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4. Vavilov's Law of Homologous Series—is it relevant to potatoes?

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Nikolai Ivanovich Vavilov published his Law of Homologous Series in 1920, but did not include any ideas on homologous variation in potatoes. The relevance of this fundamental concept of genetic diversity to potatoes is discussed in relation to disease and pest resistance in wild potatoes from Mexico and the Andes of South America.

KEY WORDS:—Disease resistance – *Globodera pallida* – late blight – pest resistance – *Phytophthora infestans* – potato cyst nematode – sticky-haired potatoes – tuber-bearing Solanums – wild species.

CONTENTS

INTRODUCTION

It was in 1920, at the third Russian Congress for Plant Breeding in Saratov, that Vavilov first presented his ideas on parallel variation in crop plants. These ideas were then published in 1922 in the *Journal of Genetics*, in a paper entitled 'The Law of Homologous Series in Variation', and further modifications were given in a paper published posthumously in English, in 1951 in Chronica Botanica. It was through his Law of Homologous Series that Vavilov began to systematize his ideas on the biological significance of the genetic diversity which he observed in primitive varieties of crop plants. The concept of parallel variation was not a new one to Vavilov. Indeed he acknowledged the contributions which several nineteenth century scientists and naturalists, including Darwin, had made. Vavilov felt it was possible to bring all the then known facts in the form of a general law to which all organisms conform—The Law of Homologous Series in Variation.

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THE LAW OF HOMOLOGOUS SERIES IN VARIATION

It is convenient briefly to review the ideas which form the basis of the Law of Homologous Series, before considering this concept in relation to potatoes. Vavilov studied the racial composition of different species, which he referred to as Linneons. He noted a number of regularities in the diversity of varieties and races, which he referred to as Jordanons. Such regularity could be seen in the similarity in morphological and physiological characters which distinguished different Jordanons. He stated, "the Linnean species, in our conception, appears to be a distinct, complex, mobile, morpho-physiological system related in its origin to a definite environment and area, and in its intraspecific hereditary variability, subject to the Law of Homologous Series" (Vavilov, 1922). Vavilov's concept of dynamic species, a consequence of post-Darwinian systematics, can be illustrated in the following way. The species radical can be considered as a stable gene complex which essentially defined the species; that is, the characters which distinguish wheat from barley, for example. The complex of variable genes, which give rise to polymorphism within the general range of a species, are subject to the Law of Homologous Series.

Vavilov then formulated the Law of Homologous Series in the following way. Each genus contains several related Linnean species, each of which can be characterized by those genes which are labile. The Law of Homologous Series is illustrated below for several related species:

$$
\begin{array}{ll}
G_1L_1(a+b+c\ldots) & G_2L_1(a+b\ +c. \\
G_1L_2(a+b+c\ldots) & G_2L_2(a+b\ +c. \\
G_1L_3(a+b+c\ldots) & G_2L_3(a+b\ +c. \\
\multicolumn{2}{c}{L_1(a_1+b_1+c_1\ldots)} \\
\multicolumn{2}{c}{L_1(a_2+b_2+c_2\ldots)}
\end{array}
$$

In this illustration G_1 and G_2 represent different genera and L_1, L_2 and L_3 represent different Linneons, which together form the species radical. In parenthesis are shown the complexes of variable genes.

Two principal conclusions result from Vavilov's law. The first is that "in general, closely allied Linnean species are characterized by similar and parallel series of varieties; and, as a rule, the nearer these Linneons are genetically, the more precise is the similarity of morphological and physiological variability. Genetically nearly related Linneons have consequently similar series of hereditary variation". The second rule or law in polymorphism, as a sequence to the first one, is that "not only genetically closely related Linnean species, but also closely related allied genera, display similarity in their series of phenotypical, as well as genotypical, variability" (Vavilov, 1922).

One important consequence of Vavilov's work on homologous variation concerns the prediction of the existence of new forms. He wrote "species and genera that are genetically closely related are characterized by similar series of heritable variations with such regularity that knowing the series of forms within the limits of one species, we can predict the occurrence of parallel forms in other species and genera. The more closely related the species and Linneons in the general system, the more resemblance will there be in the series of variations" (Vavilov, 1951).

APPLICATION OF THE THEORY

How has the Law of Homologous Series been applied in practice? Vavilov himself reported homologous variation in a wide range of cereals, including wheat, rye, barley and millets, in cotton, legumes, brassicas and other crops from the Cucurbitaceae, Papaveraceae and Compositae. However Vavilov made scant mention of the Solanaceae, and indeed it is interesting to note that even S. M. Bukasov, one of Vavilov's close colleagues, apparently did not refer to the Law of Homologous Variation in his many publications on potatoes, even though much of the early work by Russian botanists such as Bukasov has formed the basis of our understanding of patterns of variation in potatoes.

THE NATURE AND DISTRIBUTION OF THE TUBER-BEARING SOLANUMS

There are about 200 wild and cultivated tuber-bearing *Solanum* L. species. Cultivated forms of potato are found in several of the Andean countries, principally Colombia, Ecuador, Peru and Bolivia, and are generally found in farming systems at altitudes above 2500 m and up to about 4000 m. Wild potato species, on the other hand, are distributed from the south-west United States to Chile, Brazil and Paraguay in South America, from sea level to over 4000 m, and consequently in a wide range of ecological niches. This wide eco-geographical range is reflected in the wide range of tuber-bearing Solanums, which have been classified into some 21 taxonomic groups. The largest and most important of these groups is Series Tuberosa, which contains all the cultivated forms, and the wild species most closely related to them.

The Law of Homologous Series is only partially relevant to the cultivated species, in terms of tuber morphology. Cultivated potatoes represent a polyploid series and some eight species in the Andean region. On the basis of tuber morphology alone it is impossible to differentiate any one species or ploidy. This is what one would perhaps expect, considering the close phylogenetic relationships between the different species, and the fact that Andean peasant farmers have undoubtedly selected potato phenotypes which are familiar to them, and which represent varieties with known culinary qualities. These ideas are supported by the biosystematical and ethnobotanical studies conducted by Jackson, Hawkes & Rowe (1980) and Brush, Carney & Huamán (1981) in Peru. Man has clearly been a driving force for the establishment of homologous variation in such characters in cultivated potatoes.

The picture is much clearer when we consider wild potato species. The distribution of resistance genes to important pests and pathogens in wild potatoes has been considered by Hawkes (1958). His observations, and more recent ones based on extensive evaluation of wild species germ plasm have shown that Vavilov's Law of Homologous Series does have relevance to potatoes, which is illustrated in the following examples.

Late blight disease of potatoes

Resistance to late blight disease of potatoes, caused by the fungus *Phytophthora infestans* (Mont.) de Bary, can be considered from two points of view. Race specific resistance, conferring hypersensitivity to different strains of *Phytophthora*

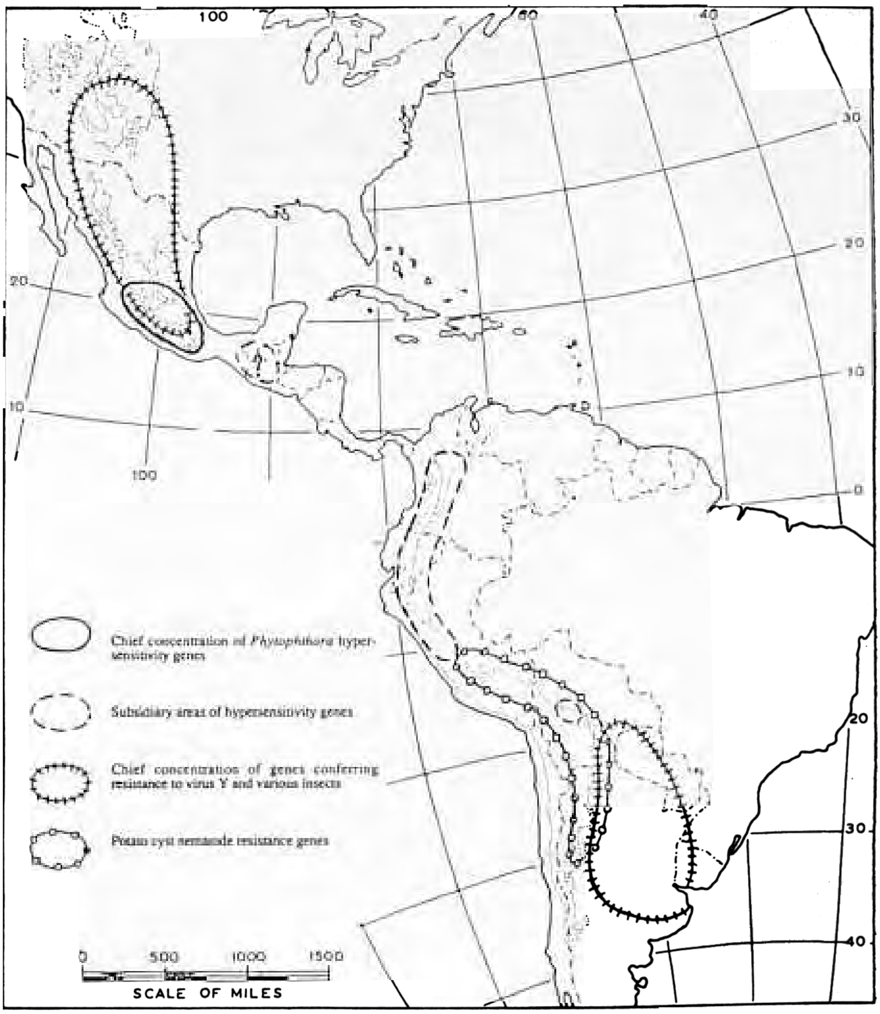

Figure 1. Geographical distribution of genes conferring resistance to certain potato diseases and pests. (From Hawkes, 1958.)

has been found in at least 12 species from Mexico, and several have been used in potato breeding. Hawkes (1958) has indicated that the geographical distribution of hypersensitivity genes lies chiefly in Mexico, but such genes have been reported also from Colombia and Bolivia (Fig. 1). The geographical distribution of species with race non-specific or field resistance to late blight is concentrated in Mexico near the Tropic of Cancer, and in the Andean region near the Tropic of Capricorn (Fig. 2), in areas often sited at altitudes between 2000 and 3500 m and where, during the rainy season, the daily rains and cool nights provide an environment ideal for the development of late blight (Van Soest, Schöber & Tazelaar, 1984). Such conditions are conducive for the development of gene complexes through natural selection, necessary to establish stable resistance. Race non-specific resistance has been reported in 15 wild species from eight taxonomic series in both Mexico and South America (Fig. 2). Although Mexico

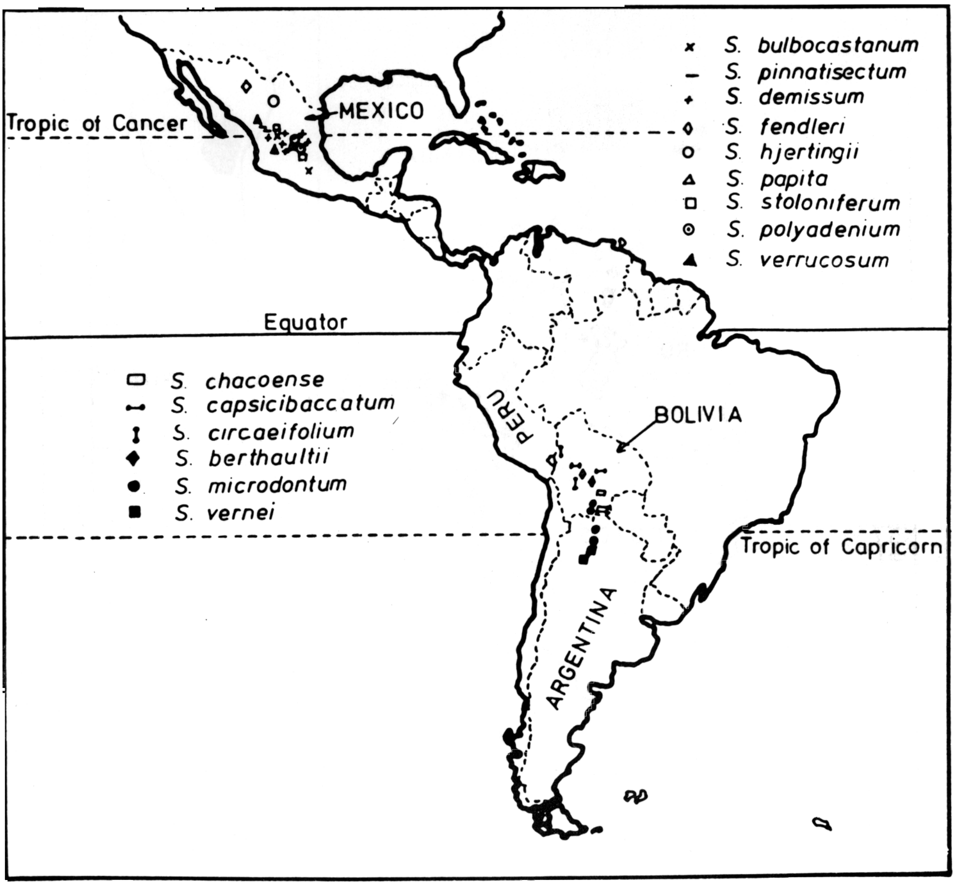

Figure 2. Geographical distribution of tuber-bearing *Solanum* species with high levels of race non-specific late blight resistance. (From Van Soest, Schöber & Tazelaar, 1984.)

is often thought of as the home of the late blight fungus, because both sexual strains of the fungus survive there *in vivo*, the presence of resistance genes in the Andean region has been due to a selection pressure which indicates that the fungus has also been present there for a long time. In this case, the Law of Homologous Series tell us something about the pathogen as well as the host.

Potato cyst nematode

With the example of the potato cyst nematode, *Globodera pallida* (Stone) Mulvey & Stone, the data are perhaps even more striking. It is apparent that the wild species of Bolivia and Argentina are extremely important as sources of resistance to this pest.

The geographical distribution of potato species, mostly from Series Tuberosa, with resistance to *G. pallida* pathotype Pa_3, is shown in Fig. 3. Van Soest, Rumpenhorst & Huijsman (1983) found a remarkable concentration of resistance genes around Potosí in central Bolivia, although the distribution extends northwards towards Oruro and Cochabamba, and southwards to the Argentine border.

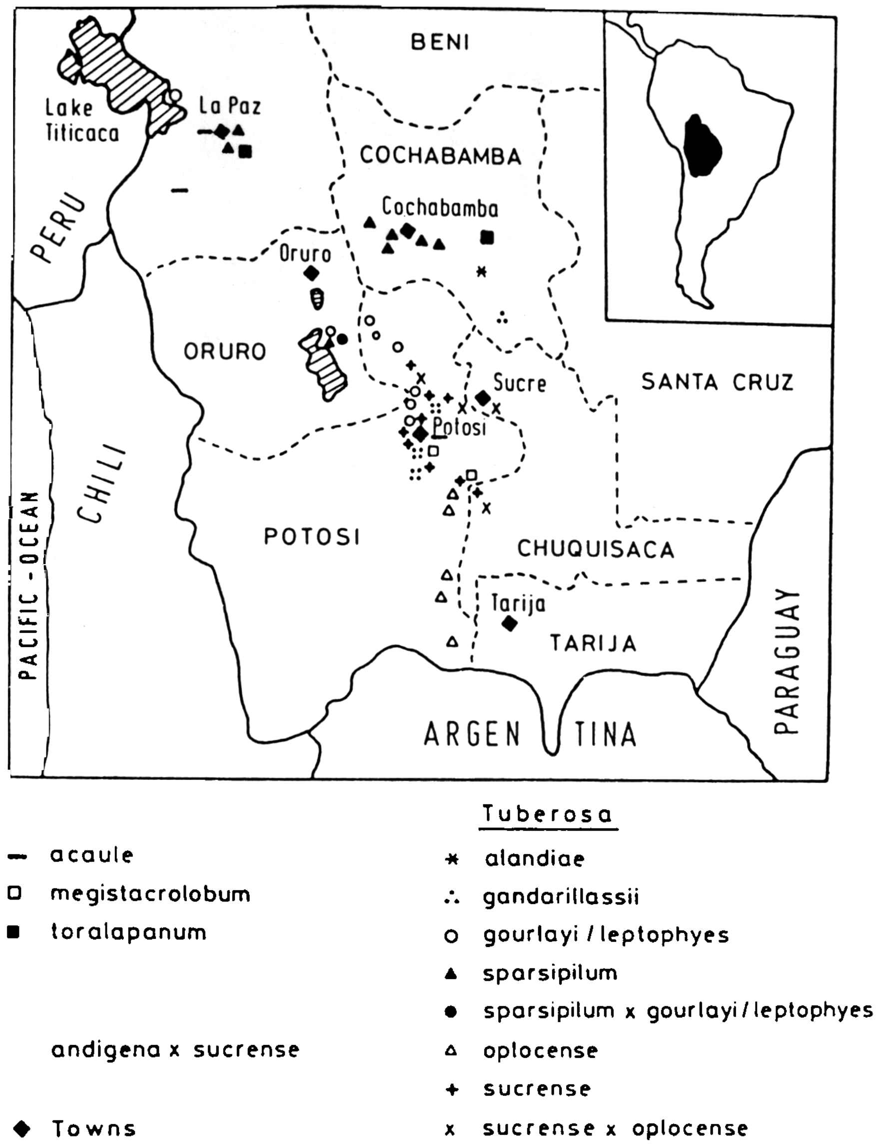

Figure 3. Geographical distribution of tuber-bearing *Solanum* species with resistance to *Globodera pallida* pathotype Pa_3. (From Van Soest, Rumpenhorst & Huijsman, 1983.)

The three-dimensional transect in Fig. 4 (abbreviations are explained in Table 1) shows that most species with *G. pallida* resistance can be found on the Cordillera Oriental and not on the Cordillera Occidental (Van Soest *et al.*, 1983). Between these two cordillera there is a high altitude plateau, the altiplano, often over 4000 m, and most of the species in the Series Megistacroloba and some Tuberosa species with resistance can be found there. *Solanum acaule* Bitt., a frost-resistant species is widespread on the altiplano. Several Peruvian Tuberosa species, including *S. bukasovii* Juz., *S. multidissectum* Hawkes, *S. marinasense* Vargas and *S. canasense* Hawkes represent the northern-most species

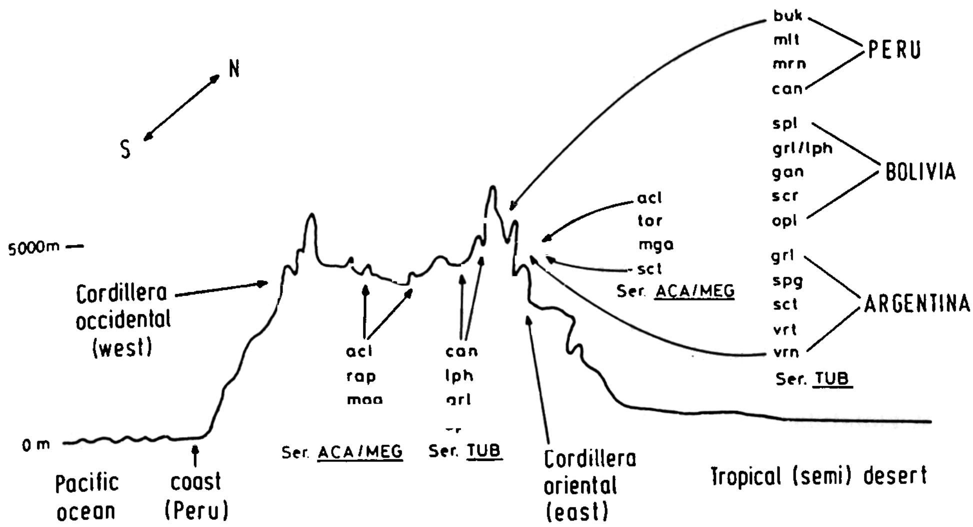

Figure 4. A schematic three-dimensional transect diagram showing the distribution of *Globodera pallida* resistance in three countries of the Andes. (From Van Soest, Rumpenhorst & Huijsman, 1983.)

on the Cordillera Oriental with resistance to *Globodera*. In Bolivia *S. sparsipilum* (Bitt.) Juz. & Buk., *S. gourlayi* Hawkes, *S. leptophyes* Bitt., *S. gandarillasii* Cárd., *S. sucrense* Hawkes and *S. oplocense* Hawkes are the important species with resistance, also on the Cordillera Oriental. Into Argentina, the list may be extended to include *S. spegazzinii* Bitt., *S. sanctae-rosae* Hawkes, *S. venturii* Hawkes & Hjerting and *S. vernei* Bitt. & Wittm. In general, cyst nematode resistance is predominantly concentrated in the Andean *Solanum* species which have their distribution at altitudes between 2500 and 4250 m. It is generally believed that the Andean part of the triangle Peru-Bolivia-Argentina is the centre of diversity or origin of potato cyst nematodes. The concentration of resistance genes would

TABLE Taxonomic series and species abbreviations used in Fig. 4

Series	Species	
ACA	ACAULIA	*S. acaule*
MEG	MEGISTACROLOBA	*S. megistacrolobum* *S. raphanifolium* *S. sanctae-rosae*
TUB	TUBEROSA	*S. bukasovii* *S. canasense* *S. gandarillasii* *S. gourlayi* *S. leptophyes* *S. multidissectum* *S. marinasense* *S. oplocense* *S. sucrense* *S. spegazzinii* *S. sparsipilum* *S. vernei* *S. venturii*

appear to support this theory. It is the co-evolution of potato species and cyst nematodes which has led to the accumulation of resistance and expression of homologous variation for this characteristic in potato species.

Sticky-haired potatoes

Another interesting example from Bolivia is the occurrence of sticky-tipped foliar hairs in *S. berthaultii* Hawkes and a newly described species, *S. neocardenasii* Hawkes & Hjerting, both from the Series Tuberosa, which help protect these species against some potato pests. There are two types of hairs, known as Type A and Type B. Type A hairs are short and four-lobed, which rupture easily when touched, releasing a sticky substance which traps or encumbers pests such as aphids and leafhoppers (Gibson, 1979). Type B hairs are long and terminate in a sticky glandular tip, which secretes a globule of sticky fluid, and which is effective against very small pests such as aphids and mites (Gibson, 1976).

The defensive mechanism of glandular hairs in *S. berthaultii* is further reinforced by what is apparently an aphid alarm pheromone, identical to E-β-farnesene, which is released from the leaves. *Solanum neocardenasii* does not possess this alarm pheromone, but protection is given by an increased frequency of Type B foliar hairs, which have sticky droplets up to eight times the size of those in *S. berthaultii* (Hawkes & Hjerting, 1989).

This combination of defensive mechanisms has been described only in these species, which are found in the general region of Cochabamba and Valle Grande in central Bolivia. The evolution of these mechanisms must have come about as a response to pest attack, although why they should have originated only in central Bolivia is difficult to explain. Gibson (1979) has described the situation near Cochabamba where *S. berthaultii* plants were free from damage by thrips, although nearby cultivated potato crops were badly damaged. It is clear, nevertheless, that species with sticky hairs merit special attention from breeders, and genetical experiments indicate a simple inheritance pattern for this character. On the basis of Vavilov's Law of Homologous Variation, it would be worthwhile looking for other species with sticky hairs in this region of Bolivia.

SIGNIFICANCE OF HOMOLOGOUS VARIATION IN POTATOES

The distribution of resistance to late blight and cyst nematode may be partially explained in terms of hybridization and introgression amongst closely related species, such as those in Series Tuberosa, but it is unlikely to account for their distribution in more distantly related species with which hydridization is difficult. Could this be analogous variation?

If the basis of the Law of Homologous Series is natural and artificial selection, then it is much more difficult to account for the occurrence of resistance genes in species in the apparent absence of a suitable selection pressure. For example, in collaborative research between the International Potato Center, Peru, and the University of Birmingham, high levels of resistance to potato leafroll virus and potato spindle tuber viroid have been found in *S. acaule* at high altitudes where both of the pathogens are not thought to survive (Carlos Arbizu, personal communication).

Nevertheless, the Law of Homologous Series is relevant and demonstrable in potatoes. Since its publication 65 years ago, the Law of Homologous Series has pointed plant breeders and investigators towards sources of diversity for crop improvement. This is precisely what Vavilov intended, for he wrote "the Law of Homologous Series shows investigators and breeders the directions for their search. It aids in the discovery of systematic links and extends the horizon of the worker, disclosing the great amplitude of species variations" (Vavilov, 1922). For those involved in plant genetic conservation, the concept of homologous variation has underpinned exploration and conservation activities. It is indeed a fundamental concept of genetic diversity, with a wide application.

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