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THE AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE.

IS MUTATION A FACTOR IN THE EVOLUTION OF THE HIGHER VERTEBRATES?[1]

THE stir created among botanists and horticulturists by the recent work of de Vries, particularly by his Berkeley lectures (1904) on 'The Origin of Species and Varieties by Mutation,' has led certain zoologists to believe that species of animals as well as plants may arise by the sudden assumption of new characters. Thus Davenport, in a recent review, expresses the conviction that 'as good an argument might be made from the zoological side as de Vries has made from the botanical.' The promulgation of these views by so eminent a student of evolution as Davenport, in connection with the circumstance that more or less similar views are held by others, has led me to reexamine certain groups of birds and mammals, of which I had previously made systematic studies, for the purpose of discovering evidence, if such exists, of the formation of species by mutation.[2]

But first let us be sure of de Vries's meaning. He states that individual plants of a certain species of evening primrose

[1] Address of the vice-president and chairman of Section F—zoology—at the New Orleans meeting of the American Association for the Advancement of Science.

[2] It is important that the terms used by de Vries should be understood. What we systematists have been in the habit of calling spontaneous variations or '*sports*' he calls '*mutations*'; what we call '*individual variations*' he calls '*fluctuations*'; and what we call the '*characters*' of species he calls '*qualities*.'

which he kept under observation for a period of years, suddenly developed abnormal new characters or 'qualities' that were inherited and gave rise to permanent new species, which continued to exist side by side with the parent species. This process he calls 'the origin of species by mutation.' While admitting the extreme rarity of occurrences of this kind, he appears to have been carried away with enthusiasm over his discovery and jumps to the conclusion that species in general originate by mutation—and in no other way!

After stating that species 'are not in the main distinguished from their allies by quantities nor by degrees; the very qualities may differ,' he goes on to say that *if* the differences in quality can not be explained 'by the slow and gradual accumulation of individual variation,' and *if* the sudden variations called sports or mutations, 'can be shown to occur in nature as well as they are known to occur in the cultivated condition, *then* in truth Darwinism can afford to lose the individual variations as a basis.' Continuing the argument, he declares: "Then there will be two vast dominions of variability, sharply limited and sharply contrasted with one another. One of them [that of individual variation] will be ruled by Quetelet's law of probability and by the unavoidable and continuous occurrence of reversions. It will reign supreme in the sciences of anthropology and sociology. Outside of these, the other [that of sports or mutations] will become a new domain of investigation, and will ask to be designated by a new name"—the origin of species by mutation. There would seem to be no doubt as to de Vries's meaning. The question is, are his assumptions justified by the facts in nature? It will be observed that he deems the perpetuation of individual variations jeopardized 'by the unavoidable and continuous occurrence of reversions.' Let me ask in all seriousness if sport variations are less likely to disappear by reversion than are individual variations?

Let us now examine the *'if and ands'* of de Vries's argument. The first of these is: *If* the differences in quality [characters] 'can not be explained by the slow and gradual accumulation of individual variations * * *.' May one venture to ask, Why can they not be so explained? Is it not true that up to the time of the announcement of his new theory a little more than a year ago it was the practically unanimous belief of zoologists and botanists the world over that the differences in quality that go to make species do originate in precisely this way? And has any reason been brought forward to justify—much less necessitate—a change in this belief? Are we, because of the discovery of a case in which a species appears to have arisen in a slightly different way—for after all the difference is only one of degree—to lose faith in the stability of knowledge and rush panic stricken into the sea of unbelief, unmindful of the cumulative observations and conclusions of zoologists and botanists?

De Vries's second and third *ifs* are: "*If* such strains [produced artificially among cultivated plants] can be proved to offer a better analogy to real systematic species, and *if* the sudden changes can be shown to occur in nature as well as they are known to occur in the cultivated condition, then in truth Darwinism can afford to lose the individual variations as a basis." The logic of this is hard to see, for is it conceivable that 'strains,' or varieties produced artificially among cultivated plants, 'can be proved to offer a better analogy to real systematic species' than species produced in the normal way by the perpetuation of individual variations? 'And if the sudden changes [sports or mutations] can be shown to occur in nature'—and I admit that they can—how does it follow that 'then in truth Darwinism can afford to lose the individual variations as a basis.' Is not this a case of enthusiasm run wild? Is it not like arguing that if it can be proved that a man ate meat for breakfast, then of course he could not have eaten bread! To my mind the striking fallacy of de Vries's argument is his assumption that because it can be shown that sports occur in nature, and that in rare cases species arise therefrom, then the theory that species are produced by the progressive development of slight individual variations must be abandoned. Why can not species originate in both ways? The occurrence of sports among animals and plants being admitted, the question arises as to what becomes of them. According to Darwin, Weismann, Dall, Jordan and a host of others they are lost by the swamping effects of interbreeding. That this is the usual result in both plants and animals I think every one will admit, for even de Vries frankly states that their perpetuation in giving rise to new species is so exceedingly rare that he is able to cite only a single authenticated case. I do not assume to be a botanist; nevertheless, for more than a quarter of a century I have been an earnest field student of plants in their relations to geographic environment. These studies have convinced me that with plants, as with animals, the usual way in which new forms (subspecies and species) are produced is by the gradual progressive development of minute variations.

But we are not now concerned with plants. The question before us is, 'Do species among the higher vertebrates originate by the sudden acquirement of new characters?' In seeking an answer I have passed in review more than a thousand species and subspecies of North American mammals and birds without finding a single one which appears to have originated in this way. Among the higher vertebrates, therefore, the conclusion seems justified that if species ever originate from sports, such mode of origin must be exceedingly rare. My own conviction is that the origin of species by mutation among both animals and plants is so uncommon that as a factor in evolution it may be regarded as trivial.

If species do not ordinarily originate in this way, it is fair to ask, 'How do they originate?' My answer is, 'By the slow but progressive acquirement of characters that have their beginning in minute variations.'

It is hardly necessary in the present connection to review the theories concerning the *inception* of variation, for whether or not we believe in the potency of dynamic influences, we all admit that individual organisms vary, and most of us are agreed that in the struggle for existence the beneficial variations are likely to be preserved, the harmful ones eliminated, by the action of natural selection. Some of us go further and believe that the universal and irrepressible tendency of organisms to vary results in the perpetuation, not only of distinctly useful departures, but sometimes also of those which, though not harmful, seem to be of not the slightest service to either the individual or the species. These, according to Dr. David Starr Jordan, owe their inception to geographic isolation. Dr. Jordan states: "The adaptive characters a species may present are due to natural selection or are developed in connection with the demands of competition. The characters, non-adaptive, which chiefly distinguish species, do not result from natural selection, but from some form of geographical isolation and the segregation of individuals resulting from it. * * * Adaptation is the work of natural selection; the division of forms into species is the result of existence under new and diverse conditions." Jordan's view is that 'the characters by which one species is actually known from the next are rarely traits of utility.'[3]

This was Darwin's view also, for he says: "It is a strange result which we thus arrive at, namely, that characters of slight vital importance to the species are the most important to the systematist." T. H. Morgan goes even further, expressing his entire disbelief in the production of species through natural selection. Had he been familiar with the characters that distinguish many of our species of mammals, birds and reptiles he could hardly have held this view, for while in some groups the characters naturalists make use of in defining species are mainly of the indifferent kind, in others they are largely of the adaptive and useful kind. Thus among mammals, birds and reptiles dozens of species and subspecies are distinguished from one another by adaptive characters alone. At the same time it should be understood that, as a rule, species are based not on one but several characters, some of which may be adaptive, others non-adaptive.

PRESSURE OF THE ENVIRONMENT.

Darwin's definition of natural selection or the survival of the fittest is: "The preservation of favorable individual differences and variations and the destruction of those that are injurious."

Whether a particular variation is beneficial or injurious depends of course on the environment. It follows that variations in order to be beneficial must be in harmony with, or meet demands of, the environment. Whether such adaptations should be attributed wholly to the slow action of natural selection, or whether one may be allowed to cherish the belief that the environment not only invites but compels variation, involves a distinction as important as it is difficult of demonstration. Is there not a hidden force which independent of, or superadded to, the general tendency of organisms to vary acts as an incentive in initiating useful variations? Have we not evidence of this in the increased length of toes and feet in species inhabiting soft or marshy ground; increased thickness of bill in birds that habitually crack seeds or nuts; increase in the length of the canine teeth in mammals that catch and hold struggling prey; increase in the size of the carnassial teeth in mammals that crunch bones of other animals; special modifications of the feet to fit them for special purposes, as for wading, swimming or grasping; and also such variations as appear to result from prolonged and oft-repeated effort, as increased length of leg in species whose welfare depends on fleetness of foot, and greater development of the external ear, or greater complexity of the internal auditory apparatus which seem to be a consequence of long continued strain in listening for the approach of enemies or of prey? This subtle influence I like to call *the pressure of the environment*.

Dall was once bold enough to assert: "The environment stands in relation to the individual as the hammer and anvil to the blacksmith's hot iron. The organism suffers during its entire existence a continuous series of mechanical impacts, none the less real because invisible."[4] These are weighty words, well worth remembering.

While a number of our ablest naturalists hold this view, the current feeling among morphologists and physiologists is undoubtedly against it. Thus Thomas Hunt Morgan in his book on 'Evolution and Adaptation' (1903), says: "We can profitably reject, as I believe, much of the

[3] SCIENCE, N. S., Vol. XXII., p. 558, Nov. 3, 1905.

[4] 'Dynamic Influences in Evolution,' W. H. Dall, *Proc. Biol. Soc. Wash.*, VI., 2, 1890.

theory of natural selection, and more especially the idea that adaptations have arisen because of their usefulness.''

Is not the fact that such diverse opinions are held by thoughtful men of science in itself an illustration of the pressure of environment? For is it not obvious—since those who spend their lives studying species in nature hold one view, while those who spend their lives peering into microscopes and inventing theories hold another view—is it not obvious that such antagonistic views are the outgrowth of different environments?

To those who admit the existence of dynamic influences it is conceivable that the inception of the resulting variations, as long ago pointed out by J. A. Allen, is not confined to a single individual, to be lost or saved by natural selection, but being the response of organisms to forces applied alike to all members of a species in a given area, takes place simultaneously in a large number of individuals and is thus established more quickly and with much greater certainty.

VARIATIONS.

It is convenient for the systematist to consider variations under four heads: (1) Fortuitous variations; (2) dynamic variations; (3) sexual variations; and (4) seasonal variations.

1. *Fortuitous variations* are such as arise without apparent cause—for it is in the nature of organisms to vary. They originate in a single individual, and occur everywhere, in all species of animals and plants. They may be beneficial, neutral or injurious. The beneficial are likely to be preserved by natural selection and increased so long as the increase is beneficial to the possessor; the neutral may either disappear or persist; the injurious are promptly eliminated. According to degree of development at the time of their first appearance they may be designated *ordinary individual variations,* or *sport variations.* This is an old story.

2. *Dynamic variations* are such as arise, apparently, in response to pressure of the environment. They are necessarily beneficial, arise simultaneously in a number of individuals, and are cumulative so long as the increased development is helpful—that is until a condition of equilibrium is established between the organism and the environment. They may be *functional* or *geographic.* Those that are functional may be *local* or *general;* those that are geographic may be *local* or *progressive.* Variations resulting from change of food habits, or from the necessity of coping with a new enemy, or from the too rapid spread of a species from one area to another, may progress to full maturity in a given locality; but in the case of ordinary geographic variations the change progresses laterally from one district to another. Thus in species that undergo geographic color variations, the change as a rule takes place so gradually that specimens from adjacent localities may be hard to distinguish, while those from the two borders of the belt of intergradation may be markedly unlike. In this case the intergrades, as well as the extremes, are in complete accord with the surroundings, the members of the species at each step along the geographic line of intergradation having attained a state of equilibrium with reference to the environment at that point.

Usually the movements of animals and plants in acquiring new territory are slow, allowing time for the necessary adjustments to take place along the line of advance, so that no great change at any one locality is required. But it is conceivable that in certain cases the advance may be too rapid for this, bringing a species into an area to which it is not yet adapted, in which case the struggle for existence would be unusually severe and the development of adaptive characters would proceed with corresponding rapidity.

Illustrations of functional and geographic variation in the same animal are afforded by the kangaroo rats (genus *Dipodomys*)—a group of American mammals highly specialized for life on arid deserts. These animals have numerous enemies and a multitude of competitors, which means that the struggle for existence is always severe. They are of small size and have big heads, big eyes, small fore legs and feet, exceedingly long hind legs and feet, and very long tails. The long hind legs and tail are special adaptations for saltatory progression—for leaping instead of running. Another general functional character is the extraordinary development of the internal organ of hearing, which forms more than half of the bulk of the skull, enabling the animal to detect the approach of its mortal enemy, the soft-footed desert fox.

In addition to functional variations of this kind, which are general or common to the group, there are others that are local in character and confined to particular species or subspecies. Of these may be mentioned the increase in size of the hind foot in forms inhabiting soft or yielding soils—an adaptation that is even more marked in certain other groups.

Turning now from functional to geographic variations, we find in certain species a marked decrease in size from the north southward. In *Dipodomys spectabilis,* which ranges from north-central New Mexico to southern Chihuahua—a distance of about 700 miles—the actual decrease in length is 52 millimeters (2 inches), or 14 per cent. of the total length. This is in accord with the general law of decrease in size from the north southward, announced by J. A. Allen many years ago.

The kangaroo rats furnish illustrations of still other matters of interest to the student of evolution. Passing the subject of color adaptations, of which much might be said, let us look for a moment at certain facts brought to light by a study of bodily proportions. Tabulation of the measurements of upwards of 500 adult specimens of the several species shows that individual variation is great, amounting in the hind foot to 15 per cent., in the total length to 20 per cent., in the length of tail to 24 per cent.—thus affording ample material for the evolution of new forms characterized by differences of proportion—but none such are developed. Indeed, the mean measurements throughout the genus are remarkably constant, the ratio of hind foot to total length varying only 2 per cent.; of tail only 4 per cent. We have here a case of wide range of individual variation coupled with surprising constancy of proportions. What does this mean? It means, if I interpret the facts aright, that all the species of the genus *Dipodomys* have come to a halt along a common line, like soldiers in a well-drilled regiment, indicating that in the course of their evolution from a generalized to a specialized type they have already reached, with respect to the environment and mode of life, a state of equilibrium or equipoise, from which any marked departure is injurious if not fatal. The possibilities in the way of divergence are shown by the large range of individual variation, which, however great, ceased long ago to operate in the production of new forms. All departures from the type are clearly disadvantageous and hence are promptly eliminated by natural selection. The operation of dynamic causes has resulted in the production of fixed conditions so far as the proportions are concerned—and no further modification need be looked for unless a marked change should occur in the environment.

SUBSPECIES.

It is obvious from de Vries's writings

that his studies of plants have been mainly with species as modified by man rather than with species in a state of nature. For instance, he says: "The same original form can in this way give birth to numerous others, and this single fact at once gives an explanation of all those cases in which species comprise numbers of subspecies, or genera large series of nearly allied forms." In the present connection it is necessary to notice only two of the fallacies embodied in this sweeping assertion—the two concerning subspecies. As a matter of fact, subspecies in nature do not occupy the same ground with the parent form, but an adjacent area; hence it is hard to see how they could fulfil his geographic requirement, which is that forms arising by mutation occur side by side with the original stock. And since subspecies differ from the parent form only by small differences, how can they arise from sports, which are distinguished from the parent form by large differences—differences of at least specific value?

From this it appears that de Vries's conception of subspecies and their relations in nature is somewhat hazy. In order to understand the relations and mode of origin of subspecies it is necessary to study them on the ground where they are formed, which means that it is necessary to consider them geographically. To do this intelligently one must study species in a region large enough to embrace belts of transition from one faunal (or floral) area to another, for it is in these transitional belts that the changes from one species or subspecies to another take place. The failure to recognize this simple but all important fact accounts for most of the current misconceptions concerning subspecies.[5]

[5] For present purposes it is immaterial whether subspecies are based on actual known intergradation (the point of view of the A. O. U. Code of Nomenclature) or on degree of relationship (the point of view of the morphologists and of some systematists), the material point being that they must be closely related to the parent form—either directly, or indirectly through other subspecies.

DO SPECIES ARISE INDEPENDENTLY OF GEOGRAPHIC ISOLATION?

According to de Vries: "We must conclude that new species are produced sideways by other forms, and that this change affects only the product and not the producer." Two of his seven 'laws' relate to this phase of the subject. These are: '(1) New elementary species appear suddenly, without intermediate steps; (2) they spring laterally from the main stem (not replacing it).' In thus burdening his mutation theory with the additional requirement that in giving off new forms the old is not altered, but continues to exist side by side with the new, he restricts its application to an exceedingly small number of cases, thereby materially weakening the theory itself. For in the case of the birth of a new species the new quality or character may be either neutral or beneficial. If neutral—of no value to its possessor—it is conceivable that the resulting new species may continue to exist in the same area with the old; but if beneficial the new species in the struggle for existence will eventually destroy and supplant the old—unless it diverges geographically so as to inhabit a separate area.

Dr. D. S. Jordan has recently expressed the belief that well-defined species arise only as a result of geographic isolation, but I am not sure that he means by this just what the reader might infer. His words are: "It is now nearly forty years since Moritz Wagner first made it clear that geographical isolation was a factor or condition in the formation of every species, race or tribe of animal or plant we know on the face of the earth. This conclusion is accepted as almost self-evident by every competent student of species or of the geographical distribution of species." A little later he says: "The contention is not that species are occasionally associated with physical barriers, which determine their range, and which have been factors in their formation. It may be claimed that such conditions are virtually universal"; and again: "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort."

J. B. Steere, in a paper on the distribution of birds in the Philippines, published in 1894, formulated the same idea in the following words: "No two species near enough alike structurally to be adapted to the same conditions will occupy the same area," and added that the facts "show *isolation* to be the first and the necessary step in the formation of species."[6]

I fully admit the potency of isolation in the production of species, but can not for a moment admit that complete isolation is a necessary factor in their evolution, mere *divarication* from a common center being in many cases sufficient. Neither can I admit that a barrier must be absolute, or that it must be interposed *between* species in order to be effective. This is proved in the case of climatic barriers, which, while not keeping contiguous species apart, nevertheless restrain each from trespassing far on the territory of its neighbor.

It is quite possible that Dr. Jordan's use of the word barrier, which occurs over and over again in his recent paper[7] is sufficiently elastic to cover most of the apparent discrepancies, so that the exceptions to his rule are really few. Still, there are in nature many groups of closely related species whose ranges follow one another in geographic series, the one beginning where the other stops, with no barrier of any kind between, as will be shown directly. In such cases it is often difficult to say whether the adjacent species have been established by differentiation from one another under existing geographic conditions, or have been developed from preexisting species along geographically divergent lines, and afterward have met by extensions of range. These points may be made clear by actual examples:

Among the kangaroo rats of the genus *Dipodomys* are two large and closely related species inhabiting our southern deserts. One of these, *D. deserti*, ranges from the Colorado and Mohave deserts in California easterly to a little east of Phœnix, Ariz.; the other, *D. spectabilis*, from a little east of Phœnix to western Texas. The geographic division between the two is an invisible line a little southeast of Phœnix in a desert area devoid of barriers of any kind, even climatic. The case, therefore, appears to be an exception to the law of isolation.

Turning now to another group, illustrations of at least two kinds of variation among closely related species are afforded by the ground squirrels of the genus *Ammospermophilus*, of which three distinct species and three subspecies are recognized. These animals resemble one another in form and markings and in the habit of carrying the tail closely appressed against the back so that its under side is uppermost and is presented to the view of the observer. In one species the under side of the tail is dark; in the others white or nearly white. The three species and their geographic ranges are (see map, Fig. 1):

Ammospermophilus nelsoni, restricted to the hot southern end of the San Joaquin Valley in California, where it occupies a detached area and is isolated by the encircling mountains, which by interposing a climatic barrier cut its range off from that of the parent species, *leucurus*. It has ac-

[6] *Auk*, XI., 239, 1894.

[7] SCIENCE, N. S., XXII., November 3, 1905.

quired a yellowish color which serves to distinguish it from all other members of the group.

Ammospermophilus harrisi, inhabiting the southwestern half of Arizona and extending south far into the state of Sonora; separated from its neighbor (*leucurus* and subspecies) on the west, north and east by two kinds of barriers—on the west by the absolute barrier of the Colorado River; on the north and east, along the southern edge of the Arizona plateau and its southerly continuation in New and Old Mexico, by the climatic barrier interposed by the elevation of the land.

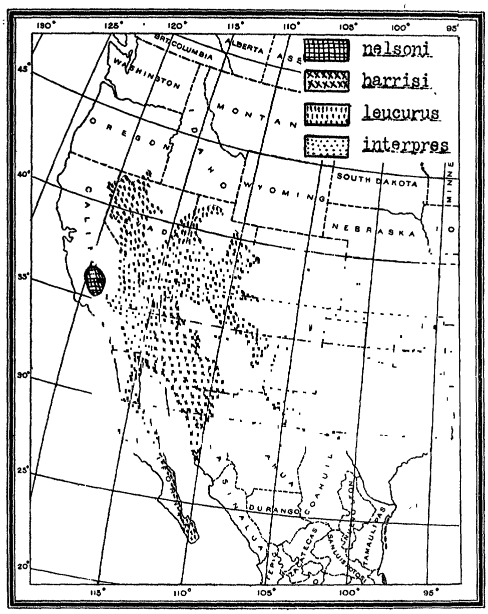

FIG. 1. Distribution of Ground Squirrels of the Genus *Ammospermophilus.*

Ammospermophilus leucurus, inhabiting the Colorado and Mohave deserts in California and thence, passing north of *harrisi,* ranging northerly and easterly over the Sonoran deserts of the Great Basin and easterly over northern Arizona to the Painted Desert and the Puerco, where it changes into subspecies *cinnamomeus,* which continues easterly to the Rio Grande Valley near the center of New Mexico. On the opposite side of the Rio Grande (east of Albuquerque) another subspecies, *interpres,* begins and follows the Rio Grande southerly and easterly as far as the valley of the Pecos. A third subspecies, *peninsulæ,* occurs in the peninsula of Lower California. It thus appears that *leucurus,* including the subspecies, surrounds *harrisi* on three sides—west, north and east—forming a complete horseshoe open only at the south. The nature of the barriers separating it from *harrisi* has been mentioned under the latter species.

Of the three subspecies of *leucurus,* two —*cinnamomeus* and *peninsulæ*—have the under side of the tail white and are only moderately accentuated color forms, continuous in distribution with the parent form and intergrading with it by imperceptible steps. The third subspecies, *interpres,* has some black intermixed in the white of the tail, and specimens from the El Paso region, where geographically *interpres* approaches nearest to *harrisi,* have more black than specimens from near Albuquerque, suggesting the possibility that intergradation may take place in the intervening area, in southwestern New Mexico. Unfortunately we have as yet no specimens from this area. If intergradation should be shown to occur, then we shall have an example of two well-defined species occupying adjacent areas and intergrading at the point of contact while remaining distinct everywhere else. In other words, the species are perfectly distinct wherever barriers exist separating their ranges, and intergrade when there are no barriers. In distribution and behavior, therefore, these animals conform to the usual rule, that closely related species separated by impassable barriers remain distinct, while those not separated by such barriers intergrade.

But the most significant and complicated case is that of the western chipmunks (genus *Eutamias*), one of the most elegant and attractive groups of American mammals. The genus occupies a vast area in western North America, extending from Lake Nipissing, Ontario, westerly to the Pacific Ocean, a distance of 2,000 miles, and from the Mackenzie River a little north of Great Slave Lake southward to the mountains of Zacâtecas in Mexico, a distance of fully 3,000 miles. Most of the species dwell in forests, but a few inhabit the great sage brush plains. Faunally they contribute distinctive species to every life zone from the Upper Sonoran to the Arctic-Alpine. In mountainous regions the species are commonly distributed in parallel belts, the borders of which are not only in absolute contact, but even slightly overlap for long distances.

As it will be impossible in the time at our disposal to consider more than a few of the species, I have selected for illustration those that inhabit eastern California, along an east-and-west line extending from the west base of the Sierra Nevada to the summit of the White Mountains. On the gradually rising slopes of the Sierra the species are arranged one above the other, from base to summit, in definite belts or strata (see diagram, Fig. 2). Field studies have shown that these belts are the same as the transcontinental life zones, each of which is characterized by peculiarities of climate and by a definite association of species of mammals, birds, reptiles, trees and shrubs. There are no gaps between the belts, the upper border of one being coincident with the lower border of the next, so that individual animals of different species meet along the border lines of the several zones. In some cases only a single species inhabits a zone, but in one case not less than three occur together. These three however, as would be expected, are so very distinct from one another that they could not possibly have arisen by mutation.

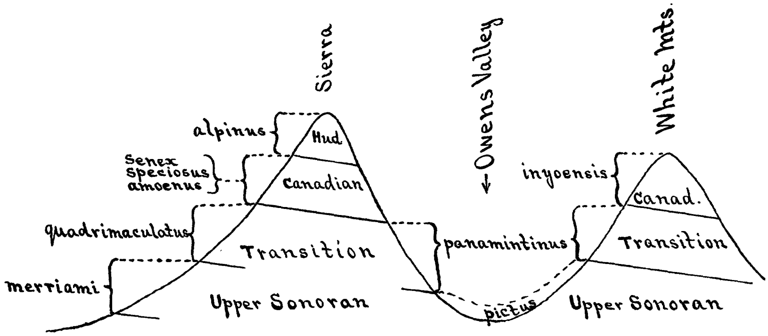

FIG. 2. Diagram Showing the Zone Ranges of Chipmunks (genus *Eutamias*) in an east-west section of the middle Sierra and White Mountains in eastern California.

Beginning at the foot of the Sierra on the west side, the first species encountered is a large, dark, long-tailed form (*Eutamias merriami*), whose range coincides with the limits of the digger pine or Upper Sonoran zone. Immediately above this is the broad belt of ponderosa pines and giant sequoias of the Transition zone. The chipmunk of the zone below does not occur here, but is replaced by a striking long-eared species (*quadrimaculatus*) which fills the zone and is restricted to it. Along the line where the yellow pines of the Transition zone change to the Murray pines of the Canadian no less than three species (*amœnus, senex* and *speciosus*) begin abruptly and range upward throughout the Canadian zone. Above this still is the Hudsonian zone, and it also has its distinctive chipmunk—a small but highly colored species (*alpinus*)—which fills the zone completely and climbs up a short distance on the alpine slopes above timber line. Crossing the summit and descending the steep east side of the Sierra, the Canadian zone is found to be inhabited by the same three species that occupy this zone on the west slope. Below this, in the nut pine belt of the Transition zone, is a brilliantly colored species (*panamintinus*) very different from any we have seen. Still lower, in the Upper Sonoran sage brush of Owens Valley, is a small gray species (*pictus*) not related to any of the others. Owens Valley is a long narrow and deep valley between the Sierra and the White Mountains. Crossing this valley and ascending the west slope of the White Mountains we reenter the nut pine belt and find the same chipmunk (*panamintinus*) that we found in the same belt on the other side of the valley (on the east slope of the Sierra). Continuing the ascent we enter the Canadian zone, which covers the greater part of the summit of the White Mountains, and in it find a widely different chipmunk (*inyoensis*), which proves to be another member of the beautiful *speciosus* group—a group we have already found represented in the same zone on both east and west slopes of the Sierra.

Thus in a distance of a hundred miles, from the west base of the Sierra to the summit of the White Mountains, are included the ranges of no less than nine species of chipmunks. This is made possible by the height and steepness of the mountains, the abrupt changes in altitude with consequent differences in temperature compressing the life zones into narrow parallel belts; whereas in level regions, as well known, these same belts are spread out broadly over the land.

The Sierra chipmunks furnish striking illustrations of the *occurrence* of species without isolation, and some of them of the *evolution* of species without isolation, for not only are there no visible barriers between the ranges of adjoining species, but the species themselves actually overlap along the zone borders, individual animals belonging to the zone above and the zone below occurring together on the same ground. But while there are no barriers *between* the species, each belongs to and is characteristic of a definite climatic life zone; and the fact that the life zones overlap slightly along the edges explains the slight geographic overlapping of the species themselves. The reason the species do not intergrade along the lines of contact doubtless is that they are not closely enough related—their differentiation into fully developed species (with the probable exception of *speciosus* and *inyoensis*) having taken place long ago.

The question now arises as to the origin of the nine species. Most of these, if studied independently of their relations in other parts of the country, resemble one another sufficiently to justify the inference that they have been derived from one another.

Far from holding this view, however, my belief is that some of them came from closely related forms in remote geographic areas, others from antecedent forms now extinct, and not more than three or four from species still inhabiting the region. The case is of a class often encountered by the systematist and student of distribution, where, without a comprehensive knowledge of the relationships and geographic distribution of the group as a whole and of its component species and subspecies, there is little hope of arriving at correct conclusions. Let us look closely at the facts, for they have an important bearing on more than one problem in evolution and distribution.

The Hudsonian species *alpinus*, now restricted to the lofty crest of the southern High Sierra, appears to be distantly related to *oreocetes* of Montana, but has no near relative.

Another of the Boreal species, *amœnus*, ranges northward over the Cascades in Oregon and is only subspecifically distinct from a form inhabiting the boreal forests of the Rocky Mountains in Colorado.

The *speciosus* group, it will be remembered, is represented in the east California section by two forms (*speciosus* and *inyoensis*), which may be called species or subspecies, as you like—the fact being that they are more closely interrelated than are any of the other forms of the region, although intergradation has not been proved. But instead of occupying different faunal zones, as do the other species, they occupy different parts of the same zone—*speciosus* inhabiting the Boreal slopes of the Sierra, *inyoensis* the corresponding Boreal crest of the adjacent White Mountains (here separated from *speciosus* by the Upper Sonoran and Transition zones of Owens Valley). But where did the *speciosus* type come from? Investigations carried on by the Biological Survey show that the same specific type still inhabits the upper slopes of the San Bernardino and San Jacinto Mountains in southern California, that a more distantly related form (*quadrivittatus*) occupies the Transition zone in Colorado, and that between the two, on an isolated mountain peak rising from the arid deserts of southern Nevada, is another species (*palmeri*), more strongly differentiated in consequence of local peculiarities of environment. These facts show not only that the *speciosus-quadrivittatus* group is a very old one, but also that its ancestors once inhabited the Great Basin itself. In those days the arid deserts of this region were in their infancy, and must have been completely bridged by continuity of coniferous forests, connecting the Sierra and Rocky Mountain areas.

The Desert Range species, *panamintinus*, which occupies the Transition zone on both sides of Owens Valley, occurs south of the White and Inyo mountains in the Coso and Argus mountains, and farther east, in the Panamint, Grapevine, Providence and New York mountains in the desert region of eastern California, and on Mount Magruder in western Nevada. It belongs to a group of which only one other species is known—*E. hopiensis*, of the high desert mesas of northeastern Arizona, southeastern Utah and southwestern Colorado. In this case, as in that of two other groups already discussed (the *amœnus* group and the *speciosus-quadrivittatus* group) the range of the type comprises localities on both sides of the Great Basin. It appears to be an aberrant offspring of the *speciosus-quadrivittatus* group and probably originated from the ancestors of that group in the bygone days when they inhabited the ancient forests of the Great Basin.

Eutamias senex appears to have originated in the Siskiyou Mountains, on the boundary between California and Oregon, as an offshoot from the redwood chipmunk, *ochrogenys*—which in turn is closely related to *townsendi* of the northwest coast of Oregon and Washington. From the Siskiyous, *senex* ranges north along the Cascades nearly to Mt. Hood, and south in the Sierra to the latitude of Yosemite Valley. In time it may be expected to push on to the south end of the Boreal Sierra in the Mt. Whitney region. *E. senex* appears to be the parent form, directly or indirectly, of two other species—*quadrimaculatus* and *merriami*—whose ranges now occupy considerable stretches along the flanks of the Sierra. It seems probable that *quadrimaculatus* originated near the north end of its present range and under existing geographic and climatic conditions. While, as we have already seen, it occupies the Transition zone, directly below the Boreal zone inhabited by *senex,* and while the ranges of the two are in direct contact for many miles, both species remain true, showing no tendency to intergrade. The history of *merriami* is by no means so simple, and the road by which it reached its present home by no means so direct. It is not an immediate offshoot from *senex,* for before attaining its present status it passed through another form, known as *pricei.* The story, as I interpret it, is this: In the northern part of California, south of the Siskiyous and west of the northern Sierra, the Boreal *senex* gave off a Transition zone form which spread and became differentiated in two directions: to the southward along the west flank of the Sierra it developed long ears and the peculiarities of coloration that distinguish *quadrimaculatus;* to the westward it developed the long tail and other peculiarities that distinguish *pricei.* The latter pressed southward through the coast ranges to Monterey Bay, south of which it underwent another change, assuming the characters by which *merriami* differs from *pricei,* and continued in the same direction to the Santa Barbara Mountains, and then easterly to Mt. Pinos, where its range forked, the north branch following the Tejon and Tehachapi Mountains to the southern Sierra and thence northward to a little beyond the Yosemite; the south branch pushing southeasterly over the Sierra Liebre, Sierra Madre, San Gabriel and San Bernardino mountains, and then south over San Jacinto and Palomar to the San Pedro Martyr Mountains of Lower California. In the Sierra region *merriami* is restricted to the Upper Sonoran zone, while its immediate ancestor, *pricei,* belongs to the Transition zone, and its remoter ancestor, *senex,* to the Boreal zone. The change from Boreal *senex* to Transition zone *pricei* and *quadrimaculatus* is merely a zone adaptation to an immediately adjoining area; the change from *pricei* to *merriami* is simpler and at the same time more interesting, for the belt occupied by *pricei,* while mainly Transition, possesses the climatic peculiarity of mild winters and relatively cool summers and fulfils the temperature requirements of both Transition and Upper Austral zones, permitting an overlapping or admixture of the distinctive species of both. In this belt *merriami* became adapted to Upper Austral conditions, so that in extending its range back to the Sierra it was natural that it should adhere to the Upper Sonoran zone.

The three Sierra members of the *senex* group (*senex, quadrimaculatus* and *merriami*) therefore have reached their appropriate zones from opposite directions—*senex* and its offshoot *quadrimaculatus* from the north by direct continuity of range; *merriami* from the south (after passing through another form) by the roundabout way of the Coast ranges and the Tejon and Tehachapi mountains.[8]

To sum up the story of the California chipmunks from the standpoint of their geographic origin: Of the nine species inhabiting the middle Sierra region, six (*senex, amœnus, speciosus, merriami, panamintinus* and *pictus*) appear to have come in from contiguous territory in their present condition—as fully formed species—although it is possible that one of them (*amœnus*) originated here and extended its range northward; and three (*quadrimacu-*

[8] The chipmunks afford admirable illustrations of a number of phases of variation and distribution besides those here discussed—as the occurrence of closely related forms end-to-end in the same zone; the spreading out of a species in certain parts of its range to cover an adjacent zone which elsewhere is avoided; the development of protective and directive coloration and markings; the utility or non-utility of characters used in the discrimination of species, and so on.

latus, inyoensis and *alpinus*) appear to have been developed within the region in the areas they now inhabit. So far as origin is concerned, therefore, we have to do with only the last three. Of these, one —*inyoensis*—was clearly derived from the *speciosus* stock by the gradual accentuation of minute variations; another, *quadrimaculatus,* appears to have originated from *senex* in the same way, as already explained, leaving only one, *alpinus,* whose *history* is by no means obvious. Since *alpinus* has no near relatives, there is little in the way of a clue to its ancestry. As already suggested, it may be the remnant of an Arctic-Alpine group, of which it and *oreocetes* of the high mountains of western Montana are the sole survivors. In any case its origin must be sought far back in the past.

I have dwelt thus at length on the California chipmunks for three reasons: (1) The problems they present to the student of variation and evolution are fairly representative of problems presented by other groups; (2) the compact distribution of the species in close-lying parallel belts in conformity with the life zones has the advantage of bringing them into near relations, so that the facts of variation and behavior are easily discerned; (3) the study of the group emphasizes the necessity of a knowledge of the geographic distribution of species in order that their interrelations and probable origins may be understood.

The term geographic distribution must not be taken to mean merely the area a species occupies, to be shown by a color patch on the map, but includes a comprehensive knowledge of the geographic environment, taking into account the climate and the aspects of nature with which each species is associated and by which it is profoundly impressed. Moritz Wagner, in a paragraph recently quoted by Doctor Jordan, said: It is 'the study of all the important phenomena embraced in the geography of animals and plants, which is the surest guide to the study of the real phases in the process of the formation of species.' To the systematist and student of evolution this knowledge is so fundamental that it is hard to see how correct conclusions can be reached without it. In studying problems in nature the geographic point of view is the natural method of approach; it is a method so full of suggestions and explanations that we can ill afford to do without it. And how can it be otherwise, for do we not all admit that organisms are profoundly affected and modified by their environment? The utter hopelessness of attempting to work out the variations, affinities and probable origin of a group of related species of animals or plants without giving heed to the geographic distribution of the various forms has just been illustrated by the case of the Sierra chipmunks. If to a knowledge of present distribution can be added a few facts from the paleontological history of the group a flood of light is at once thrown on the problem.

INTERGRADATION AND REGIONAL INFLUENCES.

In studying geographic variation in the various groups of terrestrial animals and plants one soon learns that among closely related species and subspecies some forms intergrade while others do not; and that among those that do intergrade, the change from one to another may take place abruptly in a narrow belt, or gradually, by imperceptible steps, over a wide area. These two kinds of intergradation do not usually occur in the same area, for the reason that each is associated with a definite set of geographic and physiographic conditions of which climate plays the most important part. As a general rule it may be asserted that where the geographic change from one faunal area to another is gradual, the change in the species is gradual; and conversely, where the geographic change is abrupt the change in the species is abrupt. Changes in a north-and-south direction are likely to be gradual; those in an east-and-west direction are likely to be more abrupt. In both cases, the controlling power of environment is easily recognized. It follows that one species does not change here, another there; the rule—to which there are exceptions—is that all change in a common belt or area. It thus comes about that American students of species, from Baird's time to the present, have learned to recognize certain geographic areas, usually in the form of belts, where the transition from one set of animals and plants to another set takes place. These belts of intergradation, broad or narrow as the case may be, are always flooded with intergrades, which, though the bane of the museum man, are of great importance to the student of variation and evolution.[9]

In order to make the matter perfectly clear—for it is one of no small importance to evolutionists—let me cite a few examples.

The common prairie ground squirrel or striped spermophile (*Citellus tridecemlineatus*) splits up into four geographic forms or subspecies. The range of the species as a whole extends from the plains of the Saskatchewan on the north to the coast of Texas, and from the extreme eastern edge of the prairie country in the Great Lake region westerly to and a little beyond the Rocky Mountains (see map, Fig. 3). Typical *tridecemlineatus* occupies the eastern and more humid part of this area. In ranging westward it undergoes a change, becoming paler and smaller as it enters the arid plains. The change occurs between the one-hundredth and one hundred and first meridians, from South Dakota to middle Texas, and the resulting pallid form (subspecies *pallidus*) continues westerly to the foot of the Rocky Mountains. In passing southward from the Upper Austral to the Lower Austral zone *tridecemlineatus* develops another form (subspecies *texensis*), which occupies a broad belt in Oklahoma and eastern Texas, east of the range of subspecies *pallidus*. But this is not all, for the plains form (*pallidus*) in pushing westward over some of the passes of the Rocky Mountains gives off still another subspecies (*parvus*), which occupies the Green River Basin in Wyoming, and extends thence southerly in an irregular and interrupted belt along the border between Colorado and Utah, and occurs in isolated colonies in New Mexico and extreme eastern Arizona. Between these several forms are the belts of intergradation, as shown on the accompanying map (Fig. 3).

The case is one in which a well-marked species splits into four geographic forms or subspecies in conformity with the climatic and physical features of the region inhabited. Each form is fairly constant throughout the major part of its range and develops intergrades in the transitional belt between it and the next form.

Among North American mammals and birds there are hundreds of such cases, and more than 1,000 species and subspecies, connected with other forms by series of intergrades, might be enumerated.

It may be set down as a general law that wherever a species or subspecies passes into another, intergrades occur, not side by side

[9] Among the belts of this kind are the overlapping boundaries of the life zones and certain other lines which mark the change from one physiographic or physiognomic type to another. Among these may be mentioned a strip along the western edge of the deciduous forests, where woodland gives place to prairie; a belt near the ninety-ninth meridian, where the humid prairies change to the arid plains; a belt along the east base of the Rocky Mountains, where plains forms change to mountain forms; and similar or corresponding areas in the Great Basin and in the interior of California.

with the typical form, but replacing it in the territory between it and that occupied by the new form, so that as a rule all the individuals from the transitional territory are intergrades. This fundamental fact in geographic biology seems to have escaped the keen eye of Darwin, who, in speaking of the difficulties and obstacles in the way of his theories, said:

"Why, if species have descended from other species by fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion, instead of the species being as we see them, well defined?" One of his critics, Thomas Hunt Morgan, thinks this a very serious matter. My reply to both Darwin and Morgan is that they are mistaken in their premises, for in nature transitional forms are so abundant as to be a source of annoyance and embarrassment to systematists and museum curators—men who are continually handling specimens which they desire to refer to one species or another. The only explanation I think of to account for Darwin's and Morgan's failure to recognize this fact is limited or unfavorable field experience, and limited experience in handling specimens from the peripheries of geographic areas large enough to cover the transition from one faunal division into another—in other words, failure to study the behavior of species in nature from the geographic standpoint. One might spend a lifetime in studying animals and plants in the interior of almost any of the faunal areas without encountering transitional forms or intergrades, for it is at the peripheries or borders of these areas that the intergrades occur. It would seem, therefore, that Darwin, in his effort to present fairly all objections to his theory, imagined a difficulty which does not exist, and that his critic Morgan solemnly shook his head at a man of straw.

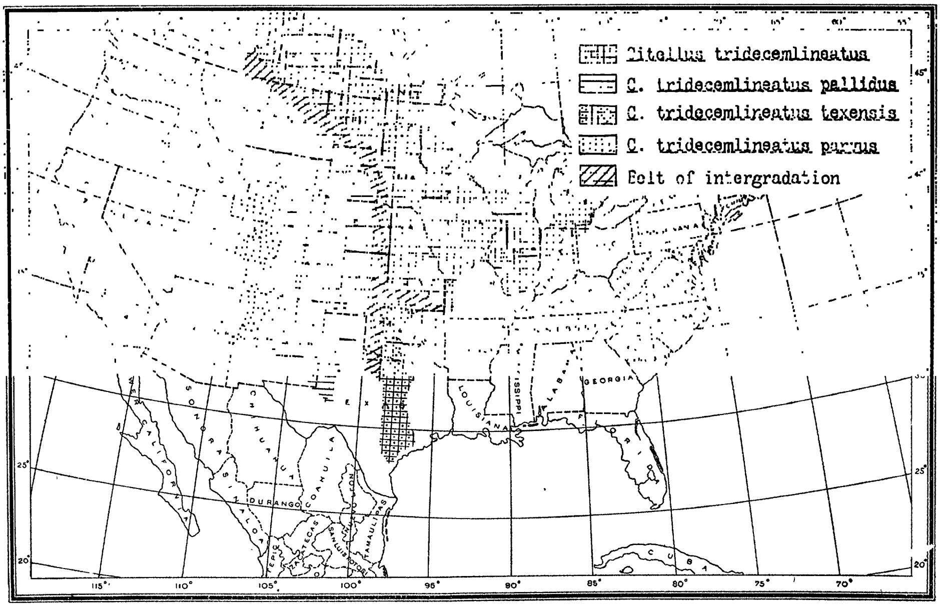

FIG. 3. Distribution of the Prairie Ground Squirrel, *Citellus tridecemlineatus* and subspecies.

Conclusion.—Inasmuch as all species have their beginnings in variations, and inasmuch as sudden or sport variations are exceedingly rare while slight variations are exceedingly common, does it not follow that the vast majority of species must originate from slight variations? My argument is not that species of plants may not in rare cases arise by the perpetuation of sport characters, as de Vries believes they do, but admitting this, my contention is that the overwhelming majority of plants, and so far as known all animals, originate in the generally recognized way, by the gradual development of minute variations. The theory of the origin of species by mutation, therefore, far from being a great principle in biology, as some seem to believe, appears to be one of a hundred minor factors to be considered in rare cases as a possible explanation of the origin of particular species of plants, but so far as known not applicable in the case of animals.

C. HART MERRIAM.

U. S. BIOLOGICAL SURVEY.

SECTION F—ZOOLOGY.

SECTION F was organized at the New Orleans meeting with the following officers:

Vice-President—Henry B. Ward, Lincoln, Nebr.
Secretary—C. Judson Herrick, Granville, Ohio.
Councilor—Herbert Osborn.
Member of General Committee—B. L. Seawell.
Press Secretary—C. Judson Herrick.
Sectional Committee—C. H. Merriam, Vice-president, 1905; Henry B. Ward, Vice-president, 1906; C. Judson Herrick, Secretary, 1905–6; C. H. Eigenmann, for one year; Henry B. Ward, for two years; Frank Smith, for three years; W. E. Ritter, for four years; A. M. Bleile, for five years.

On the afternoon of December 29 the vice-president's address was delivered by C. H. Merriam, on the subject, 'Is Mutation a Factor in the Evolution of the Higher Vertebrates?' The section met for the reading of papers on December 30, and joint sessions were held on January 1 with the Section of Physiology and Experimental Medicine, and on January 2 with the Association of Economic Entomologists. The following papers were read before the section:

Preliminary Observations on the Variation of Utethesia venusta, Dalman: MEL. T. COOK, Santiago de las Vegas, Cuba.

The literature recognizes three species (*U. bella*, *U. venusta* and *U. ornatrix*) and three varieties (*hybrida*, *terminalis* and *stretchii*) of this genus. These species cover a very wide range. The distinctive characters are primarily color characters. After examining a large number of specimens, many of which were reared in captivity, the writer concludes that intergradations are such as to reduce these three species and three varieties to one species.

Filaria loa, a Study on the Dispersal of Parasites: HENRY B. WARD, University of Nebraska.

Of the African eye worm (*Filaria loa*) the author has recently published a list of 86 old and 8 new cases. The first six cases on record were from the West Indies, as also twelve in the first 21. But since 1845 no cases have been recorded there, its introduction having ceased with the cessation of the slave trade. All cases were in negroes and most had recently come from West Africa. Five cases reported from France all originated in the French Congo, as also cases from Switzerland and Belgium. One specimen removed in Germany came from Kamerun, and five in England from Old Calabar.

Eight cases in North America since 1890 were all in missionaries and all but one came from Kamerun. Thus all extra-African cases are distinctly traceable to a known or a possible infection in the western part of that continent where the parasite is endemic. Here the review of cases indicates clearly that the parasite is distributed over the entire coast from about