GREGOR MENDEL AND HUGO DE VRIES ON THE SPECIES CONCEPT*

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Since the year 1965, the centenary of Mendel's original publication, a continuous stream of papers on his life and work has flown. Among these are translations as well as new editions in the original language of his famous paper of 1865/1866.

Although quite a number of biographical data have thrown some more light on his private and his official life, still no conclusive answer has been given to the question why Mendel's voice remained one crying in the wilderness, with only some faint echoes from Germany and from far-away Russia.

Perhaps we had better reverse that question and ask why Mendel, who certainly was a beloved and succesfull teacher, did not try to convince his pupils, friends and colleagues by a direct demonstration in the experimental garden.

Professor Carl Nägeli, whose opinion was asked for by Mendel, did not give a straightforward denial, but showed considerable diffidence in accepting Mendel's experimental data as sufficient proof for the latter's conclusions.

From his letters to Nägeli and from recently discovered manuscript notes we can infer that fundamental to Mendel's thoughts was the idea of separate hereditary characters being transmitted unaltered and independently. By his experimental work he showed that this leading idea is not contradicted by the result of crossing, as it seemed to be in the hybrid progeny. The formulation of a general law for quantitative ratios in the offspring of the hybrid was no more than a secondary, though for practical purposes very useful, result.

Mendel must have been well aware of the fact that this principle of independent and constant characters could not be accepted by his contemporaries, who at that time based their ideas on Darwin's holistic view of the species as a variable, even plastic, entity. In his own copy of one of Darwin's books, Mendel, in the margin of a sentence to that effect, jotted down the critical note: "widerlegen"! Nevertheless a formal refutation presumably did not occur to Mendel.

Another reason for uncertainty, perhaps even for a feeling of frustration, arose from the allegedly constant hybrids, as referred to in Gaertner's and Wichura's experiments and appearing in Mendel's own hybridisation experiments with *Hieracium*.

One of the above-mentioned manuscript notes reveals Mendel's rather hopeless mental struggle in defence of his *Pisum* law against that threatening phantom of the constant hybrid.

[1] Dedicated to Professor Dr. Th. J. Stomps

In his book "Intracellulare Pangenesis" of 1889, Hugo de Vries, unaware of Mendel's priority, expounded the same principle of independent and invariable hereditary characters. However, De Vries at once consolidated this thesis by adding the postulate that each of the hereditary characters is bound to a distinct particle, which he called a "pangene". By doing so, Hugo de Vries founded the Pangene hypothesis as the basic theory of Heredity and Evolution. The name Mutation Theory is a later synonym coined by De Vries himself. In very much the same way as Mendel did, Hugo de Vries attempted to obtain experimental proof for this thesis by crossing individuals differing in only a single hereditary character. He found the same regularity as Mendel's *Pisum* rule, which De Vries called "the law of segregation of hybrids".

Nevertheless the assumption is not warranted that the modern Gene Theory of Heredity has developed directly out of Mendel's work. JOHANNSEN (1909) purposely substituted the word "gene" for Hugo de Vries' term "pangene" in order to adapt it to the vague expressions used by Mendel. However, since then it has always been employed in the concrete sense of De Vries' pangene and not in that of Mendel's indistinct terms "Anlagen" or "Elemente".

The term "segregation" (French "disjonction"; German "Spaltung") is nowhere to be found in Mendel's papers.

Hugo de Vries was at the same time confronted with the problem of constant hybrids in his *Oenothera* crossings. He tried to incorporate this in his theory of pangenes by discriminating between varietal characters, which segregate after crossing and species characters that do not. Varietal differences he thought to be caused by one pangene being in a latent, inactive, condition; a species character would be controlled by an active pangene which is lacking in the other parent. Species characters could, accordingly not show normal segregation, because of the absence of an allelomorphic counterpart of the pangene.

In De Vries' train of thought, varietal characters could not contribute to the advent of a constant new species precisely because they invariably segregate. Conversely, a constant difference at the species level originates by a single mutation, which either adds a new pangene to the stock, or irrevokably destroys one.

With Alexis Jordan's investigations on *Erophila* and *Viola* in mind, Hugo de Vries at that time adopts an atomistic species concept of the "elementary" species as the smallest possible, absolutely constant taxonomic entity.

For his experimental research on evolutionary processes De Vries deliberately prefers such mutations as do not show segregation after having been crossed with the parent species.

When he came in the possession of Mendel's paper, De Vries at once recognized the cogent support for his own ideas. He expresses profound admiration for Mendel's methods of experimentation and mathematical analysis of data, and for his formulation of general conclusions. At the same time the paper induced him to pursue his own efforts concerning the exceptions to the rule of segregation with greater determination. However, as soon as the discovery of double fertilization (by Navashine and Guignard) furnished a solution for the

enigmatic phenomenon of "xenia" in maize endosperm hybrids, De Vries somewhat changed that predilection. At least he decided upon a separate preliminary publication of the "law of segregation". The significance of this term runs parallel with Mendel's "*Pisum* rule", but is not quite identical to it.

An exact retracing of the way in which Hugo de Vries finally happened to rediscover Mendel's paper is hampered by some ambiguous and contradictory statements in his own papers and published letters. The worst of these difficulties have been elucidated in publications by TH. J. STOMPS (1935 and 1954).

By collating and comparing several notes and comments in Hugo de Vries' posthumous private papers (now preserved in the Hugo de Vries-laboratory) I could fill in some of the remaining gaps and give a detailed account of the rediscovery; an abridged Dutch version of that account was published in "*Honderd Jaar Mendel*", 1965.

In contradistinction to the minimized concept of the elementary species, the ultimate picture of a species such as *Oenothera lamarckiana*, the favourite object of De Vries' experiments, finally turned out to be an extremely complex and intricate one. This image was gradually built up in the course of half a century of *Oenothera* research by Hugo de Vries and his Amsterdam disciples (Geerts, Honing, Stomps, Boedijn, Dulfer, Leliveld and others), later on linking up with the studies by Blakeslee, Renner and Cleland and their schools. The terms "twin hybrids", "balanced lethals", "complex heterozygotes", "catenation of meiotic chromosomes", etc., denote several traits of our mental picture of such singular species. We certainly have to infer that in other genera the constitution of the species image, although composed of quite different features, may show a comparable degree of complexity.

As a rule the speciation of a taxon to the level of a well-balanced and well-defined constant species will proceed along the way of a protracted gradual escalation. Initial steps in this series are mutations and mutual intercrossing, which provide a stock of genetic variation and heterozygosity, allowing for a selective adaptation to changes in environmental factors in the course of time, and according as the distributional area expands.

Further steps lead to the establishment of barriers against introgression and outbreeding. Not all these processes lend themselves so easily to an experimental approach. Taxonomists often have to resort to deductions or to more formal, sometimes even technical statistical, methods for the delimitation and the concomitant evaluation of taxa. Therefore, a taxon designated by a binary name as a "species" may have reached a very different level in the final development towards its ultimate state of an established equilibrium.

Recent ecological research and experimental taxonomy effectively contributed towards the elucidation of the factors and general trends operative during the process of speciation, but the differently constituted schemes, each of them requiring its own series of technical terms, only represent partial projections, from particular viewpoints, of the variously complicated chains of events. None of these classifications can directly be integrated in the systematic hierarchy of taxa.

B. H. DANSER (1929), being not only a pupil of Hugo de Vries but also an adept of the more conservative genetical and taxonomical ideas of Lotsy and Goethart, proposed a well-devised three-fold gradation of categories he termed "comparium", "commiscuum" and "convivium". In this way a better relative evaluation of taxa at the specific and infraspecific level may be reached, but not a categorical standardizing of these concepts for general taxonomic and nomenclatural use.

Similar systems of classification, more or less particularly adapted to various trends of ecological, genetical and taxonomical research or practice, have been proposed by Turesson, by J. Clausen's American school, by E. Mayr for zoological taxa, and by several others. Some of these proposals are synthesized into a composite doctrine under the heading "Population Biology", but the word "population" is again used for entities of different degrees of complexity and of different constitutional levels. (ANDREAS, *c.s.* 1967).

A more definite indication is intended by Dobzhansky's term "Mendelian population" (1955, transl. BREMEKAMP 1961) for a panmictic community corresponding with Danser's commiscuum.

The use of Mendel's name in the adjective to designate such a community does not seem to be very appropriate, however. Mendel deliberately concentrated his efforts on the study of individual characters, irrespective of the question whether they are limited in their occurrence to certain communities or to certain individual specimens. It is exactly by his original and fundamental concept of independent and unaltered hereditary characters that Mendel laid the foundation of genetics and thus of the whole of modern biological science.

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