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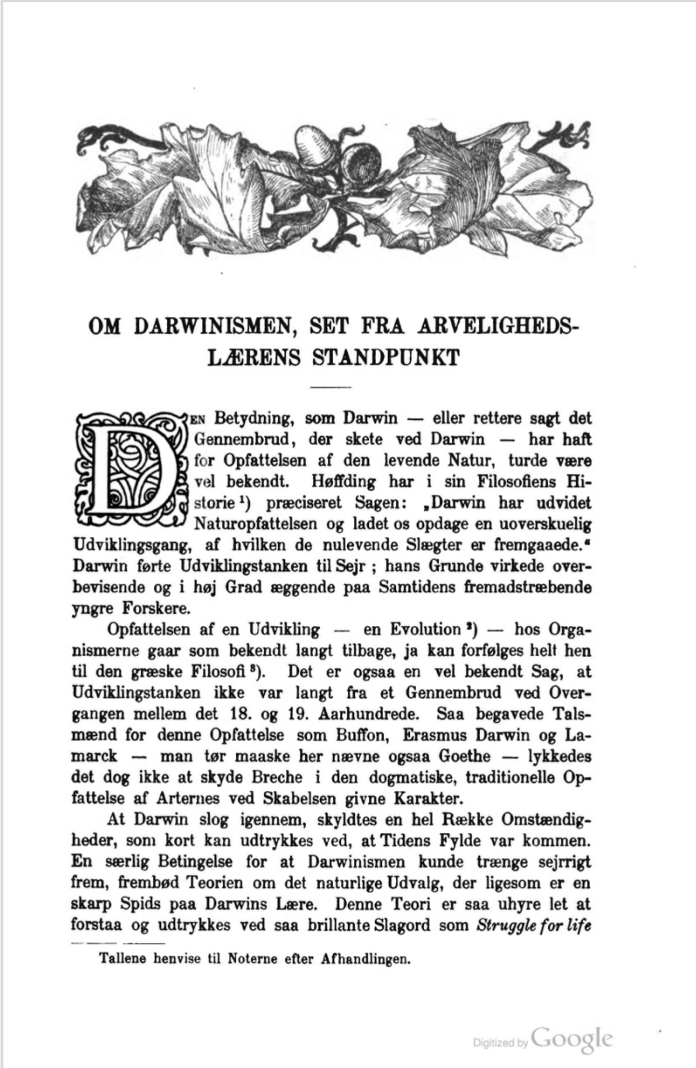
UDGIVET AF
VALD. VEDEL

1903

KØBENHAVN
DET NORDISKE FORLAG
ERNST BOJESEN


OM DARWINISMEN, SET FRA ARVELIGHEDS-LÆRENS STANDPUNKT

DEN Betydning, som Darwin — eller rettere sagt det Gennembrud, der skete ved Darwin — har haft for Opfattelsen af den levende Natur, turde være vel bekendt. Høffding har i sin Filosofiens Historie [1]) præciseret Sagen: „Darwin har udvidet Naturopfattelsen og ladet os opdage en uoverskuelig Udviklingsgang, af hvilken de nulevende Slægter er fremgaaede." Darwin førte Udviklingstanken til Sejr; hans Grunde virkede overbevisende og i høj Grad æggende paa Samtidens fremadstræbende yngre Forskere.

Opfattelsen af en Udvikling — en Evolution [2]) — hos Organismerne gaar som bekendt langt tilbage, ja kan forfølges helt hen til den græske Filosofi [3]). Det er ogsaa en vel bekendt Sag, at Udviklingstanken ikke var langt fra et Gennembrud ved Overgangen mellem det 18. og 19. Aarhundrede. Saa begavede Talsmænd for denne Opfattelse som Buffon, Erasmus Darwin og Lamarck — man tør maaske her nævne ogsaa Goethe — lykkedes det dog ikke at skyde Breche i den dogmatiske, traditionelle Opfattelse af Arternes ved Skabelsen givne Karakter.

At Darwin slog igennem, skyldtes en hel Række Omstændigheder, som kort kan udtrykkes ved, at Tidens Fylde var kommen. En særlig Betingelse for at Darwinismen kunde trænge sejrrigt frem, frembød Teorien om det naturlige Udvalg, der ligesom er en skarp Spids paa Darwins Lære. Denne Teori er saa uhyre let at forstaa og udtrykkes ved saa brillante Slagord som *Struggle for life*

Tallene henvise til Noterne efter Afhandlingen.

Translation by Nils Roll-Hansen: Wilhelm Johannsen, "About Darwinism, seen from the point of view of the science of heredity."

The impact of Darwin — or more correctly the break-through that he made — on our conception of living nature, should be well known. Høffding made it clear in his History of Philosophy[i]: "Darwin has expanded our understanding of nature letting us discover a boundless process of progressive change from which present living beings emerged." Darwin led the idea of evolution to victory; his arguments were convincing and highly stimulating for contemporary young and ambitious researchers.

It is well known that the idea of a development — an 'evolution'[ii] — of organisms goes far back, indeed it can be traced all the way to Greek philosophy.[iii] It is also well known that the idea of evolution was not far from a break-through at the turn of the 18th to the 19th century. But even such gifted spokesmen as Buffon, Erasmus Darwin and Lamarck — one may here perhaps also mention Goethe, — did not succeed in making a breach in the dogmatic, traditional view of the character of species as given at Creation.

That Darwin made the break-through was due to a large number of circumstances, which can be expressed briefly by saying that the time was ripe. A particularly important condition for the success of Darwinism was the theory of natural selection, which appears as a spearhead of Darwin's teaching. This theory is so extremely easy to understand and is expressed by such brilliant slogans as *Struggle for life*, *Survival of the fittest*, and *Natural selection* that it had not only to fill young students of nature with enthusiasm, but also penetrated broader circles to become popular or to stimulate the most ardent opposition. After Darwin the idea of evolution could not be held back; it broke all barriers.

All living beings are different, even the progeny of one and the same individual differ among themselves. And individuals belonging to one and the same species will of course not be alike, but diverge more or less in all sorts of directions. Since within each species there are born more individuals than for which there is room, a struggle for life arises, in which the competition is often very severe. The result is that the fittest, i.e., those who are best equipped for the life under the given circumstances survive.[iv] And because the properties of individuals are, to a smaller or larger degree, inherited by the progeny, natural selection can gradually bring about a displacement in the whole character of a given species. When the species spreads over areas with quite different living conditions, individuals of a certain character will best endure the struggle for existence in one place, while individuals of a different character will be better able to compete in another place, with a different set of conditions. With such selection in different places under different conditions the species could then gradually change its form or divide into new forms that little by little become so divergent that they have to be seen as different species. And when intermediate forms die out such differences will appear more and more prominent. In the course of time geographical changes leading to isolation of the emerging new forms, which are thereby prevented from hybridization among themselves or with the original stock, can be conceived to play a role in this, as can climatic changes, locally or globally for the Earth as a whole, for instance the gradual slowly proceeding cooling. Having recourse to the assistance of millions of years even large differences between organisms could be explained by successive evolution.

All of this was easy to understand. To understand this theory, in the way that it was sketched by certain German authors[1] for popular use — one might even say for the purpose of agitation, — was as easy as falling off a log. The spokespersons of this simplified Darwinism belong to, or belonged to - since most of them have now died out — the kind of thinkers who, as Brandes[2] says,[v] appear clear and penetrating because they see no difficulties.

Darwin himself indeed saw the difficulties in this matter, as is beautifully witnessed by his letters. In the course of time, in each new edition of his works, he distanced himself more and more from selection as the only or most essential main factor in the origin of species, and he approached more and more strongly to the Lamarckian view that living conditions can quite directly make an impression upon organisms and thus *also* without selection give rise to new forms, new species.

In any case, one thing is certain — that evolution has taken place and is still ongoing: new forms arise and others disappear. There is no more discussion about this point, just like there is longer any strife about the Earth being round and moving around the Sun.

Darwinism in the widest sense, the theory of evolution or descent, whatever one wants to call it, is beyond doubt in in contemporary science.[vi] This view has overwhelming support in *the unshakeable evidence of fossils* for stepwise progress in level of organization, in the striking results of *comparative anatomy*, in the facts of *animal- and plant-geography*, in the development of individual organisms themselves, and so forth; and last but not least, in the gradual accumulation of not a few cases, *where new forms have been seen to appear*.

In contemporary natural science the principle of descent is seen as unassailable or in any case indispensable. That occasionally unscientific authors or a single converted scientist, like Prof. Fleischmann[vii] at the University in Erlangen, try to overthrow this principle, make no impact and is therefore quite inconsequential. Indeed, even if one clings to the view that the idea of evolution is grounded in a false understanding of the world — like the doctrine of phlogiston in 18th century chemistry, — the principle of descent still gives

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[1] Johannsen probably had in mind Ernst Haeckel, among others.

[2] Georg Brandes (1842–1927), was an influential Danish literary critic and scholar, a spokesman for naturalism and the ‘Modern Breakthrough’.

impulse to so much research, with results which again and again fall in line with the principle, that its value as a guiding star of present biological sciences raises it to a position in which it is unassailable.

But a high degree of doubt and conflict is certainly encountered, as soon as one wants to know *how* the evolution through time is thought to have happened, and still is proceeding. Although there is agreement about the general principles, there is multicolored plurality of opinions on the specifics of how this occurs. At present there is agreement that the first priority is to understand the origin of the narrowest systematic groups. There are strong reservations towards speculations which aim to explain kinship of more distant groups. No one doubts that there can be common descent or transition for instance between reptiles and birds — in that respect the testimony of fossils appears all too striking. But such connections can be properly studied only by the 'historical' method. Only those changes that do not demand too many generations can be the object of exact investigation by methods of experiment and observation. From the standpoint of the science of heredity only the latter can be considered.

The species set up by Linnaeus and kindred thinkers were in general quite broad, and later naturalists have tended to divide these 'big' species into quite a number of subspecies and varieties. When they turned out to be characteristic and constant in appearance (with respect to plants we say 'true to seed') they were often raised to the status of valid species. Whether one is concerned with such narrowly limited 'small species' or with varieties, these groups are in any case the very narrowest classes in natural historians' systematization of the animal and vegetable kingdoms. It is the origin of such classes or systematic units that is presently being diligently studied.[viii] Before the results of many steps over long periods can at all be understood, the small steps have to be understood.

With respect to this question four main hypotheses, or, if one prefers, "theories," are presently on the agenda. They can be designated as follows: 1) The modification theory, 2) The mutation theory, 3) The theory of successive selection, and 4) The hybridization theory. Quite likely, more theories than these four ought to be mentioned — I can remind you of Nägeli's idea that organisms contain so to speak a characteristic 'drive' in the direction of increasingly higher development. Such an assumption, however, does not provide any understanding. And in any case, the literature on these matters is so extensive that it is impossible to work through unless one is willing to dedicate a lifetime to the task. The four major theories, or to be more precise, main factors in the explanation of evolution, are in no way mutually exclusive. But opinions are highly divided on their relative importance.

The theory of modification or neo-Lamarckism,[ix] maintains that living conditions — quite apart from any selection, — directly transform organisms, in such a way that, at least over the course of many generations, their inheritance is permanently modified by their environment, and to a higher or lesser degree adapted to it. The imprint gained in this way lasts at least through some generations, and also under living conditions that are different from the ones that produced them — until new conditions bring their own influence to bear. In the theory of modification, the *question of inheritance of acquired characters* plays quite an essential role. Here there are big controversies, and we are at a point where the science of heredity ought to be able to clarify the difficulties. That living conditions shape the characters of developing individuals in a more or less clear way is certain enough — but are such characters at all hereditary?

This question is of theoretical as well as practical interest. However, there is no room here for deeper scrutiny. [x] Let it simply be said that there are some influences which may often give character to the individual in high degree, and yet have no influence on the progeny, while other influences undeniably have hereditary effects. The latter is apparently the case for instance with very high or low temperatures that totally penetrate the form and structure of the organism. Just to mention some investigations from recent years, Prof. E. Chr. Hansen[3] was able to change certain properties of yeast cultures permanently by first keeping them at a high temperature for several generations. In this case however, it is only a capability that is lost — the capability to form spores — under the influence of high temperature. A new positive character has not been achieved. Similarly, from the investigations by the German zoologist Fischer into the effect of heat and cold on butterfly chrysalises it appears that the special properties of color and pattern that are caused by extreme temperature during the chrysalis stage, are sometimes inherited by the progeny, even if they are raised in a quite normal way. But first the question of how long such an influence lasts needs to be investigated. In the publication mentioned in Note ix), Wettstein has assembled other experiments and observations that more or less clearly agree with such a connection. In contrast, there are other areas in which no trace of heredity is to be found, even if the original individual was very strongly affected

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[3] Emil Chr. Hansen (1842–1909) was a Danish plant physiologist (mycologist) working at the Carlsberg laboratories where Johannsen was his assistant for a number of years. Hansen is famous for a method of ‘pure culture’ of yeast. The method built on isolating single cells of yeast as the starting point for ‘pure’ strains, and was of great importance for stable production quality in the brewing industry.

by its special living conditions. This is quite strikingly apparent in cases with effects due to abundant or sparse nourishment or to feeding methods of a particular nature. However, most practical men appear here to side with heredity. Nevertheless, the claim that the effect of feeding is highly hereditary, provided only that the progeny is fed the same diet, leaves a curious impression! This kind of heredity is not genuine. Similarly when considering the influence of exercise, for instance in race-horses — it is obvious that exercise develops the *individual* -the exercise is a necessary condition, a school to go through — but progress in breeding results nevertheless from the choice to breed from those animals that turned out to be best in training, and not from , an hereditary influence of the exercise, as maintained by the American Neo-Lamarckian zoologist Cope, who stands quite alone among scientists though many practical men agree with him. The so-called land-races of domestic animals and cultivated plants may often express modification by living conditions, but then the individuals of the land-race receive on average just 'the same diet' in the most inclusive meaning of the word. With respect to plants there are thus complaints that such races change under new conditions. It can at least be seen that *in these cases it is definitely not a pure relation of inheritance that appears*. To make such a claim, extensive new investigations would be needed. For the time being one must in each particular case try to answer the question of whether it is heredity or the influence of living conditions on the individual, or both in combination, that has determined the character of a given organism.

The theory of a 'sensitive period' in the life of the individual, proposed by Hugo de Vries is very interesting in this connection, especially with respect to plants Only during this period, usually thought of as belonging to the very earliest stages of life, can external conditions exert influence on the character of the individual, at least with respect to some properties. It is at present not possible to say to what extent this theory has general validity. What is beyond dispute however is that it contains an important and true core. Further studies can surely clarify these concepts much further.

It is to be expected that the theory of modification will be subjected to successively better testing through experimental studies of heredity, but much time and patience will be needed to illuminate what the relationships are in nature. A straight rejection of the theory of modification is not in question; in this respect a number of researchers, like Weismann and others, have been far too extreme.

The mutation theory assumes a sudden, intermittent appearance of new types, new 'small species' if you will. These new types naturally do not differ as much from their origin as distant species do, but the differences are nevertheless distinct enough not to be overlooked. This I tell you: that mutations — i.e., the sudden appearance of new types — occur is in my experience completely beyond doubt. This has often been maintained at various times and by various researchers. Through extensive investigations the eminent Dutch botanist Hugo de Vries has recorded such stepwise changes especially in the genus of evening primrose. Within the 'big' species *Oenothera lamarckiana*, a pretty yellow flowered plant, that is a native of South America, but now quite widespread in Europe, de Vries has demonstrated the sudden appearance of new forms, new 'small species', first in the wild and then in long series of cultivation. These are immediately constant, i.e., true to seed, though of course they show the variations common to all living beings, which in this connection is not important. Other researchers as well have observed similar stepwise appearance of new types which do not naturally differ much from the original type. Hugo de Vries in a large and exceedingly important work[xi] has explained in detail his own investigations and given a fascinating survey of the experiences of other researchers in the field. De Vries' view of the role of natural selection is as follows: If they cannot cope in the given conditions, all such newly arisen *types* will of course perish. In this way natural selection decides whether such a 'small' new species endures or not; but the selection of different individuals within the same species does *not* lead to successive formation of new types.

In a small pamphlet[xii], that records a lecture at the Congress of German Natural Scientists and Medical Doctors in Hamburg in 1901, de Vries briefly explains his view of the role of mutations with respect to evolution over time. I have to restrict myself to one reference and simply point out that de Vries assumes special periods in the history of a given species where mutations are particularly numerous and many-sided, periods when the species is so to speak out of balance. In other periods there is more stability in this species — but then other species may be in a period of mutation. Here we touch on a quite hypothetical point in the theory of mutation where proofs are hard to come by. What the occurrence of fossils, in themselves fully compatible with mutation theory, can tell us was discussed by the paleontologist Prof. Koken at that same congress of naturalists.[xiii] We cannot, however, go into this matter here.

The attitude of the science of heredity to the mutation theory is still in no way settled. The crucial question is whether there is any reason at all to put forward the concept of mutation as being something different from ordinary individual variation. The mathematically or statistically working English biologists, 'the Biometricians' (so named from their journal *Biometrika* that started appearing last year), led by the mathematician Pearson and the zoologist Weldon, deny the legitimacy of the concept of mutation, and therefore also hold that natural selection in combination with ordinary variability is sufficient to explain the change of types through time.

I believe, however, that these researchers have quite a mistaken view of the matter. Firstly, there are stepwise changes. Darwin himself recognizes them under the name of singular variations, and the English zoologist Bateson, who is sharply opposed to and involved in quite a bitter controversy with his two aforementioned countrymen, had already in 1894 surveyed a large number of cases that can only be explained — in a very far-fetched way, if at all — as examples of especially large individual variations. And secondly, it can be proven that the manifestations of ordinary variability are not heritable to the extent or in the way that has so far been assumed.

We have now come to *the theory of successive selection*. This is the theory called Darwinism in the narrowest sense; the theory that Darwin's famous contemporaries, the still living A.R. Wallace as well as the German zoologist Weismann, promote with enthusiasm. As we have seen, it is here that the English Biometricians also most closely belong. The theory of successive selection takes its point of departure in the familiar common variability and holds that through selection of certain deviating individuals, which are thus given permission to procreate, the type of the species concerned will be displaced in the direction of the deviation in question.[xiv]

We will leave to one side the rather loose speculations that especially Weismann and his school has produced in these matters. In particular this applies to his considerations of how large an individual variation must be in order for it to be of importance in natural selection.

If the science of heredity is to investigate these matters — as it should — then it must be according to Galileo's principle: Measure all that can be measured, and make that measurable which is not![xv] This is precisely where the Biometricians have great merits. Through anthropology and statistics, especially through the epoch-making works of Quetelet and Galton,[xvi] methods for measurement and exact evaluation of the results of measurement have been developed for use in research on heredity. And the Biometricians have understood to a high degree how to apply and improve such measurements.

It was in applying statistical methods to the English population that Galton found his so-called law of regression. As Galton found out, parents that deviate from the mean typical property, for instance in height, will have children which — as adults — on the whole deviate *in the same direction* as the parents, but to a lesser degree. Parents that deviate 3 inches from the mean height of the population, produce children that on average deviate 2 inches in the same direction. The deviation of the children is thus 2/3 of the parents. Children of deviating parents approach, when seen as a whole, toward the general character of the population; they ‘regress’ towards this character. And quite the same relation — somewhat different numerically — appeared in cultivation experiments with seed, in investigations of colors in basset hounds, and the properties of race-horses. This law of regression thus apparently expresses a general rule of inheritance within each particular species or race.

What interests us here is the following: these investigations *appear* to prove that ordinary variations around the mean character of a race are in fact hereditary to a certain degree. This appears quite clearly in the statistics, and Pearson has even shown more precisely how, using mathematics, it can be calculated how much time — that is, how many generations — it will take for continued selection of individuals that deviate the most to displace and fix the character of the race in the direction in question, that is, in such a way that selection little by little forms a new type. When a mathematician does a thing like that one all too easily takes the truth of the matter to be ‘mathematically proven’, especially when it is difficult to follow the course of the calculation. The great importance that the Biometricians attribute to the Galtonian results, is clearly expressed in Pearson’s statement[xvii]: “If Darwinism (meaning Darwinism in the narrowest sense) is the correct view of evolution, that is, if we are to think that evolution takes place through natural selection in cooperation with inheritance, then the law that clearly and distinctly expresses the character of the offspring as a function of the characteristics of earlier generations, is at the same time the foundation stone of biology and the basis upon which the study of heredity becomes an exact science”. There is nothing objectionable in the wording of this claim. I will not dispute the correctness of the view that the Galton-Pearson laws of inheritance that have been developed on the basis of the above-mentioned investigations, can express important relationships within various populations of species of organisms. And in particular these laws are likely to be relevant with respect to the evaluation of average relations of inheritance in humans, in calculations with a practical aim, and the like.

It is nevertheless easy to understand that a truly fundamental study of hereditary relationships can by no means feel satisfied by such statistical information. This is because a population or a species, a race, or however one wants to express it, is in no way always a unit. It can be a mixture of different types. Accordingly, such a population has to be *biologically analyzed* before a statistics of heredity is built — if this statistics is to say anything that is at all *certain* about hereditary relationships, and not merely produce in each case probability rules of quite limited significance.

Such analysis is cumbersome but absolutely necessary if clarity is the aim. The principle of such analysis is due to the French gardener-scholar Louis Vilmorin. He held strictly that *the offspring of every individual is to be evaluated separately*. This principle: Vilmorin's "principle of individual assessment of offspring" has been quite neglected in the science of heredity, until it was taken up again, especially by Scandinavian researchers.[4]

In a population where the choice of spouse is free or at least more or less by chance — such as in human societies,[5] — or even when mating is quite promiscuous, as in many animals and in plants with crosspollination by the help of wind or insects, this kind of analysis will be impossible. And even in the case of domestic animals there are large difficulties to be overcome, which I will not go into here.

But in plants that exhibit self-fertilization, like peas, barley, many forms of beans, etc., or which develop their seed without any fertilization at all, like dandelion, lady's mantle and others[xviii] — and where variation — the difference between individuals of the same descent — can nevertheless be as great as in other plants and in the animals — in such plants one can work with what I will call *pure lines*. That is: individuals descending from one single plant of origin. Here one is not involved with two different parents of different origin, and here one does not have an increasing number of ancestors for each earlier generation — 4 grand-, 8 great grand-, 16 great great grand-, 32 great great great grand-parents, and so on. Who can know something about the characters of *all* these ancestors? In pure lines there is only one downward branch. A population, which in this case is a continuous and homogeneous growth of absolute self-fertilizers, will then consist exclusively of 'pure lines', which to be sure are mixed but not cross-pollinated. And it appears to me that the relationships of pure lines must be the proper basis for the science of heredity, even if in most populations — above all in human populations — one does not deal with pure lines at all.

For a number of years, I have now been working with pure lines of beans, barley, and peas. And with different races of all of these cultivated plants. The characters in which I have attempted to study heredity with the support of loyal

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[4] Johannsen is referring to the work at Svalöv.

[5] Johannsen uses the term 'Samfund' not only for humans but also for plants and animals. For the latter I have translated 'Samfund' with 'populations'.

co-workers are quite diverse, but above all they can be expressed in numbers: size, relations of form, variability, chemical composition, sterility (abortive fertilizations in barley spikes), etc. — all of these are characters that are quite compatible with Galton's objects of investigation. And the result of all these investigations can briefly be specified as follows:

Within the pure lines, variability is not much smaller than within the races in question or populations as a whole. But if one selects individuals that deviate from the typical mean character of 'the line', the progeny of these individuals will on average *regress completely to the type of the line*. In other words, the individual variations are *not* heritable. Or at least so says *all my material!*

This is surely the sharpest contradiction to the claims of Galton and Pearson, and thus also to the Darwinian view that a successive shift in the type of a race can take place due to selection.

"If sometimes one answer barks against the other, then make sure they are answers to the same question," sang Richardt at the celebration of the fourth centennial of our University. [6] It now turns out that my material can be organized in such a way that it totally confirms Galton's law. Indeed, with respect to certain characters, which both Galton and I have studied (heritability of the weight of seed in self-fertilizers), my numbers illustrate Galton's laws more beautifully than his own numbers. If one adds together my 'pure lines', so that, just like Galton, I work with the population as a whole, that is, with all plants at my disposal, this is the result. Thus Galton's law is also valid for my populations. There is no barking of one answer against the other!

The population (in self-fertilizers) consists of pure lines, which each has its own type, though many lines can be quite alike. For example: Within the familiar brown trailing Princess bean there are lines with narrow seed, others with broad seed, and still others with medium breadth, that is: a breadth that corresponds to the medium breadth of the whole population concerned. For convenience we can call these lines respectively *narrow, medium* and *broad* lines. It should be kept in mind, though, that in all cases there is a great variability present. This means, for instance, that the individual seed from 'narrow' lines vary from very narrow to a little more than medium breadth, and the seed from 'broad' lines vary from less than medium to very broad, while 'medium' lines vary from quite narrow to rather broad. It is then quite easy to understand that when one simply selects narrow seed in a population these can

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[6] Christian Richardt (1831–1892) was a Danish priest and poet.

be of highly different descent. Some will of course belong to narrow lines, but a substantial fraction will belong to medium lines, and finally a few narrow seed may well belong to rather broad lines — namely individuals that deviate sharply from the type of the line! In my material all of this is exemplified.[xix]

This explains the result. The progeny of such a mixture of individually similar seed will — with respect to their heredity — be determined by the *character of the lines to which the individuals belong*. The 'personally' similar seed were in fact not of the same kind. They belonged to highly different types.[xx] And due to the large number of medium lines the progeny of all these seed *considered as a whole* approach the average of the total population: this means that Galton's law is explained in a most natural way.

Galton's law thus implies that by selecting individuals with a certain deviant property one obtains an *incomplete sorting of the pure lines*. One easily understands that with each new generation this sorting by selection will progress. On this depends the successive effect of selection. In fact, through such selection one will only obtain more or less imperfectly isolated *types which are already present*. In this way we can also understand the claim of de Vries, which he supports by a critical evaluation of the experiences of practical men, that selection for a particular property will, through a small number of generations, approach the limit of what can be achieved — namely a practically perfect isolation of lines with the same constitution.

But what is the origin of differences between these lines, all these types within one population, a growth of one pure race? That these types exist is certain. This appears not only in my investigations but generally in all refined botanical research. Thus Prof. Hjalmar Nilsson[7] at Svalöf has found, within the races of quite different agricultural plants, numerous types that can be more or less easily characterized. And Raunkiær[8] in his recently published natural history of the dandelion [xxi] has identified what he calls special lineages inside the

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[7] Hjalmar Nilsson (1856–1925) was a Swedish botanist who successfully reformed the breeding work at Svaløv by introducing classification by morphological taxonomic criteria and individual selection as a crucial step.

[8] Christen C. Raunkiær (1860–1938) was a Danish botanist known for his studies of apomixes in flowering plants. He also was a pioneer in plant ecology, known for Raunkiær's system of plant life forms as strategies to survive unfavorable seasons. Raunkiær succeeded Eugenius Warming as Professor of Botany at the University of Copenhagen.

narrowly defined species that he is studying. In a way, these lineages correspond to my ‘pure lines’ — there is nevertheless the difference that the character of my ‘lines’ is determined through exact measurement of properties expressed in numbers. Perhaps it may not yet be possible to describe the differences between the Raunkiær’s lineages with precision — but this does not mean it is less essential and real. In fact, the immediate observer will find it easier to distinguish these lineages than my ‘lines’.

So far, I see no alternative than to assume mutations here, that is, an intermittent formation of new types, as the cause of the differences between the pure lines. This is no ‘explanation’ — no more than the hypothesis that larger mutations produce new types of species provides any explanation. But the smooth, *continuous* transitions that Darwinism has been so fond of playing with, can hardly have the significance that has been attributed to them. Nature makes jumps, small and large, but jumps nevertheless. The new types thus have their origin in *discontinuous* variation. I hope also through my own investigations eventually to be able to reveal this matter more accurately.

This is how the matter stands in populations of pure lines. In this case then the theory of successive selection obviously does not fit. The important support implied by Galton’s laws of heredity, completely disappears if the results of my investigations are correct and if they apply to more than the special cases. And of this I am assured. I have already found numerous cases in the literature that can be explained most easily by applying my views, and I anticipate with confidence the outcome of the discussion that can be expected to arise concerning my work.

What then about populations without pure lines — where the lines are unceasingly crossed in mating? Indeed, will the law of the pure lines, that is the law of complete regression, also not be valid here, combined with the laws of hybridization? I will not try to pursue this thought here; that is not my present task; but I repeat, the facts and relationships of pure lines is the basis of all studies of these questions. Here Goethe’s well-known words apply: “Dich im Unendlichen zu finden, musst unterscheiden und dann verbinden.”[9] I do not dare to venture much further forward than ‘Unterscheiden’ — with respect to my pure lines.

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[9] Translator’s translation from the German: “To find your way in the infinite, you must first distinguish and then unite”.

Finally, in so far as the hybridization-theory is concerned, one will find the matter treated very thoroughly in the great work of de Vries (Note xi). The properties of hybrids and their often very great variability is presently being studied from many angles, and certain general laws are about to crystallize out of the nearly chaotic abundance of single experiences. It would lead too far astray to go into these matters. It is sufficient to emphasize that, at least in plants beyond doubt, new forms that are at least as true to seed as pure species, can come into existence through crossing of various closely related but nevertheless well separated species. How often this happens or has happened in nature is a question to which I am unable to contribute a solution. But hybridization is not necessary for the formation of new types. After all, different closely related types must be present before hybrids are possible at all!

Among the four main theories of evolution there are accordingly two that appear to deserve most confidence from the viewpoint of the science of heredity.

First and foremost is the mutation theory, which on closer scrutiny is so closely related to the theory of hybridization that they can be united into one — the theory of *intermittent*[10] *change in types*. The steps of change can be quite small, and for that matter approach continuity.

And secondly there is the *theory of modification*, which in recent years has been attracting ever more new followers, though its real importance needs closer testing.

The situation is quite different for the theory about the importance of small individual chance deviations in the struggle for existence and the supposedly successive formation of new types through natural selection of the fittest individuals. This theory, which presumably has been the worst thorn in their side for the enemies of the idea of evolution, namely because it aims to explain all purposiveness in living organisms[xxii] from chance variation and natural selection, is steadily losing ground; partly due to the rise of the mutation theory, partly due to the direct experimental critique of its positive foundation — the assumption the common individual variations are heritable — a foundation that on closer scrutiny hardly exists

As yet it is far from the last word having been said on all these questions. Here it is essentially just one aspect of the great problem of evolution that has

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[10] In other places I have used ‘stepwise’ as the translation of Johannsen’s term ‘stødvis’.

been touched on, namely how the science of evolution relates to the science of heredity. But this relation is particularly important, and there is still so much disagreement and lack of clarity on this point, that an attempt, such as the one I have made here, to provide an overview of the matter with some references to relevant literature, will hopefully not be felt to be superfluous. In any case the two areas of research that have here been juxtaposed — on the one side the question of the historical development of the living world through time, and on the other side the concentrated and exact study of relations between the character of parent and progeny — the question of heredity — may for a long time to come claim the greatest interest of biologists.

W. Johannsen

i Høffding: *Den nyere Filosofis Historie,* [11] Vol. II. 1895, p. 399ff.

ii In Danish 'udvikling" designates both the 'udvikling' of the individual, which in English would correspond with 'development', and the 'udvikling' of the whole world of living organisms — which in English would correspond with 'evolution'.

iii A very well written account of the history of the idea of evolution is given by Osborn in his book *From the Greeks to Darwin*, New York 1894.

iv In recent years it has been maintained from different quarters that this is not at all the case for human society in civilized countries. I will not discuss this topic, but refer to the very interesting article by Karl Pearson, "Socialism and natural selection" in *Fortnightly Review*, July 1894.

v G. Brandes about Ludwig Büchner in *Politiken*[12] of 16 May 1899. This interesting article is not included in his collected works.

vi A short, very popular, vividly written, illustrated presentation of the main points and most important theories in contemporary science about the descent of living beings is given by Hesse: *Abstammungslehre und Darwinismus*. Leipzig 1902. This book of 123 pages is quite inexpensive.

vii Fleischmann: *Die Descendenztheorie*. Leipzig 1901.

viii The many different forms of blackberry, which Linnaeus considered to be a single species (*Rubus fruticosus*), likewise forms of hawkweed, and the subspecies of certain species of butterflies, etc. can all be mentioned as examples of such 'small species'. Nearly all the species of the old naturalists consist of different 'small' species whether few or many in number.

ix The name is due to extensive similarity to the views of Lamarck, and brings again some honour to his much too unjustly treated memory. This theory finds support particularly amongst botanists. A short account of the theory of

[11] Harald Høffding's book was translated into English, from German, as *The History of Modern Philosophy*, 1900.

[12] *Politiken* is still a major Danish daily newspaper.

modification is given by Wettstein: *Der Neo-Lamarckismus und seine Beziehung zur Lamarckismus*, Jena (a piece of 30 pages).

x In my small publication, "Arvelighed and Variability" (*Studentersamfundets Smaaskrifter*), 1896, I have sought to throw light on questions relating to this topic.

xi H. de Vries: *Die Mutationstheorie*. 2 Vol. Leipzig 1900–1903.

xii De Vries: *Die Mutationen und die Mutationsperioden*, etc. Leipzig 1901 (64 pages).

xiii Koken, *Palæontologie und Descendenzlehre*. Jena 1902. (33pages). The paleontologists use 'mutation' somewhat differently from de Vries.

xiv The view is represented, for instance by Professor Ziegler in Jena. His lecture in Hamburg in 1901, "Ueber den derzeitigen Stand der Descendenzlehre in der Zoologie", also printed as a separate pamphlet (Jena 1902, 54 pages).

xv Høffding: "Filosofiske Problemer". *Universitetsprogram*[13], November 1902, p. 39.

xvi In this respect "Galton: Natural inheritance 1889", is a watershed in the history of the study of heredity, as it was only after the appearance of this work that measurement technique and theory penetrated the part of biology that we are interested in here.

xvii Pearson: *Grammar of Science*. 2. edit., London 1900, p. 479.

xviii Examples of the egg being able to develop without any fertilization have long been known. Thus, for instance, in certain generations of aphids, and it is well known that eggs of the queen bee which are not fertilized develop into drones. In higher plants such true virgin birth (parthenogenesis) has only been demonstrated relatively recently. Probably more cases will gradually be discovered.

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[13] "Universitetsprogram" was a series of annual lectures published as pamphlets by the University of Copenhagen.

[xix] A more detailed account of my investigations is found in the monograph "Om Arvelighed i Samfund og rene Linier" [14] (*Oversigt over d. kgl. d.Videnskabernes Selskabs forhandlinger*, 1903, 3. Hæfte, S. 235).

[xx] This is in general the case. Two individuals that are similar with respect to a given character can have a very different value as progenitors, for instance as breeding animals.

[xxi] C. Raunkiær: "Kimdannelse uden befrugtning hos Mælkebøtte". [15] *Botanisk Tidsskrift*, vol. 25 (1903), issue nr. 2.

[xxii] About the much discussed, but quite indisputable purposiveness in the general behavior of organisms, I do not wish to say anything more here. Only this, that the purposiveness, which — though only to some degree! — is found in the activity of every organism, is obviously given by the very nature of organisms as '*systems in dynamic equilibrium'* (cp. the brief and clear account of the so-called Chatellier's principle in the excellent little book *Kemiens Grundbegreber* by S.M. Jørgensen, 1902, p. 167). In this respect there is hardly any real essential difference, in spite of very large differences in degree, between organisms and other chemical-physical systems (we are not here talking about the very first origin). The aim of biological science is neither to pose nor to explain any particular principle of purposiveness, but to study the special conditions of equilibrium that are realized in the organism and determine or at least are involved in the striking regulations and adaptations to living conditions that we incessantly encounter in living nature.

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[14] This is Johannsen's famous 1903 monograph on "On heredity in populations and pure lines" first published in *Transactions of the Royal Danish Society of Sciences and letters sciences,* 1903, part 3.

[15] Translation of Raunkiær's title: "Embryo formation without fertilization in dandelions".