										Total.
	145.	150.	155.	160.	165.	170.	175.	180.	185.	190.	
145	1	—	1	—	—	—	—	—	—	—	2
150	—	—	1	2	—	—	—	—	—	—	3
155	2	1	2	—	—	3	1	—	—	—	9
160	1	1	1	5	3	1	2	1	—	—	15
165	1	1	1	4	4	3	1	1	1	—	17
170	1	—	2	2	7	12	4	5	—	—	33
175	—	—	—	3	1	9	—	1	3	—	17
180	—	—	—	1	4	9	2	3	—	1	20
185	—	—	—	—	1	2	2	1	—	—	6
190	—	—	—	—	1	—	—	—	—	—	1
195	—	—	—	—	—	—	—	—	1	—	1
Total . . .	6	3	8	17	21	39	12	12	5	1	124

$r = 0{\cdot}482 \pm 0{\cdot}046.$

TABLE LIX.—Frontal Breadth.

Offspring.	Parents.												Total.
	36.	36·5.	37.	37·5.	38.	38·5.	39.	39·5.	40.	40·5.	41.	41·5.	
36·5	—	1	1	—	1	—	—	—	—	—	—	—	3
37	1	1	1	2	—	—	1	1	—	—	—	—	7
37·5	—	2	1	—	2	—	1	—	—	—	—	—	6
38	—	1	4	4	—	1	5	2	1	1	—	—	19
38·5	1	1	1	2	2	2	—	2	—	—	1	—	12
39	—	1	2	1	4	3	13	2	—	1	—	—	27
39·5	—	—	2	—	2	6	1	1	3	1	—	1	17
40	—	—	1	—	2	2	4	3	2	—	—	—	14
40·5	—	—	—	—	2	—	—	4	1	—	—	—	7
41	—	—	—	—	—	1	4	1	2	—	—	—	8
41·5	—	—	—	—	—	—	1	1	1	—	—	—	3
42	—	—	—	—	1	—	—	—	—	—	—	—	1
Total . . .	2	7	13	9	16	15	30	17	10	3	1	1	124

$r = 0{\cdot}433 \pm 0{\cdot}049.$

TABLE LX.—Ratio.

Offspring.	Parents.										Total.
	3·9.	4·0.	4·1.	4·2.	4·3.	4·4.	4·5.	4·6.	4·7.	4·8.	
3·9	—	1	—	—	1	—	—	—	—	—	2
4	—	—	1	1	—	—	—	—	—	—	2
4·1	—	1	1	—	3	1	4	—	—	—	10
4·2	—	4	—	4	3	5	2	—	—	1	19
4·3	1	—	3	1	4	9	4	1	—	—	23
4·4	—	2	3	3	8	11	5	3	—	1	36
4·5	—	—	—	4	3	8	5	3	—	—	23
4·6	—	—	—	2	1	1	3	—	—	—	7
4·7	—	—	—	1	—	—	—	1	—	—	2
Total . . .	1	8	8	16	23	35	23	8	—	2	124

$r = 0{\cdot}235 \pm 0{\cdot}057.$

TABLE LXI.—Length of Antenna.

Offspring.	Grandparents.									Total.
	145.	150.	155.	160.	165.	170.	175.	180.	185.	
155	1	—	1	—	1	3	—	—	—	6
160	1	—	1	1	—	3	—	—	—	6
165	—	—	2	2	3	1	—	2	1	11
170	2	—	1	2	4	6	—	—	—	15
175	—	—	1	3	1	4	—	—	—	9
180	—	—	1	1	—	5	1	—	—	8
185	—	—	—	—	2	3	—	—	—	5
Total	4	—	7	9	11	25	1	2	1	60

$r = 0{\cdot}165 \pm 0{\cdot}085.$

TABLE LXII.—Frontal Breadth.

Offspring.	Grandparents.									Total.
	36.	36·5.	37.	37·5.	38.	38·5.	39.	39·5.	40.	
37	—	1	—	—	—	1	—	—	—	2
37·5	—	—	—	—	1	—	—	—	—	1
38	—	1	1	1	4	—	4	2	—	13
38·5	—	—	—	—	—	—	1	1	—	2
39	1	—	5	1	1	—	1	2	—	11
39·5	2	—	1	1	—	3	1	1	1	10
40	—	—	—	—	2	1	2	—	—	5
40·5	—	—	—	—	—	1	1	1	1	4
41	—	—	1	—	2	1	4	—	—	8
41·5	—	—	—	—	—	—	1	1	—	2
42	—	—	—	—	—	1	1	—	—	2
Total . . .	3	2	8	3	10	8	16	8	2	60

$r = 0 \cdot 231 \pm 0 \cdot 082.$

TABLE LXIII.—Ratio.

Offspring.	Grandparents.									Total.
	4.	4·1.	4·2.	4·3.	4·4.	4·5.	4·6.	4·7.	4·8.	
4·1	—	—	1	3	1	1	—	—	—	6
4·2	2	2	2	2	3	—	1	—	—	12
4·3	1	3	2	3	4	2	1	—	1	17
4·4	1	2	1	4	4	3	—	—	—	15
4·5	—	2	2	1	2	1	—	—	—	8
4·6	—	—	1	—	1	—	—	—	—	2
Total . . .	4	9	9	13	15	7	2	—	1	60

$r = -0 \cdot 002 \pm 0 \cdot 087.$