THE LAW OF HOMOLOGOUS SERIES IN VARIATION.

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(With Plates IX and X.)

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INTRODUCTION.

Evolution of the study of systematics of plants.

THE characteristic feature of the history of plant investigation, from Tournefort up to the present, has been the varied conception of systematical units. Further investigation did away with the former conception of species, as introduced by Linné. The history of systematics of plants gives a vivid illustration of attempts to arrange in a convenient and harmonious system all newly discovered morphological and physiological characteristics, the number of which grows rapidly with improved methods of discerning hereditary forms, and with the study of new specimens of the same plants, gathered in different regions. The Linnean species had to be divided into subspecies and varieties (*in sensu bot.*); varieties into races. Genetical studies of the last decades have proved even the divisibility of the minutest morphological and physiological units in systematics (races, Elementararten of de Vries), and established that, although outwardly similar, they can be different genotypically. The same is applicable to the animal world.

Lotsy, in his book *Evolution by Means of Hybridization* (1916), proposes to introduce a new terminology to distinguish fundamental units in the classification of hereditary forms. He proposes to call the old Linnean species, which, as was shown in the nineteenth century, are of collective nature—"Linneons"; races, varieties, which make up the elementary species of Jordan and de Vries he proposes to define as "Jordanons." The term "species," Lotsy would retain (as it seems to us not very successfully) for the modern conception of genetics—the genotype, as a fundamental unit covering similar hereditary groups of individuals.

Statistics of the diversity of the plant world.

Up to the present, statistics of the plant and animal world are available only for "Linneons." According to Hooker and Engler there are known altogether about 130,000—140,000 Linnean species of higher seed plants, including *Coniferae.* Families most abounding in Linneons are, according to Engler[1], those of *Compositae* (ca. 13,100), *Leguminoseae* (ca. 12,000), *Gramineae* (ca. 4000).

Although these numbers of Linneons are quite large, they give a very superficial representation of the real diversity of the plant world.

[1] Engler, *Syllabus der Pflanzenfamilien*, 8te Auflage, 1919.

Only a closer study of Jordanons and genotypes would give a true idea of this diversity.

The systematic study of numerous varieties among Linnean species, which was initiated by Lindley (Monograph on Roses), de Candolle (*Brassica*), Kraus, Metzger, and Alefeld on cultivated plants, and by Séringe[1], Jordan and Naegeli on wild plants, and is continued nowadays by plant breeders and by botanists (Swedish school of systematists: Wittrock, Dalstedt, Almquist and others), has revealed a total absence of monotypical Linneons. Linnean species, which, in the nineteenth century were regarded as uniform, in the twentieth century were separated by plant breeders and systematists into large numbers of Jordanons, easily distinguishable both morphologically and physiologically; e.g. many species of *Gramineae*, *Compositae*, *Cruciferae*, *Leguminoseae*, *Sesamum indicum*, *Viola tricolor*, *Linnea borealis*, etc. Up to the present, not many Linneons of wild and cultivated plants have been studied thoroughly, but still the data available shows an immense diversity of Jordanons among Linneons.

Thus, after investigations of local Russian and Asiatic wheats at our experimental station, the existence was proved of about 3000 Jordanons of *Triticum vulgare* Vill., perfectly recognizable morphologically and physiologically[2]. This number does not include many hundreds of varieties of hybrids created artificially by plant breeders of Western Europe during the last thirty or forty years, but only the natural local varieties of wheat.

For barley we know at least 600 to 700 Jordanons, for oats more than 600. In Rye, *Secale cereale*, many hundreds of forms, differing in hereditary morphological and physiological characters, were collected by Mrs V. P. Antropova, from different parts of Persia, Bokhara, Asiatic and European Russia. Hundreds of easily distinguished forms are found in sorghum by American investigators. Investigations in Japan and India discovered thousands of varieties in rice. Thousands of varieties might be established in Indian corn, *Zea mays*. Hundreds of varieties were found in peas, *Pisum sativum*; vetches, *Vicia sativa*; lentils, *Ervum Lens*; beans, *Phaseolus vulgaris*. Hundreds of varieties are found among Soya beans, *Soya hispida*. Jordan and Rosen found about 200 constant varieties in wild *Draba verna*. Miss Sinskaja, at our experimental station, found more than 300 well recognizable varieties

[1] *Musée helvétique*, p. 115 (Aconitum).

[2] This data is given in the address by the author and his co-workers at the All-Russian Conference on Plant Breeding, 1920. Saratov. Now in the press.

of *Eruca sativa*, a weed occurring in fields of flax in Turkestan and Bokhara. Thousands of forms, perfectly distinguishable, exist among species of *Cucurbita Pepo*, *Cucurbita maxima*, *Citrullus vulgaris*—water-melon, *Cucumis sativus*, and *Cucumis Melo*[1]. Hundreds of forms are found among wild *Linnea borealis* (Wittrock), *Picea excelsa* (Wittrock), etc.

Wild and cultivated plants.

The majority of cultivated and wild Linneons propagated by seeds, are represented by hundreds of well-defined Jordanons. There is no essential difference in this respect between wild and cultivated plants. Wild Linneons, like clover (*Trifolium pratense*), *Agropyrum cristatum*, *Agropyrum repens*, yellow alfalfa (*Medicago falcata*), *Alopecurus pratensis*, *Brassica elongata*, studied in detail at Russian Experimental Stations by plant breeders (Roudzinski, Lorch, Jegalov, Bogdan), proved to be no less variable than cultivated wheats, barleys, oats, and peas. The monotypic nature of many wild Linnean species is kept only so long as they are studied by a few specimens in the herbarium. The individual study in cultures of many samples of the same Linneon inevitably discovers its polymorphic nature.

Still greater diversity is observable in plants multiplying vegetatively or apogamically, like roses, potatoes, apples, *Hieracium* (Naegeli), and *Dahlia*.

We do not exactly know if there are really monotypic Linnean species in nature, fairly well specific and separated from other Linnean species and represented by one variety, one Jordanon only. The whole impression is that the more we study our plants and animals, the more variable they are, the more varieties we find among Linnean species. Several Linnean species of plants and animals, like roses, wheats, Indian corn, rice, squashes, *Drosophila*, seem to be extremely variable, but these have attracted more attention than others. We easily notice sharp differences in colour, size, and shape of several organs and are rather inattentive to others.

The differences of Jordanons within the limits of the same Linneon, in the shape and colour of their flowers, form and size of leaves, fruits and other organs, are very often no less marked than the differences between Linneons themselves. For instance, some varieties of *Cucurbita Pepo* are characterized by fruit the size of hen's eggs; other varieties, growing under the same conditions, bear fruit three and four feet in

[1] These plants were studied at our experimental station by Mr S. M. Boukasov and Mrs S. A. Kartashov.

diameter. Some varieties of *Sesamum indicum* have opposite leaves and fruits, others have alternate. Some varieties of wheat and rye have simple leaves, without differentiation into vaginae and plates, having no "ligula," or "auriculae"; others have the usual complicated leaves, with "ligula," and "auriculae."

Plants self-fertilized, as wheat, barley, peas, soya, etc., and cross-fertilized, as rye, maize, beet, are alike polymorphous. The seeming uniformity of several cross-fertilized wild and cultivated plants is only apparent when they are not studied carefully. The difference consists only in the heterozygotic nature of many characters in cross-fertilized plants, and in the homozygotic nature of self-fertilized plants. Some recessive characters may be hidden in cross-fertilized plants by the dominance of other characters, but by artificial self-fertilization of these plants, and by inbreeding, it is possible to re-establish them. From what we know at present from the study of Indian corn (Emerson, Collins, and others), of rye, beetroot, *Drosophila*, man himself, cross-fertilized organisms are not less variable than self-fertilized.

The above-mentioned numbers of Jordanons are in reality still greater, because, up to the present time, African and Asiatic varieties of even the most important cultivated plants, like wheat, oats, barley, peas, lentils, *Cruciferae*, are almost unknown.

Problems of the future.

There is a real need for the study and systematizing of these Jordanons, especially in cultivated plants and domesticated animals, for the benefit of geneticists, as well as systematists and agriculturists. Only the closest study of Jordanons and genotypes will give a real representation of what a Linneon is. To construct the general genetic schemes, it is necessary to know the composition of Linnean species. Before creating new varieties by crossing we ought to know what exists in nature. Even for cereals, *Leguminoseae*, and other most important plants, we have no adequate knowledge of even easily recognizable botanical varieties. Regions of ancient culture in Asia, Africa, and America still preserve numbers of varieties unknown to systematists and plant breeders.

In 1880, Alphonse de Candolle wrote in his remarkable book *La Phytographie*: "Un jour la science traitera les éléments de l'espèce comme les éléments des genres, comme ceux de la famille et tous ces groupes seront coordonnés, les uns au-dessus des autres d'une manière parfaitement uniforme" (p. 80). This day has arrived, but the task is not very simple. The closest study of some Linneons of cereals, *Leguminoseae*, *Cruciferae*, *Compositae*, and *Cucurbitaceae*, persuades one of the immensity of this work. The diversity of plants and animals is too great to admit of giving a complete list of existing forms. There comes the necessity to establish some principles and schemes of classification.

The near future promises to differentiate the Linneons still more, and to multiply the number of Jordanons and species in Lotsy's sense. Artificial hybridization threatens considerably to enlarge the external diversity of forms.

It may be expedient to define even at the present time the multiformity in Linneons, not by the number of described and possible combinations, but by the number and list of *varietal characters* through which Jordanons differ from each other, not forgetting that separate characters can be dependent on several hereditary factors or genes, involving complicated genotypical formulae. The complete genotypical composition of Linneons is a problem for the future.

The multitudinous chaos of innumerable forms obliges investigators to look for some way of simplification. The process of differentiation will go on inevitably, adding to the records of existing forms, and giving a true conception of Linneons. But parallel to differentiation it is natural to search for ways of *integration* of our knowledge of Jordanons and Linneons themselves. If some 130,000 Linneons are difficult to manage for investigation, the work with tens and hundreds of millions of Jordanons will be still more complicated.

As formerly, in the study of dead organic and inorganic worlds, so at the present, the problem before the investigator of the animal and plant world is to explore the regularities in polymorphism, and to establish its classes.

The object of this work.

Below is an attempt to integrate the phenomena of polymorphism which we define as "The Law of Homologous Series of Variation." These regularities were noted by the author during the study of innumerable varieties of cultivated and wild plants.

The ideas expounded below in some part are not foreign to biological literature. Separate facts of regular variation were known long ago. Naudin noticed them in his classical study of *Cucurbitaceae*. Darwin[1], who was in general rather the adherer of fortuitous variations in all directions in his *Origin* and *Variation*, paid attention to regular varia-

[1] Darwin, *Variation of Animals and Plants*, Part 2; "Analogous or Parallel Variation."

tion, which, as he states, "occasionally" happens in plants and animals. M. J. Duval-Jouve collected a great many data on the variation of wild Linnean species of *Gramineae*, *Juncaceae* and *Cyperaceae* in his paper on "Variations parallèles des types congenères" published in 1865 in *Bull. de la Sté. Botanique de France*, Vol. XII. His conclusions in some part come near to the statements of our study. De Vries notices in his *Mutationstheorie* the existence of series of variation. Eimer[1] in his study of Orthogenesis approached the same subject from a different point of view. Several palaeontologists (Cope, Osborn) noticed regular variation in animals. More recently Saccardo[2] and Zederbauer[3] gave extremely instructive instances of regular variation in fungi and *Coniferae*.

The detailed study of variation among many different groups, and the great number of new facts permits us to take this subject anew and to bring all known facts into the form of a general law to which all organisms are submitted.

I. VARIATION OF CLOSELY ALLIED LINNEONS.

In studying the varietal composition of the plant world, and in investigating in detail Linnean species, one can observe some regularities in their varietal diversity, in spite of their enormous polymorphism.

The first regularity one meets with is the similarity in series of morphological and physiological characters, which distinguish varieties and races (Jordanons) of nearly allied Linneons; also a parallelism in the series of genotypical as well as phenotypical variation in Linnean species of the same genus. Let us consider some examples.

Wheat. There are eight Linnean species of wheat, which represent typical collective units, well determined by their specific characters. Numerous investigations have shown that these Linneons form three genetical groups, as follows:

I. (1) *Triticum vulgare* Vill.	II. (4) *T. durum* Desf.
(2) *T. compactum* Host.	(5) *T. polonicum* L.
(3) *T. Spelta* L.	(6) *T. turgidum* L.

III. (7) *T. monococcum* L.

[1] G. H. T. Eimer, *Die Entstehung der Arten auf Grund von erworbener Eigenschaften nach den Gesetzen organischen Wachsens*, Vols. I—III. 1888—1901, Iena.

[2] P. A. Saccardo, "I Prevedibilli Funghi Futuri secondo la Legge d' Analogia." *Degli Atti del R. Instituto Veneti de Scienze, Lettere ed Arti*, Tomo VIII. Ser. 7.

[3] E. Zederbauer, "Variationsrichtungen der Nadelhölzer." *Sitzberichte d. Akademie d. Wissenschaften, Wien, Math. Nat. Klasse*, 116, Abt. I. 1907.

The eight species, *T. dicoccum* Schrank, occupies a place between the first and the second groups[1]. *Triticum vulgare* is represented by a multitude of Jordanons (varieties and races), which differ in the following characters:

1. Bearded, beardless, semi-bearded ears.
2. Ears white, red, gray, black.
3. Ears smooth, hairy.
4. Seeds white, red.
5. Winter, spring varieties; and so on.

T. compactum, *T. Spelta*, genetically closely related to *T. vulgare* repeat exactly all its varieties. So we have a complete similarity in the series of varieties in all three Linneons.

The second group of wheats, separated from the first by a considerable sterility of hybrids between them, repeats, in general, the series of variation of the first group. In *T. durum*, *T. polonicum*, *T. turgidum*, there are white, red and black eared varieties, smooth hairy eared, white and red grained, winter and spring varieties. Only beardless forms are still unknown. All existing varieties of this group of Linneons are bearded or semi-bearded. By artificial crossing, beardless durum wheats have been obtained during the last few years, at Saratov Experimental Station.

The third group of *T. monococcum*, in its wild and cultivated forms, completely repeats the former group in its variability[2].

T. dicoccoides Kcke, a wild Linnean species nearly allied to cultivated wheat, and found in great quantities by Aaronsohn in Syria, consists of a large number of varieties parallel to varieties of *T. durum*, *T. dicoccum* and other Linneons.

Numerous races included in different botanical varieties of *T. vulgare*[3], and investigated at our experimental station, showed the minutest likeness in their series. For instance, among the botanical variety *T. vulgare* var. *ferrugineum* A1, studied by Miss E. I. Baroulina, about

[1] N. I. Vavilov, "Immunity of Plants to Infectious Diseases," 1919, Ch. v. *Annales de l'Académie Agronomique Petrovskoé (près Moscow)*, Année 1918. (With a résumé in English.) "Immunity to Fungous Diseases as a Physiological Test in Genetics and Systematics, exemplified in Cereals." *Journal of Genetics*, Vol. IV. No. 1, June, 1914.

[2] K. A. Flaksberger, "*Triticum monococcum* L." *Bulletin of Applied Botany*, 1914, Petrograd.

[3] This Linnean species is divided, according to F. Koernicke (*Handbuch der Getreide*, 1885) and K. A. Flaksberger ("Determination of Wheats." *Bulletin of Applied Botany*, Petrograd, 1915), into 26 botanical varieties, each of which is of collective nature and consists of a number of races.

220 Jordanons were established, differing in structure of ears, glumes, rachis, grain, leaves, in physiological characters (immunity to fungous diseases, early ripening, etc.). The same series of morphological and physiological races were found in *T. vulgare* var. *erythrospermum* Kcke, *T. vulgare* var. *graecum* Kcke, T. var. *erythroleucon* Kcke.

Barley. Cultivated varieties of barley are represented by two genetically closely allied Linneons, which can easily be crossed: *Hordeum vulgare* L. and *H. distichum* L. The first of these has the varieties:

1. With dense and loose ears.
2. With black, yellow and red (anthocyanin) ears.
3. With hairy and smooth empty glumes.
4. With kernels hulled and without hulls.
5. With awns smooth and rough.
6. With "Kapuze" instead of awns.
7. Winter and spring varieties; and so on.

The second Linneon (*H. distichum*) completely repeats the whole series of varieties of the first one.

Until late years, only one variety of wild barley (*H. spontaneum* C. Koch), closely allied to cultivated *H. distichum*, was known. This was a winter variety, with yellowish ears. In 1916, we found in Persia and Transcaspic Province and Bokhara, a number of spring varieties of wild barley, with typical bristle spikelets, varieties with black ears, with smooth as well as with hairy, empty glumes.

Oats. Let us take a larger group of Linneons, belonging to the botanical section *Euavena*, which includes genetically nearly related Linnean species of cultivated and of uncultivated oats. A closer investigation of their numerous varieties, studied in our Bureau of Applied Botany, Petrograd, by Mr. A. I. Malzev, showed that *Avena diffusa* Asch. and Gr., *A. orientalis* Schr., *A. fatua* L., *A. Ludoviciana* Dur., *A. sterilis* L. are represented by similar series of varieties with white, yellow, gray and brown (black), flowering glumes, with hairy and smooth glumes; all these Linneons include spring as well as winter varieties, those susceptible to crown rust (*Puccinia coronifera*), as well as those which are immune, etc.

Millet. The same parallelism may be observed in Linneons which, although nearly related, are still quite distinct and cannot be crossed. *Panicum italicum* and *P. milliaceum* give an example of such distinct Linnean species, represented by a large number of botanical varieties, studied by Koernicke (*Handbuch der Getreide*, 1885), and by Russian plant breeders Arnold, Syriousov, and others at our experimental station. The series of varieties differing in compactness of panicule, in colour of flowering glumes, in the presence or absence of anthocyanin pigment in panicules, and in the size of the plants, etc., are extremely alike in both Linneons.

Cotton. If we compare the variability of Asiatic cotton, *Gossypium herbaceum,* cultivated on a large scale in Turkestan, Persia and India, with the variability of American cotton, *Gossypium hirsutum* (Upland), we notice a striking similarity in both Linnean species. Asiatic cottons were studied in detail by Leake, Gammie and others, in India, and by Zaitzev in Turkestan. In their manner of branching, in the variation of the shape of their leaves, colour of stem, and in all details of structure of fruit, colour of fibre, and other characters, one Linneon repeats the other. At the same time, these Linneons differ not only geographically but also physiologically in their origin. They can only be crossed with great difficulty, and then give mostly plants which are completely sterile[1].

Agropyrum repens and Agropyrum cristatum.

Let us take two distinct Linnean species, grown in typical wild conditions. *Agropyrum repens* and *A. cristatum,* two typical wild Linneons, meadow grasses, widely distributed over European and Asiatic Russia. These grasses were studied in detail by V. S. Bogdan, at the Krasny Kout Experimental Station (Samara Government), and by the author, in Moscow and in Saratov Government. On comparing their polymorphism we must acknowledge a striking likeness between the series of varieties represented by both plants. Both have—

1. Bearded and beardless ears.
2. Hairy and smooth glumes.
3. Yellow, red and black eared varieties.
4. Varieties with anthocyanin in ear (violet, and without anthocyanin).
5. Varieties with spreading (lying) and erect form of seedlings.
6. With thin and thick straw.
7. Loose and dense ears.
8. Ears covered with wax, and without wax.
9. With yellow and violet anthers.
10. With short and with long stems.

[1] G. S. Zaitsev, "The Results of Crossing *Gossypium hirsutum* and *G. herbaceum.*" *Bulletin of Applied Botany* (Petrograd). At present in the press.

11. Hairy and smooth leaves.
12. With narrow and broad leaves.
13. Early and late varieties.
14. Hydrophilous and xerophilous types.

Agropyrum cristatum, also, has varieties with straw full of pith, as well as the ordinary varieties with hollow straw. The former varieties are not found yet in *A. repens*, but it has not been sufficiently studied to say definitely that these forms are absent.

Brassica Napus and B. rapa.

A clear parallelism of series of varieties is to be observed in *Brassica Napus* and *Brassica rapa*. Both have annual and biennial varieties; the diversity in colour and shape of flowers and leaves, form of plants, shape and colour of fruit and seed is quite similar in both Linneons.

Cucumbers and melons, Cucurbita maxima and C. Pepo.

A striking parallelism of a series of varieties is observed in cucumbers and melons, belonging to two different Linnean species, *Cucumis sativus* and *C. Melo*, which are physiologically distinctly separated, as was shown by Naudin. Both in shape and colour of their fruit, seeds and leaves, in details of flower structure, and habits of plants, one must notice the astonishing similarity in series of variation of these Linneons, represented by a large number of well distinguished Jordanons. Some varieties of melons are quite similar in appearance and flavour to several varieties of cucumbers. This parallelism has already been mentioned by Darwin in his *Variation of Animals and Plants under Domestication*.

Very similar variability in Jordanons might be observed in *Cucurbita maxima* and *Cucurbita Pepo*, and *C. moschata*, three Linneons represented by a large number of varieties. "Three species of *Cucurbita* have yielded a multitude of races which correspond so closely that Naudin insists they may be arranged in an almost strictly parallel series[1]." These Linneons, notwithstanding their similarity in variation, cannot be crossed together, as was shown by Naudin and confirmed at our experimental station by Mrs Kartashov.

An immense number of other similar examples could be given for wild and cultivated plants. So far as we know, this kind of variation is not "occasional," as Darwin supposed it to be, *but quite general*. The data were not available in his time, but the detailed study of hundreds

[1] Darwin, *Variation*, Part II. New York edition, 1876, p. 341.

of Linnean species belonging to different families shows that there are no plants which are an exception to this rule. *Therefore, we may conclude 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.*

II. Variation of Different Genera.

Rye and wheat.

In the study of Linneons and Jordanons of closely allied genera, one can notice the same regularity in polymorphism. To compare wheat and rye—

The varietal composition of rye—*Secale cereale*—until recently has only been studied in a fragmentary and insufficient manner, notwithstanding the great importance of the culture of this cereal in Europe. As a typical cross-fertilized plant, rye has no definite constant varieties, and the separation and definition of different hereditary forms is more difficult than in wheat, which is usually self-fertilized. The predominant view met with in literature is that rye is a uniform plant, as compared with wheat.

Investigations made by Mrs V. P. Antropova and Mrs A. J. Toupikova, at our experimental station, of many samples of rye collected from different regions of European and Asiatic Russia, from Persia, Bokhara, Pamir, and Afghanistan, showed a sharp polymorphism in rye no less than in wheat. The most interesting result of these studies is that the characters which distinguish the different forms of rye appear to be strikingly similar to those marking the different forms of wheat. So it appears that rye, just as wheat, is represented by:

1. Varieties with bearded, beardless (almost), and semi-bearded ears.
2. With hairy and smooth ears.
3. By white (yellowish), red and dark brown eared varieties.
4. By varieties with violet ears (with anthocyanin), and without anthocyanin.
5. With not only the common green seeds, but also seeds of white, red or brown[1].

[1] Several varieties of Abyssinian wheat (*Triticum durum*) have brown-purple seeds, cf. A. St C. Caporn, *Journ. Gen.* VII. 1918, p. 261.

6. As in wheat, varieties with grains easily shed from flowering glumes, or *vice versa*, with seeds entirely covered in glumes.

7. Forms with hollow straw, and with straw full of pith.

8. Varieties with fragile rachis, as well as with strong rachis (as in ordinary varieties of European rye).

9. Varieties with long and short ears.

10. „ „ dense and loose ears.

11. „ „ hairy and smooth rachis.

12. „ „ broad and narrow glumes.

13. „ „ bearded and beardless empty glumes.

14. „ „ many flowers on their spikelets, or with only two flowers in a spikelet.

15. Varieties with rough or tender beards.

16. „ „ starchy or flinty seeds.

17. „ „ small and with large seeds.

18. „ „ nerves highly developed on glumes, with nerves weakly developed on glumes.

19. Varieties with smooth leaf sheaths, or with hairy sheaths.

20. „ „ ligula, or without ligula.

21. „ „ well-developed auriculae, or without auriculae.

22. „ „ smooth auriculae or with hairy auriculae.

23. „ „ violet seedlings[1] or with green seedlings.

24. „ „ broad and narrow leaves.

25. „ „ hairy and smooth leaves.

26. „ „ thin and thick straw.

27. „ „ short and long straw (stems).

28. „ „ procumbent and erect form of seedlings.

29. Early and late varieties.

30. Winter and spring varieties.

31. Resistant to and susceptible to brown and yellow rusts.

32. Varieties with ordinary simple ears, or with complicated branchy ears.

33. Varieties with leaves covered with wax inflorescence, or without wax.

34. Cross-fertilized or self-fertilized forms[2], etc.

In general, the genus *Secale* repeats in detail the series of variation

[1] In wheat some Persian varieties belonging e.g. to *Triticum vulgare* var. *ferrugineum* Al. are characterized by seedlings in colour and shape not distinguishable from seedlings of ordinary violet rye.

[2] In wheats, several varieties of *T. vulgare* are inclined to cross-fertilization.

of the genus *Triticum*, a result which was unexpected at the beginning of our studies. In the same investigation, a search was conducted for varieties similar to those of wheat previously known to us; and our presuppositions concerning the forms of rye which theoretically ought to exist were, in most cases, exactly corroborated.

Prediction of existence of rye without "ligula."

Thus we found in 1916, in Shugnan (Pamir) and in Afghanistan, several varieties of wheat (*T. vulgare*), the leaves of which were without "ligula," unknown before that time, so far as we know, in botanical literature. (See Pl. IX.) *A priori*, basing our opinion on the principle of homologous variation in nearly allied plants, we expected to find these curious forms without "ligula" in rye too; and in 1918, it was actually found among Pamirian spring rye, sown at our experimental station. (See Pl. IX.)

In literature there is no mention of the existence of varieties of rye with hairy ears. *A priori*, their existence was very probable, for in the genus of *Triticum*, all Linneons are represented by smooth eared, as well as by hairy eared, varieties. In 1918, such hairy forms were found by examining thoroughly ears of Pamirian spring rye.

Wheat, as we have seen before, is represented by bearded and beardless Jordanons. Even in Linneons, which usually are represented only by bearded varieties, as e.g. *T. durum*, there are known semi-bearded varieties (var. *Arraseita* Hochst.). *A priori*, we should expect to find the same differences in rye, and, in 1919, there were found typical long-bearded (Astrakhan rye), semi-bearded, and almost beardless varieties (the latter among specimens from Pamir and Afghanistan).

Rye and wheat belong to two genera comparatively closely allied. In some cases they produce many natural hybrids, as has happened in recent years in south-eastern Russia, some of which may even be partially fertile (single seeds)[1]. Most striking is their complete parallelism in variation down to the minutest characters.

Aegilops.

The genus *Aegilops*, which is related to *Triticum*, and grows in large quantities in natural wild conditions in southern Russia, Turkestan and Persia, as was shown by our observations, repeats in general all varieties of the genus *Triticum*. In *Aegilops squarrosa* and *Ae. cylindrica*, there

[1] G. K. Meister, "Hybrids of Wheat and Rye." *Report of the Third All-Russian Conference of Plant Breeding*, Vol. I. 1920.

are beardless as well as bearded varieties, varieties with yellow, red and black ears, hairy and smooth ears; and we know winter as well as spring varieties of these Linneons. The same division of the genus *Aegilops* into collective Linneons seems to be similar to that of *Eutriticum* (cultivated wheats). The Linnean species, *Aegilops cylindrica* and *Ae. squarrosa*, are akin to *Triticum vulgare* and to other Linneons of the same group of wheat. Both are characterized in general by hollow stems, susceptibility to yellow and brown rusts (*Puccinia glumarum* and *P. triticina*), to mildew (*Erysiphe graminis*), and to smut—*Tilletia tritici*. Other Linneons, like *Aegilops triuncialis*, correspond more to *Triticum durum* or *T. monococcum* in their immunity to these parasites, and the similarity of their straw, which is full of pith, and in the absence of completely beardless varieties[1].

As is known, Godron produced artificially hybrids of wheat and *Aegilops*, which proves the relative affinity of these genera.

Agropyrum.

The genus *Agropyrum* belongs to the group of genera closely allied to *Triticum* and to *Secale*. In 1919, we produced a sterile hybrid (F_1) by crossing *Secale fragile* with *Agropyrum villosum*. As we have shown before in the example of polymorphism of *Agropyrum repens* and *A. cristatum*, this genus in general repeats, even in detail, the series of variation of *Triticum* and *Secale*.

Vicieae.

Let us turn to the family of *Papilionaceae*. Four Linneons—*Pisum sativum*, *Lathyrus sativus*, *Ervum Lens*, and *Vicia sativa*—belonging to the systematical section *Vicieae*, were studied in detail at our experimental station. All four Linneons manifest a similar homologous series of variation like cereals. Each Linneon was represented by a large number of varieties collected from different European and Asiatic countries. All four genera proved to have varieties with white, red (pink), and violet (purple) flowers, and all manifested a striking phenotypical similarity of variation in the shape and colour of their seeds and cotyledons. In all genera were found varieties with yellow-green cotyledons, also with orange-red, and with black, brown, green, yellow, and white seeds. (See Plate X.) In all Linneons there are varieties with spotted, as well as with unicoloured seeds. In all genera were

[1] For details see N. I. Vavilov, *Immunity of Plants to Infectious Diseases*, 1919, Ch. 4.

discovered varieties with small and large seeds. The variation in the shape of seeds is found to be alike in peas, lentils and vetches, as well as in *Lathyrus sativus*; they may be flat, angular, or round. In all genera we found varieties with narrow and broad leaves, with leaves covered with wax, with coloured (violet) seedlings, and with ordinary green seedlings. All four genera have tall and dwarf varieties, early and late forms. The variation in fruits in all of them tends in the same direction.

This similarity in *Vicieae* is so clearly expressed that sometimes it was difficult to say, from an external view of the seeds, to which genus they belonged. This is the more striking as all these genera are physiologically quite independent and cannot be crossed together, in spite of many attempts made by Fruwirth[1], and at our experimental station.

Cucurbitaceae.

The most cultivated genera and Linneons of the family *Cucurbitaceae* are *Citrullus vulgaris* (water-melon), *Cucumis Melo* and *C. sativus* (melons and cucumbers), and *Cucurbita Pepo*, *C. maxima* and *C. moschata* (squashes, gourds and pumpkins). After the investigations of Naudin, it was found that these three genera, although quite distinct, belong to the closely related botanical sections *Cucumerinae* and *Cucurbitinae*, and their variability can therefore be compared.

The numerous varieties of these genera, collected from different parts of Russia, Persia and Bokhara, were studied at our experimental station during 1919 and 1920.

All three genera in their Linneons have varieties with round, oblong, and flat, simple, as well as segmented fruits. The variation of the colour of fruits is relatively similar in all genera, whether monochrome, streaked or spotted, white, green, yellow, brown, or black. Their parenchyme can be colourless, or with coloured plastids. The fruit may be sweet or bitter. Variation in the size of fruits is extremely great in all genera, beginning with small fruits of the size of apples and even smaller, and ending with the gigantic fruits, such as the ordinary squashes, melons and water-melons. The diversity in flower structure, colour and hairiness of petals and calyx, is very great in different varieties, and varies similarly in all genera. The leaves vary greatly in all three genera. Most varieties of melon have simple leaves, very different from those of the water-melon, but some resemble, in the dissection of their leaf

[1] *Pflanzenzuchtung*, Dritte Auflage, 1919.

plates, varieties of water-melon. At the same time, we know several varieties of water-melon which approach other melons in the shape of their leaves. Varieties of gourds (*Cucurbita Pepo*) have leaves differing from the simple undissected shapes to those similar to ordinary water-melons.

Probably there are not many plants which vary so greatly, or at least so conspicuously, as these genera of *Cucurbitaceae*. Sometimes it is difficult from the exterior, and even from the interior, of their fruits, to decide positively to which genus they belong. The similarity of variation in separate characters is so sharp that several very careful botanists, such as S. I. Korshinski, have classified some varieties of melon as being natural hybrids of water-melon (*Citrullus vulgaris*), and melon (*Cucumis Melo*)[1]. It is often stated quite wrongly in agricultural and horticultural literature that melons are fertilized by pollen of squashes, and give intermediate forms.

The experiences of Naudin, repeated on a large scale at our experimental station by Mrs S. A. Kartashov, have proved the impossibility of crossing these three genera. Even separate Linneons, within the limits of the same genus, e.g. *Cucurbita moschata*, *C. maxima*, and *C. Pepo*, cannot be crossed together.

The so-called intermediate forms of these plants, accepted erroneously as being natural hybrids of these genera on account of the shape of their leaves and seeds, and the flavour and shape of their fruits, are only a beautiful illustration of similar variation of these distinct genera, and of their overstepping their characters[2], including the "hybrids" of water-melon and melon described in detail by Professor S. I. Korshinski. The same phenomenon evidently is observed in the case of *Gramineae* in so-called varieties of *Festuca loliacea* supposed to be hybrids of *Festuca* and *Lolium*.

The most essential point is that, notwithstanding an exceptional diversity of varieties in these genera, their variation is very regular, and not accidental. Knowing in detail the series of variation of water-melons, we could find a similar series of varieties among melons and gourds (*Cucurbita Pepo* and *C. maxima*).

[1] S. I. Korshinski, "Bastarde zwischen *Citrullus vulgaris* and *Cucumis Melo*." *Bulletin de l'Académie des Sciences de St Pétersbourg*, 1897.

[2] A detailed article on this subject, entitled: "Hybrids between melons, water-melons and squashes," was given by the author (N. I. Vavilov) at the First All-Russian Congress on Applied Botany, Veronej, Sept. 1920, and will be published in the Report of this Congress.

Cruciferae.

Observations have also proved the striking likeness of varieties of different genera of *Cruciferae,* belonging to the section *Brassicinae,* namely—of Linneons *Eruca sativa, Brassica campestris, B. elongata, B. juncea, B. rapa,* and *B. Napus, Sinapis alba,* and *Raphanus sativus.* Linneons of these four genera show a complete repetition of a series of varieties, differing in the shape and colour of their petals and calyx, shape of leaves, presence and absence of wax on stems and leaves, shape and hairiness of fruits, colour of seedlings, hairiness of stems and leaves, as well as by many minute characters. Linneons of all four genera are differentiated into early and late varieties, into spring and winter (or biennial) varieties. In general, it was found that the more specimens of the same Linneon were studied, the closer was their parallelism of variation to that of other Linneons of the same generic section.

Capsicum and Solanum.

A clear repetition of variation can be observed in *Solanaceae.* The genera *Capsicum* and *Solanum* belong to the same botanical section, *Solaninae* (Engler). In comparing series of varieties of pepper—*Capsicum annuum,* with tomatoes—*Solanum lycopersicum,* the similarity of their hereditary variation in different organs and different characters becomes evident.

The phenomena of homologous variation in related genera may be observed in quite different botanical families of monocotyledonous, and dicotyledonous plants, as well as in *Coniferae* (Zederbauer). Notwithstanding the extinction of many links during the millennial existence of most genera and Linnean species, the rôle of natural selection and extinction, there is no difficulty, by careful study, in tracing the similarity in variation in most of the related genera.

Therefore, in general, *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 allied genera, display similarity in their series of phenotypical, as well as genotypical, variability.*

III. Variation of Whole Systematical Families.

Closer investigation of many genera within the limits of different systematical families, discloses the fact that all genera of a given family are subject to common tendencies in variation.

Gramineae.

Let us take the family of *Gramineae*, and consider the schemes of division into varieties of quite distinct genera, belonging to different generic sections of the same family. All genera and Linneons might be divided into varieties according to their density of inflorescence. Millet—*Panicum miliaceum*—is divided by systematists into three groups, according to its density of panicule:

1. Loose (branchy)—*Effusum*.
2. Densed—*Compactum*, and
3. Intermediate—*Contractum*[1].

In just the same way *Andropogon Sorghum* might be divided. Oats (*Avena sativa*) are represented by varieties with one-sided, compact panicules (*A. orientalis* Schr.), as well as by varieties with loose, branchy panicules (*A. diffusa* Asch. & Gr.). The latter are divided into varieties with more or less crowded panicules (*Steifrispe, Schlafrispe*). In general, the division of oats corresponds to that of millet and *Andropogon*. Cereals with ear-inflorescence might be divided into compact, loose, and intermediate varieties. In wheat, barley, and rye, there are all these kinds of ears among their different varieties. Varieties of maize might be distinguished quite clearly through the density of their ears. There are varieties of rice with compact vs. loose grain arrangement. Many food grasses, studied from a varietal point of view, as *Festuca pratensis, Lolium perenne, Agropyrum cristatum, A. repens, Phleum pratense, Alopecurus pratensis, Dactylis glomerata, Bromus inermis*, and others, all proved to be composed of varieties with loose and dense ears and panicules.

In the family of *Gramineae*, almost all the varieties may be divided into bearded and beardless forms.

The type of wild barley—*Hordeum spontaneum*, and wild oats—*Avena fatua*, characterized by spikelets which are brittle at the time of ripening, repeats itself in many different genera belonging to various sections, as *Secale* (*Secale montanum*), *Triticum* (*T. dicoccoides*), *Agropyrum, Oryza*, etc.

Branching ears are common not only to different Linneons of wheat, e.g. *Triticum turgidum* var. *mirabile* Kcke, but other Linneons belonging to quite different genera, with ear-shaped inflorescence, as barley, rye, *Agropyrum, Lolium, Panicum italicum*, etc.

[1] F. Koernicke, *Handbuch der Getreide*, Vol. I. Bd. 1885.

Varieties of entirely different genera of *Gramineae* might be divided into forms which have hulls and those which are hull-less, i.e. with grains tightly held by glumes, or with grains loose and easily shed out of glumes. We know such varieties in wheat (compare *T. vulgare* and *T. Spelta*), in barley (i.e. *Hordeum distichum* var. *nutans* and *H. distichum* var. *nudum*, or *H. vulgare* var. *coeleste*), in rye, in maize, in millet, in *Andropogon*.

A great many Linneons, belonging to quite different genera of *Gramineae*, studied in detail, have manifested a similar variation in the colour of their glumes. Varieties may usually be divided into white, yellow, red, gray and black (or black-brown) coloured forms. These varieties are known in wheat, barley, rye, oats, rice, millet, *Andropogon*, *Aegilops*, *Alopecurus pratensis*, *Panicum italicum* and other genera.

Nilsson-Ehle has found among cultivated oats a variety with leaves which are entirely lacking in "ligula," called by us var. *eligulatum*. We found such varieties in wheat and rye, and hope to find them also in barley. Dr Emerson and Dr Collins in America recently found aligulate maize[1]. Prof. Janishevski found such varieties among different forms of *Poa bulbosa*. Several varieties of *Panicum Crus Galli* have a small, almost undeveloped "ligula."

Most Linneons belonging to different genera may be divided into smooth and hairy varieties. Hairiness may be connected with the stems, leaves, or glumes of spikelets.

Probably all Linneons of *Gramineae* might be divided into varieties with anthocyanin in stems, and those without it; into varieties with stems and leaves covered with wax, and those without wax.

In many Linneons belonging to quite different genera, we find varieties with procumbent forms of seedlings, and those with erect seedlings.

In a great number of Linneons belonging to different sections of *Gramineae*, cases of "vivipara" were observed. (See Penzig, *Teratologie.*) Duval-Jouve in his old paper (*l.c.*) gives many examples of similarity in variation of different genera of wild grasses (*Poa, Festuca, Bromus, Brachypodium, Agropyrum*).

Even the rare and isolated characters, which are regarded as confined to distinct Linneons, could be found in other genera, as e.g. the so-called "Kapuze," or "hoods," in several varieties of barley, that is, the special metamorphosis of beards into short, thick projections. (See *Hordeum*

[1] Dr R. A. Emerson, "The inheritance of ligule and auricules of corn-leaves." *Ann. Rpt. of Nebraska Expt. Sta. Res. Bull.* 25, pp. 81—88.

trifurcatum.)[1] Thus, some varieties of wheat (*Triticum vulgare*), found by us in Persia, as well as some varieties of Chinese wheats described by Mr K. A. Flaksberger[2] under the name "*inflatum*," are by their morphological as well as their genotypical nature very similar to "Kapuze," "hooded" in barley. (We crossed them with ordinary bearded and beardless wheats.)

If we compare the following series of variable characters distinguishing different hereditary forms of wheat with those distinguishing varieties of other genera of the same family, we notice a similarity in most of them.

A SERIES OF CHARACTERS DISTINGUISHING VARIETIES (RACES, JORDANONS) OF WHEAT—*TRITICUM VULGARE* VILL.

I. *Characters of Ears (Spikes):*

1. Bearded, semi-bearded, beardless.
2. Colour of ears: white (yellow), red, gray, black (brown).
3. Hairiness of glumes: absence, presence, the degree of pubescence, the character of hairs.
4. The shape of glumes: narrow, broad, cuspidated, "hooded," etc.
5. Hairiness of the rachis: presence, absence, the degree of pubescence, the character of hairs.
6. Density of ears: loose, compact, intermediate.
7. Length of awns.
8. Length of the glume-tooth.
9. Length of the ear.
10. Number of flowers in spikelets.
11. Wax efflorescence: presence, absence, the degree.
12. The character of awns: smooth, rough.
13. Grains easily shed out of glumes, grains tightly covered by glumes.
14. Nerves of glumes: highly developed, or weakly developed.
15. Dents of nerves: weak, rough, present, absent.
16. Presence or absence of undeveloped spikelets at base of ears: presence or absence of additional spikelets in ears (very typical for several varieties of wheat).
17. Branched and simple ears.

[1] G. V. Ubisch, "Beitrag zu einer Faktorenanalyse von Gerste." *Zeitsch. f. induktive Abstammungs- und Vererbungslehre*, 1921, Ch. 25, H. 3/4.

[2] K. A. Flaksberger, "Wheats of Sounpan" (China). *Bulletin of Applied Botany*, Petrograd, 1910. John Percival, *Wheat Plant*. A monograph, 1921.

II. *Characters of Grains (Seeds):*

18. Shape of seeds: oblong, short, round, angular.
19. The size of seeds.
20. Colour of seeds: white, yellow, red, brown.
21. Character of the internal structure of seeds: farinaceous or flinty (glassy).
22. The characters of hairs on the top of grains (brush): long, short, dense, rare, etc.

III. *Characters of Plants (Vegetative Organs):*

23. Colour of seedlings: violet (presence of anthocyanin), or green (absence of anthocyanin).
24. Hairiness of leaves: presence, absence, the character of pubescence (short hairs, long hairs, rare, dense hairs, etc.).
25. Borders of leaves are ciliated, non-ciliated.
26. Leaves and stems covered by wax efflorescence, without wax efflorescence.
27. Colour of leaves: dark green, light green, variegated.
28. Length and width of leaves.
29. Length of stems (straw): tall, short, intermediate plants.
30. Straw thick, thin.
31. Straw full of pith, hollow straw.
32. Presence and absence of "ligula."
33. Presence and absence of "auriculae," size of "auriculae."
34. Colour of "auriculae."
35. Hairiness of "auriculae," presence, absence.
36. Nodes of stems: hairy, smooth.
37. Seedlings procumbent, erect, or intermediate.
38. Straw smooth and hairy.
39. The number of nodes, leaves.
40. Stems coloured by anthocyanin, without anthocyanin.
41. Leaf-sheaths hairy or smooth.
42. The number of tillers, stems, i.e. the degree of branching.

IV. *Physiological Characters:*

43. Winter and spring varieties.
44. Late and early varieties.
45. Susceptibility to brown rust (*Puccinia triticina*).
46. " " yellow rust (*P. glumarum*).
47. " " mildew (*Erysiphe graminis*).

48. Closed and opened flowering.
49. Number and length of stomata.
50. Xerophytic types, hydrophytic.

This list of variable characters is not complete; further investigation will undoubtedly increase the number of dissimilarities between different varieties of wheat. Nevertheless, it gives an idea of the great variability within the limits of one Linneon in the family of *Gramineae*. Many of the enumerated characters are independent of others in their inheritance, and in their different combinations form thousands of varieties. Those who are engaged in the study of different genera of cereals, as well as of different wild grasses, cannot deny that in *Gramineae* of quite distant genera variation manifests itself on the same lines. The knowledge of the details of a series of varieties of a single Linneon or genus might help to discover new varieties among other genera and Linneons.

The nearest families to *Gramineae* from a systematical point of view, as *Juncaceae* (Duval-Jouve) are characterized by a series of varieties similar to those of *Gramineae*.

Papilionaceae.

The same similarity of variation can be seen in *Papilionaceae*. The detailed study of variation among distant genera of this family discloses a striking unity in their differentiation into varieties, in scores of different characters of seeds, fruits, flowers, and vegetative organs. For example, if we compare the differentiation into varieties of the abovementioned section—*Vicieae*, including *Vicia*, *Ervum*, *Pisum*, *Lathyrus* and *Cicer*[1], with differentiation of Linneons belonging to sections—*Trifolieae* (*Trifolium pratensis*, *Medicago sativa*), *Loteae* (*Lotus corniculatus*), *Galegae* (*Caragana arborescens*), *Phaseoleae* (*Phaseolus vulgaris*, *Soya hispida*), we cannot help noticing the great resemblance in their mode of variation. They vary in colour of seeds (from white to black), from unicoloured to those covered with small spots or large spots), in colour of cotyledons (from green-yellowish to orange-red), in shape of seeds (from round to oblong and to flat or angular), in size of seeds, in colour of flowers (from white to violet), in shape of fruits, in structure of leaves and flowers, in pubescence of stems and leaves, in shape and colour of seedlings (green or violet, spreading or erect, etc.), and in many other characters (notwithstanding the specific nature of these genera, and the

[1] *Cicer arietinum*. *Memoirs of the Department of Agriculture of India*. Bot. Ser. Vol. VII. 1915.

botanical sections to which they belong). These variations are tending in the same direction, and the completed series of varieties of separate genera show a clear and evident regularity and likeness. It is possible to speak about systems of varieties for different genera and families.

Cruciferae and Papaveraceae.

An astonishing parallelism of variation might be observed in the family of *Cruciferae*. At our experimental station we studied in detail varieties of some Linneons belonging to the section *Sinapeae*, namely, of *Eruca sativa*, *Brassica campestris*, *B. juncea* and *B. napus* (studies carried on by Miss E. N. Sinskaja). The first Linneons established a great number of varieties differing in hairiness of fruits (presence, absence), in colour of flowers (petals) and calyx, in colour and form of seeds, in shape of leaves (beginning with quite simple forms and ending with complicated, dissected varieties), in the shape of petals, form of plants (spreading, erect), in the colour of seedlings (with anthocyanin, without anthocyanin), in structure of fruits (long, short, round, broad, narrow), in density of florescence, etc. In *Eruca sativa* we established more than 250 fixed varieties.

The Jordanons of *Brassica juncea* were studied recently by the Howards in India[1]. Comparing the varieties studied by the Howards and our varieties of *Eruca* and *Brassica*, belonging to the section *Sinapeae*, with Linneons of a quite different botanical section—*Hesperideae* (several Linneons of which (*Draba verna*, *Capsella Bursa pastoris*) were studied in detail by Jordan, Rosen, Lotsy, Shull, and others—it is impossible not to notice the striking similarity of their series of variation. We have no doubt the same series will be found in other genera, and other sections of *Cruciferae*. The mere examination of lists of varieties in "Keys to Determination of Species," in different "Floras" occasionally indicated by some authors for single Linneons, proves this regularity in variation.

The nearest family to *Cruciferae*, from a morphological and anatomical point of view, *Papaveraceae*, is characterized, as far as we can judge, from the study of varieties of *Papaver somniferum*, *Chelidonium majus* and *Corydalis solida* (sub-fam. *Fumarioideae*) by a series of variation very similar to that of *Cruciferae*.

[1] *Memoirs of the Department of Agriculture of India.* Botanical Series, 1915.

Compositae.

The numerous family of *Compositae* displays quite distinctly common tendencies in forming varieties within the limits of different genera. If we compare numerous varieties of *Hieracium*, studied carefully by Naegeli, numerous varieties of sunflower (*Helianthus annuus*), studied in detail by Miss E. M. Plachek in Russia at the Saratov Experimental Station[1], and by Dr Cockerell in America, and varieties of *Carthamus tinctorius*, studied by the Howards in India[2], we cannot help noticing the general character of varietal differentiation. Dahlias, cornflowers (*Centaurea cyanus*), *Cichorium Intybus* manifest similar series of variation in the shape and colour of flowers. The examination of catalogues, horticultural literature, and exhibitions of flowers, shows an extremely instructive similarity in direction of variation in chrysanthemums, asters, dahlias, sunflowers. The similarity is not only superficial and exterior, e.g. there are some varieties of sunflower characterized anatomically by the presence of a layer of dark cells in the skin of seeds, which prevents the seeds from attacks of larvae of sunflower moths—*Homeosoma nebulella*. The same varieties exist in *Carthamus tinctorius*, as well as in some other genera of *Compositae*. The colour of plastids in flowers of *Helianthus*, *Carthamus*, and *Hieracium*, varies in different varieties from pale yellowish to bright orange; there are known varieties with anthocyanin in petals (red sunflower and red *Hieracium*) and without anthocyanin.

The same unity of variation, with the same series of varieties, could be observed as a general rule in families of *Solanaceae*, *Cucurbitaceae*, *Chenopodiaceae*, *Caryophyllaceae*, and, we believe, in all families of the plant world. A beautiful example of parallel variation in different genera and families of *Coniferae*, is given by Mr E. Zederbauer[3].

IV. PREDICTION OF EXISTENCE OF NEW FORMS.

The immediate future will define modes of variation in different families. The series of variation specific for single families will become more exact as the varietal studies of genera become more differentiated.

[1] Miss E. M. Plachek and Prof. A. I. Stebout, "Sunflower." *Report of Saratov Experimental Station*, 1915. Miss E. M. Plachek, "Materials for the Classification of Sunflowers." *Report of the third All-Russian Conference on Plant Breeding*, Saratov, 1920.

[2] *Memoirs of the Department of Agriculture of India*. Botanical Series, 1915.

[3] E. Zederbauer, "Variationsrichtungen der Nadelhölzer." *Sitzber. d. Akad. Wiss. Wein. Math. Nat. Klasse* 116, Abt. 1, 1907.

But it is already evident that the similarity in series of polymorphism of allied Linneons, genera, and even of nearly related families, is so regular that it becomes possible to forecast, on this basis, the existence of forms and of varieties (and even Linneons), not yet discovered. Some such unknown forms might be obtained by artificial hybridization of corresponding varieties, or Linneons.

We have mentioned already some instances where predictions were fulfilled in the finding of forms of rye without "ligula," and of hairy, bearded and beardless varieties of rye. We have met many times with convincing occurrences in forecasting, according to the law of homologous variation, the existence of forms not yet described. To give some more examples—

Linnean species of wheat: *Triticum vulgare, T. compactum, T. Spelta, T. dicoccum, T. monococcum, T. turgidum*, are represented equally by winter and spring varieties[1]. But *T. durum* is usually described in literature as a species represented exclusively by spring varieties, notwithstanding its great polymorphism in many other characters. In literature, occasionally, we find remarks about the existence of one variety of wheat belonging to *T. durum*[2], but even these statements are discounted by other authors.

A priori, one would expect that such winter varieties ought to exist in great numbers, in *T. durum*, if they exist in *T. monococcum, T. Spelta*, and *T. vulgare*. Investigations were begun, and in 1918 we actually received from Mr D. D. Boukinich a large number of specimens of *T. durum*, brought from an isolated, mountainous region of Soumbar, in North Persia, near the Transcaspian Province. And, among these specimens, we found a considerable number of real winter varieties of *durum* wheats, as was shown by sowings of these samples in the spring.

On the other hand, wild Linnean species of *Triticum dicoccoides* Kcke, as well as of wild barley (*Hordeum spontaneum*), are characterized exclusively as winter plants; no spring varieties of these species being known[3]. The study of many specimens of wild barley, collected by the author in 1916 in Persia, Transcaspic Province, and in Bokhara, and sown at the experimental station, resulted in the discovery of a series of

[1] N. I. Vavilov and Miss E. S. Kouznetzov, "On the Genetic Nature of Spring and Winter Varieties of Plants." *Annals of Agricultural College of Saratov University*, Vol. I. 1921. (Résumé in English.)

[2] F. Koernicke, *Handbuch der Getreide*, 1885, Bd. 2.

[3] K. A. Flaksberger, "*Triticum dicoccoides* Kcke-Wild Emmers." *Bulletin of Applied Botany*, 1913 (Petrograd). R. Regel, "Les Orges Cultivées de Russie." *Bulletin of Applied Botany*, 1910 (Petrograd).

wild spring barleys. Among a number of varieties of *Triticum dicoccoides* obtained by us from Mr A. Aaronsohn, from Syria, we found a typical spring variety of wild wheat. Theoretically, it is very likely that spring varieties will be found eventually in *Secale montanum* Guss., which is characterized in botanical literature as a perennial plant.

Several genera of *Gramineae* contain varieties with naked grains (hull-less), as well as the ordinary hulled varieties, with grains tightly covered by glumes. Systematists know naked barley, oats, wheat. We searched for naked varieties in other genera, and found them among millet (*Panicum milliaceum*), and *Andropogon sorghum*.

It seemed probable that in *Aegilops*, *Secale*, and *Agropyrum*, as in *Triticum*, there would be forms with hollow straw, and with straw full of pith. Indeed, such varieties and Linneons were found in these genera.

Melons and squashes (*Cucurbita*) are characterized by varieties with round, oblong, flat, and segmented fruits. In literature we could find no indication of the existence of segmented varieties of water-melons (*Citrullus*), but after special search for them they were found in south-eastern European Russia, in the Astrakhan Government.

Knowing the scheme of variation of colour and shape of seeds and cotyledons, and in colour and shape of stems and leaves in *Pisum* and *Vicia*, we could establish just such a series of similar varieties in *Ervum Lens* and *Lathyrus sativus*, as well as in other genera of *Papilionaceae*. Most Linnean species of *Papilionaceae* are characterized by hairy as well as by smooth fruits. *Soya hispida* in all botanical literature is always characterized by hairy fruits. *A priori*, we expected to find sometimes a variety of *Soya* with smooth fruits. On visiting the United States we saw such a variety in the collection of the Illinois University.

Similar examples are very numerous. We are accustomed at our experimental station to investigate the varietal composition of a plant according to a scheme based on the law of homologous series in variation, and this makes it possible for us to determine many differences and to note many varieties which otherwise would escape a systematist.

V. PHENOTYPICAL AND GENOTYPICAL VARIATION.

We have spoken, so far, strictly about phenotypical differences. Jordanons, Linneons, genera, botanical families in the sense of Johannsen, are phenotypical units. But we have no doubt that the same rules apply to genotypical variation as well. The majority of differences between varieties established by old and new systematists are hereditary differences, and although all our morphological and physiological systems of organisms are systems of phenotypes, they imply genotypical differences too.

There is no doubt that under the same external aspect different genotypes may be concealed. The red colour of wheat grains may be dependent on one, two, three or more hereditary factors (genes), as was shown by Nilsson-Ehle. But genes for colour of grain may vary in different varieties. We know, e.g., two types of yellow cotyledons in peas, one dominant, the other recessive (Love); and different types of hairiness. In barley the character of crenatures depends upon five or six different genes in different varieties[1].

But this only obliges us to be careful and to study varietal differences not externally but genetically as well. It complicates the scheme of differences but does not change the statements settled before; it merely requires further and more detailed genetical investigation.

Until now, only single plants and animals, like one or two Linneons of *Antirrhinum*, or peas, maize, *Drosophila*, have been studied in detail, from a genetical point of view; and not even these in all their varietal characters and existing varieties. The study of genetics of many characters and of all types of varieties of a Linneon is not an easy task, and even for single plants looks almost hopeless to carry out in detail. The number of phenotypes by itself is so large in most Linneons (e.g. for wheat, barley, potatoes, etc.), that it looks an incredible task to accomplish. Up to the present, and for a long time yet, the knowledge will be fragmentary. So far, we have had no adequate system of phenotypes, even for most important plants like cereals. There are no complete scientific classifications for varieties of cultivated plants. In their systematical and geographical study, the investigators still work as in the pre-Columbian time. Very few Asiatic or African varieties of cultivated plants have as yet been discovered or described. The attainment of complete genetical monographies for single Linneons will still be more difficult.

At the same time, the relation of these laws to genotypical variation enables us to use them for purely genetic purposes. After the period of differential work in genetics a period of integration of all data for single plants will inevitably come.

[1] N. I. Vavilov, "On Origin of Smooth Awned Barleys." *Bulletin of Applied Botany*, 1919. (Petrograd.) Not yet published, on account of state of affairs in Russia.

The existence, e.g., in wheat, of two kinds of beards, dominant and recessive, obliges us to search for the same division in other genera of *Gramineae*. And in reality two types of bearded varieties were recently found in oats: one dominant, another recessive in crossing with the same variety[1], two different kinds of beardless varieties of oats: one recessive, another dominant.

In our crossings of *Avena nuda* var. *biaristata* Arch. & Gr. with *A. brevis* and *A. strigosa* (two hulled varieties with gray flower-glumes), all plants in F_2 as well as in F_3 of hull-less type, proved to be colourless (yellowish), showing repulsion between genes of hull-less and grey colour of flowering glumes.

On observing this, we began to study the crossings of black, hulled, with yellow hull-less varieties of barley. Here again was clearly seen the partial repulsion between genes in black (coloured) glumes, and genes of naked grain.

Moreover, all varieties of millet with naked grains, which are cultivated in Afghanistan and Bokhara, proved to be white, that is, colourless.

The genetical behaviour of the special kind of awns in barley—"Kapuze" (var. *trifurcatum*)—is very similar to that for the character of awns in wheat called "inflatum."

Many suggestions of this kind might be found by the systematical comparison of varieties of different genera of the same families, which would facilitate the comprehension of phenomena of segregation, and give useful generalizations, necessary for differential work in genetics.

In summarizing the above regularities, we state also that:

1. *Linneons and genera more or less nearly related to each other are characterized by similar series of variation with such a regularity that, knowing a succession of varieties in one genus and Linneon, one can forecast the existence of similar forms and even similar genotypical differences in other genera and Linneons. The similarity is the more complete as the Linneons and genera are more nearly allied.*

2. *Whole botanical families in general are characterized by a definite cycle (series) of variability which goes similarly through all genera of the family.*

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[1] Prof. S. I. Jegalov, "Hybrids of Oats." *Report of the Third All-Russian Conference on Plant Breeding*, pp. 80—86, 1920, Vol. I.

VI. Formulas of the Law of Homologous Variation.

The above conception may be represented by symbols in the following way. As we have seen, different Linneons and different genera are composed of an immense number of varying distinctions; at the same time this variability is similar in nearly allied Linneons and genera. For purposes of abbreviation let us call these different varying characters by letters a, b, c, d, e, f, g, h, i, j, k, etc. Their different expressions let us signify by a_1, a_2, a_3, a_4, a_5, etc., b_1, b_2, b_3, b_4, b_5, etc. For instance, the colour of glumes we signify by a, for white we shall use a_1, for yellow a_2, for red a_3, for gray a_4, and so on.

Linneons and genera consequently differ, not by these characters, but by their specific complexes of morphological and physiological nature. These differences we shall call *radicals*. There might be radicals for Linneons, as well as for genera, and whole families too.

Thus we have for two different but nearly allied Linneons of the same genus the following expression of their morphological and physiological peculiarities:

$$L_1(a+b+c+d+e+f+g+h+i+k\ldots\ldots),$$
$$L_2(a+b+c+d+e+f+g+h+i+k\ldots\ldots),$$
$$L_3(a+b+c+d+e+f+g+h+i+k\ldots\ldots).$$

L_1, L_2, L_3 are radicals distinguishing these Linneons one from another, a, b, c, d are different varying characters, as colour and shape of glumes, of leaves, stems, etc. Each of these characters is complicated and accordingly may be divided into two, three, or more morphological and physiological units—a_1, a_2, a_3, a_4, a_5, etc. Each of these morphological units may be, if necessary and possible, represented in terms of genotypical composition.

If we compare, e.g., the three Linneons of wheat, *Triticum vulgare*, *T. compactum*, *T. Spelta*, we can say that the radicals L_1 and L_2 are distinguishable from the morphological side, simply by the density of the structure of ears and stems, for L_2 (*T. compactum*) from L_1 (*T. vulgare*). *Triticum Spelta* (L_3) will be distinguished by the density of its spikelets, grains tightly covered by glumes and extremely loose ears. The varying characters a, b, c, d, etc., are the same in all these Linneons.

The same determination might be given to different genera. Let us take rye and wheat. As we have seen, their resemblance in the mode of variation is extremely close. Although every one will say there is no difficulty in distinguishing rye and wheat, there are, as a matter of fact, very few characters really specific to each of these genera which cannot be met with, although perhaps in some rare varieties, in the other, and which could be considered radicals. Let us signify the radicals of different genera by G_1, G_2, G_3, G_4, G_5, etc. We can express by formulas the composition of rye and wheat as follows:

$$G_1(a+b+c+d+e+f+g\ldots\ldots\ldots\ldots)$$
$$G_2(a+b+c+d+e+f+g\ldots\ldots\ldots\ldots).$$

The contents of the brackets are the same in both genera. The difference between their radicals, from a morphological standpoint, consists, in this case particularly, in the differences of empty glumes and flowering glumes of rye and wheat, narrow seed of rye, and a few other characters not so conspicuous and stable. As the different genera include many ordinary Linneons, some of which might be very distant phylogenetically, the more correct representation of a genus in symbols would be as follows:

$$G_1[(a+b+c+d+e+f+g+h+i+k\ldots)\,L_1, L_2, L_3, L_4, L_5].$$

But practically, at least in a good many cases, Linneon radicals might be taken in some cases into simple brackets, as they are often not divisible from ordinary alternative characters of Jordanons. In the same way the composition of different families might be represented.

Radicals of Linneons and genera could be understood as morphological and physiological complexes specific for single genera and Linneons; they could be of special genetic nature, but in this direction our knowledge is at present too limited.

If we consider from this point of view the modern classifications of plants by systematists into Linneon species and genera, we notice that in many cases they are perfectly correct, through intuition, as the specific characters of radicals were taken as a basis for the division into Linneons and genera. Several systematists like Linné, Jussieu, de Candolle, and Boissier, were very sagacious in this respect. But in many other cases it was quite different. Varietal alternative characters were often mixed with those of radicals; particularly was this the case when descriptions of new genera and Linneons were made on single plants and samples collected in one district.

From this representation of systematical units it is clear that for systematics and classification of genera and Linneons, as well as for phylogenetical purposes, only characters of radicals ought to be taken as a basis of separation.

A great number of examples of such an unsuccessful division can be seen in the family of *Cruciferae*. Such genera as *Sinapis* and

Brassica are not divisible by radicals; their division is based on varietal alternative characters, and as a result it is difficult, and even impossible, to say to which genus some varieties are related. Many Linneons of *Cruciferae* appear to be simply different varieties of the same Linneon. In the near future there must be a revision of such doubtful species, and a consequent reduction. Many new "species" described by botanists in recent systematical literature as new species are only new Jordanons.

Sometimes the characters of radicals are very sharp, as for instance in the family of *Ranunculaceae* (genera *Paeonia, Aquilegia, Aconitum, Nigella* and others), and in many *Gramineae.*

Certainly our conceptions of "Linneons," "genera," are conventional—only schemes. Characters which are alternative for most "higher" plants, are taken often as generic in mycology. But without "systems," without "schemes," it is impossible to grasp the phenomena of multiform life. Science itself is in many respects a schematization of the phenomena of nature. The adoption of the above point of view of the systematical study of variation seems inevitable. Except for some individual observations in this direction, it has not so far been taken seriously into account.

VII. Variation in Distant Families.

We have considered variation within the limits of different genetical groups united into Linneons, genera and families. But, besides, the parallelism of varietal polymorphism displays itself also in different and distant botanical families, even in different orders and classes.

Albinism.

For instance, the phenomena of albinism, or the appearance of plants without chlorophyl, or partly deprived of chlorophyl, occurs in most different families. It was observed in hundreds of genera of *Gramineae, Compositae, Papilionaceae, Chenopodiaceae, Polygonaceae, Onagraceae, Rosaceae, Scrophulariaceae, Caryophyllaceae, Cannabinaceae, Coniferae,* etc.

Gigantism, nanism.

In most different and distant families, as *Gramineae, Papilionaceae, Urticaceae, Solanaceae, Rosaceae* (*Pisum, Phaseolus, Triticum, Hordeum, Zea, Rubus, Myosotis, Oenothera, Primula, Humulus, Nicotiana,* etc.), there were established dwarf and gigantic forms.

Fasciation.

In almost all families there exists a tendency to form fasciations or enlargements of different organs, e.g. from *Compositae* to *Equisetum* (de Vries). We have seen it in peas, flax, beet, barley, sunflower, wheat, maize, buckwheat, squashes, water-melon, and several different *Cruciferae.*

Dwarfism, gigantism, albinism, and fasciation occur in the whole plant world, as well as in the animal world.

Root formation.

On a level with these general types of variation there are also narrower kinds of variability, inherent, nevertheless, to many families genetically rather distant. So, e.g., many genera of some families are apt to form swelling of their roots, as beet, turnips, radish, carrots. This peculiarity is a trait of many families, but what is more remarkable is that in the process of their formation the varietal differences repeat themselves in most distant families. For example, beet, belonging to *Chenopodiaceae*, has varieties with oblong, cylindrical, rhombic, spherical, and flattened and segmented roots. Similar varieties can be found among turnips (*Brassica rapa*) belonging to *Cruciferae*, in carrots belonging to *Umbelliferae*, etc., which means that forms of roots are crystallized in definite directions in genetically different families.

Shape of fruits.

The same may be seen in fruits of different families, e.g. apples, melons, tomatoes, peppers, squashes, water-melons. In all these quite distinct plants, varieties differing in the shape of fruits give the same series of variation—round (spherical), oblong, flattened, cylindrical, pyriform and segmented (cantaloupes in melons, "scrijapel" in apples).

Colour of flowers and fruits.

The colour of flowers is determined chiefly by two groups of pigments—yellow or orange, of plastids and pink (rose-red) or violet anthocyanin pigments dissolved in cell-sap; the last group is often accompanied by a special kind of pigment—flavone, pale yellow, also soluble in cell-sap. Series of varieties in anthocyanin colouring, from white (absence of anthocyanin), through pink (rose), to dark violet and blue, are similar in most different Linneons belonging to quite distinct families. Compare variation in cornflowers, *Iris*, *Aquilegia*, *Linum*, *Cichorium, Hysopus, Myosotis, Matthiola,* peas, vetches, lilac, *Hyacinthus*, etc.

Red, pink or white cornflowers (*Centaurea cyanus*), pink flax (*Linum usitatissimum*), and pink lilies of the valley are rare, but still they exist, as do many rare minerals, and one has to consider them in constructing a system of genotypes and phenotypes in plants.

Varietal differences in colour of plastids are similar in a great many Linneons: pale yellow, yellow, orange. Compare e.g. varieties of *Hieracium, Nasturtium, Helianthus,* and many other genera.

When a Linneon is characterized by the presence of both pigments, of anthocyanin as well as of coloured plastids like flowers of dahlias, tulips (*Tulipa Gesneriana*), *Cheiranthus cheiri, Viola tricolor, Helianthemum vulgare,* we have more complicated but also regular series of polychroism.

The distribution of pigments is not altogether irregular, and it is possible to recognize types in different varieties and plants, and these types repeat themselves in different families.

A similar variation in anthocyanin colouring is observed not only in flowers, but in fruits of many distant genera: *Atropa belladonna, Daphne mezereum, Fragaria vesca, Ribes rubrum, Rubus idaeus, Solanum nigrum, Vitis vinifera,* and many others (Wheldale).

Nearly all seedlings in some varieties are coloured by anthocyanin, in others they are colourless. The same is observable with the stems.

Variation in other characters.

Linneons of nearly all families are divided into varieties with hairy leaves, stems, fruits, and petals, and those with smooth organs. Almost all plants could be divided into dense and loose varieties, according to the density of their inflorescence. Many plants are characterized by varieties with procumbent as well as erect form of seedlings.

Zederbauer (*l.c.*) points out that several types of varieties in shape of stem and branches (vv. *pendula, pyramidalis, nana*) are common in *Coniferae* and dicotyledonous families *Salicaceae, Betulaceae, Fagaceae, Juglandaceae,* and, we believe, they are common in herbaceous plants too.

Thousands of Linneons are represented by both single and double flowers.

Most families with zygomorphic flowers have peloric varieties (*Labiateae, Scrophulariaceae, Papilionaceae*).

Winter and spring varieties, genetically distinct, are common in most herbaceous families and genera of plants.

Teratology gives thousands of clear examples of common variation in most plants[1].

In general parallelism is noticeable in organs having the same form and function. To this category are related the phenomena of "unabhängiger Entwicklungsgleicheit" or "Homogenesis" of Eimer by which he accounts for the acquiring of similar characters by different groups of plants and animals.

Series of varieties in distant families.

We have observed in detail large numbers of varieties among different genera of *Gramineae, Cucurbitaceae, Papilionaceae, Cruciferae, Compositae, Linaceae, Urticaceae.* In general, we came to the conclusion that a great many varietal morphological and physiological differences are similar even in most distant families. There is e.g. very little in common in phylogeny between squashes (*Cucurbita Pepo*) or water-melons (*Citrullus vulgaris*) and wheat or barley. Nevertheless, there are many common varying morphological and physiological characters which vary in the same direction in both families. The shape of petals varies in *Cucurbitaceae* very similarly to that of glumes in cereals—there are varieties in both families with pointed petals of perianth (in case of wheat of glumes) as well as with blunt petals. In both families we know varieties with sharply developed nerves in perianth, or *vice versa*, with very weakly developed nerves. Types of hairiness in different varieties, although at first sight very unlike in both families, are strikingly alike in *Cucurbitaceae* and *Gramineae* on close examination of varieties. There are varieties of squashes (*C. Pepo*) with naked seeds, similar to the naked varieties of cereals. In the shape and form of seedlings, there are common varietal differences in both families.

Homologous and analogous variation.

The origin of these organs might not be quite the same in different families—they might, from a formal morphological point of view, be only analogous and not homologous. The same genotypical difference in the sense of modern genetics, might vary in different families. But, nevertheless, the similarity in variation allows us to construct simple general schemes of morphological and physiological variation.

The difference between homologous and analogous organs, as well as between homologous and analogous variation, is in many cases not easily discernible. Some authors, competent enough to know the

[1] Penzig, *Teratologie*, 1, 2, Bd. Second edition, 1920.

difference between homology and analogy, are prepared to deny the essential difference of these two kinds of variation (Lotsy, *Evolution by Means of Hybridization*). In any case, the great majority of varietal characters, not only within the limits of single genera and families but even in distant families, are homologous from a morphological point of view (colour, shape, etc.).

If we follow the above-mentioned symbolic designation, we must own that although the radicals for families might be extremely different, as in the case of *Cucurbitaceae* and *Gramineae*, the contents of brackets will be similar for both families in a considerable degree.

Origin of new forms and the law of homologous variation.

Summarizing all above said, it is clear that after detailed study of any particular Linneon it would be possible, according to the law of homologous variation, to forecast the division into varieties (Jordanons) of other genera and Linneons. To some extent the same divisions into Linneons, and even genera too, are subject to the same rules.

Moreover, this concerns not only the existing diversity of forms, but also new forms appearing from hybridizing distant forms or through mutation.

The origin of new forms was studied in *Oenothera Lamarckiana*, where a great number of varieties originated during observation. If one compares the series of varieties obtained from *Oenothera* by de Vries with that obtained from *Rubus* by Lidforss[1], in hybrids of different Linneons, one cannot help noticing the remarkable parallelism in the varietal composition of *Oenothera* mutants and *Rubus* hybrids.

The same similarity in the series of new forms (we mean forms not representing simple combinations), obtained as a result of distant crossings, could be observed in hybrids of different Linneons of wheat, and of hybrids of wheat and rye. In both crossings hybrids showed new forms with extremely narrow leaves, or with extremely broad leaves, plants with very hairy stems and leaves, the appearance of very late, as well as of very early forms, varieties with branching ears, the development of awns on empty glumes, dwarf plants, as well as giant forms, albino plants, etc., partly as a result of "cryptomery" in the sense of Tschermak, partly as a result of abnormal development very common in the offspring of distant hybrids. *Heliantlhus* and *Oenothera* are very little related—

[1] *Zeitschrift für induktive Abstammungs und Vererbungslehre*, 1914.

writes T. D. A. Cockerell—yet in breeding and studying sunflowers one is constantly reminded of phenomena previously recorded in connection with evening primroses. The parallelism in variation is such that one is led to ask what, precisely, do we mean by a "new variation[1]."

Mutations in closely related Linnean species and genera all tend in the same direction. T. H. Morgan, C. B. Bridges, A. H. Sturtevant, A. Weinstein and H. J. Muller[2], found it for different species of *Drosophila*, E. B. Babcock for *Juglans*[3]. De Vries, R. Gates, Stomps and other investigators established the same for different species of *Oenothera*[4].

E. Baur, in the fourth edition of his *Einführung in die experimentelle Vererbungslehre*, 1919 (pp. 193—194), in the Chapter on Mutations, notices the remarkable parallelism of mutations in different related Linnean species of plants and animals, homologous series of mutations, "ganz merkwürdige homologe Reihen."

In general, in comparing mutations in different plants and animals, one notices general lines of variation even in distant groups of organisms.

VIII. VARIATION IN FUNGI AND IN ANIMALS.

Doubtless the same regularity in variation manifests itself not only in "higher" but also in "lower" plants, as well as in animals.

Ascomycetes and Basidiomycetes give a complete parallel series of Linneons and genera. The same differentiation into the smallest units, "biologic species," is noticeable in both classes. P. A. Saccardo in his article "I Prevedibili Funghi Futuri secondo la Legge d'Analogia[5]" has noticed the existence of series of forms in fungi, and has given a system for their division according to a series of variation in single families. In general his system has proved to be too artificial; he took for the basis of classification the characters of varieties of "higher plants"; his division of great groups as genera is based, not on separation

[1] "Suppression and Loss of Characters in Sunflowers." *Science*, Vol. XL. No. 1025, 1914, p. 283.

[2] T. H. Morgan, *Physical Basis of Heredity*, 1919. A. H. Sturtevant, "A Parallel Mutation in *Drosophila funebris*." *Science*, 1918, Vol. XLVIII. A. Weinstein, "Homologous genes and linear linkage in *Drosophila virilis*." *Proc. of the National Acad. of Sciences*, Vol. VI. No. 11, 1920.

[3] "Studies in *Juglans*, III. A parallel mutation in *Juglans hindsii*." *U. C. Pub. Agr. Sci.* 2. 3, 1916.

[4] R. R. Gates, *Mutations and Evolution*. London, 1921.

[5] *Degli Atti del R. Instituto Veneti de Scienze, Lettere ed Arti.* Tomo, VIII. Ser. VII. Or in *Tabulae Analogical Omnium Gener. Fung. Syll.* Vol. XI. 1896—97.

of radicals, but pre-eminently on varietal characters. But still some of his predictions were afterwards justified. And, undoubtedly, Saccardo's beginnings in this direction are of great importance in systematics.

Comparative animal and plant anatomy discovered a common plan of construction for distant classes and families. The facts of hereditary variation among Linneons, genera and families of animals, known nowadays in great numbers, are a proof of the general plan in variation. Exterior characters of many animals show an evident subordination to the law of homologous variation. Colour of hair, the same structure of hairs, and horns, in their variation, show a similarity not only in near Linneons and genera, but also in different families; and, as genetics has shown, from a genotypic as well as from an external point of view[1]. The series of known mutations in rabbits, rats, and mice are extremely alike.

The systematical division of many genera into Linneons in zoology, shows in some cases a clear series of homologous variation. Palaeontology gives many examples of this kind. Gastropoda, Goniatites, and in general, fossil-molluscs, show beautiful examples of the existence of these series of variation. Many examples could be taken from Rotatoria, etc.

Looking over botanical and zoological, as well as palaeontological literature on variation and systematics, one could find many data for parallel series of variation in different genera and families. In *Pangenesis* and *Mutationstheorie*, we find many facts signifying the existence of parallel variation. "Suchen wir in irgend einer Flora," writes de Vries in *Mutationstheorie*, p. 454, "diese abgeleiteten Varietäten zusammen, so fällt sofort auf, dasz dieselbe Abweichung in der verschiedensten Familien, Gattungen, und Arten widerkehrt. Überall bilden die Varietäten Reihen von parallelen Formen." *Mutationstheorie*, I. p. 454. Variation does not take place in all directions, by chance and without order, but in distinct systems and classes analogous to those of crystallography and chemistry. The same great divisions into orders and classes manifest regularities and repetitions of systems.

IX. Phenomena of Mimicry and Convergence.

Phenomena of mimicry.

The so-called mimicry—the imitation by one genus of another in shape and colouring, which may be of some profit in living beings, undoubtedly is in most cases only a repetition of similar cycles of variation

[1] A. Lang, *Ergebnisse der Mendelforschungen.* Jena, 1914. Castle, *Genetics and Eugenics*, 1920.

in different families and genera. Eimer was quite right when he explained the phenomenon of mimicry in butterflies by independent development of the same types of variation in different genera and families. Mimicry may be regarded as a general phenomenon of repetition of form characteristic for the whole organized world, and by no means as an exception, illustrating the rôle of selection in creation of forms, as was supposed by Darwinists[1].

At our experimental station we observed a striking case of such mimicry in plants, namely in *Papilionaceae*, studied in detail by Miss E. I. Baroulina[2]. Vetch (*Vicia sativa* L.) is often found as a weed in sowings of lentils. Several varieties of vetches are so similar to ordinary lentils in the shape, colour and size of their seeds, that they cannot be separated by any sorting machine. Most of these varieties flower and ripen simultaneously with lentils, and are perfect mimics of their "models"—lentils. We began to study both plants in detail. Many samples of lentils (*Ervum Lens*) and vetches (*Vicia sativa*) were gathered from different parts of Russia and from Persia, Bokhara and Afghanistan. As a result it was found that not only vetches exist which in shape, colour, and size of seeds are inseparable from ordinary lentils, but also that there exist varieties of lentils which are quite similar in their seeds to ordinary round black seeded vetches. The whole series of varieties (a number of which are represented on Plate X) showed clearly that the similarity between these two different genera is so great that it would be difficult, even for an expert eye, to divide several varieties of vetches from lentils by their seeds. This example gives one of the best illustrations of the idea of homologous series in variation which we have in the plant world. In the colour of their flowers and in many other characters lentils show similar series of variation to vetches.

The rôle of natural selection in this case is quite clear. Man unconsciously, year after year, by his sorting machines separated varieties of vetches similar to lentils in size and form of seeds, and ripening simultaneously with lentils. The same varieties certainly existed long before selection itself, and the appearance of their series, irrespective of any selection, was in accordance with the laws of variation.

The phenomena of "mimicry," from our point of view, are general for all classes and families, and those usually impressive forms of mimicry,

[1] See R. C. Punnett, *Mimicry in Butterflies*. Cambridge, 1915.

[2] E. I. Baroulina, "On Vetches (*Vicia sativa*) weeds in lentils." (Mimicry in Plants.) *Report of Third All-Russian Conference on Plant Breeding*, held in June, 1920, Vol. 1.

which are found, for example, in butterflies, give an excellent illustration of the law of homologous variation[1].

The phenomena of convergence, or similarity in characters, which is known in many existing and fossil animals and plants found in similar or sometimes in different surroundings, represents also the phenomena of parallel variation, if not homologous, at least analogous. These phenomena are also of general character and no exception. There are already many data on convergence in most different groups of plants and animals, and their number increases every year. The same division of placental mammals into various orders of carnivorous and insectivorous is parallel to the orders of implacental beasts. Countess Linden established many cases of convergence in Gastropoda[2], without any relation to their affinity and biological surroundings. Dr F. Alverdes recently published a work on parallel development of birds and mammals[3]. It seems as though nature cannot differ indefinitely, but creates analogous or similar forms in different families and orders.

St G. Mivart, in his book *On the Genesis of Species* (New York, 1871), devoted much attention to the coexistence of closely similar structures of diverse origin. He regarded these phenomena as contradictory to Darwin's theory of "Natural Selection." It seems that Mivart was the first who used the expression "The Law of Homologous Variation" (see p. 196).

External conditions to which naturalists of the last century ascribed phenomena of convergence, acted as a factor in selection and elimination without creating forms, but leaving and sorting those which were best suited to their surroundings.

X. General Conclusions.

Parallelism in varietal polymorphism, and the existence of regularity in differentiation of greater groups as Linneons, genera, and families, is a great help in the study of varieties in self- and cross-fertilized plants and animals. Instead of searching for unknown forms, the investigator can definitely look for, and foresee, forms lacking in a system, by noticing

[1] R. Punnett, *Mimicry in Butterflies.* Cambridge, 1915. H. Eltringham. "On Specific and Mimetic Relationships in the genus Heliconius." *Trans. of the Entomological Society of London*, 1916.

[2] Linden, Gräfen U. v. "Unabhängiger Entwicklungsgleicheit bei Schneckengehäusen." *Biologisches Centralblatt*, Bd. XVIII. 1898.

[3] Dr F. Alverdes, "Die gleichgerichtete stammesgeschichte Entwicklung der Vögel und Säugetiere. *Biologisch. Centr.* 39 Bd. September, 1919.

the similarities with the nearest known Linneons and genera. In this respect a biologist places himself in the position of a chemist, who classifies substances according to their place in a system, and creates them through synthesis.

The investigation of polymorphism and the description of new forms become full of scientific meaning and interest. New forms have to fill vacancies in a system. The collections of immense numbers of butterflies and beetles in our museums and herbariums will play a more worthy rôle in the immediate future than ever before. For a systematist is not a man who knows all the curiosities of nature, but one who grasps the order and sense of it all.

The existing systems of Linneons and varieties ought to be fundamentally changed, and constructed according to a general plan. Instead of occasional characters, which usually determine species and varieties, it would be more rational to follow a general system. The greatest problem of systematists is to build up a general well sustained monotypical system, where similarity and homological series of variation would be considered as the fundamental basis, instead of an indefinite tangle of names impossible to remember. This may seem rather revolutionary for systematists, and it must be done very carefully, in consideration of existing orders. It would be easier to arrange in general systems of minutest systematical units, varieties and races which are as yet almost untouched by systematists. We have tried this for cultivated plants, and have found it expedient. Instead of remembering endless forms, usually named after occasional places of origin or in honour of persons, we have the possibility of studying a system and introducing into it individual additions, where it may be necessary to do so, for single Linneons and genera. We realize well the size and difficulty of the whole problem. Without a differential work, and without studying in detail, the integral work will be groundless. To integrate it is necessary to differentiate. We know that perhaps a century will pass before botanists and zoologists will create, through collective work, an organized world system; but this way is historically necessary and inevitable.

Analogy with chemistry.

The above-mentioned analogy of the present day position of the biologist and chemist is deeper than it might seem at first. We have spoken conventionally about characters, colours, hairiness, beardedness, etc. Chemistry says little about the exterior of its substances; it considers the chemical nature of its compounds and their formulas. Numerous chemical substances are reduced to a harmonious system of combinations of a few elements. The biologist is still far behind. During the last decades, however, genetics has advanced greatly and is rapidly overtaking chemistry—at least the old chemistry of complicated organic compounds. Genetics is creating a laconic language of signs for hereditary factors, determining external characters. The biologist has learned to analyze organisms, and to get a hold on methods for the synthesis of new forms.

The regularities in polymorphism of plants, established by a minute examination of variation in different genera and families which we have examined, can be compared to homologous series of organic chemistry, e.g. carbohydrogen (CH_4, C_2H_4, C_2H_2, ...). Its series of compounds differing from each other, are still characterized by many common properties in reactions, by definite cycles of compounds, by definite reactions of exchange and adhesion. Every single hydrocarbon gives a series of compounds similar to that of other hydrocarbon.

In general, genera (G_1, G_2, G_3, ...) and Linneons (L_1, L_2, L_3, ...) of plants and animals display, in just the same manner, their homologous series of varieties, corresponding to different homologous series of hydrocarbons.

$$\begin{array}{ll} G_1L_1\,(a+b+c\ldots) & G_2L_1\,(a+b+c\ldots) \\ G_1L_2\,(a+b+c\ldots) & G_2L_2\,(a+b+c\ldots) \\ G_1L_3\,(a+b+c\ldots) & G_2L_3\,(a+b+c\ldots) \end{array}$$

$$\begin{array}{llll} L_1a_1, & L_1a_2, & L_1a_3, & \ldots \\ L_2a_1, & L_2a_2, & L_2a_3, & \ldots \\ L_3a_1, & L_3a_2, & L_3a_3, & \ldots \end{array}$$

Where a, a_1, a_2, a_3, ... are different characters which distinguish different varieties. The series of forms are strikingly analogous to homologous series of organic chemistry.

Besides their chemical structure, different forms of organized nature are characterized by physical structure, and perhaps it would be better to trace also the analogy of homological series of plants and animals, with systems and classes of crystallography with definite chemical structures (Crystallo-Chemistry of Fedoroff).

We leave the question, in detail, of these analogies, which is already discussed in literature (Johannsen, Lehmann, Tischler).

Further investigations will establish more precisely the law of homologous variation in plants and animals, and it may be possible to bring the same series into mathematical expression. The variation in form might be reduced to some geometrical scheme.

The problem of the origin of species cannot be separated from the problem of variation. A great many forms are undoubtedly only different combinations of the same genes, some primary types. The study of variation will give us the possibility of establishing these primary types, the fundamental series of variation of organisms.

The idea of the homologous series in variation in its essence is only a development of the general idea of Goethe's "Metamorphosis of plants," the idea of the unity in variety of C. Dresser[1].

In conclusion, we take the liberty of expressing our strong conviction that the most rational and expedient method of studying the diversity of plants and animals open to breeders of both, even for practical purposes, is through the establishment of parallelism and homologous series of variations.

[1] Christopher Dresser, *Unity in Variety*. London, 1860. Recently there appeared several works devoted to the general uniformity of phenomena of life, history, psychology. See f. i. K. Marbe, *Die Gleichförmigkeit in der Welt*. Bd. I and II. München 1916—1919. P. Kammerer, *Das Gesetz der Serie*, 1919.

DESCRIPTION OF PLATES.

PLATE IX.

Fig. 1. *Triticum vulgare eligulatum*—found in North Afghanistan and Shugnan (Pamir).

Fig. 2. *Triticum vulgare ligulatum*—ordinary wheat.

Fig. 3. *Secale cereale eligulatum*—found in North Afghanistan and Shugnan (Pamir).

Fig. 4. *Secale cereale ligulatum*—ordinary rye.

PLATE X.

Parallel variation in colour and in shape of the seeds and cotyledons of vetches (*Vicia sativa* L.) and lentils (*Ervum Lens* L.).

Drawn by Miss M. P. Lobanova.

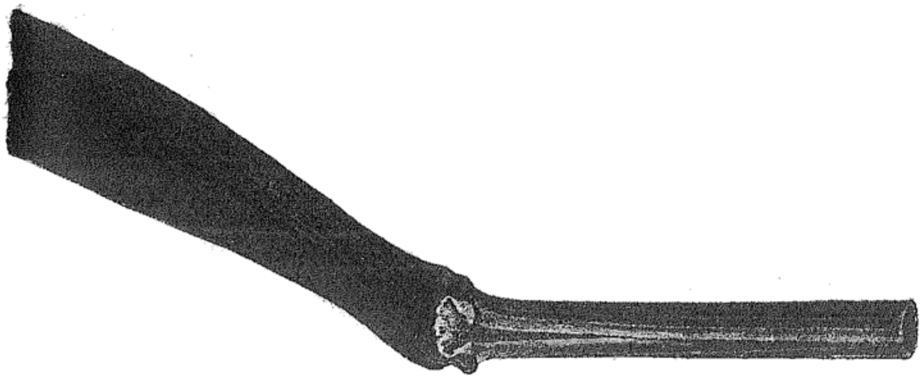


Fig. 4.

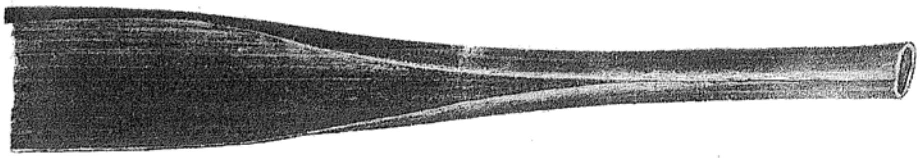


Fig. 3.

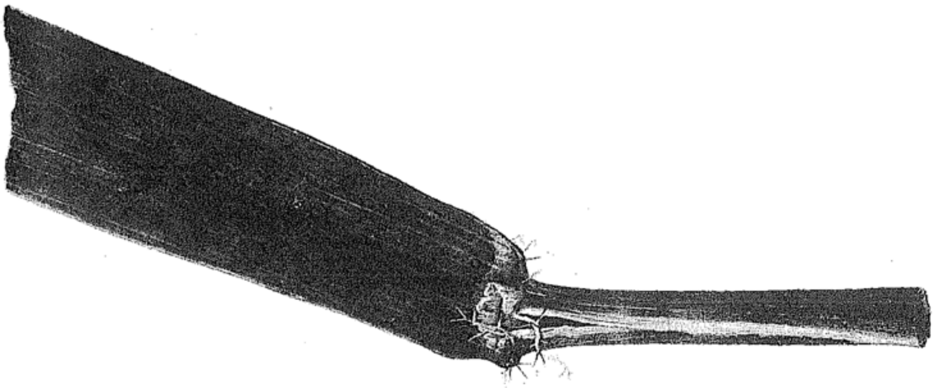


Fig. 2.

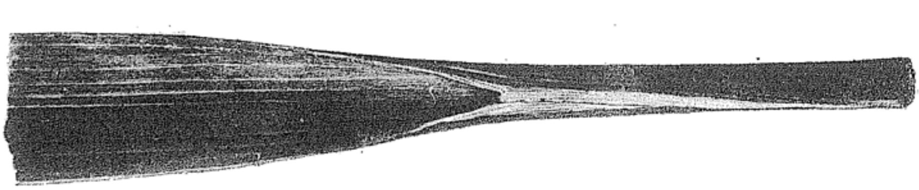
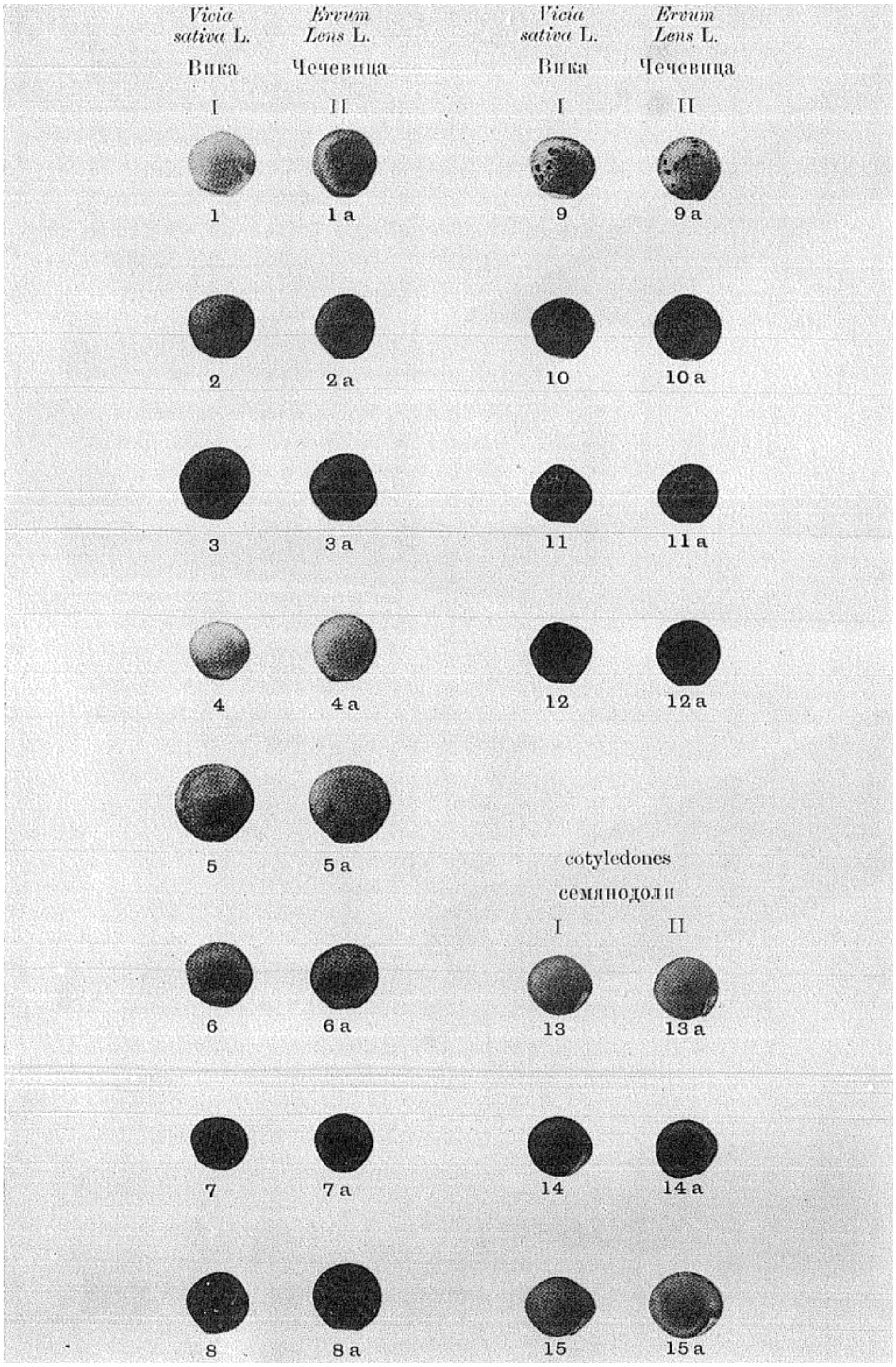


Fig. 1.


Vicia sativa L.
Вика
I
Ervum Lens L.
Чечевица
II
1
1 a
2
2 a
3
3 a
4
4 a
5
5 a
6
6 a
7
7 a
8
8 a
9
9 a
10
10 a
11
11 a
12
12 a
cotyledones
семянодоли
13
13 a
14
14 a
15
15 a