ington, he displayed to a degree that excited our greatest admiration a capacity for the dual duties of research and administration." As one of the world's leading paleontologists and revealer of Primordial Faunas, he outshone by far even the illustrious Barrande of Bohemia, and in this country he was one of the outstanding men of all science, evidenced by his presidency of the National Academy of Sciences from 1917 to 1923. Five medals (Bigsby and Wollaston of England, Gaudry of France, Thompson and Hayden of this country), and honorary degrees from Cambridge, St. Andrews, Christiania, Paris, Hamilton, Chicago, Hopkins, Pennsylvania, Yale, Harvard, and Pittsburgh further testify to the high place he held at the seats of learning in America and Europe.

CHARLES SCHUCHERT

NEW LIGHTS ON EVOLUTION[1]

I

THE past two decades or more seem to have been marked by too great a confidence in the experimental method as a universal solvent of biological problems. It would be as unreasonable to expect the physicist alone to be able to unriddle the mysteries of inanimate nature, without any aid from the fundamental science of chemistry, as to assume that the much more complex problems of living matter can be resolved by the investigation of functions and activities alone. Living beings are so much more a product of their past history than of present environment that the historical and comparative study of animate matter will always be of fundamental importance. For the moment many biologists have lost their sense of proportion and have over-emphasized the experimental side with a consequent sterility and loss of interest in the science. Biology from its very nature will apparently always be more a historical and comparative science than an experimental one. For its normal development the experimental and structural study of organisms should obviously go hand in hand.

One of the most interesting tendencies of the present time is the vivid revival of the interest in biology. We are accustomed to regard the epoch, which began with the appearance of the "Origin of Species," as marked at the outset with misunderstanding and lack of interest. It is worth while accordingly to remark that the first edition of fifteen hundred copies of Charles Darwin's immortal volume, published as you will remember in 1859, was exhausted at the time of issue and that within less than a year three other editions, comprising thousands of copies, were called for. I may remind you that the full title of Darwin's great book is the "Origin of Species by Natural Selection." The severest criticisms of the work as a matter of fact have been based on its author's supposed opinion that natural selection alone is able to account for the origin of species. In one of his chapters, however, Darwin states that it is the internal factor of variability which is of the greatest importance in connection with the origin of the species. The only reason that he did not deal at greater length with the subject of variability in living organisms was the complete ignorance, then and since on the part of biologists, as to the cause of variability. In another of his chapters Darwin makes the illuminating and indeed, in the light of very recent events, prophetic statement, that the greatest degree of variability is found in the larger groups of plants and animals. Within the limits deliberately set by himself, Darwin produced a book which will always rank as the greatest classic of the biological sciences.

We may now turn to the question of the present position of the problem of the origin of species, and in this connection we can not do better than refer to some of the recent utterances of the Nestor of American evolutionary biologists, Professor Henry Fairfield Osborn, director of the American Museum of Natural History. In a series of essays devoted to the theme of the teaching of evolution (Charles Scribner's Sons, New York, 1926), he remarks on page 29: "In my opinion natural selection is the only cause of evolution which has thus far been discovered, and demonstrated."

In his recent Oxford address on evolution, delivered on the occasion of the meeting last summer of the British Association for the Advancement of Science, in that venerable university, Osborn points out that as the result of the manifold activities of naturalists in more recent years we are now in the position to state the conditions under which new species make their appearance although not their cause. The most important element from the naturalist's standpoint is apparently isolation such as is found in islands of the sea or in the case of fresh water forms in rivers once connected but now separated by geological change. Such species are in general distinguished by the fact that they do not intergrade with their more nearly related species. His general conclusion is that: "We know the *modes* by which subspecies and species originate; in fact, there is little more on this point to be known. But this very knowledge renders the problem of *causes* infinitely more difficult than it appeared to Darwin."

The question of the origin of species is in fact much too large a one to be attacked successfully by any one line of biological investigation. Of late

[1] Public lecture delivered under the auspices of the Royal Canadian Institute and the University of Toronto.

years it is the geneticists who have expressed themselves with the greatest confidence and positiveness on the subject of the origin of species. Of these perhaps the most judicial is William Bateson, whose recent untimely death we all deplore. Although earlier he shared the confidence, characteristic of his group, his latest view was that we know nothing whatever about the origin of species. Naturally enough such pessimistic utterances, which are not confined to the author just cited, have been seized upon by the so-called fundamentalists, as showing that biologists have in reality no knowledge of the basal problem of their science. A consideration of the full significance of recent discoveries in biology, particularly in the case of plants, seems however to lend little support to a position of pessimism or negation. On the contrary, these recent investigations have tended to show that many hitherto unexplained phenomena are accounted for by the factor of hybridization.

An illuminating feature of the Darwinian method was the comparing of plants and animals in nature with those under cultivation and domestication. He pointed out that the best cows and the best cabbages are both the result of deliberate and continued selection of the part of man, in other words, are the consequence of what Darwin called artificial selection. Similarly he made it clear that in the long course of geological time those plants and animals best suited to their natural environment survived. To this natural weeding process he applied the apt title of natural selection. The possibility of selection whether natural or artificial depends on the inherent variability of living organisms, as was long ago pointed out by Darwin himself. The cause of variability is now apparently well in sight as the result of recent comprehensive investigations on the minute structure of important cellular elements in plants and animals. It has long been known on the plant side that the crossing of different natural species led to the production of offspring of infinite variability. Although this situation has for years been a commonplace among the producers of new varieties of cultivated plants, the matter has not until recently been followed backwards to the minute but highly important details of the reproductive cells. The biologist of late has been paralleling the path of the chemist in attempting to resolve his problems by reference to minute ultimate structures. Naturally he can deal with only the smallest units of structure clearly recognizable by the microscope, particularly those entering into the organization of the nucleus of the cell.

When two species are crossed, the result is a hybrid. The sterility of hybrids has been long and even popularly known, as witness the cases of the mule and the mulatto. Recognized hybrids among animals are relatively rare, but among plants the occurrence of hybrids both natural and artificial has become a commonplace. The structural peculiarities of the most minute elements of the reproductive cells of hybrids present a subject of fundamental interest and importance which has only recently received the attention which its significance demands. I have been occupied for many years in this fruitful field and have reached conclusions, the general tenor of which I shall try to summarize for you to-night; namely, that hybridization offers an explanation for variability and that variability accounts for the origin of new species.

Some twenty years or more ago a Swedish botanist, Rosenberg, gave the first clear description of the nuclear peculiarities of reproduction in hybrids. He noted that in a natural hybrid between two species of sundew, namely, *Drosera rotundifolia* and *D. longifolia*, the reproductive cells presented very interesting conditions in their divisions. In the species *D. rotundifolia* when the mother cells, which produce the four pollen grains characteristic of the genus Drosera, undergo their first division, the nuclear substance appears in the form of ten so-called chromosomes. In *D. longifolia*, on the other hand, there are twenty chromosomes under the same conditions. In the hybrid between the two species, the number of chromosomes in the body cells is the sum of ten and twenty, namely, thirty. In the division of the mother cells of the pollen grains of the hybrid, however, a very interesting condition presents itself. There are present ten *double* chromosomes and ten *single* ones. The doubles are called bivalents and the singles univalents. The double chromosomes are regarded by Rosenberg as consisting of pairs derived one from each of the two parents. The ten singles on the other hand represent the remainder of the chromosomes of *D. longifolia*, which have failed to find mates. Equally interesting is the behavior of the chromosomes in division. In the somatic cells the conduct of the chromosomes is quite normal, but in the reproductive division the univalent or single chromosomes lag and are frequently left out when the two nuclei, formed after division, are completed. The laggards frequently form one or more additional and smaller nuclei. While the parent species produce their pollen grains in the normal number of four, the hybrid has more than four pollen grains produced by each mother cell. Further, the pollen of the hybrid is largely sterile. It is thus clear that the hybrid Drosera differs from both its parents in a number of well-marked features. Although the first observations in this important field were made on the natural hybrid described above, subsequently similar phenomena have been observed in numerous artificially produced hybrid plants. We have thus arrived at clear criteria for hybridism based on the study of the cytological changes in the dividing mother cells of the reproductive elements. It is an interesting fact that these abnormalities are not found in the vegetative or somatic divisions. This no doubt is the reason that their importance in the study of the origin of species has received so late a recognition.

Rosenberg quickly noted that similar peculiarities appeared in the reproductive divisions of the very variable dog-rose of Europe, Rosa canina, and one of his students, Taeckholm, carried out observations on European roses in general with similar results. Simultaneously Blackburn and Harrison made parallel observations on the roses of England. Abnormal reproductive divisions in the roses of Europe, western Asia and northern Africa, united with a large degree of variability and likewise marked sterility, make it more than probable that the multiplication of species of roses in the European area is the result of hybridism. Our eastern American roses are of pure race, but in America another huge and variable rosaceous genus, Crataegus, the hawthorns, has been shown by investigations carried on by Dr. A. E. Longley to be largely of hybrid origin. Hybridism in fact is extremely common in the larger genera of the Rosaceae. Not only have the criteria of hybridism (sterility and abnormality in the reproductive divisions) been clearly discerned in many of the Rosaceae, but although the field is as yet new and comparatively unworked, numerous examples have already presented themselves in the Compositae, Myrtaceae, Betulaceae, Fagaceae, Proteaceae, Gramineae, etc., etc. We are in fact already in the position to state with confidence that hybridism has played a large rôle in the multiplication of species among the higher and even the lower plants.

We may at this stage consider, so far as plants are concerned at any rate, the cause of the high variability, noted by Darwin, as an outstanding feature of larger groups. It receives its natural explanation as the result of hybridization in nature, since precisely in these very large groups we find sterility, abnormalities in reproductive divisions and in the production of pollen. Further the conclusion recently set forth by Osborn and cited in an earlier paragraph, that isolated species are constant and not connected by intermediates with other isolated species, is attributable to the absence of the possibility of hybridization. On the other hand, where species grow in proximity, they may naturally be connected with every possible sort of hybrid intergradation.

Animals

We may now turn our attention to the animal side. Here known hybrids are infinitely less common than is the case with plants. I have chosen the Orthoptera for investigation in this respect. This group is particularly favorable by reason not only of its great extent but also on account of the large size of the reproductive cells, which make them suitable for cytological study. The grasshoppers and locusts belonging to this group are distinguished for their numerous and extremely variable species. It is in fact said that there are as many as thirty thousand species of grasshoppers in the larger sense in North America, and hundreds of new species are described every year. In the reproduction of animals the sperms are produced in fours precisely as are the corresponding pollen grains on the plant side. If one examines microscopically the reproductive gland or testis of almost any grasshopper, locust or cricket, one usually finds present huge quantities of sterile sperms, particularly in the earlier stages of activity of the gland. These abortive sperms naturally suggest a comparison with the correspondingly sterile pollen of the hybrid Drosera and that of numerous species of roses, hawthorns, etc., etc. The earlier formed sperms present the same abnormalities as present themselves in the divisions of hybrid plants. It is at once reasonable and scientific to suppose that the huge multiplication of species in certain Orthoptera is like the similar multiplication of species in large groups of plants, due to hybridism. The peculiarities in relation to sterility and abnormal conduct of the chromosomes in the reproductive divisions are not confined to the Orthoptera, but have been unwittingly described in large and variable genera of snails, butterflies, moths, spiders, flies (Diptera), etc. I assume accordingly that the variability found in the large groups of animals, since it is accompanied by the same cytological abnormalities and the same sterility as is found in known and suspected hybrid plants, is likewise an indication of the rôle played by hybridism in the formation of new species. Hybridization appears also to be responsible for the phenomenon known as parthenogenesis.

II

Parthenogenesis

An interesting abnormality in reproduction is presented by many plants and animals. Normally the formation of offspring depends on the fertilization of the egg of the female by the sperm of the male. In a number of cases, however, eggs are able to produce new individuals without previous fertilization. This phenomenon is known as parthenogenesis. It is well illustrated among plants by the common dandelion. In this species, the pollen grains are for the most part abortive and even where they reach a certain size lack the two nuclei which are present in normal pollen grains of other flowering plants. It is possible to remove entirely the anthers or pollen-producing organs in the young flower by excision with a sharp razor, and with them the stigmata or receptive surfaces connected with the ovaries. The flowers under these circumstances set seed precisely as if nothing had happened. My observations on the pollen mother cells reveal the fact that their divisions show all the cytological peculiarities of hybrids. There are, for example, both bivalent and univalent chromosomes, which lag after the hybrid manner in division. Further the lagging of the chromosomes is responsible for the formation of small and supernumerary nuclei, which give rise to small abortive pollen grains. Finally, the pollen as a whole is completely sterile and consequently incapable of effecting fertilization. Similar observations have been made on the cudweeds (Antennaria), the hawkweeds (Hieracium), the ladymantles (Alchemilla), etc., etc. I have observed an interesting case in the common broomrape, a parasite, known as *Orobanche uniflora*, which is at the same time parthenogenetic and presents all the peculiarities of known hybrids. On the basis of detailed agreement in essential features with known hybrids, there seems to be no reasonable doubt that parthenogenesis in plants may be a favorable variation following previous hybridization. This view has been ably put forward by Ernst before the cytological peculiarities of hybrids were as clearly formulated and understood as they are at the present time. Winkler's criticisms, which represent the narrowness of view which so often characterizes the pure experimentalist, are accordingly of slight importance.

The cytological evidence seems clearly to indicate that parthenogenesis is the result of previous hybridization in plants and it is of interest in the present connection to discover if the evidence points towards a similar conclusion in animals. One of the most striking cases of parthenogenesis is presented by the green-flies or aphids as well as related parasitic insects. My own studies show here the same peculiarities as in parthenogenetic and hybrid plants. There are univalent lagging chromosomes, which often form supernumerary nuclei and a very large amount of sterility is presented by the sperms, which are frequently highly abnormal. The univalent laggards have been noted by the zoologists, but under a misapprehension as to their significance have been called "sex chromosomes." It is, however, in view of the whole situation, quite impossible to put this interpretation upon them. The described cytological conditions in connection with parthenogenesis in ants, bees and wasps, lead to the conclusion that these too, so far as they are parthenogenetic, are of hybrid origin. A similar statement holds for parthenogenesis in certain parasitic worms.

An interesting case is presented by the grouse-locust, Apotettix Eurycephalus, in which Nabours has recently described parthenogenesis. On request he has kindly furnished me with suitable material and I have been able to observe not only a high degree of lagging in the chromosomes, but also a marked degree of sterility. It is of interest in this connection to note that Harrison had already suggested on the basis of Nabours's work that the species under consideration is of hybrid origin.

Mutation

A great deal of attention has been focussed in recent years on the so-called phenomenon of mutation or saltatory origin of species. Stock illustrations of this condition are the evening primrose (Oenothera), *Drosophila melanogaster* and the Boston fern. There is little doubt both from the experimental and morphological standpoints that most of the species of Oenothera are of hybrid origin. Their extreme variability in many instances, their usually high degree of sterility and the cytological peculiarities, particularly of the more sterile species or subspecies, clearly testify to a heterozygous origin. The Boston fern, which originated some time ago in a greenhouse in Cambridge, has been investigated in my laboratory and it shows both the extreme sterility and the special cytological characteristics of a hybrid. Elsewhere the present author has shown that *Drosophila melanogaster* is, on the basis of its extreme variability and its cytological abnormalities, of hybrid origin.

There can scarcely be any reasonable doubt that so-called mutation in general is associated with previous hybridization. The so-called mutating forms present usually the high variability, the sterility and the cytological peculiarities of known hybrids. Further, Tower's experimentally produced hybrids of the potato-beetle are described by him as showing subsequent mutations.

General Conclusions

It will be obvious to the reader who has followed the data and descriptions of the preceding paragraphs that striking abnormalities are frequently found in the divisions of the reproductive cells of both plants and animals, where these are highly variable or belong to large groups or genera. These peculiarities present an inescapable resemblance to the conditions found in known hybrids. It follows that the high degree of variability noted long ago by Darwin, in large groups of plants and animals, has its natural explanation as the result of hybridization.

It seems clear that the phenomenon of parthenogenesis in plants and animals is likewise to be explained as a successful result of previous hybridization. Since the general sequel of hybridization is sterility, the only outlook for the offspring of a hybrid union is either the development of improved sexual fertility or the appearance of parthenogenesis.

The peculiarities of so-called mutating forms find their rational elucidation in the study of the phenomena, variational and cytological, of known hybrids. It accordingly follows that mutation, so far as it is a real cause of the origin of species, is merely the appearance of more or less constant offspring, following a previous hybrid union.

In our study of the origin of species we have now apparently, after many years of comparatively ineffectual effort, reached a point of view which will enable us to explain some at least of the fundamental causes of variation, fluctuating or fixed. One-sided attack has been shown to be futile. The great merit of Darwin's work is its many-sidedness. To-day, too, it seems clear that for permanently valid results in biology, structural and experimental work must go hand in hand. Moreover, observations in the field and observations in the laboratory must supplement one another for the most fruitful results.

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SCIENCE AS CULTURE

ONLY about ten per cent. of the undergraduates who, since the war, have taken general chemistry at ten leading colleges and universities[1] pursue further chemical courses. But one student in forty-five does postgraduate work in chemistry.

It would require an exhaustive study of registrar's records and post-collegiate careers to determine how many graduates make any direct or indirect use of chemistry in their life work; but this is not necessary to confirm the common observation that they would be only a small fraction of those who take an introductory course in the science.

What, then, should be the purpose of such a course? "To state the laws and define the conceptions of the science in terms of experimental facts"[2] is the object set forth, more or less aptly, in the prefaces of twoscore college texts. Hundreds of courses, described in the curriculum as "Chemistry I—general chemistry, lectures and laboratory work," are given each year, more or less successfully attaining this object. From the student's point of view, a firm foundation of chemical science with a year's training in scientific methods of work and scientific habits of thought is shooting wide of the mark. Judged by standards of interest and utility for the majority, it would be more profitable to teach ice-skating to the Hottentots.

Those who have given thought to this subject will not even debate these facts. It is conceded that pandemic chemistry, suggested by Bancroft,[3] serves the needs of the average student better by treating chemistry as a cultural subject. Such a course—the pioneer, I believe—was introduced tentatively at Marshall College under Professor Phelps two years ago, and at Harvard, Yale and Cornell, possibly elsewhere, too, similar experiments are being made. The subject is in the air—very much in the air—but the thought seems to be condensing that two distinct Chemistry I courses, professional and pandemic, must of necessity be developed best to serve the different needs of students who plan to follow medicine, engineering, or one of the natural sciences and those who will make no professional use of chemistry.

This thought I would examine in its nascent state. It will be easier to analyze before it crystallizes.

For this task I have no professional equipment. However, during the better part of ten years, I have served as liaison officer between the three groups who, after all, are most concerned with the practical results of chemical education; the industrial chemists, the chemical manufacturers and the industrial consumer of chemicals. From this coign of vantage it is my business to survey the chemical fields without becoming lost in the towering forests of chemical theory or being bemired in the swamps of chemical commercialism. This point of view is certainly interesting and perhaps helpful.

The time when a knowledge of the Greek and Roman classics was the hallmark of an educated man has past. To-day, even their cultural value is fast diminishing. To know Eros is nowadays not so important as to know what Freud believes about love. The fire Prometheus stole is less use to us than the energy generated by photosynthesis. Phoebus's chariot has become an internal combustion engine; radio replaces Mercury; the metamorphosis of cellulose into rayon, lacquers, celluloid, artificial leather, explosives and what not transcends the myths told

[1] Harvard, Yale, Princeton, Williams, Virginia, Ohio State, Michigan, Illinois, Northwestern and California. The records are not satisfactorily complete for this purpose; but the data are sufficient to assure representative results. Technical schools and universities where engineering courses are notably stressed were purposely omitted.

[2] Alexander Smith, "Inorganic Chemistry."

[3] Walter D. Bancroft, *Jl. Chem. Educat.*, 3, 396 (1926).