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## CONTENTS

<i>The Problem of the Origin of Species as it appeared to Darwin in 1859 and as it appears to us To-day:</i> DR. HENRY FAIRFIELD OSBORN .....	337
<i>The Journal "Science" and the American Association for the Advancement of Science:</i> DR. J. McKEEN CATTELL .....	342
<i>The Relation between the Cost of Research and the Cost of Publication:</i> PROFESSOR WILLIAM ALBERT NOYES .....	347
<i>The First Greenland Expedition of the University of Michigan:</i> PROFESSOR WM. H. HOBBS .....	348
<b>Scientific Events:</b>	
<i>Statistics of the Physicians of Germany in 1926; The Royal Photographic Society's Exhibition; The Conference on Bituminous Coal; The Mohonk Cancer Symposium; The Tenth International Congress of Zoology</i> .....	349
<i>Scientific Notes and News</i> .....	352
<i>University and Educational Notes</i> .....	354
<b>Discussion:</b>	
<i>The Teaching of Evolution in Arkansas:</i> C. BUSH. <i>The Concilium Bibliographicum:</i> G. E. GATES. <i>The Discovery of Vitamins:</i> DR. E. C. VAN LEERSUM. <i>A Logic Poem:</i> DR. CHRISTINE LADD-FRANKLIN .....	354
<b>Quotations:</b>	
<i>A Berthelot Memorial</i> .....	358
<b>Scientific Books:</b>	
<i>Pierce on the Physiology of Plants:</i> DR. BURTON E. LIVINGSTON .....	359
<b>Scientific Apparatus and Laboratory Methods:</b>	
<i>A Simple Method of using Safety Razor Blades for Microtome Sections:</i> ROBERT A. NESBIT. <i>Estimation of the Colloidal Material in Soils:</i> DR. GEORGE JOHN BOUYOUCOS. <i>Permanent Cultures:</i> DR. FREDERICK BAUER .....	361
<b>Special Articles:</b>	
<i>The Filterable Cell of the Rous Chicken Sarcoma and the Question of the Causative Agent:</i> DR. WARO NAKAHARA. <i>Glass as a Fourth State of Matter:</i> DR. GEORGE S. PARKS and DR. HUGH M. HUFFMAN .....	362
<i>The Division of Chemical Education of the American Chemical Society:</i> DR. B. S. HOPKINS .....	364
<i>Science News</i> .....	x

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## THE PROBLEM OF THE ORIGIN OF SPECIES AS IT APPEARED TO DARWIN IN 1859 AND AS IT APPEARS TO US TO-DAY<sup>1</sup>

*The first of these objects, that is, the establishment of a belief in descent with modification, was always held by my father to be the more important of the two; for I once heard him say, if a recollection of about fifty years' standing may be trusted, that "after all, evolution is the great thing, not natural selection."*—LEONARD DARWIN, "Organic Evolution," pp. 1, 2.

NEARLY one hundred years ago Charles Darwin began to collect facts for "The Origin of Species," his immortal work, which was cautiously withheld from publication until 1859. There still prevailed the zoology of Linnæus and Buffon and the paleontology of Cuvier. In Lesson's "Mammalogie" (1827) the number of mammalian species is exactly 1,124, as compared with the 13,000 species and subspecies of mammals known at the end of the year 1925. Birds increased from 3,600 to 23,939; reptiles and amphibians from 543 to 9,000; fishes from 3,500 to 20,000. Darwin's species stood apart like isolated mountain peaks, whereas to-day living species and subspecies are often comparable to mountain chains composed of lesser peaks completely connected by ridges known as intergradations. It is not the number of species and subspecies which is significant, but the facts as to habit and habitat which are recorded with them. Similarly, it is not the number of fossil species now known as compared with those of Darwin's time, but the *linkage* of families, genera, species, subspecies, and even of "ascending" and "descending mutations" reaching back over hundreds of thousands, if not millions, of years.

This twenty- to one hundred-fold disparity in our knowledge simply intensifies our admiration for the courage of Darwin in boldly substituting a natural for a supernatural conception of the origin of species. It is true that Darwin's most influential authority was not the current zoology and paleon-

<sup>1</sup> Read at the opening of Section D (Zoology) of the British Association, at the Oxford meeting, August 5, 1926. This is the fourth of a series of papers on the origin of species, the first having appeared in *Nature*, June 13 and 20, 1925, under the title, "The Origin of Species as Revealed by Paleontology." The fifth, under the title, "The Origin of Species, V: Speciation and Mutation," will appear in the *American Naturalist*.

tology of his day but Nature itself, whereby even in 1859 he absolutely established the Law of Evolution, as well as the directing and standardizing principle of Natural Selection. It is, however, not this broader aspect of evolution, but the more concrete problem of the *modes* and *causes* of the origin of species which we are considering to-day.

Let us re-examine these causes in the light thrown by naturalists and observers on the invertebrates and vertebrates as distributed over the great continents of Europe and Asia, of North and South America, of Australia, considered not alone with their present boundaries but also with their former land connections secured by elevation to the hundred fathom line. In this connection I present a new zoogeographic and paleogeographic map of the world, prepared with the aid of Bartholomew of Edinburgh. We shall see that the results of zoological and paleontological research are entirely harmonious and concordant, but that zoology, while clearly teaching certain principles of the origin of species, leaves blank many gaps which are completely filled by paleontology.

Thus these two branches of biology are complementary in demonstrating that, through observations after the very naturalistic manner of Darwin in the voyage of the *Beagle* and through the very Lyell-Darwin methods by which the natural origin of species was originally discovered, *the problem of the origin of species has entirely changed in the last hundred years*. In fact, were the great naturalist living to-day, he would be foremost in modifying his own opinions, speculations and theories.

Greatly enhancing the value of the recent work of our field naturalists is the fact that the results reached in fishes, amphibians, reptiles, birds and mammals were recorded entirely independently of each other. Where the conclusions reached are harmonious or concordant they have the convincing value of entirely independent testimony. Also, these results are doubly valuable because they are for the most part assembled without biological purpose or intent, not to prove or to disprove any particular theory, but recorded simply as actual observations.

This is generally true of all field naturalists, who are more concerned about Nature than about the interpretation of Nature. The interpretations upon which our field naturalists do venture, such as the "direct action of environment" and "Lamarckian inheritance," are often lacking in real biological analysis. For such analysis, therefore, we must allude to five biological principles which have developed from laboratory experiments, and the generalizations growing out of them, beginning chiefly in the year 1880. These are as follows:

(1) Weismann's sharp distinction of the germ-plasm from the body plasm, from which follows the equally sharp distinction between truly germinal specific characters and bodily modifications by environment or habit; (2) the experimental failure of the inheritance effects of adaptive habit, known as Lamarckism; (3) the apparent failure of the environment to modify immediately the germ-plasm in creating adaptive specific characters; (4) the sharp limitations of the originative powers of Natural Selection as conceived by Darwin; (5) the sharp distinction between the continuous and discontinuous (or mutational) origin of specific characters.

In fact, the outstanding speculations of Darwin's and Herbert Spencer's time as to the causation of the origin of species have been pared down by laboratory analysis to a mere vestige of their former selves, and the overweening confidence of one school of causation after another has been displaced by diffidence, doubt, or even agnosticism, as expressed in the final address of William Bateson, whose recent death we lament at this meeting. To sum up, intensive laboratory and experimental research has added vastly to our knowledge of the functions of animals and of the heredity mechanism but has greatly increased the difficulties inherent in the problem of the origin of species. It is the *modes* and the *causes* of the onward progressive movement of the germ-plasm resulting in the consecutive origin of new adaptive specific forms which are rendered still more mysterious by the negative results of laboratory research.

#### DISTINCTION BETWEEN SPECIATION AND MUTATION

So far as the *modes* of the origin of species are concerned, these negative results of the laboratory are more than offset by the positive results obtained by our field naturalists and explorers who are independently discovering a considerable number of species-in-the-making at the present time. In other words, we now understand the contemporary origin of species after modes and under conditions wholly unknown to Darwin in 1859. Geographic *isolation*, to which Darwin's attention was first directed by Wagner, with all the incidental influences of physical or chemical change, of enforced change of habit, of competition with a new life environment, perhaps of stimulus to the germinal energies themselves, seems to constitute the chief complex of causes in the origin of new species; this complex is summed up in the principles which Osborn terms *tetraplasia* and *tetralinesis*. An extreme phase of isolation is *insulation*, where species are scattered among a number of islands. A like isolating mode among fishes is seen in the complete separation of rivers and streams

formerly connected. In this complex of four coefficient causes, all involving energy, the specific germinal substance itself undergoes change, extremely slow but continuous, so that a new stage is very gradually reached, formerly known as a "geographic variation" but now known as a "subspecies." Between subspecies living in islands and separated rivers there are naturally no *intergrades* or intermediate stages, but in a number of independent examples among fishes, amphibians, reptiles, birds and mammals, true intergradation has been observed linking one subspecific form with another in a continuous germinal life-chain. Such survival of intergrades may be instanced as proof of *complete continuity* between subspecies and, consequently, between species.

This appears to be the normal and natural mode of origin of the greater number of specific forms as observed in zoology; such mode has been termed "speciation" by recent British and American authors. In exactly the same field of observation and by the same observers, apparently as an abnormal mode due to some irregular influence on the specific germ-plasm, is seen the discontinuous or sudden origin of new characters, ranked by some observers as specific, after the manner termed "chance variation" by Darwin and "mutation" by De Vries. *Mutation* thus appears to be a real phenomenon, but a relatively rare one; such mutational origins need to be protected by geographic or climatic isolation from interbreeding with normal species.

Thus *speciation* through continuity stands in contrast with *mutation* through discontinuity. There is no question as to germinal change in mutations, but may the same be said of subspecies? In answer to this doubt it has recently been shown by experiment (Sumner, 1924) that many, if not all, subspecific characters are *stable under changed conditions of environment*. Consequently, while under suspicion as to reality, often vexatious and unconvincing, and always annoying to the systematist, *well-authenticated subspecies are of priceless value to the biologist who seeks to ascertain the conditions under which new species arise*. It proves that many "geographic variations" and "subspecies" are really germinal transitions, intermediates and intergradations from "species" to "species" of the higher kind known to Darwin.

The above is a summary of principles gathered from a very large number of independent observers whose names will be fully recorded with the titles of their papers in the complete series of notes on which the present paper is based. Outstanding names are those of Adams in the gastropods, Jordan, Berg and Regan in the fishes, G. A. Boulenger in the amphibians, E. G. Boulenger in the reptiles, Chapman and

Griseom in the birds, Osgood and Sumner in the mammals. The whole list of observers in the vertebrates alone comprises more than a hundred names. For the annotation of this extensive literature I am indebted to members of the corps of zoologists of the American and British Museums and of the Zoological Society of London.<sup>2</sup>

#### EXAMPLES OF GEOGRAPHIC ISOLATION AND SPECIATION

It appears that speciation arises only where one or all of the energy coefficients of Osborn is changed. In amphibia especially, geographic isolation does not invariably result in the origin of new species, because all the conditions of the new habitat may be identical with those of the old. A most striking example of complete intergradation between "species" is that of the molluscan genus *Io* of the Tennessee River, which now presents all the living intergrades between the smooth and the spinose forms as we pass downstream. In fishes, skeletal intergrades are observed as we pass from northern to southern waters (Berg) or from colder to warmer marine habitats; these intergrades consist in the number of vertebrae, of fin rays and of scales, and in body form and color, and Berg concludes that all the individuals of certain geographic areas simultaneously produce similar new specific characters.

Among amphibians the entire region around the Mediterranean affords G. A. Boulenger a series of subspecies of the edible frog, *Rana esculenta*, more or less connected by intergrading forms. Among reptiles E. G. Boulenger observes the speciation of the skink, *Chalcides ocellatus*, a species which, like the edible frog, surrounds the Mediterranean, in which the difference between two isolated subspecific forms is so great that *were it not for the wonderfully complete manner in which they are connected they could not be denied full specific rank*. As among fishes, intergradations are observed in all the skeletal characters, as well as in the coloring and the scales. Completely supporting these observations are those of many of the recent herpetologists who conservatively use the word "variety" where other authors use the word "subspecies," who imply that intergradations occur wherever a sufficiently large number of specimens is examined. Chapman, with extensive collections of South American birds at his command, records exactly similar results:

The ornithologist finds large forms occupying colder areas, dark ones humid areas, and pale ones arid areas;

<sup>2</sup> These data will be published in full in a sequel to the present paper, in the *American Naturalist*, No. V in the series on the origin of species.

and as the [environmental] conditions which obviously produce these variations in size and color merge one with the other, so do the [specific and subspecific] forms themselves intergrade. That these variations are inherent [*i.e.*, germinal, constitutional, hereditary] and not merely the temporary impress of physical environment on the individual, is apparently shown by the fact that they are often as well marked in the nestling as in the adult.

Chapman also observes a distinct case of "mutation" within the genus *Buarremon* in the presence of a black pectoral feather-band, which is established as a specific character by isolation or geographic discontinuity. Like the single case with black dorsal band observed within the genus *Troglodytes*, the mutation does not intergrade and is thus recognized as of discontinuous or mutational origin. Stresemann finds partial melanism as well as albinism arising as not infrequent mutational characters, but fails to show that these are adaptive. Chapman and Griscom in their North and South American field work distinguish clearly between intergrading and non-intergrading kinds of birds. In a collection of 1,500 specimens of the house wren, *Troglodytes*, these observers have noted a considerable number of cases of *complete* intergradation between subspecies, and those familiar with the marked physiography of South America, with (a) its cold and arid Pacific coastal belt, (b) its Andean Mountain chain subdivided by Chapman into numerous vertical life-zones each clearly demarcated until we reach the boreal summits, (c) its vast Amazonian forest plain, (d) its pampas and plains of the southeast, and (e) humid forests bordering the Straits, may anticipate wide speciation in other forms of animal life in this continent. It is noteworthy that these observers have discovered in *Troglodytes* only one example of mutation in the sense of De Vries. It can not be questioned that isolation is the most important factor in the speciation of birds, especially in its extreme form of insulation.

Among mammals the great transverse geographic range from Scotland across Eurasia and North America of three species of the deer family affords a striking example of geographic speciation: the stag (*Cervus*) yields twenty-three species and subspecies; the moose (*Alces*) yields eight subspecies; the reindeer (*Rangifer*) yields twenty-one subspecies. This is in wide contrast to the knowledge of Darwin (1837-1859), to whom were known only two species of stag, one species of moose, and one species of reindeer. Far more significant, however, are the observations of Osgood and Sumner on the deer-mice of the genus *Peromyscus*, which range through the temperate region of North America to the Pacific coast. From a collection of 30,000 specimens Osgood

finds that a subspecies is characteristic of every distinct climatic region and sub-region. These subspecies listed by Merriam and Osgood have been accepted with great reluctance, especially by naturalists unfamiliar with the excessively sharp geographic and climatic barriers of the western United States. Our hesitation to accept these subspecies as of real germinal or genetic value has been entirely removed by the persistent observations and experiments of the biologist Sumner, largely in the identical collecting grounds of Osgood, and we must welcome these combined observations and experiments as the most convincing demonstration of the principle of *speciation continuity* thus far afforded. Between at least six of these subspecies complete intergradations occur. Classification becomes like dividing the lines of the spectrum. After eight years of transfer from an arid to a humid environment, or vice versa, these subspecies retain their original characters. Even profound change of environment does not yield a new subspecific form, nor are changes of habit inherited in eight years of experiment.

(1) The summary of eight years' experiment proves the comparative stability of subspecies of the Deer-mice (*Peromyscus*) under very marked new environmental physical conditions. (2) Merriam-Osgood subspecies are proved to be stable under changed conditions of environment, by transplantation experiments; *i.e.*, a desert subspecies, *P. m. sonoriensis*, reared for eight years in a humid environment, is entirely unmodified in the direction of the humid subspecies, *P. m. gambeli*. (3) This doubly proves (a) that characters of the desert *P. m. sonoriensis* are germinal, not environmental; (b) that humid environment makes no modification whatever toward increased depth of color in eight years and in seven to twelve generations. (4) Similar results from transplantation of *P. m. rubidus* and *P. m. sonoriensis* are obtained: reared in an entirely new environment, they do not converge toward each other or toward the local humid subspecies *P. m. gambeli*.

#### SPECIATION A SECULAR PHENOMENON

Whereas an inheritable mutation may be produced by a single experiment, 40,000 years, the lapse of time since the last glaciation, is a moderate estimate of the time required to produce a subspecies. In the case of all the genera cited above—*Cervus*, *Alces*, *Rangifer*, *Rana*, *Chalcides*, *Troglodytes*, *Peromyscus*—we are observing subspecies arising in a region which was profoundly affected by the fourth glaciation with its pluvial climate, a region in which new subspecies have arisen *pari passu* with the modern demarcations of habitat and of habit. That specia-

tion is an incredibly slow process is attested by the case of the newly discovered *Pliohippus* of Leidy, which early in Pliocene time assumed all the characters of the modern *Equus*. The entire speciation process of plants and animals has been going on perhaps for a thousand million years, as estimated on purely physical grounds, and in a recent conversation with Sir Ernest Rutherford it was agreed that another thousand years of research may be required for an understanding of the highly complex physico-chemical basis of life.

#### CONCORDANT OBSERVATIONS IN ZOOLOGY AND PALEONTOLOGY

As distinguished from the speciation observed in zoology, in paleontology we deal with secular speciation, in which, quoting from the first of Osborn's series of papers on the origin of species, we observe the adaptive action and reaction of the heredity germ over long periods of time. We also observe the secular action of natural selection (Darwin's selection factor), the secular direct reaction to environment (Buffon's factor), the secular adaptive action of habit (Lamarck's factor), the secular adaptive reaction to the living environment (Darwin's factor). We sharply separate Darwin's factor of selection, which has no energy content, from the above four energetic forces of evolution, namely, heredity, physical environment, living environment, and individual development or ontogeny. These are the principles of tetraplasy and tetrakinesis.

This momentary lapse into speculative as distinguished from purely observational consideration of the problem of the origin of species may clarify the transition from zoology to paleontology.

In paleontology an entirely new series of principles is discovered in speciation which are quite beyond the eye of the zoologist. Chief among these new principles is that dimly perceived by Darwin in the words "analogous variation"; it is that of germinal or evolutionary trend in a definite direction, the "mutations richtung" of Neumayr. Out of this springs Osborn's principle of *rectigradation* observed in the rise of adaptive characters from the germ-plasm, that is, new specific characters which pass continuously from the most rudimentary and inefficient into the most efficient and highly developed stages. It may be a matter of interest to members of the British Association to recall that this principle was presented to the Association in 1889 by the present speaker. Through unbroken observation during the intervening thirty-seven years this *rectigradation* principle has been confirmed in four great orders of

hoofed mammals, namely, the horses, the rhinoceroses, the titanotheres, and the proboscideans. Research on the two latter groups fills two great monographs aggregating nearly a million words and covering, in the case of the Proboscidea, the analysis of the mode of origin of more than 350 species and, in the case of the titanotheres, the chief stages of specific development extending from Lower Eocene through Lower Oligocene time, when these animals suddenly disappear.

An epitome of these observations is presented in three diagrams in which the three outstanding principles discovered in paleontology are observed: First, the unbroken continuity of speciation, which becomes absolute as the gaps are filled by discovery. Second, the constitutional predisposition to speciate in certain predetermined directions which must be inherent in the germ-plasm of ancestral forms. Third, that these constitutional predispositions are not released except through adaptive reaction to new conditions of life; they are not, therefore, of the nature of inherent perfecting tendency, but, rather, of the nature of a *potentiality* to appear when the need for them arises. For example, the rhinoceroses have the potentiality of developing two horns, an anterior horn on the nasal bone and a posterior horn on the frontal bone. But in the fourteen branches into which this great subfamily subdivides in its migrations to all parts of the earth, this double potentiality is seldom availed of, sometimes not availed of at all.

#### CONCLUSIONS

We seem to have reached an entirely new era in research on the problem of the origin of species, marked by the decline and death of speculations and theories advanced upon the very limited knowledge of the first half of the nineteenth century. Through zoology and paleontology we have reached a solution of the least difficult half of the problem with which Charles Darwin was confronted: 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 causes of "variation," to use the term he employed for the evolutionary process, lie in the way before us. They may be resolved or they may prove to be beyond human solution. We must resolutely face these alternatives, and in the meantime continue our synthesis over every field of biologic research.

HENRY FAIRFIELD OSBORN