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B. T. GALLOWAY, *Chief of Bureau.*

METHODS AND CAUSES OF EVOLUTION.

BY

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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., July 30, 1908.

Sir: I have the honor to transmit herewith a paper entitled "Methods and Causes of Evolution," by Mr. O. F. Cook, of this Bureau, and recommend its publication as Bulletin No. 136 of the Bureau series.

The doctrine of evolution is now being made of practical use in the solution of problems of breeding and acclimatization. The nature of evolution must be understood before the effects of selection and environment upon the characters of organisms can be correctly appreciated as a guide in our efforts to improve plants or to avoid the degeneration which appears in many of our domesticated varieties. The distinctions made in this paper will assist in the practical application of the ascertained facts of evolution, and will help to avoid confusion from numerous conflicting theories which have been developed without bringing evolution into relation with the physiology of plants.

The accompanying report contains a brief statement of the present status of our knowledge of these important subjects, particularly on the sides relating to agriculture. It summarizes in direct and simple form the results of more detailed studies already published by this Department and in scientific journals.

The author wishes to acknowledge helpful criticisms from Prof. Willet M. Hays and from several of his colleagues, Messrs. Walter T. Swingle, T. H. Kearney, W. R. Maxon, Frederick V. Coville, C. S. Scofield, and David Fairchild. The paper has also been read by Dr. Alexander Graham Bell, who has made the following significant comments regarding the function of natural selection:

> I, too, entertain the feeling that natural selection does not, and can not, produce new species or varieties, or cause modifications of living organisms to come into existence. On the contrary, its sole function is to prevent evolution. In its action it is destructive merely, not constructive—causing death and extinction, not life and progression. Death can not produce life; and though natural selection may cause the

death of the unfit, it can not produce the fit—far less evolve the fittest. It may permit the fit to survive by not killing them off if they are already in existence; but it does not bring them into existence or cause improvement in them after they have once appeared. We must look to other agencies for the causes of evolution. A closed gate may block a road, but it does not push the traveler into a new path, or, indeed, cause him to move at all. It is a mere static obstruction, not a dynamic force. In a similar manner natural selection prevents evolution along certain lines; but it is not a dynamic force compelling progress along other lines. The motive power of evolution must be sought elsewhere.

Respectfully,

B. T. GALLOWAY,
Chief of Bureau.

Hon. JAMES WILSON,
Secretary of Agriculture.

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METHODS AND CAUSES OF EVOLUTION.

INTRODUCTION.

Evolution is the branch of science concerned with the study of organic change. That species are subject to change is a fact as general and as fundamental in the organic world as gravitation is in the inorganic, and no less important in its relations to human progress. Our knowledge of evolution is far from complete, but it affords our only insight into many important problems.

The further development of the art of agriculture by which we live and even the progress of the human race itself are dependent upon knowledge of the conditions and factors which bring about changes in organisms. Our attempts to ameliorate varieties or to avoid degeneration are experiments in evolution. To know how species have developed in nature affords a necessary basis of judgment in the investigation of methods of improvement of domesticated types.

The problem of evolution is not to be solved without understanding how species are constituted, since it is only in species that evolution is known to take place. The higher plants and animals maintain their existence in nature not as separate individuals or in small, isolated groups, but as large groups of freely interbreeding individuals—the groups we call species. The lines of descent of a normal species are united by free interbreeding into a vast network or fabric in which progressive variations are accumulated and built up into new organs and functions. This constructive process also bears the name evolution.

The members of species are not normally uniform, but are normally diverse. Continuous interbreeding among the diverse members of a species is accompanied by continuous changes in the group as a whole, though without diminishing the normal diversity of descent. The more advanced the evolution of a group the greater are the diversities found among the members of the same species.

Natural selection and other agencies of the environment have not been found to cause the evolution of species. After fifty years of

study of evolution it is becoming apparent that constructive evolutionary changes are spontaneously put forth by species, which tend to these evolutionary motions as naturally as inanimate objects tend to remain at rest. Too much emphasis has been laid upon evolution as a process of formation of new species and too little upon evolution as a process of change in species already formed.

Species are multiplied by the subdivision of older species, but evolution goes on whether species are subdivided or not. If two parts of a species become separated the two groups no longer share the new characters which may be attained by each, and thus gradually become different. This occurs even under apparently identical natural conditions, in neighboring islands, mountains, or valleys. Facilities for interbreeding are necessary to keep the same characters distributed throughout a specific group. The formation of more species is one of the results of evolution, but is not a cause of evolution. Evolution and species-formation are different problems.[a]

The recognition of evolution as a property inherent in all species of plants and animals opens the way to the solution of many practical problems. It is not necessary that breeders undertake to produce evolutionary changes, for these take place spontaneously without our interference. Our power over evolution is to control and direct, to accelerate, retard, or reverse it. Some of the means of attaining our purposes are already known to us, and the chances of learning others are greatly increased by clear conceptions of the evolutionary facts and relations encountered in the work of the breeder.

Objections which have been urged against mechanical theories of evolution do not hold against the present interpretation of the facts, for selection and other external conditions are not reckoned as primary causes of evolutionary progress. Their functions are regarded as only secondary and directive. The theory that selection causes evolution, notwithstanding its wide popularity, seems not to be well founded. It stands in the way of further progress in evolutionary science and interferes with a full development of the art of breeding.

EVOLUTION PROCEEDS BY CONTINUOUS CHANGES OF CHARACTERS.

To maintain a distinction between methods and causes conduces to clear thinking in evolution. How evolution proceeds is one question; what actuates the motion is another. By treating these two questions separately much confusion of issues may be avoided.

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[a] Cook, O. F. Evolution Not the Origin of Species, Popular Science Monthly, 64:445, 1904; republished in the Annual Report of the Smithsonian Institution for 1904 under the title The Evolutionary Significance of Species. See also Factors of Species-Formation, Science, n. s., 23:506.

Evolution may be considered as a fact, and the modes or methods of evolutionary change may be studied quite apart from any explanation or theory of the cause of evolution. The regular courses of the heavenly bodies are taken as evidence of the fact of gravitation, although the underlying causes still remain unknown.

Darwin ascertained that evolution is accomplished through continuous, gradual changes in the characters of species. He had a wide acquaintance with species in nature and with the facts of variation. He found in the differences between natural groups evidences of gradual evolutionary divergence. He saw that the evolutionary courses of species could be traced from their characters, much as hunters follow animals by their tracks. Those who have a like acquaintance with species in nature find similar facts and accept Darwin's conception of the method of evolution.

Studies of the classification and geographical distribution of wild species have special value in training the judgment in evolutionary matters. The evidence that evolution is accomplished through continuous changes of characters can not be appreciated adequately by those who know plants and animals only as domesticated breeds and have not become acquainted with the similarities, differences, and internal diversities of species in nature.

NATURAL SELECTION UNLIKE ARTIFICIAL SELECTION.

In addition to showing that continuous changes represent the method by which evolution proceeds, Darwin advanced a theory of the cause of evolution—natural selection by environmental agencies. He applied to natural species analogies drawn from domesticated breeds. The selective action of the environment and of the struggle for existence was supposed to interfere for the preservation of useful variants in nature, to keep their new characters from being "swamped" by interbreeding, in the same way that artificial selection is used to preserve the peculiarities of domesticated breeds.

In reality, natural selection is not similar to artificial selection; there is a complete biological opposition. Natural selection eliminates deficient and aberrant individuals, but preserves the species as a great multitude of diverse, broadly interbreeding organisms. Artificial selection disregards the species, but saves some of the aberrant forms and restricts their descent to narrow lines of consanguinity. Nature has been searched in vain for proofs of the origin of new types from selected individuals or from narrowly restricted varieties. Natural selection by preserving a broad network of descent permits a gradual and completely continuous evolution.

Darwin had learned from his studies of classification and geographical distribution that species in general evolve by gradual subdivision and divergence, as branches grow on trees, but the analogies of

artificial selection are not in accord with this idea of complete continuity. They do not lead us to think of trees as having inherent powers of growth, but as growing because they are pruned.[a]

The breeder cuts off all except the most proficient individuals after careful selection among small fluctuating differences. He seeks in this way to obtain the highest and most uniform expression of a particular character, but this artificial specialization of characters in narrow-bred varieties is not the same as the free evolutionary progress of broad-bred natural species.

To keep a few individuals away from the network of descent of their species is not nature's method of evolution. Narrow artificial selection turns its protégés into paths of degeneration. Natural selection does not separate the fittest individuals from others of their kind. It leaves them to interbreed and share their progress with millions of the less proficient. Only the unfit suffer from nature's discrimination. The more prosperous the species the greater the number of interbreeding individuals. Only when species are verging on extinction do they approach the condition of narrow breeding shown in domesticated varieties.

NATURAL SELECTION NOT THE CAUSE OF EVOLUTION.

Darwin retained much of the pre-evolutionary idea that species are normally stationary, and was accordingly led to infer that changes of characters must be brought about through changes of external conditions. Species were not supposed to have an inherent power of making progressive changes without environmental interference or even in spite of it. Variability was recognized, but variations were not thought of as resulting in evolution unless selection interposed. The adaptive fitness of many species to particular environments seemed to indicate that the causes of evolutionary progress were in the environment.

It is the office of natural selection to guide the evolutions of species in directions of fitness to their environments, but not as a cause of evolution, not through any power to actuate the evolutionary motions of species. The influences of selection are more often exerted in holding species back than in carrying them forward. Adaptation is not the whole of evolution, but only a particular kind, a specially directed

[a] "Each new variety or species, when formed, will generally take the place of, and thus exterminate, its less well-fitted parent. This I believe to be the origin of the classification and affinities of organic beings at all times; for organic beings always *seem* to branch and subbranch like the limbs of a tree from a common trunk, the flourishing and diverging twigs destroying the less vigorous—the dead and lost branches rudely representing extinct genera and families."—Darwin, Charles, On the Tendency of Species to Form Varieties, etc. Proceedings of the Linnean Society of London, 1857, p. 53.

form of evolution. If continued variation is assumed, it is to this that the evolutionary progress must be ascribed, not to natural selection. Selection merely limits the directions that progressive variations may take.[a]

A logical fallacy, as well as a biological error, is involved in assuming that the selecting away of a part of a supposedly stationary species would change the characters of the remainder. Only the statistical averages of the survivors of such a species would be shifted, not their evolutionary positions. Selection would leave the surviving members of a group more uniform, but it would not carry them farther on the course of development. Progress toward uniformity means that some of the characters are suppressed instead of new differences being added. Greater uniformity marks an agricultural improvement in a domesticated variety, but is not a measure of evolutionary progress in a natural species.

Some of the most effective evidence of the supposed power of selection to produce changes of characters has been drawn from the phenomena of mimicry among butterflies. Harmless species sometimes show very close resemblance in wing colors to members of other families protected against birds by distasteful secretions. But even mimicry can be understood by recognizing that selection tends to restrict evolution better than by supposing that selection has dragged the mimetic species away from their relatives and painted them with new colors to resemble unrelated types. Likeness exists before differences develop. It is only necessary to suppose that selection has preserved similarities when these were of use, while the related groups have been free to diverge in colors, as in other characters. Mimicry affords striking proof that selection can lead two or more species to evolve in parallel or converging directions, but it does not show that selection is the motive power of evolutionary change.

If species were not already evolving, natural selection would have no influence over them; there would be no motion to be resisted and guided toward greater utility. That selection should not be expected to originate new characters has often been recognized, but it is equally unreasonable to suppose that existing characters would be modified by selection if species were normally stationary. The facts of adaptation abundantly corroborate the Darwinian conception of evolution as a process of gradual change in the characters of species, but they afford no proof at all that selection can cause adaptive variations or carry along the evolutionary progress of species.

Strangely enough, the general popularity of the doctrine of evolution has been due largely to this theory which made selection appear

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[a] Cook, O. F. Weevil-Resisting Adaptations of the Cotton Plant. Bulletin 88, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1906.

as the cause of evolution, the side of Darwinism which has been most persistently questioned by students of nature. Many intelligent people think they can see clearly that natural selection, working through variability, causes species to evolve, but among biologists this has continued to appear doubtful. The scientific literature of the last half century abounds in protests declaring that the alleged cause is inadequate and the reasoning inconsistent with the facts.

Philosophical writers found in natural selection an extremely attractive hypothesis which made the organic world a result of its environment. Those who are not deterred by the biological difficulties begin by accepting natural selection as the cause of evolution, and then argue that the changes are continuous because they are results of continuous selection. This is to reverse Darwin's method of reasoning, for he used the facts of gradual evolution to support the theory of selection. The withdrawal of the theory of selection does not weaken the doctrine of continuity, but leaves it the more firmly established.

Darwin's first concern was not to demonstrate the theory of natural selection, but to implant in the minds of his readers the general conception of organic evolution. He made free use of any facts, suggestions, or theories that seemed likely to aid in establishing the basic idea of evolution. Many of his readers could understand the argument for natural selection as a cause of evolution, while very few could appreciate the mass of detailed evidence proving the more fundamental fact that the changes of characters are gradual and continuous. The theory of selection soon overshadowed the fact of continuity. Darwinism came to mean merely natural selection. Advocates and opponents alike have allowed themselves to forget that Darwin's perception of the method of evolution was independent of his theory of cause.

THE SIGNIFICANCE OF USELESS CHARACTERS.

Useless characters have more bearing than useful characters upon the question of evolutionary methods and causes. No interpretation is adequate that does not provide for the evolution of useless characters. If useless differences can be evolved without selection, the same may be expected for useful differences. To suppose that selection is the cause of evolution no longer appears necessary.

The theory of selection requires us to believe in the utility of all characters and in the development of each character through the selective origination of a new species. Darwin appreciated the difficulties of his hypothesis and continued all his life to seek additional evidence. Many other naturalists have joined in the search, and a large literature of adaptations has accumulated. New and

interesting uses of many characters have been discovered, but the results do not support the assumption of utility for all characters. The examination of any group of species or genera shows that the useless differences vastly outnumber those for which any environmental use can be assigned or even imagined.

Possibilities of former utility in characters now useless may be admitted, but the preponderance of useless differences is far too great to be thus explained away. The issue is not so plain among the complex structures and diverse habits of the higher animals and plants. Conclusive evidence comes from the lower orders, where many species and genera have the same habits and live under the same conditions and yet display endless differences of form and structure. There may still be doubt regarding the present or past utility of any particular character, but there can be no question that diversities of characters are out of all proportion to selective diversities of environment.[a]

A useful character has an evolutionary advantage, for it can develop and spread through the species without being hindered by the natural selection which discriminates against useless and injurious characters. Any change not forbidden by the limiting factors of environment and competition can go on by mere evolutionary propensity. The evolutionary progress of a useful character is no less spontaneous than that of a useless character. Selection need not be thought of as carrying along the useful character, but only as hindering the development of injurious characters. Selection works through restriction of descent—restriction of evolution.

A species evolving in the direction of longer hair would be able to resist increasing degrees of cold, but it is not necessary to think that the cold causes the longer hair to be evolved. The utility of a new variation depends upon the environment at hand when the variation is put forth. Thus, utility is a consequence of evolution; to say that it is the cause of evolution is to reverse the true relations of the facts. Instead of selection causing the evolution of the useful character, it is the advance of evolution that enables the higher standards of selection to be applied without destroying the species. The evolutionary progress of the species is not a result of selection, but an antecedent condition.

To gain clear perceptions of evolutionary factors we may lay aside this historical assumption that selection is the motive power of evolution, the active principle, agency, or cause by which evolution is brought about. Evolution is to be conceived in the mind as entirely independent and distinct from selection.

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[a] Cook, O. F. Evolutionary Inferences from the Diplopoda. Proc. Entomological Society of Washington, 5: 84. 1902.

ABRUPT VARIATIONS NOT INCOMPATIBLE WITH CONTINUOUS EVOLUTION.

The failure to distinguish adequately between the theory of selection and the fact of gradual change has led some writers to suppose that the idea of continuous evolution must be given up when the theory of selection is rejected. Hence, they return to the older notion of fixity of species and make use of the idea of evolution only to the extent of supposing that new species originate from older species by abrupt transformations of individuals, instead of being created altogether anew. Sudden changes of characters often occur, variously known as "sports," "mutations," or "extraordinary births," and these have been taken as new species and as true examples of the method of evolution.

Abrupt variations in the characters of individuals do not necessarily conflict with the method of evolution as a continuous change in the network of descent of the species. A single sheep may jump the fence, but this does not prove that a new flock is to be formed, for the others usually follow. The motion of the flock would still be gradual, no matter how far the individual sheep might jump. An individual variation, however wide, would not have evolutionary value and permanence unless the new character were able to spread to other members of the species, and thus become established in the network of descent.

A new character is like a new pattern in a fabric. Substitutions among patterns already designed are not to be confused with the working out of new patterns. Sudden alternations among old characters do not compel us to believe that new characters are made suddenly. The facts of continuous change shown in natural species enable us to think of new characters as woven by gradual changes and combinations of older characters through the interweaving of the lines of descent of the species.

REVERSION, MUTATION, AND MENDELISM.

A narrow-bred uniform variety shows only one set of characters, so that the characters of a diverse individual mutant appear to be new. But if we observe a sufficient series of mutations as they spring from the same uniform variety, a wide range of individual diversity is found, like that of the wild species from which our cultivated varieties are derived. It becomes evident that selective narrow breeding has not destroyed the ancestral diversities, but only suppressed them. Though showing only one set of characters in its external visible form, the narrow-bred variety still transmits a long series of latent differences.[a]

[a] Cook, O. F. Heredity Related to Memory and Instinct. The Monist, 18: 363. 1908.

To ascertain that an individual plant or animal has brought a really new character into expression it would be necessary to have a complete account of its ancestry, to know all the characters which are being transmitted along the lines of descent. Such knowledge is not to be obtained from the pedigrees of a few generations of narrow-bred individuals. The wild species gives the best idea of the normal diversity of ancestral characters. When the wild species no longer exists our only resource is to apply the analogies of diversity shown in other related wild types.

The ranges of diversity shown in wild species are not equal, but they are generally very much wider than in narrow-bred domesticated varieties. Thus, aboriginal cotton varieties from Central America, though often as well isolated and as distinct from each other as natural species, have an individual diversity corresponding to that of our whole series of varieties of Upland cottons and even greater. The mutative variations of our Upland varieties often show some of the forms of diversity which are regularly present in the Central American series, but are not represented in any of the Upland varieties now cultivated in the United States.

The sudden mutative changes in our Upland cottons which fall outside the range of diversity of the Central American types are in the nature of abnormalities, such as the shortening of joints, fasciation of branches and flowers, and partial or complete absence of lint. Such a degeneration does not constitute a new character in any truly evolutionary sense. It is merely a failure to bring an old character into normal expression.

By hybridizing two narrow-bred varieties we can often recall to expression many of the diverse characters of the aboriginal species—characters which may have been suppressed for so many generations that they appear to us as entirely new. Thus, the characters of mutations and of hybrids may have the same origin in the store of latent diversities which even the most uniform varieties continue to transmit.

Hybridization serves our purposes best in plants grown by vegetative propagation, but mutations are preferable in species grown from seed, because the change of expression is more definitely "fixed" from the first, without the need of the series of selections used for fixing the characters of hybrids, sometimes ineffectually.

Thus, characters which have been supposed to originate suddenly in mutative variations can be viewed with better reason as reversions or as degenerations; often they partake of the nature of both. That the great majority of mutations are obviously abnormal and inferior in fertility, even to the degenerating stocks from which they spring, is a sufficient reason for refusing to regard them as true examples of a constructive evolutionary progress.

Many instances of abrupt variations, or "sports," were known to Darwin, but he considered that sudden changes of characters indicate abnormality. He was too familiar with the evidences of continuous change in natural species to look with favor upon the idea of evolution by sudden jumps from one species to another. The following passages may serve to show his general conclusion regarding the group of facts now commonly described as mutation and Mendelism:

> The ordinary result of a cross is the production of a blended or intermediate form; but in certain cases some of the offspring take closely after one parent-form, and some after the other. This is especially apt to occur when the parents differ in characters which first appeared as sudden variations or monstrosities.[a]
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> When two breeds are crossed their characters usually become intimately fused together; but some characters refuse to blend and are transmitted in an unmodified state either from both parents or from one.
>
> From this fact, and from the several slight, aggregated differences which distinguish domestic races and species from one another, not being liable to this peculiar form of transmission, we may conclude that it is in some way connected with the sudden appearance of the characters in question.
>
> Some few characters, however, are incapable of fusion, but these are unimportant, as they are often of a semimonstrous nature and have appeared suddenly.[b]

Although the sudden changes and the "peculiar form of transmission" shown in mutative varieties are often connected with abnormalities, other forms of alternative expression of characters are general in nature and must be reckoned as entirely normal. Sexual differences represent a form of alternative expression of characters quite as definite as in the so-called "Mendelian hybrids" in which contrasted parental characters "refuse to blend."

It is a most familiar fact that sexually diverse parents produce sexually diverse offspring, and in equal numbers when averages are considered. Darwin and others have shown that the characters expressed in only one sex are transmitted by both sexes. There is much additional evidence that sexual diversity arises from the unequal expression of alternative characters, not from unequal transmission, and the same interpretation can be applied to all the facts of Mendelism. Considered as a phenomenon of alternative expression, Mendelism finds a place in a connected series of phenomena as one of many forms of diversity which may exist among the members of the same species. The assumptions used to explain Mendelism as a phenomenon of alternative transmission are too complicated to secure

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[a] Darwin, Charles. The Descent of Man and Selection in Relation to Sex, New York edition, p. 172. 1896.

[b] Darwin, Charles. The Variation of Animals and Plants Under Domestication, New York edition, pp. 69, 72, and 157. 1897.

credence when the possibility of a simpler interpretation is once appreciated.[a]

ADJUSTMENTS OF CHARACTERS TO EXTERNAL CONDITIONS.

Another form of alternating expression is found in the changes of characters, often very abrupt, by which organisms are able to adjust themselves to different conditions of existence. Before the possibilities of alternative expression were realized, these environmental changes were supposed to represent a power of the environment to form new characters in organisms, a supposition no longer required. The alternative characters of the same species are like the two or more forms which the same chemical substance may take in crystallization.

Environmental changes, like mutations, are to be considered as alternative expressions of characters already developed; they do not represent the progressive changes by which new characters are originated. One alternative character need not be considered more normal than another, seeing that freedom of substitution among many alternative characters is a normal condition in species.

The finely divided leaves which some amphibious plants put forth when growing in water are as truly characters of the species as the entire leaves shown by plants growing on dry soil. Even the same individual when transplanted from one habitat to the other changes the character of its leaves. The environment merely calls one alternative or another into expression, just as the pupils of our eyes open in the darkness and contract in the light. It is not necessary to suppose that characters which are changed with changes of environment are products of environment or that such changes add anything to the evolutionary progress of the species.

How the external influence works upon the internal adjustments so as to call forth a substitution of one alternative character for another is still unknown, but there is no lack of evidence that such relations exist. To take the adjustments of such characters as examples of evolution is another way of confusing the result with the cause.

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[a] Cook, O. F. Mendelism and Other Methods of Descent. Proc. Washington Academy of Sciences, 9: 189. 1907.

A Mendelian method of inheritance, by the alternative transmission of contrasted characters in pure germ cells, could have no direct relation to evolution. It has been shown by Mr. G. H. Hardy (Science, n. s., 28: 49) that a character inherited in the Mendelian fashion would not tend to spread through a species. The proportion in which such a character was represented in a group would not increase with successive generations, but would preserve a constant average after the second generation, if there were no selection or other interference.

The power of external conditions to influence expression is not limited to the substitution of one environmental character for another. The phenomena of acclimatization, no less than those of mutation, require to be brought into relation with the facts of normal diversity. Transfers of cotton and other plants to new conditions are often followed by striking changes of characters far beyond the range of ordinary environmental accommodations. Sometimes all the individuals of the same planting change in the same way,[a] and sometimes a wonderful individual diversity is aroused.

Instead of rare mutations of a few individuals of an otherwise uniform variety, there is a promiscuous mutation of all the individuals at once, each in a different direction. To believe that the same environment makes all these diverse characters anew is obviously unreasonable. But when the normal diversity of the members of species is recognized, and the fact that such diversities are transmitted, it becomes possible to understand that an unwonted condition may recall many ancestral diversities into expression by disturbing the internal relations which govern the expressions of the characters. The result is the same as though the plants were making experiments with all the various degrees and combinations of their ancestral characters to see which might be best adapted to the strange surroundings. Thus, the planting of a variety under new conditions may serve the same purpose as hybridization in recalling diverse characters to expression.

CHARACTERS NOT DIRECTLY MOLDED BY ENVIRONMENT.

In the century before Darwin many students of nature interpreted facts of adaptation as indications of evolution. But instead of appreciating evolution as progressive change in species, most of the pre-Darwinian evolutionists dwelt upon the idea that the organisms were directly molded by their environments into adaptive conformity. They assumed that all of the diversities found among members of the same species are due to inequalities of environment, and pointed to the results of environmental limitations and adjustments as true examples of evolution. This idea of evolution as a direct result of environmental influences has continued to find supporters. Many attempts have been made to substitute the teaching of Lamarck for that of Darwin, or to supplement natural selection by alleged environmental factors.

Darwin's superior insight enabled him to take an important step in advance of his predecessors. He agreed with them that adapta-

[a] Dr. C. A. White, of Washington, D. C., has described such changes in the tomato and calls them aggregate mutations. The Mutations of Lycopersicum, Popular Science Monthly, 47: 151.

tion shows relation to the environment, but judged that the relation is not direct. He recognized also that evolution pertains to species, not merely to organisms in mass, and he found in natural selection the way by which evolutionary changes in species are influenced indirectly by their environments. Those who have rejected selection and returned to Lamarck's theory of adaptive evolution through a direct molding of characters by the environment have not made good their case. To find that selection does not produce new characters does not prove that they are produced by the environment. It has not been shown that the environment has any active constructive influence in descent, either in individual organisms or in species at large.

The environment often appears to change the characters of organisms, but there is no indication that these changes represent progressive evolution. All forms of environmental influence thus far discovered can be interpreted in one or two ways, either as limitations of existing characters or as substitutions. Mutilations, diseases, and similar abnormalities imposed by the environment often destroy organisms or weaken their progeny, but are not known to contribute anything to evolutionary progress. The substitution of one character for another as following an environmental change or interference can not be accepted as the formation of a new character, now that organisms are known to inherit and transmit characters in latent form and to bring one or another into expression with or without relation to external conditions.

DIRECTIONS OF EVOLUTION NOT FIXED.

Other writers have turned away from the external environment to seek the causes of evolution in internal substances or mechanisms of heredity. From minutely detailed studies of species of Hieracium, Naegeli gained a conception of evolutionary motion as tending to carry species in definite directions, and incorporated this idea into a theory of the structure of protoplasm. He refused to accept Darwin's opinion that species are variable indefinitely in all directions, but declared that they vary in single definite directions.

The facts are again matters of observation. The members of a normal sexual species have many kinds of diversity, showing that many evolutionary changes can go on simultaneously in the same species. It has been found that Hieracium is parthenogenetic; that is, the flowers frequently develop seed without fertilization. This explains the unusual constancy of characters, for parthenogenesis is like vegetative propagation in being exempt from the indiscriminate diversity shown in normally sexual groups. The variations of parthenogenetic plants are not shared among the different lines of

descent, but follow separate courses and gradually diverge in definite directions. Nevertheless, these more definite changes are not to be accepted as examples of normal evolution, for they lead toward sterility and extinction if sexual reproduction does not intervene.

Naegeli's conception of internal causes of evolution through protoplasmic mechanisms of heredity has been borrowed and combined with many other theories, sometimes even with the idea of evolution by environmental causation. Weismann denied the inheritance of characters imposed on the bodies of organisms by the environment, but conjectured that heritable characters might be imposed by the environment directly upon the germ cells. This made it possible to think of evolution as carried forward by environmentally directed variations, so that adaptation would be explained without natural selection. A return toward Lamarck's doctrine became possible for those who wished to reject natural selection because it did not explain variation.

That natural selection is not responsible for all that has been ascribed to it does not justify a neglect to appreciate its true power of leading the evolutions of species toward adaptation. If the directions of evolution were fixed in advance or controlled by internal mechanisms, the preservation of the species would depend altogether upon coincidence. Selection would have no power to influence the direction of evolution.

Adaptations are too numerous and too finely specialized to be explained as mere coincidences; they are joint products of evolution and selection. Though not adequate to prove that the evolutionary motions of species are caused by the selective agency of the environment, the testimony of adaptation is ample to show that the evolutionary directions of species are not definitely determined by internal agencies or mechanisms.

DIVERSITY A FACTOR IN NATURAL EVOLUTION.

The problem of evolution always leads back to the discussion of variation, because this term is used to cover all the differences found among the members of a species. Somewhere among the internal diversities of the species are characters which at some future time will become the common property of the whole group and serve to distinguish it from other species in which these characters do not develop. The problem is to fix upon the truly evolutionary differences.

Several kinds of differences have been used as examples of evolution, as shown in the previous pages. Some writers have looked upon the fluctuating individual differences of narrow-bred varieties as the means of evolutionary progress, while others have considered that

new species are formed by sudden mutations. A third doctrine treats of environmental variations as representing evolution; a fourth would illustrate evolution by the smaller and more definite changes found in parthenogenetic and self-fertilized varieties.

There is still another type of diversity which seems to have more significance in evolution than any of the preceding. This is the normal diversity of natural broad-bred species, the differences found in species before descent is restricted—differences manifest even when the conditions are so uniform as to call forth no environmental variation.

To distinguish this diversity of normal descent from fluctuating and environmental variations, the word "heterism" has been used. Heterism can be eliminated by restricting descent to narrow groups or to individual lines, and can thus be distinguished from the fluctuating differences that are always to be detected, even in the most uniform of our narrow-bred domesticated varieties.

Fluctuating differences have been subjected to careful statistical study and have been found to conform to mathematical curves of chance distribution, like curves made from the records of a marksman shooting at a target. This conception of chance deviation from a fixed standard of heredity evidently does not apply to sexuality and other normal forms of diversity among the members of species. Fluctuations continue to be shown alike on all the lines of descent into which a species may be separated, but heteristic differences are separately expressed on different lines of descent when a species is subdivided by selective narrow breeding. The fact that all characters fluctuate leaves the fluctuating variations without special significance in evolution, though they are of interest in showing that uniformity is an artificial ideal not to be attained in practice, even under experimental conditions.

Sexual differences represent a very highly specialized form of heterism, but all gradations of diversity are found between sexual differences and mere environmental variations and fluctuations. Though evolution is a gradual process it is not necessary to suppose that advance takes place only by the selective accumulation of infinitesimal fluctuating differences. Normal diversity of descent provides for free substitutions and alternations in the expression of a much wider range of characters.

In diversities of descent rather than environmental or fluctuating variations are to be found causes of evolution, factors of change in the characters of species. Heterism does not serve the purposes of evolution alone. It has a physiological value in reproduction. High-grade organisms are the offspring of diverse parents. The higher

we go in the scale of life the more numerous and complex are the provisions for securing this diversity of parentage. Heterism thus contributes to evolution in two ways, by maintaining the vitality of the species and by furnishing the characters by which the species can change.

BROAD BREEDING A FACTOR IN NATURAL EVOLUTION.

Another cause of evolution is free interbreeding among the members of a species to maintain a broad network of descent. A species is an evolutionary unit because its members travel together along the path of development. Unless new characters were distributed through the species by broad interbreeding there would be no such evolution as that shown in nature. Characters would remain the exclusive property of single lines of descent, as in varieties of plants propagated from cuttings.

Complex structures are not developed without binding the species into a broad, continuous network. Among all the higher types of plants and animals the processes of descent are normally sexual and thus insure the weaving of a network of descent. Constructive evolution ceases whenever the network is cut into narrow strands or individual lines of descent; changes continue to take place, but leading toward degeneration.

The theory that natural selection is the cause of evolution led Darwin and many later writers to regard free interbreeding among the members of a species as an obstacle or hindrance to evolution. Broad breeding would hinder evolution if progress were dependent upon the selective restriction of descent, as in domesticated varieties. Broad breeding does not conflict with evolutionary changes in the network of descent of a natural species; such changes are facilitated by the distribution and combination of the characters of the component organisms.

The evolutionary prosperity of a normal species means large numbers, wide distribution, and abundant individual diversity. It contrasts at every point with the results of narrow selection, and warns us that the systems by which we breed our domestic animals and plants are contrary to the conditions of normal evolution.

Evolution is still to be defined as a process of change in the characters of species, but several kinds of changes in the characters of species have to be distinguished from the genuinely evolutionary changes. The paring away of species by selection, the dividing of species by isolation, the adjustments of characters to external conditions, and the suppression of characters by narrow breeding are processes as

different from evolution as they are from each other. They can all be studied from the evolutionary standpoint, but they do not represent evolution itself. They are not the progressive, constructive changes through which the world of organisms has come into existence. They show some of the consequences of evolution, but do not reveal its true nature or its motive power.

NARROW BREEDING A FACTOR IN DOMESTICATED VARIETIES.

Changes occur under conditions of narrow breeding which would not take place if descent remained unrestricted, but these changes do not represent a true evolution. Narrow breeding induces degenerative variations, but is at the same time our readiest means of making such variations serve our economic purposes. Any type is degenerate which is no longer on the pathway of constructive, progressive evolution.

The practical importance of our agricultural improvements of plants and animals is not lessened by the fact that they are not evolutionary improvements, but include many kinds and stages of degeneration. Nor is it any less a part of evolutionary science to study these valuable degenerations and ascertain the best methods of producing them. Breeders of specialized varieties have the problem of increasing desirable degenerations as much as possible, with as little as possible of injurious degeneration, such as weakness or sterility.

It is here that the belief in selection as the cause of evolution brings confusion and discord into the art of breeding. Darwin concluded, after weighing much evidence, that persistent narrow breeding always results in degeneration, because it violates a general law of nature. He makes the following statement:

> These two great classes of facts, namely, the good derived from crossing and the evil from close interbreeding, with the consideration of the innumerable adaptations throughout nature for compelling, or favouring, or at least permitting, the occasional union of distinct individuals, taken together, lead to the conclusion that it is a law of nature that organic beings shall not fertilize themselves for perpetuity.[a]

As long as selection is represented as the chief agency of evolution, the teaching of science will appear to favor the indiscriminate application of narrow breeding instead of warning against its dangers and limitations. The idea that selective restriction of descent is the cause of evolution is not in accord with a law of nature against close breeding. To hold that organic progress depends on selection and isolation is to place evolution in conflict with itself. It amounts to saying that

[a] Darwin, Charles. Variation of Animals and Plants Under Domestication, New York edition, 2:159. 1897.

evolution is everywhere working to prevent evolution, since every adaptation to facilitate interbreeding is at the same time an obstacle to the restriction of descent required by the theory that selection causes evolution.

When diversity of descent and broad breeding are recognized as the conditions of normal reproduction and evolutionary progress, this contradiction disappears and the meaning of the law against perpetual narrow breeding becomes plain. It no longer appears as a merely arbitrary regulation applied to some species and not to others, but reveals essential requirements of organic existence and evolutionary progress. Broad networks of descent are necessary to maintain efficiency of reproduction and organic vigor in the species. To destroy the network of descent removes the support of the organic structure.[a]

Degeneration comes to narrow-bred organisms as surely as clocks run down when they are no longer wound. Some clocks run only a day; others may not need rewinding for a week, a month, or even a year. Species differ widely in their ability to live by vegetative propagation, parthenogenesis, self-fertilization, or other forms of descent in narrow lines. Nonsexual methods of reproduction are often very useful to supplement normal sexuality, but exclusive dependence on restricted descent evidently brings extinction to wild species as well as to domesticated varieties. Nonsexual methods are not found in consistent use in whole species, genera, and families of plants, but in a few narrowly restricted forms closely related to normally sexual types.

Deterioration is slower with vegetative propagation and other similar processes of descent in individual lines than with less discriminate forms of narrow breeding, but all forms of restricted descent lead ultimately to infertility and degeneration. Line breeding is superior to narrow breeding, but not superior to broad breeding. The elaborate contrivances of plants to secure cross-pollination show at once how difficult and precarious are the processes of sexual reproduction, and at the same time how indispensable.

MUTUAL RELATIONS OF PRINCIPAL FACTORS.

Diversity and broad breeding are not merely causes of evolution, but are necessary to normal processes of descent among all higher types of organisms. Evolution not only results from diversity and interbreeding, but at the same time brings increased diversity and improved adaptations for still broader breeding.

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[a] Cook, O. F., and Swingle, W. T. Evolution of Cellular Structures. Bulletin 81, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1905.

The facts are concrete and their relations obvious. The members of each species are diverse (heterism). They freely interbreed among themselves (symbasis). They produce successive generations (descent). Later generations differ from the earlier (evolution). Without diversity, interbreeding has no significance, and descent is not accompanied by evolution. Heterism, symbasis, descent, and evolution form a continuous series, a complete chain of phenomena. For some purposes the four processes may be described as distinct, but physiologically they are mere phases or aspects of organic existence, each at once requiring and assisting the others.

Thus, the constitutions of species and the methods by which they are propagated show that they are in motion. We no longer seek to prove that species evolve; we see that they do and understand why they must continue to do so as long as they remain groups of normally diverse, broadly interbreeding organisms.

Diversity and interbreeding do not appear as causes of evolution in the same way that natural selection was supposed to be the cause. They are rather the general conditions or means of evolution. An actuating cause of evolution, in the narrow sense of an agency which takes hold of normally stationary species and changes their characters, it is not necessary to seek, since species do not tend to remain stationary in nature, nor do domesticated varieties continue constant even when breeders strive for uniformity.

The search for causes never ends. There is always something unknown behind the facts we are able to understand. The most that we can hope to do is to maintain the right direction in our inquiries. To have known that the causes are in the species and not in the environment would have saved many wanderings.

The only relations thus far established between evolution and environment are negative; the environment often hinders or limits evolution, but has not been found to cause any constructive change. On the other hand, normal diversity and free interbreeding have direct relations with evolution, for they represent essential conditions of the existence of species. Without them our species would not have the characters they now possess.

The true nature of evolution as a progressive change in the network of descent of a species, accomplished through diversity and interbreeding, was understood by Goethe a century ago. The statement of his evolutionary conclusions in metrical form may have caused them to be overlooked as scientific discoveries, but it is evident that he perceived the essential relations more clearly than the later writers who have ascribed evolution to environmental agencies or to restriction of descent. Goethe was an active investigator of natural phe-

nomena and represents himself as having studied and solved the problem of evolution, as shown in such passages as these:

Years ago it was a pleasure
Of the eager spirit's days,
Searching for the course and measure
Of creative Nature's ways.
Lo, a unity eternal
Stands in manifold revealed;
Large or small kinds, great or little,
Point one law in every field.
Always changing, yet enduring,
Far and near, by land or main,
Forming now, and now transforming—
Wondrous goal that I attain!

Radiant this truth has shown,
Vital more than any:
Nothing living lives alone,
Always there are many.

Behold we now the primal art,
The ancient Weaver-woman's part;
One tread uplifts a thousand lines
While back and forth the shuttles go,
And meeting strands together flow,
Each stroke a thousand unions twines;
Her web by no mere chance is made,
Forever has her warp been laid,
The Master-workman's one behoof
Content for aye to throw the woof.

EVOLUTION PROBLEM DISTINCT FROM DESCENT PROBLEM.

Many investigators have thought to reach the problem of evolution through the problem of descent. By learning how characters pass from one generation to another it was hoped to learn also how characters are changed during series of generations. The problem of descent was supposed to include the problem of evolution.

It now appears that evolution may throw light upon descent rather than descent upon evolution. Descent is carried on through individual organisms and conjugations of germ cells, but evolution is conducted through species. Until we recognize diversity and interbreeding as of physiological value, the elaborate complexities of descent by sexual reproduction appear wasteful and meaningless.

A species is a mutual physiological organization for the improvement of descent, instead of being a merely arbitrary assemblage of organisms fenced in by hostile environments and compelled to compete with each other in a struggle for existence. Adaptations for strengthening the network of descent by diversity and interbreeding exceed environmental adaptations in number and complexity. Adaptations for interbreeding are a permanent gain for the

species, while environmental adaptations may have only temporary advantage. The more perfect the adaptation to special conditions the smaller are the chances that the species can survive a change of environment.

Geology repeats in many different groups the lesson of the earlier extinction of the more specialized types and the preservation and continued progress of the less specialized, those able to maintain themselves under a wide range of conditions. The new types which appear to have arisen suddenly in remote geologic ages were already widely distributed. Instead of being confined to limited areas where interbreeding would be restricted, the species must have contained vast numbers of individuals, more than in the later times when these same groups become subdivided in their turn into many genera and species.

The higher we go in the scale of existence the greater is the need that we study cells and organisms in their social or collective relations. In the lower groups reproduction can be accomplished by simple splitting of single cells, but in the highest groups it requires the cooperation of two extremely complex organisms, each composed of millions of cells. In man and in many other social species, numerous individuals contribute to the nurture of the young, to bring them to fully developed maturity, and thus complete the process of descent. To maintain evolutionary progress a still wider cooperation is required, a huge assemblage of interbreeding individuals which constitutes a species.

Galton considered the system of double parentage as necessary to sustained efficiency of reproduction among the higher plants and animals, but this conception falls short of the full indications of evolutionary facts. Not merely double parentage, but a highly multiple ancestry is required to maintain a succession of complex organisms. The species rather than the individual is the true unit of organic existence and of evolutionary progress. Evolution may prove to be as essential a factor in descent as descent is in evolution. There is a general evolutionary physiology of species and varieties, as well as a special physiology of descent shown in the reproduction of individual organisms.

Cells may be thought of as containing mechanisms of descent, but species are mechanisms of evolution. The problem of evolution is much more accessible to our observation than the problem of descent, and comes first on the normal route of inquiry from the known to the unknown. Though closely allied, the two problems lie on different planes and can be studied separately. In bringing them into relation we should be careful not to bring them into confusion. We do not need to seek in the cells for the functions performed by the species.

To defer the recognition of evolutionary facts because our knowledge of descent remains incomplete would be much like refusing to walk or to practice manual arts until we should have a complete explanation of the mechanism of contraction in the cells of muscles, on which our bodily movements depend. It may be long before we can gain any complete understanding of the physiology of descent, of the activities and relations of cells in organisms, but this need not prevent our gaining knowledge of the physiology of evolution, the relations of lines of descent in species.

EVOLUTION INHERENT IN SPECIES.

A normally constituted species can carry forward changes of characters without environmental or selective causation. Under natural conditions of free interbreeding, new variations and combinations of characters are to be thought of as tending to spread and to transform the species or to accentuate the normal and desirable diversity of descent inside the species. The evolutionary development of a species is as spontaneous as the growth of the individual plants and animals of which the species is composed. External conditions influence the evolution of species, just as they influence the development of individual organisms, but both forms of growth are manifestations of life, not effects of inanimate surroundings.

Environmental utility influences the rapidity of extension and uniformity of expression of characters, but useless characters can also spread and serve the species physiologically by ministering to a healthful diversity of descent. The state of free interbreeding found in natural species is most favorable for evolutionary progress; no rare or exceptional conditions have to be imagined.

Evolution is analogous to history. The importance of events is determined by the conditions and the sequences in which they occur. Species are not carried along by their environments, nor compelled by internal clockworks to change at particular times or to go in definite directions. Nevertheless, the timely putting forth of a new character may have a profound influence upon the subsequent history of a species. Variation is genetic, for species tend to evolve, but it is not definitely directed or determined (orthogenetic). A character once formed tends to further development, and thus finds the range of greatest utility or of most harmonious combination.

Though evolution is often described as a doctrine of transformation, the earlier theories really taught only the selective substitution of one species or variety for another; they did not provide for the transformation of species. They represent evolution as possible only when descent is restricted by selection or other means of isolation, and require at every step highly improbable coincidences between varia-

tion and isolation. An advantageous new character, if not prepotent, would be preserved and extended only when opportunely separated from the unmodified type, but a prepotent variation, whether useful or not, can gradually pervade and transform the species. There is no need that it be isolated from the parental stock or that it wage a selective warfare of extermination against its nearest relatives.

CONCLUSIONS.

Relation of evolution to species.—The evolution of the higher types of plants and animals is an essentially complex process, not to be accomplished without the association of organisms in species and not to be understood without recognizing that the association of organisms into species has a concrete physiological significance. Evolution is change in species. Unless we learn how species are constituted we do not become acquainted with the results of evolution or with the conditions under which it takes place.

The constitution of species.—Species in a normal condition of evolutionary progress are large groups of diverse, freely interbreeding organisms. The joining of the lines of descent of each specific assemblage into a huge, continuous network provides for endless individual diversity by free combinations and substitutions among gradually changing characters. New characters must combine harmoniously with old characters and must spread through the network of descent of the species.

The method of evolution.—A comparison of the diversities found among members of the same species with the diversities of separate species shows that evolutionary changes in the characters of species are completely gradual and continuous. Species are found in nature in all stages of division and divergence. Evolution does not depend on occasional originations of new species, nor upon abrupt changes of characters in individual organisms, but it is shown in gradual changes of the characters of the organisms of which species are composed. Species may be differentiated without any new characters being added, or new characters may arise in a species though no subdivision takes place.

Causes of evolution.—The differentiation of species and the attainment of new characters and functions are results of evolution made possible by the facts that the members of species are normally diverse, and that there is free interbreeding in the networks of descent. Evolution is not caused by the struggle for existence, nor limited to characters of environmental fitness. Harmless and even harmful characters may be acquired by species in the same way as beneficial adaptations.

Expression of characters distinct from transmission.—The number of characters that organisms inherit from their ancestors and transmit to their descendants is much greater than can be brought to visible expression in any individual. Reversions show that characters may be transmitted in latent form for many generations and then suddenly reappear. On the other hand, characters long expressed with regularity may suddenly disappear, as often occurs in mutations. Many of the differences which have been used as examples of evolution represent mere substitutions and alternations among characters already evolved by the species, instead of evolutionary progress toward new characters.

Influence of external conditions on expression of characters.—The conditions of existence often influence the expression of characters in individual organisms, calling some characters into expression and leaving others latent. In different environments the same species, or even the same individual organism, may put forth different characters.

By varying expressions of their characters, organisms are able to adjust themselves to wider ranges of environmental conditions, but this versatility does not indicate that the environment is responsible for the formation of new characters or for the evolutionary progress of species. Doctrines of environmental causation of evolution tend to deceive us with the false hope of making over inferior breeds by environmental manipulation, instead of leading us to appreciate the primary importance of normal descent.

Influence of selection on expression of characters.—Changes induced by the narrow artificial selection of domesticated plants and animals are not true examples or equivalents of natural evolution. The removal from a group of all the individuals which show a certain character tends to suppress this character. The selective suppression of characters renders the members of a group more uniform, but it does not make new characters. Selection works by eliminating differences; evolution comes by introducing them. Selection is an analytic process, while evolution is synthetic. Evolution can be guided through selection, but the guidance must not be too narrow or conditions essential to the continued existence of organisms are destroyed. The teaching that evolution is caused by the selective action of the environment and hindered by interbreeding among the members of the species reverses the facts of nature. The environment permits some changes and forbids others, and can thus limit the directions in which the changes proceed, but the changes are put forth by the species, instead of being actuated by the environment.

Status of domesticated varieties.—Uniform domesticated varieties are small groups in which the normal diversity has been suppressed by selection. The greater uniformity is secured at the expense of normal

diversity and free interbreeding, the primary conditions of constructive natural evolution.

The idea that uniformity is to be sought for its own sake or that "pure-bred" uniform types are essentially superior to those showing greater individual diversity finds no warrant in the general facts of evolution. It is misleading and dangerous to advise that all domesticated types of plants be made uniform by breeding from single individuals. To the extent that it is necessary to obtain uniform commerical products, restriction of descent to individual lines may be justified, but not on the ground that it represents a normal or truly evolutionary condition.

Evolution must continue to furnish the materials for breeding. It is vain to expect that the work of breeding in any economic group can be finished by securing narrow strains, however superior. Narrowly selected breeds must continue in the future, as in the past, to follow in a gradual succession, the older and weaker being discarded for the newer and more vigorous, more recently derived from broadly interbreeding stocks.

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