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THE RISE OF GENETICS[1]

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THE new developments in science that occur from time to time can generally be traced either to the invention of a new method or to the discovery of a new fact that has far-reaching consequences, or to the elaboration of a new theoretical principle that suggests new lines of investigation. In the latter case, it is the prerogative of science, in comparison with the speculative procedure of philosophy and metaphysics, to cherish those theories that can be given an experimental verification and to disregard the rest, not because they are wrong, but because they are useless.

In the case of genetics the situation was in some respects different from any of these procedures; for it began with the discovery of a discovery that had been made 35 years before. We can date the beginning of genetics, then, from the resurrection of Mendel's paper in 1900. Its rehabilitation was not, however, due to a literary find, but to a need resulting from similar experiments by de Vries, Correns and Tschermak that unveiled a series of phenomena identical with the facts of Mendel's earlier work.

The significant fact is that when the time was ripe to appreciate its fundamental significance, Mendel's forgotten paper was discovered with the result that the activities of hundreds of biologists, as the program of this present Congress bears witness, had the direction of their scientific careers entirely redirected, or begun along new lines. The discoveries that rapidly followed, showing that the same laws applied widely to the other plants and to animals also, brought about realization that a great step forward in biology had been made.

But before we consider the rise of genetics after the year 1900, it is proper on this occasion to pay

[1] Address of the president of the Sixth International Congress of Genetics at Cornell University, Ithaca, New York, August 25, 1932.

tribute to the earlier work in hybridizing that furnished the background of procedure to which Mendel himself probably owed a considerable debt. Let us pause for a moment and recall a bit of history, for it would be unfair to forget or to underrate everything prior to the first year of the present century.

If to-day we express surprise that Mendel's paper remained unnoticed for 35 years, let us recall that this is a not unfamiliar experience in biological science. Between the experimental proof of sex in plants by Camerarius (1694) and the prize essay of Linnaeus on the sex of plants (1760) sixty-six years elapsed.

At about this time the scientific study of hybridizing may also be said to have been begun by Linnaeus and his students, and especially by Kohlreuter in several memorable papers (1760–66).

Then, thirty-three years elapsed before Sprengel's (1793) observations on the natural crossing of plants by insects, which made clear that cross-fertilization is of wide-spread occurrence in flowering plants.

More interesting, perhaps, to modern geneticists are the pioneer experiments on peas that, in a very real sense, were the precursors of Mendel's work. It is not as generally known as it should be that some of the facts on which Mendel's results with garden peas rested had been recorded by several earlier experimenters. In 1823 Thomas Knight, 42 years before Mendel, described a cross between a pea with a gray seed-coat and one with a white that gave seeds which were uniformly gray-coated. These seeds when grown produced in the next year both gray and white seeds. John Goss had in 1822 also reported experiments with garden peas and found the first generation of offspring had seeds like the paternal race. From these in the next generation he obtained peas of two kinds, one like those of the original grandpaternal race, the others like those of the grandmaternal. Separating these he found that the blue peas produced in F_3 only blues, and the white peas both blues and whites. Here is an example of what to-day we call dominance and recessiveness, as well as segregation in F_2. In the same year (1822) Alexander Seton reported similar results. Nearly fifty years later Thomas Laxton (1868–72), working with peas, recorded numerous facts similar to those first spoken of, and in addition he mentioned cases in which two pairs of contrasted characters were present. Assortment between the pairs was found—which result is familiar to students to-day and which Mendel's work established.

Amongst the earlier hybridists the name of Naudin (1861–64) is most often referred to as a forerunner of Mendel, and it is sometimes stated that he anticipated Mendel's discoveries. His principal prize paper appeared in 1863, two years prior to Mendel's paper before the Brunn Society, and was followed by two others in 1864 and 1865. Naudin laid emphasis on the identity of individuals of the first generation hybrids, including reciprocal crosses. He insisted on the intermediate character of the F_1 hybrid, with the important reservation that the intermediate forms do not stand always equally distant from the two parents. We now know that, taken character by character, sometimes an intermediate condition, sometimes complete dominance, may be found. But whichever condition holds for a particular character, the phenomenon of segregation in the germ-cells of the F_1 hybrid remains unaffected.

Naudin stated explicitly that in the second and later generations there is a mixture of forms, including some which are like the original parents and others that approach these in various degrees. Then follows his most important deduction, namely, that the second generation results find their explanation in the disjunction of the two specific essences derived from the parents in the ovules and in the pollen of the hybrid. Here we have a highly significant contribution, for, not only did Naudin see clearly that the results are explicable on the principle of disjunction (or, as we say now, segregation), but that this, taking place both in the egg and in the pollen, gives the kinds of characters that appear. So important historically is this fact that there should be included his specific statement showing that he had a perfectly clear idea as to how disjunction accounts for the diversity in the second generation. If, he says, a pollen grain bearing the characters of the male parent meets an egg of the same kind, a plant that is a reversion to the paternal species will result; similarly for the maternal species. But if a pollen grain of one kind meets an egg of the other kind, a true cross-fertilization takes place like that of the first generation and an intermediate form will result. It will be agreed, I think, on all hands that this was a brilliant interpretation of results based on first-hand experience. It falls short of Mendel's work in two or three important aspects: (1) The failure to put the hypothesis to a test by back-crossing; (2) the failure to see what the numerical results should be on the basis of disjunction of the elements in the hybrid. His use of the words "disordered variation" in the F_2 and later generations brings out the essential difference between Naudin and Mendel. It is the orderly result of disjunction or segregation that is the important feature of Mendel's work; and finally, the clearness with which Mendel stated and proved the interrelation between character-pairs in inheritance, when more than one pair is involved, places his work distinctly above everything that had gone before. Nevertheless, the genial abbot's work was not entirely heaven-born, but had a background of one hundred years of substantial progress that made it possible for his genius to develop to its full measure.

If, in this brief review, I have neglected to bring in the names of a number of well-known selectionists whose work has been in the main in the field of agriculture, it is not because I do not realize the importance of their work or the great difficulties they overcame, but because, for the moment, we are interested especially in the development of our theoretical knowledge of genetics.

So far I have spoken only of plants. What part, may be asked, has the study of animals played in the pre-Mendelian history of genetics, *i.e.*, down to 1865?

The question of sex in plants that took botanists a hundred years to decipher was not so difficult for zoologists. If we may accept the traditional story, it was not unknown in the Garden of Eden. Aristotle had a good deal to say about it. The credit of finding a sex-determining mechanism can properly be claimed by zoologists, but this happened only in the opening years of the present century.

Hybridizing was also familiar to zoologists, but in pre-Mendelian times occupied only a relatively small part of their interest. What was known has been recorded by Darwin in his "Animals and Plants under Domestication." This scattered and loose information was incorporated after 1859 in the discussions of the theory of evolution.

The chief contribution of zoologists to present-day genetics was along different lines. In the latter half of the last century there was great activity in the field of cellular morphology. The important facts concerning chromosome-division and the extraordinary changes that take place at the time of maturation of the germ-cells and at fertilization were first made out by zoologists. The names of Kölliker, Flemming, Fol, Van Beneden, Hertwig and Boveri are landmarks in the history of cytology. Correspondingly for plants the names of Hofmeister, Strasburger, Du Bary and Guinard run a parallel course.

Weismann's theoretical contributions have also played an important historical rôle. "The Continuity of the Germ-plasm" served to counteract the all-too-prevalent influence of Lamarck and his successors, whose views if correct would undermine all that Mendel's principles have taught us. Weismann's speculations on the origin of new variations by recombination of elements in the chromosomes, while not to-day acceptable as stated by him, nevertheless focused attention on an important subject. His discussion of the interpretation of the maturation divisions played, I believe, a leading rôle in directing attention to a subject that was destined very soon to have great importance for genetics.

Thus at the end of the last century some extraordinary advances had been made in unraveling the changes that take place in the maturation of the germ-cells. These advances led to the recognition of a mechanism that was to place the theoretical elements of Mendel's hypothesis on a firm foundation of fact. But this, however, was not apparent until 1903.

GENETICS AT THE BEGINNING OF THE CENTURY

We come now to the fateful year 1900, when three lines of fundamental significance for genetics were ready to be brought together. I refer, of course, to the mutation theory of de Vries, to the rediscovery of Mendel's paper, and to the application of the discoveries in cytology to the new theories.

The intimate connection between the mutation theory, as first propounded, and the origin of the characters that follow Mendel's laws was not immediately evident, since de Vries laid emphasis on the many character changes that result from each progressive mutational step. In fact, at about this time de Vries recognized three types of mutational changes: Progressive changes—changes that introduce something new, leading to the sudden appearance of a new elementary species; retrogressive changes, the result of something lost or becoming latent; and degressive changes, in which old characters are revived.

This nomenclature, in so far as it is purely descriptive and based on characters rather than changes in the germ-plasm, covers broadly many of the facts with which we are familiar to-day. But in the light of the work of the last 30 years, especially when applied to genes, this description can no longer be accepted as fundamental; for now we have information that gives a more consistent picture of the changes produced by the genes. For example, the evidence from hybridizing elementary species, on which de Vries based in part his distinctions, has to-day a different interpretation. We no longer hold that a progressive change introduces an entirely new, unpaired element into the germ-track, for the unpaired chromosome in cases of heteroploidy can surely not be regarded as the usual step for progressive evolution. Again, the permanence of certain hybrid combinations, whenever such exceptional cases arise, are not now regarded as due to the introduction from each parent of a new unpaired element, but can be interpreted in different ways in different cases.

It was the emphasis that de Vries laid on mutational changes in the germinal material as sharply discontinuous, irrespective of the effect on the character, that has had important and far-reaching consequences for genetic work and theory.

The groundwork for discontinuous phenotypic variation had in 1894 been laid by Bateson's contribution on discontinuous variation. While we recognize that some of the examples Bateson collected are not inherited but phenotypic (which confused the picture), nevertheless his insistence on the importance of discontinuity prepared the way for the acceptance of the more fundamental distinction that de Vries had made.

But I wish to emphasize that the revolution in our ideas that took place at this time was not so much due to the insistence on discontinuity of somatic structures, but discontinuity in the hereditary elements. An example will serve to illustrate the difference. When a gene changes, its effects on new characters, taken individually, are generally very different. Some of them may be sharply marked off from the original character. The character showing the greatest effect is the one generally picked out for genetic work. But at the same time there are changes in other organs that are less conspicuous—some of the characters are so little affected or so variable that, taken by themselves, they would give a picture of continuity rather than of discontinuity. They would often pass unnoticed were not attention drawn to them by the discovery of the major change.

For the theory of evolution some of these inconspicuous changes may be more significant than the more obvious discontinuous change. In fact, if evolutionary advances are more often through invisible physiological mutational changes rather than morphological ones, we can better understand the paradoxical situation in which taxonomists find themselves, to wit, that the sharp structural differences, that are used for diagnostic separation of species, relate to characters that seem often to be unimportant for the well-being of the individual. The new point of view is a complete inversion of much of the thinking in which the evolutionary theory indulged in the past.

As I have said, the rapid expansion of genetics after 1900 has been intimately connected with the applications of the chromosome theory to the experimental work in genetics. The integrity of the chromosomes and their continuity from one cell-generation to the next, the constancy in number of the chromosomes in each species and the absence of mixing of the materials of the conjugating chromosomes at the time of meiosis have furnished the basis on which genetics rests.

I think we can not overemphasize the significance of this relation between the theoretical side of genetics and the factual side as observed in the known behavior of the material basis of heredity. To put the matter bluntly, the recognition that there is a mechanism to which genetic theory must conform, if it is to be productive, serves to keep us on the right track and acts as a check to irresponsible speculation, however attractive it may seem in print.

Some one may reply that it is not always an advantage to keep one's nose to the grindstone. Granted! but realizing how often ingenious speculation in the complex biological world has led nowhere and how often the real advances in biology as well as in chemistry, physics and astronomy have kept within the bounds of mechanistic interpretation, we geneticists should rejoice, even with our noses on the grindstone (which means both eyes on the objectives), that we have at command an additional means of testing whatever original ideas pop into our heads.

EXPANSION SINCE 1900

I come now to the expansion of the Mendelian theory that has taken place in the last 30 years. If I refrain from giving the names of the numerous contributors to this advance, it is because many of the discoverers are before me in person; or, if not, will get reports of the congress. Future congresses will probably be better able to evaluate individually the merits of those who have made the significant contributions in this generation.

It must have been evident to many geneticists after 1903 that if the chromosomes are the bearers of Mendel's elements, there would be only as many independent characters as there are chromosomes, provided the then current idea of the integrity of the chromosomes were true. This would place limitations on Mendel's second law—the law of independent assortment. In fact, the genetic evidence can now be said to have firmly established that there are more characters independently inherited, within stated limits, than there are chromosomes.

But linkage also turned out to have its limitations, and these very limitations made it possible to determine the localization of the genes in the chromosomes. I refer, of course, to crossing over. Since localization of the genes is to-day the basis of much of the quantitative work in genetics, I may be allowed to elaborate it somewhat.

The outstanding genetic fact is that these interchanges take place only between homologous chromosomes—*i.e.*, between members of the same pair.

The second important genetic fact is that when the interchange takes place, large blocks of the chromosomes are exchanged. This can be proven only in cases where more than two loci are involved, and best when a considerable number of well-spaced genes have been located. Until recently the evidence that large blocks of genes are involved in crossing over was known only genetically. No certain cytological proof was known. To-day, however, the proof has been found. No doubt this cytological evidence will be presented and discussed at this congress.

It has also been determined on genetic evidence that more than one interchange may take place between a pair of chromosomes, which can be checked only in cases where there are enough intermediate loci between two pairs to serve as markers.

A moment ago I said that crossing over has furnished the basis for the theory of localization. May I give an illustration, in the hope of removing a criticism of the localization technique that is based, I believe, on a misunderstanding? It has been said, for example, that the changes made from time to time in the genetic map of the Drosophila chromosomes discredit the method by which the localization is determined. It might as well be said that the method by which the atomic weights in chemistry were gradually improved discredited the procedure of the chemist.

Two illustrations will serve our present purpose. Let us suppose a new mutant character is found and its chromosome group—*ie.*, its linkage group—determined by familiar methods. We may proceed, then, to find its relation to two known loci in that chromosome. If these are far apart, the cross-over data will give only its approximate position. Having found this, it may turn out that the locus lies near another gene in that region, but whether above or below may be uncertain. We next proceed to find its more exact location with respect to this third gene, using either of the other two genes as a second point. In this way the new gene is more accurately placed with respect to the third locus. Further work will then be necessary if there are other genes in this region.

The second illustration concerns a distinction between crossing-over data given in the actual experiment and its conversion into map distance. For very small values, say 5 points, the two are the same because double crossing over is not present. But in longer distances the crossing-over data may depart widely from the map figures because double crossing over makes the figures too low. In Drosophila, for example, the sex chromosome is 70 units of map distance, but the crossing-over data are found to give not over 50 units. In this case the map distance has been built up piece by piece through the summation of crossing-over data of loci so near each other that double crossing over is eliminated.

In other animals and plants, where few loci have as yet been found, the cross-over data are generally put down as map distance. This may be far from the real map distance, and since the actual amount of double crossing over in such less-worked-out forms is unknown, and since crossing over is different in different species, the loci must be regarded as only provisional.

There is another factor to be taken into account. The theory of localization was based in a general way on the assumption that crossing over in one region of a chromosome has the same frequency as in other regions. The Drosophila workers have long known that this is not exact, and in fact they had invented methods to show that crossing over is different in different regions.

The crowding of the genes in some regions of the genetic map and their scarcity in other regions has been shown to be due to the different frequencies of crossing over per unit of absolute distance in the cytological chromosome. This seems to be a fundamental relation for all chromosomes. In the X-chromosome of Drosophila, which appears to be a special case, most of the genes are crowded at the two ends of the chromosome with a middle region of undetermined length having few or no genes, in the sense that the Y-chromosome is empty of genes. These facts do not invalidate the purpose for which the maps were invented, since the relative position of the genes remains the same. It is their position relative to each other, allowing very precise prediction of the topographical relation of a new gene to all other known genes, as determined by corrected cross-over data, that is important.

This brings us to one of the most recent fields of modern genetics—the study of the redistribution of the linkage group by translocation. Treatment with x-rays has been found to be a prolific source for material of this kind, but it should not be forgotten that translocation had been discovered and utilized for genetic interpretation several years before x-rays were used. Even to-day, with much evidence before us, the way in which x-rays bring about this result puzzles us. In a crude way we might picture the electron shooting holes in the chromosomes, thus breaking them apart. But when the relative sizes of the electron and the chromosome are considered, it is difficult to see how such a disruption would result from a single shot.

Even more surprising is the fact that the broken end of a piece may reunite with the end of some other chromosome and, acquiring thereby an attachment fiber, form a new linkage group. Of course it does not follow that such a reunion occurs whenever a chromosome is broken. It is only those cases where reunion does occur that are recovered and studied by geneticists. When no such union is brought about the piece, lacking an attachment point, will be lost, and the zygote containing it will probably die.

As I have said, the astonishing fact remains that the broken end becomes at times attached to the end of another chromosome. Without the objective evidence of this union that we have to-day, it might have been supposed that the broken-off fragment would rather have made, or retained, a side-to-side union with a corresponding part of its homologous chromosome. However, since the conditions of the cell that permit conjugation of like chromosomes occurs only once in the life-cycle, such a union is not, then, to be expected if the breaking has occurred after that event. If it had occurred earlier in the germ-track the piece would no doubt have been lost before meiosis came on. Here, then, we have a field inviting speculation. Let us hope that it will not long remain there, but that evidence concerning these puzzling relations may soon be forthcoming.

In this connection I need hardly recall to mind that, on the current theory of crossing over, the linear order of the genes is broken at the same level in two of the strands, and a new lengthwise reunion of the broken ends takes place. Whether this breaking and reunion is a comparable process to that seen in translocation we do not know, and it would be unprofitable at present even to make guesses.

POLYPLOIDY

In even a passing review of present-day genetics, the numerous problems connected with the increase in number of the chromosomes, or polyploidy in technical language, can not be ignored. But how can one hope even to summarize the work that is pouring in with the arrival of every new number of the genetics journals? The importance of polyploidy for the evolution doctrine is perhaps clear, but needs cautious handling in the light of the past history of phylogenetic interpretation of the facts of comparative anatomy. I hope that that history, at least, will not be repeated when the story of genetics comes to be written, for, in the light of recent work on the exchange of limbs between non-homologous chromosomes, and on translocations, the comparison of chromosome numbers without this knowledge may be very misleading. The determination of the linkages of the genes is the only safe basis for such comparisons.

At present I can do no more than briefly indicate some of the obvious and salient points. In many families of plants, and also in a more limited number of animals, chromosome groups are present that are multiples of a basal number, usually of the haploid number of the lowest member of the group. These are frequently double or triple, or quadruple groups of a basal number, generally assumed to be the haploid number. A good many of our cultivated plants are also known to show multiples of a real or postulated basal number of chromosomes. It is natural to assume that, in many cases, this has come about by the actual doubling of the whole chromosome group rather than by breaking of the chromosomes, that would also lead to doubling their number. It is more consistent to assume that doubling is the method by which the number of chromosomes is increased, because of the evidence from the sizes of the chromosomes, from their method of conjugation and from the relation of chromosomes to the attachment-fiber.

There are several known ways in which we can bring about a doubling of the number of chromosomes in a cell. The usual way is to suppress the cytoplasmic division of the cell at the time when the chromosomes divide. When this is done the chromosomes do not reunite, but the descendants of that cell will forever possess twice the original number of chromosomes. Theoretically, the process might go on forever, unless there are upper limits of a physiological nature preventing an indefinite increase. Doubling of diploids gives tetraploids. These crossed to diploids give triploids. Double tetraploids (or octoploids) crossed to tetraploids give hexaploids, and so on.

This work furnishes an opportunity for the solution of certain genetic problems of theoretical interest, for, without this knowledge, some of the known genetic ratios would have been difficult to interpret. With this knowledge they are found to conform to recognizable general principles.

It is perhaps ungracious to point out that the mere study of chromosome numbers in different species may in itself become mere hackwork. It looks as though it may become as popular for academic work as section-cutting of embryos was at an earier period. It is more generous, perhaps, to regard the work on chromosome counts as pioneering, and therefore preliminary work in the search for new materials, some of which will certainly be of value for deeper-lying genetic problems. This is especially evident in the study of hybrids whose parents, whether cultivated or wild types, have different numbers of chromosomes. The erratic behavior of the chromosomes, often seen in the maturation of the germ-cells of such hybrids, clearly explains the exceptional and often abnormal results that follow. Without this information we might be tempted to indulge in much profitless and arbitrary speculation.

Not only are we familiar with cases where a multiplication of the same group of chromosomes is brought about within the species, but there are a few cases where an increase has been brought about by crossing distinct species with different numbers of chromosomes, and chromosomes that do not mate at meioses. These situations are full of interest for students of genetics, presenting a wide range of new possibilities.

Of great importance for the genetic interpretation of polyploidy in terms of chromosomes is the identification of chromosomes that carry specific genes. Only a few years ago this was known in only one animal, but the number of cases is steadily increasing. Until information of this kind becomes more general there will be, as at present, a good deal of guessing as to the relation of chromosome groups having different numbers of chromosomes.

(*To be concluded*)

SCIENTIFIC EVENTS

MUNICIPAL RECREATION AREAS

THE National Recreation Association has issued a statement in regard to recreation areas that have been donated to cities in the United States.

According to this statement park and recreation areas, valued at more than $100,000,000 and comprising 75,000 acres, have been donated to municipalities in the United States, according to a study made by the National Recreation Association.

These parks comprise one third of all municipal recreation areas, the remainder having been secured by the expenditure of municipal funds. Some cities, including New Brunswick, New Jersey; Oneonta, New York, and Raleigh, North Carolina, reported that every acre of their existing parks was secured through gifts.

Typical of the varied types of areas given are the Edwin Gould Playground of 6.5 acres in Dobbs Ferry, New York; Percy Warner Park of 700 acres in Nashville, Tennessee, and the Littauer Park and swimming pool of 4.1 acres in Gloversville, New York. H. C. Frick, of Pittsburgh, willed 151 acres, now known as Frick Park, to the city and in addition left a fund of $2,000,000, the income from which was to be used for maintaining, improving and adding to the park.

Northampton, Massachusetts, the home of former President Coolidge, was given an area of 103 acres, known as Look Memorial Park. A fund of $450,000 was also given by Mrs. Fannie B. Look for developing and maintaining the park. Fred Morgan Kirby in 1921 gave Wilkes-Barre, Pennsylvania, $250,000 to develop Kirby Park, adding $120,000 in 1924 and creating an endowment of half a million dollars.

A variety of motives inspired the park gifts. One applicable to many gifts is the desire to perpetuate the memory of a citizen who has given special service to his community or to the nation. In Summit, New Jersey, for example, the citizens, desiring to provide a lasting memorial to Hamilton Wright Mabie, made a fund to purchase and improve a tract of land opposite the Civic Center. The area, known as the Mabie Memorial Playground, possesses natural beauty and has been equipped with many recreation facilities, including tennis courts, a shelter house and playground apparatus. The Cauldwell Playground in Morristown, New Jersey, is a memorial to a former mayor, as is the David N. Ropes Playground in Orange of the same state.

Lieutenant Clayton C. Ingersoll Memorial Park of 110 acres in Rockford, Illinois, was given by the parents of the young man for whom the park was named. He was killed in the war.

Mr. and Mrs. William Allen White, of Emporia, have developed an area of fifty-one acres as a city park, naming it "Mary's Garden" in memory of their daughter. Among the restrictions accompanying the gift are that the name White will never be used in connection with the park and that the donors shall have five years in which to spend as much of their own money as they wish in improving the park.

Robert Greer Playground in Elizabeth, New Jersey, was given by the father of a boy killed by an automobile. The donor of Pope Park in Hartford, Connecticut, offered this area to the city, stating, "A large part of the success of any manufacturing business depends upon the health, happiness and orderly life of its employees." He made it a condition that the city buy another tract of land so situated as to benefit the employees of all the factories in that section of the city.

THE COST OF SCIENTIFIC JOURNALS

THE *Wistar Institute News* says: "On August 15, 1932, a circular letter was addressed to the editors of all journals published by The Wistar Institute. The responses from editors have been so gratifying in their support of the institute's policy that it seems advisable, in order to aid the editors in their arduous and thankless task, to publish the letter in *The Wistar Institute News*."

The letter, signed by Dr. M. J. Greenman, director of the institute, reads:

> During 1931, The Wistar Institute published more pages in its several journals than during any previous year (8,091 pages). During the first six months of 1932 there has been a very considerable increase in the number of pages over the first six months of 1931. At the same time the individual support of journals is decreasing.
>
> It would appear that some men who write papers are not interested in supporting journals. Perhaps there is a very good reason for this.