cases of salt poverty, sodium chloride as well (these being materials which the organism can not afford to lose), while at the same time these epithelial cells, like those of the intestines, have also to perform the duty of excreting the combined substances of the blood by means of their specific secretory activity.

Diuresis, therefore, represents the fusion of two principal processes—one concerning the gomeruli, which is in its main features mechanical in its nature; the other pertaining to the urinary tubules, which is not yet explicable on any physico-chemical hypothesis. The process of resorption from the urinary tubules has a distinctly biological, that is, teleological character; water and salt are only reabsorbed when the organism does not possess these in excess. If one administers an abundance of water, the urine acquires a highly watery character, while after the administration of an abundance of sodium chloride there is a failure on the part of the tubules to reabsorb salt, as Loewi has shown. The process of reabsorption adapts itself, therefore, to the requirements of the organism.

Although I believe that the theory of renal function which I have here presented is the one which has the best experimental foundation, I readily concede that it leaves many facts still unexplained. For example, it is difficult by means of this hypothesis to explain the constitution of the urine in diabetes insipidus as well as the complete retention of chlorine under certain conditions, and I fancy that we shall have to suppose, as Cushny has done, that there is some kind of combination of sodium chloride with the blood tissue which hinders its filtration. The theory of diuresis and the action of diuretic drugs further possesses a practical interest. If, for example, it be true that caffeine acts diuretically through local specific dilation and not through irritation of the secretory cells, as was formerly supposed, then, as Loewi thinks, we are justified in its administration during long periods in the course of nephritis in which, in many instances, the vessels of the kidneys are abnormally contracted. And there is some reason to believe that the vasodilator action of the caffeine not merely induces an increased diuresis but exerts a favorable influence upon the pathological condition of the kidney itself.

In conclusion, I desire to express my appreciation of the courteous attention you have accorded me. HANS MEYER.

THE EVOLUTION OF SPECIES THROUGH CLIMATIC CONDITIONS.

IN a recent article in SCIENCE,[1] entitled 'The Origin of Species through Isolation,' President David Starr Jordan has presented much evidence bearing upon the influence of geographical isolation in the formation of species and races of animals and plants. He dwells especially upon the agency of barriers in interrupting the flow of life and isolating groups of individuals of a species, which groups of individuals, either with or without material change in the conditions of existence, 'may become in time an entirely distinct species if the barrier is really insurmountable.' This is impliedly recognized as only one of various influences that tend to modify species, but in this connection, in marshalling the evidence in favor of the proposition of the origin of species through isolation, hardly any reference is made to the part played by other agencies in the evolution of new forms. In this way, rather undue importance is given to a single and well-recognized factor in the problem of evolution. The purpose of the present paper is not to

[1] N. S., Vol. XXII., No. 566, November 3, 1905, pp. 545–562.

question or controvert any of the evidence, or in any way to belittle the principle of evolution by isolation, but to bring forward other well-known facts that bear on the problem of evolution through environment unassisted by isolation or obvious physical barriers.

Says President Jordan, in his opening paragraph:

> It is now nearly forty years since Moritz Wagner (1868) first made it clear that geographical isolation (räumliche Sonderung) 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. But to those who approach the subject of evolution from some other side the principles set forth by Wagner seem less clear. They have never been confuted, scarcely even attacked, so far as the present writer remembers, but in the literature of evolution of the present day they have been almost universally ignored. Nowadays much of our discussion turns on the question of whether or not minute favorable variations would enable their possessors little by little to gain on the parent stock, so that a new species would be established side by side with the old, or on whether a wide fluctuation or mutation would give rise to a new species which would hold its own in competition with its parent. In theory, either of these conditions might exist. In fact, both of them are virtually unknown. In nature a closely related distinct species is not often quite side by side with the old. It is simply next to it, geographically or geologically speaking, and the degree of distinction almost always bears a relation to the importance or the permanence of the barrier separating the supposed new stock from the parent stock.

With the above I am in hearty accord, except with the declaration that geographical isolation is a 'factor or condition in the formation of every species, race or tribe of animal or plant * * * on the face of the earth'; especially if the isolation here meant implies a physical barrier, 'geographical or climatic,' to the continuous range of closely allied forms, as the general context seems clearly to involve. That isolation is an important factor no intelligent biologist will be disposed to deny; that it is not the only important factor, or, as regards incipient species, the chief one involved there is ample evidence, well-known to a large number of present-day investigators.

President Jordan, however, appears to have mainly in mind species, or fully segregated forms, rather than incipient species, or intergrading geographic phases; as when he states, as 'practically a universal rule': "A barrier which prevents the intermingling of members of a species will with time alter the relative characters of the groups of individuals thus separated. These groups of individuals are incipient species and each may become in time an entirely distinct species if the barrier is really insurmountable."

In illustration of his theme, the author cites examples of mammals, birds, fishes and mollusks, which serve very well to illustrate the points at issue; except that incipient species, as well as fully segregated forms, are claimed to owe their existence to barriers, either geographic or climatic, which is not generally the case, taking the term 'barrier' in its commonly accepted sense.

Doubtless President Jordan well knows that among birds and mammals, and especially among the former, many wholly distinct congeneric species, or forms that are known not to intergrade, are often much more nearly alike, structurally and in color and size, than are the extremes in many groups of forms that are known to intergrade completely through geographically intervening forms, as notably in the song sparrow (*Melospiza cinerea*) group; and that many other conspecific groups of wide distribution show nearly parallel variations, as the horned larks, and, to a lesser

extent, many species of woodpeckers, jays, the bob-whites, some of the pipilos, juncos, wrens, titmice, etc. As to exploit all of these cases would require a good-sized volume, only two or three can be taken for illustration in the present connection.

In the first place, to facilitate treatment, certain general well-known laws of climatic or geographic variation may be recalled, which are of so nearly universal application that the exceptions, generally easily explainable, may be ignored. First, in relation to size. In the northern hemisphere, in nearly all types of both birds and mammals of obviously northern origin, there is a gradual decrease in general size from the north southward in the representatives of a conspecific group, most marked, in the case of birds, in non-migratory, or only partly migratory, species, the most southern representatives of such groups being from one fifth to one third or more smaller than the most northern representatives of the same groups. At the same time, but less generally, there is a relative increase in certain peripheral parts, as the length of the tail, the thickness or length of the bill (according to its form) in birds, and often the ear, tail and feet in mammals.[2]

[2] As already intimated, there are some exceptions to the rule of decrease in size southward, which are covered by the following propositions, first formally propounded in 1876 (*Bull. Geol. and Geogr. Surv. Territories*, Vol. II., No. 4, July, 1876, p. 310) in relation primarily to mammals and later (*Bull. Nutt. Ornn. Club*, Vol. III., April, 1883, pp. 80–82) restated with more direct reference to birds, as follows:

"(1) *The maximum physical development of the individual is attained where the conditions of environment are most favorable to the life of the species.* Species being primarily limited in their distribution by climatic conditions, their representatives living at or near either of their respective latitudinal boundaries are more or less unfavorably affected by the influences that finally limit the range of the species. * * * Different species being constitutionally fitted for different climatic conditions, surroundings favorable to one may be very unfavorable to others, even of the same family or genus. Hence:

"(2) *The largest species of a group* (genus, subfamily, or family, as the case may be) *are found where the group to which they severally belong reaches its highest development, or where it has what may be termed its center of distribution.* In other words, species of a given group attain their maximum size where the conditions of existence for the group in question are the most favorable, just as the largest representatives of a species are found where the conditions are most favorable for the existence of the species.

"(3) *The most 'typical' or most generalized representatives of a group are found also near its center of distribution, out-lying forms being generally more or less 'aberrant' or specialized.* Thus the Cervidæ, though nearly cosmopolitan in their distribution, attain their greatest development, both as respects the *size* and the *number* of the species, in the temperate portions of the northern hemisphere. The tropical species of this group are the smallest of its representatives. Those of the temperate and cold-temperate regions are the largest, where, too, the species are the most numerous. Most of the species of this family also have a wide geographical range, and their representatives respectively present great differences in size with locality, namely, a very marked decrease in size to the southward. The possession of large, branching, deciduous antlers forms one of the marked features of the family. These appendages attain their greatest development in the northern species, the tropical forms having them reduced almost to mere spikes, which in some species never pass beyond a rudimentary state. * * *"

Secondly, and coincidently with the decrease in size southward, is a change in coloration, which may be described in general terms as a restriction in area of all white markings and a corresponding increase in the area of the dark markings, together with, generally speaking, an increase in the intensity of color in markings or areas of other tints than black or white, as yellows, greens, browns, etc., and also in iridescence, in birds of metallic tints. The birds of latitudinally extended breeding ranges in eastern North America rarely present exceptions to these rules; and many

of the mammals of the same region exhibit perfectly parallel variations. Nor are these rules restricted to eastern North America, but prevail throughout the northern hemisphere, and also in the southern hemisphere, with, however, the conditions reversed, the increase in size and intensity of colors being from the south northward. High mountains in low latitudes represent, in respect to these phenomena, the higher latitudes nearer sea-level.

It is equally well known that, in continentally dispersed groups, pallid tints accompany desert areas and arid conditions of climate, and that increase in depth of color, particularly in gray, brown and olive tints, is an inseparable accompaniment of regions of heavy rainfall and a moist climate, so familiarly illustrated in the northwest coast region of North America. Furthermore, there are various other areas in the world where the animal inhabitants are collectively characterized by some special feature of coloration, as excessive lightness of color—hoariness, or increase in area of light or white markings in eastern Siberia, or redness or blackness of coloration in parts of Africa, etc. In other words, regional areas of peculiar climatic conditions impress upon their animal inhabitants a certain distinctive phase of coloration, developing in some instances wholly new specific types, in others merely forms that intergrade with others of the immediately adjoining districts.

To return now to our starting point in eastern North America, the variation in size from the north southward is as gradual and continuous as the transition in climatic conditions; there are no barriers, in the ordinary sense, and no abrupt transitions. In conspecific groups the phase inhabiting Canada or the northern border of the United States, in species of wide breeding range, differs more from the phase inhabiting southern Florida and the Gulf coast than do many congeneric species known to be completely distinct; and were these phases isolated by a wide geographic interval they would have to be recognized in nomenclature as distinct species. It would also be the same if they were found living together, the differences between them are so marked. In reality, however, these very distinct phases are merely the extremes of a single continuous intergrading series or unbroken sequence of individuals of one and the same species.

In passing westward from the Atlantic seaboard to and across the arid interior of the continent, and thence to the Pacific coast and northward to Alaska, other forms of the same conspecific groups may come into view, so distinct from their eastern representatives and from each other, that many of them were originally described as distinct species, and for many years were so recognized, till the accumulation of material from many intermediate points showed them to be connected by insensible gradations over the intermediate regions, and that their true status was that of incipient species, or merely geographic forms, distinct enough when birds of distant and limited areas are compared, but inseparable when those of intermediate regions are taken into account. There are also, in these cases, no barriers beyond the gradual climatic transition from one area to another. This, at some points, owing to topographic conditions, may be abrupt, but in general is too diffused to prevent the continuous spread of the species.

In illustration of these points, we may take the downy and hairy woodpeckers (*Dryobates pubescens* and *D. villosus*), both species of continental distribution, and each with its half dozen or more commonly recognized subspecies, varying enormously in color and in size when those of

eastern North America are compared with each other, or either of these with the Rocky Mountain forms, and these again with the northwest coast and southern California birds.

The eastern flickers (*Colaptes auratus*), the western flickers (*C. cafer*), and the eastern pileated woodpecker (*Ceoplœus pileatus*), have also been divided into subspecies, mainly on the difference in size between the northern and southern representatives of the species. The bob-white (*Colinus virginianus*) has in the east its northern and southern forms, differing markedly in size and coloration, with another pallid form in Texas, which passes into a group of very diverse forms in different parts of Mexico, some of them having black instead of white throats, uniform chestnut instead of barred black and white underparts, and others with various other combinations of characters, yet all retaining their characteristic *bob-white* call, and so blending with each other and the northern forms as to be found to be specifically inseparable, though they have usually been accorded the status of species.

The horned larks (*Otocoris alpestris* group), ranging from the Arctic regions to northern South America, and embracing nearly a score of forms, some of them extremely diverse, are found to completely intergrade, though the various forms have special breeding areas, and have obviously attained their differentiations under the most diverse climatic conditions. Yet they are separated by no appreciable barriers, and contiguous forms completely intergrade, forming an unbroken chain from one extreme of the series to the other.

The almost hackneyed case (at least to ornithologists) of the song sparrows (*Melospiza cinerea* group), nearly continental in dispersal and differentiated into about twenty recognized forms, may well close this series of illustrations. Many of the forms of this group are so different that, when compared without the connecting links, they seem like remotely related species, almost different enough for subgeneric separation. Between the great gray song sparrow of the Aleutian Islands and the little song sparrow (*pusillula*) of the San Francisco salt marshes the difference in size is enormous, the length of the wing being 85 mm. in the Alaska bird and 56 mm. in the San Francisco bird, the northern bird having probably more than twice the bulk of the southern one. Between them are some eight Pacific coast forms, by means of which there is continuous gradation between these extremes. Between the desert forms of the interior and the coast form at Sitka, there is much less difference in size, but the former is a pale gray bird, while the latter is deep intense rufous.

The recognized Pacific coast forms, from Lower California to the Aleutian Islands, excluding several insular phases, are nine in number, between which there is no abrupt barrier, either climatic or geographic, and consequently we find the successive and gradual mergence of all; but if a few of the links were dropped out, the remaining forms might readily be taken for distinct, fully segregated species, so much do they mutually differ.

Almost numberless similar illustrations might be cited among North American mammals. In general, the geographic ranges of conspecific groups in mammals are less extended, but they are of sufficiently wide range to include a great variety of environmental conditions, which result in marked modifications of size, color and structure.

Indeed, mammals being sedentary, they are even more susceptible to climatic modification than birds. Some of the more

widely dispersed species of squirrels, spermophiles, voles, field rats and mice, hares, gophers, pouched rats and mice, deer, shrews, moles and bats, afford admirable illustrations of differentiation without isolation. To cite a single notable case, the Virginia deer ranges over eastern North America from New England and southern Canada to Central America, varying greatly but gradually, in size and other features, till in the southern forms the size is only about one half of that of the northern, with disproportionately reduced antlers.

Variations of this nature, however striking, can not be due to isolation, for in the cases here in view there is no isolation, but continuous distribution, and consequently complete intergradation. The amount of differentiation, between the more extreme phases in various directions, is great enough, were these several forms isolated, or separated by geographic intervals, to warrant their recognition as well-marked species. All that is requisite to constitute them species is the extinction, through some physical cataclysm or other cause, of the connecting links, over portions of the intermediate areas by which even the extremest phases are at present connected. Doubtless in the past many species, and perhaps genera, have had their origin in the dismemberment of such groups of incipient species, through violent physical changes in the distribution area of widely dispersed specific types.

At present these connecting links between the leading phases of highly diversified conspecific groups are a nuisance and a stumbling block to the systematist in labeling collections, since between each properly namable form there is an area, more or less extended, where none of the forms are typically represented, but which is occupied by troublesome intergrades, approaching one form, usually, more than another, and in various degrees. These intergrades, furthermore, offer a temptation to aspiring young naturalists to give them a name, thus 'bridging the difficulty by doubling it.' If these areas of intergradation could be transformed into areas of isolation many problems in nomenclature and much trouble in identifying specimens would be eliminated.

The facts already set forth explain why two or more subspecies are never found in the same breeding area—a proposition discussed at some length in the paper here under consideration. They also show why insular forms, if separated somewhat remotely from the parent stock, assume the character of species rather than subspecies, and owe their existence to isolation. But insular forms exhibit various degrees of distinctness from the parent stock, depending upon the completeness and duration of the period of isolation. Theoretically there can be no intergradation between insular forms, particularly in land mammals—not so clearly in the case of birds, with their exceptional powers of locomotion; but in the case of forms inhabiting islands but little removed from a neighboring mainland, the environing conditions may be so similar that not time enough has elapsed to develop a well-marked type through the action of isolation, in which case the normal range of individual variation in the insular and the stock forms may be sufficient to cause an overlapping of the characters through occasional individual aberration. This might be mistaken for actual intergradation, while it is in fact merely an overlapping through individual variation. To this condition is probably due the recent tendency to give slightly differentiated insular forms the rank of subspecies rather than that of full species, to which theoretically they should be entitled.

I have long been a believer, in common

with many of my fellow-systematists, in the evolution of species and races by environment, which, of course, includes evolution by isolation. This seems far more rational than evolution by natural selection, as this process was originally defined. But since the inefficiency of natural selection, pure and simple, to produce the results formerly attributed to it became evident the significance of the term has been expanded to embrace evolution through climatic influences, including also the factor of isolation. The inefficiency of natural selection, as originally defined, in the evolution of species and races was the subject of frequent comment by the present writer in various papers published some thirty years ago, in opposition to which was urged the direct action of environment in the origination of incipient species. The discussion was eventually summarized in a paper published in 1877, entitled 'The Influence of Physical Conditions in the Genesis of Species.' This paper, of some thirty-three pages, appeared in a short-lived and not widely known magazine,[3] and thus doubtless escaped the attention of many investigators interested in such problems. The facts of geographic variation were here presented at some length.

In discussing Darwin's statement[4] regarding the method of the action of natural selection, namely: 'I believe that natural selection generally acts slowly in effecting changes, *at long intervals of time, and only on a few of the inhabitants of the same region,*' the direct and simultaneous action of climatic conditions upon all of the individuals inhabiting the same region was dwelt upon at length. Thus, to quote a few passages:

> The local races of any given region, as compared collectively with those of contiguous regions, and the manner of their mutual intergradation, point plainly to some general or widely acting cause of differentiation. This is indicated by the constancy of the results, so many species, belonging to numerous and widely distinct groups, being similarly affected. * * * There is, however, a vast amount of unquestionable proof of the direct and constant action of climate and other conditions of life upon animals, and that such geographical variations as the thicker and softer fur of mammals inhabiting cold regions, smaller size and brighter colors at the southward, etc., do not require the action of natural selection, in its strict and proper sense, for their explanation. It is well known, for instance, that a flock of fine-wooled sheep, when taken to a hot climate, rapidly acquire a coarser and coarser fleece, till, in a few generations, it nearly loses its character of proper wool, and becomes simply hair; that the change affects simultaneously the whole flock, and is not brought about by one or two individuals acquiring a coarser fleece and through their descendants modifying the character of the herd. Furthermore, in the case of sheep, it is well known that certain countries are very favorable to the production of a fine fleece, and that fine-wooled breeds, even by man's aid, can not be perpetuated in other regions. Again, it is a fact of common observation that in birds and mammals colors become more or less faded toward the moulting season simply by the direct action of the elements—the tints of the fresh and the long-worn plumage or pelage being more or less strikingly different in the same individuals—and that this contrast at different seasons is more marked in arid than in moist regions, through the greater bleaching effect of a dry heated atmosphere and the more intense dazzling sunlight of regions that are not only cloudless, but lack the protection afforded by abundant vegetation.

But climatic conditions were not claimed in this essay as the only agent in the evolution of species and races. President Jordan has referred to the song birds of the family Drepanidæ in the Hawaiian Islands, with such remarkable diversity in the form of the bill and other features, which he ascribes, perhaps properly enough, in part to natural selection and in part to isolation. Upon such cases the following paragraph from my long-forgotten paper has some bearing:

[3] *The Radical Review*, No. 1, May, 1877, pp. 108–140.

[4] 'Origin of Species,' 5th ed., p. 168.

While so much is claimed * * * as due to climatic causes, it is admitted also that habits and food, and other conditions of life than those resulting from climate, have a marked effect in determining modifications of form and color among animals. A scarcity of a favorite kind of food will undoubtedly force species to subsist upon the next best that offers, which may be so different as to modify certain characters and fit the species to live upon the less desired food. A change of food may lead to modification of dentition, the muscles of mastication, and the organs of digestion, and, correlatively of other organs or parts of the body; the modification, however, arising simultaneously among all the descendants of the individuals thus driven to a change of diet, instead of appearing first in a single individual and becoming perpetuated in its descendants alone. Entomologists have found that, among insects of the same species, the forced or voluntary use of different food-plants gives rise to modifications of color and structure, and hence results in what have been termed phytophagic varieties or subspecies, and that man can also affect such changes at will by simply changing the food of the species. Again, the geological character of a country is well known to have a marked effect upon the size and color of animals inhabiting it, as is strikingly illustrated among molluscous animals, whose abundance, and even presence, is largely dependent upon the constituents of the soil. Over regions of the United States, for example, where the underlying rock is non-calcareous, the species are both few in number and sparsely represented. In respect to the fresh-water mussels, those of the same species from different streams are easily distinguishable by differences in the thickness of the shell, in color, shape, and ornamentation, so that the character of the shells themselves affords a clew to the locality of their origin. At some localities the species tend to become tuberculous or spinous * * *; at other localities, they acquire a very much thickened shell, or different colors, the same characteristics appearing simultaneously in quite diverse species, and thus becoming distinctive of particular localities. [After reference to mammals of certain regions being influenced in relation to size by the presence of calcareous or non-calcareous soils, and to the birds of the Galapagos Archipelago, with their short wings and large bills, etc., there follows:] The sedentary life necessitated by the confined habitats of species thus situated would naturally act more or less strongly on the organs of flight, and a reduction in the size of the wing would follow; not necessarily through the round-about process of natural selection, through the modification originally of a single individual, but by the direct action on all the individuals alike of the changed conditions of life.

There are thus what may be termed regional modifications due to the direct action of environment, independently of natural selection, in its original, restricted sense, or of isolation. The modifying influence may be either primarily climatic or due to peculiar constituents of the water or soil and the resultant vegetation. In a sense the two latter conditions may act as barriers, with the resultant effect of modified isolation. In general, however, in birds and mammals, in which regional modifications are so patent, the main factor is climate, the action general, and the transition between regions gradual. While all these influences may be as active on islands as on continents, there is in the former the powerful agency of isolation superimposed upon all the other agents that tend to the differentiation of animal forms.

J. A. Allen.

SCIENTIFIC BOOKS.

The Evolution Theory. By Dr. August Weismann, Professor of Zoology in the University of Freiberg in Breisgau. Translated with the author's cooperation by J. Arthur Thomson, Regius Professor of Natural History in the University of Aberdeen, and Margaret R. Thomson. London, Edward Arnold. 1904. 2 vols., illustrated. Pp. 416 and 405.

No one, in the last thirty years, has contributed more to the discussion and investigation of evolutionary problems than has August Weismann. The present work marks the culmination of his long series of stimulating writings. His fertility in hypotheses and keenness of criticism are well known; not less noteworthy is his readiness to withdraw hypotheses when disproved, or to modify them to conform with new discoveries. Thus, the