

INHERITED VARIATION IN PLANTS

IN a series of articles published in this Review I endeavoured to sum up our present knowledge about the direct action of surroundings, considered as a factor in the evolution of new species. After having sketched, in a first article,¹ the development of Darwin's ideas on this subject, I analysed next the experimental researches into the effects of changed conditions of life upon plants and animals that had been made during the last twenty years.² Darwin lived only to greet the first steps made in this direction. But since then it has been proved by the most varied experiments that changes which we formerly believed would require scores of years to be produced by a natural selection of accidental variations are obtained in the experimental field or the laboratory in the lifetime of the individual by a mere change of environment.

Many biologists believed that by these researches the theory of evolution was going to be placed on a solid experimental basis. However, since 1888 it began to be contested by Weismann and his followers that such changes could be inherited, and thus might lead to the appearance of new species. So I discussed, in a fourth article,³ the hypotheses of Weismann. I pointed out that the origin of his hypotheses was anti-Darwinian. They were born, as he himself acknowledged in 1876, from his desire 'to combine in a theory of evolution a teleological principle with a mechanical principle'—that is, causality and purpose⁴—this desire leading him to admit the existence of a 'matter endowed with a soul,' represented by an immortal germ-plasm. As to the modifications which Weismann had to introduce later on into his germ-plasm hypothesis so as to make it agree with established facts, they are such that the difference between him and those who recognise the hereditary transmission of acquired characters is now only (as Delage has shown it) *as to the means of transmission*—direct

¹ *Nineteenth Century and After*, January 1910.

² *Ibid.* July, November, and December 1910.

³ *Ibid.* March 1912.

⁴ *Studien zur Descendenztheorie*, Leipzig 1876; English translation by R. Meldola.

or indirect—of the exterior influences to the reproductive cells. The biologist can thus safely return once more to empiric research, for ascertaining by experiment how far the transmission of acquired characters is actually taking place.

These experiments we have now to analyse, limiting our remarks to plants, and leaving the similar researches about animals for a subsequent study. True, that the results of all such researches have been obscured by many secondary matters introduced into the discussions, so that it is not easy to sum them up for the general reader. But the recent appearance of several general works by Karl Goebel, Kammerer, Przibram, Semon, and La Plate,⁵ where all these questions are discussed in full, and the deep interest of the main question will, I hope, facilitate my task.

I

It is well known that trees which shed their leaves every autumn in our temperate zone have a tendency to become evergreens when they grow in a moist, tropical climate. A certain modification of structure takes place in this case, and it permits the tree to grow, to flower, and to bear fruit without needing a period of rest. The fact is well known; but it was important to know whether this modification is transmitted by the thus modified trees to their descendants, and whether it is retained when the latter are grown in a temperate climate. That such variations are transmitted by grafts and cuttings was well known. But that they should be transmitted by seed was doubted. Now, Professor Ed. Bordage, who has spent twelve years in Réunion, a French island in the Indian Ocean to the east of Madagascar, gives to both the above-mentioned questions an affirmative reply. The peach-trees obtained in Réunion, by seed from European trees, fully retain their leaf-shedding habit when they are grown in the cooler climate in the interior of the island. On the contrary, if they are grown in the hot and moist climate of the coast region, they retain it only for a number of years, and the period during which they remain leafless is gradually shortened. As a rule, after ten years they still remain leafless for six weeks every winter; and most of them require full twenty years of growth in

⁵ Karl Goebel, *Einleitung in die Experimentelle Morphologie der Pflanzen*, Jena 1908; Paul Kammerer, *Die Abstammungslehre*, Jena 1911; Dr. Hans Przibram, *Phylogense, eine Zusammenfassung der durch Versuche ermittelten Gesetzmässigkeit tierischer Artbildung*, being vol. iii. of his *Experimental-Zoologie*, Vienna 1910, with many coloured plates; Richard Semon, *Das Problem der Vererbung 'Erworbener Eigenschaften'*, Leipzig 1912; Dr. I. Plate, *Selektionsprinzip und Probleme der Artbildung*, fourth enlarged edition, Leipzig 1913. I take this opportunity to express my very best thanks to those institutions, such as the Carnegie Institution, the Russian Biological Station at Villefranche, the Svalöf Seed-Institute, and those numerous authors who have favoured me either with letters or by sending me their special publications.

the hot and moist seashore belt to become nearly complete evergreens. But when the seeds of the thus modified trees are sown in Réunion, they produce individuals which have inherited the evergreen character to the same degree as the mother-plant had acquired it. And this character is retained in the second generation, even when the tree is grown in the cooler part of the island, at an altitude of 3300 feet, where the peach-trees whose mother-plants have not previously been modified by the tropical climate continue to shed their leaves every autumn.⁶

Speaking of this observation of Professor Bordage, R. Semon makes the remark that the Réunion peach-trees, having obtained this new character in one generation, their descendants probably would return to the leaf-shedding habit if they were grown in Europe.⁷ Very probably so—but not unless the mother-plants had retained the acquired structure for a few years only. A rapidly established equilibrium of forces can be upset with the same rapidity, while an equilibrium of long standing requires a long time to be upset: this may be taken as a general law of Nature. At any rate, we have here a definite new habit—evidently the result of a modified structure—acquired in a new environment, inherited to the same extent, and retained by the progeny of the modified individuals, even when this progeny is grown under conditions approximating to those under which the grandparents used to grow before the modification took place.

Of another instance of a cumulative inheritance of an acquired character, observed by Lesage, I have already spoken in previous articles.⁸ As to inherited variation in the stems and the roots, due to changes in nutrition, we have many instances of it in our cultivated plants. Darwin knew them and mentioned them in words which modern biologists would do well to remember: 'But scarcely any modification,' he wrote, 'seems so easily acquired as a succulent enlargement of the stem or root—that is, a store of nutriment laid up for the plant's own future use.' And he mentioned, as instances in point, our cultivated radishes, our beet, the turnip-rooted celery, the Italian variety of the common fennel, as also the experiments of Mr. Buckmann, who proved 'how quickly the roots of the wild parsnip can be enlarged, as Vilmorin formerly proved in the case of carrot.'⁹

In all these cases, well-established varieties, now propagated

⁶ E. Bordage, 'A propos de l'hérédité des caractères acquis,' in *Bulletin scientifique de la France et de la Belgique*, 7e série, t. liv., Paris 1910. In chapter x. of *Variation* Darwin had already mentioned cases of a similar character.

⁷ Richard Semon, *Das Problem*, etc., p. 64.

⁸ *Nineteenth Century and After*, July and November 1910.

⁹ *Variation in Domestic Animals and Plants*, i. 402 and ii. 330 of the 1905 edition.

by seed, were obtained by a combination of an inherited, definite and cumulative variation due to a new environment and selection. Variation was provoked by growing descendants of wild plants in especially favourable conditions (rich soil, proper watering); the characters acquired in these conditions were inherited, and the variation continued to increase up to a certain degree; and then a selection was made by choosing for further propagation the seeds of those individuals which offered the desired variation, and rejecting those which did not offer it.

I know, of course, that there are now biologists who treat the facts of inherited variation taken by Darwin from the gardeners and seed-growers as 'unscientific.' But it is not possible to re-read Darwin's work on *Variation*, where he analysed, sifted, and discussed these facts, without recognising, on the contrary, the full scientific value of Darwin's assertions. One understands also at the same time why Darwin, in proportion as he advanced in his studies of variation, attributed more and more importance to the direct action of surroundings in producing those useful changes without which Natural Selection would have had no material to choose from. I will even permit myself to say that a number of arguments produced in the discussions of later years would never have appeared in print if their authors had been as well acquainted with *Variation* as they are with *Origin of Species*.

II

In a previous article the remarkable series of experiments made by Gaston Bonnier, of the French Academy of Sciences, upon the adaptations of plants to an Alpine and a Maritime climate has already been mentioned.¹⁰ As, however, in the literature on the Weismann side these experiments are either not mentioned at all, or their earlier portion only is referred to, I must once more return to the Alpine portion of these experiments, and analyse their bearing upon the question of inheritance of 'acquired characters.'¹¹

¹⁰ *Nineteenth Century and After*, July 1910.

¹¹ Gaston Bonnier, 'Recherches expérimentales sur l'adaptation des plantes au climat Alpin,' in *Annales des Sciences Naturelles*, 7e série, Botanique, t. xx. 1895, pp. 217-360, with 11 plates. Weismann, in his *Essays*, in *Keimplasma*, and in *Vorträge*, and the chief representative of the Weismann school in this country, Prof. J. A. Thomson, in *Heredity* (1908), do not mention them at all. In an elaborate and richly illustrated work, by the Berlin professor Erwin Baur, *Einführung in die experimentelle Vererbungslehre*, Berlin 1913, which represents an excellent compendium of Mendelism, only the earlier part of Bonnier's experiments is spoken of. Prof. Baur writes to me, however, that he has already made the necessary additions for a second edition of his work, which, I am sure, will soon be required.

The substance of these experiments can be given in a few words. Taking a great variety of plants originating from the plains, Professor Bonnier divided each of them into two parts, and planted the two parts in different surroundings: one of them in the plain, at a low level, and the other in the Alps, or the Pyrenees, at different altitudes, up to 6600 feet. After a year or two, and again four, six, and eight years later, the changes of general form and anatomical structure that took place in the plants grown at a high altitude were carefully described and illustrated by photographs and engravings. In several cases Bonnier studied also the modifications obtained by growing specimens of the same plants in ice-boxes, in darkened surroundings, and so on, and compared them with the modifications obtained by a change of climate. Finally—and this is an important part of the experiments—after the low-level plants had grown for one, two, four and six years on a high Alpine level, parts of them were taken back to a low level, and notes were taken there of the speed with which changes in an opposite direction took place.

It hardly need be said that the changes produced in the general aspects, the separate characters, and the anatomical structure of nearly all plants, after they had grown in an Alpine climate, were exactly those that are characteristic for the Alpine species of the same genera. On the other hand, these changes were identical with those which took place in low-level plants when they were grown in conditions artificially imitating those of an Alpine environment. All taken, Bonnier experimented upon 105 different species belonging to 34 different families, and in nearly all cases the results were the same. Almost all the plants planted at a higher altitude took, more or less, the characters of the respective Alpine species¹²: not only in their general aspects, but also in their tissues and cells, where intimate physical changes went on in consequence of the new functions performed

¹² To mention a few illustrations, our familiar friend, the Nodding Silene (*S. nutans*), after a six years' growth in the Alps, took all the characters and inner structure of the Alpine specimens of the same species, as they had been described by A. Wagner. The same with our common Potentil (*P. Tormentilla*); with the Lady Mantle (*Alchemilla vulgaris*, L.), which became rampant and acquired thicker leaves; with the Umbellifer *Bupleurum furcatum*, L., which, after a ten years' growth at a high altitude, became strikingly like to the Alpine species of the same genus, as one may see it in the photographs given by Bonnier (p. 262). The same change took place in the Common Golden-rod (*Solidago Virga-aurea*, L.), which assumed all the characters of *S. alpestris*, Perr. et Souq.; in the Wood Cudweed (*Gnaphalium sylvaticum*, L.), which took the aspect of *Gn. norvegicum*, Gumm.; the Thistle (*Carduus defloratus*, L.), which, after several years' life on a high level, took more and more the aspects of *C. carlinae-folius*, L.; the Basil Thyme (*Calamintha Acmos*, Clairv.), which was an annual in the plain, and became perennial in the Alps, approaching in its aspect the *C. alpina*. And so on.

by the cells and the tissues. Besides, these changes were—to use Darwin's expression—'cumulative.' They increased from year to year; and they acquired more and more stability.

Alpine plants, as everyone knows, are chiefly perennials. Their seeds cannot ripen during the short Alpine summer, and they propagate by the buds of their root-stocks, 'crowns' (Lily of the Valley), or 'runners' (Strawberry). Their mode of propagation is thus vegetative. The bushes propagate by producing new stems from their roots, while the perennial herbs die at the end of the summer, and new stems—complete new plants—grow every summer out of the buds of the root-stock, taking every year a more and more distinctly Alpine character. Besides, the inner structure of the root-stock itself is gradually modified. The whole plant thus takes a new Alpine character to such an extent that the botanist cannot but classify it as a distinct Alpine species. More than that. If, after a two years' stay in the Alps, a piece of the root-stock of the modified plant is taken back to the plain, it produces for two years plants having an Alpine character. But if the plant be kept in an Alpine climate for four or six years, and then only part of its root-stock is taken for propagation to a low level, its buds continue to give birth to Alpine plants in the lowlands for four, five, or six years. Unfortunately, the experiments were not continued for a longer period.

These being the facts observed by Bonnier, what light do they throw upon the part played by the direct action of environment in producing new varieties and species? If we put this question to a Weismannist, he will tell us that they throw no light at all, because 'the acquired "Alpine" habitus was and remained entirely personal.' This is what the Danish Professor W. Johannsen says in a very valuable book on the elements of heredity.¹³ No propagation having taken place *by seed*, a plant which grew out of the buds of the root-stock, or the runner of a perennial, remains for a follower of Weismann *the same individual*, no matter how different it may be from its ancestors. There is no *inherited* variation: we have only an *individual* variation, the possibility of which—it is added—nobody contests, as we know quite well that individuals vary when they are placed in new conditions. A propagation by *buds* which we have in the propagation by root-stocks, runners, cuttings, grafts, tubers, and so on, is for them nothing but a 'subdivision of the same individual.'

For those who know that to vegetative propagation by cuttings, tubers, bulbs, grafts, and so on, we owe thousands of new varieties and species of our cultivated plants, this assertion must

¹³ *Elemente der Exakten Erblchkeitslehre*, enlarged German edition, Jena 1909, p. 350.

sound rather strange. Our gardens and orchards are full of new varieties of fruit-trees, vegetables, ornamental bushes, and flowers obtained in this way; and while most of them are still propagated by buds, there are many other varieties, such as the eatable radishes, carrots, occasionally tulips, and so on, which are also propagated by seed, and nevertheless 'remain true'—that is, reproduce the variety primarily obtained by bud propagation. And we ask ourselves: Must we really consider the millions of fruit-trees, palms, rose-bushes, vegetables, dahlias, and so on, which our gardeners have propagated for scores of years by cuttings, grafts, tubers, and bulbs, as 'subdivisions' of those few individuals with which the new variety originated? Is it not paying too high a tribute to biological dialectics? The more so, as we know, or ought to know by this time, that propagation by buds is *not* a mere subdivision of the body-cells of a plant, as Weismann described it in 1888. Even under the Weismann germ-plasm hypothesis, every bud of a tree, a root-stock, or a tuber, if it is capable of reproducing the whole individual with its body-plasm and germ-plasm, contains *the same germ-plasm* that is contained in an ovule or in a grain of pollen. Therefore, shall we not better accept Darwin's view of the subject when he wrote that 'the difference between seminal and bud reproduction is not so great as it at first appears; for each bud is in one sense a distinct individual'¹⁴? Each bud contains, at any rate, like the ovule, *the germ of a complete new individual*.

The origin of the conception which refuses to see in vegetative propagation the appearance of new individuals lies in one of the early teachings of Weismann. When he revived, under the name of Amphimixis, the hypothesis of Professor Brook (already rejected by Darwin), according to which *all variation* was due to *sexual reproduction*, he evidently was compelled to refuse the name of inherited variation to variation propagated in a vegetative way. But the Amphimixis hypothesis could not stand; it was soon abandoned, even by its author; and with its abandonment goes also the fundamental difference that Weismann tried to establish between 'seminal' and 'vegetative' propagation.

In fact, in 1888, at the outset of his work on heredity, Weismann went even so far as to deny any transmission of germ-plasm

¹⁴ *Variation*, ii. p. 468. Perhaps I may also give here the opinion of a contemporary botanist, the Geneva Professor R. Chodat, who has seriously discussed in his *Principes de Botanique* (Genève 1907) the question of variation and heredity. 'Some have tried to go further,' he writes. 'They have asserted that in multiplication by grafts and cuttings, all the new individuals being originated by the fragmentation of the old one, represent the very same individual. We are going to see that such a view cannot be defended. For us, individuality ceases where there is disjunction: the individual is a harmonic

when a bud is transplanted by means of grafting¹⁵; and this assertion was accepted by his followers, who therefore described the experiments of Bonnier as an illustration of a purely 'individual' variation.

Need I add that Darwin, who had studied 'bud-variation' (that is variation inherited by bud propagation) with infinitely more care than Weismann had in 1888, held a very different view?

We have seen [he wrote] that varieties produced from seed and from buds resemble each other so closely in general appearance that they cannot be distinguished. . . . The law of analogous variation holds good with varieties produced by buds as with those produced by seed. The laws of inheritance seem to be nearly the same with seminal and bud varieties. Finally, the facts given in this chapter prove in how close and remarkable manner the germ of a fertilised seed and the small cellular mass forming a bud resemble each other in their functions (*Variation*, ch. xi. vol. i. pp. 526-527 and 529 of 1905 edition).

The same is true of Julius Sachs, whose authority in the physiology of plants will hardly be contested by the zoologist followers of Weismann. For him, as soon as the connexion of a daughter-plant with its parent plant has been destroyed by the dying off and final rotting of the older part of the runner or the rhizome, we have 'a new independent plant.' In such cases, Sachs speaks of 'the properties of the parent plant' being usually transmitted to 'its descendants.'¹⁶

whole, whose parts are consequently in a harmonic dependency' (p. 640). Further on, criticising Weismann's hypothesis of specialised 'determinants,' he makes the following correct remark: 'Consequently, if a fraction of a root, a leaf-stalk, or a leaf contains all that is required for becoming the starting-point of a complete individual, it is because it has in it *all* the supposed determinants' (p. 673). In other words, the bud contains the same germ-plasm as the seed.

¹⁵ 'Grafts,' he wrote, 'are parts of the soma [the body-cells] of a previously existent tree, and we are not therefore concerned, in this method of propagation, with a succession of generations, but with the successive *distribution of one and the same individual* over many wild stocks. If, as I presume, the English in Ceylon do not care to eat wild cherries but prefer the cultivated kinds, it follows that the branches [of the cherry-trees] which bear fruit in that island have not been developed from germ-cells at any time since their introduction, and there is nothing to prevent them from gradually changing their anatomical and physiological characters in consequence of the direct influence of climate.' ('On the Supposed Botanical Proofs of the Transmission of Acquired Characters,' in *Essays upon Heredity*, vol. i., Oxford 1891, pp. 420-421). The italics are mine. Is there now a botanist who would maintain that only somatic cells are transmitted in grafts, and that a plant ought to have *not* been developed from germ-cells, in order to be able to reproduce a variation due to the direct influence of climate?

¹⁶ *Lectures on the Physiology of Plants*, lecture lxi. pp. 721-723 of the English edition. For illustrations to confirm that in the immense majority of cases vegetative and seed propagation are identical as to their results, see, among others, Erwin Baur's *Einführung*, l.c.

As to Weismann himself, he, of course, was soon compelled to modify his views on vegetative propagation; and in his main work, *Das Keimplasma*, he not only came to the same conclusions as Darwin: he expressed them in almost the same words. Speaking of varieties obtained in cultivated plants, he recognised that those were right who saw 'in the influence of changed outer agencies the causes of modification,'¹⁷ and he admitted, like Darwin, the cumulative effect of changed environment.

Of course, I do not mean by that [he wrote] that there are not influences of surroundings and food which, after a prolonged action, would not be capable to modify most of the determinants of a certain part of the body, and thus to produce purely climatic varieties, in whose appearance natural selection has taken no part.¹⁸

And after having owned that when he wrote first he had not 'sufficiently appreciated at that time the variation of the germ-plasm itself under the directly acting agencies,' he added these words, which I permit myself to underline:

The ultimate cause of bud-variation must be the same as that of variation from seeds—that is, differences in the feeding of the germ-plasm, the word 'feeding' being understood in its widest sense, thus including variations of temperature and so on (p. 579).

In a still later work Weismann returned once more to bud-propagation, and here he definitely gave up his previous idea of 'grafts being parts of the soma'—that is, of the body-cells only. He recognised at last the fact, well known to every botanist, that

an enormous number of cells is spread over the body of the plant, each of which can become, under certain circumstances, the origin of a bud—that is, contains the complete germ-plasm in a latent state (*in einem gebundenen Zustande*), such as is required for producing a complete plant.

Consequently he speaks of 'the appearance of a new individual through budding.'¹⁹

All this sounds so elementary that I would not have dwelt upon this matter if there were not fervent Weismannists who continue to repeat the mistake which Weismann made at a time when he evidently was not yet sufficiently acquainted with the subject of bud-variation.

It is certainly a matter of regret that since 1895 nobody has made the experiment of transplanting some Alpine-born perennials to a level where they might ripen their seed, and then

¹⁷ *Das Keimplasma, eine Theorie der Vererbung*, Jena 1892, p. 573.

¹⁸ *Keimplasma*, p. 577. See also Darwin's *Variation*, ii. 300.

¹⁹ *Vorträge über Descendenztheorie*, 2nd revised edition, Jena 1904, Bd. ii. pp. 29 and 1.

sowing it. A continuation of Bonnier's experiments is most desirable. But to dismiss them, such as they are, by saying that they deal only with 'individual variation,' is totally to misunderstand bud-variation. On the contrary, when we remember that nearly all Alpine and Arctic plants are perennials, which propagate by buds and not by seed, and when we think of the immense numbers of perennials covering the woods, the meadows, and the steppes of the earth, we see what an immense number of varieties and species must have originated precisely by means of bud-propagation, especially in the earlier post-glacial flora.

III

To Professor Georg Klebs we owe an important series of experiments, carefully conducted for several years in order to study the modifications, or 'metamorphoses' as he describes them, obtained in plants under the influence of changed environment.²⁰ His first experiments, chiefly made with the Houseleek (*Sempervivum*), of which he spoke before the Royal Society in a Croonian Lecture in 1910, have already been mentioned in this Review²¹; but his subsequent experiments, dealing especially with the inheritance of the 'metamorphoses,' offer a still deeper interest.

The leading idea of this last series was to cultivate the plants in a rich soil, in a warm frame, and after the main flower-bearing branches (the 'terminal inflorescences') had been produced, to cut them off; whereupon 'side inflorescences'—i.e. flowering branches growing from the sides of the stem—made their appearance. The flowers borne by these side inflorescences, described by Professor Klebs as 'neogene' flowers, offered quite a number of variations in the numbers of their petals and stamens, as also metamorphoses of the same—stamens transformed into petals, and the like.

Further experiments proved that these modifications were inherited. When the just-mentioned side inflorescences were planted in the soil, or when their modified 'neogene' flowers were self-fertilised and their seed was sown, it appeared that some of the modifications reappeared in the second generation, even

²⁰ *Willkürliche Entwicklungsänderungen bei Pflanzen*, Jena 1903; 'Ueber Künstliche Metamorphosen,' in *Abhandlungen der Naturforschenden Gesellschaft zu Halle*, Bd. xxv., Stuttgart 1906, pp. 133 seq., and in a separate edition; 'Ueber die Nachkommen künstlich veränderten Blüten von *Sempervivum*' in *Sitzungsberichte der Heidelberg Akademie der Wissenschaften*, Jahrgang 1909; and *Proceedings of the Royal Society*, vol. 82, 1910, Croonian Lecture. Also 'Ueber die Rhythmik in der Entwicklung der Pflanzen,' and 'Ueber das Verhältnis der Aussenwelt zur Entwicklung der Pflanzen,' same *Sitzungsberichte*, 1911 and 1913 (separate reprints).

²¹ *Nineteenth Century and After*, July 1910, p. 67.

though the latter was grown under the ordinary conditions of garden culture. In some individuals they were even reinforced. At the same time, some other modifications were *not* inherited, and Professor Klebs intends to make further researches in order to see what are the conditions furthering inheritance.

In another series of researches Professor Klebs took a species of *Veronica* which had never been cultivated, and in its wild state offers very few anomalies. He cultivated cuttings of this plant in different conditions: some of them in a garden soil, others in nutritive solutions, others again under glass, or in a darkened space. After having obtained in these conditions a development of leaves, instead of flowers, on the flowering branches, and thus transformed reproductive organs into vegetative, he planted these branches, and cultivated them, so as to obtain 'neogene' (modified) flowers. Their seed was collected and sown, and the results, carefully described and tabulated, were very interesting.

To begin with, in three years a relatively very constant species of *Veronica* gave a great number of modifications which were not previously known, and probably never existed before. As to the inheritance of these modifications, and their persistence after the plants had been taken back to their normal conditions of growth, the results varied, both for the different new characters and the descendants of different stocks. At any rate, a tendency towards producing leaves instead of flowers *was* inherited in a sense: it was maintained when the descendants of a modified plant (obtained in a glass-house) were grown in conditions more normal, on a moist bed. Besides, the tendency towards a leaf-metamorphosis was 'undoubtedly increased.'²²

Altogether the conclusions of Professor Klebs may be summed up as follows: (1) 'Most of the anomalies [the so-called inheritable "sports" and "mutations"] can be obtained, like individual variations, through the action of modified surroundings'; and (2) 'Most of the anomalies, after having appeared accidentally in separate individuals, can be transmitted to their descendants; by means of a good supply of nourishment and selection they can be made inheritable race characters.'²³ Being drawn from a wide

²² *Abhandlungen*, l.c. p. 285 (p. 153 of separate reprint). The same experiments were made with Beet, as also with Scurvy Grass (*Cochlearia officinalis*), the Creeping Bugle (*Ajuga reptans*), *Lysimachia* (*L. thyrsofolia*) and Sorrel (*Rumex acetosa*).

²³ *Abhandlungen*, loc. cit. p. 255. In another place (p. 286) Professor Klebs writes: 'New races can originate as a result of changes in environment. These changes provoke inner changes in the plants, in consequence of which, according to the intensity of the [external] action and the time it has lasted, the possibilities of the forthcoming structure become visible as new characters; they become reinforced and are maintained in different degrees of hereditary trans-

series of well thought out experiments, these conclusions deserve full attention.

One more remark must be made in connexion with these researches. In speaking of the 'metamorphoses' which he obtained by experiment, Professor Klebs shows how great was the service that Goebel rendered to biology by proving that every real change of form in a plant means a modification in the functions of some of its organs. This fact renders it highly improbable that the evolution of new forms should result from a succession of accidental modifications of the elements of the germ-plasm.

At the same time, Professor Klebs was brought, by his many years' experiments, entirely to part with the conception of an immutable species, which still underlies many of the present-day discussions:

All properties of a species—Professor Klebs writes—however definitely inherited they may seem to be, can be altered within certain limits. In fact, all of them must be liable to change, as they are the products, on the one side, of certain given specific possibilities (*Fähigkeiten*), and on the other side of the ever-changing external world.²⁴ Only experiments can decide to what an extent variability can go and determine the conditions that caused it.²⁵

This is the language of Lamarck. With all that, Professor Klebs does not exaggerate the importance of his experiments. He fully recognises that they do not solve the question as to whether it is possible to obtain experimentally new species. But the very fact that certain changes, produced in the mother-plant under exceptional conditions, reappear in the seedlings of the second generation, when they are grown under normal conditions, must not be minimised. And this fact does not stand alone. More and more similar facts become known. And even if it were found later on that under normal conditions the acquired new characters would gradually disappear, the fact of an hereditary transmission to the nearest generations would retain its importance.²⁶ It certainly renders it very probable that modifications produced by changes in environment, if they have lasted for a considerable number of years, will be retained for a correspondingly longer period. And

mission' (*Potenzen der vorauszusetzenden Struktur als neue Merkmale sichtbar werden, sich steigern, und sich in verschiedenen Graden der Erbllichkeit erhalten*).

²⁴ In his work, 'On the Relations of the Outer World to the Evolution of Plants' (*Sitzungsberichte*, 1913), he gives striking data in proof of all the characters of a species being liable to change under the influence of changed conditions. And he attempts an explanation of this fact on the ground of purely physico-chemical causes, without any incursion into the domain of teleology for which a number of 'Neo'-Lamarckians have a decided predilection.

²⁵ *Ueber künstliche Metamorphosen*, p. 206.

²⁶ *Sitzungsberichte*, 1909, pp. 27-29 of the separate reprint.

we have already seen that the observations of Bordage and Bonnier give hints in the same direction.

Speaking further of the countless experiments that have been made lately to verify the Mendelian rules relative to crossings, and in which some writers saw a disproof of the inheritance of characters acquired under the direct action of environment, Professor Klebs makes a very true remark. When we obtain bastards by crossing a blue-flowered variety of some plant with its white-flowered variety, and see that the hybrids follow the Mendelian rules, we must not forget that under certain external conditions the blue-flowered individuals also will produce white flowers, independently from any crossing, and the white-flowered individuals, under certain conditions, also may produce blue flowers.²⁷ The fact that the causes which produce blue, white, and variegated flowers are transmitted by heredity in certain proportions is well proved; but how far the variability of plants under external influences may go to modify their forms, structure, and colours has yet to be studied.²⁸

IV

Some interesting experiments dealing with inherited variation were made with our familiar Shepherd's Purse (*Capsella bursa pastoris*) by Professor Zederbauer. He noticed during a journey to Asia Minor that this weed gradually changes its aspect along the route followed by man from the Steppes, nearly 3300 feet high, to the higher pasture grounds, or *jailas*, reaching an altitude of nearly 7000 feet. On the lower levels the Shepherd's Purse has a stem 12 inches to 16 inches high, thickly haired, Dandelion-like leaves, and whitish flowers. On the higher level—where, notwithstanding a careful search, it was found only near the camping-places of the shepherds, thus showing that the weed had followed man—the same plant becomes dwarfed (like the variety *pygmaea*, Holmboes), has long roots, small, dry, or 'xerophytic' leaves, and red flowers. It thus has the same characters which A. von Kerner and Bonnier found characteristic for plants growing in an Alpine climate.²⁹

That the high-level Shepherd's Purse must have originated from the low-level plants has to be concluded, not only from a

²⁷ *Abhandlungen*, 1906, pp. 220-221.

²⁸ It would be impossible to enter here into the discussion of this question. So I must refer the reader interested in it to De Vries's *Mutationslehre*, Leipzig 1901-1904, and *Arten und Varietäten*, Berlin 1906; Correns's *Ueber Vererbungsgesetze*, Berlin 1905; E. Strasburger, *Die Stofflichen Grundlagen der Vererbung*, Jena 1905; E. Ziegler, *Die Vererbungslehre in der Biologie*, Jena 1905; J. P. Lohs, in *Recueil de travaux botaniques Néerlandais*, t. i. 1904; and so on.

²⁹ Zederbauer, *Botanische Zeitschrift*, Jahrgang lviii., Vienna 1908, p. 233.

study of its extension along the routes followed by man, but also from the fact that the same high-level variety was obtained by experiment. When seed, collected from the low-level plants, was sown in the high Alps at Bremerhütte, it soon produced plants similar to the high-level plants of Asia Minor. On the other side, when seed collected in Asia Minor at an altitude of about 6700 feet was sown in the Vienna Botanical Garden, 'the assimilation organs [the leaves] changed at once under the new conditions of life'; while 'the reproductive organs (the flowers and the seeds), as also those which are in a near connexion with them (the flower-bearing stems), displayed on the contrary a greater steadiness of character, changing very little, or not at all.'³⁰ For four consecutive generations, in 1903-1906, the stems and roots offered no substantial changes, the habitus of the plants remained Alpine, only the leaves were modified.³¹

The results of these experiments are so definite that Professor MacDougal, who formerly was sceptical as regards an hereditary transmission of somatic modifications (the modifications in the cells of the body),³² and who is now doing such excellent work at the Arizona Desert Laboratory in the way of going deeper into these questions, fully recognised in 1911 the inheritance of the characteristic features of the Alpine form. They are—he wrote—'clearly direct somatic reactions; and that they have become fixed and fully transmissible is demonstrated by the fact that in a series of generations grown at lower levels the stem characters, as well as those of the reproductive branches and floral organs, retained their Alpine characters, although the leaves, as might be expected, returned to a mesophytic form with broad laminae.'³³

The observations and experiments of Professor Zederbauer are thus especially valuable, as they give us an instance, taken from free Nature, of that definite and cumulative variation under the direct action of new environment, which Darwin came to consider necessary for the evolution of new varieties and species with the aid of Natural Selection.

³⁰ Zederbauer, *loc. cit.* p. 288.

³¹ *Loc. cit.* pp. 234-235.

³² See his 'Address before the American Association for the Advancement of Science, Chicago, 1907-8,' in *Science*, New Series, vol. xxvii. p. 123.

³³ D. T. MacDougal, 'Organic Response,' in *The American Naturalist*, vol. xlv., January 1911, p. 39 of separate reprint. After having quoted the words of Professor MacDougal to the same effect (from *Science*, N.S., vol. xxxiii. 1911), R. Semon expresses the hope, which all students of this question will share with him, that 'the comprehensive experiments which are now carried on in several Acclimatisation Laboratories in America will contribute to place the very promising researches of Bordage and Zederbauer on a broader basis' (*Das Problem*, pp. 65-66).

V

An instance of inherited variation in plants which has often been quoted, and also often contested in the present controversy, is that of Schübeler's experiments on wheat. This well-known Norwegian botanist wrote on the influence of climate on cereals in the 'fifties of the nineteenth century. Later on he himself made some experiments, chiefly on a certain summer wheat which used to take in Germany an average of 100 days to ripen. Sown in Norway, where the summer days are longer, and the plants are thus exposed for a longer time to daylight, the same wheat ripened in 75 days.³⁴ And when, after a few years' culture in Norway, seeds of that wheat were sown in Germany, they produced wheat which ripened much more quickly than previously—namely, in 80 days. It was concluded, therefore, that this wheat had acquired in the higher latitudes a character which was transmitted to its progeny.

Other similar variations were mentioned lately—the most typical being those observed by Wettstein on flax and Cieslar on trees.

The Vienna professor, R. von Wettstein, experimented for six years on flax, and he found that,

if we examine the same sort of flax in regions possessed of a different climate, we find that it offers various adaptations to the local conditions, both as to the times it requires for ripening and various peculiarities of form. The shorter the warm period in a given locality, the more rapid is the development of the sort of flax which is cultivated in this locality. And if the seeds of this sort be sown in another locality, the plants they produce do not take at once the structure appropriated to the new conditions; they retain for some time their adaptation to the previous conditions of life.³⁵

A similar observation was made by A. Cieslar. Trees growing at different altitudes differ, as foresters know, in the rapidity of their growth. These characters are inherited. When Pines and Larches were grown from Alpine seed in the lower valleys they retained the feature of slow growth.³⁶

Several objections were raised against the conclusions of

³⁴ The rapid ripening of barley in the province of Yakutsk is well known. Professor Beketoff explained it by a long exposure to daylight in high latitudes during the long summer days.

³⁵ Dr. R. von Wettstein, *Der Neo-Lamarckismus und seine Beziehungen zum Darwinismus*, Jena 1903, pp. 20-21.

³⁶ A. Cieslar, in *Centralblatt für das gesammte Forstwesen*, 1890, 1895, and 1899, quoted by Wettstein, *loc. cit.* p. 21; 'Die Bedeutung Klimatischer Varietäten,' etc., in *Zentralblatt*, 1907. The experiments made with different Gramineae by Weinzierl, who obtained under the influence of a greater intensity of light in the Alps new, morphologically different acclimatisation races, belong to the same category. I know that they are mentioned by Wiesner in *Der Lichte Genuss der Pflanzen*, Leipzig 1908, but I have not yet consulted that work.

Schübeler, and they apply also to those of Wettstein, Cieslar, and several others,³⁷ the chief of them being those of the Danish professor, W. Johannsen, the author of an elaborate work on the elements of the science of heredity. He pointed out that the wheat cultivated by Schübeler was not 'a single pure race.' Like all our domesticated plants, it represented 'a population,' a mixture of different races. Some of these races ripened sooner than the others, and when this mixture, imported from Germany, was sown in Norway, the rapidly ripening sorts came to maturity during the short northern summer, while the later sorts contained in the mixture did not ripen at all. There was *no variation*; no new characters were acquired—merely an unconscious selection took place. And when the seeds were taken back to Germany the later-ripening sorts had been eliminated.³⁸

Johannsen's suggestion *may*, of course, be correct; but nothing has yet been produced to give it any *probability*. One would like to know how it happened that 'the early-ripening pure lines' should not have been eliminated during the long succession of years that this summer wheat was cultivated in Germany before its seed was taken to Norway. What was it that prevented the individuals which ripened their seed in 80 days from dropping it on the ground during the 20 additional days that the wheat had to stand in the field before the harvest began? We know, indeed, that when wheat is ripe, a delay of two or three days in harvesting means the loss of 10 per cent. or more of the crop. And then would it not be necessary to prove that when the German wheat was harvested in Norway, 80 days after it had been sown, instead of 100, only a portion of the 'mixed population' had come to maturity, so that the crop was reduced in proportion? So long as this has not been done, Professor Johannsen's suggestions can hardly be considered as a disproof of the conclusions of Schübeler, Wettstein, Cieslar, and many others.

³⁷ N. Wille, in *Biologisches Centralblatt*, vol. xxv. 1905, especially pp. 564 and 569, has tried altogether to discredit Schübeler's work. But Professor R. Semon (*Das Problem*, p. 63) has already shown that 'Wille took no notice of the experiments made by Schübeler himself; he believed that this writer had drawn his conclusions exclusively from other people's reports and from an old Swedish paper.' Let me add that the data which Wille gives concerning the rapidity of growth of cereals in different parts of Norway, and which he opposes to the conclusions of Schübeler as to the influence of light, might have been of great value; but the altitudes of the different localities and the amount of sunshine having not been indicated, they are of no use in this controversy.

³⁸ W. Johannsen, *Elemente der exakten Erblchkeitslehre*, German enlarged edition, Jena 1909, pp. 351 *seq.* This argument is frequently produced on the Weismannist side. For a good summary of the question see Erwin Baur's 'Die Frage der Vererbung erworbener Eigenschaften im Lichte der neuen experimentalen Forschung mit Pflanzen,' in *Archiv für Soziale Hygiene*, Bd. viii. 1913.

It must also be added that Dr. H. Nilsson-Ehle, who certainly has acquired at the Swedish Experimental Seed Station of Svalöf a wide experience of 'mixed' and 'pure' races of cereals, warns us against hasty conclusions in this direction. His experience has also brought him, like Professor H. Nilssen, to the conclusion that the old races of cereals, hitherto considered pure, represent in reality mixtures of maybe twenty or thirty different races. But he also points out how difficult it is to distinguish between what is a racial inheritance and what is individual, fluctuating modification, due to the always fluctuating exterior conditions. The 'races' overlap each other, and 'a small change in the average character can easily be due to the exterior conditions which are never the same in an experimental field.'³⁹ In fact, although care is taken to grow all the individuals of a pedigree culture under the same conditions of soil, manure, temperature, moisture, and sunshine, these conditions, as Nilsson-Ehle reminds his readers, are not fully realised. The outer conditions—he writes—are never the same in two adjoining beds, still less so in different years. Not even—shall I add?—for two plants on the same bed, or even two pods, or two ears of the same plant. The Jersey growers know that quite well, and therefore they take separate care of each one of the half-dozen apples, or pears, or the bunch of grapes which they single out for an exhibition, or for selling them to the dealers who supply choice fruit for dinner-parties. This is why such 'characters' as the size or the weight of individual beans, the shade of colour in the grains of wheat or oats, and the like, are so unreliable in the supposed 'pure lines.' Even if they are inherited for two or three generations in accordance with the Mendelian rules, this must very often be due to the fact that the effects of an especially healthy (or unhealthy) constitution, due to accidental combinations of external influences, are felt in the next two or three generations.⁴⁰

In these researches, as in all others, we thus come to the result that always the *two* factors of variation must be taken into account: the inheritance of the previously established characters, and the transmission, be it only for a few generations, of the new variations due to the direct action of the surroundings. This is also why Nilsson-Ehle, even though he considers the

³⁹ Dr. H. Nilsson-Ehle, 'Om lifstyper och individuell variation,' in *Botaniska Notiser*, 1907, pp. 113-140; analysed by Dr. C. Fruwirth in *Journal für Landwirtschaft*, Berlin 1906, p. 296.

⁴⁰ Thus H. Tedin, one of the Swedish explorers of this subject, points out that the amount of protein contained in different sorts of barley can hardly depend upon the 'pure line,' or 'sort.' It is, to begin with, a result of the soil, the manure, the climate, the weather (Fruwirth, *loc. cit.* p. 311). And we know how such a 'character' influences all others.

inheritance of newly acquired characters as problematic, adds nevertheless that

the possibility of a real acclimatisation of a constant form through the prolonged action of the surroundings cannot be denied without further proof. For deciding the question definitely a long succession of experiments would be required.⁴¹

This attitude of doubt, I must add, is the attitude now taken more and more by those botanists who a few years ago considered the inheritance of acquired characters as absolutely impossible.⁴²

VI

The researches briefly passed in review in the preceding pages undoubtedly represent a substantial addition to our comprehension of evolution. In addition to what Experimental Morphology had already taught us as regards variations due to changing conditions of life, we now learn that each time experiments were made to ascertain whether such variations are inherited, the reply was: 'Yes, they are inherited, with certain limitations—provided the modifying causes acted for some time and at the proper time. Different characters are inherited in different degrees, and the number of generations which will retain the variation depends upon the number of ancestral generations influenced by the modifying conditions.'

It thus appears that variability, which Darwin described as a 'handmaid to Natural Selection,' offers to her lady such a profusion of variations that the lady's preferences are determined beforehand. All that she has to do is to weed out those, probably sickly, individuals which are not plastic enough and do not answer rapidly enough the requirements of a changed environment by corresponding structural changes.

Already in 1862, when Darwin began to prepare his work on *Variation*, he saw the importance that this distinctive feature of variability would have for the theory of evolution, and he recognised—not without a touch of quite natural regret—that it would diminish the importance of Natural Selection.⁴³ But, as an honest student of nature, he did not say that his critics had to

⁴¹ 'Sammanställning af höstvetes sorterernas vinterhärdighet'; analysed in German by Fruwirth, *loc. cit.* p. 293.

⁴² It would be impossible to analyse here the immense amount of work done lately in the study of the 'pure lines,' and especially the Mendelian rules of inheritance in crossings. So I must refer the reader to the already mentioned work of W. Johannsen and to two works of Erwin Baur—one in the *Archiv für Soziale Hygiene*, 1913, Bd. viii, pp. 117-144, and his last, already mentioned book.

⁴³ *More Letters of Charles Darwin*, London 1903, vol. i. p. 214. Also *Life and Letters*, ii. 390. Compare also *More Letters*, ii. 235, 300.

prove that : he was the first to collect data in favour of this view ; so that in *Variation* he himself substantially reduced the part he attributed at the outset to Natural Selection.

Since that time evidence in favour of the direct action of environment has rapidly accumulated, and now the hereditary transmission of its effects finds acceptance with a growing number of followers. Biologists begin to see that at the bottom of the present controversies there lies still the pre-Darwinian conception that the agencies which have been at work in centuries past to mould a species, and the effects of which are transmitted by heredity, are so powerful that no amount of action of a new environment can alter them ; and, in proportion as they better study heredity, they abandon this conception.

Of course, a Palm remains a Palm, whether it be grown in Tunis, or in the warm coast-region of the Riviera, or in a glass-house at Ghent ; and a South African Cactus retains its weird features in the Mortola garden—if it grows at all. But it must not be forgotten that the imported plants are placed, as much as possible, in conditions similar to those of their mother-countries—otherwise they perish—and yet all of them undergo certain changes. When we see a Buttercup or a Shepherd's Purse growing in the prairies of both Southern Siberia and Southern Canada, we must not exaggerate the differences of climate in these two regions, nor must we forget how much this same Buttercup varies in our own meadows, according to its growing on a dry ground, or half immersed in water. We have just seen how much stable a species as the Shepherd's Purse varies when it is taken from Fontainebleau to the Alps, or from a high plateau in Asia Minor to Vienna. Altogether, when we think of the variability of all our plants, or of the numbers of 'genotypes' of wheat or oats established by our seed-growers, the hundreds of 'small species' of *Draba* produced by Jordan, and the modifications of nearly all species obtained at the Alpine, Maritime and Desert Experimental Stations, we understand why botanists begin to consider every race of a species merely as a temporary equilibrium between two factors : the resistance to change opposed by the inherited features, and the transforming influence of the surroundings. The species thus appears like the course of a river that has been determined first by the general relief of the country, and then has never ceased to be altered by all sorts of local physiographical processes.

It may be asked, however, 'Why should the modifications produced in plants by new surroundings ever prove to be useful? Why should they represent adaptations to new conditions?' Taking a familiar example from an English garden, we see that with certain frost-resisting Rhododendrons, such as the Hima-

layan species, the leathery leaves, covered with a sort of felt on the under side, and usually standing upright, droop as soon as it begins to freeze, and roll themselves into a tube. When the frost is over they return to their natural position. Similar movements, we all know, are performed by the leaves of scores of plants as soon as the temperature of the air sinks after sunset. What is the cause of these 'adaptive' movements?

They so well answer a purpose that there are biologists who attribute them to an inherited 'instinct.' Others explain them as a result of Natural Selection, which means the survival of those plants which 'by chance,' for some unknown cause, began to perform these movements. But neither of these two 'explanations' reduces a complicated fact of unknown origin to simpler, elementary facts of which we comprehend the cause. This is why, after the experimental researches made by Sachs, Goebel, Wiesner, Warming, Costantin, Kny,⁴⁴ and so many others, botanists come now to the opinion that, as Johannsen has expressed it, 'adaptation—the self-preserving reaction—is a *necessary consequence*, or, to express it more correctly, an expression of the fact that organisms are systems in equilibrium.'⁴⁵ I should even suggest that in 'adaptations' we have the effects of that fundamental principle of the Newtonian philosophy—the equivalence of *action* and *reaction*, from which Mendeléef derived all the laws of chemical reactions.⁴⁶

Finally, modern research having shown that *time* is an important element for obtaining inheritable variation, it is interesting to see how Weismann, the chief adversary of the inheritance of acquired characters, accounted for this fact. Since he published (in 1888) the essay in which he denied the possibility of an hereditary transmission of acquired characters in plants,⁴⁷ he re-studied the subject, and in his next work, *The Germ-Plasm*, he evidently had to explain why, under his germ-plasm hypothesis, the effects of the modifying influence of the surroundings were transmitted in certain cases, especially when these influences had acted for a certain time. His explanation was : that when a plant or an animal is placed in new conditions of life, the nutrition of the germ-plasm determinants of a given organ may be altered. But the determinants of every organ are many, and not all of them will be affected at once. Therefore it may be necessary that a number of generations should be submitted to the modifying influence, before the majority of the determinants of that organ are modified, so as to produce a modified organ in

⁴⁴ *On Pressure Favouring Cell-Division, and Consequently Growth.*

⁴⁵ *Loc. cit.* p. 357.

⁴⁶ In a lecture delivered in 1889 before the Royal Institution, and published in the Appendix to his *Principles of Chemistry*, London 1891, vol. ii.

⁴⁷ *Essays upon Heredity*, Oxford 1891, pp. 397-430.

the progeny. This explanation is quite probable, and it can be accepted, equally well, under Darwin's Pangenesis hypothesis, or any other hypothesis of inherited germs or 'physiological units.'

In conclusion, I can only express, in common with Professor D. T. MacDougal, the hope that decisive facts proving this inheritance will soon be obtained now that the subject is studied empirically at several experimental stations of the United States.⁴⁸ This is also the opinion of those botanists who have lately paid attention to Experimental Morphology as a branch of plant physiology. The results of the later years' experiments have certainly turned the scales in favour of the inheritance of acquired characters, and proved the importance of the direct action of environment in the evolution of new species.

The same change of opinion is taking place as regards the animal world. But this vast subject must be treated separately.

P. KROPOTKIN.

⁴⁸ D. T. MacDougal, 'Organic Response,' Presidential Address delivered before the Society of American Naturalists, reprint from *American Naturalist*, vol. xlv. January 1911. See also Giesenhagen, 'Erblichkeit in Pflanzen,' *Archiv für Entwicklungsmechanik*, xxx. pp. 310 seq.

VENETIAN SCHOLARS AND THEIR GARDENS

Veri paradisi terrestri per la vaghezza del aere e del orto, luogo de' ninfe e de' semi-dei.—ANDREA CALMO.

Few Italians take greater pleasure in flowers and gardens than the people of Venice, the city in the sea. These dwellers in the lagoons, whose houses rise from the water's edge, and who seldom own more than a few feet of ground, are passionately fond of plants and blossoms. They cultivate every inch of soil within these narrow bounds, and grow vines and acacias round every *traghetto* and *osteria*. Their balconies are hung with wistaria and Virginia creeper, their roofs and window-ledges are gay with flower-pots. Every visitor to Venice remembers the glimpses of leafy arbours, of palm and myrtle and pomegranate, that charm his eyes as his gondola glides along the Grand Canal, the flowery paradise behind the iron gates of Ca' Foscari and Casa Rossa, the gardens of Palazzo della Mula and Palazzo Venier, the trailing roses and white convolvulus of the loggia at Ca' Capello—that fair house which few of us to-day can see without a sigh for the gracious presence which has passed away. Even in the densely populated quarters of the city, at the back of the Carmine and San Pantaleone, spacious gardens are still to be found, where you can walk between rows of tall cypresses and rosy oleanders, and discover ancient wells, carved with the arms of Venetian families, hidden in a tangle of briar rose and jessamine, or, following Byron's example, pick bunches of purple grapes from the pergola overhead. The palace where Bianca Capello lived still retains its stately Renaissance terraces, adorned with classical peristyles and moss-grown statues, nymphs and fauns, and planted with avenues of ilex and cypress. And there are other gardens in the outlying parts of the city where you can wander at will among tall Madonna lilies and bowers of honeysuckle, and look across the pearly lagoon to the long shores of Lido and the open sea, without hearing a sound but that of the waves lapping against the low sea-wall. But these, for the most part, are only fragments of what they were, and we are reminded of the saying of our fellow-countryman Lassels, who declared that in Venice gardens were as wonderful things as