THE ORIGIN OF THE MUTATION THEORY.

AT the time when Darwin published his book on the *Origin of Species* biological science was in a very different condition from what it is now. Hardly ten years had elapsed since Schleiden and Schwann discovered the fundamental law that all living organisms are built up of one or more ordinarily almost innumerable cells.

Mohl's contention that protoplasm is the essential and in fact the only living part of the cell is almost contemporaneous with Darwin's book (1849 and 1851). The presence of a nucleus within the cells began to be recognized. Hereditary problems were almost only discussed by breeders.

The *Textbook of Botany* by Julius Sachs appeared in 1868; it was the first to introduce into botany really scientific methods. When I was a student at the University of Leiden (1866-1870) systematic and descriptive morphological studies prevailed. Microscopical study of tissues was new and cytology had hardly reached us. Under these conditions a student interested in the causal relations of the phenomena of life naturally turned his mind to physics and chemistry. The prominent question of those days was the validity of physical and chemical laws in the living body. The idea dawned upon us that this question chiefly related to the protoplasm but hardly needed a proof for the cell walls and the tissues built up of them.

Once convinced that the phenomena of life are regulated by the protoplasm we naturally looked for methods of studying this relation. Many different ways presented themselves, and among these four seemed to me the most promising. They were the study of respiration, of galls, of osmosis and of variability. I tried all of them and at the end chose the last. Respiration was the source of energy; it was a phenomenon common to animals and plants, and one of the main links which connected both kingdoms in our knowledge at that time. I devoted many years to its study, chiefly in a comparative way, and chose it for the subject of my inaugural address when I was called to the chair of plant physiology in the University of Amsterdam (1878).

But galls seemed to promise far more. They are built up of the ordinary qualities of the plants combined in a new way to fit the requirements of their insects, and this combination is brought about under the influence of some stimulus given off by the insect. To discover the nature of these stimuli and the laws by which they so effectively change the growth of the tissues, seemed to me a scope worth the devotion of a whole life. I made a large collection of galls, in search of the species which would be the most appropriate to attack this line of research. I concluded for those of the willows, belonging to the genus Nematus. But at that period I met with Mr. M. W. Beyerinck who was far beyond me in the study of the life history of the galls, and so I left this pathway. I have, however, read a course upon galls and their bearing on the broad problems of biology about every third year from that time on.

The study of osmosis and of the turgidity of the cells led to the discovery of the semi-permeable membranes of the protoplasm and their significance for growth and movements as well as for the study of isotonic coefficients and the determination of atomic weights, as, e. g., in the case of the sugar raffinose. But its promise of elucidating hereditary questions diminished with every new discovery.

In 1880 I started a course on variability. I had been interested in this question chiefly by making a herbarium of monstrosities, and monstrosities were at that time almost all we knew of variability. Moreover I had visited the celebrated agriculturist W. A. Rimpau at Schlanstedt in Saxony and stayed repeatedly for some weeks on his estate in order to study his selection of cereals and sugarbeets. This induced me to take up a thorough study of agricultural and horticultural selection and I soon found that Darwin's books were the best guides for this literature. Especially from the pamphlets of Vilmorin, Verlot and Carrière I took a large part of the facts for elaboration of my lessons.

I read this course every second year from 1880 to 1900, and each time introduced into it the principles and methods which I found in the literature. This consisted partly in rare pamphlets which I succeeded in collecting only gradually, partly in articles scattered in agricultural and horticultural journals. In the meantime I increased my collection of monstrosities but soon perceived that collecting is not the right way to gain an insight into them. Therefore I preferred revisiting the same spots in nature for successive years and found the monstrosities regularly repeated. This induced the idea of their being heritable phenomena, a conception wholly new at that time, although the inheritance of the cockscomb or *Celosia* was, of course, known to every horticulturist. Then I turned to cultivation, made races of fasciated and twisted forms and studied the inheritance of pitchers and analogous deviations.

Parallel to these experimental studies I tried to penetrate into the theoretical side of the question, and this led to the publication of my book on *Intracellular Pangenesis* in 1889, of which the Open Court Publishing Company published an English translation by Prof. C. Stuart Gager in 1910. Freed from the hypothesis of the transportation of germs through the tissues, Darwin's pangenesis coincided with my own conception of the material basis of protoplasmic life and of the hereditary qualities. This study brought about the conviction that variability must at least consist in two essentially different principles. One of them is the origin of new qualities and their accumulation through geological times, producing the continuous development of higher forms from lower. This form is what we now call mutability. The other is our present fluctuating variability. It determines the degree in which the single qualities will show in different individuals. I proposed this difference between mutability and fluctuating variability at the conclusion of my book, but said to myself: It is all right to deduce the theoretical necessity of this conclusion, but it would be of far higher importance to prove the actual existence of these two types of variation.

I set at work at once, first in the field but soon in the garden. I cultivated over a hundred wild species, and some of them through many years. Fluctuating variability was everywhere present. Then I chanced to meet with Quetelet's *Anthropométrie,* which had appeared in 1870, applied his methods to plants and saw that here the same general laws prevail. Different forms of curves of variation were determined in the corn marigold (*Chrysanthemum segetum*) and other plants (1894-1899), and it became clear that they changed the properties only in the directions of more or less development, but gave no indication whatever of an origin of new qualities. Fluctuation and mutability must therefore be principally distinct.

Mutations must of course be rare, but some few of them occurred in my garden in well-guarded breeds. They were sudden, without visible preparation or transitions. The peloric toadflax appeared in 1894, the double corn marigold in 1896; they sufficed to prove the reality of mutations and gave an experimental basis for the appreciation and the study of the sudden appearance of new varieties in horticulture.

Besides them, one species proved to be rich in such sudden changes. It was Lamarck's evening primrose, a species originally wild in the eastern United States and collected there by Michaux, but which has since disappeared in America. It has, however, won an extensive distribution in England, Holland, Belgium and France, preferring the sand dunes along the coast. I observed its mutations for the first time in 1888 and since then it has never ceased to produce them. The number of mutants amounts to more than a dozen, some of them being progressive, as for instance the giant type or *Oenothera Lamarckiana gigas,* published in 1900, others retrogressive like the dwarfs and a brittle race called *O. rubrinervis.* Ordinarily they are constant from seed, but some show a splitting and are therefore considered to be half-mutants only, as *O. lata* and allied forms. The changes are always sudden and without transitions and occur so regularly in about 1% of the individuals that they constitute an unexpected but excellent material for experimental researches.

In my course on variability I laid especial stress on the pedigrees of definite systematic groups. The families of the euphorbiaceous and the umbelliferous plants afforded a very demonstrative material, and the hypothesis of the descent of the Monocotyls from the Dicotyls through types allied with the common buttercups, proposed at that time by Delpino, proved to be very convincing and instructive. Systematic atavisms, as shown in the leaf-bearing seedlings of the leafless species of Acacia and analogous instances were added to these discussions. They showed that evolution in nature is partly progressive and partly retrogressive. Progression means differentiation and specialization, it governs the main lines of the pedigree of the animal and vegetable kingdoms. But retrogression, consisting in the loss of previously developed qualities, must be responsible for a large part of the diversity of forms in nature. And since it is easier to lose a thing than to acquire a new quality, the cases of retrogression must be far more numerous in nature than those of actual progression.

Therefore there must be two kinds of mutations and even in our experimental cultures progressive ones must be rare, and retrogressive ones comparatively more frequent. This is exactly what we see in the mutations of the evening primrose.

Alongside of these studies I tried hybridization. Opium poppies afforded a useful material and led to the rediscovery of Mendel's law. At that time this conception was believed in by nobody, it was rather considered as an idealistic fiction. But the splitting of the poppies confirmed that of Mendel's peas, and numerous garden varieties behaved in the same way. I was fortunate enough to be the first to publish this result (1900) and pointed out that it is especially retrogressive variations which follow this law, whereas progressive ones produce constant hybrids, at least in many instances.

Paleontological studies strengthened the idea of the origin of species by means of sudden variations instead of a slow and gradual development. This side of the question has since been taken up by Charles A. White and other paleontologists. From my own studies I deduced the contention, that life on this earth has not lasted long enough for such a slow development as Darwin's theory of selection supposed. Darwin calculated some thousands of millions of years as required for his theory, but geologists and physicists only allow about forty or at most a hundred millions of years for the development of all animals and plants. The hypothesis of sudden mutations delivers us from this difficulty. And so it does for many other objections which were still being used as weapons against the whole principle of evolution in the form proposed by Darwin.

It has always been my conviction that the improvement of industrial practice is the main aim of all science. Biological science has to be a basis for agriculture and horticulture. The discipline of heredity should be crowned by the advance in our knowledge concerning the breeding of animals and plants. With Dr. Wakker I studied the diseases of the flower bulbs cultivated all around Haarlem (1883-1885), and since then I regularly sent contributions to the journal of our agricultural society. From 1892 to 1894 I was editor of the journal of the Dutch Horticultural Society in order to have an easy access to horticultural establishments in the Netherlands as well as abroad, and collected all the evidence I could find concerning practical plant-breeding. As a matter of fact this was very scanty but it led me to a connection with the Director of the Swedish agricultural station at Svalöf, Dr. Hjalmar Nilsson, whose celebrated method of plant improvement rested on the same scientific basis as my own experiments.

My book on the mutation theory is the combination of all these preliminary studies into a regular discussion of the main principle. I had the great advantage of my steadily repeated courses on heredity, which constituted, if I may say so, a first unpublished edition, with all the many faults inherent to first trials on a new field. The book appeared in 1900, and an English edition,[1] prepared by Prof. J. B. Farmer and A. D. Darbishire, was published by the Open Court Publishing Company in 1909. It tries to show that the origin of species is a natural phenomenon and that it is possible to subject it to experimental study. In nature the mutations have produced the whole evolution

[1] *The Mutation Theory.* 2 vols.

of all living beings; in the garden we can, of course, only expect to see their very smallest steps. The identity of retrogressive mutations in nature, in horticulture and agriculture and in the experimental garden seems now to be beyond doubt. But progressive changes, which are the most important, are at the same time the rarest, in nature as well as in cultivation. In regard to these the theory relies on its broad arguments and the question whether the directly observed progressive mutations afford a material for the interpretation of the ways of nature is still under discussion.

The theory is based upon arguments taken from widely different branches of nearly all natural sciences. It conduces of necessity to experimental research, but this, of course, is still in its first infancy. It promises, however, to become some day of important service to science at large as well as to the practice of breeders.

HUGO DE VRIES.

LUNTEREN, HOLLAND.