

VAVILOV'S SPECIES CONCEPT AND THE EVOLUTION OF VARIATION

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ABSTRACT In 1931 N.I. Vavilov formulated a polytypic species concept, put forward the ideas of multiformity of species, relativity of taxonomic criteria and the theory of peripheral accumulation of recessive characters. From the evolutionary point of view he considered species as knots in evolutionary chains. It is suggested that the linnaeons and jordanons of Lotsy and Vavilov correspond to successive stages of speciation which seem closely related to ecosystem evolution. The fossil angiosperm *Trochodendroides* exemplifies such evolution of variation.

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1. INTRODUCTION

1987 was a centennial year of the Russian scientist Nicolai Ivanovich Vavilov. In the late 20s and the 30s he made a gigantic effort to modernize Soviet agriculture by spreading a net of experimental selection stations all over the country and even abroad — one was established in New York; by introducing new varieties, for which he travelled to 65 countries all over the globe; and by founding research institutes for genetic and evolutionary studies, which he stimulated by his own deeply original and provocative ideas. As a theorist he is remembered mostly for his law of homologous variation (Vavilov, 1922) and the geographical pattern of genetic polymorphisms (Vavilov, 1926, 1927). His ideas on species and speciation are less known though his "Linnean species as a system" (1931, 1967) can hardly be denied a prominent place among the evolutionary classics. This is his most mature work and embodies his earlier views on variation, which are brought into a framework centered on the concept of species as a system. If valued not by its length but by concentration of ideas and their factual backing — which is from many years of scrupulous field observations and experimental work — it is second to none of the voluminous writings which made up the foundation of the modern paradigm. The aim of the following comments is not only to render historical justice to Vavilov but also to show that his views are still pertinent to the current discussions of species and speciation. All the following citations are from the second edition of his lecture on "The Linnean species as a system" delivered at the V International Botanical Congress in Cambridge in 1930 (Vavilov, 1967).

2. WHAT IS A SPECIES?

Vavilov's concept of biological species was a direct outcome of work by himself and his coworkers E.I. Barulina, E.N. Sinskaya, K.A. Flacsberger, S.V. Yuseptchuk and others on natural and experimental variation in wild and cultivated plant species. Using morphological and chorological analysis, inbreeding, interbreeding, and physiological experiments they found many taxonomic species to be diverse in the sense that they concealed a multiplicity of forms, some of which seemed good species. In *Lathyrus odoratus*, *Pisum sativum*, *Phaseolus vulgaris*, *Solanum*

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tuberosum, *Cucurbita mixta*, *Avena strigosa* and many other species the number of the recognizable discrete races and varieties increased tenfold, while in the Abyssinian *Triticum durum* they amounted to thousands. But the variation was far from chaotic. The awnless form common in *Triticum vulgare* was found in the Abyssinian *T. durum*. The liguleless wheat *T. vulgare*, first found on the Pamir Mountains in Central Asia, was mimicked by *T. durum* on Cyprus and then liguleless varieties were observed in rye, oats, maize, and millet. Such amazing parallelism allowed several predictions which came true. These inspired Vavilov (1922) to formulate a law of homologous variation (parallel variation was admittedly observed earlier, but not in such a regular fashion). He then set out to define biological species as a dynamic system of homologous variation. Among those who influenced him were de Vries, Jordan, Lotsy, Turesson, and above all, Shull, whose lecture on the genetic basis of taxonomic units at the International Congress of Plant Sciences in Ithaca, 1926, he attended. (In modern American literature on plant genetics I found a few references to G.H. Shull, but not this particular work on species.) He, however, felt that Shull's species concept was somewhat deficient, especially in respect to historical and geographical aspects of speciation. At the same time Vavilov sought an aphoristic definition of the kind given by the then well-known botanist V.L. Komarov (later a supporter of Lysenko): a species is a morphological system plus geographic distinctness. Elaborating on this, Vavilov defined a "Linnean species" as "an isolated complex dynamic morpho-physiological system bound in its origin to a certain environment and area" (p. 79).

I wish he had been less aphoristic, because this formula seems inadequate to convey the essence of his species concept, which was implicitly related to homologous variation. According to Vavilov's views, each species had a potential to vary in a regular pattern, which can be predicted by comparative studies of related species. This potential, either realized or restricted by some environmental factors, is the essence of a species as a dynamic system. Such systems, exemplified by the thoroughly studied *Triticum vulgare*, *T. durum* and *T. monococcum*, are "facts of nature", while their subordinate forms are also "facts of nature" but of less significance.

A few comments on the species essence seem pertinent here. Emerging from the Plato-Diogenes controversies, the essence problem survived through the ages. It is evolving with us, hence there is no solution once and for all. Nominalistic solutions of the kind "let us consider species groups with no more than 25% morphological or reproductive overlap" had been proposed from time to time but they were never completely successful. The essence remained. It was conceived of as the morphological, functional, geographical or historic unity, unique ecological role, shared gene pool, competition for reproductive resources, or all this and something else.

A dog recognizes all cats as a natural unit; there is nothing nominalistic about it. For primitive people ability to sort out species was an important adaptive trait. Their species concept was by necessity essentialistic or else it would have been of little adaptive value. Our taxonomic intuition is still traceable to the purely adaptive approach of our wild ancestors. We still tend to recognize species as consistently similar organisms which maintain some distinct place in our environment, which deserve some special attitude. This still is their essence.

Organisms do cluster in various ways. There are geographical, ecological, reproductive clusters (or topodemes, ecodeemes, gamodemes according to the useful but little-used terminology of Gilmour and Gregor, 1939) and some others can be distinguished on effort. But we pick out as species those clusters which can be treated as units for most practical and intellectual purposes. In other words, species reflect our ideas of organisms which are essentially similar in occupying and holding some particular place in our worldview. Humans are considered a single

biological species despite the obvious morphological, physiological, genetic, geographical and historical differences among their major races. In addition to interbreeding there are important ethical and political reasons, and above all, as a fact of nature humanity as a whole seems more important than its races. The cognitive parallelism revealed by the structuralist analysis of mythology is an essential evidence of unity. Notably, species is one of the universal ideas owing their origin to the cognitive parallelism. What Vavilov did can be seen as an early attempt at the structuralist viewpoint, unfortunately swept out by the wave of vulgar essentialism in his country and the recurrent advocacy of nominalism in the west.

3. POLYTYPIC SPECIES

A major thesis of Vavilov's paper on species is that "monotypic species do not exist" (p. 60). He refers to his work on several hundred plant species, some of which, previously considered monotypic, have revealed their heterogeneity. More strikingly, their laboriously exposed variability mimicked that of better-known admittedly variable species — observations from which the law of homologous variation has emerged.

Vavilov forcefully put forth the polytypic species concept before other people with whose names it is usually linked. What is more, he attempted a holistic description of the polytypic species as a system bounded by the homologous variation of its elements, a system in which polymorphisms not just happen but make sense in comparison with related species showing parallel variability ("creativity", I think, would be more in the spirit of the Vavilov's idea of a species' essence and its outward expression as homologous polymorphisms).

Classical taxonomists starting with Linné himself have sought an invariant species type while considering variations spurious. In contrast, for Vavilov it is the pattern of variation which is typical for a species. Citing the examples of homologous variation in wheat and other cereals, he concluded that "varieties within species, firmly established now in distinction from the views of Linné, arise with a certain regularity" (p. 67). At the same time Vavilov seemed somewhat reluctant to discuss the causes of this remarkable regularity. To this day they are far from evident. In the most general terms their meaning may be that each genetic as well as epigenetic system has a variation repertoire of its own, a definite set of polymorphic states, and the more similar such systems, the closer their polymorphisms.

Vavilov was aware of the problem of excessive lumping, which eventually made the polytypic species concept unpopular among taxonomic practitioners. He avoided it by admitting different kinds of species.

4. MULTIFORMITY OF SPECIES

Reminding us of Darwin's remarks on different kinds of species, some fairly distinct and others slightly if at all different from varieties; of Lotsy's broad polytypic linnaeons and homogeneous jordanons; of Turesson's coenospecies, comprising distinct but interbreeding entities; and of his own vast experience with species of cereals and other wild and cultivated plants, Vavilov concluded that species differ with respect to their distinctness, integrity, origin and mode of differentiation. This was formulated as a general statement of species multiformity: "Analysis of a great number of Linnean species with the methods of differential systematics, differential geography, and ecology as well as the modern methods of genetics, cytology and anatomy reveals great factual multiformity of species" (p. 79).

Forty years later Dobzhansky published his influential paper "Species of *Drosophila*. New excitement in an old field", in which he wrote: "As the situation appears to be now, there is one consideration which seems unlikely to be changed: there is not a single kind but there are several kinds of species and of processes of speciation in *Drosophila* and, of course, even more in the living world at large" (Dobzhansky, 1972, p. 669). But is it not the point where Vavilov should be remembered?

5. RELATIVITY OF TAXONOMIC CHARACTERS

If there are different kinds of speciation, there should be different kinds of taxonomic criteria as well. If morphological divergence proceeds hand in hand with ecological and genetic differentiation then we have very good species. But one or another mode of divergence may prevail. Reproductive isolation seems much more important in birds than plants. But how many plant taxonomists view species with an ornithological eye!

To keep closer to nature, taxonomic criteria should be as flexible as nature is itself in its modes of speciation. This in essence is Vavilov's "rule of relativity of taxonomic characters" (p. 78).

But why there are many kinds of speciation? In answering this we can hardly avoid a more fundamental question — why speciation at all? One obvious reason for speciation is for cooperation of organisms as members of ecological communities with differentiation of ecological roles, or niches, while speciation aims toward more effective performances in each of the roles. Effectiveness in turn is due to coadaptive genetic complexes which must be protected from disturbing genetic inflows. Hence reproductive isolation is necessary or at least desirable and, if not achieved momentarily by a happy chance, it would develop gradually by means of disruptive selection. These modes of speciation, both more or less confirmed by experiment and observation, emphasize reproductive isolation as a cornerstone of a species and, by implication, its major recognition criterion. However in the first case isolation is at the leading edge while in the second it is at the rear of the respective speciation process, so at least some incipient species can be recognized by their ecological preferences and other criteria much before reproductive isolation is, if ever, completed.

But what happens when an ecosystem, instead of continuing on the endless path of differentiation, is disturbed, its niche structure reshuffled and simplified? If species have to change their performances, may not a gene inflow be beneficial for them rather than detrimental? Actually in disturbed environments introgression often happens not only among plants but also among animal species. It can be seen as a mean of a species gene-pool enrichment, while reproductive isolation then appears retrograde and no longer useful as a species criterion. Even diagnostic morphological characters, fairly reliable under stabilizing selection, might degrade to mere intraspecies variation. In this way, I believe, Vavilov's relativistic taxonomy can be linked to ecosystem evolution.

6. SPECIATION

In line with the Hegelian dialectics of continuity and discreteness, Vavilov interpreted species as "knots in the evolutionary chain" (p. 83). According to his examples given in the last chapter of the paper (pp. 80-83), continuity is manifested mostly within the Linnaean species, between their constituent jordanons and races, while the boundaries of the large polymorphic species systems are far more distinct. A metaphor of "knots", or relatively discrete evolutionary stages, can be seen as an elaboration on the now well-known statement of Darwin that periods of change were shorter than species durations, a precursor to the modern punctuated-

equilibrium theory. However, while the problem of evolutionary reality is at least temporarily resolved by the notion of species as knots or punctuations, our ideas of just what happens at punctuations are as vague as they were in the Darwinian time.

Eldredge and Gould (1972) have adopted the Wright-Mayr model of peripheral speciation by founder effect and genetic revolution. In this model speciation is random, but Vavilov had something important to say about marginal populations also. He showed that recessive character states ("genes") tended to concentrate toward the periphery of a species' range in many plants as well as in *Homo sapiens*. This and not the founder effect might produce the genetic differentiation of marginal populations. This "pioneer effect" can be seen as not casual but causally related to some specific marginal conditions, primarily to the lower population density, less stringent intraspecies competition and relaxed stabilizing selection. The adaptive strategy under these conditions is mostly fine-grained (Levins, 1968), where more genetic polymorphisms can be tolerated as neutral or semineutral.

In disturbed environments certain marginal conditions are imposed on all surviving populations, releasing their potential genetic variability or even augmenting it via introgression or transduction of exogenous genetic material (preceding section). The ensuing macropolymorphic populations might serve as genetic depots for the segregating adaptively more constrained strains when the marginal conditions give way to stability and specialization (or coarse-grained strategy and K-selection, which amounts much to the same thing).

Under periodic fluctuations speciation might proceed in two more or less distinct stages: an accumulation of rather loosely linked polymorphisms in the disclimax populations and then segregation of the coenotically bounded successional and climax populations showing more restricted and correlated variation. Taxonomic evolution of these evolutionary stages would roughly correspond to the Lotsy-Vavilov linnaeons and jordanons.

7. A PALEONTOLOGICAL EXAMPLE

Historical accidents conforming to the above scheme might be numerous, but most of them are overburdened with technical details, by themselves arguable. I would risk just one example, hopefully less complicated. *Trochodendroides* is one of the dominant Late Cretaceous and Palaeocene fossils, originally a leaf-genus, but applied also to the whole plant, of which infructescences and seeds are also known. (In palaeobotany different plant parts are usually described under different names but in some cases their attribution to the same plant is fairly certain.) Several species, such as *T. rhomboideus*, *T. microphylla*, *T. sachalinensis* appeared in the Late Cretaceous of North America and eastern Asia.

Each of them was morphologically and geographically well defined. In the North American *T. rhomboideus*, the leaf blade was rhombic, proximally cuneate, apically broadly triangular, with an undulate margin in the distal part (Lesquereux, 1874), while in the Asiatic *T. sachalinensis* it was obovate or elliptical, apically long- or short-pointed, with a serrate or crenate margin (Krassilov, 1979). *T. arctica*, appearing in the latest Late Cretaceous, was more variable, showing leaf varieties similar to both *rhomboideus* and *sachalinensis*, that is obovate, proximally cuneate, with an undulate margin, and broadly ovate with a dentato-crenate margin (Krassilov, 1979). Was it homologous variation or introgression between the North American and Asiatic species? One guess may be as good (or bad) as another. Notably the Bering land bridge may have expanded at this time as a result of the end-Cretaceous regression.

To the close of the period, and especially after the Cretaceous/Tertiary boundary event, which is recognized by many palaeontologists as a major environmental crisis, *Trochodendroides*, supposedly a pioneer tree, became more numerous and variable. Heer (1868) recognized three species -- *Trochodendroides*

(then "*Populus*") *arctica*, *T. richardsonii* and *T. raddachii* in the early Palaeocene of Greenland. He described also six varieties of *T. arctica* (Heer, 1883). Subsequent authors paid little attention to leaf polymorphisms, trying to establish as many species as possible. An example of this is a taxonomic treatment of trochodendriods from the White Mountain locality on the Bureya River (Amur Province, Soviet Far East) by Kryshstofovich and Baikovskaya (1966). They recognized no less than thirteen leaf species, all of which were subsequently reduced to varieties on the basis of the minor venation pattern, cuticle and associated reproductive organs. In the White Mountain locality *Trochodendroides* is abundant, covering bedding planes of the siltstone and sandstone flood-plain facies. Several hundred specimens were measured and assessed in relation to their blade shape and margin, characters diagnostic for many plant species. The blade-shape morphologies (rounded, ovate, elliptical, cordate, etc.) combine freely with the leaf-margin morphologies (entire, undulate, crenate, serrate, festooned, etc.). A bimodal shape-frequency distribution (Krassilov, 1976, fig. 2) might be evidence of the influence of the long-short shoot differentiation with divergent leaf morphologies. The former species names were retained as designations of the discrete morphotypes, while a few intermediate specimens remained unassigned. The following morphotypes have been described (Krassilov, 1976, p. 56-60, Plates XVI-XX, text-figs. 3): (1) "*arctica*" — blade broadly obovate or rhombic, base cuneate, apex rounded, truncate or bluntly pointed, margin undulate or irregularly crenato-dentate; (2) "*genetrix*" — blade broadly obovate, base vaguely cordate, apex short-pointed, margin undulato-serrate; (3) "*richardsonii*" — blade large rounded or broadly ovate, base truncate or cordate, apex broadly rounded or inflated, margin coarsely dentate or festooned, teeth trapezoid; (4) "*smilacifolia*" — blade ovate or broadly triangular, base truncate or cordate, apex longly pointed, margin crenato-serrate; (5) "*speciosa*" — blade rounded-rhomboid or ovate, base broadly cuneate, apex shortly pointed, margin irregularly crenato-dentate or crenato-serrate; (6) "*elliptica*" — blade elliptical, margin irregularly dentato-serrate; (7) "*crenatum*" — blade broadly elliptical, margin regularly crenate; (8) "*amurensis*" — blade broadly elliptical or ovate, base rounded, apex longly pointed, margin crenato-serrate; (9) "*fibrillosa*" — blade elliptical, base rounded, slightly cordate, margin entire; (10) "*hyperborea*" — blade ovate, base slightly cordate, apex attenuate, margin minutely serrate; (11) "*phosphoria*" — blade elliptical, base cuneate, margin crenate; and (12) "*praetrinervis*" — blade broadly elliptical or ovate, margin entire.

Among these only (1), (4), (5), (6) and (12) have their "homologues" in the Late Cretaceous leaf populations, while almost all morphotypes were found by the present author and his coworkers in the Palaeocene of western Kamchatka and recognized from drawings and photographs of the coeval North American trochodendroids in Heer (1868, 1882), Brown (1939, 1962) and other authors. The Eocene leaf population from the Due geological section in western Sakhalin (Krassilov et al., 1986) and the Oligocene of the Rachnoi Peninsula near Vladivostok (Krassilov and Alexeenco, 1978) comprise two morphotypes each, corresponding to the "*arctica*" and "*crenata*" of the Paleocene populations in the first case and to the "*crenata*" and "*speciosa*" in the second. The Amur province *Trochodendroides* had large panicles of paired fruits while the same or closely related American species had simple racemes. Some paleobotanists have even questioned the possibility of such a polymorphism in reproductive traits, which normally show considerable constancy (Crane and Stockey, 1985). But a large number of whole panicles preserved in the Amur province localities testify to their regular shedding as reproductive entities (not just occasional shedding of a receme-bearing shoots). The later Palaeocene and Eocene species, often assigned to the extant genus *Cercidiphyllum*, still appear closely related but better defined, with less variable leaf characters and fairly constant reproductive morphologies.

I see what happened at the Cretaceous-Palaeocene boundary as an evolutionary appearance of a macropolymorphic linnaeon, *T. arctica*, in which the genes of several Late Cretaceous lineages were reshuffled, then spread again in a number of the late Palaeocene - early Eocene jordanons. In cyclic processes like this the initial linnaeon formation appears rapid. This stage is marked by loosely (if at all) correlated polymorphisms in different character sets while the strengthening correlations can be taken as a sign of ongoing differentiation of fordanon. Sudden mutational restrictions of gene flow can be involved in the latter process but generally it is gradual and the ensuing fordanon systems can be stable through geological ages, up to the next serious environmental crisis. Thus the punctuated equilibrium of speciation might result from the periodicity of ecosystem evolution, which might also impose some — otherwise inexplicable — regularities on the species longevities.

In conclusion I feel that if species were knots in the evolutionary chain, the chain itself was knotted by the higher-level ecosystem evolution, in the context of which speciation is to be fully understood. One reason why Vavilov's species concept did not gain the popularity it deserves might be its complexity, and perhaps I am adding further complications. But simplicity is hardly a reliable sign of truth.

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