Occasional Papers

OF THE

CALIFORNIA
ACADEMY OF SCIENCES.

III.

SAN FRANCISCO.

1893.

EVOLUTION OF THE COLORS

OF

NORTH AMERICAN LAND BIRDS

BY

CHARLES A. KEELER.

San Francisco:
California Academy of Sciences,
January, 1893.

Committee of Publication:

H. W. HARKNESS, H. H. BEHR,
T. S. BRANDEGEE.

Editor: TOWNSHEND STITH BRANDEGEE.

PREFACE.

The present paper has been written more with the hope of stimulating thought and inciting research in a new and as yet almost untrodden field of ornithological inquiry, than with the expectation of reaching definite results. The subject is as yet too new and difficult to be reduced to even the semblance of an exact science, and accordingly all the views here set forth are more or less provisional and tentative. I have constantly proceeded upon the assumption that a poor theory is better than no theory, provided it be not considered as final, since it affords an opening wedge for the further study of a subject. Accordingly many of the views here set forth are hardly to be considered as more than guesses, and it is expected that future study will serve to show their fallacy. If they lead to this further study, however, and to more exact and comprehensive work by others, I shall be glad to see them overturned and their places filled by more worthy hypotheses.

In the preparation of the work I have received much valuable assistance, which I here take pleasure in acknowledging. Much of the examination of specimens was done at the United States National Museum, the authorities of which kindly placed their collection of birds at my disposal. To Mr. Robert Ridgway I am indebted for innumerable personal favors during my stay in Washington. His Manual of North American Birds has formed the systematic basis for this paper. Dr. L.

Stejneger assisted me very materially by his criticism and suggestions, he having devoted more attention to this subject than any other American ornithologist. Dr. Elliott Coues furnished me with several useful terms (some of them new), as well as many suggestions which have been of value. Mr. F. C. Test of Washington, Mr. Witmer Stone of the Philadelphia Academy of Sciences, and Dr. J. A. Allen and Mr. Frank M. Chapman of the American Museum of Natural History, have aided my work, both by placing their collections at my disposal and by furnishing me with valuable facts and suggestions. Dr. Allen's important contributions to the subject here discussed have been of far more service than the mere quotations indicate. To Mrs. Katharine Brandegee and Mr. Frank H. Vaslit I desire to return thanks for their kind and painstaking revision of the proof, also to Mr. Walter E. Bryant, who read the proof for scientific terminology.

BERKELEY, Cal., December 21, 1892. C. A. K.

CONTENTS OUTLINE.

I. INTRODUCTION.

THE INHERITANCE OF ACQUIRED CHARACTERS............ 2

Theoretical Aspect of the Subject............................ 2

Heredity. Introduction; 2; Lamarck, originator of the doctrine of use and disuse, 2; Hilaire, originator of the doctrine of environmental influences, 2–3; Darwin, doctrine of pangenesis, 3; Brooks and Galton's modifications of this, 5; Morgan, criticism of pangenesis, 5; Spencer, physiological units, 6; bearing of theories of heredity upon transmission of acquired characters, 7; Weismann, 7; value of his work, 8; immortality of protozoa, 8; mortality of metazoa, 9; Naegeli's nucleoplasm theory criticised, 10; immortality of germplasm precluding the inheritance of acquired characters, 10; Vines' criticism of Weismann, 11; Weismann's reply to Vines, 13; Ryder, theory of heredity opposed to Weismann, 17; Morgan on cellular continuity, 19; Eimer on same, 20; summary of argument between Weismann and his opponents, 21.

Pammixis. Morgan's criticism of, 22; Cunningham's criticism, 23; Romanes on cessation of selection, 23; other theories to account for degeneration, reversal of selection (Romanes), economy of energy (Darwin), disuse (Lamarck), retardation (Cope), 24.

Practical Aspect of the Subject................................ 27

Consequences of Dispensing with the Inheritance of Acquired Characters. Cunningham, general consequences, 27; inability of accounting for origination of new characters, 27; inheritance of acquired characters by protozoa admitted, 28; Osborn, why should this factor become obsolete?, 28; Romanes, all variations must be directly acquired, 28.

Evidence of Observed Cases of Transmission. Abnormal Transmissions. Cunningham on why mutilations are not transmitted, 29; Morgan, the transmission of mutilations not a proof of the inheritance of acquired characters, 29; Weismann on mutilations, 30; experiments with white mice, 31; Cunningham's criticism of his observations on the feet of Chinese ladies, 31; Eimer, instances of observed cases of transmission of mutilations, 32–34; inheritance of artificially induced epilepsy in guinea pigs, 34.

NORMAL TRANSMISSIONS: observed instances of change due to environment, 34; examples of changes in goldfish and brine-shrimp, 34-35; discussion of the validity of these examples as proofs, 35; after effects in plants illustrative of an hereditary rhythm, 36; change in environment not established in one generation, but only the predisposition to change, 37; inheritance of acquired habits, 38; Elliott's examples, 38; these not proofs of inheritance, 39; Darwin's instances criticised by Ball, 40; results which can be best explained by transmission of acquired characters, 41; Romanes' examples of instinct due to the transmission of acquired characters, 41–42; æsthetic faculties of man, 42; Spencer's three forms of evidence of transmission, 43; the first and third form untenable, according to Romanes and Ball, 43–44; correlation as a proof, 44; the giraffe as an illustration of correlation, 44; Ball's criticism of this illustration, 45; further discussion of correlation, 46; Osborn on paleontological proofs of transmission, 46–48; Poulton's reply to Osborn's evidencs, 48; summary of discussion, 49–50.

VARIATION AND NATURAL SELECTION 50

Scope and meaning of natural selection, 51; not creative (Schurman), 51; conditioned by variation, 52; variations quantitative rather than qualitative, 52; how are new parts originated?, 53; variations must be advantageous to be favored by selection, 53; Romanes on useless variations favored by selection, 54.

THEORIES EXPLAINING VARIATION 54

Spencer's physiological units, 55; Weismann on sexual combinations, 55; variations according to this view must be within the extremes of ancestral modification, 55; Hartog's objection, 56; Lloyd Morgan's theory of organic compounds, 58; objections to this view, 59; Three views of the origin of variations, 59; spontaneous, uninfluenced by environment, 59; due solely to environment, 60; inherent tendency to vary in a specific direction, 60; conservative variations, 61; progressive variations, 61; Brooks' secondary laws of variation, 62; conclusion concerning variations, 62.

LAWS CONDITIONING EVOLUTION 64

LAWS OF DEVELOPMENT 65

Bathmism, or growth force, 65; law of extent and density; 66; phylogenic extent and density, 67; metabolism, 67; law of sexual intensification, 68; Gulick's criticism of Brooks' theory of male progressiveness, 72; acceleration and retardation, 73; cause of acceleration, 74; the originator of the fittest, 75; bearing of the law of phylogenic extent and density upon acceleration and retardation, 76; law of concentration, 77.

LAWS OF STRUCTURE 77

Homology, 77; successional relation, 77; parallelism, 78; adaptation, 78; geratology, 78; bilateral symmetry, 79; correlation of growth, 79.

Laws of Heredity 79
Uninterrupted or continuous transmission, 79; interrupted or latent transmission, 79; sexual transmission, 79; mixed or mutual transmission, 79; abridged or simplified transmission, 80.

SEXUAL SELECTION 80
Law of battle, 81; preferential mating, 81; Darwin's and Wallace's views compared, 82; relation of color of male to vitality and vigor, 82; color as related to integumentary expanse and complexity, 83.

Evidence of Selection by the Female 84
Peckham on sexual selection among spiders, 84; Wallace's explanation of sexual display by male birds, 85; the house-finch as an illustration of selection, 86; objection that each bird finds a mate, 87.

Difficulties in the Theory of Sexual Selection and Alternative Hypotheses 88
Beddard on sexual dichromatism without selection, 89; difficulty of believing in a highly developed æsthetic sense in birds, 90; Stolzman's view of bright colors and appendages of male birds, 91; Romanes' reply to Wallace's objections, 92; Wallace on the æsthetic sense in relation to sexual selection, 93; Poulton on the same, 94; Morgan on the æsthetic taste of birds, 95; the beautiful in inorganic nature contrasted with the beauty of birds and insects, 96; Weismann on novelty as the cause of sexual selection, 97; Romanes on the beautiful among the lower forms of life, 97; coloration viewed from a general standpoint, 98; colors which have been evolved with reference to some percipient being, 99; implications of the theory of sexual selection, 100; Grant Allen on the mechanical explanation of the pleasure derived from color combinations, 100; the pleasure given to birds by color combinations is of this lower order, 101; synthesis of factors involved in the production of the sexual character of birds, 102.

THE NATURE OF SPECIES 103

On the Meaning and Limitations of the Term 103
Natural and artificial modes of classification, 103; the basis of a natural system, 103; relativity of the term species, 104; definition of species as used in science, 105.

On the Relation of Evolution to Species 106
Species necessary for rationality in evolutionary progression, 106; Romanes on the preservation of the species by natural selection, 106; objections to Romanes' view, 107; reproduction as growth beyond the individual as an explanation of the origination of altruistic characters and traits, 108; necessity for natural selection to preserve family, and in some instances the tribe, but not the species, 109.

ISOLATION AS A FACTOR IN THE EVOLUTION OF SPECIES. 110

Physiological Selection.................... 110

Romanes' three difficulties in natural selection considered as a theory of the origin of species, 110; explanation of physiological selection, 111; sterility of species, 111; variations in the reproductive system as correlated with other variations, 113; on the swamping effects of interbreeding and the inutility of specific characters, 114; objections to physiological selection by Meldola and Galton, 115; Romanes' reply to these objections, 116; Wallace's objections, 117; Romanes' reply to Wallace, 118; Seebohm's criticisms, 121; Romanes' answer, 122; Dyer's criticisms, and Romanes' refutation of his objections, 123; conclusions concernphysiological selection, 124.

Gulick on Isolation.. 125

Resemblance and difference between the view of Romanes and Gulick, 125; criticism of his views, as ignoring the origin of variations, 126; necessity for isolation established, 127; forms of isolation, 128 *et seq.*

II. THE COLORS OF NORTH AMERICAN BIRDS.

ON MODES OF PLUMAGE CHANGES.......................... 132

By the feather itself becoming altered in color, 133; by the wearing off of the lengthened lighter-colored tips of the feather, 135; classification of different modes of plumage change, 137.

GENERAL PRINCIPLES OF COLOR IN BIRDS 137

On the physical and mechanical causes of color effects, 137; statement of the theory of bird colors to be elaborated, 139; law of assortment of pigments, 140; examples illustrating this law, 140; on generalized and specialized colors, 142.

THE PROPORTION AND DISTRIBUTION OF THE COLORS IN NORTH AMERICAN GENERA......................... 143

On the general distribution of the fundamental colors among North American genera, 143; the bearing of these facts on the law of the assortment of pigments, 145; the proportion and distribution of black, 146; white, 151; black and white as cognate colors, 152; the proportion and distribution of red, 153; red and yellow as correlative colors, 154; examples showing this interdependence, 155; the proportion and distribution of yellow, 157; blue, 157; generalizations from foregoing facts, 158.

THE PATTERN OF MARKINGS.................................. 159

On Individual Feathers 159

Feather markings as affected by the general laws of growth, 159; Eimer and Kerschner on feather markings, 162; secondary pigmentation to be accounted for by metabolism, 163; examples illustrating the method of pigment assumption, 163; successional taxology, 164; further examples of successional taxology, 164; study of the pattern of markings on the wing of *Falco sparverius*, 165; the significance of successional taxology, 169; natural selection as a factor in the origination of feather marks, 170; repetitive marks, 171; hybrid feathers, 172; examples of hybrid feathers, 173; classification of the different forms of hybrid feathers, 174; explanation of the different forms of hybrid feathers, 174; pseudo-hybrids, 177.

ON THE GENERAL PATTERNS OF BIRD COLORS....... 179

Eimer's law of posterior–anterior progression of markings, 179; markings of the primitive plumage, 180; characteristic types of markings, and those which seldom or never occur, 180; Dr. Harrison Allen on the relation between large masses of muscular and nervous tissue and color patches, 182; on the location of color patches on the most conspicuous parts of the body, 183; the superciliary stripe, 185; on the markings of the head, 186; relation between laws of growth and selection in the production of these markings, 190; wing markings, 190; tail markings, 191.

RECOGNITION MARKS.. 193

Markings considered from the standpoint of their utility, 193; Poulton's classification on this basis, 194; protective colors (procryptic), 195; aggressive colors (anticryptic), 197; false warning colors (pseudosematic), 198; warning colors (aposematic), 200; recognition marks proper (episematic), 200; Wallace on recognition marks, 200; Todd on directive colors, 201; classification of recognition markings, 201; recognition at a distance and at close range, 203; recognition markings among the grouse, pigeons and hawks, 204; tail markings of the Caprimulgidæ, 207; law of sexual recognition, 209; socialistic markings, 210.

VARIATION OF COLOR WITH SEX, AGE AND SEASON........ 211

Individual variation in bird markings, 211; epigamic colors, 211; Darwin's classification of birds according to the variations in plumage with sex, age, and season, 212; additional classes, 213; revised table of classification, 214; male like female, young like adult, 214; male like female, young differ from adult, 216; resemblance of sexes differing with the seasons, or both sexes alike and varying with the seasons, 218; male more conspicuously colored, young like female, 221; male more conspicuously colored, young with peculiar first plumage, 222; male more conspicuously colored, young of each sex resembles its respective adult, 223; adult male more conspicuously colored, young male unlike adults of either sex, 224.

THE DIRECT INFLUENCES OF THE ENVIRONMENT.......... 225

Beddard on the general effects of food on color, 226; Stejneger's theory of melanism and albinism, 226; Sauermann's experiments in changing color by food, 227; influence of temperature, moisture and sunlight on food, 229; instances where intensifying and bleaching has been the result of the presence or absence of sunlight, 230; Garman on the bleaching power of sunlight, 231; objections to Garman's theory, 231; pale colors of the under parts of animals due to the absence of sunlight, 232; reconciliation of this view with the bleaching effect of sunlight, 233.

GEOGRAPHICAL DISTRIBUTION AS A FACTOR IN THE EVOLUTION OF COLORS............................. 234

General survey of the faunal areas of North America, in their relation to extralimital faunas, 234; birds of the Boreal area, 235; absence of brilliantly colored genera among boreal forms, 236; reasons for this lack of specialization among northern forms, 237; brilliancy of tropical species, 238; Beddard on special relations of color to geographical distribution, 238; on the resemblance of the colors of Sturnella and Macronyx, 239; Ridgway on the relation between color and geographical distribution, 241; *Spinus psaltria* as an instance of melanism as related to distribution, 241; other examples of melanism toward the south, 243; intensification in yellow toward the tropics, 243; intensification of red with change in climate, 244; increase in blue from north to south, 245; *Cyanocitta stelleri* studied with reference to the connection between color marks and geographical distribution, 245; J. A. Allen on the relation between climate and geographical races, 247; *Melospiza fasciata* as an instance of the result of climatic influence, 248; the ice age as a factor in isolation, 249; examples of forms produced by an east and west isolation, 250; examples of north and south isolation, 252; varieties or closely related species whose ranges overlap, 253; particular instances where the different races cannot have been produced solely by climatic influences, 255; Myiarchus as an example of species which have been produced by climatic influences alone, 256.

ORDERS, FAMILIES, AND GENERA OF NORTH AMERICAN BIRDS, CONSIDERED FROM THE STANDPOINT OF THEIR EVOLUTION....................................... 257

BIBLIOGRAPHY....................................... 337

EXPLANATION OF PLATES................................ 345

INDEX... 349

THE EVOLUTION OF THE COLORS OF NORTH AMERICAN LAND BIRDS.

I. Introduction.

A few words of explanation may be said with regard to the greatly disproportionate length of the introductory portion of this work. To the uninitiated the most perfect harmony is commonly thought to prevail concerning the great problems of evolutionary philosophy, but once within the circle of current scientific thought and the reverse is found to be true. Instead of harmony, discord is discovered. There is hardly one of the important doctrines concerning which a consensus of scientific opinion has been attained. To be sure, all maintain that Darwinism or natural selection is a factor in evolution, but while some hold it to be the only factor, and all-sufficient in the creation of species, others believe it to be a very minor agency, and relegate it to the post of inspector-general of the army of life. With regard to sexual selection the same diversity of opinion prevails, one school advocating sexual selection as the sole agent in producing the brilliant colors and varied plumes of male birds, etc., the other extreme asserting that sexual selection as a factor in evolution is a myth. Still greater is the diversity of opinion and more intense the feeling in regard to that momentous question which is at present agitating the troubled sea of scientific thought—the transmission of acquired character.

In view of all this disagreement, it is quite impossible to undertake any general scientific investigations in the field of evolution without a tolerably thorough survey of the whole ground. With this end in view, and merely as a preparation for the more particular investigations of the work, these preliminary pages have been written. The tenability of the theories here advanced need not materially affect the work of the second part, although the theories concerning the special investigations in the evolution of color in birds are largely founded upon the principles laid down in Part I. Although this first part is necessarily of a general character, nothing has been inserted which has not some bearing upon the investigations which follow. An attempt has been made to discuss the general principles of evolution according to a logical system, the subject of the inheritance of acquired characters being treated first, as it is the most fundamental question in dispute.

The doctrine of evolution is by no means modern in its conception, having been dimly foreshadowed from the days of Aristotle; but it was first suggested in a plausible scientific form by Jean Lamarck, who, in 1809, published his Philosophie Zoologique. He attempted to account for the changes in organic forms almost exclusively by the principles of the use and disuse of parts of which doctrine he was the originator. His views were hardly noticed at the time they were announced, but a little later Geoffroy St. Hilaire was more successful in calling the attention of the scientific world to his own closely related theory of the action of the environment in producing the changes in organic beings; although his views were not generally accepted by the naturalists of the day. The nature and extent of his theory is explained in the following words of Haeckel.* "He conceives the organism as passive, in regard to the vital conditions of the outer world, while Lamarck, on the contrary, regards it as active. Geoffroy thinks, for example, that birds originated from lizard-like reptiles, simply by a diminution of the carbonic acid in the atmosphere, in consequence of which the breathing pro-

---

*History of Creation, I., p. 117.

cess became more animated and energetic through the increased proportion of oxygen in the atmosphere. Thus there arose a higher temperature of the blood, an increased activity of the nerves and muscles, and the scales of the reptiles became the feathers of birds," etc.

The principle of use and disuse, and the transmission of acquired characters, are very closely related and stand or fall together. Darwin, in his Origin of Species, and throughout all his subsequent writings, accepted them both as supplementary to his own doctrine of natural selection, in accounting for the origin of species. It was, of course, generally admitted that an individual could, during the course of its life, acquire characters peculiar to itself, or could modify its parts by use or disuse. Moreover, it was commonly held that such modifications could be transmitted by the individual to its offspring. To this view Darwin was committed, and in order to explain it in a rational way he formulated the provisional hypothesis of pangenesis, which he describes in the following language: "This important distinction between transmission and development will be best kept in mind by the aid of the hypothesis of pangenesis. According to this hypothesis, every unit or cell of the body throws off gemmules or undeveloped atoms, which are transmitted to the offspring of both sexes, and are multiplied by self division. They may remain undeveloped during the early years of life or during successive generations; and their development into units or cells, like those from which they were derived, depends on their affinity for, and union with other units or cells previously developed in the due order of growth."*

Mr. Romanes has presented Darwin's hypothesis of pangenesis† in so able and comprehensive a manner

---

*Descent of Man, p. 228.

†Weismann's Theory of Heredity by George J. Romanes. Contemporary Review. May 1890, pp. 686–699.

that in order to convey a proper understanding of the subject I cannot do better than quote his words in full. It is stated in the following seven assumptions:

"1. That all the component cells of a multicellular organism throw off inconceivably minute germs or "gemmules," which are then dispersed throughout the whole system.

2. That these gemmules, when so dispersed and supplied with proper nutriment, multiply by self division, and, under suitable conditions, are capable of developing into physiological cells like those from which they were originally and severally derived.

3. That while still in this gemmular condition, these cell seeds have one for another a mutual affinity, which leads to their being collected from all parts of the system by the reproductive glands of the organism; and that, when so collected, they go to constitute the essential material of the sexual elements—ova and spermatozoa being thus nothing more than aggregated packets of gemmules, which have emanated from all the cells of all the tissues of the organism.

4. That the development of a new organism, out of the fusion of two such packets of gemmules, is due to a summation of all the developments of some of the gemmules which those two packets contain.

5. That a large proportional number of the gemmules in each packet, however, fail to develop, and are then transmitted in a dormant state to future generations, in any of which they may be developed subsequently—thus giving rise to the phenomena of reversion or atavism.

6. That in all cases the development of gemmules into the form of their parent cells depends on their suitable union with other partially developed gemmules, which precede them in the regular course of their growth.

7. That gemmules are thrown off by all physiological cells, not only during the adult state of the organism, but during all stages of development. Or, in other words, that the production of these cell-seeds depends upon the adult condition of parent cells; not upon that of the multicellular organism."

This theory has subsequently been varied in its details by Brooks, Galton, Herdman, and others. According to Brooks the ovary is passive and does not aid in the transmission of acquired characters, but the sperm cells contain gemmules which are thrown off from such parts as are undergoing change. Galton believed to a considerable degree in the continuity of the germ plasm, although also holding that acquired characters are inheritable. For example, he says, "From the well-known circumstance that an individual may transmit to his descendents ancestral qualities which he does not himself possess, we are assured that they could not have been altogether destroyed in him, but must have maintained their existence in a latent form. Therefore each individual may properly be considered as consisting of two parts, one of which is latent and only known to us by its effects on his posterity, while the other is patent, and constitutes the person manifest to our senses."* These latent characters he considered to be transmitted from generation to generation by means of a portion of the gemmules of the fertilized ovum which remained undeveloped. Although at first adopting an hypothesis of pangenesis he afterwards abandoned this for a theory of the continuity of the germ-plasm not unlike that of Weismann.

Lloyd Morgan criticises the pangenetic hypothesis in the following well chosen words: "The existence of

---

* On Blood Relationship, Proc. Roy. Soc., 1872, p. 394.

gemmules, then, is unproven, and their supposed mode of origin not in altogether satisfactory accordance with organic analogies. Furthermore, the whole machinery of the scheme of heredity is complicated and hyper-hypothetical. It is difficult to read Darwin's account of reversion, the inheritance of functionally acquired characters and the non-inheritance of mutilation, or to follow his skillful manipulation of the invisible army of gemmules, without being tempted to exclaim—What cannot be explained, if this be explanation? and to ask whether an honest confession of ignorance, of which we are all so terribly afraid, be not, after all, a more satisfactory position."*

Haeckel's plastidule theory and Spencer's theory of physiological units do not differ very essentially from Darwin's hypothesis of pangenesis, although Spencer's idea is a much less crude one. He finds that the units of which an organism is composed have the property of arranging themselves in a definite form or sequence, and then proceeds to enquire into the nature of these units. He first shows that they cannot be chemical, for the chemical composition of the various organic bodies which arrange themselves in such diverse shapes is essentially alike in all cases. Neither can morphological units be accepted as final. The simple cell is the morphological unit, but certain tissues arise directly out of the formative substance without the intervention of a cellular stage. Moreover, certain non-cellular organisms, such as Rhizopods, are capable of transmitting peculiar specific characters. From these exceptions it is evident that this formative power does not reside in cells; and consequently both chemical and morphological units are disposed of. Spencer then argues for

---

* Animal Life and Intelligence, p. 137.

physiological units in the following terms:* "If, then, this organic polarity can be possessed neither by the chemical units nor the morphological units, we must conceive it as possessed by certain intermediate units, which we may term *physiological.* There seems no alternative but to suppose, that the chemical units combine into units immensely more complex than themselves, complex as they are; and that in each organism, the physiological units produced by this further compounding of highly compound atoms, have a more or less distinctive character."

Before considering the subject of heredity in further detail, it may be well to pause a moment to consider its bearing upon the question in hand—the inheritance of acquired characters. Obviously the nature of the mechanical process by which heredity is made possible must most decisively determine what the possibilities of heredity are—just what characters can be inherited, and what characters cannot (if any such exist). Darwin began with the assumption that all characters could be inherited and framed his theory of heredity upon this assumption. In this he was followed by the various subsequent writers on the subject, with the exception of Spencer, whose theory does not appear to be designed with the express view of accounting for the inheritance of acquired characters, but rather to have been constructed inductively.

Such was the state of the case when, in 1885, Mr. A. E. Shipley in an article in "The Nineteenth Century," called the attention of English and American scientists to the views of Prof. August Weismann, of Freiburg. Since then two editions of an English translation of the collected essays of Prof. Weismann on the subject of

---

*Principles of Biology, I, 183.

heredity have appeared, the second in 1891. Prof. Weismann's views, although not entirely original, are stated with such a rigid consistency to all the consequences which they involve, are fraught with such unusual and daring speculations, and so vitally affect many of our scientific dogmas, that they have caused a remarkable revolution in the scientific world. By many English biologists these new views have been received with great favor. Wallace has thrown the weight of his approval with them. With such avidity have they been accepted that one is almost tempted to feel that a reaction must ultimately follow. In America the case has been directly the reverse. Instead of meeting with favor they have been passed by in silence, questioned, doubted, denied, and even in some cases treated almost with scorn and ridicule. Against such an extreme as this also, reaction seems inevitable.

The chief value of Weismann's work, regardless of how correct or incorrect it may ultimately prove to be, is the fact that he has attacked the problem of heredity from an entirely new point of view, and has set the scientific world to thinking. It will be advisable to consider his speculations in some detail, as bearing directly upon the subject under discussion.

Weismann commences his discussion with an inquiry into the nature of death. He asks why mortality should be a necessary consequence of life. In unicellular organisms reproduction takes place by fission. The life of one amœba comes to an end by the division of the parent into two equal halves, each of which forms a new individual. "But," as Weismann says, "this process cannot be truly called death. Where is the dead body?—what is it that dies? Nothing dies; the body of the animal only divides into two similar parts, possessing the same constitution. Each of these parts is exactly like its parent, lives in the same manner, and finally also divides into two halves. As far as these organisms are concerned, death can only be spoken of in the most figurative sense."* From this view of Weismann's in regard to the immortality of protozoa there has been but little dissent. The most serious objection that has been raised to it is that of Maupas, who has shown that even among amœba conjunction is occasionally necessary to effect rejuvenescence, and who holds that, in consequence of this, even unicellular organisms are mortal. Geddes and Thomson have well stated,† however, that Maupas' experiments, instead of being contradictory to Weismann's view, should be inserted as a saving clause, for in a state of nature this rejuvenescence by coalescence does take place when needed and neither the organism as a whole nor any part of it dies.

Having established the immortality of unicellular organisms, Weismann attempts to account for the introduction of death into the economy of nature on the principle of the advantage to the race as a whole, of the sacrifice of the old and decrepit to the young and vigorous. The weaknesses and fallacies of this part of his theory have been pointed out with especial force by Lloyd Morgan.‡

The fact seems to be tolerably well established that in protozoa death never normally ends the career of the organism, although of course violent death by accident is perfectly possible, while in metazoa death is the natural outcome. Or, as Weismann explains it, there is no limit to the number of times an amœban cell can divide itself, but the cells of a more complex organism are lim-

---

* Essays upon Heredity, 1891, I, p. 26.

† Evolution of Sex, Humboldt Library, p. 240.

‡ Animal Life and Intelligence, pp. 184 and 193.

ited in their powers of reproduction and ultimately wear out. To this latter rule Weismann makes one important exception, viz: the germ cells. In the case of some insects and other invertebrates it has been demonstated that almost at the commencement of embryonic development the reproductive cells are set apart. In the case of these organisms it is evident that there is an immortal chain of reproductive cells from one generation to another. Observation has proved, however, that it is only in rarely exceptional cases that the reproductive cells are thus set apart, and that in ordinary metazoa they appear after the embryo is well advanced toward maturity. Weismann argues very reasonably that it is at variance with the laws of development to assume, as Nægeli does, the existence of a nucleoplasm which first develops into the more complex body cells and then becomes simplified into reproductive cells; and he accordingly substitutes an hypothesis of his own. He assumes the existence of germ-plasm intermingled with the body plasm and capable of producing the latter, although body plasm cannot be converted into germ-plasm. There is, then, in the higher metazoa, not an immortal chain of reproductive cells, but an immortal chain of germ-plasms.

From this standpoint the heredity of acquired characters is obviously impossible. The germ-plasm cannot be influenced by the body plasm. The hypothesis, from its very nature places an effectual barrier against the inheritance of acquired characters, and in case it could be demonstrated as true, it would be necessary to explain all such supposed cases of transmission in some other way. This is what Weismann and his followers have done, but before considering the evidence for and against such transmission of acquired characters, it will be advisable to consider how well founded this theory is.

Prof. S. H. Vines has criticised it in an article entitled "An Examination of Some Points in Prof. Weismann's Theory of Heredity," which appeared in *Nature*, October 24, 1889 (pp. 621–626). Prof. Vines admits the immortality of protozoa, but questions the explanation of Prof. Weismann as to how the immortal protozoa evolved into the mortal metazoa. He objects to Weismann's suggestion of unequal fission as being no explanation, and asserts that if unequal fission were the cause it would be necessary to assume that a potential mortality already existed in protozoa. "It is impossible to conceive," he says, "that unequal fission can take place in a cell consisting throughout of essentially the same kind of substance." Furthermore, as Prof. Vines points out, Weismann claims that the germ-plasm is located chiefly in the nucleus of the germ-cell, but does not explain of what the remaining portion of the germ-cell consists. Obviously it must be somatoplasm, which is mortal, despite the fact that Weismann has asserted that the entire germ-cell is immortal. Prof. Vines suggests as an explanation of the paradox, "the assumption that the substance of the nucleus determines the nature and character of the cell." Admitting the above explanation that the protozoon contains both somatoplasm and germ-plasm, it is easy to understand how unequal fission might separate the one from the other, thus originating two forms of cells, mortal and immortal; but this Weismann is not likely to admit, asserting as he does that the germ-plasm becomes changed into somatoplasm.

"It is not a little remarkable," says Prof. Vines, "that Prof. Weismann should not have offered any suggestion as to the conception which he has formed of the mode in which the conversion of germ-plasm into somatoplasm can take place, considering that this assumption is the key to his whole position. He has been at considerable pains to controvert the view that somatoplasm may be converted into germ-plasm; but in making the attack he has overlooked the necessity for defense." Prof. Vines then gives quotations from Prof. Weismann illustrative of his theory of heredity, and of his assertion that germ-plasm must be a substance of great stability in order to be able to transmit all of the complex modifications which it acquires. He then continues his objections as follows: A part of the germ-plasm, Weismann claims, goes to the formation of the somatoplasm of the developing embryo, while what remains goes to the formation of the nucleus of the germ-cells of the embryo. But the germ-plasm of the ovum, Prof. Vines claims, cannot influence the somatoplasm of the embryo, even from Prof. Weismann's standpoint. "This function cannot be discharged," he says, "by that portion of the germ-plasm of the ovum which has become converted into the somatoplasm of the embryo, for the simple reason that it has ceased to be germ-plasm and must therefore have lost the properties characteristic of that substance. Neither can it be discharged by that portion of the germ-plasm of the ovum which is aggregated in the germ-cells of the embryo, for under these circumstances it is withdrawn from all direct relation with the developing somatic cells. The question remains without an answer." So much for the criticism from Prof. Weismann's own standpoint. From Prof. Vine's position it is open to a still more vital attack. Claiming as he does that the possibility of germ-plasm being converted into somatoplasm is an unwarrantable assumption on the part of Prof. Weismann, Prof. Vines cannot but assert that the entire theory of germ-plasm which is built upon this assumption, must collapse. Furthermore, inasmuch as the embryo is not formed solely from that part of the nucleus which is purported to be the chief bearer of the germ-plasm, but from the whole nucleus plus a portion of the cytoplasm of the ovum, it is evident that the somatoplasm must have some constructive powers as well as the germ-plasm; but this is the very thing denied by Prof. Wiseman, and if true, what would be the necessity of introducing the germ-plasm at all. The somatoplasm alone would be able to be `the bearer of hereditary characters, and we would then have a continuity of somatoplasm instead of a continuity of germ-plasm.

Prof. Weismann's reply to the criticism of Prof. Vines* is of especial interest for it contains an epitome of his theories brought up to date. From it, it is possible to comprehend which of his views he still holds and which he rejects, a task of some difficulty in depending upon the series of his collected essays. In reply to the objection of Prof. Vines that an immortal cell could not have changed into a mortal cell by fission unless there already existed within it a latent principle of mortality, Prof. Weismann appeals to the division of labor, saying: " From the one cell which performed all functions comes a group of several cells which distribute themselves over the work. In my opinion, the first such differentiation produced two sets of cells, the one the mortal cells of the body proper, the other the immortal germ-cells." Surely Prof. Weismann does not consider immortality a function of amœban cells, or, if he does, cannot hold that mortality is another function possessed by the same cells! His explanation of the distinction between immortality and eternity is opportune and may throw some light on the subject. By biological immortality Weis-

---

* Prof. Weismann's Theory of Heredity; Nature, February 6, 1890, pp. 317-323.

mann simply means that an organism has the potential power of renewing the cycle of its existence, as long as the environment conditioning its existence remains suitable. While it can be destroyed, it does not bear within it the seeds of decay. "If, then," says Prof. Weismann, "this true immortality is but cyclical, and is conditioned by the physical constitution of the protoplasm, why is it inconceivable that this constitution should be under certain circumstances and to a certain extent, so modified that the metabolic activity no longer follows its own orbit, but after more or fewer revolutions comes to a standstill and results in death? All living matter is variable; why should not variations in the protoplasm have occurred which, while they fulfilled certain functions of the individual economy better, caused a metabolism which did not exactly repeat itself, *i. e.*, sooner or later came to a condition of rest?"

This explanation, although rather vague, does indeed seem to throw some light upon the way in which mortality might have originated, but his appeal to panmixia to aid him seems wholly unwarrantable. He says: "I believe that organs no longer in use become rudimentary, and must finally disappear solely by 'panmixie'; not through the direct action of disuse, but because natural selection no longer maintains their standard of structure. What is true of an organ is true also of its function, since the latter is but the expression of the qualities of material parts, whether we can directly perceive their relations or not. If, then, as we saw, the immortality of monoplastids depends on the fact that incessant metabolism of their bodies is ever returning exactly to its starting point, and produces no such modifications as would gradually obstruct the repetition of the cycle, why should that quality of its living matter which causes immortality — nay, how *could* it be retained—when no longer necessary?" The above passage is open to two objections. First, he assumes panmixia as proved. In discussing this subject later on it will be shown that, on the contrary, panmixia appears to be largely untenable. Secondly, panmixia means a cessation of natural selection. If we assume with Weismann, as there seems every reason to assume, that the original unicellular organisms, and their living representatives to-day, possess a potential immortality or possibility of indefinite existence, we certainly cannot assume that some are more immortal than others. But if potential immortality be a natural attribute of life, why should natural selection be necessary to preserve this attribute, or from what could it make its selection? If natural selection is not requisite to maintain this standard of immortality, panmixia, assuming its potency in other instances, could have no influence in causing mortality, being merely the negative of natural selection.

Prof. Weismann then replies to Prof. Vine's criticism of his theory of embryogenesis and the continuity of germ-plasm. He asserts that Prof. Vine's criticism is due to a misconception, that he does not claim that germplasm is ever converted into somatoplasm. In his second essay he had indeed contrasted the somatoplasm or the entire substance of the body with the germ-plasm or entire substance of the germ-cells, not having arrived at the time at the conclusions of Strasburger and O. Hertwig, that hereditary transmission was effected solely by the chromatin of the nuclear loops. This view he had adopted when the fourth essay was written, and his theory was accordingly somewhat modified. He made use of Nageli's term, idioplasm, in an essentially different manner, applying it to the chromatin not only of the ovum-nucleus, but also of every cell in the body. This idioplasma he asserted to be the vital formative principle of every cell, what remained being merely nutritive. The general term somatoplasm was then of course abandoned. There are, then, according to this theory, two series throughout the body, one formative, the other reproductive. The formative, which is the chromatin of the nucleus, passes under the general term of idioplasma. When present in the germ-cells it is called germ-plasm; in the body cells, "somatic idioplasm." The nutritive substance is what was previously known as somatoplasm. To it also a new term was given, "cytoplasma." Having made these distinctions, Weismann explains his idea of embryogenesis. This takes place, according to his theory, by the successive halvings of the nuclear loops or germ-plasm. "Each fresh cell-division," he says, "sorts out tendencies which were mixed in the nucleus of the mother-cell, until the complex mass of embryonic cells is formed, each with a nuclear idioplasma which stamps its specific histological character on the cell." A minute part of the idioplasm he assumes to remain unchanged when the first transformation occurs, in order to preserve the continuity of the germ-plasm. This fragment of germ-plasm migrates in an inactive condition from cell to cell, until it comes to the spot where it develops into the germinal cells of the next generation.

How, then, does the controversy between Prof. Vines and Prof. Weismann rest? Briefly, Prof. Vines has shown that Weismann has not accounted for the introduction of mortality in the order of life, although it is upon the assumption of such a differentiation of cells into mortal and immortal that his entire theory rests. Vines has not shown, however, that such a differentiation is impossible. Weismann, on the other hand, has refuted the charge of the inconsistency of assuming that germ-plasm can be converted into somatoplasm, although the reverse is impossible. From the destructive, it may now be well to turn to the constructive form of criticism.

There have been two theories recently advanced in opposition to Weismann's—one by J. A. Ryder and the other by Lloyd Morgan. Ryder has presented his theory in an article entitled "A Physiological Hypothesis of Heredity and Variations," in the "American Naturalist.* He considers Weismann's views to be fanciful and visionary and admits of no possible compromise. He agrees with Morgan that the introduction of a hypothetical germ-plasm, instead of making the question of heredity more simple, in reality complicates matters. He believes with H. Milne Edwards and Huxley that in the division of labor of the various cells of the body, all have been specialized beyond the point where further embryonic development is possible, with the exception of the reproductive cells which remain unspecialized, and hence capable of development. Spencer confirms this view of the simplicity of the reproductive cells. He says: †"The marvellous phenomena initiated by the meeting of the sperm-cell and germ-cell, naturally suggest the conception of some quite special and peculiar properties possessed by these cells. It seems obvious that this mysterious power which they display, of originating a new and complex organism, distinguishes them in the broadest way from portions of organic substance in general. Nevertheless, the more we study the evidence the more is this assumption shaken—the more are we led towards the conclusion that these cells have not been made by some unusual elaboration, fundamentally different from all other cells, * * * the organs for preparing sperm-cells and germ-

---

*Vol. 24, p. 85.

†Principles of Biology, I, pp. 219–220.

cells have none of the specialty of structures which might be looked for, did sperm-cells and germ-cells need endowing with properties essentially unlike those of all other organic agents. On the contrary, these reproductive centers proceed from tissues that are characterized by their low organization."

Besides the accusation of producing unnecessary confusion by the introduction of the mystical germ-plasm, Ryder has a much more serious charge to prefer against Weismann. He claims that the isolation of the germ-plasma in the germ-cell is in conflict not alone with the principles of metabolism, upon which modern physiology stands, but also with the law of the conservation of energy. "Modern physiology," he says, "as well as the doctrine of the conservation of energy, positively forbids us to interpose any barrier between the plasma of the parent-body and that of the germ-cells, as is done by the promulgators of the hypothesis of the continuity and isolation of the germ-plasma." What, then, is Ryder's theory? Briefly this: All cells of the body have some reproductive power, as shown by the healing of a wound among the most specialized organisms, by the restoration of a lost limb among lower forms, or of a lost organ, as the eye, for example, by still lower, and by the power of the lowest metazoa and some plants of forming a new individual from a fragment of the parent. The lower in the scale of life we penetrate, the more generally diffused and potent do we find this regenerative power. The logical inference from this is that reproductive force is most powerful where the specialization is least. The reproductive cells would accordingly be the least specialized cells of the body. Moreover, they are the only cells which are normally passive and functionless. The specific molecular character of the reproductive cells, then, according to Ryder, together with the molecular tendencies of all the cells of the body form the efficient force for the production of a new individual. This theory would allow, nay, even necessitate, the inheritance of acquired character. Prof. Ryder states this as follows: "Molecular impressions experienced in the course of variations in the modes of manifestation of, or of disturbance of the balance of the metabolism of the parent-body, are supposed upon this view to be transmitted as molecular tendencies to the idle or passive plasma of the germ-cells. Variations in the molecular constitution and tendencies of the germinal matter are supposed to thus arise at different times in the same parent, and that, consequently, successive germs may be thus differently impressed."

The above view does not seem to be fundamentally different from Haeckel's plastidule theory, although Ryder classes the latter with those from which his own is a departure. The chief objection to it is its vagueness, and it is to be hoped that Prof. Ryder may elaborate it at some time. There appears to be nothing expressed in Lloyd Morgan's views contradictory to the theory above stated. Morgan lays the greatest stress upon cellular continuity. He regards "the sharp distinction between body-plasm and germ-plasm as an interesting biological myth." He expresses his views on cellular continuity as follows:*

"The nucleus is the essence of the cell. And the doctrine of cellular continuity emphasizes the fact that the nuclei of all the cells of the body are derived by a process of divisional growth from the first segmentation nucleus which results from the union of the nuclei of the ovum and the sperm. In this sense, then, however late the germinal cells appear as such, they are in direct

---

* Animal Life and Intelligence, p. 142.

continuity with the germinal cell from which they, in common with all the cells of the organism, derive their origin. In this sense there is a true continuity of germ-cells."

Morgan, like Ryder, believes the reproductive cells have been set apart in the division of labor, and in this he is in accord with Weismann. The agreement is not carried out in the details, however. Morgan says:* "Cell-reproduction is, however, in the metazoa of two kinds. There is the direct reproduction of differentiated cells, by which muscle-cells, nerve-cells, or others reproduce their kind in the growth of tissues or organs; and there is the developmental reproduction, by which the germinal cells under appropriate conditions reproduce an organism similar to the parent. The former is in the direct line of descent from the simple reproduction of amœba. The latter is something peculiarly metazoan, and is, if one may be allowed the expression, specialized in its generality."

Prof. Eimer† expresses himself in similar terms with regard to the continuity of body cells. He says: "If the body of the multicellular organism is thus, even according to Weismann's ideas, of secondary importance in comparison with the germ-plasm, if the latter corresponds to the unicellular organism, it follows that the multicellular is just as immortal or mortal as the unicellular. And thus it is impossible to see why, between the germ-plasm of the multicellular on the one hand, and that of the unicellular on the other, there should exist this profound difference, that the latter acquire characters during life and transmit them by heredity, the former not, how the former any more than the

---

*l. c., p. 143.

†Organic Evolution; English Translation, p. 71.

latter can nourish itself and grow without being influenced in its nature by its nurture."

The above discussion of the views of Weismann and his opponents is merely intended as a statement of the case in an unprejudiced light so that a provisional conclusion may be reached, at least on some of the points in dispute. A brief summary of the details in which the two factions agree and differ may now be given: They agree:

(1.) In the immortality of protozoa.
(2.) That mortal metazoa have been evolved from immortal protozoa.
(3.) That the reproductive cells have been set apart by the principle of the division of labor.

Weismann claims:

(1.) That there are two forms of plasma, germ-plasma which has a formative and cytoplasma which has a nutritive function.
(2.) That the germ-plasma has the immortality of protozoa, while the cytoplasma is mortal.
(3.) That the two plasmas are mutually isolated.

Hence:

(4.) That whatever may affect the cytoplasma of the body-cells can have no influence on the germ-plasma of the ovary. Or, in other words, that acquired characters cannot be inherited.

His opponents claim:

(1.) That there is only one form of plasma which may be called either somatoplasm or idioplasm.
(2.) That, inasmuch as every individual is formed by repeated cell divisions of the germ-cell, there is an immortality of somatoplasm.
(3.) That the inheritance of acquired characters is not in opposition to any known biological law.

According to Ryder's hypothesis acquired characters must be inherited, but this hypothesis not yet having been demonstrated does not afford a proof that such characters are inherited. Morgan, on the contrary, points out the difficulty of framing an intelligible theory which will satisfactorily explain such inheritance, although at the same time claiming that there is no theoretical evidence against it. This being the state of opinion in regard to the theories, it will be well to look to the so-called proofs of the inheritance of acquired characters; but before so doing one other theory of Weismann's bearing upon the subject must be examined, viz: panmixia, or "pammixis," according to the corrected version.

Panmixia, according to Weismann, means the "suspension of the preserving influence of natural selection," over an organ, part or function no longer necessary for the welfare of the species. So far all very well. We cannot quarrel with Weismann for giving a name to this cessation, but we can disagree with him as to the result which will be brought about; and this Lloyd Morgan has done so ably that I cannot do better than refer the reader to the passage.* Weismann claims that by this failure on the part of natural selection to maintain the standard of excellence of an organ, it will degenerate and ultimately disappear. Lloyd Morgan shows that pammixis can only produce a reduction from the survival mean to the birth mean. Selection, by eliminating such individuals as possess inferior parts, makes the standard of excellence of the survival mean considerably above the standard of birth mean. If then, selection cease to operate, the birth mean standard will be again restored. Or, to express it in figures,

---

*Animal Life and Intelligence, p. 189.

if the birth mean standard of an organ equal 3, and the survival mean 5 when selection is operative, the standard cannot possibly fall below 3 when selection ceases.

Mr. J. T. Cunningham criticises pammixis as follows:* "The fallacy of this argument is so obvious that it is surprising it should be for a moment accepted. For what is stated of the maxima variations is equally true of the minima. In the absence of all selection the minima variations will be combined in sexual union with variations superior to themselves, and therefore in each successive generation the minimum will be raised. Thus the only possible result of pammixis, on Weismann's theory of variation, will be the production of uniformity in a disused or useless organ, and the degeneration or disappearance of such an organ will be absolutely impossible."

In an article on "The Factors of Organic Evolution,"† Prof. Geo. J. Romanes calls attention to the fact that he had enunciated the principle of pammixis under the name "Cessation of Selection," as early as 1873. He had not claimed, however, that this cessation of selection could of itself produce the total disappearance of an organ or part. As an instance of this, he supposes a structure to have been raised from 0 to an average of 100, and then to have become wholly useless, so that natural selection would be no longer operative in maintaining the standard. Reversal of selection would then set in, due to economy of growth, and variations 101, 102, 103, etc., would be eliminated, while variations 99, 98, 97, etc., would be favored. To continue the explanation in the writer's own words: "For the sake of definition, we shall neglect the influence of economy

---

* The New Darwinism, Westminster Review, July, 1891, p. 23.

† Nature, XXXVI, Aug. 25, 1887, pp. 401-407.

acting below 100, and so isolate the effects due to the mere withdrawal of selection. By the conditions of our assumption, all variations above 100 are eliminated, while below 100 indiscriminate variation is permitted. Thus, the selective premium upon variation 99 being no greater than upon 98, 98 would have as good a chance of leaving offspring which would inherit and transmit this variation as would 99; similarly, 97 would have as good a chance as 98, and so on." He then shows how there would be a constant tendency toward reduction in the part, but that the greater the reduction the less possibility of future reduction would remain. "Thus," he says, "theoretically the average would continue to diminish at a slower and slower rate, until it comes to 50, where the chances in favor of increase and diminution being equal, it would remain stationary."

Prof. Romanes then gives examples of parts which he thinks have degenerated through cessation of selection. He considers the cases where the phylogenic stages are omitted in the developing embryo to be instances in point, and argues that such omissions cannot be explained by economy of growth, for in allied forms where economy would be equally operative the structure persists. Neither can the absence of such parts be due to disuse, Prof. Romanes contends, for they were not generally produced by use. The case of hard coverings, which are developed by natural selection as a protection to certain animals, and afterwards lost when their period of usefulness is past, is also cited as an example of degeneration without disuse.

Pammixis, then, is not new as a theory, nor is it the only available explanation of degeneration. Romanes himself suggested three alternatives. Besides reversal of selection, he has stated two other factors, as follows: "The first of them is inheritance at earlier periods of life, which progressively pushes back the development of a rudiment to a more and more remote embryonic stage of growth; and the second is the eventual failure of the principle of inheritance itself. For, 'whether or not we believe in Pangenesis, we cannot but deem it in the highest degree improbable that the influence of heredity is of unlimited duration.'" The former of these two factors is the same as Prof. Cope's principle of retardation, while the latter has also been independently stated by Cope, as will be seen in a subsequent quotation. There are, then, five theories besides pammixis by which degeneration of parts may be explained, viz: (1) reversal of selection, (2) economy of energy, (3) disuse, (4) retardation, and (5) the failure of heredity. In some cases the loss of an organ or member is an advantage, and then natural selection may aid in eliminating it. An instance of this is to be found in insects inhabiting islands, which would be blown to sea and perish if they possessed the power of flight, and in which the wings are aborted or entirely absent. There are many cases, however, in which there is no such direct advantage to be discovered in the reduction of a part. To some of these cases the principle of economy enunciated by Darwin might well apply. This principle assumes that the organism has a given amount of force to expend, and that if one part be useless the growth force which has been expended in maintaining it will be diverted to some other channel. Thus birds, like the ostrich, in which the wings are aborted, have legs proportionately powerful. The third principle is disuse. It is universally admitted that whenever a part is not used during the lifetime of an individual it degenerates to a certain extent. The principle of disuse merely assumes that such acquired degeneration can be inherited. Cope enunciated the fourth and fifth principles, independently of Romanes.* When any part or the whole of an individual is retarded in its growth, so that the animal begins to breed before reaching maturity, Cope holds that the descendents will be deficient in such parts as were not fully developed in the parent. The statement of the action of this law in producing degeneration of parts is as follows: "'Retardation' continued terminates in extinction. Examples of this result are common; among the best known are those of the atrophy of the organs of sight in animals inhabiting caves. * * I would suggest that the process of reduction illustrates the law of 'retardation' accompanied by another phenomenon. Where characters which appear latest in embryonic history are lost, we have simple retardation—that is, the animal in successive generations fails to grow up to the highest point of completion, falling farther and farther back, thus presenting an increasingly slower growth in the special direction in question. Where, as in the presence of eyes, we have a character early assumed in embryonic life, retardation presents a somewhat different phase. Each successive generation, it is true, fails to come up to the completeness of its predecessor at maturity, and thus exhibits 'retardation;' but this process of reduction of rate of growth is followed by its termination in the part long before growth has ceased in other organs. This is an exaggeration of retardation, and means the early termination of the process of force-conversion, which has been previously diminishing steadily in activity."

The subject of use and disuse need not be considered in further detail. From the above it is evident that there are many explanations of the phenomena of degeneration and that pammixis cannot be at best more than one of several factors.

---

* Origin of the Fittest, p. 13.

Having disposed of the theoretical aspect of the question of use and disuse and the inheritance of acquired characters, a few words on the practical side of the case may now be in order. In the first place it will be advisable to enquire what an acceptance of the views of Weismann involves. Some of the consequences are well shown by Mr. J. T. Cunningham, in his introduction to the English translation of Eimer's Organic Evolution. He calls attention to the abnormally lengthened tongue of the woodpecker, which can be greatly protruded and thrust into holes to extract insects. The lengthened tongue, the Neo-Darwinians claim, has been produced solely by the selection of those individuals in which it was longest. They cannot but admit with the Lamarckians, however, that constant exercise of the tongue in the individual, especially the constant stretching to which it would be subjected in the effort to reach farther, would increase its length; but in admitting this they have involved themselves in the paradox of assuming that the tongue has become lengthened during the course of ages, and that it has also been lengthened in the individual by the Lamarckian factor of use and disuse, but that the lengthening which has occurred in the race is in no wise related to the lengthening that has taken place in the individual. "Which is very like the argument," says Cunningham, "that the *Iliad* and the *Odyssey* were not written by Homer, but by another man of the same name who lived at the same time."

Another difficulty in the way of the Neo-Darwinian argument to which Cunningham, among others, has called attention, is its inability to account for the origin of totally new characters. Even though it may be able to account for the lengthened neck of the giraffe by selection, it is impossible, Cunningham argues, to explain the origin of horns by this principle. From what is the selection to be made? "No other mammals," he says, have ever been stated to possess two little symmetrical excrescences on their frontal bones as an occasional variation; what then caused such excrescences to appear in the ancestors of horned ruminants? Butting with the forehead would produce them, and no other cause can be suggested which would."

An inconsistency which has been pointed out by Romanes, Osborn and Le Conte, is the fact that the Neo-Darwinians admit the Lamarckian factors among protozoa. Romanes has pointed this out with especial clearness in his article entitled "Weismann's Theory of Heredity."* He calls attention to the fact that inasmuch as natural selection is unavailing without variation, and that variation, according to Weismann's view is due to the sexual admixture of different traits, there can be no individual variation among unicellular and parthenogenetic organisms, and hence natural selection cannot be a factor in producing new forms. Weismann, indeed, sees this to be the case and admits that modifications in such animals must be due solely to the direct action of the environment. Two objections have here been interposed. Prof. Osborn asks why, if the direct action of the environment was once a factor of evolution, as Weismann admits, it should ever have ceased to be such if its period of usefulness did not terminate.† Now it is apparent that the period of usefulness of the Lamarckian factors does not terminate with the protozoa, and consequently natural selection itself would have tended to preserve them. Prof. Romanes' suggestion was not stated in the form of an objection, although such is clearly implied. It is in brief as fol-

---

*Contemporary Review, May, 1890, pp. 686-699.

†American Naturalist, xxiii, p.

lows: The germ-plasm of Prof. Weismann is a highly stable substance unaffected from within or without. Variations occur by sexual admixture, but as there is an immortal chain of germ-plasm all variations may be ultimately referred back to the unicellular organism, and hence all variations must have been due originally to the direct actions of the environment in producing changes in the protozoa.

In considering the observed cases of transmission of acquired characters, the subject of the supposed transmission of mutilations may be first discussed. As is well known, many cases of such transmission are on record, but Weismann has shown that a large number of these are untrustworthy. Undue significance however, has been attached to the validity of such cases. In his introduction to the English translation of Eimer's Organic Evolution, Mr. J. T. Cunningham has made a suggestion, the importance of which has been generally overlooked. He says: "The fact that artificial malformations are not usually inherited is no argument against the inheritance of acquired characters. In all animals, from the lowest up to reptiles, recrescence of lost parts takes place, and the reappearance of lost parts in the next generation in mammals and birds seems to me to be simply recrescence slightly postponed."

Lloyd Morgan, speaking of the evidence of the inheritance of acquired characters, says:* "Attempts have been made to furnish such evidence by showing that certain mutilations have been inherited. I question whether many of these cases will withstand rigid criticism. Nor do I think that mutilations are likely to afford the right sort of evidence one way or the other. We must look to less abnormal influences. What we require is evidence

---

*Animal Life and Intelligence, p. 163.

in favor of or against the supposition that *modifications* of the body-cells are transmitted to the germ-cells. Now these modifications must clearly be of such a nature as to be receivable by the cells without in any way destroying their integrity. The destruction or removal of cells is something very different from this. If it were proved that mutilations are inherited, this would not necessarily show that normal cell-modifications are transmissible. And if the evidence in favor of inherited mutilations breaks down, as I believe it does, this does not show that more normal modifications such as those with which we are familiar, as occurring in the course of individual life, are not capable of transmission."

Weismann has devoted some attention to the reported cases of the inheritence of mutilations, and has reached the conclusion that all the published instances are either untrustworthy or of such a character that they do not conclusively prove that a case of mutilation has ever been inherited.

In commenting upon his explanation of reputed cases of the transmission of rudimentary tails, he says:* "We have seen that the rudimentary tails of cats and dogs, as far as they can be submitted to scientific investigation, do not depend upon the transmission of artificial mutilation, but upon the spontaneous appearance of degeneration in the vertebral column of the tail. The opinion may, however, be still held that the customary artificial mutilation of the tail, in many races of dogs and cats, has at least produced a number of rudimentary tails, although, perhaps, not all of them. It might be maintained that the fact of the spontaneous appearance of rudimentary tails does not disprove the supposition that the character may also depend upon the transmission of artificial mutilation.

---

* Essays on Heredity, 1891, I, p. 443.

"Obviously, such a question can only be decided by experiments; not, of course, experiments upon dogs and cats, as Bonnet rightly remarks, but experiments upon animals the tails of which are not already in a process of reduction. Bonnet proposes that the question should be investigated in white rats or mice, in which the length of the tail is very uniform, and the occurence of rudimentary tails is unknown."

Weismann accordingly performed these experiments, and there can be no doubt that they have been done in a thorough and scientific manner. The result has been purely negative, mice of the fifth generation bearing young with the tails of normal length. Weismann, indeed, admits that these experiments do not constitute a complete disproof of a possibility of transmitting mutilations, but justly claims that, in comparison with the cases of such supposed transmission occurring completely in a single generation, and where but one parent was affected, the possibilities of transmissions were infinitely greater in his experiment. If, however, the suggestion of Cunningham, that the non-inheritance of mutilation in higher animals is comparable with regeneration of lost parts among lower forms, but delayed to the following generation, we can easily understand that while mutilations might be inherited, the contrary would be the rule, and such inheritance would be due to an abnormal condition of the organism. Cunningham, furthermore, not unjustly, insinuates that even the cautious Prof. Weismann may have been betrayed into asserting a little more than he knew in order to prove his point. For example, he says:* "Prof. Weismann mentions the feet of Chinese ladies, which he says are still, when uncompressed, as large as if the

---

* Organic Evolution, Translator's Preface, p. x.

practice of artificially compressing them had not been practiced for centuries. But he does not tell us whether he ever saw a Chinese young lady, or if he has made any observations on the feet of Chinese young women." Eimer has mentioned a number of cases of supposed mutilation which I have not seen refuted. In arguing for the inheritance of mutilations, he says:* "That injuries, when continued for an extremely long time, may be inherited is proved, to my mind, by atrophied (rudimentary) organs. The degeneration of these organs depends incontestably on disuse; in consequence of disuse the blood-supply is diminished, in consequence of the decrease of nutrition degeneration takes place. If we consider the course of gradual degeneration, *e. g.* of the tail as it must have taken place in the higher mammals, to have proceeded in this purely physiological manner from the tip toward the root, the process is much the same as if the tip of the tail had been in many successive generations amputated, and the shortening had been inherited and then the shorter tail thus acquired had been farther shortened artificially, and so on. In any case, in the degeneration of the tail an acquired character has been inherited by the offspring, a character which, in the causes of its origin, is closely similar to a perpetually repeated mutilation. Great periods of time, however, have been necessary in this case for the accomplishment of a final result."

This example of Prof. Eimer's seems, however, to be an assumption of the validity of the point in dispute. His opponents could, of course, claim that the reduction in the length of the tail was due solely to the selection of the shortest. His examples of observed cases of inheritance of mutilations, however, do not appear to be

---

* Organic Evolution, Eng. translation, p. 176.

susceptible of the criticism of a misinterpretation of the facts. Two only need here be given.* "A. Decandolle describes one such case with the assurance that it is perfectly true. In the year 1797 a girl twenty-one years old was thrown from a carriage, and in consequence had a scar about five centimeters wide over the left ear and temple which remained without hair. Married in 1799, she bore a son in 1800, in whom the hair was absent from the same area and remained so. The son of the man, born in 1836, had no such defect, but it was present in his grandson born in 1866, and in 1884 in this last individual when he was eighteen years old the peculiarity was disappearing.

"Dr. Meissen of Falkenberg, records in the number of Humboldt for June, 1887, the following case of inheritance of an injury in his own family: 'When I was seven or eight years old I had the chicken-pox, and I recollect with complete distinctness that I scratched one of the pustules on the right temple in consequence of which I had a small white scar at this spot. Exactly the same scar, which I had of course ceased to think of, on exactly the same spot, was present on my little son, now fifteen months old, when he came into the world. The resemblance is so perfect that it surprises everyone who sees the little mark.'"

It is unnecessary to multiply examples of reported cases of the inheritance of mutilations. A single trustworthy instance is sufficient to offset an indefinite amount of evidence to the contrary; more especially when the Neo-Lamarckians themselves assert that such inheritance, if it occurs at all, is abnormal. The explanation given by Weismann of the inheritance of epilepsy in guinea pigs as described in the experi-

---

* l. c., p. 177.

ments of Brown-Séquard and Obersteiner appears forced and inexcusably far-fetched, but it will be unnecessary to dwell longer upon such cases. Suffice it to say, that epilepsy superinduced by severing certain peripheral nerves has been transmitted to the following generation, but that Weismann evades the experiment, first by suggesting that it was merely the predisposition to the disease—due to a general derangement of the nervous system that was inherited, and secondly suggesting that the disease was transmitted by microbes penetrating the reproductive cells.

An almost endless number of instances have been reported of the transmission of acquired characters, while the Neo-Darwinians have replied to many of them, explaining the facts after their own fashion. It will be obviously impossible to give all of the cases which have been brought to light, but a few representative ones may be detailed. The evidence divides itself into two classes; viz: observed instances of transformation which appear to be due to the direct action of the environment; and, second, structures, functions, or traits which could only have resulted from the inheritance of acquired characters.

In the first category may be mentioned the case of the Japanese goldfish of Dr. Wahl, which Prof. Ryder records,* which, by close confinement and abundant food, were greatly modified, "enormous and abnormally lengthened pectoral, ventral, dorsal, double and caudal fins" being developed. "Some of the races of these fishes have obviously been affected in appearance by abundant feeding," he states, "as is attested by their short, almost globular bodies, protuberent abdomens and greedy habits," etc. Lloyd Morgan gives some interesting instances

---

*Am. Nat., vol. 24, page 89.

of observed cases of the direct action of the environment in affecting a race. One of the finest is the transformation of the brine-shrimp, *Artemia*, reported by Schmankewitsch: "One species of this crustacean, *Artemia salina*," says Lloyd Morgan, "lives in brackish water, while *A. milhausenii* inhabits water which is much salter. They have always been regarded as distinct species, differing in the form of the tail lobes and the character of the spines they bear. And yet, by gradually altering the saltness of the water, either of them was transformed into the other in the course of a few generations. So long as the altered conditions remained the same the change of form was maintained."

What is to be said of such cases? Do they constitute a proof positive of the inheritance of acquired characters? At first sight they certainly do appear to be conclusive and final, but a candid examination of them compels us to admit of the possibility of a different interpretation. The two examples mentioned are fairly representative of a large number of similar instances. The whole difficulty with them lies in the fact that when the organism is restored to its former conditions the change does not persist. Does the son of a blacksmith inherit the strong arms of his father? Probably he does, but this is not equivalent to asserting that he inherits the strength *acquired* by his father in following his vocation. It is not improbable that his father became a blacksmith because he was naturally strong or was predisposed to develop unusual strength. We must first in every case assure ourselves that the predisposition does not exist in the animal and only requires a favorable environment to be developed. Secondly, it must be demonstrated that there is a progressive change from one generation to the next. This there apparently was in the case of the goldfish, for a period of six years was required for the production of some of the forms. But even in cases where the change lasts only as long as the altered environment is operative, although the permanent transmission of acquired characters is not demonstrated, it is rendered highly probable. Cunningham gives an excellent analogy illustrative of this. He says:* "If a plant with a vertical stem is placed in a horizontal position, the light coming from above, the end of the stem will bend up toward the light, partly by growth, partly by flexure. Such a plant was so placed, and, after a certain time, when the upward flexure was established, it was turned round so that the tip pointed downwards. Of course the flexure was gradually reversed until the tip pointed upwards again. After the same interval the plant was reversed once more. This was continued for some days, the plant being reversed at regular intervals. At last, when the time came for turning the plant round, the operation was not performed, it was left undisturbed. But then the plant began to reverse its flexure of its own accord, and actually turned its tip downwards, away from the light. By the regularly repeated reversal of position a rhythm had been set up in the life of the plant, and even when the cause which excited this rhythm ceased, the rhythm continued."

Weismann himself gives some instances of these "after-effects" in plants, such as the case of the sunflower, which is as follows:† "If vigorous plants of the sunflower, grown in the open air, be cut off close to the ground and transferred to complete darkness, the examination of a tube fixed to the cut surface of the stem will show that the escape of sap does not take place uniformly, but undergoes periodical fluctuation, being strongest in the afternoon and weakest in the early

---

* The New Darwinism, Westminster Review, July, 1881, p. 416.

† Essays upon Heredity, 1891, I. p. 416.

morning. Now the cause of this daily periodicity in the flow of sap depends upon the periodical changes due to the light to which the plant was exposed when it was growing under normal conditions. When plants which have been grown in darkness from the first are similarly treated, the flow of sap does not exhibit any such periodicity." In commenting on these instances, Weismann says: "All this is certainly very interesting, and it proves that periodical stimuli produce periodical processes in the plant, which are not immediately arrested when the stimulus is withdrawn, and only become uniform gradually and after the lapse of a considerable time. But I certainly claim the right to ask what connection there is between these facts and the transmission of acquired characters? All these peculiarities produced by external influences remain restricted to the individual in which they arose; most of them disappear comparatively soon, and long before the death of the individual."

From the theoretical standpoint of Prof. Weismann this is doubtless correct. But it has been shown, I think, that Prof. Weismann's theory of the continuity of germ-plasm is not only unproven but highly improbable. Moreover, it has been shown that the continuity of the body plasm is highly probable. But if this be true, then there is, to say the least, a strong analogy between a rhythm which can be established in the somatoplasm and repeated during the life of the individual and a rhythm which can be established in the history of a race.

Cunningham has well pointed out, however, that the Neo-Lamarckians do not claim that a change due to the environment can be established in a single generation. All that is claimed is, that when a particular environmental influence is continued from generation to generation, the offspring successively inherit a progressive predisposition to be modified, until, in the course of time, the modification takes place, when the cause is no longer operative, as in the case of the after effects just considered.

Mr. D. G. Elliot, in a recent address on the inheritance of acquired characters delivered before the American Ornithologists' Union,* relates an instance of the observed inheritance of an acquired habit in birds as follows: "Currituck Sound, in North Carolina, where wild fowl are accustomed to pass the greater portion of the winter, is a great resort of sportsmen, who pursue the birds in every way to accomplish their destruction. This, at length, was carried to such a degree that the fowl had no place left for them to rest during the day. Some years ago the gunners were surprised to find that whenever the weather permitted, as soon as a gun was fired in the early morning the birds would rise and betake themselves to the ocean, and remain congregated on the water just beyond the line of the breakers, and would not return until night closed in. This custom was acquired by birds of succeeding years, until the habit has become apparently established. Now it may be said that this is not an *acquired* habit, but the result of example, the old birds leading the young to the sea. But this would be to assume that the majority of the birds which commenced this habit had survived to return to this locality every winter. And even if the young, without at first comprehending the reason for so strange a proceeding, merely followed the old birds, is it reasonable to suppose they would remain in such an unusual locality throughout the day, deprived of their food, which could be obtained in profusion on the other side of the narrow beach? It must have been something

---

* Auk, ix, Jan. 1892, pp. 77–104.

more powerful than the mere example of the flight of the old birds to the ocean, witnessed by the young for the first time, which compelled them to remain. Can we not more reasonably presume that it was the knowledge acquired by the parents that this was a secure method to escape from a threatened danger, and transmitted to the young, who assumed the habit as a part of their nature?"

Mr. Elliot then mentions numerous cases of the change of nesting habits in birds. He alludes to the instance reported by Coues in Birds of the Northwest, of the geese of the Yellowstone, which build in trees instead of on the ground, which is the usual habit of these birds. He furthermore calls attention to the case noted by Audubon of the change in nesting habits of the herring gulls on White Head Island, in the Bay of Fundy, which during the lifetime of a single man had deserted the ground in favor of trees owing to the persecution to which they had been subjected. "A remarkable effect of this transmission of an acquired character," says Mr. Elliot, "is that the young hatched in the trees do not leave the nest until they are able to fly, while those hatched in nests on the ground run about in less than a week and conceal themselves at the sight of man among the moss and plants."

But cannot these instances of Mr. Elliot's be otherwise interpreted? I think they can. It is impossible to prove the inheritance of acquired habits by citing examples which could best be thus explained, but which might be otherwise accounted for. In the first instance mentioned, the majority of the birds which commenced the habit *might* have survived. Or, a smaller number might have been sufficient if we admit that birds have sufficient language to give warning of danger. Moreover, Mr. Elliot's argument that the inducement of obtaining food would be so strong as to compel the young birds to ignore the example of their elders really reflects upon his own assumption, for it seems difficult to conceive that a new adjustment of such force as this instinct is supposed to be, could be inherited in the course of a few generations. The argument derived from the change in nesting habits appears to have still less force. Mr. Elliot assumes that nest building is an instinct, but this assumption is unproven and has been emphatically doubted by Wallace. In his Philosophy of Birds' Nests,* he says: "At all events, till the crucial experiment is made, and a pair of wild birds, raised from the egg without ever seeing a nest, are shown to be capable of making one exactly of the parental type, I do not think we are justified in calling in the aid of an unknown and mysterious faculty to do that which is so strictly analogous to the house-building of savage men."

Darwin has given many instances of the inheritance of acquired habits which, however, have been skillfully combated by William Platt Ball.† He cites, for example, the inheritance by a colt of the paces of her mother, but suggests that "selection of the constitutional tendency to these paces, and imitation of the mother by the colt, may have been the real causes." He calls attention to the fact that the songs of birds are not inherited, but are learned from their parents, and says: "If use-inheritance has not fixed the song of birds, why should we suppose that in a single generation it has transmitted a newly-taught method of walking or trotting." He speaks of the supposed inheritance by dogs of the intelligence acquired by contact with man, which he explains thus: "But selection and imitation are so

---

*Natural Selection, pp. 108–109.

† Are the Effects of Use and Disuse Inherited? Humboldt Library, pp 31–33.

potent, that the additional hypothesis of use-inheritance seems perfectly superfluous. Where intelligence is not highly valued and carefully promoted by selection, the intelligence derivable from association with man does *not* appear to be inherited. Lap-dogs, for instance, are often remarkably stupid." It seems to me that Ball does not establish his point in this instance. To be sure, it might be claimed that thoroughbred dogs had attained their intelligence through selection alone (although this I should be inclined to question), but such dogs are generally, if not universally, bred with one especial end in view,. either speed, hunting qualities, fighting qualities, beauty or eccentricty; but how often are they bred for intelligence? Moreover the most intelligent dogs are not infrequently curs. A large number of the most remarkable stories of canine sagacity are told of animals without a pedigree. But these dogs have not been selected at all, for the most part. What is the fate of a large litter of puppies of a cur? A part of them are generally destroyed in early infancy, and this in a manner practically impartial so far as intelligence is concerned. The rest are generally given away, but what evidence have we that the less intelligent of them are killed by their new masters, while the more intelligent survive to perpetuate the race?

Romanes has called attention* to the inheritance of an instinct in dogs which he considers especially invulnerable in support of the inheritance of acquired habit. For an instinct to have been established solely by natural selection, it must be of sufficient importance to be essential to the life of the race, so that those individuals possessing it may alone survive. This is not the

---

* The Factors of Organic Evolution. Nature. August 25, 1887–XXXVI, p. 406.

case with the instinct which dogs possess of turning around several times before lying down, in order to trample down a bed, a relic of primitive comfort which surely could not have become established by the survival of the fittest. "Or," says Romanes, "if this instance be held doubtful, what shall we say to the courting instincts in general, and to the play-instincts of the bower-bird in particular, which are surely quite without meaning from any utilitarian point of view? And these instincts naturally lead to the æsthetic faculties of mankind, few of which can be possibly ascribed to natural selection, as Mr. Spencer very conclusively shows."

Weismann and Ball have both combated this, as, indeed, they are bound to do to be consistent with their theory. Thus Ball says: "The emotional susceptibility to music and the delicate perceptions needed for the higher branches of art, were apparently the work of natural and sexual selections in the long past. Civilization, with its leisure and wealth and accumulated knowledge, perfects human faculties by artificial cultivation, develops and combines means of enjoyment and discovers unsuspected sources of interest and pleasure. * * * But modern æsthetic advance seems to be almost entirely due to the culture of latent abilities, the formation of complex associations, the selection and encouragement of talent, and the wide diffusion and imitation of the accumulated products of the well-cultivated genius of favorably varying individuals. The fact that uneducated persons do not enjoy the higher tastes, and the rapidity with which such tastes are acquired or professed ought to be sufficient proof that modern culture is brought about by far swifter and more potent influences than use-inheritance." What has Mr. Ball shown in the above paragraph? If he has proved anything it certainly is that natural selection has not originated, even if it has been instrumental in the development of the æsthetic faculties. In speaking of the culture of latent abilities he has yielded a most important point. There was obviously a time in the evolution of organic life when piano playing, or, in more general terms, appreciation of harmony, was not even a latent faculty. It would be taxing our credulity to assume, for example, that amœba possessed it. Then it must, at some time, have come into existence as a latent faculty, and later on been developed by use, or culture, as Ball calls it; and this developed faculty has been inherited.

Spencer published in the *Nineteenth Century* for April and May, 1886, two essays, which have since appeared in a separate form, entitled "The Factors of Organic Evolution." "Among the most important criticisms of this work is the one by Romanes in an article bearing the same title, which appeared in *Nature* August 25, 1887; and Ball's criticism in his pamphlet, "Are the Effects of Use and Disuse Inherited?" Spencer gives three forms of evidence in proof of the inheritance of acquired characters—(1) the crowding of teeth in dogs and reduced size of the jaw in civilized man; (2) the correlation of different parts of the organism, and (3) the apparent direct influence of the environment in altering the surface of an organism.

Romanes and Ball agree that Spencer has failed to prove his first point. Romanes says, in regard to this: "Be it observed, I am not disputing that disuse may in both these cases have co-operated with the cessation of selection in bringing about the observed result. Indeed, I am rather disposed to allow that the large amount of reduction described in the case of the dogs as having taken place in so comparatively short a time, is strongly suggestive of disuse having co-operated with the cessation of selection. But at present I am merely pointing out that Mr. Spencer's investigations have here failed to exhibit the crucial proof of disuse as a reducing cause, which he assigns to them; it is not true that in this case disuse 'remains as the only conceivable cause.' "*

The third argument, as Romanes asserts, is too theoretical to be considered as a proof, but the second, in regard to the correlation of parts of the organism is of great importance, and, according to the opinion of Romanes, "virtually proves the truth of the Lamarckian assumption."

So important is this particular case that it is worthy of a somewhat extended consideration. Spencer takes the giraffe as illustrative of his point. He calls attention to a statement of Darwin's that "the prolonged use of all the parts together with inheritance will have aided in an important manner in their co-ordination." "A remark," observes Spencer, "probably having reference chiefly to the increased massiveness of the lower part of the neck; the increased size and strength of the thorax required to bear the additional burden, and the increased strength of the fore legs required to carry the greater weight of both. But now I think that further consideration suggests the belief that the entailed modifications are much more numerous and remote than at first appears; and that the greater part of these are such as cannot be ascribed in any degree to the selection of favorable variations but must be ascribed exclusively to the inherited effects of changed functions." Mr. Spencer then describes the mechanism of locomotion in the giraffe, the short hind limbs which must keep pace with the long fore limbs, and the consequent complex series of changes of bones, muscles and nerves which must have taken place in order to bring

---

* l. c. p. 405.

about this result. This might very easily be explained, indeed, by the effects of inherited use and disuse. "If the effects of use and disuse of parts are inheritable," says Mr. Spencer, "then any change in the fore parts of the giraffe which affects the action of the hind limbs and back will simultaneously cause, by the greater or less exercise of it, a remoulding of each component in the hind limbs and back in a way adapted to the new demands; and generation after generation the entire structure of the hind quarters will be progressively fitted to the changed structure of the fore quarters, all the appliances for nutrition and innervation being at the same time progressively fitted to both." But the factors of use and disuse aside, we must assume that all of these complex changes occurred simultaneously. It might be contended that slight variations in one direction which were advantageous might take place in one generation, and the correlative changes in other parts at some future time. In reply to this Mr. Spencer says: "Besides the fact that until this secondary variation occurred the primary variation would be a disadvantage, often fatal, and besides the fact that before such an appropriate secondary variation might be expected in the course of generations to occur, the primary variations would have died out; there is the fact that the appropriate variation of one bone or muscle in the hind quarters would be useless without appropriate variations in all the rest—some in this way and some in that—a number of appropriate variations which it is impossible to suppose."

Mr. Ball either cannot or will not see the force of Spencer's objections. He says: "All that is needed is that natural selection should preserve the tallest giraffe through times of famine by their being able to reach otherwise inaccessible stores of foliage. The continual variability of all parts of the higher animals gives scope for innumerable changes and nature is not in a hurry. Mr. Spencer, however, says that the chances against any adequate readjustments fortuitously arising must be infinity to one. But he has also shown that altered degree of use does not cause the needed concomitant variation of co-operative parts. So the chances against a beneficial change in an animal must be, at a liberal estimate, infinity to two. Mr. Spencer, if he has proved anything, has proved that it is practically impossible that the giraffe can have acquired a long neck, or the elk its huge horns, or that any species has ever acquired any important modification."

Mr. Ball then draws attention to the facts which Wallace has adduced in his recent work, "Darwinism," proving that constant and independent variation is the rule among all animals and plants. He then says: "The lengthened wing might be gained in one generation, and the strengthened muscle at a subsequent period; the bird in the meanwhile drawing upon its surplus energy, aided (as I would suggest) by the strengthening effect of increased use in the individual." This explanation is open to two objections: First, the one already raised by Mr. Spencer, that before the second correlative variation appeared the first would be lost; and, second, the suggestion of Cunningham in regard to assuming that use could develop the character required, but that the individual thus favored could not transmit the variation, but that posterity must wait for the same variation to arise spontaneously. This hypothesis is so forced, illogical and absurd, that so long as a better one can be found it should be adopted.

But one more class of evidence need be discussed, that furnished by paleontology. Prof. Henry F. Osborn has called special attention to this subject on two different occasions.* He says: "The evidence is of a direct and indirect character. The direct evidence is that by actual observation in complete paleontological series, the origin of adaptive structures is found to conform strictly to the lines of use and disuse. The indirect proof is that the natural selection of chance variations is unsupported by observation and is inadequate to explain the various phenomena of the second class." Special attention is drawn to the evolution of teeth, in which every gradation may be traced from the simple conical reptilian tooth to the highly complex molars of some mammals. Osborn has enunciated the two following laws of cusp growth:

"(1) The primary cusps first appear as cuspules, or minute cones, at the first points of contact between the upper and lower molars in the vertical motions of the jaw.

(2) The modeling of cusps into new forms, and the acquisition of secondary position, is a concomitant of interference in the horizontal motions of the jaws."

From the above laws it is evident that the variations in the race are the same as the variations in the individuals, caused by the use and disuse of parts, and a causal connection between the two is inferred. This proof of the inheritance of the characters of use and disuse has been criticised by Poulton. In a foot-note to Weismann's Essays upon Heredity,† he says: "One of the most remarkable forms of this revival of Lamarckism is the establishment in America of a 'Neo-Lamarckian School,' which includes among its members many of the most distinguished American biologists. One of the arguments upon which the founders of the school

---

* Proc. A. A. A. S., 1889, pp. 273–276. Am. Nat. March, 1891, p. 191.

† Page 437.

have chiefly relied is derived from the comparative morphology of mammalian teeth. The evolution of the various types are believed to be due to modifications in shape, produced by the action of mechanical forces (pressure and friction) during the life of the individual. The accumulation of such modifications by means of heredity explains the forms of existing teeth.

"It may be reasonably objected that the most elementary facts concerning the development of teeth prove that their shapes cannot be altered during the lifetime of the individual, except by being worn away. The shape is predetermined before the tooth has cut the gum. Hence the Neo-Lamarckian School assumes, not the transmission of acquired characters, but the transmission of characters which the parent is unable to acquire!"

In replying to the criticism of Mr. Poulton, Osborn says: "To the objection that the teeth are entirely formed before piercing the gum, and that use produces an actual loss of tissue as contrasted with the growth of bone, it may be said that by our theory, it is not the growth itself but the reactions which produce this growth in the living tissue, which we suppose to be transmitted." Osborn also criticises Weismann's theory as follows: "In Weismann's variation theory the preponderating influence must be conservative; however it may explain progressive modification, or even correlation of old characters, it does not admit that the genesis of new characters should follow definite lines of adaptation which are not pre-existent in the germ-plasma. We find that new characters of the second class do follow such purposive or directive lines, arising simultaneously in all parts of the organism, and first appearing in such minute form that we have no reason to suppose that they can be acted upon by selection. The old view of nature's choice between two single characters, one adaptive, the other not adaptive, must be abandoned, since the latter does not exist in the second class."

I have attempted to present a fair statement of both sides of the case in this controversy in regard to the inheritance of acquired characters, and to all of the important arguments which have been adduced both pro and con, illustrated by typical examples. It will be remembered that the scepticism in regard to the possibility of acquired characters being transmitted arose from the theory of heredity enunciated by Prof. Weismann. A study of the different theories of heredity disclosed the fact that while Darwin's hypothesis of pangenesis, or any subsequent modification of it, was a merely formal and provisional scheme for explaining the supposed facts of heredity, Weismann's theory of germ-plasm appears to be a speculative deduction from real facts which the facts themselves do not warrant. That consequently, although this theory may be true, it appears rather visionary and certainly should not be unconditionally accepted as true or even as a working hypothesis, unless the facts dependent upon it can be thus best explained. The practice of stretching facts to fit into a theory is a habit which cannot be too strongly condemned.

If Weismann's theory of germ-plasm is unproven there is no apparent reason why acquired characters may not be inherited. An examination of the testimony on this point seems to indicate that both sides have cited cases which did not prove their point. Many so-called proofs which have been brought forward by the Neo-Lamarckians in reality prove nothing, but, on the other hand, some of the interpretations of the Neo-Darwinians appear forced and illogical.

It is obvious that a single established case of inheritance of an acquired character would be sufficient to prove the principle, however many other cases might be differently explained. And it seems to me that some fairly well established, if not absolutely convincing, cases have been adduced. Furthermore, the Neo-Darwinians maintain the illogical assumption that the changes which are observed in the individual have no possible causal connection with the changes which take place in the race, this assumption being contradictory to the law of correspondence of the ontogenic and phylogenic series. Lastly, it is impossible to explain, from the Neo-Darwinian point of view, simultaneous variations of an adaptive nature.

From all this we may come to a provisional conclusion that acquired characters are transmissible. We are justified in using this assumption as a working hypothesis, and in feeling confident that future investigation will place it upon a footing where it is beyond the possibility of refutation.

VARIATION AND NATURAL SELECTION.

The end of science is the establishment of natural law, which is merely the orderly relationship existing between phenomena, and consequently cannot be considered as an ultimate cause. Thus gravitation is merely a name for the observed relation between bodies, but does not in any way tell us why these relations exist. Evolution is a term expressive of change in form, and modern biology is striving to determine the precise laws conditioning such changes as occur in organic beings. There are two sets of changes—ontogenic and phylogenic. It has become the fashion of late years among certain scientists to attribute changes of the second class solely to the action of natural selection, and it thus becomes necessary in inquiring into the laws of evolution to consider first this principle, and determine what it can effect.

It will be necessary to understand clearly the scope and meaning of the term natural selection, or Darwinism, as it is frequently called in recognition of its enunciator, before inquiring into what it can accomplish. Darwin himself used the term in two different senses, more narrowly as synonymous with Spencer's term survival of the fittest and in the broader interpretation of the cause of modifications including the facts of variation. In this latter application, however, it is inaccurate and misleading. Indeed, the process, is as a rule, not one of selection, as Lloyd Morgan has pointed out,* but rather of rejection, in which case natural elimination becomes a more correct term. But how can any change be brought about in a species by this process? Prof. J. G. Schurman in a chapter on the Metaphysics of Darwinism† writes as follows of natural selection: "There have been objections to the theory, especially to the somewhat startling assumption that the results of man's purposive selection in breeding could be attained and that, too, on a much larger scale—by the blind and purposeless operations of nature; but granting all that the hypothesis requires of us, we are still in presence of the fact that natural selection, or survival of the fittest, can accomplish nothing until it is supplied with material for 'selection,' until there has appeared upon the field an antecedent 'fittest'—a fittest organ, function, habit, instinct, constitution, or entire organism. Natural selection produces nothing; it only culls from what is already in existence. The survival of the fittest is an eliminative, not an originative, process."

So obvious is the above assertion that it needs no discussion. A variation must be originated before it can

---

* Animal Life and Intelligence, p. 79.

†The Ethical Import of Darwinism, pp. 77–78.

be selected. We find then, that before variations can occur in the phylogenic series they must take place in the ontogenic series, or in other words, natural selection is strictly conditioned upon individual variation. It therefore becomes a matter of no small moment to enquire into this subject, from the standpoint of observation to determine what are the possibilities of variation, and from the theoretical aspect to establish the conditions of variation. Wallace, more than any other scientist, probably, has given attention to the recording of individual variations, and his most recent work, Darwinism, furnishes us with a large number of facts of this sort. An inspection of the instances there given* and of cases adduced by other writers, as Semper in his Animal Life, discloses the fact that they are all quantitive and not qualitative. Variations may occur in size, in shape, in position, in number and in color. Variations in size are most numerous and most marked, perhaps, but such variations if in any special direction entail variations in shape. Variation in the position of parts is almost equally great, perhaps, although less readily observed and consequently less frequently recorded. Variations in number may be trivial and unnoticeable, or may become monstrous as with six-fingered men and two-headed calves. Besides the above mentioned deviations I know of none, except the occasional suppression of parts, either internal or external.

The above variations might at first sight appear sufficient to produce changes in structures already in existence, but the old difficulty still remains of accounting for the origination of new parts. Wallace's answer to this is certainly apologetic.† Have we a right to assume

---

* Darwinism, pp. 41–82.

† l. c., pp. 128–131.

that variations occurred in past geological ages different in nature from those which occur to-day? If we do not do so, from which class of the variations above enumerated were feathers evolved, or horns, for example? Singularly enough, Wallace, an avowed opponent of Lamarckianism, triumphantly appeals to the principles of use in the one difficult variation which he does really explain, the shifting of the eye of the flatfish.* If individual variation does not normally originate new parts, such as horns, for example, and I know of no reason either theoretical or practical for assuming that it does, then there must be some other factor occasionally called into play; but if some factor exists which must be operative at rare intervals it is but reasonable to assume that it is constantly operative to some extent rather than to suppose that it is lying idle until natural selection is obliged to call upon it to lend a helping hand.

The above considerations lead to another frequently urged difficulty that even supposing the necessary variations did occur, we are obliged to assume that they were advantageous. That incipient modifications of an organism are always advantageous is considerable of an assumption. It seems incredible, indeed, that some very pronounced distinctions can be of utility. Thus it seems difficult to explain, by utility or adaptation, the fact that in California a species of magpie is found identical with the one found east of the Sierra Nevada Mountains, with the exception of being smaller and having the bill bright yellow instead of black. The birds are well isolated geographically throughout the greater part or the whole of their range, so the difference could hardly be accounted for by the theory of recognition markings. This is but one of a great number of instances of a similar nature

---

*l. c., pp. 129–130.

which might be adduced. Examples of insular species are especially noteworthy in this regard.

Mr. Romanes has considered these difficulties at some length in a book which has but just appeared.* The Duke of Argyll in advocating design in nature, made use of the above objections to natural selection, and it is to him that Mr. Romanes addresses his reply. It is hardly necessary to say that the difficulties above stated were not mentioned with a view to show the necessity for design in nature, or some direct supervising power to control the origination of variations, but merely to call attention to the proposition that natural selection, with the help of purely fortuitous variation, does not seem sufficient to account for all structural and specific details. Mr. Romanes, in his reply to the Duke of Argyll, shows how careful it is necessary to be in any particular instance in saying that a character is of no use. Thus the eye must have been of use in its most incipient stages as a black pigment spot which indicated vaguely the presence of light to the nerves in its vicinity. The wing in its incipient stages must also have been of use, as Mr. Romanes points out. Even if a variation were of no use at first it might be indirectly preserved by natural selection through correlation of growth. "Mr. Darwin, who has paid more attention to this matter than any other writer, has shown, in considerable detail, that all the parts of any given organism are so intimately bound together, or so mutually dependent upon each other, that when one part is caused to change by means of natural selection, some other parts are very likely to undergo modification as a consequence."

The theories which have been put forth to explain variation are, for the most part, very incomplete. Darwin

---

* Darwin and After Darwin. I—The Darwinian Theory, pp. 350-373.

freely confesses his ignorance on this point, saying: "Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part has varied."* Spencer suggests a number of causes for variation.† He considers the influences of environment in altering functions to be one factor in determining variations, asserting * * * "that organisms produced by the same parents at the same time, must be more or less differentiated both by insensible initial differences, and by slight differences in the conditions to which they are subject during their evolution." He then appeals to first principles to show that no two parts of a homogeneous substance can be exactly alike, and that consequently there must always be a difference at least in the number of physiological units composing a reproductive cell. Thus we have a clue to the differences existing in the young of a single litter.

Weismann's theory of variation is probably the most carefully worked out in its details, and is perfectly consistent with his theory of the isolation of the germ plasm. It appears impossible, however, that any progressive modification could take place according to this view, for it depends exclusively upon the number of ahnenplasmas of each sex which enter into combination, this number being largely determined by the amount of surplus germ plasm which is disposed of in the extrusion of the two polar cells. But variation according to this theory, it would seem, must be strictly conservative, for all modifications must be within the extremes of ancestral modification. Thus, let us suppose that every living individual of some species has been measured, and that 500 represents the number of units in the

---

* Origin of Species, p. 73, Humboldt.

†Principles of Biology, I, pp. 257–272.

smallest individual of the species, and 550 in the largest. There could be, then, no variation due to sexual admixture which fell below 500 or rose above 550, and hence no progress would be possible.

Another difficulty in Weismann's theory of variation has been recently communicated to *Nature*, by Prof. Marcus Hartog.* He argues from the assumption that Weismann's theory is proved, and the result is, as he says, indeed a startling one. He first presents five theses expressing the main assumptions of Weismann's theory, which Poulton has since admitted to be an impartial and correct statement of the case. They are as follows:

"I. Each primitive germ-cell of either sex, contains a number of ancestral germ-units, the ahnenplasmas; and this number is constant, for the species at least.

II. These ancestral germ-units are far more constant and unchangeable in character than the species itself.

III. They lie associated together in the germ-cell without loss or alteration of their individual peculiarities.

IV. The number contained in the mature ovum and spermatzoon is reduced by one-half, and in the fertilized ovum or oosperm the number is restored to the normal by the summation of the ahnenplasmas of the two fusing cells. This process is comparable to the shuffling of two packs of cards by taking half from each and joining the talons or remainders to form a new pack.

V. The possible combinations under this process are so numerous as to explain the variations among the offspring of sexual union.

Accepting these statements, we next inquire, How

---

* Nature, October 29, 1891, p. 613.

are we to conceive of these ancestral units, the ahnenplasmas? Two hypotheses may be given in answer to this question:

A. Each ahnenplasma unit corresponds to an individual of the species itself; and if put under proper tropic conditions, would, singly, reproduce such an individual.

B. The ahnenplasmas correspond to the primitive Protozoan ancestors, which, according to theory, could alone reproduce modifications due to external causes (acquired modifications)."

Prof. Hartog then shows that if hypothesis A be accepted the ahnenplasmas must have varied with the race, but this would make the shuffling process superfluous as an explanation of variation, and would also be contradictory to thesis II.

"According to hypothesis B," he continues, "the ahnenplasmas of all Metazoa being similar and Protozoan, if the *numbers are equal* and the shuffling fair, any two parents may beget any offspring whatever; on the plane of thesis V, a lioness might be expected to bring forth a lobster or a starfish or any other animal, which as we know, does not take place in nature. The only escape from this result is to assume the postulates—(1) that the number of ahnenplasmas varies from species to species; (2) that the *number* in the combination and not the *character* of the ahnenplasmas determines the species. And as there is not a particle of evidence for the latter postulate, we may say that on hypothesis B, the theory breaks down by its non-conformity with the facts.

We have then the dilemma, from which I see no escape, that the theory is inconsistent, on A with itself, on B with the facts."

It is too soon to attempt to pass judgment upon this objection, as the subject is still under discussion. Certain it is, however, that the replies which have been made by Poulton and Trow are incorrect and Hartog demonstrates their inconsistency with the views of Weismann by a letter from that gentleman.

Lloyd Morgan suggests as an hypothesis of variation a modification of Spencer's theory of physiological units, which has much to commend it, viz., the organic combination of the elements of the two sexes into a specifically new compound. Morgan explains the need of this hypothesis as follows:* " * * * if, in sexual union, there is a mere mixture, a mere commingling of hereditary characters, it is quite impossible that new characters should result, or any intensification of existing characters be produced beyond the mean of those of ovum and sperm. * * * Let us suppose, for the sake of illustration, that a pair of organisms have each an available store of forty units of growth-force, and that these are distributed among five sets of organs, *a* to *e*, as in the first two columns. Then the offspring will show the organs as arranged in the third column.

	Parents		Offspring.
a	10	10	10
b	8	10	9
c	9	5	7
d	7	9	8
e	6	6	6
	40	40	40

" There is no increase in the set of organs *a*, which are strongly developed in both parents; and no decrease in the set of organs *e*, which are weakly developed in both parents. By sexual admixture alone there can be no increase or decrease beyond the mean of the two

---

[*] Animal Life and Intelligence, pp. 150, 151.

parental forms. If then the union of sperm and ovum be the source of new or more favorable variations other than, or stronger than those of either parent, this must be due to the fact that the hereditary tendencies not merely commingle, but under favorable conditions combine, in some way different indeed from, but perhaps analagous to, that exemplified in chemical combination."

According to this theory it is of course possible that new variations could be originated by sexual admixture. It would also help to explain the presence of useless specific characters, which would, according to the old view, be obliterated by the swamping effects of intercrossing. "If, however," says Morgan,* "on the hypothesis of combination, we have definite organic compounds, instead of, or as well as, mere hereditary mixtures, if, in other words, variations take definite lines determined by the laws of organic combination (as the nature and properties of chemical compounds are determined by the laws of chemical combination), then this difficulty disappears." It would account also for the introduction of new parts or organs, and for their preservation before they had reached a point of usefulness. The chief objection to this view, aside from its purely hypothetical nature, which the author freely concedes, is the fact that it appears to prove too much. There are three general hypotheses concerning modifications: (1.) The variations may be "spontaneous," or due to some unknown cause, and occurring in all directions indiscriminately, as Wallace and other Neo-Darwinians claim, so there would be ample material for natural selection to work upon. According to this view external influences have nothing to do with variations. (2.)

---

*l. c., p. 152.

Variations may be caused chiefly by the response of the organism, or of its parts, to influences external either to the organism as a whole or to the parts thus affected. Or (3) variations may, as in the first instance, be wholly independent of external influences, but due, not to the selection of such modifications as happen to be suitable, but to inherent properties of the organism itself, or to predetermined properties of the combinations of organisms. It is Nägeli who advanced the first part of this third hypothesis, while Morgan's organic combination theory would, if pushed to its logical conclusion, it seems to me, lead to the second part. If certain combinations must inevitably lead to certain fixed and definite results, regardless of environment, not only the incipient stages but also the more advanced condition of an organism should be due exclusively to the operation of this force.

In reality there are but two alternatives in regard to the origin of variations. They are due either to some force or tendency or property resident within the organism itself, whether it be Weismann's sexual combination of different germ-plasmas, Nägeli's idioplasm with the inherent tendency to vary in the right direction, or Morgan's organic compound of sexually different elements which must on uniting produce a new given result; or to the workings of forces outside of the whole organism or of the parts affected. The possibility, of course, exists of both alternatives being valid. There is, however, a very fundamental objection to the first class of forces as being sufficient to originate variations, viz.: that it is at variance with the law of the conservation of energy, as suggested by Ryder, that an organism can create anything new within itself without the aid of any force external to it—a feat no less difficult than for a man to lift himself by the straps of his boots. The delusion of supposing that it is only a very little which is created new each time only serves to confuse the mind.

It is still not inconceivable that both external and internal forces may influence variation. There is no possible doubt that sexual combination is productive of variations, but I think it has been shown that these are not progressive. It is doubtless this factor which produces individual variation in species which have remained unmodified through long geological ages. This class might well be termed *conservative variations*.

It is a fact well known to gardeners and breeders that when a species is placed under entirely new environmental conditions it is apt to produce variations which are well marked, known as sports. It is such variations as these, due to the influence of environment, which, it would seem, are originative of new characters and might be called *progressive variations*. According to this view not only certain unusual modifications are due to environment, but all variations which are new have been thus produced. It must not be supposed that the environment acts definitely upon the organism, compelling it to vary in a single direction. Such may be the case in some instances, but not universally. Change in nutriment may produce very different results in different individuals, even of the same species, and would thus furnish natural selection with a very diverse, although by no means unlimited, assortment to pick from. Climate would often act in a more direct manner in modifying organisms as will be seen later on in considering the varieties of North American birds. Use and disuse of parts would also be productive of definite variations. According to the principles above stated, variations may be classified as follows:

I. *Conservative.* Occurring in all directions within the limits of variation of the species. Produced by sexual combination of unlike individuals.

II. *Progressive.* Produced by the action of environment upon the whole organism or by the interaction of parts.
  1. *Definite.* Direct action of environment in one direction, including use and disuse.
  2. *Indefinite.* General action of environment in producing variations which can be accumulated by natural selection.

Dr. W. K. Brooks in his book on heredity (p. 213) quotes the following secondary laws of variation which should be borne in mind:

(1) "Specific characters are more variable than generic characters." (Darwin, Origin of Species, p. 122.)

(2) "Species of the larger genera in each country vary more frequently than species of the smaller genera." (l. c., p. 44.)

(3) "A part developed in any species in an extraordinary degree or manner, in comparison with the same part in allied species, tends to be highly variable." (l. c., p. 119.)

(4) "If any given character is very variable in one species of a group, it will tend to be variable in allied species, and if any given character is perfectly constant in one species of a group it will tend to be constant in allied species." (Walsh, Proc. Ent. Soc. Phila., Oct. 1863, p. 213.)

The above discussion has answered the question, is natural selection creative? in the negative. An attempt has been made to show that it is not even admissible to assume unlimited variation as affording material for natural selection. Prof. Schurman goes even a step farther than this with regard to the origin of variations. He says:* "They originate, we know not how, in the nature of the organism. Nor would the state of the case be essentially altered if it were domonstrated, in opposition to Darwin, that every organic modification was occasioned by some external stimulus. For the change thus set up in the organism in response to the foreign excitation would obviously derive its character from the constitution of the organism, just as, to use Darwin's own example, the peculiarity of a flame is due to the constitution of the combustible materials, and not to the igniting spark." Prof. Schurman is arguing for a theistic conception of the origin of variations, and hence, of the creation of species, but his conclusion here does not effect the scientific, but only the metaphysical aspect of the case. As stated in the introduction to this chapter, natural law does not explain first cause, with which, indeed, science is not concerned. The ultimate reason for the enlargement of a muscle when exercised, for example, cannot be ascertained, but, nevertheless, if it could be shown why such exercise produced in successive generations variations in the direction of increased dimension, we would have as good an explanation of the cause of those particular variations as we have of the cause of the earth's attraction by the sun through gravitation. That variations are conditioned by the reaction of the organism on the influences of the environment, is undeniable, but this does not detract from the validity of an explanation of the origin of variations, so far as science is concerned. An analogy may illustrate this better, perhaps. Certain qualities of the mind are developed by education. It is possible to formulate the exact process by which these mental traits were brought about and it is justifiable to state

---

* The Ethical Import of Darwinism, p. 81.

that the origin of these qualities is known, and the cause of their presence in the mind, despite the fact that had not the mind the potential possibility of developing them they could never have been introduced.

LAWS CONDITIONING EVOLUTION.

If the above considerations upon individual variation contain within them even a flimsy core of truth; if natural selection even in its widest interpretation be not creative; then, indeed, it is necessary to discard the dogma of chance so much preached by the scientists of the day, and admit that just as the formation of the crystal is due to the working of natural law, so, too, is the evolution of man and of all the diversified life of the globe due to workings of the same natural law. Prof. Cope, Prof. Hyatt and Haeckel have placed especial stress upon the importance of the laws of biology, and it will be necessary to consider some of the laws which they have enunciated. The laws governing the evolution of life may be stated under three heads: (1) laws of development, (2) laws of structure, and (3) laws of heredity. They may be diagramatically classified as follows:

I. Laws of development.
    1. Bathmism or growth force.
    2. Phylogenic extent and density.
    3. Metabolism.
        a. Anabolism
        b. Katabolism.
    4. Sexual intensification.
    5. Acceleration and retardation.
    6. Law of concentration.
II. Laws of structure.
    1. Homology.
    2. Successional relation.

    3. Parallelism.
    4. Adaptation.
    5. Geratology.
    6. Bilateral symmetry.
    7. Correlation of growth.
- III. Laws of heredity.
    1. Uninterrupted or continuous transmission.
    2. Interrupted or latent transmission.
    3. Sexual transmission.
    4. Mutual or amphigonous transmission.

Of the laws of development, growth force or bathmism, as Prof. Cope has termed it, is the most fundamental. Protoplasm is a great store house of energy from without. It, alone, is capable of converting into its own substance foreign matter—inorganic among plants and organic among animals. By this conversion of foreign substance into the body of the organism, growth is induced, but this growth requires an expenditure of energy. The Century Dictionary refers to the following passage of Cope's for a definition of bathmism:* "It is here left open whether there be any form of force which may be especially designated as 'vital.' Many of the animal functions are known to be physical and chemical, and if there be any one which appears to be less explicable by reference to these forces than others, it is that of nutrition. Probably in this instance force has been so metamorphosed through the influence of the originative or conscious force in evolution, that it is a distinct species in the category of forces. Assuming it to be such, I have given it the name of *Bathmism*."

Bathmism, then, is the vital force inducing growth. Prof. Cope has stated as a fundamental law of bath-

---

* Method of Creation, p. 26.

mism* * * * "that growth-force, uninfluenced by inherited peculiarity, or any stronger influence locating a nutritive fluid, must *develop extent in the direction of least resistance, and density on the side of greatest resistance*, when not too great. The illustration of this statement would be that of a globular mass of cells brought to the point of junction of two media, as water and earth or air and earth, elongates in the direction of the medium presenting the least resistance, *i.e.*, air." This law may be further illustrated by the growth of the foliage of a tree. When a tree is located in the midst of a forest, it is crowded on all sides and accordingly expends its energy in growing upward. If, on the other hand, a barrier be placed to its upward growth, the foliage will become dense and matted at the point of obstruction. This law of extent and density, as enunciated by Prof. Cope, is apparently intended to account for the distribution of force in individuals or species only, but it seems to me possible that a broader interpretation may be put upon it than Prof. Cope had intended to imply. As an analogy representing the differentiation of life the structure of a tree has been commonly used, the spreading branches of which illustrate the divergent course of life through past geologic ages, while the leaves and terminal buds constitute the life of to-day. But the analogy of the tree may serve another purpose. It has been stated that the growth of a tree is conditioned by Cope's law of extent and density. This is a law of ontogony. But just as the perfect tree represents the direction of organic progress, so the law of growth force which conditions the growth of the tree, conditions also the growth of organic beings as a whole. In other words, life as a whole has made progress or

---

* Origin of the Fittest, p. 30.

developed in extent along the lines of least resistance and multiplied in forms on the same plane, or has developed in density along the lines of greatest resistance. This may be called the Law of Phylogenic Extent and Density. According to this view, living matter has within it the potential possibility of indefinite growth and modification. The growth is limited as Spencer has shown by the mass outrunning the surface, while modification is limited (1) by the possibilities of environment to create variations, and (2) by the ability of the organism to adapt itself to its environment. If it be asked how an organism can adapt itself to an environment which is itself the cause of the variations, the reply is by the selection of such environmental variations as are adaptive, or conversely by the elimination of such as are unadaptive. Living matter, then, like a gigantic tree or bush, spreads out in all directions where the environment offers least resistance, and man was not an accident or happy coincidence in the aimless wanderings of blind forces, but rather the inevitable outcome of natural law.

Metabolism, according to the Century Dictionary, is "the sum of the chemical changes within the body, or within any single cell of the body, by which protoplasm is either renewed or changed to perform special functions, or else disorganized and prepared for excretion." Geddes and Thomson in their work on the Evolution of Sex, have especially emphasized the importance of the laws of metabolism in the development of species. Metabolism should be clearly distinguished from bathmism or growth force. The latter is a force analogous to electricity, for instance, which conditions the growth of an organism; while the former is an expression of the changes continually taking place in protoplasm. There are two phases of metabolism. When the protoplasm is in a passive growing state and storing away energy, it is spoken of as anabolic, but when it is in a disruptive condition, giving out energy and breaking up into simpler compounds it is said to be katabolic. The metabolism of an organism is constantly varying between the anabolic and katabolic state, although of course not in rhythms of definite duration.

Messrs. Geddes and Thomson have devoted a considerable space in their work on the Evolution of Sex to establishing the principle that the male nature is naturally katabolic, the female naturally anabolic. They have enforced this principle by many examples and arguments, and it is justifiable, it seems to me, to use it as a working hypothesis. The law of sexual intensification proposed by me in a recent paper on the Colors of West Coast Mammals* is based upon this principle. Among west coast mammals are certain species which have assumed a black color in harmony with their surroundings, which are dark in hue, owing to the volcanic rock of which the soil is formed. A particular species was taken as an example, the black-headed ground squirrel (*Spermophilus grammurus atricapillus*), and an attempt was made to account for the black color. For three reasons it was assumed that the ancestors of this species were paler in color, probably gray or brown: (1) Because black is never a primitive color but rather a mark of specialization. (2) Because the races and species which are not black occupy a much greater geographical area, the black form being very local; and (3), because the young are paler than the adult. If the preceding discussion has established the impossibility, or even the improbability of natural selection exercising a creative power, it becomes proper to ask how the black

---

* Zoe, ii, pp. 203-216.

color of this race was produced from brown or gray ancestors. It is found that the male averages considerably darker than the female, although females may be found as dark as the lightest males. This is in accordance with the principle enunciated by Geddes and Thomson, that the tendency of the male is katabolic, of the female anabolic. The surplus of energy of the male would be expended in pigment, making the color more intense than in the female.

It will now be necessary to anticipate two of the laws of heredity as quoted in Zoe from Haeckel.* "A third law of conservative transmission may be called the law of sexual transmission, according to which each sex transmits to the descendants of the same sex peculiarities which are not inherited by the descendants of the other sex. * * * A fourth law of transmission, which has here to be mentioned, in a certain sense contradicts the last, and limits it, viz.: the law of mixed or mutual (amphigonous) transmission. This law tells us that every organic individual produced in a sexual way receives qualities from both parents, from the father as well as from the mother."

Now, according to this law of mutual transmission, there would be a constant tendency for the characters of the male and female to combine more or less in the offspring. This tendency, if acting alone, would result in an average color for both sexes. The females would become darker and the males lighter. The katabolism of the males, however, would tend to keep them at an average distance in advance of the anabolic females, and a tolerably constant ratio would be established. If, then, there were nothing to hinder the female from approaching the characters of the male, the latter would

---

* History of Creation, 1, pp. 209–210.

be constantly pushed ahead by katabolism and drag his mate after him. Thus, in the case in point, suppose the following proportions of color existed in a pair of these ground squirrels:

	MALE.	FEMALE.
Brown	10	20
Black	60	40
White	30	40

In accordance with the law of mutual transmission the two sexes are approaching the average: brown 15, black 50 and white 35. As the first ratio had been adjusted by the difference in metabolism which is supposed to be constant, the real goal toward which the male of the next generation is advancing is shown in the following proportion:

	1ST GENERATION.				2D GENERATION.		
	MALE.		FEMALE.		MALE.		FEMALE.
Brown	10	:	20	::	x	:	15
Black	60	:	40	::	x	:	50
White	30	:	40	::	x	:	35

The male of the second generation would then have the proportion of colors as follows: brown 7.5, black 75, and white 26.25, the black having increased considerably. In nature no such rapid increase as this is supposed to occur. The conservative law of sexual transmission and innumerable limiting and modifying circumstances would retard it.

After attaining a certain goal it would be impossible for any further intensification to take place in the male, as, for example, when it had become perfectly black. The color of the male then becoming stationary, it would be possible for the female to become more and more like the male in accordance with the law of mixed transmission, the characters of the one sex being transferred to the other. This, apparently, has actually taken place in another black form, the jack-rabbit of Espiritu Santo Island, Lower California, *Lepus insularis*, in which both male and female are equally black. This law, as stated in Zoe, referred only to transformations of color, but would apply equally to any form of modification. Variations, according to the principles stated in this chapter, are due to influences of the outer world upon the organism. One of the most potent environmental influences is nutriment. If there be an abundance of nourishment during a period of time, the tendency will at first be anabolic, or constructive. There is, at such times, a storing away of energy for future use. Geddes and Thomson have shown that a preponderance of females is born in times of plenty, of males in times of want. After a time of bountiful nourishment suppose a period of scanty food supply to follow. There will be a tendency toward katabolism, which means a breaking up of the energy which has been accumulating, a tendency toward variation and a preponderance of males. The males being more katabolic than the females, will tend to vary in advance of the latter in every direction in which a surplus of energy might be expended. In noting the different kinds of variation which have been observed it was found that they might consist of differences in size, shape, position, number, color or the addition of parts. It is obvious that any increase of size of the whole organism or of any particular part is due to an increase in the number of constituent cells, while variations in shape are due simply to a different distribution of the cells or to an increase or decrease in the number in any particular region. Variations such as ordinarily occur in organisms then, are apparently either variations in number or position. Number and position depend on the amount and location of growth-force, which in turn is conditioned by the metabolism of the organism, which last is determined by nutrition. The law of sexual intensification would thus seem to be applicable to any form of modification, which may be encouraged by natural selection, in which the male takes the lead, but would in no wise serve to originate any new part or structure.

At first sight this law might appear to be a mere restatement of the view of Dr. W. K. Brooks. According to his view, the male cells are the bearers of gemmules inducing variation, and in hard times the variable males being in preponderance, would induce progressive variation. Rev. J. T. Gulick has criticised this view as follows:* "There can be no doubt that in many species the males are more variable than the females, and that in some of the same species the proportion of males increases with the degree of adversity; but this does not seem to be sufficient ground for maintaining that the increase in the proportion of males will increase the variability of the offspring. Increase in the number or amount of the variable element does not necessarily involve increase in the variability of either element, or in the offspring of both. I find need of additional factors in order to bring these facts into any relation to the increase of variability. Granting that the sperm-cell is the source of variation and the germ-cell the source of fixity, and that increased tendency to variation in the offspring will be secured by an increased range of variation in the sperm-cells, it does not follow that increase in the relative number of males will increase the range of variation in the sperm-cells, and therefore in the offspring."

This difficulty, which implies that, however great the majority of the variable sex may be, unless each one

---

* Journ. Linn. Soc., xxiii, p. 317.

found a mate the variability of the species would not increase, does not, of course, apply to the law of sexual intensification, which has, it seems, been placed upon a firm basis through the researches of Messrs. Geddes and Thomson.

Cope first enunciated the law of acceleration and retardation. Two passages may be cited from his writings explanatory of this law: "I believe that this is the simplest mode of stating and explaining the law of variation; that some forms acquire something which their parents did not possess; and that those which acquire something additional have to pass through more numerous stages than their ancestors; and those which lose something pass through fewer stages than their ancestors; and these processes are expressed by the terms 'acceleration' and 'retardation.'"* On another occasion he had expressed the law thus: "It was also shown that, if the embryonic form were the parent, the advanced descendant was produced by an increased rate of growth, which phenomenon was called *acceleration;* but that if the embryonic type were the offspring, then its failure to attain to the condition of the parent is due to the supervention of a slower rate of growth; to this phenomenon the term *retardation* was applied." †

With regard to the cause of acceleration Prof. Cope first made the following suggestion:‡ "The successively higher degree of oxidization of the blood in the organs designed for that function, whether performing it in water or air, would certainly accelerate the performance of all the vital functions, and among others that of growth. Thus it may be that *acceleration* can be accounted for, and the process of the development of the

---

* Origin of the Fittest, p. 297.

† l. c., p. 125.

‡ l. c., p. 143–144.

orders and sundry lesser groups of the vertebrate kingdom indicated; for, as already pointed out, the definitions of such are radically placed in the different structures of the organs which aërate the blood and distribute it to its various destinations.

"But the great question: What determined the direction of this acceleration? remains unanswered. One cannot understand why more highly oxidized blood should hasten the growth of partition of the ventricle of the heart in the serpent, the more perfectly to separate the aërated from the impure fluid; nor can we see why a more perfectly constructed circulatory system, sending purer blood to the brain, should direct accelerated growth to the cerebellum or cerebral hemispheres in the crocodile."

The above statement of the cause of acceleration is in reality no explanation, for after all the real question is what determined the direction of the acceleration, for which Prof. Cope does not here attempt to account. In the paper on the Method of Creation of Organic Forms* he offers another explanation, which appears to be final. He asks, "What are the influences locating growth-force?" and answers, "The only efficient ones with which we are acquainted are: first, physical and chemical causes; second, use; and I would add a third, viz.: effort." To this third influence Prof. Cope ascribes a most important function—that of originating new parts; to it, indeed, may be attributed, according to Prof. Cope, the origin of the fittest. He says: "You cannot rub the sclerotica of the eye without producing an expansion of the capillary arteries and corresponding increase in the amount of nutritive fluid. But the case may be different in the muscles and other organs (as the pig-

---

* l. c., p. 195.

ment cells of reptiles and fishes), which are under the volition of an animal. Here, and in many other instances which might be cited, it cannot be asserted that the nutrition of use is not under the direct control of the will through the mediation of nerve force. Therefore I am disposed to believe that growth-force may be, through the motive force of the animal, as readily determined to a locality where an executive organ does not exist, as to the first segment or cell of such an organ already commenced, and that effort is, in the order of time, the first factor in acceleration."

All that can be said to the above is that it may be true, but that it has not yet been demonstrated. There is, indeed, a vast difference between the assumption that use can modify a part which already exists, and the assumption that desire or effort can originate something which does not exist. Moreover, even if effort be a valid factor in creation, it cannot, it seems to me, have the general application ascribed to it by Prof. Cope. For example, it could apparently have no influence upon the origination of new colors. Does the bird desire to be protectively colored? If so, it must decide what colors would be most in harmony with its surroundings and then make an effort of will to have these colors developed; all of which is, on the face of it, inconceivable. Or by what imaginable sort of effort could feathers be originated? Effort, then, if it can be shown to have any creative power, must be relegated to a very special field, and cannot be considered as the sole or even principal originator of the fittest.

What then can be considered the originator of the fittest? This I have attempted to indicate in the discussion of variation. It is an emphasis of the Hilairian rather than the Lamarckian factor. It is rather more in accord with the views of Eimer than Cope, although both are considered of importance. It is the recognition of the importance of physical and chemical causes, as the originators of new parts. The environment produces changes of which natural elimination destroys the least advantageous, leaving only the fittest to survive. There are metabolic rhythms in life. When the anabolic tendency is in the ascendent life is non-progressive, or there may even be retardation; but when the katabolic tendency is in the ascendent, life progresses along lines determined: first, by the nature of the variations, and second, by the operation of natural selection or elimination.

It may be of interest to note the bearing of the law of phylogenic extent and destiny. In the growing tree whenever its progress is checked in any direction, if the resistance be not too great the foliage becomes dense and matted. So with life as a whole. When a new plan of organization was originated, nature ran riot for a time in the wealth and multiplicity of forms she displayed. Take for example the age of reptiles. In their palmy days they were without competitors; climate and vegetation conspired for their well being; the soil had not been cultivated and was capable of bearing an immense crop. This was a period of acceleration. There was no resistance to the upward progress of growth-force and it advanced rapidly along certain lines. Having originated this great variety and multiplicity of forms quite suddenly, comparatively speaking, a barrier was presented to their future progress. The climate may indeed have remained as propitious and the food as abundant, yet an obstacle to their advance was introduced. And this obstacle was apparently simply the fact that they had reached the goal of their specialization. The growth-force was still there to be expended and was used in increasing density or mass to speak figuratively, or in other words, in the great multiplication of such species as already existed. In course of time the conditions of life became less favorable to them, more powerful antagonists arose, and they began to dwindle. Retardation began, and to-day there are left a few poor fragments of that mighty host that lived in the age of reptiles.

Prof. Alpheus Hyatt's law of concentration is very closely related to the preceding, being in fact a form of acceleration. Prof. Hyatt thus alludes to it:* "The law of concentration in development seems to express an invariable mode of action of heredity, in the earlier reproduction of hereditary characteristics of all kinds and under all conditions. In progressive series it acts upon healthy characteristics and appears to be an adaptation to favorable surroundings, and in retrogressive series upon pathological characteristics, and is probably an adaptation to unfavorable surroundings usually leading to the extinction of the series or type."

This ends the discussion of the laws of development. Of the laws of structure and heredity little need be said. For the sake of completeness, however, and especially as it will be necessary to refer to them in the second part of the work, it will be advisable to include a brief statement of them. Prof. Cope, in the Chapter on Evolution and its Consequences,† states the following four laws of structure:

"1. *Homology.* This means that animals are composed of corresponding parts; that the variations of an original and fixed number of elements constitute their only difference. * * *

"2. *Successional Relation.* This expresses the fact

---

* Fossil Cephalopoda in the Museum of Comparative Zoology. Proc. A. A. A. S., 1883, xxxii, p. 360.

† l. c., pp. 6–7.

that species naturally arrange themselves into series in consequence of a mathematical order of excess or deficiency in some feature or features. Thus species with three toes naturally intervene between those with one and four toes. * * *

"3. *Parallelism.* This states that while all animals in their embryonic and later growth pass through a number of stages and conditions, some traverse more and others traverse fewer stages; and that, as the stages are nearly the same for both, those which accomplish less resemble or are *parallel* with the young of those which accomplish more. * * *

"4. *Teleology.* This is the law of adaptation so much dwelt upon by the old writers, and admired in its exhibitions by men generally. It includes the many cases of fitness of a structure for its special use, and expresses broadly the general adaptations of an animal to its home and habits."

5. *Geratology.* Prof. Hyatt has enunciated this principle of distorted or pathological types.* It is the law that there "is an exact correspondence between the life of an individual and the group to which it *belongs:* namely, the young and adolescent stages having direct correspondence and repeating the past history of its own group to a greater or less extent, the adult corresponding to the present with all the peculiarities and differences of its group, and the metamorphoses of old age to the pathological modifications and changes found in the types which arose in the unfavorable localities, or which were found as a rule to terminate the history of the group in time."

To this list may be added the following special laws of structure, both of which may be more or less closely related to homology:

---

* Proc. A. A. A. S., xxxii, p. 349.

6. *Bilateral symmetry.* It is not clearly apparent why bilateral symmetry should be so prevalent in organic structures, whether it be due to some fundamental law of growth, or persistence of type, or to some principle of utility. Wallace has advocated the last view with regard to the bilateral symmetry in the colors of animals, arguing from the fact that where protective or recognition markings are no longer of utility, as with domesticated animals, bilateral symmetry is lost.

7. *Correlation of growth.* This law has been most clearly enunciated and established by Darwin. Owing to the close interdependence of parts in organisms, anything which affects one structure in the body may cause a similar or corresponding modification to appear in some other structure which is not directly influenced.

The laws of heredity may be condensed after Haeckel, thus:*

1. *Uninterrupted or continuous transmission.* Children are in general like their parents. This is expressed by the phrase "like produces like," or more accurately "similar things produce similar things."

2. *Interrupted or latent transmission.* Among certain lower forms of life there is an alternation of generations, the children being like the grandparents, the parents a different organism. "If we express this general law and the succession of generations by the letters of the alphabet, then A = C = E, whilst B = D = F, and so on."

3. *Sexual transmission.* Each sex transmits to its offspring certain peculiarities not possessed by the other sex, as, for example, the antlers of a deer.

4. *Mixed or mutual* (amphigonous) *transmission.* "This law tells us that every organic individual produced in a sexual way receives qualities from both parents, from the father as well as from the mother."

---

* History of Creation, pp. 205-213.

5. *Abridged or simplified transmission.* In embryonic development the organism does not pass through all ancestral stages, but omits a portion of them in order more rapidly to reach a state of maturity.

Having clearly defined my attitude in regard to the non-creativeness of natural selection and the necessity of qualifying it by the laws of development, structure and heredity, it will in the future frequently be found convenient to speak figuratively of selection as the originator of this or that character. Whenever a use is found for any structure or peculiarity of a species it is justifiable to assume that such a character has been encouraged by selection or elimination, and this is a most important, although not the ultimate step, in determining how the feature under consideration came about. It is indeed the only step which can be explained in most cases, the causes of the origination of anything new being so intimately dependent upon the nature of the organism, that comparatively little is known of them.

Two forms of selection still remain for consideration, sexual and physiological. Both have a direct and vital bearing upon the subject of the colors of birds; for if sexual selection be a valid factor in evolution it is undoubtedly an agent in the production of the bright plumage and gay ornamentation of male birds; while if the hypothesis of physiological selection be correct much light is thrown upon specific color marks which would otherwise appear useless. It thus becomes important to consider both of these theories with considerable care.

SEXUAL SELECTION.

Darwin originated the theory of sexual selection and Wallace has been his most determined opponent. Both should be heard from before a decision is reached. Darwin says;* "This form of selection depends, not on

---

* Origin of Species. I, p. 108.

a struggle for existence in relation to other organic beings or to external conditions, but on a struggle between the individuals of one sex, generally the males, for the possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring." There are two forms of sexual selection, the law of battle which is universally admitted, and "preferential mating" as Lloyd Morgan has termed it,* which is doubted by many. It is known that the males of many animals, especially among mammals and birds, fight among themselves for a female, the victor carrying off the prize. There can be little doubt that in such cases the more powerful males become the parents of the race, and that every advantage which they may possess in the way of strength, agility, or special weapons, such as antlers or spurs, will be selected in accordance with the law of battle. Preferential mating is thus described by Darwin:† "Amongst birds, the contest is often of a more peaceful character. All those who have attended to the subject, believe that there is the severest rivalry between the males of many species to attract, by singing, the females. The rock-thrush of Guiana, birds of paradise, and some others, congregate; and successive males display with the most elaborate care, and show off in the best manner their gorgeous plumage; they likewise perform strange antics before the females, which, standing by as spectators, at last choose the most attractive partner. Those who have closely attended to birds in confinement well know that they often take individual preferences and dislikes. Thus Sir R. Heron has described how a pied peacock was eminently attractive to all his hen birds. I cannot here enter on the necessary details, but if man can in a short time give beauty and an elegant carriage

---

* Animal Life and Intelligence, p. 198.

† l. c., p. 109.

to his bantams, according to his standard of beauty, I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect."

Darwin's theory of sexual selection with regard to the colors of birds is simply this, that both sexes were originally dull colored and alike, but the females, in selecting those males for mates which were more brightly colored than their fellows, have gradually brought about the brilliant and diversified plumage of the male birds of to-day. Wallace takes a directly opposite view, as expressed in the following passage: * "I have long held this portion of Mr. Darwin's theory to be erroneous, and have argued that the primary cause of sexual diversity of color was the need of protection, repressing in the female those bright colors which were normally produced in both sexes by general laws; and I have attempted to explain many of the more difficult cases on this principle ('A Theory of Birds' Nests,' chap. VI. ante)."

Mr. Wallace then proceeds to elaborate his views, explaining how the colors of male birds have become more brilliant without reference to sexual selection. He makes the valuable suggestion that brilliant colors are concomitants of a healthy organization, dull hues of a diseased system. The vitality of the male he considers to be greater than of the female, especially during the breeding season, and the brilliant colors and long plumes which are donned at that time are due to the necessity for this vital energy to find some outlet. "The greater intensity of coloration in the male" he says, † "which may be termed the normal sexual difference, would be

---

* Natural Selection 1891, pp. 364–365.

† l. c., p. 366.

further developed by the combats of the males for the possession of the females. The most vigorous and energetic usually being able to rear the most offspring intensity of colour, if dependent on, or correlated with vigor, would tend to increase. But as differences of colour depend upon minute chemical or structual differences in the organism, increasing vigor acting unequally on different portions of the integument, and often producing at the same time abnormal developments of hair, horns, scales, feathers, etc., would almost necessarily lead also to variable distribution of colour and thus to the production of new tints and markings." In following out this line of argument Mr. Wallace suggests that color is proportionate to integumentary development, reaching its maximum among butterflies and birds where there is the greatest expanse and variation of wings, but it has been asked why, if this hypothesis be a true one, bats are generally so dull colored, or beetles so brightly. "The endless processes of growth and change during the development of feathers, and the enormous extent of this delicately organized surface," he says,* "must have been highly favorable to the production of varied colour effects, which, when not injurious, have been merely fixed for purposes of specific identification, but have often been modified or suppressed whenever different tints were needed for purposes of protection." This appeal to the extent and structure of the feather can have but little weight, for, in the majority of cases, it is the exposed edge of the feather alone which is colored; the basal half being as a rule white or some dull shade of buff or gray.

Whether the appeal of Mr. Wallace to the general laws of growth is or is not justifiable as an explanation

---

*l. c., p. 369.

of the markings of birds, the question with which we are at present concerned is whether the female exerts any choice of a mate dependent upon color, and whether, if she does so, it is possible that the markings of a species might in course of time be changed by this means. Wallace asserts that there is no evidence that the female is in any way influenced by color in choosing a mate. Among butterflies it does indeed seem incredible that any such selection can take place, and Mr. Wallace presents the argument against this in the strongest possible light. His argument is controverted by Poulton, however, with considerable force.* Prof. Geo. W. and Elizabeth G. Peckham have published a paper entitled Observations on Sexual Selection in Spiders of the Family Attidæ,† in which they advocate the factor of sexual selection in the production of the colors of spiders. They show that in this group the female is fierce and pugnacious, which trait, according to Wallace, should be accompanied with a surplus of vitality and accordingly with brilliant colors, as he claimed to be the case with the humming-birds. But in this group the males are nearly always brilliantly colored, while the females are inconspicuous. On the other hand, the dull colors of the female could not have been originated for protection, for "all the species of this family have covered nests." The most important part of the paper is devoted to a minute description of the courting habits of different species of Attidæ. In conclusion the authors sum up the results of their observations as follows: "The fact that in the *Attidæ* the males vie with each other in making an elaborate display, not only of their grace and agility but also of their beauty, before the females, and that the females, after attentively watching

---

* The Colors of Animals, 291–297.

† Natural History Society of Wisconsin.

the dances and tournaments which have been executed for their gratification, select for their mates the males that they find most pleasing, points strongly to the conclusion that the great differences in color and in ornament between the males and females of these spiders are the result of sexual selection." Indeed, anyone who will attentively follow the account of these elaborate and painstaking investigations of the courting habits of this family of spiders, must admit that in this instance at least, there is considerable reason to believe that sexual selection has played an important part in the modification of color.

Among birds it is difficult if not impossible to secure such definite results from observation. It is known, however, that many male birds display their markings before the female in a very elaborate way. Darwin pointed this fact out as being especially confirmatory of his theory of sexual selection. It is thus explained by Wallace:* "At pairing-time the male is in a state of excitement, and full of exuberant energy. Even unornamented birds flutter their wings or spread them out, erect their tails or crests and thus give vent to the nervous excitability with which they are overcharged. It is not improbable that crests and other erectile feathers may be primarily of use in frightening away enemies, since they are generally erected when angry or during combat. * * * But if those portions of the plumage which were originally erected under the influence of anger or fear became largely developed and brightly colored, the actual display under the influence of jealousy or sexual excitement becomes quite intelligible." Mr. Wallace, in the above passage, has introduced a new theory explaining the brilliant colors of male

---

*l. c., p. 377.

birds, which it seems to me would need far greater proof to establish than the theory of sexual selection which it is intended to supplant. According to this new hypothesis the brilliant crests, etc., of birds have been largely developed in order to frighten away enemies, but it would require a great amount of observational evidence to demonstrate this. On the contrary, in the majority of cases the colors of the male bird are not in the least calculated to inspire an enemy with fear. Let us take a familiar example and compare the two views as explanations. The house-finch (*Carpodacus mexicanus frontalis*), is now at the height of the courting season and certainly displays a great amount of energy in the prosecution of his love-making. Three or four males may frequently be seen following a single female from fence to fence, or tree to tree. The wings are slightly lowered and the birds either face the object of their devotions displaying the bright crimson of the head, throat and breast, or hop directly away exposing the rump patch of the same color. Their vivacious song is also a feature of the courtship. The dull colored female eventually flies away with one of the competitors for her favor and the remaining males start in quest of other mates. It would of course be utterly impossible to assert that the female had chosen the most brilliantly attired of her suitors, but it is indeed a significant fact that several males, or at least two, have presented themselves to her, displaying their charms of song and dress, and that one of them is successful without any fighting with his competitors. Another fact of some importance,—I have seen a single male house-finch paying assiduous attentions to a female, and utterly repulsed and deserted by the object of his devotions. From the above it is evident that it is not mere perseverance which determines which male shall be successful, as Mr. Wallace has argued, but the choice is really made by the female.

Mr. Wallace has, however, interposed another objection of great importance. He says: * "Again, evidence collected by Mr. Darwin himself, proves that each bird finds a mate under any circumstances. He gives a number of cases of one of a pair of birds being shot, and the survivor being always found paired again almost immediately. This is sufficiently explained on the assumption that the destruction of birds by various causes is continually leaving widows and widowers in nearly equal proportions, and thus each one finds a fresh mate; and it leads to the conclusion that permanently unpaired birds are very scarce, so that, speaking broadly, every bird finds a mate and breeds. But this would almost or quite neutralize any effect of sexual selection of color or ornament, since the less highly-colored birds would be at little or no disadvantage as regards leaving healthy offspring." If it were indeed true that every male bird found a mate there would be a serious difficulty in the way of sexual selection, but Mr. Wallace has not established this in the passage above quoted. It seems quite as natural to suppose that there are always a number of birds who have not found mates, and that consequently there are constantly a supply of bachelors and old maids on hand to mate with any unfortunate widow or widower. Collectors of birds have often commented on the fact that several males are nearly always shot to one female. To be sure the duller colors and more retiring habits of female birds would insure their protection, but even where special search is made for them they are found to be less common than the other sex. This is noted, moreover, among species in which the sexes are alike. If there be such a preponderance of males as seems

---

*l. c., p. 370.

highly probable, then, of course, every bird does not find a mate, and Mr. Wallace's objection is invalidated. Prof. and Mrs. Peckham have shown that among the *Attidæ* every male does not get a mate. They say: *"In spiders, as the females gradually become adults, they have a choice from among a number of males, as these mature several days earlier. The males will pair as often as they have the opportunity, and as the mating season lasts for two or three weeks, the more brilliant males may easily be selected again and again."

Of considerable significance as showing the unsettled state of scientific opinion upon this difficult question, is the fact that two eminent English naturalists have each just published a work in which the subject is discussed, and have arrived at directly opposite conclusions. Prof. Frank E. Beddard, in his book entitled Animal Coloration, concludes that sexual selection, if operative at all, is a very insignificant factor, while Prof. George J. Romanes, in the first volume of the series on Darwin and After Darwin, writes to the contrary in the following emphatic sentence: † "And, as regards the particular case now before us, I think I have shown, as far as space will permit, that in the phenomena of decorative colouring (as distinguished from merely brilliant colouring), of melodious song (as distinguished from merely tuneless cries), of enormous arborescent antlers (as distinguished from merely offensive weapons), and so forth—I say that in all these phenomena we have phenomena which cannot possibly be explained by the theory of natural selection; and, further, that if they are to be explained at all, this can only be done, so far as we can at present see, by Mr. Darwin's supplementary theory of sexual selection." Inasmuch as these two scientists have

---

* l. c., p. 60.

† p. 400.

arrived at these opposite conclusions from consulting in the main the same works that have been referred to in the preceding discussion, it may be profitable to notice the grounds for their decisions.

Prof. Beddard, in his chapter on Sexual Coloration,* first enumerates instances of sexual dimorphism and dichromatism among forms where sexual selection is obviously precluded by the nature of the case, as, for example, among some species of Echinoderms. He states that even among birds when the sexes are different in color the female is sometimes as beautifully marked as the male, as in certain species of curassows, parrots, and the upland goose. He contends with Wallace that these brilliant colors are most common and striking in butterflies and birds where the nature of the expanded surface would facilitate their development. He points to the very slight exhibition of sexual dichromatism in mammals, and cites instances showing the dependence of sexual dichromatism in birds upon the sexual organs.

What is to be said of those objections to sexual selection? His first objection is, indeed, a valid one so far as it goes, viz., in showing that there can be sexual diversity in color and form without any selection, but this by no means disproves sexual selection in forms where it might be possible. As regards certain isolated instances of birds in which the female, although differently colored from the male is equally beautiful, there is much room for argument. In the first place it would be necessary to know in each specific instance in what the degree of difference consisted. Certain colors in birds have complementary colors which are more primative but not necessarily less beautiful. Thus many scarlet male birds when kept in captivity become yellow, which color is often characteristic of the female of the

---

* pp. 253–282.

same species. A bird might accordingly develop a brilliant scarlet color in its plumage through the instrumentality of sexual selection, while the female, through partial inheritance, would be colored yellow upon corresponding parts of the body. In the same manner various colors in one sex might be imperfectly inherited, producing a female bird but little inferior to her mate, although quite differently marked. The instance of the upland goose (*Bernicla magellanica*) in which "the female is a rich brown diversified by white marks, while the male is black and white," would be a case in point. To the suggestion that the structure of the feather offers greater facilities mechanically, for the display of color, the objection has already been raised that only the tip of the feather is colored. In another connection I have suggested * that the absence of brilliant colors in mammals, may be due to the fact that they are characteristically nocturnal in their habits, and the faculty of color perception would very naturally be less exercised and less highly developed than among birds. That the color of birds may be influenced by the removal of the sexual organs is an undoubted fact, but it does not throw any light upon the origination of the color. Even though a color had been developed by sexual selection, it would eventually become an attribute of one sex only, and might be expected to change if the bird were unsexed.

Prof. Beddard also calls attention to the difficulty of believing in a highly developed æsthetic sense, which has been urged by Wallace with such force. He alludes to the excitability during the breeding season of animals among which there is no pairing, but this does not appear to be as significant as he imagines. Granting it to be a fact that low forms of life do show signs of excitability

---

* Zoe, ii, p. 209.

during the breeding season, which is due to the state of their nervous organization, and granting, even, that the excitement shown by birds at this time may be due to the same cause, to a large extent, this does not account for the fact that the male birds display their ornaments in a painstaking and elaborate way. Prof. Beddard states Mr. Stolzmann's view as set forth in the Proceedings of the Zoological Society.* This theory is indeed an ingenious one and may be used as supplementary to the theory of sexual selection. It is based upon the assumption that male birds are much more numerous than the females, an assumption which Mr. Wallace rather too hastily discarded. Mr. Stolzmann suggests that this preponderance of male birds would be a disadvantage to the species, for the unpaired males would be apt to annoy the setting females and prevent the raising of the brood. Accordingly those species in which the males greatly predominated would stand less chance of perpetuating their kind than species in which the sexes were more evenly divided, and any device by which the surplus males could be killed off would enable such as were left to rear their offspring with greater success. Such a device is to be found, according to Mr. Stolzmann's view in the long tail feathers and brilliant colors of many male birds. If Mr. Stolzmann's view be correct then natural selection, it would appear, must be causing individuals to assume instruments for their own destruction in order that the species may live. This conclusion is arrived at from a merely superficial consideration of the case, however. Natural selection is in reality only preserving the lives of the greatest number of individuals. In any given generation the fittest individuals to survive would be those males which were least ornamented, but these would be the least fit to

---

* 1885, p. 615.

leave offspring, because from their very advantages over the females in point of numbers and strength, they would prevent them from rearing their young. Consequently these unornamented and inconspicuous males would leave fewer offspring than the conspicuous males which were fewer in numbers. The survival of the fittest, then, should be regarded in the long run as the survival of the individuals best fitted to leave offspring.

And now it may be well to enquire how this theory might be made to support sexual selection instead of opposing it, as Prof. Beddard intended it should. A very weighty objection to sexual selection has been raised by Mr. Wallace, viz., that even admitting the fact of selection on the part of the female bird its influence would be entirely neutralized by natural selection, for if these ornaments were developed solely for the sake of beauty, the individuals possessing such charms would be at a disadvantage in the struggle for existence, and perish. If the paradox can be demonstrated, on the contrary, that these disadvantageous appendages which have been acquired for the purpose of adornment, are in reality an advantage, this difficulty is entirely done away with.

Prof. Romanes does not consider Mr. Wallace's objections in great detail, but takes issue with him on the leading points in question. He says:* "There is no conceivable reason why mere *brilliancy of color*, as an accidental concomitant of general vigor, should have run into so extraordinary, so elaborate, and so beautiful a *design of colors*. Moreover, this design is only unfolded when the tail is erected, and the tail is not erected in battle (as Mr. Wallace's theory of the erectile function in feathers would require), but in courtship; obviously, therefore, the purpose of the pattern, so to speak, is cor-

---

* l. c., pp. 394–395.

related with the act of courtship—it being only then, in fact, that the general purpose of the whole structure, as well as the more special purpose of the pattern, becomes revealed." Mr. Romanes also calls attention to the fact that in many cases, such as the appendage of the bell-bird, a very elaborate structure has been evolved which is used only in courtship. Such a tube as the bell-bird's inflatable tube, which is present only in the male, certainly could not have been developed by any excess of vitality, or in accordance with any general laws of growth.

Mr. Romanes is inclined to throw aside the difficulty of constancy in æsthetic taste in birds a little too lightly. He says: * "Although we know very little about the psychology of the lower animals, we do observe in many cases that small details of mental organization are often wonderfully constant and uniform throughout all members of a species, even where it is impossible to suggest any utility as a cause."

In commenting on the display of ornaments by male birds, Mr. Wallace writes: † "But it by no means follows that slight differences in the shape, pattern, or colors of the ornamental plumes are what lead a female to give the preference to one male over another; still less that all the females of a species, or the great majority of them, over a wide area of country, and for many successive generations, prefer exactly the same modification of the color or ornament." Or to put the difficulty in the words of Lloyd Morgan, ‡ "Sexual selection of preferential mating involves a standard of taste; that standard has advanced from what we consider a lower to what we consider a higher æsthetic level, not along

---

[*] p. 399.

[†] Darwinism, p. 285.

[‡] Animal Life and Intelligence, p. 205.

one line, but along many lines. What has guided it along these lines?" There are apparently but two views to take in regard to the beautiful in life, either that which appeals to the æsthetic tasté of man in animal and floral colors has been developed solely for the utility of the individual possessing it, in accordance with the general laws of growth (such as the direct action of the environment, the structure of the integument, etc.), in which event any beauty which it may possess for man is purely incidental or a mere coincidence; or else it has been produced by the selection of the most beautiful, generally by the female.

Even Wallace admits that the beautiful colors of flowering plants have been produced by the selective agency of insects which aid in fertilization. Prof. Peckham has shown that in all probability the brilliant colors of some spiders have been produced by the selective agency of the female, while the argument for sexual selection in birds has a great deal in its favor. But it is not a little remarkable that those things which appeal to man as beautiful should be the same ones that affect animals as low in the scale as insects. Mr. E. B. Poulton believes this æsthetic sense to be generally present in the animals as well as in man. He says: *"If an artist, entirely ignorant of natural history, were asked to arrange all the brightly colored butterflies and moths in England in two divisions, the one containing all the beautiful patterns and combinations of color, the other including the staring, strongly contrasted colors, and crude patterns, we should find that the latter would contain, with hardly an exception, the species in which independent evidence has shown, or is likely to show, the existence of some unpleasant quality. The former division would contain the colors displayed in courtship

---

* l. c., p. 316

and when the insect is on the alert, concealed at other times.

"The immense difference between the two divisions, the one most pleasing, the other highly repugant to our æsthetic susceptibilities, seems to me to be entirely unexplained if we assume that the colors of both are intended for the purposes of recognition. But these great differences are to be expected if we accept Mr. Darwin's views; for the colors and patterns of the latter division appeal to a vertebrate enemy's sense of what is *conspicuous*, while those of the former appeal to an insect's sense of what is *beautiful*. It is, of course, highly remarkable that our own æsthetic sense should so closely correspond with that of an insect. I believe, however, that it is possible to account for this wonderful unanimity in taste."

Mr. Poulton accounts for it by supposing that "our standards of beauty are largely derived from the contemplation of the numerous examples around us, which, strange as it may seem, have been created by the æsthetic preferences of the insect world." But this does not explain why insects should have the same standards of beauty as man. Morgan indeed takes a stand decidedly opposed to Poulton. Thus he says:* "To sum up, then, concerning this difficult subject, the following are the propositions on which I would lay stress: (1) What we term an æsthetic sense of beauty involves a number of complex perceptual, conceptual, and emotional elements. (2) The fact that a natural object excites in us this pleasurable emotion does not carry with it the implication that the object was evolved for the sake of its beauty. (3) Even if we grant, as we fairly may, that brightly colored flowers, in association with nectar, have been objects of appetence to insects; and that

---

* Animal Life and Intelligence, p. 413.

brilliant plumage, in association with sexual vigour, has been a factor in the preferential mating of birds;—this is a very different thing from saying that, either in the selection of flowers by insects, or in the selection of their mates by birds, a consciously æsthetic motive has been a determining cause. (4) In fine, though animals may be incidentally attracted by beautiful objects, they have no æsthetic sense of beauty. A sense of beauty is an abstract emotion. Æsthetics involve ideals; and to ideals, if what has been urged in these pages be valid, no brute can aspire."

There is certainly much truth in these propositions of Mr. Morgan. His second statement, however, seems to need some qualification. As previously stated, the beauty in nature must be a pure accident or else have been evolved, because it appealed to the sense of beautiful in the lower animals. A landscape or beautiful sunset generally appeals to our sense of the sublime rather than the beautiful. But there are many objects in inorganic nature that certainly do appeal to our sense of the beautiful. Crystals may be beautiful both in form and color, but when such is the case the beauty cannot be looked upon as anything but a coincidence. Objects in the organic just as in the inorganic world may or may not be beautiful, but in this case the beauty cannot be always considered incidental. If a feather is beautiful it is doubtless a mere accident, inasmuch as it was evolved for utility, and the same may be said of the leaf. But if flowers, insects and birds, display beautiful effects which bear an observed relation to the inter perceptual and emotional faculties of these organisms, it is but reasonable to assume a causal connection between them, and to suppose that these beautiful effects have been evolved by insects and birds, because they gave them pleasure. Mr. Weismann, in speaking of the tailless cats of Japan, suggests that novelty may be the motive for choice in sexual selection. He says:* "We thus see how a slight but striking variation may at once cause an energetic process of artificial selection, which helps this variation to predominance: a hint for us to be careful in passing judgment upon sexual selection, for the latter also works upon such functionally indifferent but striking variations. In the case of the cats, man has favored a particular variation, because the novelty rather than the beauty of the character surprised and attracted him. * * * I see no reason why the same process should not take place in animals by the operation of sexual selection."

If the colors of birds and insects had been produced for the sake of novelty, as Weismann suggests, we might indeed expect to find occasional or even frequent examples of beauty among them, but the rule would be that glaring contrasts would prevail. There would be no harmony in the arrangement or contrast of colors, and the majority would possess the characteristics of those insects that are branded with warning colors.

Mr. Romanes, in his recent work, devotes more attention to the beautiful in the lower forms of life than has been previously done, and affords an excellent explanation of its occurrence. He says:† "Turning, then, to the animal kingdom below the level of insects, here we are bound to confess that the beauty which so often meets us cannot reasonably be ascribed either to natural or to sexual selection. Not to sexual selection for the reasons already given; the animals in question are neither sufficiently intelligent to possess any æsthetic taste, nor, as a matter of fact, do we observe that they exercise any choice in pairing. Not to natural selection,

---

* Essays upon Heredity, I, 1891, p. 443.

† l. c., p. 408.

because we cannot here, as in the case of vegetables, point to any benefit as generally arising from bright colors and beautiful forms. On the principles of naturalism, therefore, we are driven to conclude that the beauty here is purely adventitious, or accidental. Nor need we be afraid to make this admission, if only we take a sufficiently wide view of the facts. For, when we do take such a view, we find that beauty here is by no means of invariable, or even of general, occurrence. There is no loveliness about an oyster or a lob-worm; parasites, as a rule, are positively ugly, and they constitute a good half of all animal species. The truth seems to be, when we look attentively at the matter, that in all cases where beauty does occur in these lower forms of animal life, its presence is owing to one of two things—either to the radiate form, or to the bright tints." Mr. Romanes then shows that neither of these circumstances have primarily any reference to beauty, and we must consequently conclude that the beauty of such structures is a purely accidental feature of their organization.

But having shown this to be the case, might it not be justifiable to extend the conclusion, as Mr. Wallace has done, and decide that wherever beauty is found in animate nature it is accidental and due to the mechanical or organic necessities of the case? Clearly the generalization should not be made without looking at the question from other aspects. On looking at color in the broadest possible manner, it is found to be of two sorts: colors incidental to the nature or properties of a substance or organism, as the red of blood, green of leaves, brown of earth and blue of sky; and colors which do not appear in any way mechanically essential to the organisms possessing them, but to have been produced for an effect upon some percipient being. It is hardly necessary to call attention to the fact that all color is color only in so far as it is seen as such, being, from a mechanical point of view, nothing but molecular vibrations. In spite of this fact, some colors appear to have been brought about from some relation existing between the being possessing them and some other percipient being or beings, while other colors are purely adventitious. It is indeed difficult in many cases to distinguish between the two kinds, although there are some instances in which opinion is practically unanimous. For example, no one can deny that certain animals are protectively colored; but in asserting that an animal is protectively colored, the implication is necessarily made that there are or have been other animals in the same environment which would see it if it were colored otherwise. Accordingly, in these protectively colored species, the colors are not adventitious but have been produced with the view of not being seen. Warning colors and recognition marks, on the other hand, have been produced for the purpose of being seen. If, then, these three great classes of colors in animals—protective, warning, and recognition—have been produced in order that the animal possessing them may be seen or not seen, as the case may be, is it logical to assume that the colors which appeal to us as beautiful, although it is impossible, in the majority of cases, to draw any sharp line between them and such as may be more or less of use for protection or recognition—is it logical to assume that these beautiful colors have been produced without any reference to some other individual perceiving them? Why, in this one instance of the colors which above all others attract the human eye, and, apparently, the eye of all the higher animals, should we assume that they have been produced without any reference to their fellow beings which are continually seeing them?

Having stated at some length the leading arguments for and against sexual selection, it will be appropriate to end the discussion with some provisional conclusions concerning it. In the first place, it will be necessary to distinguish between the origination and guidance of sexual colors. Critics of the theory of sexual selection frequently appear to imagine that its acceptance requires the assumption that a female bird has simply to get fixed in her mind in some unaccountable manner a particular style of dress for her lord and master, and then by a patient process of trying on one garment after another, and with perfect scope to embellish the dress at her pleasure, she will at last get one to suit. The more rational view is, that the female simply passes judgment upon the attire of the male, accepting that which is most pleasing to her sense of sight.

Grant Allen, in his suggestive little volume on Physiological Æsthetics, treats of the physical basis of color perception, and of the harmony and discord of color. He says:* "We have seen * * * that certain masses of colour are in themselves, apart from any effects of combination, pleasurable stimulants of the optic nerve. They may thus be regarded as the analogues of musical tones, which we saw to be similarly gratifying in isolation, because they aroused normal amounts of action in fully-nurtured and under-worked nervous structures. But most pleasures of colour are not so simple in their nature as these, nor do those we have already considered rank very high in æsthetic value. Savages are pleased by yards of red or blue cloth, and even cultured eyes are often attracted by a colour of unusual purity and richness, unrelieved by contrast or harmony; but the greater number of artistic effects depend upon combinational considerations." He then shows why certain combinations of colors are more pleasing than others. A particular

---

* p 161.

color fatigues only such nerves of the eye as respond to it as a stimulant. Just as in music when the beats are too frequent a dissonance is produced, so in looking at a combination of colors if the recurrent interferences are too frequent a discord is produced and the colors do not please.

The eye of the bird is a more perfect mechanical contrivance than the human eye, and is doubtless fully as sensitive to the stimulus of various shades of color. To be sure, it has been ascertained that birds see colors entirely differently from mammals. Blue, for example, is apparently excluded from their list.* Lloyd Morgan says:† "If these facts be so, it is not too much to say that the colour-vision of birds must be so utterly different from that of human beings, that, being human beings, we are and must remain unable to conceive its nature. The factors being different, and the blending of the factors by overlap being, by specially developed structures, lessened or excluded, the whole set of resulting phenomena must be different from ours." This difference in the colors perceived by birds, however, does not in the least interfere with the mechanical basis of color harmony as laid down by Grant Allen. A female bird would naturally prefer for a mate an individual in which the feathers were not soiled and bedraggled, and also one in which the colors did not produce any mechanical jar (roughly speaking) upon the delicate optical mechanism. Accordingly, given certain base colors, these might be separated, refined, purified, intensified and even arranged in certain patterns in order to produce a harmonious and agreeable combination and contrast.

To state briefly the factors operating in the production

---

* Color-Vision and Color-Blindness. R. Brudenell Carter: Nature, xlii, p. 56.

† Animal Life and Intelligence, p. 285.

of the brilliant colors and plumes of male birds they are as follows: Katabolism of the male supplies a surplus of energy to be expended (Geddes and Thomson); some color must be present in birds as in all objects, and its distribution is limited (but not determined) by the nature of the integument and the general laws of growth (Wallace); birds and some insects (?) have a visual apparatus which is sensitive to contrasts of color and is more easily fatigued by certain shades and patterns than by others, and consequently certain combinations are more pleasing than others; the female bird (generally) chooses a mate from among a number of suitors, conforming to what is more or less pleasing or disagreeable in the plumage of the males (Darwin); owing to the surplus of males, the conspicuous plumes and colors which are thus developed by the choice of the female bird, are a positive advantage to the species, reducing the numbers of the predominant sex, and their preservation is thus insured by natural selection (Stolzmann); in many cases the female bird inherits the bright colors of the male, but these colors are more frequently suppressed by the action of natural selection, from the greater necessity for protection on the part of the female during the process of incubation (Wallace).

According to the view thus summed up, each one of the investigators who have contributed to the subject have presented only a portion of the truth and have attempted to make it stand for the whole. This synthesis seems to satisfy all the various objections which have been raised against sexual selection, and to supply a tolerably complete explanation of secondary sexual characters in birds.

THE NATURE OF SPECIES.

Throughout all the foregoing consideration of the various theories and speculations regarding the factors of organic evolution, it will be noticed that little has been said about the nature and origin of species. This has been left for the conclusion, as the final problem for evolution to solve. In the first place, a few words on the term species will be necessary. In its broadest or logical interpretation, any set of individuals having some characteristic or group of characteristics in common, constitutes a species. Species may be determined upon an artificial or upon a natural basis. For example, the human race might be divided into species depending upon the occupation pursued, when we would have a species of hunters, a species of mechanics, one of doctors, another of lawyers, and so on, *ad infinitum*. This would, indeed, be, to a certain extent, a natural classification, from one point of view. Or we might divide mankind more arbitrarily into species according to height, weight, disposition, or attainments, which would be a classification into artificial species. A natural system differs from the foregoing in showing real relation through common ancestry. To be sure, in the classification of the human race according to occupations, a true relation through common ancestry is shown, for the progenitors of the human race undoubtedly all had much the same occupation, from which all subsequent pursuits have been evolved; but a natural system of division must do more than indicate a real connection by evolutionary succession—it must show that particular connection or group of connections which is most vital to the nature or being of the thing classified. In fact that which is used as a basis for a natural classification must be that which is most fundamental to the being classified, and each stage in division must be based upon that quality or property which most vitally conditions it, and is common to all subsequent groups which may be contained within it. To illustrate: A natural classification of man must be based upon life, which, from a scientific point of view at least, is the most vital and fundamental property of the being under consideration. The next stage in the classification would be a division into the animal and vegetable life, and the third the placing of man in the vertebrate series of animals. It will be observed that this third process of division is simply a particular form of the fundamental property with which we started. Continuing in this same manner, we should ultimately get a classification of men into the various races, Caucasian, Ethiopian, Mongolian, etc., and a subdivision of each of these into the various tribes or nationalities, as Germans, French, Italians, Americans. It is possible to go even a stage farther, and divide Americans into Yankees, New Yorkers, Southerners, etc., but a point is ultimately reached where no further division is possible because no characteristic can be found of any number of individuals which is a more special expression of some more universal and necessary property of their being.

The point to be emphasized in this discussion is the fact that logically any group, however extensive or restricted, may be regarded as a species in relation to the next more inclusive group which contains it, and constitutes its genus. Thus, logically, the vertebrates form one species of the genus animal. Furthermore, science is more or less arbitrary in the making of species, unless only the most ultimate and special division of a group be considered as such. Such a distinction of species is never made, however, for what scientist would venture to make the Yankee a distinct species, *americanus*, of the genus *Homo*, even though every individual had a nasal twang which unerringly indicated the section from which he came? The Code of Nomenclature of the American Ornithologists Union* contains the following apt sentences on this subject: "There is no inherent zoological difference between a 'generic' and a 'specific' name,—the *nomen genericum* and the *nomen triviale* of earlier zoologists. Both alike designate a 'group' in Zoology,—the one a group of greater, the other a group of lesser classificatory value. Some necessary distinction, which has been misconceived to exist between these two names, is simply a fortuitous matter of the technique of nomenclature, apparently arising from the circumstance that the generic and the specific names form the contrasted though connected terms of a binomial designation. Recognition of the scientific fact, that a 'species,' so called, is not a fixed and special creation, as long supposed, but simply a group of the same intrinsic character as that called a 'genus,' though usually less extensive, and always of a lower taxonomic rank, has done more than any other single thing to advance the science of Zoology; for the whole theory of evolution turns, as it were, upon this point."

From the above it is apparent that the decision of whether any particular group of individuals constitutes a species or some greater or lesser taxonomic division, must be more or less arbitrarily settled. In general, however, it may be said that a species in science is a group of individuals morphologically isolated from every other group by at least one peculiar character.† Wherever a group is not completely isolated, but connected by living intervening forms with some other

---

* pp. 26-27.

† The word morphological is here used in its broadest interpretation, as distinguished from physiological, and of course includes color changes.

group, it is called a variety. Species and varieties, then, do not always represent real taxonomic values, for two extreme varieties of one species may be morphologically very much less alike than two closely allied species. It all depends upon the accident of destruction of intermediate forms.

Having now clearly defined the nature of a species and the relativity of its value, it is time to consider the relation of evolution to species. The end of evolution is the establishment of successively higher types. Progress must be orderly, and species are merely crystallized forms of orderliness. If each individual were to start off on its own independent track there would be no unity in nature. Organisms would not hold together, and life as a whole would present no feature of rationality. Real progress would be defeated, and evolution would end in chaos. But in recognizing that species are the indispensable instruments of orderly evolution, is it necessarily implied that species are the outcome of natural selection? This implication certainly does not inevitably follow, even using the term natural selection in its widest sense, and admitting it as an important factor in evolution.

Before considering this fundamental question as to whether or not natural selection, aided, of course, by all the factors of heredity and variation, can originate species, it will be well to enquire what it is that natural selection preserves—the individual or the species. Mr. Romanes, in the Darwinian Theory* says: "Next, it must be clearly understood that the life which it is the object, so to speak, of natural selection to preserve, is primarily the life of the *species;* not that of the *individual.* Natural selection preserves the life of the individual only in so far as this is conducive to that of

---

* Darwin and After Darwin, i, pp. 264–265.

the species. Wherever the life-interests of the individual clash with those of the species, that individual is sacrificed in favour of others who happen better to subserve the interests of the species. For example, in all organisms a greater or less amount of vigour is wasted, so far as individual interests are concerned, in the formation and the nourishment of progeny. * * * * Again, all unselfish instincts have been developed for the sake of the species, and usually against the interests of the individual. An ant which will allow her head to be slowly drawn from her body rather than relinquish her hold upon a pupa, is clearly acting in response to an instinct which has been developed for the benefit of the hive, though fatal to the individual. And, in a lesser degree, the parental instincts, wherever they occur, are more or less detrimental to the interests of the individual, though correspondingly essential to those of the race."

Let us view these words of Mr. Romanes in the light of what has just been said concerning the nature of a species. Discarding any teleological conception as unworthy of scientific consideration, why should natural selection preserve the species rather than any other more or less inclusive taxonomic group? Natural selection is the result of a struggle for existence. This struggle for existence, as Darwin has shown, is most keen among those individuals that are most alike; just as among men, doctors come into closer competition with one another than they do with lawyers, or a dry goods merchant will have a harder contest with his fellow dry goods merchants than he will with a hardware merchant. The struggle for existence is then, first of all, a struggle of individuals of one species among themselves, in which battle only the fittest will survive. But how could the self-sacrificing ant to which Mr. Romanes alludes, pass muster in such a struggle for existence of individual with individual; or how could any altruistic trait be evolved? Mr. Romanes, it seems, has not adequately shown this. The parental instinct does not constitute a strictly corresponding instance, for the survival of the fittest must of course mean the survival of those individuals best fitted to leave offspring. In the case of the dry goods merchant just referred to, he would only be the fittest individual to survive in the long run, if he were able not merely to win his place among his competitors, but to maintain it through his heirs. Reproduction is merely growth beyond the individual, and accordingly the longer the line of potential descendants which an individual leaves, the longer will that individual survive, speaking broadly. Consequently, no sexual individual is really complete. It can only become complete by perpetuating itself, which demands a mate.

In this view of reproduction a clue may be found to the introduction of altruistic traits. Every individual's bodily immortality is conditioned by the existence and well being of some other individual. The survival of the individual is thus clearly wrapped up with the survival of the family, and natural selection would therefore encourage any tendency which would promote the family, even to the disadvantage of certain members of it. Thus the habit of feigning lameness by some birds to lure an enemy from the young, is a source of danger to the parent but a protection to the young. If in any case, however, the danger to the parent were greater than the protection to the young, the habit could not have been acquired, for whenever the parent were lost through the exercise of this altruistic habit, the young would in the great majority of cases die of neglect, and the habit would not become established.

To admit that it is the family rather than the single individual which natural selection preserves, is far different from granting that the species, or even the race or tribe is what natural selection especially favors. Let us pass on next to a consideration of this point. The family, as we have seen, is absolutely indispensable to the life of the individual, in the widest sense, but this is not the case with the tribe. The individual can have a potential bodily immortality without the tribe, and in a large number of cases this actually occurs. However, it sometimes happens that by associating in a community with similar interests, a greater number of individuals can enjoy an immunity from some common danger. This would only occur when the struggle for existence was more severe with some outside enemy than with each other, which would be a comparatively exceptional state of affairs.

This has not brought us any nearer to Mr. Romanes' main proposition, that it is the life of the species which natural selection preserves, and not that of the individual. In point of fact, natural selection does not preserve species with anything like the persistence with which she perpetuates genera, nor are genera as lasting as orders. What natural selection really preserves are those individuals which are capable of perpetuating something higher or more perfect. A species is an aggregate of individuals in which some new feature of excellence is universally present, and from the very fact of their possessing this new feature they will stand a better chance of being preserved as a whole, than another group of individuals which lack this higher or advantageous characteristic. To return to the analogy of the dry goods merchants, which, by the way, is a true analogy because natural selection is actually in operation in this instance: their struggle for existence, as previously pointed out, is more intense among themselves than it is with the hardware or shoe merchants.

Now, if in some large city, a portion of the dry goods merchants should introduce some new feature, such as keeping open evenings and lighting their stores with electricity, while the other dry goods merchants were unable to afford this innovation, a new species of dry goods store would arise, every individual of which would be at an advantage over the old species. The struggle for existence would then go on between the different individuals of the new species and those who were able to afford the most brilliant illumination or to keep open the longest would survive, while the others would die. In this sense natural selection is protecting the species regardless of the individual, but in a deeper sense it is protecting the individual regardless of the species.

PHYSIOLOGICAL SELECTION.

Mr. Romanes has also raised the deeper question, has natural selection, even in its widest sense, originated all new species? His original paper on Physiological Selection was read before the Linnean Society, May 6, 1886,* and shortly afterwards an abstract appeared in the columns of Nature. This communication aroused a great storm of opposition, Wallace in particular enlisting himself with the enemy. Romanes asserts that there are three cardinal difficulties in the way of natural selection, considered as a theory of the origin of species. These are: (1) the difference between species and varieties in respect of mutual fertility; (2) the swamping effect of free intercrossing upon an individual variation; and (3) the inutility of a large number of specific characters.

---

* Journ. Linn. Soc. xix, pp. 337–411.

To overcome these three difficulties he has proposed a new factor, physiological selection or the segregation of the fit. It is a known fact that isolation favors the production of new species. Oceanic islands in particular attest to this. According to Mr. Romanes, however, the advantage of geographical isolation is not always offered to incipient species, which often branch off in the midst of the parent stock. It is a noteworthy circumstance, however, that of all parts of an organism the reproductive organs are most susceptible to change, and if a variation in these parts should occur among a number of individuals making them sterile with the rest of the species but fertile among themselves, they would be physiologically isolated even in the midst of their associates. In the words of the author, this view enables us to regard many, if not most, natural species as the records of variation in the reproductive systems of ancestors.

In considering the three difficulties in the way of natural selection the author adduces considerable evidence to show that the difficulties are real. He asserts that the fundamental or primary difference between species is sterility, this being a common distinguishing feature in nearly every instance. Other differences consist in innumerable distinctions of structure, color or markings, which he calls secondary differences. Inasmuch as these secondary differences are never exactly alike in two species while the primary difference is always the same, he demands an explanation of the constancy of this distinction, asserting that all previous theories have dealt only with the secondary differences. Even where geographical isolation has originated species it is not possible to account for the almost universal sterility existing between them. "The consequence is," he says, "that most evolutionists here fall back upon a great assumption: they say that it must be the change of organism which causes the sterility—it must be the secondary distinctions which determine the primary. But the contrary proposition is surely at least probable, namely, that it is the sterility which, by preventing intercrossing with parent forms, has determined the secondary distinctions—or, rather, that it has been the original condition to the operation of the modifying causes in all cases where free intercrossing has not been otherwise prevented." The author then proceeds to show that it is not logical to suppose that any one of so infinite a number of changes could have the same effect in modifying the reproductive system. Furthermore, these changes constantly occur among domesticated animals without affecting the fertility of the breed. Darwin has shown that among wild species the ratio between structural affinity and the degree of sterility is not always constant, some very distinct species being found to hybridize with facility; but this is not in accord with the view that the sterility is universally due to structural differences. "Mr. Darwin further shows that, 'independently of the question of fertility, in all other respects there is the closest general resemblance between hybrids and mongrels.' Clearly, this fact implies that natural selection and artificial selection run perfectly parallel in all other respects, save in the one respect of reacting on the reproductive system, where, according to the views against which I am arguing, they must be regarded as differing, not only constantly but also profoundly. Lastly, Mr. Darwin concedes—or rather insists—that 'the primary cause of the sterility of crossed species is confined to differences in their sexual elements.' A general fact which assuredly proves that the primary specific distinction is one with which the organism as a whole is not concerned: it is merely a local variation which is concerned only with the sexual system. Why, then, should we suppose that it differs from a local variation taking place in any other part of the organism? Why should we suppose that, unlike all other such variations, it can never be independent, but must always be superinduced as a secondary result of changes taking place elsewhere?"*

After stating at length his reasons for believing that variations in the reproductive system may arise independently of variations in the organism, Mr. Romanes qualifies this by admitting that in some cases the variation in the sexual organs may be correlated with other variations in the system, and may have been primarily caused by natural selection; but in granting this he shows that natural selection simply becomes one of the causes determining physiological selection. "If," he says, "we thus regard sterility between species as the result of what I have called a local variation, or a variation arising only in the reproductive system—whether this be induced by changes taking place in other parts of the organism, to changes in the conditions of life, or to changes inherent in the reproductive system itself—we can understand why such sterility rarely, though sometimes, occurs in our domesticated productions; why it so generally occurs in some degree between species; and why as between species it occurs in all degrees."

As to the evidence of this infertility between individuals of the same species, which is a necessary assumption of the theory, many cases of failure to interbreed have been adduced by Darwin and others. Or the time of flowering or mating may be accelerated or retarded in certain individuals, thus isolating them from the rest of the race.

---

* Nature xxxiv, pp. 338–339.

The second difficulty of the doctrine of natural selection as the originator of species, according to Mr. Romanes, is the swamping effect of interbreeding. Wherever any geographical barrier cuts off a portion of a race the section so isolated is found to develop into a new species. In fact, it is evident that if occasional variations arise in individuals in the midst of others in which they do not occur, they will soon be eradicated by interbreeding with the dominant class, however advantageous they might be. Physiological selection would of course prevent this.

Mr. Romanes' third difficulty is a question of fact. Are all specific characters useful? Natural selection concerns itself solely with adaptations caring nothing whatever for species as such. In case the specific character is also an adaptive character, it is reasonable to suppose that it has been developed by natural selection; but if, as Mr. Romanes contends, a large number of specific characters are of no use, some other factor must have developed them, which factor Mr. Romanes considers to be physiological selection. He asserts, moreover, that without isolation evolution would be linear in direction but never branching. The struggle for existence is most intense in the most populous districts, and consequently the evolution of new species should be most rapid in such regions, but the evolution of new forms in a crowded district would be especially difficult, in fact practically impossible without some form of isolation. Physiological selection would afford this needed aid.

That so revolutionary a theory as this appeared to be should not be immediately accepted by scientists was not to be wondered at. To be sure it had been suggested previously in Mr. Belt's Nicaragua and in a letter to Nature by Mr. Catchpool, but Mr. Romanes for the first time elaborated it and pointed out some of its bearings upon the doctrine of natural selection. Mr. R. Meldola was one of the first critics of the new theory.* He asserted that the principal difficulty pointed out by Mr. Romanes was "the sterility of natural species as compared with the fertility of domesticated races." Inasmuch as the struggle for existence is most intense between those individuals which are most alike, anything which would cause them to vary would be an advantage which natural selection would make use of. The prevention of intercrossing by inter-sterility would be such an advantage and natural selection would accordingly favor it.

Mr. Francis Galton, soon after offered another suggestion regarding physiological selection.† According to his view certain individuals of a race are isolated from the rest by having similar sexual likes and dislikes which cause them to interbreed rather than to mingle with the rest of the tribe. In replying to the above two criticisms, Mr. Romanes attempts to show that neither Galton nor Meldola have really opposed his views. Mr. Galton had objected to physiological selection on the ground that the intersterility which it presupposes would not be externally apparent, and consequently many infertile unions would result. There is nothing to show, however, that infertile unions do not take place at times, and Mr. Galton's hypothesis of psychological selection simply supplements among the higher animals the more universal factor of physiological selection.

In replying to Mr. Meldola's criticism, Mr. Romanes shows that it is not his theory of physiological selection which is called in question, but simply whether natural selection may not in every case underlie and condition

---

* Nature xxxiv, pp. 384-395.

† l. c. pp. 395-396.

it. "But surely," he says, "the burden of proof here lies on the side of my critic. If he can show any sufficient reason for going much farther than I have ventured to go in out-Darwining Darwin—or for holding that natural selection may not merely help in inducing stertlity in some cases, but has been the sole cause of it in all cases—then I should welcome his proof as showing that the principles of physiological selection ultimately and in all cases rest on those of natural selection. But, clearly, it is for him to prove his positive: not for me to prove what I regard as an almost preposterous negative."*

Mr. Meldola also noted the difficulty that physiological selection must always be subservient to natural selection, because if a race developed through isolation did not possess some advantage over the main stock—the struggle for existence being most severe among most closely related forms—it would not be able to compete with the dominant type of the species. In reply to this Mr. Romanes states that if the character distinguishing the new form be indifferent as regards utility the individuals possessing it will be on an exactly equal footing with those which do not possess it, more especially if as at first, the variation be simply of the reproductive organs. The fact that the individual possessing this variation has reached the breeding age is in itself a guarantee of its fitness to survive, and it was to emphasize this fact that the alternative name of the "segregation of the fit" was proposed.

Mr. Wallace has however presented a more sweeping and serious line of criticism than any of the preceding, and it is to this that attention must next be directed. His objections were stated in an article entitled "Romanes *versus* Darwin. An Episode in the History of the

---

* l. c. p. 408.

Evolution Theory."* Mr. Wallace objects most emphatically to the view that any specific characters are without use. He points to the progress which has been made of late years in discovering the use of structures or characters which were formally thought to be of no utility, and calls particular attention to the colors of the higher vertebrates as illustrating his point. He mentions the fact that while the colors of wild animals are so generally constant (white or pied varieties being speedily obliterated) domestic breeds exhibit the greatest inconstancy and diversity in this respect; proving, as he thinks, that the colors of all wild animals must be useful, even though we cannot always see how they are so, and that their lack of uniformity under domestication is due to the fact that they are no longer of utility. He then gives illustrations of the various forms of adaptive markings—protective and warning colors and recognition markings. He says: "This need of easy recognition by each species of its own kind and of the sexes by each other, will probably explain at once those slight diversities of colour and marking, which, more commonly than any other characters distinguish closely allied species from each other, and also the constancy and bilateral symmetry of the colouration of wild animals."

With regard to the swamping effects of free intercrossing, Mr. Wallace says the difficulty is removed by conceding "that the same variation occurs simultaneously in a number of individuals inhabiting the same area." Mr. Romanes had denied this, but Mr. Wallace presents an array of facts taken from Mr. J. A. Allen's Winter Birds of Florida, in support of his contention.

So far as the infertility of species with one another is concerned, Mr. Wallace denies that the facts support

---

*Fortnightly Review, xlvi, pp. 300-316.

Mr. Romanes' side of the argument. He points out that experiments in hybridizing are generally made with very distinct species, and that even these are sometimes fertile, while if two closely related forms hybridize they are said to be one species. He quotes Dean Herbert's experiments as proving that in several large genera of plants not only are the hybrids often fertile but sometimes more so than the parent stock, whence he concludes "that the sterility or fertility of the offspring does not depend upon original diversity of stock; and that if two species are to be united in a scientific arrangement on account of a fertile issue, the botanist must give up his specific distinctions generally, and intrench himself within genera."

"Really close species," says Mr. Wallace, "which have probably originated by one remove from a common ancestor have never yet been crossed in large numbers and for several generations, under appropriately natural conditions, so as to afford any reliable data. The mere fact that not only animals of distinct genera, but even those classed in distinct families—as the pheasant and the black grouse—sometimes produce hybrid offspring in a state of nature, is itself an argument against there being any constant infertility between the most closely allied species, since if that were the case we should expect the infertility to increase steadily with remoteness of descent till when we came to family distinctions absolute sterility should be invariable."

To these criticisms of Mr. Wallace, Mr. Romanes replied in an article in the Nineteenth Century,* entitled Physiological Selection. He freely grants that Mr. Wallace has proved that some specific characters are useful, but insists that this is not sufficient to prove that all points of specific difference are so. The theory of

---

* xxi, pp. 59-80.

natural selection is based upon the assumption that certain characters are useful, but we are not justified in arguing from this that all characters have been developed by natural selection and are therefore useful. Darwin himself freely conceded the inutility of many characters, and, as Mr. Romanes says, " there is positive evidence to show that the slight changes of form and colour which chiefly serve to distinguish allied species are often due to what Mr. Darwin calls 'the direct action of external conditions,' such as changes of food, climate, etc., as well as to mere independent variation on isolated areas, and in some of our domesticated productions, etc.; and in none of these cases do the specific changes which result present a meaning of any kind." In refuting Mr. Wallace's argument on the utility of color Mr Romanes, in a footnote, quotes Darwin to the effect that "each of the endless variations which we see in the plumage of our fowls must have had some efficient cause; and if the same causes were to act uniformly during the long series of generations on many individuals, all probably would be modified in the same manner," and he adds: "The obvious truth of this remark serves to dispose of Mr. Wallace's argument in the *Fortnightly*, that 'the general constancy of colouration we observe in each wild species,' of itself furnishes sufficient proof that the colouration must be 'a useful character.' Moreover, when using this argument Mr. Wallace forgets that uniformity of colouration (whether useful or unuseful) is preserved in wild species by free intercrossing. Where this is prevented—as by isolation or migration—variations of colour very frequently do take place, just as in the then analgous case of our domesticated strains."

Concerning the swamping effects of intercrossing, Mr. Romanes shows that the variations cited from Mr.

Allen's paper as quoted by Wallace would not be sufficient to originate any new structure. He says: "It is easy to see how natural selection could alter the general size of the body, the relative sizes of parts, degrees of colouration, etc., without encountering any great difficulty from intercrossing. But if it were required to produce, say, a fighting spur on a duck, clearly it could not be done by natural selection alone, or when depending only on 'accidental variations.'" Mr. Romanes has here granted far too much to his critic; for, if physiological selection is not a necessary factor in the modification of size, shape (relative sizes of parts), and color, all closely related species which depend upon such features for their specific identity (and they constitute a very large proportion of species), would be excluded from the operation of the segregation of the fit. Nor would this factor particularly assist in the production of spurs and horns, for example. It is thought by many that such structures are due to the factor of use, in which case physiological selection would indeed become restricted in its function.

In replying to Wallace's criticisms of his view of sterility between species, Mr. Romanes says: "Under this head Mr. Wallace's criticism amounts to nothing more than a vague suggestion to the effect that all other naturalists may have hitherto exaggerated the generality of some degree of sterility between species. But he allows that it is 'a widespread phenomenon,' and gives no reasons for differing from Mr. Darwin's careful estimate of its frequency, he does not really furnish me with any material to discuss."

Mr. Seebohm in the introduction to his work entitled The Geographical Distribution of Charadriidæ, also makes a sweeping criticism of physiological selection, and as he and Mr. Wallace argue on the same lines upon certain points, it may be well to pass on now to a brief survey of his objections. The central idea of his argument is that variations are never spontaneous, but always due to a definite cause, so that "the inevitable new species will be produced even in defiance of increased fertility between the diverging forms." He lays great stress upon geographical isolation, however, and doubts that any new species of bird has arisen without the aid of this factor. He propounds a rather novel explanation of the mutual infertility of natural species as compared with the fertility of domesticated breeds. Briefly stated it is this: Domestic animals are species which from some unknown reason are capable of adapting themselves to a great variety of circumstances. Just as the individual as a whole is capable of surviving in various environments, so also, it may be supposed, the germ cell of the male of such individuals would have a greater vitality, and would be capable of surviving in an unusual ovarian environment. A proportion is thus established between the individual and its seed—as the stable individual is to the plastic individual so is the reproductive element stable or plastic. He calls attention to the fact that in a state of nature fertile hybrids occur most frequently among the *Phasianidæ* and *Anatidæ*, "the very families to which most of our domestic birds belong." This is certainly a very plausible and ingenious theory, and I am not familiar with any attempted refutation.

Unlike Mr. Wallace, Mr. Seebohm freely grants that "specific differences are frequently, if not usually, without utilitarian significance," but he considers that this is due to the fact that they have been brought about by definite variation without reference either to natural or physiological selection. Upon one point, however, he and Mr. Wallace agree, namely, that granting all that physiological selection demands, the chance of all the necessary contingencies arising contemporaneously would be so slight as to make the theory unworkable. Mr. Seebohm says: "To make it work we must presuppose:—1st, the special variation of the reproductive organs must occur in two inviduals, otherwise the possible ancestor of the new species would have no descendants; 2nd, it must occur at the same time in both; 3d, it must occur at the same place; 4th, the two individuals must be of opposite sexes; 5th, they must each of them possess some other variation, or their progeny would not differ from that of the rest of the species; and 6th, the variation must be the same in both, or appear simultaneously in the majority of their children, otherwise it would be swamped by interbreeding within the physiologically isolated family." Obviously Mr. Seebohm does not think it possible for all these contingencies to be realized, and that from their failure to co-operate the theory of physiological selection must break down.

Along the same lines as this Mr. Wallace also objects to the segregation of the fit. In reply, Mr. Romanes asserts that while it is true that the chances against these physiologically isolated individuals mating may indeed be thousands to one, so is it also true that the number of fertile unions among animals compared to the origination of every new species is in the proportion of thousands to one, and he says: "I confess it appears to me a somewhat feeble criticism to represent that the conditions which my theory requires for the origin of a new species are probably about as rare in their occurrence as is the result which they are supposed to produce." He furthermore states that the variations in fertility of the sexual organs are not due to chance, as his critics have assumed. They may be due to the change in season of flowering or pairing, or to difference in food or climate, or they may even be originated by natural selection itself. Indeed, Mr. Wallace has suggested as an "alternative hypothesis" to physiological selection, that specific sterility is due to a relation existing between the external coloring and sexual compatibility, so that whenever a change in color is produced, the individuals so changed will not be fertile with the parent stock. Mr. Romanes clearly shows that instead of being an alternative hypothesis, if tenable at all, it merely furnishes us with an additional indirect cause of the infertility demanded by physiological selection. Mr. Romanes gives a number of forcible reasons for not granting this theory the prominent function attributed to it by Mr. Wallace. Thus he asserts that "many species which are mutually sterile differ very little in color," while "most species which are mutually fertile differ considerably" in this respect. Furthermore, "in the case of natural species, it often happens that a great difference in respect of fertility occurs, according to which has acted as the male and which as the female, yet in both these crosses the colour of each species is, of course, the same."

The controversy which Mr. Romanes had with Mr. W. Thiselton-Dyer, in the columns of *Nature* in 1889, respecting physiological selection, did not serve to elucidate many new points. Mr. Dyer's objections to the terms physiological selection and the segregation of the fit, need not here detain us, for Mr. Romanes had previously justified their use. The discussion centered upon the relation between natural and physiological selection. Mr. Romanes has so clearly expressed this in an admirable figure that to quote it, will be a sufficient epitome of the argument. He says: "In short, species are like leaves, successive and transient crops of which are necessary to the gradual building up of adaptations, while these, like the woody and permanent branches, grow continuously in importance through all the tree of life. Now, it is the office of natural selection to see to the growth of these permanent branches; physiological selection has to do only with the deciduous leaves."

Having now stated the principal arguments for and against physiological selection, with as little bias as possible, it only remains to pass judgment upon their merits. This, however, does not appear to be an easy task; but as usual in such cases, it will probably be found that both sides are partly in the right and partly wrong. Thus, with regard to sterility, natural species are as a general thing sterile *inter se*, while domestic races are usually fertile, but these conditions are by no means uniformly constant. Physiological isolation might explain this state of affairs, while Mr. Seebohm's hypothesis has quite an aspect of plausibility,—or both views might be correct; whereas, various secondary factors have been instrumental in bringing about this condition. There seems to be hardly any evidence, however, that sterility with the parent stock is generally one of the first variations of a diverging race, but if this be not so, then the chief aim of the theory—viz. to account for the early stages of divergence—fails.

Isolation may be advantageous in preventing the swamping effects of free intercrossing, although Mr. Romanes has granted that the size, shape, or degree of coloration, may be modified without its aid. Furthermore, geographical isolation is an ever-present factor, while a slight change in habits on the part of certain individuals would effect their isolation. psychological isolation, as suggested by Galton, may also be a valid factor, while the operation of physiological selection itself need not be excluded.

Thirdly, some specific characters, at least, are apparently of no conceivable use, but these may be due to the direct action of the environment or to the use and disuse of parts.

As regards the bearing of the above discussion upon the evolution of the colors of birds, in the light of the evidence adduced, it would hardly seem justifiable to use physiological selection, unless the facts admitted of no other rational explanation. It is always an easy loophole for escape in accounting for any difficult character, and for this very reason should be treated with especial caution.

GULICK ON ISOLATION.

One of the most valuable contributions made of late years to the literature of evolution is the series of articles upon isolation by the Rev. J. T. Gulick. His views coincide with those of Mr. Romanes upon many important points, while their theories overlap to a certain extent. Without considering in detail the relationship between their respective views, it may be said that they both agree that many specific characters are useless, and that isolation is a necessary factor in their origination, but Gulick does not emphasize physiological isolation as Romanes has done; while he asserts, contrary to Romanes, that not only species, but larger groups as well require isolation as a factor in their origin. His central idea is this: no two groups of individuals of one species contain exactly the same proportion of variations in their aggregate number; accordingly, if two or more miscellaneous groups are isolated, inasmuch as free intercrossing is no longer practicable to preserve the average, each division will necessarily start off on an independent line, irrespective of its environment. Futhermore, natural selection without isolation could not produce divergent, but only linear evolution. Natural selection implies a contest between a more and less favorable class of variations, in which the less favorable class perish. As an example, a race horse might be evolved by artifical selection from a common stock, but in order to produce a dray horse from the same stock, the two varieties would have to be isolated from the earliest stages of their divergence.

The tendency of this view of Mr. Gulick's is to overestimate the self-sufficiency of the organism to originate new forms by virtue of an assumed inherent tendency to vary indefinitely. In other words, he sometimes appears to assume, in conformity with Nageli, that each organism contains within itself the potentiality of developing all the forms which may be subsequently derived therefrom; that free intercrossing suppresses this tendency to vary, but isolation enables each group to develop any little idiosyncrasies toward which it may have a leaning, and by successive stages of isolation these are piled up into new characteristics or structures. Thus, in summing up the result of his survey of the various forms of selection, he finds: *" First, that all the forms of Reflexive Selection are due to the relations of members of the same species to each other, and are liable to change without any change in the environments. Second, that Active Natural Selection is due to change in the successful use of the powers of the organism in dealing with the environment, and is not dependent on change in the environment. Third, that Passive Natural Selection, which is due to the exposure of the organism to a different environment, is often produced by the organism's entering a new environment without there being any change in either the new or the old environment. Fourth, that when Passive Natural Selec-

---

* Journ. Linn. Soc. xxiii, p. 337.

tion is produced by change in the environment, the more effective forms of Selection do not appear till the organism has so multiplied as to produce what I call Superlative Natural Selection through intense competition between rival individuals of the same species in gaining possession of limited resources. And, fifth, that Passive Comparative Natural Selection, which depends on change in the environment, without special rivalry between the members of one species, also depends on variation in the adaptations of the organism, many of which variations do not depend on that change in the environment which has produced the change in the Natural Selection, nor, indeed, on any change in the environment except those physical changes by which the world has passed from its primitive gaseous to its present partially liquid and solid state, rendering it a fit abode for organisms."

He thus entirely ignores the origin of variations and assumes that inasmuch as the environment in the various forms of selection cited does not produce the variations definitely and directly, it can have no influence whatever in their origination. If the discussion of variation in the preceding pages has any force whatever, this conclusion certainly should not seem an inevitable one.

An attentive consideration of Mr. Gulick's views seems to make one fact undeniable, viz. that some form of isolation is indispensable to divergent evolution. His elaboration of the various forms of isolation is so extensive that anything more than a brief outline of it would be impossible in the present connection. This much is, however, necessary to even a general understanding of the factors of organic evolution. The following is Mr. Gulick's classification table of the forms of segregation:

- A. Environal Segregation.
  - (a) Industrial Segregation.
    - Sustentational.
    - Defensive.
    - Nidificational.
  - (b) Chronal Segregation.
    - Cyclical.
    - Seasonal.
  - (c) Spatial Segregation.
    - Geographical.
    - Local.
      - Migrational.
      - Transportational.
      - Geological.
  - (d) Fertilizational Segregation.
  - (e) Artifical Segregation.
- B. Reflexive Segregation.
  - (a) Conjunctional Segregation.
    - Social.
    - Sexual.
    - Germinal.
    - Floral.
  - (b) Impregnational Segregation.
    - Segregate Size.
    - Segregate Structure.
    - Prepotential Segregation.
    - Segregate Fecundity.
    - Segregate Vigour.
  - (c) Institutional Segregation.
- C. Intensive Segregation.
  - (a) Assimilational Intension.
  - (b) Stimulational Intension.
  - (c) Suetudinal Intension.
  - (d) Correlated Intension.
  - (e) Integrational Intension.
  - (f) Selectional Intension.
  - (g) Fecundal Intension.
  - (h) Eliminational Intension.

The following brief definitions will explain the above terms:

A. ENVIRONAL SEGREGATION—Isolation due to the relations of organism to environment.

(a) *Industrial Segregation.* "Activities by which the organism protects itself against adverse influences in the environment, or by which it finds and appropriates special resources in the environment."

1. Sustentational. "Different methods of obtaining sustentation by members of the same species."

2. Defensive. "Different methods of protection against adverse influences in the environment."

3. Nidificational. Differences in nesting habits in the same species.

(b) *Chronal Segregation.* "Segregation arising from the relations in which the organism stands to times and seasons."

4. Cyclical Segregation. Among certain insects "the life cycles of the different sections of the species do not mature in the same years."

5. Seasonal Segregation. Change in time of flowering or breeding of a section of a species.

(c) *Spatial Segregation.* Isolation in space.

Geographical. Physical or climatic barriers to free intercrossing.

Local. Due to the wide distribution of species with inadequate powers of locomotion or migration.

Spatial segregation may also be subdivided in conformity with the causes producing it, thus:

6. Migrational, "caused by powers of locomotion in the organism."

7. Transportational, "caused by activities in the environment that distribute the organism in different districts."

8. Geological, "caused by geological changes divid-

ing the territory occupied by a species into two or more sections."

(d) 9. *Fertilizational Segregation.* Repugnance of insects to visiting different plants interchangeably prevents hybridization.

(e) *Artificial Segregation.* Artificial selection.

B. Reflexive Segregation. "Segregation arising from the relations in which the members of one species stand to each other."

(a) *Conjugational Segregation.* Due to "the instincts by which organisms seek each other and hold together in more or less compact communities."

10. Social. "Produced by the discriminative action of social instincts. The law of social instinct is preference for that which is familiar in one's companions; and, as in most cases the greatest familiarity is gained with those that are near of kin, it tends to produce breeding within the clan," etc.

11. Sexual. "Produced by the discriminative action of sexual instincts."

12. Germinal. "Caused by the propagation of the species by means of seeds or germs any one of which, when developed, forms a community so related that the members breed with each other more frequently than with the members of other communities."

13. Floral. Self-fertilization of flowers.

(b) *Impregnational Segregation.* Physiological selection *par excellence.*

14. Segregate Size. Inability of varieties to interbreed, owing to difference in size.

15. Segregate Structure. Due to "lack of correlation in the proportionate size of different organs, and by other incompatibilities of structure."

16. Potential and Prepotential. "Caused by more or less free distribution of the fertilizing element to-

gether with the greater rapidity and power with which the sexual elements of the same species, race, or individual combine, as contrasted with the rapidity and power with which the elements of different species, races, or individuals combine."

17. Segregate Fecundity. Relation of species or varieties *inter se*, when free crossing between "members of the same species or variety results in higher fertility than the crossing of different species or varieties."

18. Segregate Vigor. "Relation in which species or varieties stand to each other when the intergeneration of members of the same species or variety produces offspring more vigorous than those produced by crossing with other species or varieties."

(c) *Institutional Segregations.* "Produced by the rational purposes of man embodied in institutions that prevent free intergeneration between the different parts of the same race."

C. INTENSIVE SEGREGATION. When two or more sections of a species are mutually isolated by any of the above forms of segregation and are subject to the influences of a highly complex transforming agency, there is a reasonable certainty that the different divisions will be differently acted upon. In succeeding generations there will be increasing degrees of divergence and segregation, which is termed the law of Intensive Segregation. The different forms of intension are due to difference in food, influence of the environment, use and disuse, correlation of growth, selection, etc. In this case, it will be noticed that Mr. Gulick takes due notice of the influence of the environment, despite his assertion that variations may, in many instances, be wholly independent of it.

It is time to bring this introduction to a close and hasten on to the more special considerations for which it is a preparation. The idea which I have attempted to emphasize in the preceding pages is that life has evolved in accordance with tolerably definite and unvarying laws, and that the element of chance, if any such there be, is a very limited one. The living forms of to-day are looked upon as the result of the interplay of organism and environment, progress being urged on by the laws of development and held in check by the laws of heredity; while the organic cosmos is under the ceaseless and untiring scrutiny of natural selection, which, like a wise mother, is perpetually passing judgment on the acts of her children and abmonishing them when they go astray.

II. The Colors of North American Birds.

ON MODES OF PLUMAGE CHANGES.

I am not aware of any important addition to the subject of the changes of plumage in birds since William Yarrell, in 1835, published a paper entitled "Observations on the laws which appear to influence the Assumption and Changes of Plumage in Birds."* He there distinguished four "modes by which changes in the appearance of the plumage of birds are produced":

(1.) "By the feather itself becoming altered in color."

(2.) "By the bird's obtaining a certain number of new feathers without shedding any of the old ones."

(3.) "By an entire or partial moulting, at which old feathers are thrown off and new ones produced in their places."

(4.) "By the wearing off of the lengthened lighter colored tips of the barbs of the feathers on the body, by which the brighter tints of the plumage underneath are exposed."

---

* Trans. Zool. Soc. of London, i, pp. 13–21.

This first mode of change is doubted even by many ornithologists of to-day, and yet the testimony presented in Yarrell's paper seems to be conclusive on the point. To be sure, it does seem difficult to understand how a feather, in which there is no circulation, in fact no life, apparently, can alter its color. Mr. Yarrell tried the experiment of marking certain feathers in a bird which he suspected to be changing color, and succeeded in actually observing the addition of pigment. He also says: "On the breasts of several *golden Plovers*, some of the feathers were entirely white, the colour peculiar to all the feathers of that part of the bird in winter; some were entirely black, being the colour assumed at the breeding season; while others bore almost every possible proportion of well-defined black and white on the same feathers; from which it appears that the same cause of particular colour in new feathers can also partially or entirely change the colour of old ones."

Mr. F. O. Johnson first called my attention to the tails of some Arizona hooded orioles *(Icterus cucullatus nelsoni)* in his collection. They represent various stages of transition from yellow to black. I have since examined all the specimens of this bird in the National Museum and the American Museum of Natural History in New York, besides a number in private collections, and from this ample material cannot but conclude that the transition in this species is by an addition of pigment without moult. Plate VI shows a tail in a state of change. The primitive color of the tail in this species is yellow, but in the adult male entirely black. The tail figured was of an immature male in changing plumage. The feathers are still yellow for the most part, but one has become almost completely black, only a part of the tip being left yellow. In other feathers little spots of black were visible, while in still others the general shade of a part of the feather was dusky, as if only a thin layer of black pigment had been deposited. In other specimens various stages of transition were observable, from the example figured to instances where the entire tail was black with simply a few little isolated irregular patches of yellow.

Dr. C. Hart Merriam has published an instance of a seasonal change of color occurring by the introduction of pigment without moult, although his views are not accepted by Mr. Ridgway in his Manual. With regard to Allen's ptarmigan *(Lagopus lagopus alleni)*, the bird in question, Dr. Merriam writes:* "The large series of wings sent by Mr. Comeau demonstrates beyond a question that individual feathers do change color. Most of them are already pure white excepting the shafts of the six outer primaries, which, as usual in winter specimens of *Lagopus albus*, are black. The quantity of black varies greatly in the different wings. In those in which the change is most advanced it is merely a narrow strip of pale sooty-brown, extending along the middle of the upper surfaces of the shafts of the six outer primaries, and is confined to the middle half of the exposed part of each, so that the basal half, and a considerable apical portion, together with all the rest of the wing, is pure white," etc.

Mr. Witmer Stone called my attention to specimens of *Terpsiphone cristata* from Western Africa in the collection of the Philadelphia Academy of Sciences, in which an apparent transition of color of the tail without moult is shown, but of an opposite character from the instances above cited, viz.: from dark to light. The tail in the first stage is colored a reddish brown or rufous, this color changing to black, and the black to white, apparently without any moult. In the orioles

---

* Auk. ii, pp. 202-203.

this change does not appear to be confined to the tail, but the black patches of the head and throat seem to be developed in the same manner. Thus figure 11 of Plate I shows a feather from the throat of *Icterus cucullatus nelsoni* which is changing from yellow to black. Figure 12 represents a feather from the back of the head of *I. bullocki*, taken from an immature male of the second year, in which the black was appearing in spots upon a field of yellow.

It is impossible to say without more complete investigations, and perhaps some experiments upon living birds just how general this change by increase or decrease of pigment is, but it is probably quite a limited mode of transition.

The fourth mode of change, *i. e.*, by the wearing off of the dull tip of the feather, leaving the bright under part exposed, is a very common one, among land birds. Dr. Coues has called my attention to a term in the Century Dictionary covering these two classes of change—aptosochromatism, which is defined as change of color of the plumage without loss or gain of any feathers. He very kindly suggested two new words to indicate these two forms of aptosochromatism; *acraptosis*, meaning the falling off of the tip of the feather, and *acroptosis*, implying that the tip is not cast. Plate I shows a number of acraptotic feathers. Figure 6 is a frontal feather of the western yellow-throat (*Geothlypis trichas occidentalis*) in winter plumage. The basal portion of the feather is much darker than in most feathers, in fact almost black, the median portion a clear ash, and the tip brown. This brown terminal third is inclined to be worn and very brittle. It is so broad that it completely conceals the under portion, but in spring it all crumbles away leaving nothing but the clear ash. Along the line of demarkation of black and ashy the black base is sometimes broader and the ashy edging so narrow that the tip wears down to the black. Figure 7 is a feather from the back of the head of the western warbler (*Dendroica occidentalis*), in winter plumage. In this instance the brown edging wears off leaving a yellow feather with a black dot at the tip. In full plumaged birds all this black wears away leaving the head uniform yellow. Figure 8 is a feather from the breast of the rusty blackbird (*Scolecophagus carolinus*), in winter plumage. In the above two instances the brown was so complete as to produce a uniform color, but with the rusty blackbird it is less regular, causing a mottled effect. The brown tip wears off in spring leaving the plumage clear black. Perhaps the two most interesting examples of all, however, are represented in figures 9 and 10 of feathers from the backs of the two species of snow-buntings (*Plectrophenax nivalis* and *P. hyperboreus*), nearly in breeding plumage. In *P. nivalis* (fig. 9), the broad white terminal portion has almost entirely worn away leaving the black base exposed, but it does not wear off thus in *P. hyperboreus*, the black remaining white through the breeding season.

Mr. Yarrell says: "Young birds of the year in various species, after the autumn moult, continue through the winter to assume, by degrees, the more intense colours characteristic of adults, without changing the feather. This colour commences generally at that part of the web nearest the body of the bird, and gradually extends outwards till it pervades the whole feather." He calls attention to the influence of the sexual organs in changing plumage. Many birds appear to become more brilliant in color as the breeding season approaches without either a moult or the wearing away of the tips of the feathers (*acraptosis*). This I believe is the case with the house finch (*Carpodacus mexicanus frontalis*).

Changes of plumage, then, may be classified as follows:

I. Substitution of feathers.
  1. By renewal (moult).
  2. By addition.
II. Modification of feathers (aptosochromatism).
  3. By shedding of tip (acraptosis).
  4. By change of pigment (acroptosis).
    a. By addition. { Different pigment. / Intensification of same pigment.
    b. By loss.

The first class, namely, the substitution of feathers, has not been discussed because its bearing upon our subject is less direct, and because it is more familiarly known. It need only be noted here that all birds have an autumn moult, while some have a more or less complete spring moult in addition, either in both sexes or in the male only.

GENERAL PRINCIPLES OF COLOR IN BIRDS.

Having devoted so much space to the fundamental problems underlying all transitions in animals, it will not be possible to consider at any length the general principles of coloration in nature. Indeed, the subject has already been touched upon in discussing sexual selection. However, a few words more are necessary.

Colors may be classed, as Poulton has suggested, as structural and pigmental, depending upon the manner in which they are produced. The structural colors are of three sorts—those due to thin plates, one upon another; those due to diffraction, where the surface is broken by fine parallel grooves; and those due to refraction, where the light passes through a transparent wedge-shaped substance or prism. All of the above classes are due to the reflection and interference of light waves, and probably all occur to a greater or less extent among birds, although authorities disagree as to which form is the commonest. The iridescent colors are due to these structural peculiarities. White is due to the presence of minute bubbles of gas contained in the feather which breaks the structure so that the light is refracted in all directions, much on the principle of pulverized glass. The worn, dull plumage of birds, at the close of the breeding season, is due to a similar though coarser form of this same agency. Frequently the outer edge of the wing feathers becomes dull brownish, or even nearly white, from becoming worn and abraded, even though its natural color be black.*

The vast majority of color effects, particularly among birds, are due to chemical pigments. Many of these pigments have been chemically analyzed and named, and it is found that the same color in different species is not always due to the presence of one pigment, but to different ones. "Thus," says Beddard† "the brown colour of birds is chiefly due not to one pigment, but to two apparently distinct pigments, which give different chemical reactions; to these two pigments their discoverer, Krükenberg, has given the name Zoorubin and Pseudozoorubin. An inspection of the feathers would not enable one to tell with certainty which of the two substances was the cause of the colour; but an extract of zoorubin can always be detected by its change to a beautiful cherry red on the addition of the minutest trace of blue sulphate of copper."

The theory of bird colors which I shall attempt to elaborate in the succeeding pages is as follows: Pig-

---

* For fuller discussion of structural colors, see Dr. Gadow, Proc. Zool. Soc., 1882, p. 409; Poulton, Colors of Animals, pp. 3-11.

† Animal Coloration, pp. 2-3.

ment is a chemical composition thrown off from the system of the bird, probably as a product of waste, and lodged in the integument. The chemical substance thus generated varies in different groups of birds, but is probably generally constant in the species of one genus, or frequently in an entire family. A certain genus would thus be capable of generating only a given number of fundamental colors, but natural and sexual selection by combining and rearranging this limited assortment, can produce a great variety of effects. Besides black and white, most North American genera appear to contain but two fundamental colors, but in the tropics, three frequently occur in a single genus. If the pigment be regarded, to some extent at least, as a product of waste due to superabundant vitality, as Wallace maintains, it is not difficult to understand how among some tropical birds a third chemical product might be generated in addition to the usual two. As an illustration of this view, let color be compared to a variety of skin diseases. Each genus of birds in general, we may say, developes two kinds of skin disease which are bound to be in the system of every species. One of them may sometimes be suppressed or they may be combined in such a way as to be no longer recognizable, but they will still be present.

This theory could not be demonstrated without further study of the chemical properties of pigment. If it could be shown that in closely allied species the color, although the same, was produced by different pigments; or that in the same or closely allied species, where one color gave the appearance of being a combination of two other colors which occurred in the same or allied species, there was no real connection in the pigments, chemically; the theory would certainly become very weak. Until such experiments have been made, however, it is necessary to depend upon appearances, and here there are many facts that seem to support the view. Thus Plates XVIII and XIX seem to be in accordance with it. It will be noticed that in the genus Dendroica olive green is, especially in the female and young, the prevailing color of the group. It is not a little significant that in coloring these two plates it was found that in order to produce this color all that was necessary was to mix black with gamboge yellow, in about equal proportions —black and gamboge being the two most characteristic colors of the specialized males.

It might at first sight appear as if this was a modification from complexity to simplicity, but this is not really the case. If the system of the bird from which the present genus Dendroica was evolved normally produced two pigments which were lodged in the integument, unless some controlling and distributing force were brought to bear upon them, they would naturally be mixed and combined at first, and only after a long process of selection would the real colors become apparent.

This principle may be termed the Law of Assortment of Pigments. If true at all it will be found to have a very wide applicability in the evolution of colors of birds, and, indeed, to underlie all the other principles of color differentiation, although, of course, conditioned by all the more general laws of evolution. The best examples of it are to be found, as might be expected, among the most highly specialized genera, where the colors have changed from some dull hue to distinctly colored patterns. Thus woodpeckers are generally colored black and white and scarlet. The combination of the black and scarlet would produce a brown, which is still the body color of some species, as *Dryobates arizonæ*. In the genus Tyrannus the original color was probably an olive green, although in many instances where the bird is found in arid districts, this color has been bleached out to a brownish or grayish. The more special colors are black and yellow. The male of *Pyrocephalus rubineus mexicanus* is scarlet and brownish black. The female is colored a plain brown olive, which is a mixture of red and black. The blue jays are generally colored some shade of blue in the adult, together with black and white, but a mixture of these shades would produce the grays of the young and of the less specialized forms as Perisoreus and Picicorvus. The adult male red-winged blackbirds are black and scarlet, the female brown. The meadow lark is brownish or grayish in its generalized color, and black, white and yellow in the specialized shades. I am not certain that the combination of black and yellow (olive-greenish) together with white would produce the grayish-brown of the back, but if this instance be an exception, it is not a very glaring one. The term brown is a very loose one and may cover a great variety of color effects. It may be produced either by a combination of black and red, or of black and green; or it may be due to the structure of the feather. If a certain amount of gas bubbles are contained in a feather where the pigment is dark, it will produce a brown effect, or a black feather with a frayed edge may appear brown. There is probably no white pigment in birds' feathers, this effect being structural or due to the absence of pigment.

Among the orioles, the colors of the specialized males are black and yellow (the orange being merely an intensification of this) while the primitive color as exhibited by the females and young is olive green. Plates XVI and XVII showing the heads of a number of representative species in the generalized and specialized stage illustrates this instance. It might appear that *Icturus spurius* with its reddish brown color was an exception to this law, but an attempt will be made later to explain this instance in accordance with it.

Enough examples have now been given, I trust, to show that, as a rule, the shade of color which we agree to call the primitive color is a composite which, when more or less completely resolved into its component elements, gives the two specialized tints of the species or genus. A word may be said as to the criterion of a general and special color. In the first place, in accordance with the law of the correspondence of the ontogenic and phylogenic series, or the tendency of the individual to repeat ancestral stages, if the young differ from the adult in color (unless the latter be a degenerating form), it will represent an earlier and more generalized type. Furthermore, in an adult male bird the color which is spread over the greater part of the body is ordinarily the generalized color, while the detailed markings represent the more specialized hues. This is directly analogous to the geographical distribution of animals. If we have two allied species of animals, the one found upon the mainland, the other upon an island, or the one spread over a wide area and the other in a limited section, we should conclude that the species having a restricted range had sprung from the species having a wide range. More especially would we conclude this if the limited form had some mark of superiority to the other. It is found that among birds the limited markings are, as a rule, of a purer or more sharply defined color than the body color. Notice, for instance, the crest of the kinglets or the breast of the rose breasted grosbeak. In cases of high specialization, as with the orioles and tanagers, for instance, the generalized colors may be completely superseded by the specialized, in which case the female and young, alone, would show any trace of them.

Specialized colors may be classed under four heads, according to the degree of their development: (1) local in the male sex only; (2) local in the species; (3) universal in the male sex only; (4) universal in the species. As an example of the first may be mentioned the ruby-crowned kinglet (*Regulus satrapa olivacea*), red-winged blackbird (Agelaius), etc.; of the second, the kingbird (*Tyrannus tyrannus*); of the third, the scarlet tanager (*Piranga erythromelas*); and of the fourth, the California woodpecker (*Melanerpes formicivorus bairdi*).

THE PROPORTION AND DISTRIBUTION OF THE COLORS IN NORTH AMERICAN GENERA.

It may be well at the outset to take a comprehensive view of the various colors as they appear among North American genera. There are two hundred and nine genera represented among North American birds. Black is present to a greater or less extent in a hundred and thirty-five, and white in a hundred and sixty-nine of them. Pure red occurs in only thirty-three genera, although there are eighty-three besides in which it is present in some such combination as reddish brown, vinaceous, pink, etc., making a total of a hundred and sixteen genera in which some red pigment appears. Pure orange occurs in but ten genera, while yellow is found pure in fifty, and in combinations such as ochraceous in twenty-nine others, making a total of seventy-nine genera in which yellow pigment is found. Green is present in twenty-two genera, but in fourteen of them it is metallic, and hence may not be due to a green pigment. Green in combination, particularly with olive, is found in twenty-seven genera, being metallic in only two or three instances. There are accordingly about thirty genera that have green pigment. Blue occurs pure in twenty-three genera, in seven of which it is metallic or iridescent, while bluish-black or bluish gray is present in thirty-five other genera, giving a total of something like fifty-one genera with blue pigment. Purple is by far the rarest of the colors, only six genera showing it pure and seven in combination, while out of these thirteen instances it is iridescent in ten. Gray and brown are the most difficult colors to assign to a given number of genera, because they frequently occur only in the young, while in a large number of instances the two hues are more or less combined. In general, however, it may be said that gray occurs pure in a hundred and thirteen genera, and in combination in thirty-nine others, making a total of a hundred and fifty-two. Brown is found pure in a hundred and twenty-nine instances, while in combination it exists in forty-three additional genera,—a hundred and seventy-two in all. These somewhat dry statistics of the relative abundance of the different colors may be shown more clearly in the following condensed table:

Total number of genera..................209

Brown	172	Yellow	79
White	169	Blue	51
Gray	152	Green	30
Black	135	Orange	10
Red	116	Purple	3

The above facts are susceptible of more than one interpretation. The very large number of genera in which brown is present may be accounted for by the fact that brown affords better protection, and that where it appears it is a protective color which has been developed by natural selection. The same argument might be applied to gray, while black and white usually occur in such limited areas that they may be looked upon simply as recognition markings. There is, however, another view which seems to be more in harmony with the facts. Brown and gray are generally present in species in which the markings are not highly specialized. Moreover, these colors very frequently occur in the young of species which are highly specialized in the adult, as, for example, in the red-headed woodpecker (*Melanerpes erythrocephalus*). The presence of brown or gray in almost every genus of North American birds, either in the young or the adult stage, would seem to indicate that these are the most primitive colors, and that where they still occur it is due to a lack of specialization in this respect. To be sure, in many cases this specialization may be retarded in many instances by the positive advantage of protection, or protection on the contrary may enable it to continue. As an excellent example of these two cases may be mentioned the goldfinches. The pine finch (*Spinus pinus*), retains the primitive plumage, perhaps from the need of protection, while the goldfinches (*Spinus tristis* for example), have become specialized in color without sacrificing protection. They frequent during the summer the yellow compositæ, in the vicinity of which they can be detected only with great difficulty.

This view would be in harmony with the law of assortment of pigments. The tendency would be to progress from such mixed shades as brown and gray to the pure colors. The need of recognition would in any event be sufficient to account for the early and universal tendency to produce limited areas of black and white. It might at first sight appear as if the fact that green is less frequently found than either of its constituent elements, yellow and blue, would militate against the law of the assortment of pigments. This discrepancy is only an apparent one, however. The green pigment of the bird is a different chemical substance from either the yellow or the blue. It might be that in certain instances, especially among tropical birds, that a green color was produced simply by a combination of yellow and blue pigments, in which case we shall have the primitive color of the bird, as indicated either by the young stage, or by the body color of the adult, green, and the specialized colors, yellow and blue. In general, however, the green is probably either a different pigment, or, as is frequently the case, in olive greens, produced by a combination of yellow and black.

It may be well to consider next each of the primary colors (together with black and white) more particularly. More species are wholly or largely black than any other of the primary shades. The following are exclusively or almost completely black:

Catharista atrata.
Crotophaga ani.
Crotophaga sulcirostris.
Corvus.
Molothrus æneus.
Scolecophagus.
Quiscalus.
Progne subis.
Phainopepla nitens.

Still larger is the list of species in which black covers a large proportion but not the entire surface of the body:

Colinus virginianus cubanensis.
Pseudogryphus californianus.
Cathartes aura.
Urubitinga anthracina.
Campephilus principalis.
Xenopicus albolarvatus.
Sphyrapicus thyroideus.
Pica pica hudsonica.
Dolichonyx oryzivorus.
Molothrus ater.
Agelaius.
Spinus psaltria mexicana.
Sprophila morelletti.
Euetheia bicolor.
Calamospiza melanocorys.

A number of species are colored a very dark brown or gray, showing a strong tendency towards black. The list of these is as follows:

Parabuteo unicinctus harrisi.
Buteo harlani.
Buteo abbreviatus.
Buteo swainsoni.
Buteo fuliginosus.
Falco columbarius suckleyi.
Archibuteo lagopus sancti-johannis.
Ceophlœus pileatus.
Leucosticte atrata.
Junco hyemalis.
Sayornis nigricans.

There are thus something like forty-five or fifty North American species which show a very strong tendency toward melanism. The relation of geographical distribution to this subject will be discussed at a later stage of our inquiry. Besides these species in which black is the sole or predominant hue, there are a number in which it figures quite largely. Thus the genus Pipilo contains two groups, *erythrophthalmus* and *maculatus* in which the back, throat and breast are mainly black. The American redstart *Setophaga ruticella* has the black distributed in precisely the same manner, while in the painted redstart *(S. picta)* there is a still greater predominance of black. Indeed, there is a curious parallelism between the colors in these two widely separated genera which may be only a coincidence or may be a matter of profound significance. At any rate it is a subject of great importance in an investigation like the present, to scrutinize all these apparent coincidences and see if they may not have some real meaning. In the first place, then, *Pipilo erythrophthalmus* and *Setophaga ruticilla* both have the black of the male distributed over the same parts of the body. There is the same abrupt contrast between the black of the breast and the white of the belly. The sides of the breast are red in both species, although in the one it is a bright flame reddish-orange *(Setophaga)* while in the other it is chestnut or rufous. There is a light patch on the wing, orange in Setophaga and white in Pipilo. The tail markings are decidedly different, however, being basal in Setophaga and terminal in Pipilo. In both species the black of the male is replaced in the female by brown. Perhaps the most curious point of resemblance, however, is the fact that both species which belong to the eastern states, have western or southwestern representatives *(Setophaga picta* and *Pipilo maculatus)* in which there is a greater amount of black, and in which the sexes are colored alike. To be sure, the difference in structure, size and general appearance between these two birds is so great as to apparently preclude any possibility of kinship, yet the parallelism is complete in so many points that it is difficult to believe it to be a mere coincidence.

There are, however, several species in which the color of the back, head, throat and breast is black or some very dark shade, in abrupt contrast to the pure white of the breast. Such, for instance, is the case with *Junco hyemalis* and *Sayornis nigrescens.*

Again, the area of black may be the same, but the under parts some color, such as yellow or brown, instead of white. As examples of this *Icterus parisorum* and *I. spurius* may be cited. The general style of coloration in the rose-breasted grosbeak *(Habia ludoviciana)* is the same, although the black is interrupted on the back by a patch of rose color. This species forms a connecting stage between such forms as Pipilo, Setophaga, Junco and Sayornis, where the black extends from the back around the throat and breast, and such forms as the Blackburnian warbler *(Dendroica blackburniæ)*, where the entire upper parts are black and the entire lower parts light colored. In the magnolia warbler *(D. maculosa)*, the black is still an important feature of the back, but less evenly distributed, not covering the top of the head, and frequently broken by olive green. It also appears in decided streakings upon the breast and sides.

In general, it may be said that the tendency is for the dark markings, whether black or some other shade, to occur in the greatest masses upon the back. As will be seen later, this might be accounted for by supposing that light is inclined to favor the deposit of pigment, and as the back has always received a more considerable share of it than the breast, a rhythm had in the course of ages been established, inclining the larger amount of pigment to those parts of the body. As if to bid defiance to any such laws as we may make upon the subject, a number of species are found in which this order is directly reversed. Thus, in the chestnut-colored longspur *(Calcarius ornatus)* the top of the head and entire lower parts, except throat are black. The same parts are colored black in the grassquit *(Euetheia bicolor)* and in the bobolink *(Dolichonyx oryzivorus)*. In all these cases the upper parts contain the lighter markings.

These black markings seem as a rule to spread from certain well marked areas. Those on the lower parts appear to spread from the throat or breast patch, while those of the upper parts usually come first on the head. This is by no means universally the case, as, for instance, with the genus Icterus (Plates XVI–XVII). In the females the only patch of black is the one on the throat. It does not extend from there at first, however, but the back darkens, as in the adult of *Icterus cucullatus.* In *Icterus bullocki* the black has extended over the head, while in the next stage, *Icterus galbula,* the patches on throat and back of head become confluent. The point to be noted is that there is no species in which the top of the head is black while the back remains light colored.

Sometimes when the entire bird is black or some dark shade, its antecedent stage is black above and light below. A good example of this is the purple martin *(Progne subis),* the male being entirely dark glossy blue black, while the female has the under parts gray and white. Among the blackbirds, the females frequently have the under parts lighter than the back. This is noticeable in Scolecophagus and extremely pronounced in Agelaius. In Xanthocephalus, the breast of the female is mixed with white. In the hawks it is frequently the case that a melanistic phase will occur in which the bird is dark above and below, whereas, in the normal phase the breast is light colored. Such is the case, for example, with *Buteo borealis* and *B. swainsoni.*

Some of the tanagers (*Piranga erythromelas*, for instance), present a rather unusual localization of black, the wings and tail alone being shaded thus. In the Louisiana tanager (*Piranga ludoviciana*) the back as well as the wings and tail is black. *P. erythromelas* undoubtedly represents a more advanced stage, in which the black has become restricted to these regions.

Perhaps the most instructive example of the way the black spreads from the breast, as a center of pigmentation, is the female of Williamson's sapsucker (*Sphyrapicus thyroideus*). The final color of the male is an almost uniform black, varied on the breast by only one patch of red on the throat. Every stage may be traced from the young female with white under parts, through the adult female with a black patch upon the breast, and the different stages of its extension in the young males to the final plumage of the adult.

The most complete example with which I am acquainted of the spreading of black upon the back is the green-backed goldfinch and its allies (Plate VII). *Spinus psaltria* has a black cap upon the top of its head, and the shoulders are usually dark. In *S. psaltria arizonæ* both of these areas of color have become more extended and the dark on the shoulders is a more pronounced and uniform black. In addition to this, black feathers are interspersed throughout the back. In the third variety, *S. psaltria mexicana*, the black is the predominant color of the back, while in still more extreme races no trace of the green can be detected.

Three methods of turning black have been observed among the examples above cited. (1) The general tone of color may darken uniformly, approaching a black, as in *Junco hyemalis* and *Sayornis nigricans;* (2) masses of color may spread until they meet, as in Icterus; or (3) dark spots and irregular mottlings may become fused into continuous patches, as in the *Spinus psaltria* group. This latter is the most universal method, and the other two may be combined with it to a greater or less degree.

As we are not concerned at present with the causes of colors, but rather with the facts of the distribution and localization of the different primary shades, we may rest content for the present with this survey of black as it appears among North American birds, and take up white.

One of the first points which is noticeable with regard to white is its close interrelation with black. Next to brown, white is more universally present among North American genera than any other color. In spite of its prevalence, however, there is not a single species which is pure white, and only a very few in which it is predominant. The fact that black and white both occur in the same species so frequently might first be considered as a mere coincidence, due to the fact that both are very prevalent, or it might be regarded as a question of utility, white setting off black, or *vice versa*, in a conspicuous manner, and affording a useful recognition mark. This may indeed be a partial explanation, but I think not the fundamental one. We have such species as the dusky seaside sparrow *(Ammodramus nigrescens)*, and the black and white warbler *(Mniotilta varia)*, in which the black and white are about evenly distributed in streaks over the body. Among the woodpeckers a considerable number have black and white markings in about equal proportions. The general black color of the lark bunting *(Calamospiza melanocorys)* is relieved by a broad white patch on the wing. The bobolink *(Dolichonyx oryzivorus)* has almost as much white and buff in its make-up as it has black. The shiny-crested flycatcher *(Phainopepla nitens)*, although for the most part black, has the inner webs of the primaries white. Perhaps the most remarkable case, where no utility can be conceived, is the white-necked raven *(Corvus cryptoleucus)*, which has the feathers all around the neck pure white at the base. It would be difficult to understand how this could be an advantage, being entirely concealed by the overlapping tips of the feathers. The tendency toward albinism is common among the crows, while in the magpies *(Pica)* and the flute bird of Australia *(Gymnocitta)* white figures largely in the plumage.

As a recognition of some sort of interdependence between black and white, as they exist among birds, I would suggest that they be termed Cognate Colors.

Although, as before stated, there are no exclusively white birds in North America, the winter dress of the ptarmigans (*Lagopus*), approaches very close to this. In the following species white is the prevailing color:

Elanoides forficatus.
Elanus leucurus.
Falco islandus.
Scotiaptex cinereum lapponicum.
Bubo virginianus arcticus.
Nyctea nyctea.
Plectrophenax nivalis.
Plectrophenax hyperboreus.

In no instance is a species colored in some uniformly pale shade approaching white, the anthesis of the dark color of *Sayornis nigricans*. There are thus only about four species of ptarmagin (*Lagopus*), which are almost exclusively white and eight other species in which it figures as the prominent color. Among nearly all North American genera some white is present, and in a large proportion of species. When occurring in large masses it is usually on the breast and under parts, as previously intimated. It generally persists longest on the abdomen and under tail coverts. Plate XIX of the genus Dendroica furnishes illustrations of the way in which the color fades out into white on the under tail coverts. I know of no instances in which large masses of white occur upon the upper surface of the body except such as the bobolink and a few others in which the under parts are largely black.

The only North American species which is exclusively red is the summer tanager (*Piranga rubra*). In the following species red is the prevailing color:

Pyrocephalus rubineus.
Pinicola.
Carpodacus.
Ergaticus ruber.
Leucosticte.
Cardinalis.
Piranga erythromelas.
Piranga hepatica.

Two classes of red birds may be distinguished—those in which the color occurs in clear, well defined patches as in Pyrocephalus, Piranga and Cardinalis, and those in which the plumage is everywhere suffused with red, but the color not sharply marked out, as in Pinicola, Carpodacus and Leucosticte. Carpodacus is more or less intermediate between these two styles. When pure red is present in smaller amounts it generally occupies well defined local areas. Red crests are frequent, *i. e.*, in most of the woodpeckers where the color sometimes spreads over the entire head as in *Melanerpes erythrocephalus*.

Among the species having a crest of scarlet or some bright red may be mentioned *Milvulus forficatus*, *Tyrannus verticalis*, *Passerina versicolor*, *Acanthis* and *Regulus calendula*. Red or rose colored throat patches are found in Sphyrapicus, Platypsaris and *Habia ludoviciana.* There is a curious resemblance in the colors of this latter species with the becards (Platypsaris). In both cases the tendency is toward black on the upper parts of the body, white on the lower parts, and a rose colored breast. The red-winged blackbirds (Agelaius), are unique in the red shoulder patch. It is a noteworthy fact, and one which is too apt to be looked upon, as a matter of course, that scarlet, or any other brilliant color, when occurring only in limited areas, is never in an inconspicuous place, as upon the abdomen, for instance.

The presence of red in connection with slaty gray in a few instances, as in *Pyrrhuloxia sinuata* and *Pinicola enucleator*, may be worthy of note. The most significant interrelation of colors, however, and one which I believe to be of wide application in the explanation of bird colors, is that between red and yellow. Whether these two colors are produced by the same or a different pigment I am unable to say; but, however this may be, there is a high degree of probability that the red is simply an intensification of the yellow. There is much evidence to show that yellow is a more primitive stage than red, and that the latter has always, or nearly always, been developed from the former. What the factors in this intensification may be I will not attempt to state, merely suggesting that heat, moisture and food may play an important part. The term CORRELATIVE COLORS will be an appropriate one by which to indicate this interrelation.

Now, as to the evidence of this dependence of red upon yellow. Plate V indicates a number of instances of correlative colors. What I have attempted to show is that when red occurs in a group of birds, yellow will be found in the same group, and that the yellow represents a more primitive stage of development than the red. For instance, in the family Icteridæ we have the red winged blackbirds (Agelaius) with a scarlet shoulder patch. In the same family is the yellow-headed blackbird *(Xanthocephalus xanthocephalus)*. This fact in itself would be of little significance, but may be explained in accordance with the law of assortment of pigments together with the correlation between red and yellow. Of far more significance are the colors in the grosbeaks *(Habia)*. In the male rose-breasted grosbeak *(H. ludoviciana)* the breast patch and under wing coverts are bright rose red, while exactly the same areas in the black-headed grosbeak *(H. melanocephala)* are a clear gamboge or lemon-yellow. As if still more emphatically to emphasize the fact that this yellow was really a more primitive stage of the red, the females of both species have these parts colored a paler yellow. The fork-tailed flycatcher *(Milvulus tyrannus)* has the crown patch a bright lemon-yellow, while the crown patch of the scissor-tailed flycatcher *(M. forficatus)* is scarlet. So also the kingbird *(Tyrannus tyrannus)* has a crown patch of orange-red. In the gray kingbird (*T. dominicensis*), according to Ridgway's Manual, it is orange colored, while in the thick-billed kingbirds (*T. crassirostris*) it is lemon-yellow. In this genus then, the stage of transition from red through orange to yellow is present. Among the woodpeckers the crown patch is ordinarily red, but in three-toed woodpeckers (*Picoides*) it is yellow.

The brilliant red of the scarlet tanager *(Piranga erythromelas)* is replaced in the western tanager *(P. ludoviciana)* to a large extent by yellow, the scarlet being developed in the latter species in limited areas. The females and young of both are yellow. In the flickers, which are so intimately related, as shown by their habitual hybridization, the one species is yellow *(Co-*

laptes auratus) where the other one is bright red *(C. cafer).* The ruby-crowned kinglet *(Regulus calendula)* has a cap of scarlet while in the golden-crowned kinglet *(R. satrapa)* it is orange and yellow. The meadow-lark of South America *(Sturnella defilippii)* is rose-red where the North American species *(S. magna)* is yellow.

Having now cited instances of different genera of the same family and different species of the same genus in which red and yellow are correlative, let us examine some of the closer genetic relationships. The Arizona hooded oriole *(Icterus cucullatus nelsoni)* is colored yellow, varying from saffron to gamboge. In the hooded oriole (*I. cucullatus*) the color is "orange or dull orange red,"* while in the fiery oriole (*I. cucullatus igneus*) it is "intense orange-red, sometimes almost scarlet." The male redstart (*Setophaga ruticilla*) is marked with rich orange-red, the same areas in the female being yellow. In the genus Sphyrapicus and also in Melanerpes, the markings are largely bright scarlet, but supplemented by yellow, as if a part of the color had been intensified by sexual selection, for example, and the rest left unaffected. In the winter plumage of the red-winged blackbirds the shoulder patch is yellow instead of red. The house finch *(Carpodacus mexicanus frontalis*) when kept in captivity loses its bright red tints, which are replaced by yellow. The same is true of the crossbills (*Loxia*), and would probably be found to hold good for Pinicola and Leucosticte. Canaries fed upon cayenne pepper turn red, although this may possibly not be a converse instance.

I have now given a considerable number of examples covering all degrees of genetic affinity, of this correlation of red and yellow. One of the strongest points in favor of the validity of this correlation as an explana-

---

* Ridgway's Manual.

tion of color changes from yellow to red is the fact that there are so few exceptions to it. The vermilion flycatcher (*Pyrocephalus rubineus mexicanus*) is a partial exception to it, although the female is sometimes tinged with a salmon color which is not far from yellow. The female cardinal grosbeak (*Cardinalis virginianus*) is dull brownish or reddish, but the head and under parts are more or less tinged with yellowish. Acanthis with its red head is not far removed from the goldfinches (*Spinus*). The becards (*Platypsaris*) and the red warbler (*Ergaticus ruber*) form the only complete exceptions to the rule with which I am familiar, but a knowledge of allied South American forms might bring them also under the law of correlation.

There are no North American birds which are exclusively yellow in color. In the following species it is the predominant hue, or figures very conspicuously:

Xanthocephalus xanthocephalus.
Sturnella magna.
Icterus.
Coccothraustes vespertinus.
Spinus.
Piranga ludoviciana.
Dendroica æstiva.
Sylvania pusilla.
Geothlypis trichas.
Vireo.

It is conspicuously present among the warblers *(Mniotiltidæ)*, and in such of the vireos as *Vireo flavifrons and V. flavoviridis.* As a rule it is found upon the under surface of the body, especially when in large masses. In fact, when the tendency is for the whole bird to be thus colored, it will be noticed that the yellow upon the back is apt to be less pure, with more of an olive or greenish tinge, as in *Dendroica æstiva*, the females of Piranga, etc.

Two North American species are almost exclusively blue in color—the indigo bunting *(Passerina cyanea)*, which has the lores black, and the arctic bluebird

(Sialia arctica), in which the belly and under tail coverts are white. In the following, blue is the conspicuous color:

Cyanocitta.
Aphelocoma.
Cyanocephalus cyanocephalus.
Dendroica cærulea.
Guiraca cærulea.
Passerina amœna.
Euphonia elegantissima.

It is a fact worthy of note that blue very rarely occurs in limited patches or markings. There are a number of species in which the general shade of color is approaching a clear blue, as in the blue-gray gnatcatcher *(Polioptila cærulea)*, the yellow-rumped warbler *(Dendroica coronata)*, and a number of others of the same genus; but where do we find, among North American birds, species with blue heads, ear coverts, throat patches, wing markings, or spots in general? The green-jay *(Xanthoura luxuosa)* with its bright blue head is a striking exception.

It will not be necessary to consider green at any length, for the simple reason that there are hardly any species in which a pure green figures at all, the above-mentioned jay and the parrots being exceptional cases. The metallic greens, as in the humming birds, are probably not pigmental in nature, and hence must be excluded. As an olive green it is frequently found, however, but we are at present concerned only with the pure colors.

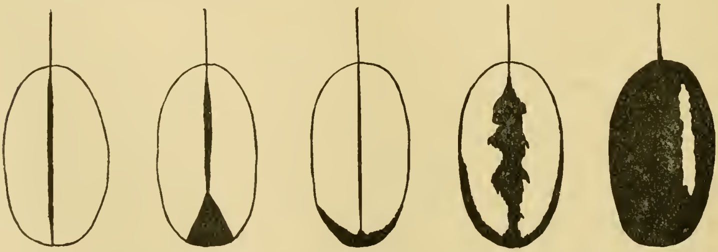
A few generalizations from the forgoing facts may now be in order. It will be noticed that with a very few exceptions (Buteo and Dendroica) pure color in large masses occurs in small genera. Black forms are scattered through various families, from the lowest to the highest. White reaches the climax of its development among the Falconidæ and Bubonidæ; red among the Fringillidæ and the allied Tanagridæ; yellow among the Mniotiltidæ, and blue among the Corvidæ. When any of these colors occur in considerable masses in combination with some other color, it is generally with brown, black or olive green, and seldom with any other very pronounced shade.

PATTERN OF MARKINGS.

In the preceding discussion of the distribution of color masses it has been found difficult to keep clear of a closely related subject, to which attention must next be directed, viz.: the pattern of markings, both as distinguished from and as related to their colors. These markings must be regarded in two ways; first, as to the pattern, mode of development, etc., of the markings upon individual feathers, and second, the general effect of feather markings in the pattern of the entire bird.

In an investigation of color patterns, the laws of growth and structure stated in the introduction, should be kept in mind. The law of growth force or bathmism is especially important in this connection. Pigment is a definite chemical. substance which travels through the various branches of the feather, advancing farthest and most rapidly along the lines of least resistance and accumulating in masses where the resistance is greatest. Now the pigment cells must reach the various parts of the feather by way of the shaft, and we should *a priori* expect to find that the resistance would be least right down the shaft. It might spread out a very short distance on the barbs but the main tendency would be toward the tip. This would produce a streaked feather as the most primitive form. Having reached the tip it would encounter an obstacle, and then would develop in mass. This route of the pigment might be illustrated by a panic-stricken mob running down a street. They would naturally keep in the road where travel was easiest rather than branching off into the fields where their progress would be impeded by the unevenness of the ground, fences, etc., but if a large body of water should finally interpose a barrier to their course they would, upon reaching it, come to a halt at first while the multitude would press on from behind causing a mass at the end.

This phase would represent a feather with a terminal spot. If the crowd ceased to press on in the rear they would spread along the margin of the water corresponding to a feather with a black band at the tip. In this instance the pigment would desert the base of the barbs and spread out into their ends. If a second invasion of the mob occurred later, and it happened that the road along which they were escaping traversed the center of peninsula, the last resort of the people would be to flee over the rough ground in all directions from the road, and we should have first a stage corresponding to a feather with a pigmented border and pigmented center but a clear space between the two, and finally a uniformly pigmented plume, when the crowd had filled the entire space. Nothing more would remain but for them to pack in tighter and tighter which in the case of the feather would result in the intensification of the color. The accompanying diagram is a conventional representation of these feather changes.



This example of a mob may seem a fanciful one, and not calculated to prove anything, but indeed it is not so. If the laws of growth have any sort of universal validity, and I am firmly convinced that they have, the line of movement of a mob of men along the lines of least and greatest resistance would typify any form of involuntary movement along the same lines. The question simply is to determine which are the real points of greatest and least resistance. The sequence of color assumption here exemplified may be infinitely varied in detail, but will, I think, be found tolerably uniform in general. Different forms of feathers may offer different degrees of resistance in the various parts of their structure, but I think it will be found true in the main that the pigment will pass down the shaft most readily, while there can be no possible exception to the obstruction at the tip. The channel of pigmentation may be diverted along the sides, however, and thus not give rise to any terminal spot or band.

I have thus far assumed that there was some force analogous to the blind terror of a mob which urged the pigment cells away from the source of danger, the body. This is probably not strictly true, however. It is more likely that it is the warm sunlight which, with its genial touch, causes them to crowd forward; to leave the prison in which they were born, and press on joyfully into the free air of the outer world. Capillarity or a variety of undetermined forces might also tend to draw them outward. The number which were thus enticed to the surface would depend simply upon the amount of surplus energy, or whatever else it may be, which results in the formation of pigment in the system of the bird. As a species grows older and more vigorous, and more completely adapted to its environment, the sum total of pigment would increase, and accordingly, if no other tendency were at work in a contrary direction, there would be a development towards a uniform pigmentation of each feather.

The subject of the lines of pigmental development has received more attention at the hands of the German scientists than from any others.[*] The researches of Eimer in particular are in accordance with the view here stated. It seems that among nearly all animals (at least among the vertebrates), the earliest form of color is the longitudinal streak. These longitudinal markings are finally broken up into spots (when the tendency to assume a uniform color does not assert itself) and the spots ultimately fuse into cross bars.

This view of the general succession of patterns has been commonly accepted, although denied by Kerschner, who asserts that the longitudinal barring is the oldest form of marking. As his conclusions were based upon a limited number of forms, the eye spots of the peacock's tail having claimed his special attention, they cannot be considered to be of general validity. Häcker has devoted special attention to pigmentation in the thrush family, although he considers the water birds also to a certain extent in the paper cited below. With the exception of the primitive streak he finds the clear feather with a pigmented border to be the earliest form, which may be modified into a spot as in the thrushes. The coloring of the interior of the feather he considers to be due to a secondary pigmentation.

---

[*] On this subject see Th. Eimer, Untersuchungen über das Variiren der Mauereidechse, etc., 1881. Ueber die Zeichnung der Vögel und Säugethiere. Jareshefte des Vereins für vaterld. Naturk. in Wurttemberg, 1883, p. 556. Zoolog. Anzeiger, 1882–83. Humboldt, 1885–1887.

Dr. Kerschner, Zur Zeichnung der Vogelfedern, in: Arbeiten aus dem Zoologischen Institut zu Graz, I. Band, Nr. 4. Leipzig, 1886.

V. Häcker, Unter nichungen über die Zeichnung de Vogelfedern. Zool. Jabrb., III, Jan. 15, 1888, pp. 309–316.

With regard to this secondary pigmentation, metabolism may be introduced as an explanation. When a species is katabolic the surplus of energy might be expended in the formation of pigment. This would become distributed in the feathers in accordance with the laws determining the location of growth force. It would become fixed there by the conservative laws of heredity, and then a state of anabolism might follow. At the beginning of the next katabolic period, in accordance with the rhythm of metabolism of Geddes and Thomson, more pigment would be produced and again distributed, this being the secondary pigmentation of Häcker.

Let us see now how the facts agree with these theories. The first group of feathers on Plate II is a series from the under parts of a Californian woodpecker (*Melanerpes formicivorus bairdi*) commencing on the sides and extending up on the breast. It will be noticed at once in how many respects it tallies with the ideal instance previously considered. The feathers of the belly are white, but along the sides and the upper portion of the belly there is a black streak down the shaft. In some instances the shaft alone is thus marked, but generally the base of the barbs is similarly affected. On the feathers located on the lower part of the breast the line has become broader, and black pigment has appeared on the borders of the feathers. Both areas of black next increase, although the inner one spreads most rapidly, until the white area has been confined to two small islands which ultimately disappear in the clear black feathers which form the patch upon the upper chest. This sequence of stages is in accordance with the law of successional relation (see *ante*, pp. 77–78), and undoubtedly indicates the phylogeny of the black feathers. Certain it is that the feathers of the abdomen are less developed with regard to pigmentation than those on the flanks;

the flank feathers are less developed than the feathers of the lower breast, and these in turn less advanced than a stage higher up on the breast. Through all this a regular sequence of successional relation is maintained, and we, consequently, feel justified in assuming that the different parts of the body of the bird represent different stages in the evolution of the feathers. Being unfamiliar with any word expressive of this relation so closely akin to ontogeny and taxonomy, I would suggest the term SUCCESSIONAL TAXOLOGY.

As before stated, the assumption of a uniform pigmentation by a feather is by no means universally along the ideal development of Melanerpes. Thus, in the yellow-breasted sapsucker (*Sphyrapicus varius*) the transition is from the original streaked form through a barred type to a uniform black. The successional taxology in this species as indicated by the feathers along the border line of the black throat-patch is represented in a tolerably typical series in Plate II. The streaked type generally occurs farthest from the black patch, but these feathers are inconspicuous and largely concealed, so that no streaked pattern appears in a general survey of the bird. In the next phase the streak becomes slightly tilted to one side (fig. 8), or it may divide and extend out on both sides enclosing a white spot (fig. 9). Continuing to descend, it approaches a position in which it is at right angles to the shaft, forming a bar (fig. 10) and presently a second bar makes its appearance along the edge of the downy basal portion (fig. 11). The two bars next fuse, frequently passing through the stage indicated in figure 12 and end by becoming perfectly black.

I cannot see that this series can be explained by the general laws of growth previously used, but would suggest that it may not improbably be a case of correlation.

The back of *Sphyrapicus varius* is barred, and this barred stage in the progression from the primitive streak to the uniform black pigmentation may well be due to correlation of pattern. The bars may be of utility on the back, whereas they cannot be on the breast, because they are so concealed as to be almost invisible. In Williamson's sapsucker (*Sphyrapicus thyroideus*), the barred markings surrounding the black patch on the breast of the female assert themselves very strongly, but this may be simply an advanced form of correlation. They are also much more conspicuous on the back in this instance, and we should therefore expect to find them correspondingly developed on the breast if it was a case of correlation. In the Californian woodpecker, in which the breast feathers do not pass through the barred stage in becoming black, it is to be noted that the back is never barred at any stage of its development. Figures 14–17 of Plate II show the transition from the barred to the uniform black type taken from the border of the black throat-patch. It may be remarked that these instances illustrate Cope's law of parallelism previously stated (see *ante*, p. 78), this last instance being especially instructive in this respect, because in the male these parallel stages are no longer repeated as in the female.

The most systematic study of successional taxology in the pigmentation of feathers can be made upon the wing and tail, where the exact relation of feathers is fixed. Here the interesting fact is disclosed that all changes in the pattern occur according to a defininite orderly sequence. Plate III represents the feathers from the wing of a sparrow hawk (*Falco sparverius*) in their natural order. Figures 1–5 are the feathers of the spurious wing. In fig. 1 the barring is evident, but has not yet strongly asserted itself, being irregular on the upper part of the feather. The second feather has two complete bars and a triangular subterminal dot. The tendency, however is towards a more complete pigmentation, and in the third feather the bars have run together somewhat along the line of the shaft. The triangular patch has become extended upward along the shaft also. In the fourth feather this darkening of the feather has proceeded another stage, while in the last of the set (fig. 5), the outer web is almost entirely black, and the inner web has succeeded in closing in an island of light, a tendency which had been developing through the whole series. In the primary coverts no such transition is observable except the gradual loss of one of the bands (figs. 6–15). The primaries themselves, however, present an interesting series of changes (figs. 16–25).

In the first place it will be noticed that the number of bands is largely dependent upon the size of the feather. If there is a little more room at the basal portion another bar will be formed. In the first feather (fig. 16) there are eight white bars. In the next two which are the longest there are nine (counting the spots). In the fourth (fig. 19) there are only eight, this number persisting in the fifth and sixth, although the basal bar is very indistinct. In the seventh feather (fig. 22) there are but seven bars, this number being reduced to six in the last three—and the sixth one very inconspicuous.

It seems to me we have here a fact of considerable significance. This basal bar, or even two or three of them perhaps, could never be of any use because they would be concealed in life by the coverts, and must therefore be repeated from some general law. Just as soon as there is a little space at the base of the feather another bar of pigment crowds in. It seems probable that this is to be accounted for by the law of repetition, so closely akin to the law of correlation. Instead of the repetition of parts we have here the repetition of color pattern.

The two fused spots of the second feather (fig. 17) are probably not homologous with the two bands of the first feather, but are two additional spots. This may be due to the fact that the terminal portion which contained them has become aborted. At any rate, the character of this first feather is so different from the second that an abrupt transition of pattern might be anticipated. It will be noticed that there are two other tendencies manifested in this series—for the lowest spot to increase in size and for the white bands to be crowded toward the edge of the feather; both of which tendencies take place gradually and regularly. On the opposite wing the markings are very similar, feather for feather. Merely in slight details do they differ, as for instance in regard to the fusion of spots, which is not so decidedly pronounced in the second feather and more nearly approached in the third. Again there is a tenth white bar, which is barely indicated in the second feather of the wing figured but well marked on the same feather of the other wing.

There is a more marked change between the last primary and the first secondary (fig. 26). The subterminal spot which has been gradually enlarging suddenly breaks out into a broad terminal band of bluish with a white spot still left. A trace of black has also persisted along the line of the shaft. As a sort of premonitory symptom of the coming light band, a small spot of white is noticed at the base of the last three primaries.

The next important change occurs in what I take to be the first of the tertiaries (fig. 34) where a decided tendency toward the elimination of the black bars first asserts itself. This rapidly advances until the simple stage of figure 39 is reached. The same sort of transition occurs in the secondary coverts, the last five of which are figured (figs. 40–44). It is difficult to say whether the spot which first appears near the tip of the fifth secondary (fig. 30) spreads toward the shaft forming the spot in fig. 36 and afterwards becomes reduced to a spot on the shaft as in figs. 38–39 or whether the marking in fig. 36 is of distinct origin. The former view, however, is the more probable one.

This same sequence of stages seems to hold for all the forms which I have examined, and the uniformity of successional taxology will doubtless be found to be the normal condition of wing markings. The wing of the Californian woodpecker affords an excellent illustration of this. Some of the changes from feather to feather are rather sudden, but an examination of any particular feather would enable one to predict in general what the pattern of the next one was to be, so inevitably is each new character foreshadowed in the antecedent feather. The general color of the wing feathers in this species is dark brown, with a conspicuous band of pure white crossing it. The first primary is uniformly dark, with the exception of a small gouge of white close to the base of the inner web. In the second primary the white has spread into a patch about thirty mm. long, and extending from the inner edge almost to the shaft. In the third it has become still more elongated, and spread not only to the shaft, but across it on the outer edge. In the fourth and fifth primaries the white continues to spread until it occupies almost the entire basal half of the feather. A little dark pigment at the extreme base of the fifth feather asserts itself in the sixth, forming a well marked patch of brown. This spreads down the shaft in the seventh feather, and in the eighth has isolated the white in two patches, a long one along the inner edge of the feather and a shorter one midway along the outer edge. In the ninth primary this outer white patch has vanished, the one on the inner edge persisting in a long line on the edge of all the secondaries. The first secondary is well marked off from the last primary by a spot of white at the terminal end of the white border. A second spot is gradually constricted off from the end of the border, and the first one dwindles into insignificance.

It is time now to ask the meaning of this successional taxology in the color pattern. If the successional taxology represents different evolutionary stages of progression, as I believe it does in some cases, it is easily understood. For example, in the feathers of Melanerpes, previously described, it is only necessary to assume that the under part of the body is becoming black, but the tendency has been stronger on the upper part of the breast than lower down, to understand this successional relation perfectly, as different degrees of completeness in evolution in different parts of the body. This is a beautiful example of Cope's law of acceleration and retardation. The growth force has been accelerated on the upper breast and retarded on the belly. With regard to wing feathers, however, the explanation is not so simple. Here, instead of one part of the body exhibiting a general stage of development, and other parts successively higher stages, we find feather following feather in uniform steps of transition, when in many cases it is simply impossible to say that one stage is higher than another. Certainly there is not an ideal mode of coloration being approached through successive stages, as is the case with feathers becoming black, but rather a variety of individual patterns combined to produce one effect.

Thus far little has been said of general effects. The question has been discussed as if it were supposed that all colors were produced strictly in accordance with these laws and utterly regardless of any external influences which might modify the patterns. We must, however, frankly acknowledge that, while all internal and constitutional laws of development must rigidly limit and condition the assumption of pigment by a feather, a large proportion of color markings are produced by external causes—natural and sexual selection, direct action of the environment, etc. For example, the general laws of the location of growth force might have caused the pigment to have lodged in the tips of the feathers of the thrush's breast, but the effect would have been one of mottling. Then natural selection might have taken advantage of this and emphasized and defined the markings, and left each one distinct and isolated as a spot. And thus it is with the wing bars and bands under consideration. They have doubtless been produced by selection for some effect, and indeed it might be argued that the orderly sequence from feather to feather was due solely to the fact that in this manner the general effect might best be secured. This view, however, can, I think, easily be shown to be untenable. For example, upon the last primary of a wing of the Californian woodpecker (*Melanerpes formicivorus bairdi*), which I examined, was a mere suggestion of a white dot below the strip of white on the inner side of the feather. It was so small that it might easily have been overlooked in an examination of the feather, and most certainly could have had no more influence on the general appearance of the feather than a speck of dust. Upon the feather next it, the first secondary, a well marked spot appears in exactly the same place, while in the secondaries successively following the first this spot slowly dwindles away. Now it might of course be argued that this spot had been a useful character at some past time, but was becoming obliterated. This objection wholly misses the point, however, which is, not why does this little dot which can be of no utility exist but why does it occur as anticipating a larger spot? This is only one instance out of an innumerable number of cases where a well marked character in one feather is led up to by anticipatory stages. I would suggest that the term REPETITIVE MARKS be used to designate these characters. These repetitive marks, from their very nature, cannot be useful characters nor can they be rudimentary. The most probable explanation of them appears to be that they have been developed in accordance with the law of repetition. This is a form of correlative development, but it does not appear by any means adequate to completely explain the case. In a general way it might be understood that if a definite manifestation of growth force were located in one feather, there would a tendency to repeat this less and less completely in succeeding feathers. It might seem, however, that this repetition precedes and leads up to the complete form rather than follows it. Of course it is difficult to say which end is the beginning of the series, but it might seem at first glance as if it should begin with the first primaries and end with the tertiaries, these latter being less specialized. In reality, however, it seems more rational to suppose that the tendency works from the simple to the complex. Going from the secondaries toward the primaries it is found that while certain characters are becoming more developed others are fading out. Thus in wing of the sparrow-hawk (Plate III), proceeding from the tertiaries towards the primaries the black bars are found to be progressing in complexity, while at the same time the black subterminal spot of fig. 39 diminishes and lingers on as a repetitive spot to fig. 30. All that can be said of this successional taxology in marks as exhibited on the wing feathers is that it is not due to selection or any external force, but rather to some unknown principle of repetition or correlation.

Thus far the discussion has been confined to black and white, or brown and white markings. As soon as colored feathers are brought into consideration the factor of selection immediately becomes more prominent. It is a noteworthy fact that along the line of division of two patches of color the feathers are not uniformly colored, some the one shade and others the other, on the contrary the two colors in a large number of cases appear on the same feather. It will be found convenient to designate these as HYBRID FEATHERS. Take for instance the rose-breasted grosbeak where the black, white and rose color come together on the breast and sides of the head. Some of the feathers are colored black and white, the shaft dividing the two, and each color contiguous to the general patch of that color. Others are colored rose and white, the rose generally at the base of the feather and adjacent to the rose patch, the white at the tip of the feather and helping to cut the white line of the breast from the rose of the throat. Many rose and black feathers are to be found, the shaft generally dividing the two colors, although sometimes there is merely a black spot at the tip. The point to be noticed is that the colors are not as a rule distributed in accordance with any law of growth force, but in any way which will produce the general effect of a rose colored patch with moderately sharply marked limitations, bordered with black on the sides and white below. Occasionally a very interesting feather is found which beautifully illustrates the interplay of internal and external effects. Such a one, for instance, was marked according to the ideal mode of pigment deposition with a dark tip and border, but only on the side nearest the black patch, the pigment having been directed to that side of the shaft by natural selection but still insisting upon following the conventional route of travel.

The Californian woodpecker (*Melanerpes formicivorus bairdi*) affords several especially fine illustrations of color for effect regardless of the laws of growth. Thus at the line of demarcation of the white of the frons and the scarlet of the occiput, which is quite clearly cut, nearly all the feathers are literally cut in two by the color, the basal half being white and the distal end scarlet. Along the sides of the head many of the feathers are scarlet terminally and black basally, but I fail to discover any feathers at the base of the scarlet patch which are black terminally. Here again we have an illustration of how natural selection must still be limited. The scarlet was able to come in upon the white pigmentless feathers or the white to encroach upon the scarlet, but the black did not seem able to get a foothold upon the tips of the scarlet feathers in a corresponding manner.

The throat markings are interesting as being remarkably free from hybrid feathers. This is particularly the case with the feathers of the black jugular patch where it meets the yellowish crescent of the throat, hybrids being almost wholly absent here. They also play a very subordinate role at the lower end of the throat crescent where it joins the black of the breast, although some of the feathers here have a narrow edging of black. The red-shafted flicker (*Colaptes cafer*) presents some interesting features with regard to hybrid feathers. The red malar streaks, or moustaches, occupy a tolerably distinct pterylographical area, and are well separated from the feathers of the throat by a bare tract. Accordingly hybrid feathers are almost or wholly wanting on the inside edge and rare on the outside of the streak. The black crescent on the breast is of especial interest because strongly marked hybrid feathers form both the upper and the lower line of the patch. The upper line is formed by white feathers with the distal half sharply black, and the lower edge by black feathers with the distal end edged with white. This is rather unusual, for the rule is that when the base and tip of a feather are differently colored on one side of a patch they preserve the same relative positions upon the other side.

In order to study these hybrid feathers more systematically I shall make the following classification:

I. Hybrids (feathers of two or more colors helping to define a patch).
  1. Symmetrical.
    a. Lateral.
    b. Transverse { Relative positions uniform.
      Relative position insterchangeable
  2. Asymmetrical.
    a. Sharply marked.
    b. Indistinctly defined.
II. Pseudohybrids (feathers of two or more colors not helping to define a patch).
  1. Sharply marked.
    a. Both colors showing.
    b. Only one color showing, the other concealed.
  2. Tinged with some foreign color.

I will now explain each of these divisions and give examples. I have restricted the term hybrid feathers to such as are divided into two or more parts by color and in which each color shows in the general pattern of the bird. Where two colors show in a feather but have no significance in defining a patch, I have termed them pseudohybrids. In a large proportion of cases patches of color are marked on one side at least by true hybrid feathers. When the feathers are divided into two tolerably uniform parts they may be considered as symmetrical. Then the question is are the divisions lateral or transverse? This is determined in the main by the position of the patch. If the feathers in question occur on the side of a patch they are ordinarily divided laterally. Thus the white streak down the back of the downy woodpecker (*Dryobates pubescens*) is defined along its sides by feathers which are, in general, white on the inner side of the shaft and black on the outer. So also with the streaks on the head of the meadow lark (*Sturnella magna*), the boundaries of which are fixed by feathers which are white on one side and brown on the other. Examples of tranverse symmetrical hybrids have already been given, no better case being known than such as the dividing line between the white and red across the head of the Californian woodpecker (*Melanerpes formicivorus bairdi*).

When a band occurs, as for instance, across the head or breast, cutting some uniform ground color into two areas, the line of demarcation is generally made by hybrid feathers on one side only. Thus the breast of the belted kingfisher *(Ceryle alcyon)* is white, but crossed by a broad, well-defined band of blue. The white feathers along the upper border of this blue strip are edged with blue, and both the blue and white in a single feather are visible. Accordingly the line separating the white from the blue along this edge is not made by the tips of feathers of one color overlapping another, but cuts right through the center of the visible part of the feather. The blue feathers along the lower edge of the blue patch, on the contrary, were not, in the specimens examined, edged with white. In other words, the lower border of the blue patch is marked off simply by the tips of the blue feathers overlapping the white feathers. This state of affairs is due to the fact that in all the feathers of the breast the relative position of the colors is constant, that is, if there be two colors, the white will occupy the base of the feather and the blue the tip. This is probably due to the fact that the breast of this species was white, and that the blue pigment which came into these white feathers, in following out a general law of pigment distribution, sought the tip of the feather in every case. Or the converse may be true, that the breast was blue, and that in becoming white the base of the feather was uniformly affected first.

The black crescent on the breast of the red-shafted flicker *(Colaptes cafer)* has already been mentioned as a case where the relative position of the colors on the hybrid feathers is interchangeable. In other words, both the upper and the lower border of the black patch is defined by hybrid feathers—the upper border by light feathers with black edgings, the lower border by black feathers with light edgings.

We come next to the asymmetrical hybrids. It would be wrong to suppose that there is a sharp distinction between these two classes. Hybrids which are not asymmetrical are really quite the exception. The distinction is made to express the difference between hybrids where a definite plan is followed to produce the effect, as by the cutting of the feather in two, more or less regularly either transversely or laterally, and hybrids where no regularity is observed, but the two colors distributed on the feather more or less at random. Many of the hybrid feathers on the throat of the rose-breasted grosbeak *(Habia ludoviciana)* are of this asymmetrical type. So also are they on the back of the neck of the golden-crowned sparrow (*Zonotrichia coronata*) where the black, white and brown are all mingled, but the area of each color sharply defined.

Asymmetrical hybrids are sometimes not sharply defined as in the preceding instances, but the two colors blend more or less at the point of meeting. This is the case in the vermilion flycatcher (*Pyrocephalus rubineus mexicanus*), where the scarlet feathers along the border of the crown are brown, basally, but the two colors are not sharply separated on the feather. This is also the case with the white and slate-colored hybrids of *Junco hyemalis*.

Besides these hybrid feathers, which help to define patches of color on the bird, there are other feathers which are of two or more colors, but which are of no apparent utilitarian significance. These I have called pseudohybrids. They are especially interesting as showing the sort of material furnished to natural selection with which to produce effects. It is evident that along the line of demarcation of two colors the pigments are apt to get confused as to which is their proper route, and hence both come upon the same feather, by accident, as it were. Natural selection has frequently used this chance commingling for the production of effects, but has not always done so. Thus true hybrids are almost wanting in the crown patches of the goldfinches, but pseudohybrids are not uncommon. They are feathers in which the black of the crown and the olive of the back are both present, but instead of helping to define the black patch they rather tend to break up the symmetry of its boundary. This is especially noticeable in specimens of *Spinus psaltria* and *S. lawrencei*. In the latter the feathers along the edge of the crown patch are pseudohybrids, and the same is true of those between the yellow and gray of the breast.

Another class of sharply marked pseudohybrids are those in which one color is completely concealed by overlapping feathers. Such pseudohybrids are very common and are interesting as being in most instances apparently vestiges of some former color of the bird. This under color is of no more utility than a rudimentary organ. A good illustration of this class is presented by the feathers of the black throat patch of the meadow lark (*Sturnella magna*). These feathers generally have a white basal portion and a black terminal portion, with a more or less decided tinge of yellow upon the white nearest the edge of the black. This is plainly a relic of the time when the breast was all yellow, for only the black is now visible, and the white and yellow bases could be of no possible utility. These feathers are very common in patches of bright color, as the scarlet head of the Californian woodpecker, where the feathers are black below the scarlet. It is interesting to note that the extent and distinctness of the subterminal line line of black on the scarlet feathers decreases in orderly succession from the feathers of the frons backward toward those of the nape. This is directly parallel with the extent of the scarlet on the head of the different forms now living. The scarlet in these decreases and the black increases from the frons backward. In general, it may be said that true hybrids occur only along the border line of two color areas, while pseudohybrids are sometimes the only form found throughout an entire color patch.

There is but one other form of pseudohybrid to be considered and this an uncommon variety. In the red-winged black birds the line of division of white and scarlet upon the shoulder is made by the scarlet feathers overlapping the white. In other words, there are no true hybrids. Frequently in *Agelaius tricolor* an infusion of pink or buffy is noticed upon the white feathers as if some of the scarlet pigment had run in upon the white by mistake. *A. gubernator* frequently has a blush of scarlet upon the buffy feathers.

We come next to the general patterns of bird colors. These are so infinitely varied and complex that it will be almost impossible to bring them under any universal law or laws, but at least a few generalizations must be made. Eimer has stated* "that the appearance of new characters always takes place at definite parts of the body, usually the posterior end, and during development—with age—passes forwards, while still newer characters follow after from behind. Thus during life, *e. g.* in lizards, a series of markings pass in succession over the body from behind forwards, just as one wave follows another, and the anterior ones vanish while new ones appear behind." This development from posterior to anterior is illustrated by many examples among birds, but seems to me to have far too many exceptions to be held as as a general law of development. The successional taxology of markings on the under parts of many of the hawks, conforms to this rule. Upon the breast the markings are simple streaks, but from this stage they pass into spots and from spots into bars which are most distinctly marked upon the lower part of the flanks and belly. This is especially well shown in the western red-tailed hawk (*Buteo borealis calurus*). It is also well illustrated by a large number of the woodpeckers, especially in the genera Dryobates and Picoides which have the flanks barred and the breast streaked or plain. The reverse is true with the Californian woodpecker, where, as we have already seen, the markings simplify instead of specialize as we approach the abdomen (see *ante* p. 163 and Plate II, figs. 1–6). So also in the lark bunting (*Calamospiza melanocorys*), the specialization begins at the anterior end. In immature males the throat first becomes black, and in a series of males it is found that the tendency is for it to spread from this

---

* Organic Evolution, p. 28.

point downward to the tail in tolerably uniform succession. The Louisiana tanager (*Piranga ludoviciana*), is doubtless colored somewhat after the fashion of the primitive color of the scarlet tanager (*P. erythromelas*), which had a yellow ancestor; and here the specialized color, the scarlet, first asserts itself upon the anterior part of the head and throat, spreading thence down the back and breast, to a greater or less degree depending upon the perfection of plumage of the bird.

Many of the conclusions concerning the feather patterns will apply also to the pattern of the bird as a whole. Thus, just as the streaked feather is the most primitive so also is the streaked plumage. This is exemplified by the young of a large number of birds. Thus the breast in many of the sparrows, such as Zonotrichia, Chondestes, Spizella, Junco, Amphispiza, Peucæa, and Pipilo, which is pure white or buffy in the adult is streaked in the young, and in many instances the back also is streaked. The pine siskin (*Spinus pinus*), seems to have preserved this primitive plumage with very little variation, in its adult state. Again, just as the accumulation of pigment at the point or on the edge of the feather is an early stage, so do we find many young birds with a mottled plumage such as would be produced in this manner.

Looking at birds broadly, the endless modification of pattern and infinite variety in the form and position of color areas is simply bewildering. Out of this chaos, however, it is possible to bring some semblance of order by showing what forms of marking never or seldom occur and what forms are most often repeated.

In the first place there are no birds marked with an asymmetrical pattern. It seems hardly fair to explain this fact wholly by the law of bilateral symmetry, for this law does not apply in the least to individual feathers. Still there is probably a general tendency to repeat the same pattern on both sides of the body, just as there seems to be a tendency to repeat a general style of marking on the lower that has been produced on the upper part of the body. The asymmetry of hybrid flickers is an abnormal case, and would hence not be an exception to the rule of bilateral symmetry, which is intended only for normal forms.

Although a streak may occur either just over or through the eye, I know of no instance where a streak runs near or through the eye at right angles to the superciliary stripe. I know of no species which has either the throat or the top of the head barred, nor can I think of any instance where any definite pattern of color occurs on the back proper. Neither does any instance come to me where a single streak down the middle of the back (as in *Dryobates pubescens*) is continued without interruption over the top of the head to the bill, nor where a similar streak on the under parts, extending down the throat and median breast, (as the carmine of *Pyrrhuloxia sinuata*) extends also down on the abdomen and under tail coverts. I can think of no species in which a single transverse band or bar crosses the back below the nape (where it occurs in *Dolichonyx oryzivorus*, for example), nor of any instance where such a band or bar crosses the under parts of the body below the breast. No instance is recalled where large spots of any kind occur either on the throat or head.

It may seem like an idle task to enumerate these forms of marking which do not occur, but by next noting what styles are most common, the two will be brought out in strong relief. The head is by far the most complexly marked part of the body. Of the head markings the superciliary stripe is the most universal, being characteristic not merely of birds but also of many reptiles and mammals. Next most common is the throat patch which is not strictly but mainly confined to the pterylographical region lying between the lower jaw bones and extending downward along that line. A transverse stripe on the frons either of light or dark is very common, as in *Melanerpes formicivorus bairdi*, *Geothlypis trichas*, *Dendroica dominica*, etc. So also a transverse band on the nape is common as in *Cyanocitta cristata*, *Dolichonyx oryzivorus*. A median line on the head is common, as in *Sturnella magna*, *Regulus satrapa*, *Tyrannus tyrannus*, the young of Habia, and many others. A contrasted transverse band terminating the throat patch is common, as in *Hesperocichla nævia*, *Cyanocitta cristata*, etc. In fact, whenever the breast has any diversity of marking a breast patch of some sort is the general rule. The belly is only very exceptionally marked, and then either simply streaked or barred, or more rarely, spotted as in Colaptes, but the flanks are usually marked either a darker shade than the belly or streaked or barred. The under tail coverts are frequently streaked, barred, or colored quite differently from the belly as in the cat bird (*Galeoscoptes carolinensis*) and Californian towhee (*Pipilo fuscus crissalis*). The rump patch is very often marked by some conspicuous color as in the yellow-rumped warbler (*Dendroica coronata*) and the flicker (*Colaptes auratus*). The wing and tail markings are strikingly varied and characteristic of species.

In accounting for these patches of color and their distribution in diverse patterns it will be necessary, it seems to me, to abandon wholly or largely internal laws of growth as explanation. Dr. Harrison Allen has published a paper on the Distribution of Color Marks of the Mammalia* in which he elaborates the view that the distribution of pigment is favored by the presence of

---

* Proc. Acad. Nat. Sci. Phil., 1888.

large masses of muscle lying beneath the surface or by nerve terminals, which produce great local activity and excess of nourishment in particular parts of the body. Inasmuch as the large masses of muscle and important nerve terminals are more or less constant, especially among species of the same genus, whereas the areas of color may be profoundly different, it does not seem possible that this factor can be a very strong one, if operative at all among birds. The frequent occurrence of a patch of color on the breast where the largest muscles of the body are situated, might be, to some extent, due to this influence however. With regard to the great frequency of a strongly marked throat patch Dr. Stejneger suggested to me the possibility that the constant vibration of the throat in singing might be a factor in the specialization of its color. There could not be any direct connection between the motion of the throat and singing, however, because sometimes the patch is distinguished by the presence of pigment as in Harris's sparrow (*Zonotrichia querula*) which has a black throat, while in the same genus even, a species occurs in which the throat is marked off by the absence of pigment—the white-throated sparrow (*Zonotrichia albicollis*). Moreover, the canary, which shakes its throat as if it would burst, has not produced any perceptible difference in this region, nor has the mocking bird (*Mimus polyglottos*) in which the throat and breast are uniform white. Dr. Stejneger's theory has suggested to me another view which is not open to these objections. The frequent vibration of the throat, especially during the courting season, would make it almost the most conspicuous part of the body, and it seems highly probable that whenever any suggestion of pigment occurred there it would be retained and encouraged by sexual selection. It might also prove a useful recognition mark in many instances.

According to this same principle of the conspicuousness of moving parts, other markings may possibly be explained. A considerable number of birds have the edge of the wing along the shoulder, decidedly marked with yellow, white, rose, etc. It is especially on the under side of the wing and not very readily seen when the bird is at rest. During the courting season the males of many species have a habit of rapidly vibrating their wings in a slightly lowered position. I have noticed this among the sparrows such as Gambel's sparrow (*Zonotrichia leucophrys gambeli*), and I think the western savanna sparrow (*Ammodramus sandwichensis alaudinus*). It is probable that this habit obtains with the grasshopper sparrow (*A. savannarum passerinus*) in which the wing is so conspicuously edged with yellow, and has been developed by selection in the same manner as the throat patch. Frequently the under wing coverts are colored peculiarly and sometimes very beautifully, as in the rose-breasted grosbeak. When the male bird is paying his addresses to the female this patch would be sometimes obscured and sometimes visible, and accordingly more conspicuous and beautiful than if always in plain sight. Audubon, in his plate of this species, represents a male facing a female with wings raised to show this patch, but it may be that he drew it thus in order that the spectator might see the marking, and not because he had ever seen the birds in that attitude. The rump is very frequently colored differently from the back and tail (as in *Dendroica coronata*), or when colored the same is more intense (as in *Carpodacus mexicanus frontalis*). When courting, the wings and tail are lowered and the rump accordingly is very conspicuous. The under tail coverts are frequently colored differently from the belly or tail, and generally in species which live amongst the underbrush dodging about with the tail frequently thrown up in the air. This patch of color would accordingly be of great use as a recognition marking—but this subject will be more fully discussed later.

It thus seems that the markings of the throat, under tail coverts, rump and under wing may be explained by selection. These markings are determined in their shape chiefly, if not entirely, by the part affected, and hence present no particular difficulties. With the head markings the problem is, however, not so simple. We have already seen that lateral markings are common upon the head while transverse markings occur only in special parts and there less frequently than the others. The superciliary stripe is much the commonest of marks, and being generally white in color, there seems far more probability that it is due to some internal principle than is the case with any other bird marking. The fact that frequently where no superciliary stripe occurs in the male it is present in the female or young would also seem to indicate that it is constitutional rather than utilitarian in nature. Instances of this sort are the bay-breasted warbler (*Dendroica castanea*), red-winged blackbird (*Agelaius phœniceus*), bobolink (*Dolichonyx oryzivorus*), etc. There are at least a hundred and six North American land birds in which the white superciliary stripe occurs, from the bob white (*Colinus virginianus*) at one end of the list, to the wood thrush (*Turdus mustelinus*) at the other. In the genus Dendroica it is especially prominent, being present in eleven species and generally very sharply defined. It is also present in nine species of the genus Vireo, and among a large number of warblers of other genera than Dendroica, as well as many of the Fringillidæ. It is not always, although generally, a narrow sharply defined line. In the western night hawk (*Chordeiles virginianus henryi*), for instance, its boundary is not sharply defined, while in the chuck-will's-widow (*Antrostomus carolinensis*) it is a very broad band. In the California jay (*Aphelocoma californica*) it is sharply defined but is composed of a series of fine white streaks or spots, and hence is not a continuous line. It hardly seems within the bounds of reason to suppose that all the species which exhibit this mark are the descendants of a common ancestor which possessed it, and that it has persisted without significance for so long a time, although this would not perhaps be any less conceivable than the retention by man of the pineal eye. On the other hand, it can hardly be held that the superciliary stripe is a recognition mark, because it is very often inconspicuous in life, although sometimes very noticeable,as in the varied thrush (*Hesperocichla nævia*), where it forms one of the very best characters for recognizing the bird instantly, even though at a distance. Among many of the warblers, vireos and sparrows, where it is present in closely allied species, it would not serve, however, as a help in detecting the species.

There is one thing which seems to be of some significance—that this marking so universally present in the most diverse groups is a streak and not a bar. This fact together with the circumstance that it is frequently present in the female or young and not in the adult, and that the reverse is never (?) the case, would indicate that it is a marking of great antiquity, and has probably no very great utilitarian significance, except in exceptional cases where natural selection has made use of it for a recognition mark.

In general the markings of the head are lateral rather than tranverse. They may be reduced, for the most part, to certain types or modifications and combinations of these. Plate IV represents the various patterns of black among North American land birds. Nearly all the characteristic head patterns are produced by the black and white combinations here figured. There are five general types of markings, all more or less simple and rudimentary. They are all lateral, and it seems probable that all transverse markings have been derived from them. I have attempted in this diagram to show how all the head patterns of North American birds are related to these five types. Of course the relations between the widely different forms here associated are not supposed to be genetic, but the diagram is merely intended to show, by means of the arrows, how the various patterns may have been derived by the modification of the types. It is not difficult to see why these five patterns should be the simplest and earliest developed. In the first place they follow the general trend of the feathers, which would be more natural than to cross it. Then they follow pterylographical areas more or less. It is easy to see how types 1 and 2 might be bounded by the eyes and upper edge of the ear coverts, while type 3 includes little besides the ear coverts. Types 4 and 5 occupy definite feather tracts separated by bare spaces, and their origin is accordingly not far to seek. *Polioptila plumbea* is figured as a representative of type 7, which includes also such species as *Dendroica striata, Sitta carolinensis* and *Galeoscoptes carolinensis*. It is a simple black cap. Type 2, the superciliary stripe or band is illustrated by *Zonotrichia coronata, Seiurus auricapillus* and *Regulus satrapa* belonging in the same category. The line through the ear coverts, type 3, is the commonest form existing among North American birds. The figure represents *Saxicola œnanthe*, but the class includes also the following: *Psaltriparus melanotis, Dendroica coronata, Dendroica olivacea, Oporornis formosa, Lanius, Passerina cyanea,* besides numerous species where this marking is associated with other head markings, or where it is present but not black in color. The fourth type—the malar steak, represented by *Colaptes auratus* in the plate, is less commonly met with alone; but type 5, *Dendroica virens* in the diagram, which is the throat patch, is very common. There are only a few forms, however, such as *Dendroica occidentalis* and *Amphispiza bilineata* where it occurs as the only black patch upon the head.

The combinations of these five types follow next. Fig. 6 is *Dendroica tigrina*, which presents a combination, not of types 1 and 2, but of 1 and modification *a* of type 2. Fig. 7, *Dendroica blackburniæ*, is a combination of 1 and 3, the black cap and ear covert. This is a very common form, being presented with greater or less deviation from the type by such forms as *Sitta canadensis*, *Certhiola bahamensis* and *Pitangus derbianus*. Fig. 8 is the combination of types 1 and 4, as shown in *Dendroica striata*. Fig. 9 is a combination of types 1 and 5 illustrated by *Parus atricapillus*. Fig. 10, of *Ampelis cedrorum* is equivalent to 2*a* plus 5, and figure 11, *Helminthophila chrysòptera*, equals 3 plus 5. Fig. 10*a*, *Parus hudsonicus*, is a combination of types 1, 2 and 5; while fig. 11*a*, *Mniotilta varia*, is a combination of types 1, 3 and 5.

There is little difficulty in understanding these types and their combinations as markings which have followed the feathers along natural areas of the birds' heads. They may thus be in part accounted for in accordance with the location of growth force along lines of least resistence, although natural selection has played a not unimportant part in shaping and defining them. Upon leaving the types and considering the various modifications, it becomes immediately evident that here the part played by selection must have been a far more important one. Can any law of growth be suggested, for example, for chopping off a black line right through the middle of the ear coverts as in fig. 3*a*, *b* and *d*, and fig. 10*e* ? By attentively following the arrows, it will be seen how either by the modification or combinations of patterns, or both, each form may be derived from some preceding form, more or less completely. Figs. 10*e*, 11*c*, *d*, *e*, alone fail to be reduced to a community with the other patterns. It is unnecessary to encumber the text with the names of the various species, which are not essential to the point under consideration, and may be found in the explanation of plates. A few words should be added concerning the nature of some of the relationships here indicated. By a reduction of the posterior extent of the black cap in fig. 1, fig. 1*a* is produced. A continuation of this reduction would lead to fig. 1*b;* while the cutting off of the front of the black cap would give fig. 1*c*, which process continued would end in fig. 1*d*. Fig. 2*a* is hardly more than a narrowing of the band of fig. 2, but fig. 2*b* is a combination of this with fig. 1*b*. In fig. 2*c* the band has become extended posteriorly abruptly downward, while in 2*d* the angle is changed and it is extended not merely downward but forward.

It will not be necessary to continue an interpretation of all the transitions indicated in the diagram. I desire simply to show that all the head markings of birds can probably be interpreted as modifications of certain fundamental types which are probably the parent forms from which all have sprung. They are in fact closely allied to the primitive streaked plumage, and may be looked upon as merely an aggregate of streaks in definite parts of the head.

It may now be more readily apparent why some forms of marking never occur while others are so general. It is necessary to keep in mind two general influences, the internal forces of growth regardless of the effect to be produced, and external selection, which looks only at the effect. We have now seen how selection would tend to produce the most striking effects of form and color of marking upon those parts which are most exposed, and especially those parts which are most constantly in motion—the head, throat, wings, tail, rump and under-tail coverts. At the same time, other things equal, these effects would always be produced in the easiest and most natural way, rather than in direct opposition to the laws of growth.

With regard to the wing markings, the laws of development apply when the individual feathers alone are taken into consideration, but the general effect of wing marking is produced in a great variety of ways which has no obvious relation to laws of growth or mechanical forces. Wing markings are generally white in strong contrast to some very dark shade, generally brown, and are obviously recognition marks of some sort. It might be thought that the white was due to degeneration if it uniformly occurred at the tips of the feathers where the wear is the greatest; but in point of fact, while it is very often situated thus, it also occurs at the base or through the middle of the feather. Thus the cedar wax-wing (*Ampelis cedrorum*) has no white wing bars, while the Bohemian wax-wing (*Ampelis garrulus*) which is so closely related, has a wing-bar formed by the white spots at the terminus of the primary coverts, another on the tertiaries, and a vertical line down the wing formed by the white and yellow spots on the outer edge of the tips of the primaries. It surely cannot be held that any internal law of growth, or external mechanical force which produced such a variety of effects in the one species could have been almost or wholly in-operative in a species of the same genus so closely allied. In the rose-breasted grosbeak, the band of white situated apparently in almost the same place as in the wax-wing, is produced not by white terminals on the primary coverts, but by a broad patch of white at the base of the primaries themselves, which is partly cut off by the coverts, leaving only a white band. In the Californian woodpecker (*Melanerpes formicivorus bairdi*) the white markings on several of the feathers run through the center of the primaries leaving both the base and tip uniformly dark.

The tail markings also vary in different forms to such an extent as to be inexplicable by any factor but selection. There are, on the other hand, certain points in regard to them which demand an appeal to internal laws for explanation. It is a noticeable fact that the two outer tail feathers have the markings most strongly developed, and that they decrease as we approach the central feather. Of course, it would be said that the outer feathers are the most conspicuous, and the markings would be of more use here than on the inner feathers, and this is doubtless the true explanation in such forms as the junco (*Junco hyemalis*), where only the two outer feathers are thus marked. In the blue jay (*Cyanocitta cristata*), on the other hand, the tail is marked with a terminal band of white, which diminishes in a regular sequence towards the center. The two central feathers have only a minute tip of white, which would be invisible even to the closest scrutiny at the distance of a few feet, and hence could not have been produced by selection. This is another example of repetitive marks, it seems to me. Natural selection has developed this white bar on the outer feathers as a recognition mark, and it has been repeated according to the law of correlation in a decreasing series toward the center. In the course of time these inner marks might become of sufficient size for natural selection to make use of, and then they would rapidly increase in size. The tail of the belted kingfisher *(Ceryle alcyon)* is an interesting instance of this sort. When the tail is in a normal position of rest, the two outer tail feathers almost or quite touch. The bars on these two feathers are so symmetrically placed that they invariably meet, forming one continuous line. On the outer web, just opposite the tip of each bar, is a spot of white. This complex arrangement has obviously been due to selection, for by no law of pigment distribution could the bars on one feather be made to match the bars on the opposite feather with such perfect accuracy. On the innermost feather of the tail the bars are present, but so very faint as to be scarcely discernable, and on the successive feathers passing outward they become more and more sharply defined.

Certain birds display a curiously converse form of tail marking, having the greatest specialization on the two inner tail feathers. This is markedly the case with some of the woodpeckers, such as *Sphyrapicus varius*, which has the outer tail feather barred distinctly on its outer web, and less so on the inner web, this marking repeated but much less complete on the next feather within, followed by two feathers entirely unmarked and with the two inner feathers the most strongly barred of all. Sometimes these two inner feathers are barred on both outer and inner web, the black predominating on the former, and the white on the latter (young); while sometimes the outer web is black without marks, and the inner web white with narrow bars of black (adult). Of course, this instance is at variance with the rules, but becomes intelligible when it is seen that the inner webs of the upper tail-coverts, and sometimes the entire feather, indeed, is white. A conspicuous line of white is thus begun down the middle of the rump and carried out on these two tail feathers. As the tail is flattened against the tree these feathers would stand out very distinctly and a broad line of white would be the result, very characteristic of the bird in question. The barring is of no utility, but a mere repetition of the tendency to form bars on the outer tail feathers, as is shown by the fact that the bars become obliterated with advancing age, until in highly plumaged individuals these inner tail feathers are almost uniformly black on the outer and white on the inner side of the shaft.

RECOGNITION MARKS.

We may now consider the subject of color markings from an entirely new point of view. Thus far the question has been looked upon largely, if not entirely, from the standpoint of the dead bird. An attempt has been made to show that both the distribution of pigment upon the feather and the formation of general patterns of color were to a greater or less extent dependant upon the laws of growth resident within the organism. In considering this problem, however, the ubiquitous natural selection was constantly dogging our footsteps and demanding a hearing, but it is now time to listen to its cause argued by an advocate for its rights and not simply tolerate its presence as a necessary evil.

Darwin was inclined to attribute the diversity of color in birds rather to the action of sexual selection than to natural selection. Accordingly such instances as the conspicuous white tail of the rabbit he found difficulty in explaining. It is to Wallace that we must turn for an elucidation of the real meaning of these conspicuous colors. He has shown that a large number of color marks, which had been previously thought to be of no significance, were in reality of use as a means of recognition by the individuals of a species among themselves, or by the individuals of one species of other allied forms. Mr. E. B. Poulton has elaborated and systematized the various theories of color marks, principally as originally presented by Mr. Wallace, and I will use his classification and terminology as given in his work On the Colors of Animals, merely simplifying it so as to exclude such classes as are not found among birds. His table of colors classified according to their uses may be modified for the present purpose as follows:

A. APTATIC COLORS (*deceitful*). Causing an animal to resemble its environment, or to be mistaken for some other species.
- I. CRYPTIC COLORS. Protective and aggressive resemblance.
  - 1. *Procryptic*—Protective.
    - *a*. General protective resemblance { Variable. / Constant.
    - *b*. Special protective resemblance.
  - 2. *Anticryptic*—Aggressive.
    - *c*. General aggressive resemblance { Variable. / Constant.
    - *d*. Special.
- II. PSEUDOSEMATIC COLORS. False warning and signaling.
  - 1. *Pseudaposematic*—Deceptively suggesting something dangerous to an enemy.
  - 2. *Pseudepisematic* (alluring colors). Deceptively suggesting something attractive to prey.

B. SEMATIC COLORS (*signaling*). Warning and signaling colors.
- I. APOSEMATIC COLORS. Warning colors.
- II. EPISEMATIC COLORS. Recognition marks.
  - 1. *Directive.*
    - *a*. Recognition by distant stragglers.
    - *b*. In close flight.
    - *c*. In migrations.
  - 2. *Discriminative.*
  - 3. *Sexual.*
  - 4. *Socialistic.*
    - *d*. In darkness of night.
    - *e*. In burrow.
    - *f*. In care for young.

C. EPIGAMIC COLORS. Colors displayed in courtship.

Let us now consider these various classes and see how they may help in the elucidation of the color problem. Omitting the more inclusive divisions as sufficiently clear, let us commence immediately with (1) *Procryptic colors*. This includes all of that large class of forms whose colors harmonize with their environment for the purpose of protecting them from enemies. In many cases it is extremely difficult to say whether an apparent adaptation to a given environment is due solely to natural selection, or solely to the direct action of the environment, or to the co-operation of these two factors. In many instances, such as the white of Arctic animals and the pale color of desert forms, the latter view will probably be found to be correct; but as the influences of the environment are to be discussed later, nothing more need be said upon the subject at present.

These protective colors may vary with a changing environment, as is the case with the ptarmigan (Lagopus), which is dark in summer and white in winter, and possibly with some of the goldfinches such as *Spinus psaltria*, which is bright yellow and olive green during the summer when the yellow Compositæ, upon which it is almost invisible, are in bloom, and buffy and olive brown in winter when it is almost equally inconspicuous among the dry weeds. It seems probable that this is a case of a bird which acquired its yellow breast largely by sexual selection, and afterwards this character was made use of by natural selection as a variable protective color. The house-finch *(Carpodacus mexicanus frontalis)* varies with the seasons also, and its winter coat is a protective one, but the summer dress does not happen to be of a color which can be turned to account.

By far the greater number of general protective colors are constant, and harmonize with the most prevalent environment only. Nearly all of the Gallinaceous birds are colored upon the upper part of the body some mottled shade of brown or dun, which blends wonderfully with the ground upon which they alight. The perfection of protection of the colors of the nighthawk and whip-poor-will which sleep in exposed places during a large part of the day, is a source of wonder to every country boy. Most of the smaller flycatchers are so obscurely clad and blend so completely with the branches upon which they alight, that in walking through the forest the observer frequently knows them simply as *vox, et prætera nihil.* The horned lark as it squats upon the plain is often nothing but a song in the air, and defies the closest scrutiny. Most of the sparrows, in the general style of their dress—Zonotrichia, Spizella, Melospiza, Peucæa and Passerella, are colored harmoniously with their environment. The buff and olive green of most of the vireos make them very difficult to detect, even when singing close at hand. So also with the wrens, titmice and thrashers.

It will be noticed that species habitually found near the ground are generally colored brown, while species found among the trees are either greenish or olive, as with so many of the vireos, warblers, etc., or gray, the colors thus blending either with the leaves or branches. I would suggest that there is great probability that the habits of birds have been more or less determined by their colors. If, for example, the natural color of the pigment of a group of birds was olive green or gray, those individuals which formed the habit of living among the trees would survive, those frequenting the ground, being more conspicuous, would perish. Still more probable is it that, other things being equal, the brown birds which got up among the trees would be destroyed, while those which remained near the ground would live.

I am not sure that any instance exists among North American land birds of (*b*) special protective resemblance. The nearest approach to it is the perfect imitation of the bark of the tree by the markings of the back of the brown creeper (*Certhia familiaris americana*). This is in reality only an unusually complete case of general protective resemblance. Mr. Wm. V. Praeger has suggested an instance among wading birds which should be inserted here as illustrating this very unusual class. He says:* "To the protective colors which are unusual among the shore birds I had always considered the neck and head marking of the genus *Ægialitis* a striking and curious exception, till a short time ago, when looking at an *Æ. semipalmata*, which I had wounded, trying to hide by crouching in a hollow in the sand; and while admiring the perfect blending of its brown shades with the surroundings, I saw in its white rings one of the commonest objects of the sea shore—the empty half of a bivalve shell. The white about the base of the bill was the "hinge," the collar the outer rim, and the top of the head the cavity of the shell, filled—as they usually are—with sand. In the cabinet drawer the resembance is not so noticeable, but such resemblances rarely are, and it was striking among the natural surroundings when I first observed it, and it is most perfect when the bird is crouching as it does in the presence of danger or when on its eggs."

(2) Anticryptic colors differ from the preceding merely in the fact that they are used by rapacious birds in approaching their prey, instead of by harmless species in avoiding danger. (*c*) General aggressive colors are illustrated by the mottled plumage of most of the owls, the burrowing owl *(Speotyto cunicularia hypogæa)*, being a particularly good example. These forms are all

---

*Auk, viii, p. 236.

constant in their color and I know of no species which is marked with general variable anticryptic colors. The snowy owl *(Nyctea nyctea)*, would come nearer answering the requirements than any other species, but the change in this species is dependent more upon age than season, and it would accordingly not apply. Of (*d*) special anticryptic colors, the belted kingfisher *(Ceryle alcyon)*, is a partial example, and the only one with which I am familiar. The colors of this bird are such that they blend, not with the environment of the bird particularly, but with the water and sky as seen by the fish as its foe descends upon it from above.

(II) *Pseudosematic* colors are seldom met with among birds—at least among North American species. Wallace has suggested that many of the plumes and appendages of birds may be used to frighten enemies, but I have been unable to detect any instances of their use for this purpose. Ordinarily, when an enemy threatens, a bird will seek safety in flight, rather than try the doubtful experiment of frightening a foe by its formidable appearance. There are some cases of protective mimicry among birds, although I know of none among North American species. "A most extraordinary case," says Dr. Stejneger,* "is that of the Indian, so-called drongo-cuckoo *(Surniculus dicruroides)*, which, as indicated by the name, so exactly imitates the king-crow, or drongo-shrike *(Dicrurus)*, inhabiting the same locality, in size, form and color, that there is required considerable attention in order not to confound them, though the arrangement of the toes, of course, at a closer inspection is alone sufficient to separate them. This imitation is the more strange since it has even extended to the curiously furcated tail, a feature elsewhere entirely unexampled among the cuckoos." Further study may bring

---

* Riverside Natural History, iv, p. 380.

to light instances of these (1) *pseudaposematic* colors among North American birds.

There is at least one excellent illustration of (2) *pseudepisematic* colors, however, among our native birds. Dr. Stejneger quotes Mr. Charles W. Beckham on the case in point, referring to the kingbird *(Tyrannus tyrannus)*:[*] "Several years ago, in May, I saw one of these birds occupying an exposed perch on a pear tree in bloom, about which many bees were darting. Several times I observed that the bird caught the insects without leaving his perch by quickly turning his head and 'grabbing' them. My attention being thoroughly aroused, I noticed that many of them seemed to fly directly towards him; the majority appearing to 'shy off' at a short distance and change their course, but very few that came within reach escaped him. The question naturally suggests itself: Did the thrifty Hymenoptera mistake the fully displayed orange-red crown (I could see that the crest was erected), for a flower? Once since I have observed the same phenomenon, but not as well as upon this occasion. Mr. C. C. Nutting, who has spent considerable time studying the birds of Costa Rica and Nicaragua in their native haunts, states that he has seen *Muscivora mexicana* perched upon a twig, and waving its curious and brilliant fan-shaped crest after the manner of a flower swayed by a gentle breeze and thus attracting insects within reach."

It is not impossible that the crest of the kinglets and other insect eating species similarly adorned, even though developed by sexual selection may have afterwards been used for attracting insects. It would require a long series of careful observations to demonstrate this point however.

---

[*] Riverside Natural History, iv, p. 469.

By far the largest number of useful markings are included under the head of (B) SEMATIC COLORS. As a general rule the ground color of a bird is the protective color while many of the detailed markings are for recognition. Warning colors (I. *Aposematic*) are apparently almost as rare in the bird world as the false warning marks. The only genuine example with which I am acquainted is to be found among the water birds. It is the conspicuous white patch upon the head of the tufted puffin (*Lunda cirrhata*) which is very prominent when the bird is upon its nest at the end of a burrow, serving as a warning for intruders to avoid the sharp and indeed dangerous beak which they are sure to encounter.*

The (II) *Episematic colors* however, are very conspicuously represented among all classes of birds. These are what are commonly known as recognition marks. White, particularly in contrast to black, or some other dark shade, is most frequently used for this purpose. The markings of the wing and tail can doubtless be explained in this way in nearly every instance. It is upon this class of markings that Wallace lays the greatest stress, as accounting for a large proportion of the diversity of markings and patterns in the bird world. In explaining these markings he says:† "If we consider the habits and life-histories of those animals which are more or less gregarious, comprising a large proportion of the herbivora, some carnivora, and a considerable number of all orders of birds, we shall see that a means of ready recognition of its own kind, at a distance or during rapid motion, in the dusk of twilight or in partial cover, must be of the greatest advantage and often lead to the preservation of life. Animals of

---

* cf. Zoe iii, pp. 161–162.

† Darwinism, p. 217.

this kind will not usually receive a stranger into their midst. While they keep together they are generally safe from attack, but a solitary straggler becomes an easy prey to the enemy; it is, therefore, of the highest importance that, in such a case, the wanderer should have every facility for discovering its companions with certainty at any distance within the range of vision.

Some means of easy recognition must be of vital importance to the young and inexperienced of each flock, and it also enables the sexes to recognize their kind and thus avoid the evils of infertile crosses; and I am inclined to believe that its necessity has had a more widespread influence in derdermining the diversities of animal coloration than any other cause whatever."

Mr. J. E. Todd, entirely independently of Wallace, published in 1888 a similar theory of animal colors, calling them directive colors.* He makes the following classification of directive colors: 1. "Marks and tints, promoting recognition at a distance, to guide in straggling flight and to bring stragglers together [A]. 2. Those indicating the attitude of the body and its probable movement [B] in darkness of night, or in dens; [C] in close movement of large numbers, by day as well as by night; [D] in intercourse of the sexes [E] in the care of young."

In a previous paper† I have proposed a somewhat different classification of recognition markings. Neither Wallace nor Todd seem to have drawn a sharp line of distinction between such recognition marks as enable an individual to find those individuals with which it is to his advantage to consort, as for example, such marks as enable stragglers to regain the flock; and those recog-

---

* American Naturalist, xxii, pp. 201–207.

† Zoe ii, pp. 210–216.

nition marks by which individuals are enabled to mutually avoid one another, as, for instance, the distinctions of species by characteristic marks, by which infertile crosses are prevented. These two classes may be termed respectively directive and discriminative recognition marks. A third class includes such marks as are of use in the intercourse of sexes, the care of young, or in the darkness of holes or burrows. For these the term socialistic marks may be used.

In the paper in Zoe cited above I found difficulty in explaining these recognition marks in harmony with the survival of the fittest, for the individuals possessing these marks are not thereby benefited but rather benefit others. In the introduction to this paper (see *ante* p. 108), I have indicated the manner in which these might be explained through the necessity for the survival of the family.

Directive marks may be of three sorts: those which enable stragglers at a distance to regain the flock—especially well illustrated by a flock of moving sandpipers, which as they wheel about now flash into sight as a fluttering mass of shining white and then disappear, like a flash light which throws its rays now upon one point of the compass and now upon another—those which enable a bird to follow its companion or companions through dense underbrush, as for instance some of the towhees, (*Pipilo*), which are so conspicuously marked with black and white, and which always frequent the densest tangle of the bushes—and those which enable migrating birds to follow their leaders. As migrations are so largely conducted by night, call notes and the general manner of flying are probably more relied on for purposes of recognition than color marks, although I am inclined to think that the latter may at least in some instances also be called into play. Todd has suggested a number of different methods in which recognition at a distance may be effected. Thus one means is "by having the general color more or or less strikingly contrasted with the environment," as with crows, buzzards, bluebirds, woodpeckers, etc. It seems hardly possible that colors such as the complex patterns of the woodpeckers, for example, can have been developed merely in order that the general effect shall be in contrast with the environment. With the crows and blackbirds, however, which habitually consort in flocks, it is quite possible that means of recognition has been at least one factor in the production of the black color.

It is difficult in many instances to say definitely whether a certain mark should be classed among those which are useful for recognition at a distance or in close flight. The white rump-patch and flash of scarlet serve to distinguish the red-shafted flicker *(Colaptes cafer)* as far as the bird can be seen, and the same may be said of the superciliary stripe and wing bars of the varied robin *(Hesperocichla nævia)*. The markings of Audubon's and the yellow-rumped warblers *(Dendroica auduboni* and *D. coronata)* are especially good recognition features. They are probably of more use near at hand than at a distance although they might be of service at tolerably long range, and especially during migrations. These markings are most conspicuous just as the bird takes flight, at which time the yellow rump patch and white markings of the tail combine in a pattern which irresistably catches the eye. The meadow lark *(Sturnella magna)* just as it settles down on the ground exposes the white outer tail feathers, which do not appear as a rule either when the bird is at rest or in flight. Allusion has already been made to the reddish under tail coverts of the Californian towhee *(Pipilo fuscus crissalis)*. As the bird hops rapidly about among the bushes they are frequently exposed, and when it alights quickly the tail is frequently thrown forward as if the bird had lost its equilibrium for the instant, thus showing this patch of contrasted color. It is without doubt an instance of a recognition character which would be of great use as a directive mark to birds living in the dense underbrush.

The white patch on the wing of the shiny-crested flycatcher *(Phainopepla nitens)* is concealed when the bird is at rest, but very conspicuous in contrast to the black of the body when the bird is in motion. The wing band of Townsend's solitaire *(Myadestes townsendii)* is concealed when the bird is at rest, but conspicuous in motion. In many species the white outer tail feathers are folded out of sight while the bird remains passive, but are noticeable the moment the bird starts to fly. Such, for instance, is the case with Junco, Anthus, etc. The subterminal or terminal spots or bars on the tail are always more conspicuous when the bird is in motion than when at rest.

The grouse, pigeons and hawks, present so many interesting modifications of recognition markings upon the tail that it may be worth while to consider them in a little more detail. In the genus Dendragapus the tail is black, tipped with a distinct band of ash gray in the dusky grouse (*D. obscurus*), and with a narrower band in the sooty grouse (*D. obscurus fuliginosus*), which is almost entirely wanting in Richardson's grouse (*D. obscurus richardsonii*). In the Canada grouse (*D. canadensis*) the tail is tipped with ochraceous rufous, while in Franklin's grouse (*D. franklinii*) it is black to the tip. The black tail is doubtless a directive recognition mark, but the modification in the terminal bar is in all probability a character belonging to the class of (2) discriminative marks. When, from differences in climate, food, or selective influences two forms occupying adjacent territory have differed to such an extent that the sexual organs are affected and they are no longer fertile *inter se*,[*] any mark by which they might distinguish their own kind from the other stock, would serve in the perpetuation of the race by preventing infertile crosses. These different wing bars in the genus Dendragapus may not improbably be characters of this sort. In the band-tailed pigeon (*Columba fasciata*) the terminal third of the tail is lighter and is separated from the basal portion by a broad band of blackish. It may be in this instance that the black bar was originally developed as a discriminative mark, and that now, when no longer needed for this purpose on account of the isolation of the species from allied forms, natural selection has turned it to account as a directive mark. In the passenger pigeon (*Ectopistes migratorius*) the tail markings are highly complex. They are thus described in Ridgway's Manual: "Shading from dusky on middle feathers through gradually lighter shades of gray, to white on outer webs of lateral pair, the inner web of each feather (except middle pair) with a transverse blackish spot, preceded by one of rufous." The necessity for directive recognition marks would be especially necessary in a species moving in such large flocks, from which individuals or small parties would constantly get astray. It may be that the complex pattern on the tail feathers was evolved first as a discriminative mark, for except in size, the species might easily have been confused with the mourning dove *(Zenaidura macroura)* which has the tail marked with a simple irregular subterminal band of dusky. The white-fronted dove *(Engyptila albifrons)* has an especially characteristic form of recognition marking on the tail, all but the middle pair of feathers being black, broadly tipped with white. The

---

[*] See discussion of physiological selection *ante*. p. 123.

white-winged dove *(Melopelia leucoptera)* has the terminal fourth of the tail white, the basal portion of the feathers (except middle pair) being slaty.

Among the hawks the tail is often the most characteristic mark of recognition at a distance. The marsh hawk *(Circus hudsonicus)* may always be distinguished at a distance by his white rump patch, and the black markings on the head of the sparrow-hawk *(Falco sparverius)* serve to distinguish it, and yet both these species, and nearly all other hawks have some characteristic marks upon the tail. Thus the tail of the marsh hawk is tipped with white, with a broad blackish subterminal band and several narrower bands anterior to it. Accipiter has the tail crossed by several bands of blackish and narrowly tipped with white. The tail of Parabuteo is black, with the base and tip white, while in many species of Buteo it is crossed by a subterminal band of blackish and with a white tip. There are very many variations in the form of tail marking in the genus Buteo, and these are doubtless discriminative marks which were originated soon after the different forms began to diverge. Among the red-tailed hawks *(Buteo borealis)* the general color of the tail is a striking example of a directive mark by which the species may be known at a long distance. The different races vary in the detailed characters of the tail, and these marks are apparently discriminative in nature, all the members of the genus having them in some form. In the broad-winged hawk *(Buteo latissimus)* the ground color is blackish, crossed by from two to four broad bands of light brownish gray, while in Swainson's hawk *(B. swainsoni)* there are nine or ten bands. In the white-tailed hawk *(B. albicaudatus)* the ground color is white, crossed by a broad subterminal band of black, and anterior to this by five bars or lines of slate or dusky. If we suppose the various species of this genus to be the descendants of a common ancestor, we can hardly interpret this great diversity in the distribution of the bars on the tail to any principle but natural selection producing discriminative recognition marks.

The tail-markings among the Caprimulgidæ are peculiarly characteristic. They are interesting because, instead of affording merely specific distinctions, they form generic characters also. In the whip-poor-wills *(Antrostomus)* the three outer tail feathers are tipped with white on the inner web in the male. In the poor-will *(Phalænoptilus)* all but the inner pair are broadly tipped with white in the male, and less broadly in the female. The tail markings in the parauque *(Nyctidromus)* are very peculiar. They are thus described in Ridgway's Manual: "Outer tail-feathers nearly uniform blackish; next mostly white, the outer web edged with dusky; four middle tail-feathers without any white, their ground-color mottled brownish-gray, relieved by irregular 'herring-bone' blotches of dusky along the shaft." In the night-hawks *(Chordeiles)* the males have a broad bar of white on all but middle feathers near the tip of the tail. The variations in the tail patch of the different forms of the genus Antrostomus presents so many interesting features that a tabular view of them may serve to bring the points before the mind:

ANTROSTOMUS.

carolinensis..	♂ terminal third of three outer tail-feathers white or buffy. ♀ no white or buffy on tail.	
cubanensis...	♂ four outer tail-feathers with white tip. ♀ three outer tail-feathers with buff tip.	White patch occupying less than terminal third, and decreasing in extent from exterior feather
macromystax	♂ three outer tail-feathers with white tip. ♀ three outer tail-feathers with buff tip.	
vociferus—Tail patch more extended.		♂ White patch occupying more than terminal third, and increasing in extent from exterior feather ♀ No white tail patch
vociferus arizonæ—Tail patch less extended.		

There are many interesting questions opened by this survey of the tail markings of the Caprimulgidæ. The initial markings were doubtless discriminative in nature coupled in many instances with other marks such as the wing bars and throat patch, and were of use at the time when each of the present four genera was a species diverging from a common stock. As the species became more and more distinct, and in some instances more completely isolated geographically, these marks were no longer of necessity for purposes of discrimination and gradually became of service as directive marks. Then, as the species of Antrostomus began to divide up into a number of forms, a new set of discriminative marks became necessary. The white patch occupying less than the terminal third and decreasing in extent from the exterior feather would present a very different general effect from the patch occupying more than the terminal third and increasing in extent from the exterior. If these markings be discriminative in their nature it is possible to understand why they would be more constant and more completely developed in the male than in the female, or how they may even be wholly lacking in the latter. The female selects the mate and not the male; and it would be quite possible for natural selection so to adjust matters that the female would always prefer to mate with a male marked in one manner. Those females which selected for mates individuals differently marked (*i. e.*, belonged to a different race, and consequently sterile when crossed), would leave no offspring and the tendency would accordingly be for those only to survive which selected mates of the one pattern. In this manner by a process of natural selection a form of sexual selection having no relation whatever to æsthetic choice, but simply to the survival of the fittest would be instituted. Wherever a marked character is present in the male which seems to be more of a mark of recognition than of beauty, and absent in the female, it may be explained, it seems to me, according to this principle which may be called the LAW OF SEXUAL RECOGNITION. The crown patches of the white-crowned sparrow *(Zonotrichia leucophrys)*, and the golden-crowned sparrow *(Z. coronata)*, the black cap of the male gnatcatcher *(Polioptila)*, the black throat patch of the male house-sparrow *(Passer domesticus)*, and many other instances, are examples of the workings of this law. This law of sexual recognition might frequently be coupled with the law of sexual intensification, so that both sexes would progress along a certain line, the males in advance, until the latter had reached the goal of specialization, after which the female would "catch up" to the male. Markings which had thus been sexual recognition marks would become ordinary discriminative marks and finally directive marks.

These sexual recognition marks are closely connected with the fourth and last class, viz.: socialistic markings. These are such marks as assist in the domestic and social relations of the family. They are particularly well represented among mammals—the white face markings and ringed tail of the raccoon *(Procyon lotor)* being an admirable example, but instances are not lacking among birds. Here, however, it is more difficult to distinguish them from other forms of recognition marks, but future study with this end in view will undoubtedly disclose many examples. In the corner of my sleeping room, just opposite the foot of the bed, stands a mounted western great horned owl *(Bubo virginianus subarcticus).* On awakening one morning before dawn a white spot caught my eye which at first I was unable to account for. It soon occurred to me that it was the white throat patch of the owl, and such it proved to be, standing out with wonderful clearness as relieved by the dark plumage surrounding it. It is easy to see how valuable this mark would be to a family of owls in the prosecution of their domestic duties. The white throat patch of the night-hawks *(Chordeiles)* would be similarly useful. The conspicuous white markings on the eyebrows, chin and chest of the burrowing owl *(Speotyto cunicularia hypogæa)* is an admirable instance of a socialistic mark which is useful in the darkness of the burrow. Many of the white markings about the heads of woodpeckers doubtless serve the same purpose, and also the white throat of the belted kingfisher *(Ceryle alcyon)* and the white breasts of the white-breasted swallow *(Tachycineta bicolor)* and the violet green swallow *(T. thallassina).* In these instances the white color is of that peculiar purity that would be especially conspicuous in the darkness of a burrow. The white feathers of downy young birds are doubtless of no utilitarian significance so far as their origin is concerned, but would nevertheless serve to mark the position of the bird in the nest if in a dark burrow or hole.

VARIATION OF COLOR WITH SEX, AGE AND SEASON.

Before natural selection can be established as a factor in the differentiation of color-patterns, it must be shown that the markings are not perfectly constant. Probably nowhere in the system of the bird is there such scope for individual variation as in pigment distribution. In the first place, no two feathers are ever marked exactly alike. On comparing the pattern even on the right and left wing of the same bird very marked individual differences are at once apparent, although the general effect may be the same. Besides, these individual feather differences which are universally present but which do not alter the general appearance, variations of a more striking nature are not uncommon. The pattern may be more or less sharply defined or intensely colored even in birds of the same age, sex and locality. As a good example of variation in the markings of the tail, I have figured the three outer tail-feathers of the downy woodpecker *(Dryobates pubescens)* in very pale, normal and in extremely darkly barred examples (Plate I, figs. 1–3). Again, the general color may be paler or darker, differences of this sort being very striking in some species, as the meadow lark *(Sturnella magna)*, for example; or, on the other hand, a species may be so constant that the closest scrutiny fails to show any well marked individual differences.

I have by no means attempted in the above survey of recognition marks, to give all the instances under each class, for nearly all birds have them to a greater or less extent, but merely to illustrate and establish the validity of the different forms of recognition markings included in the classification given. A consideration of (C) EPIGAMIC COLORS opens up an entirely different field. These are the colors displayed in courtship, and if the conclusions arrived at with regard to sexual selection have any validity (see *ante*, pp. 99–102) they do not so much belong to the class of useful markings as to the division of beautiful colors.

Darwin devotes a large portion of his work on the Descent of Man to a consideration of sexual selection in birds. He there tabulates the rules or classes of cases under which birds may be grouped according to the constancy or variability of the style of coloration with sex, age or season, this purpose being to show how heredity acts with regard to the transmission of sexual characters. His classification, which is an amplification of Cuvier's, is as follows:

"I. When the adult male is more beautiful or conspicuous than the adult female, the young of both sexes in their first plumage closely resemble the adult female, as with the common fowl and peacock; or, as occasionally occurs, they resemble her much more closely than they do the adult male.

II. When the adult female is more conspicuous than the adult male, as sometimes, though rarely, occurs, the young of both sexes in their first plumage resemble the adult male.

III. When the adult male resembles the adult female, the young of both sexes have a peculiar first plumage of their own, as with the robin.

IV. When the adult male resembles the adult female, the young of both sexes in their first plumage resemble the adults, as with the kingfisher, many parrots, crows, hedge-warblers.

V. When the adults of both sexes have a distinct winter and summer plumage, whether or not the male differs from the female, the young resemble the adults of both sexes in their winter dress, or much more rarely in their summer dress, or they resemble the females alone. Or the young may have an intermediate character; or again, they may differ greatly from the adults in both their seasonal plumages.

VI. In some few cases the young in their first plumage differ from each other according to sex; the young males resembling more or less closely the adult males, and the young females more or less closely the adult females."

To these classes as given by Darwin the following may be added:

VII. When the adult male is unlike the adult female, the young of both sexes may differ from either sex of the adult, as with the blue-bird (*Sialia sialis*).

VIII. When the adult male is unlike the adult female, the young male sometimes has a peculiar first plumage, while the plumage of the young female is like that of the adult female, as in many of the woodpeckers.

These classes may be more clearly presented in a table commencing with the most developed forms in which the characters originating first have been transferred first to the female and secondly to the young, and proceeding down from this point through the classes where the inheritance is less and less complete. Darwin has called attention to the fact that these various divisions are not sharply marked, but shade into one another, so that in many instances it is difficult to say definitely to which class a particular species should be assigned. It should also be remembered that while in a large number of instances sexual selection has been the factor which has produced the difference, it is not always so, sexual intensification, sexual recognition and other factors having played a part.

- Male like female.
  - 1. Young like adult (IV).
  - 2. Young like some ancestral stage of the adult (III).
- Resemblance of sexes differs with the seasons; or both sexes may vary with the seasons (V).
  - Male like female.
    - 3. Young like winter plumage of adult.
    - 4. Young differ from adults at any season, or intermediate between summer and winter plumage of latter.
  - Male in breeding plumage differs from female.
    - 5. Young with peculiar first plumage.
  - Male unlike female in both plumages
    - 6. Young like female in winter.
- Male unlike female.
  - Female more conspicuously colored — young like male (II).
  - Male more conspicuously colored.
    - 7. Young like adult female (I).
    - 8. Young with peculiar first plumage (VII).
    - 9. Young male more or less like adult male; young female like adult female (VI).
    - 10. Young male unlike adult of either sex; young female like adult female (VIII).

When the plumage of the male and female is the same there is generally no variation with seasons, but among some forms, especially some of the water birds and waders, a bright plumage is assumed during the breeding season by both sexes, corresponding to the male plumage of species which are sexually dissimilar, while the dull plumage of winter is analogous to the ordinary dress of the female among forms sexually different in colors. The most complete stage of transmission of peculiar characters is (1) that in which the species has but one phase of plumage, at all times of its life, and in both sexes. The following list of species and genera belonging to this class is based upon an examination of specimens in the National Museum. It makes no pretense of being complete, but will serve to indicate representative forms. An asterisk indicates that there is a slight difference in the shade or intensity of color of adult and young:

Dendroica dominica.
*Icteria virens.**
Vireo.
Clivicola riparia.
Stelgidopteryx serripennis.
*Spinus pinus.**
Ammodramus.
Melospiza.
Passerella.
Picicorvus.
Cyanocephalus.
Pica.
*Cyanocitta.**
Aphelocoma.
Perisoreus.
Corvus.
*Sayornis.**
Contopus.
Empidonax.
Chætura.
Geococcyx.

It is a noticeable fact that most of the birds in the above list are more or less dull colored forms. The yellow-throated warbler *(Dendroica dominica)* and yellow-breasted chat *(Icteria virens)* are the only two in which yellow figures at all prominently, and the genera Cyanocitta and Aphelocoma are the only ones in which blue occurs. Besides these there are the highly specialized crows and magpies, and all the rest are without distinctive marks, save the peculiar Geococcyx, which, as will be shown later, is doubtless a degenerate form, so far as color goes, at least. This lack of forms with elaborate patterns of color in this first list is what would naturally be expected; first, because elaborate colors are generally assumed first by the male, and only occasionally the female has been enabled to acquire them; and second, because these dull colors are apt to represent old established types which have found their protection in their insignificance, so that there would have been ample time for the female to have acquired what small degree of specialization the male had attained.

There are a large number of forms belonging to class

2, where the adults are alike, but the young have a peculiar first plumage. The following is a list of North American species coming under this class:

Merula migratoria.
Myadestes townsendii.
Helminthophila swainsoni.
Helminthophila ruficapilla.
Helminthophila virginiæ.
Helminthophila luciæ.
Dendroica nigrescens.
Seiurus.
Lanius.
Ampelis.
Petrochelidon lunifrons.
Chelidon erythrogaster.
Tachycineta.
Chondestes.
Spizella.
Junco.
Amphispiza.
Peucæa.
Pipilo.
Tyrannus.
Melanerpes erythrocephalus.
Malanerpes torquatus.

Among the species in this list no little variety and specialization of color and markings is to be met with. These are the forms in which the female has caught up with the male, which originally led in the evolution of color, or else species in which the colors of the two sexes evolve *pari passu*. It is difficult to decide in which class to place many of the above species, although where the colors are very elaborate and decorative, as in the waxwings (Ampelis), the red-headed woodpecker *(Melanerpes erythrocephalus)*, and the violet-green swallow *(Tachycineta thalassina)*, it is safe to assign them to the former category, whereas, when the colors are obviously of use for purposes of recognition, as with the wag-tails (Seiurus), butcher birds (Lanius), lark-finch (Chondestes), and Junco, the latter alternative is a possible one. Still, the colors of the genus Pipilo are largely recognition marks, and yet the female of the common towhee of the Eastern States *(Pipilo erythrophthalmus)* is colored differently from the male, although in the very closely related *P. maculatus* group the sexes do not differ. This seems to show that the characters of the genus were acquired first by the male, as sexual discriminative marks, and afterwards perhaps transferred to the female as general directive marks.

It is an interesting matter to determine in what manner, and to what extent the young, among these species differ from the adult. Among a large number of them the young are spotted or streaked. When the adults have any distinctive mark or patch this is generally wanting in the young, while the colors of the immature bird are apt to be paler or duller than those of the adult. As examples of species in which the young are spotted or streaked may be mentioned the robin *(Merula migratoria propinqua)*, Townsend's solitaire *(Myadestes townsendii)*, water wag-tails (Seiurus)—spotted on the back with rusty—waxwings (Ampelis), lark-finch *(Chondestes sgrammacus)*, chipping sparrows (Spizella), Junco, etc. A instances where the young are colored similar to the adult but without the distinctive markings of the latter the following may be mentioned: The chestnut crown-patch of the Nashville warbler *(Helminthophila ruficapilla)*, is somewhat variable in the extent of its development, but is wanting in the young of both sexes and present in full-plumaged adults. Lucy's warbler *(Helminthophila luciæ)*, has, besides the crown-patch, a chestnut patch on the rump which is also wanting in the young. The black-throated gray warbler *(Dendroica nigrescens)*, is marked with a black throat in the adult male which may or may not be developed in the female, and is always wanting in the young stage. The crown-patch of the kingbirds (Tyrannus), is wanting in the young. Perhaps one of the most complete changes from the young to the adult plumage takes place in the red-headed woodpecker *(Melanerpes erythrocephalus)*. The areas of the markings are the same for the young and the adult, the markings of the wings and rump being especially constant. In general, however, the brilliant crimson, dark blue and white colors of the adult are replaced by mottled brownish and grayish hues in the young. In all the above instances the adult colors were probably first acquired by the male for recognition *(Dendroica nigrescens)*, sexual beauty *(Melanerpes erythrocephalus)*, or use in some other manner (Tyrannus). The following are cases where the plumage of the young is in general similar to the adult, but markedly paler or duller. Swainson's warbler *(Helminthophila swainsoni)*—young darker than adult, sooty-colored; shrikes (Lanius)—young with colors duller on breast and smoky brown on back, wavy markings on breast pronounced; cliff swallow *(Petrochelidon lunifrons)*, and barn swallow *(Chelidon erythrogaster)*—young paler; white breasted swallow *(Tachycineta bicolor)* and violet-green swallow *(T. thalassina)*—bright colors of back of adult replaced in the young by plain brown.

Where there are seasonal differences in plumage it is decidedly difficult to make sharp distinctions of classes. Frequently the sexes differ very decidedly in their breeding dress, but only very slightly in winter, the male then assuming a plumage like that of the female. In such istances the young generally resemble the winter plumage of the adults, but may differ in being still more plainly colored. The following list includes these forms:

Dendroica auduboni.
Dendroica coronata.
Dendroica maculosa.
Dendroica palmarum.
Cinclus mexicanus.
Geothlypis trichas.
Loxia.
Acanthis.
Leucosticte.
Spinus.
Plectrophenax.
Calcarius.
Guiraca cærulea.
Calamospiza melanocorys.
Dolichonyx oryzivorus.
Xanthocephalus.
Agelaius.
Scolecophagus.
Otocoris.

The above list stands midway between those species in which the adult female is like the adult male, and such as differ in the adult plumage. It includes such forms as vary with the seasons in which the male may or may not be different from the female in summer, but is not markedly so in winter. This division of forms displaying seasonal differences is perhaps the least modified type of sexual adornment, for the male simply puts on his courting garb for a brief season, when it is obviously assumed to attract the attention and admiration of the female.

(3.) In the water-ouzel *(Cinclus mexicanus)* the sexes are alike, but in winter the breast is much suffused with white. The young plumage is like that of the adult in winter. In this class the colors are obviously not sexual, but the more primitive plumage appears during the winter months. The increased vigor during the breeding season has produced acceleration in the development of pigment at that time of the year.

(4.) As an example of this class may be mentioned the palm warbler *(Dendroica palmarum)*, in which species the sexes are alike, the colors becoming broken and obscured in the winter plumage. The young are a plain dusky, streaked above and below.

(5.) In Audubon's warbler *(Dendroica auduboni)*, the yellow-rumped warbler *(D. coronata)*, and the magnolia warbler *(D. maculosa)* the plumage of the male in summer is similar to that of the female, but all the markings greatly accentuated and intensified. In winter the sexes are very much alike, while the plumage of the young is considerably less specialized than that of the female.

The changes in plumage of the crossbills (Loxia) is especially complex, for the male frequently passes through three phases of plumage—first a gray phase, then yellow, and finally red. In general, it may be said that the adult male is red, the female yellowish, and the young dusky gray, but whether the yellow plumage of the male is simply a mark of immaturity or a seasonal difference, I have not been able to determine.

(6.) The red-winged blackbirds (Agelaius) present some interesting features in the changes of plumage. Not only does the male differ from the female in summer, but both sexes also change in winter, and the plumage of the young resembles but is not identical with that of the female.

The uniform black of the males is in winter broken up by rusty terminals to the feathers, while the brown and gray streaks of the female become duller in winter, and the white tinge on the lower parts less marked. The changes in the red wing-patch are shown in Plate XII. The adult males in summer are colored with a patch of brilliant red or crimson. In winter it is yellowish much broken up with dusky and black mottlings. The wing patch of the adult female *Agelaius phœniceus* and *A. gubernator* in summer plumage is a pale reddish tinge greatly interrupted with mottlings, while the wing patch of the summer female of *A. tricolor* is a dull crimson, mingled with bluish black mottlings. The last figure represents the adult female in winter, or young, phase of the shoulder marking, the color being there a plain unmodified brown. The various stages of transition from the unspecialized to the most highly developed phase are thus to be found in this group by studying the variations of age, sex and season.

The third division includes those forms in which the adult male is, at all seasons of the year, unlike the female. Instances where the female is more conspicuously colored than the male are very rare, and I do not think there is any example of this group among North American land birds. The phalaropes form one of the most notable illustrations of the class. When the male is more conspicuously colored than the female and there is no marked seasonal change, the young may differ to a greater or less degree from the adults. The following is a list of species in which (7) the young are like the adult female:

Mniotilta varia.
Protonotaria citrea.
Helminthophila chrysoptera.
Helminthophila pinus.
Helminthophila ruficapilla.
Parula americana.
Dendroica tigrina.
Dendroica æstiva.
Dendroica cærulescens.
Dendroica blackburniæ.
Dendroica cærulea.
Dendroica virens.
Dendroica townsendi.
Dendroica occidentalis.
Dendroica vigorsii.
Setophaga ruticilla.
Geothlypis agilis.
Geothlypis philadelphia.
Geothlypis macgillivrayi.
Sylvania mitrata.
Sylvania pusilla.
Sylvania canadensis.
Vireo atricapillus.
Phainopepla nitens.
Progne subis.
Coccothraustes vespertina.
Pinicola enucleator.
Cardinalis.
Pyrrhuloxia sinuata.
Habia.
Piranga æstiva.
Icterus.
Quiscalus.
Trochilus.

It is a noteworthy fact that every species in this list has some mark of specialization, while nearly all are highly modified forms. This is the class which, more than any other illustrates sexual selection—the males having been originally marked like the present females and young, and the brilliant and varied hues of the male warblers, humming birds, cardinals, and tanagers of to-day have doubtless been assumed principally as sexual charms.

Of species in which the male is more conspicuously colored and the young have a peculiar first plumage, the following are representative examples:

Dendroica pensylvanica.
Dendroica castanea.
Dendroica striata.
Piranga ludoviciana.
Piranga rubra.
Spinus lawrencei.
Pipilo erythrophthalmus.
Passerina.
Spiza americana.
Molothrus ater.
Pyrocephalus rubineus.
Sphyrapicus varius.
Melanerpes carolinus.
Sialia.

This class, like the preceding, is made up of brightly colored species without exception. The colors are sexual ornaments, but in every instance have been partly acquired by the female, which thus stands in an intermediate position between the generalized plumage of the young and the specialized plumage of the adult, marking three stages of evolutionary progress. Thus the colors of the female western tanager *(Piranga ludoviciana)* lack the brilliancy and purity of the hues of the male, while the young, in their first plumage are streaked above and below. The summer tanager *(P. rubra)* is colored in a corresponding manner, as is also the scarlet tanager *(P. erythromelas)*. A specimen of this species in the collection of the National Museum—a male in full plumage—is colored a deep yellow, with black wings, entirely different from the greenish yellow of the female. This is proably an instance of reversion to an earlier plumage, or may possibly be simply the correlative of the red pigment, due to some derangement in the bird's system. The adult female of Lawrence's goldfinch *(Spinus lawrencei)* is without the black of the head, and with all the colors somewhat duller, while the young are plain dusky with a little yellow on the wings and a decided tendency towards a streaked plumage. In the indigo bunting *(Passerina cyanea)* the bright blue of the male is replaced by a dull brown, while the plumage of the young is like that of the female, but streaked above and below. The bluebird *(Sialia sialis)* is a familiar example of this class, the colors of the female being much duller than those of the male, and the young having a mottled breast.

The next class (9) includes those species in which the male is more conspicuously colored than the female and the young of each sex resembles its respective adult. The following forms are representative of the class.

Habia ludoviciana.	*Sphyrapicus thyroideus.*
Picoides.	*Melanerpes aurifrons.*

In the three-toed woodpeckers *(Picoides)* the adult male differs from the female chiefly in the yellow crown patch, which is lacking in the latter. The young do not materially differ from the adults. In the golden-fronted woodpecker *(Melanerpes aurifrons)* the general plumage of the young is like that of the adult except that the colors of the former are duller, particularly the yellow of the belly. The adult female differs from the adult male chiefly in lacking the red on the head, and with the yellow of the head duller. In the young male the markings of the adult are indicated but very dull, while the yellow of the young female is so pale as to be almost buffy. Williamson's woodpecker *(Sphyrapicus thyroideus)* is interesting as coming one step nearer to class 10, and also of note from the fact that the female is so markedly different in color from the male. The young female is like the adult female, having a barred plumage, but the yellow of the belly is decidedly paler. The young male has the plumage marked in uniform masses of black and white like the adult, but the bright yellow is replaced by white and the red throat patch is lacking.

In the rose-breasted grosbeak *(Habia ludoviciana)* we have approached one step nearer to class 10 showing how these different divisions shade into one another. In this species the young male is intermediate in plumage between the adult male and female. The general color is brown like the adult female instead of black like the male, but the characteristic rose-colored patches of the adult male on the under wing coverts are fully developed in the young, and the patch of rose on the breast is present, but much interrupted. The young female is almost like the adult, but the yellow paler and colors less pronounced. This species exhibits four stages of evolutionary progress, and it is possible to trace the phylogeny of the adult male from the plain brown streaked bird with pale salmon-yellow under wing coverts (young female) to the more pronounced pattern of the adult, although still obscured by streaks, and with the yellow of the wing coverts more strongly developed (adult female), through the stage in which the yellow patch, by the action of sexual selection in intensifying the correlative color becomes changed into rose, and an irregular patch of the same is developed on the breast (young male), until finally the black, white and rose plumage, in well defined patches, is assumed by the adult male.

The last class (10) which, however, has already been encroached upon, includes those species in which the adult male is more conspicuously colored than the adult female, and the young male unlike the adults of either sex, but the young female generally like the adult. The best examples of this class with which I am familiar are to be found among the woodpeckers, especially Dryobates and Xenopicus. Here the general color and markings do not vary much with age or sex, but the head markings are very peculiar. The red head markings of the adult male are upon the nape, those of the young male cover the top of the head, being, in fact, not only differently located, but more extensive. The head of the female is unmarked with red in the adult.

Mr. Charles Richmond informs me that the young female often has the top of the head marked with yellow. Specimens in the National Museum collection failed to demonstrate this, as the sex of the young is in many instances undetermined. This peculiar head marking of the young seems to point to but one thing—to a different and perhaps more highly developed ancestral plumage. At any rate, the crown patch, which once extended over the entire head, has now become restricted to a comparatively narrow line across the nape.

THE DIRECT INFLUENCES OF THE ENVIRONMENT.

In the preceding discussion of the factors involved in the evolution of the colors of North American birds, the distribution of pigment in accordance with the internal laws of growth was first considered, then the utility of the various colors and their patterns, and the manner in which natural selection had been instrumental in their development, and finally beautiful colors, which had been evolved by sexual selection, and the manner in which the laws of heredity had tended to reproduce, first in the female, and afterwards in the young, at successively earlier and earlier stages, in accordance with Cope's law of acceleration, the characters which had been acquired by the male. We have yet to observe how these various markings may be modified by the direct action of the environment — by the influences of food, temperature, moisture, etc. — in a way which is of no utility to the species. If the results of environmental influence were a detriment to the species, the race would either die out or become adapted to the change, but if these direct influences were an advantage, they would be seized upon by natural selection, and made the most of.

Eimer considers that the part played by the direct influence of the environment in the evolution of colors is a very important one. In his "Organic Evolution" he discusses the changes caused by food, climate, and the direct action of the color of the environment upon the nervous system. This latter influence, which is so important a factor in the changes of color of the frog, for example, probably does not affect birds to any extent whatever, and need not be discussed here. Comparatively few experiments have been attempted to determine to what extent food may affect the colors of birds. With regard to the effects of food upon color, Mr. Frank Beddard says:* "If the nature of animal colours is borne in mind, it seems impossible to doubt the modifying action of food; those that are due to structural peculiarities of the parts coloured (*e. g.* feathers of many birds) may be altered just as much as those that are caused by the deposition of pigment; for the 'structural' colours depend largely upon pigment for their manifestation.

The mere increase in the deposition of pigment may lead to an alteration of colour, oftenest perhaps in the direction of melanism; and there is evidence that various substances, when taken into the body, do influence the amount of excreted matter. Where there is an obvious relation between waste matter and the skin pigments, it cannot be doubted that variation in the amount only of the food may lead to colour changes."

These remarks of Mr. Beddard's are along the line of a theory of melanism and albinism, suggested to me by Dr. Stejneger, viz.: That there is a general tendency among birds to assume a uniform coloration—generally black, which is prevented from asserting itself in most instances by natural selection, etc. White, Dr. Stejneger regards as a mark of degeneration, and, just as

---

* Animal Coloration, p. 48.

animals (more especially man) in old age have their hair turn gray or white, so species or genera, when on the wane, may become albinistic. This might be considered an exemplification of Hyatt's principle of geratology (see *ante*, p. 78). If a species is in its prime, it would tend to be superabundantly nourished—the adjustment of the means of living being so perfect—and the surplus of vitality would gradually expend itself in an increase of pigment. If the pigment were a dark one, the more closely the feathers were crowded with it, the blacker the plumage would become. If a species, on the contrary, had passed its prime and were wearing out, it would be imperfectly nourished, and less and less pigment would be deposited until an albino form would result. Both the black and white coloration, as previously suggested, might be of use as recognition marks, and thus the assumption of such a plumage would be hastened by natural selection. If, on the other hand, the black or white, instead of being of use for recognition, was a detriment to the species, by making it over-conspicuous, the result would probably be the extinction of the race.

One of the few direct influences of food which have been observed upon the colors of birds is the effect of cayenne pepper. Dr. Sauermann has experimented with a number of species, with some interesting results.* These observations have been recorded by Beddard in his Animal Coloration, together with other notes on the effects of food upon color. Canaries have generally been experimented upon, the unfledged birds being fed with food mixed with the pepper. Beddard reports Dr. Sauermann's experiments as follows:† "Cayenne pepper, of course, is a composite substance, from which a number of chemical substances can be extracted; the red

---

* Archiv. Anatomie und Physiol., 1889; Physiol., Abtheil., 543.

† l. c., p. 54.

colour is caused by a pigment termed capsicin, which can be separated from the pepper; and it might easily be supposed that the change from yellow to red in the feathers of the canary was simply caused by a transference of the pigment * * * but Dr. Sauermann has shown that it is not so. Yellow-coloured canaries were not in the very slightest degree affected by the pigment alone; but, curiously enough, parti-coloured birds did react,—the brown parts of the feathers becoming distinctly lighter in hue. It is a fatty substance (triolein) which appears to convey the pigment, and produce thus a changing of the colour from yellow to red; and further experiments were made with other birds, showing that it is not only canaries which are influenced by their food in this way. Some white fowls, belonging to a special breed, showed traces of yellow among the feathers after feeding with cayenne; but in this case there were not racial but individual differences in susceptibility, for all the specimens of the birds experimented with did not react to the stimulus.

A similar series of experiments was made with some other colours: it was found with carmine that the yellow colour was destroyed and the birds became white. This unexpected effect is explained by the fact that a mixture of violet and yellow produces white. The proof that the fatty constituent, triolein, plays the chief part in the colouring of the feathers may perhaps help to explain the very singular fact that the Amazon parrots change from green to yellow when fed upon the fat of certain fishes.

With regard to the white fowls referred to, the experiments made by Dr. Sauermann were particularly interesting. The interest lies in the fact that the pigment was not absorbed equally by all the feathers; only special tracts were affected; the breast feathers, for instance, became red, while the head remained white. It is therefore quite credible that in a state of nature partial alteration of colour may be produced by a change of diet."

It is difficult to say whether the change in color of the caged housefinch *(Carpodacus mexicanus frontalis)* from red to yellow is due principally to a change in food, or to the confinement and general deterioration of the system from captivity. Food, nevertheless, plays some part in this, as well as in many changes in the color of birds in a wild state, which, with the present lack of experimental data, are far too complex even to be surmised.

With regard to the influence of temperature, moisture and sunlight, however, it is less difficult to arrive at some general conclusions. Mr. Frank M. Chapman, I believe, first directed my attention to one of the most obvious and immediate influences of the environment upon color. In certain species a mark is left upon each primary indicating where the superimposed feather covered it. In the grackles *(Quiscalus)* each primary is a dark brown except the tip which is not covered by the overlying feather, this part being glossy black. So exactly is the boundary defined that the rounded edge of the overlying feather is clearly marked. There can be no possible doubt that this marking is due to the direct influence of the environment, and it seems not improbable that sunlight has been the agent. An analogous, though in a way quite different, effect is shown on the wing feathers of the blue bird *(Sialia)*. Here also each primary leaves its impression upon the next feather, but the concealed part, instead of being duller, is brighter blue, the exposed tip being dull brownish.

It is a very important, and, at the same time, a very difficult matter to determine just what is the effect of sunlight upon pigmentation. By some it has been argued that sunlight favors the deposition of pigment, and has been instrumental in the production of the brilliant colors of tropical birds. Others, on the contrary, maintain that the effect of sunlight is to bleach the plumage, and that the pallor of desert forms has been thus induced. No one, so far as I know, has had the temerity to advocate that both these apparently antagonistic views may be correct, and yet an impartial consideration of the matter seems to force us to this position. Mr. Beddard has discussed in a very fair and unprejudiced manner the influence of light upon pigmentation.* He has given a number of examples showing that light frequently does not produce more brilliant coloration, and that animals living in the darkness may lose their color from causes other than absence of light, but he has also adduced a number of cases in which the color was undeniably due more or less completely to light. Thus he says: "As a general rule, those insects whose pupæ are exposed are brighter in color than those insects whose pupæ are concealed, either in the ground or in a dense cocoon." He mentions the larva of a tiger beetle *(Cicindela campestris)*, "which lives in a hole, from which its head and thorax alone protrude; and these are of the same green as the perfect insect, while the rest of the body is of the usual whitish yellow of a grub" (Andrew Murray, Disguises of Nature, p. 9), and adds: "Here light may have been influential in distinguishing the two halves of the body." Perhaps the best instances of the influence of light upon pigmentation are the experiments of Cunningham upon young flounders, which developed pigment upon the white under side of the body when placed in an aquarium with mirrors on the bottom, and Poulton's instance of the pale cave-dwelling amphibian, Proteus, which became gradually darker

---

* l. c. pp. 61–70.

after being removed into the light. The very general absence of color in cave-dwelling animals is itself a very strong argument in favor of the influence of light in developing pigment. "What we do find," says Beddard, in commenting upon the argument that the lack of pigment in cave-dwelling forms is due simply to the need for color being obviated, "is a uniform absence of pigment, which is highly suggestive of a direct action of the environment—and an environment obviously different from that which has caused or permitted the bright and varied coloration of deep-sea animals."

Mr. S. W. Garman published in the Proceedings of the American Association for the Advancement of Science in 1877, * a paper on Variation in the Colors of Animals, in which he advocated a view which appears in direct opposition to the evidence above adduced—viz.: that the pale colors of animals are produced by the bleaching power "exerted by the confusing blending prismatic reflection of sands and snows," etc. This law of the bleaching power of reflected light he considers as the universal cause of pale or white coloration, accounting for the pallor of desert forms and the white or pale color of the underparts of so many animals. Besides the evidence above adduced which goes to negative this view I need only to call attention to the white-bellied and violet-green swallows which have such pure white breasts and yet spend nearly all their time in the free open air far above any influence of reflected light, and the fish crow and raven which live along the sands of the sea shore where the reflected light is full as bright as on the desert, and yet show not the slightest intimation that they have any idea of relinquishing their proverbial garb of black.

Again, it will be found that the abdomen is far more frequently white than the breast—in fact the color gen-

---

* Vol. xxv, pp. 187-204.

erally grows paler from the breast towards the tail—but the abdomen is more protected from the direct influence of reflected light than the breast, because, especially during the middle of the day when the influence would be strongest, it would be protected by the bird's shadow. This is supposing that the bird is habitually upon the ground, but if it were habitually among the trees or bushes it would be protected by them.

I would accordingly suggest the very opposite view of the white color of the under parts of animals. We have seen that color is a normal product of growth, which would at first be thrown out upon the integument in a perfectly indiscriminate manner. The influence of sunlight would, in the course of time, tend to attract the greater amount of pigment to that part of the body most exposed to the light. Thus there are many instances where two pigments have apparently combined upon the back, and perhaps the upper part of the breast, while only one, and that one not very intense, remained upon the belly, often fading into pure white on the under tail coverts. This state of affairs may be frequently found among the warblers, where the back is a dark olive green, and the breast a light yellow. Plates XVIII and XIX of the colors of the genus Dendroica well illustrate this point, for it will be noticed how uniformly the abdomen and under tail coverts are pale colored and unmarked. According to this view there would be a general tendency for the bulk of pigment to be directed to that part of the body which received the most sunlight, but if it happened that some advantage, either from recognition, protection, or sexual adornment, was to be gained by retaining patches of color upon the breast, or by having the breast uniformly colored some dark shade, natural selection would counteract the influence of sunlight.

But how, it may be asked, can this view be reconciled with the undoubted bleaching effect of sunlight upon desert forms? It seems to be a general rule that dryness as well as heat is necessary to produce the pallor. Sea coast species are generally darker than inland forms, even among such as the savanna sparrows (Ammodramus) which live much of the time on the sands of the beach. However, it may be said that moisture in the air means much foggy and cloudy weather when the sunlight is obscured, while dryness means that the sun is constantly shining. One fact which should be borne in mind is that the moist sea coast climate does not produce more brilliant colors, but rather darker and duller hues than the normal. The facts seem to show that the maximum of sunlight and moisture together favors the development of the most pure and brilliant coloration, sunlight without moisture has a tendency to burn and bleach, while moisture without sunlight produces darker and duller colors. Nor need this be particularly difficult to understand. The intense heat and dryness of the desert might well leave the plumage in a state bordering on pathological, so drying and parching the feathers that pigment could not well be deposited. The heat and dryness may also have an influence upon the structure of the feather itself, leaving it in a condition analogous to the "worn" plumage at the close of the breeding season, which is much paler. This burnt or worn appearance of the feathers of desert birds may often be noticed. On the other hand, moisture alone might well have a direct influence on the pigment cells in making them darker, or it might be a condition favorable to the deposition of more pigment.

A complete discussion of the relation between climate and color demands a few preliminary remarks on the general principles of the geographical distribution of animals, particularly with regard to the land birds of North America.

GEOGRAPHICAL DISTRIBUTION AS A FACTOR IN THE EVOLUTION OF COLORS.

Inasmuch as the geographical distribution of life bears such an important relation to the evolution of species, a knowledge of the past and present distribution of birds must throw some light upon the subject of the evolution of their colors. It will accordingly be necessary to briefly glance at the distribution of birds in North America, and to note the bearing of the question upon their colors.

The land mass which now forms Europe and Asia was, according to Wallace, the original home of the primitive vertebrates, whence, at a slightly later period, they migrated to North America. Spreading southward over South America and Australia they were very early cut off from North America, and the fauna of Australia has never since intermingled with any other. At one or two successive later periods communication between North and South America was established, resulting in a very considerable intermingling of forms. The present fauna of North America, as Dr. C. Hart Merriam has shown, is derived from two centers, a northern and southern.* According to his second provisional biogeographic map of North America † the principle life areas are as follows: treeless area extending across the northern edge of Alaska, southeast to the southern border of Hudson's Bay, and thence across a narrow strip of the northern coast to the Atlantic; a Boreal area occupying nearly all of British Columbia and extending

---

* cf. North American Fauna, No. 3.

† The Geographic Distribution of Life in North America, Proc. Biol. Soc., Wash. vii.

south on the Sierra Nevada Mountains irregularly into northern Lower California, upon the Rocky Mountains irregularly into Arizona and New Mexico and in more isolated spots of the Alleghany Mountains south to Tennessee and North Carolina; the Upper Sonoran area lying in the center of the continent including the Great Basin region, the upper prairie and Mississippi Valley district, and touching both the Atlantic and Pacific in restricted areas; the Lower Sonoran area, comprising the south Atlantic and Gulf States the greater part of Mexico and Lower California; the Lower Californian area, occupying only the Cape region; and the Tropical area extending from Central America north along both coasts of Mexico, and the southern extremity of Florida, and including the West Indies. Between the Boreal and Sonoran areas extends a transition region in which the life is typical neither of the northern nor southern area, but rather a more or less complete intermingling of the two.

The birds of the Boreal area are similar to the birds of the northern Palæarctic region, becoming practically identical in the circumpolar zone, and progressively distinct southward. There seems to be little doubt that the birds of this northern region are, for the most part, the descendents of the original land birds of this district. Especially is this the case with such forms as are typical of the Boreal area. The birds of the Sonoran area, while originally descended from the same stock, present forms which have probably come from the Neotropical region since the decline of the ice age. It is possible, indeed, that the upper and lower Sonoran areas represent two separate invasions from the south. The tropical fauna of North America is, in all probability, comparatively speaking, a very recent feature.

Wallace furnishes the following list of Boreal genera of birds "which have as much right to be considered typically Nearctic as Palæarctic:"[*]

1. Regulus,
2. Certhia,
3. Sitta,
4. Parus,
5. Lophophanes,
6. Lanius,
7. Perisoreus,
8. Pica,
9. Corvus,
10. *Ampelis,*
11. Loxia,
12. Pinicola,
13. Linota,
14. *Passerella.*
15. *Leucosticte,*
16. *Euspiza,*
17. *Plectrophanes,*
18. Tetro,
19. Lagopus,
20. *Nyctala,*
21. *Archibuteo,*
22. Haliæetus.

Mr. Wallace's list of typical Nearctic genera of land birds consists chiefly of Boreal forms. This is to be accounted for by the fact that the Boreal area contains the most primitive Neotropical birds and consequently the most typical genera. The list is as follows:

1. Oroscoptes,
2. Harporhynchus,
3. Sialia,
4. Chamæa,
5. Catherpes,
6. Salpinctes,
7. Psaltriparus,
8. Auriparus,
9. Gymnokitta,
10. Picicorvus,
11. Mniotilta,
12. Oporornis,
13. Icteria,
14. Helmintherus,
15. Helminthophaga,
16. Myiodioctes,
17. Phænopepla,
18. Xanthocephalus,
19. Scolecophagus,
20. Pipilo,
21. Junco,
22. Melospiza,
23. Spizella,
24. Passerculus,
25. Poœcetes,
26. Ammodramus,
27. Cyanospiza,
28. Pyrrhuloxia,
29. Calamospiza,
30. Chondestes,
31. Centronyx,
32. Neocorys,
33. Empidias,
34. Sphyrapicus,
35. Hylatomus,
36. Trochilus,
37. Atthis,
38. Ectopistes,
39. Centrocercus,
40. Pediocœtes,
41. Cupidonia,

? Ortyx,

42. Oreortyx,
43. Lophortyx,
44. Callipepla,
45. Cyrtonyx,
46. Meleagris,
47. Micrathene.

Taking these two lists as a whole, it is surprising what a lack of brilliant and diversified color they present. There are some notable exceptions, to be sure, but they are very few. Regulus is adorned with a coronet of flame or scarlet, Ampelis from the far north displays its beautifully varied, although not gaudy, attire; Sialia tries to appear unassuming in luxurious blue; Oporornis,

---

[*] Geographical Distribution of Animals, ii, p. 119.

Icteria and Sylvania (Myiodioctes) make the northern woods and swamps gay with their parti-colored attire, while Dendroica, which should have been included in the list, is still more varied and resplendent in its dress; to say nothing of the Trochilidæ or the beautiful partridges of the west—Oreortyx, Callipepla, and the rest. The Trochilidæ may be excluded from this list as unquestionably of Neotropical origin, leaving only two or three of the warblers in the list of really brilliant colored species representative of the Nearctic region. Furthermore, it is noticeable that with the exception of the blackbirds and humming-birds, irridescent or metallic colors are almost wanting.

It thus becomes apparent that there is some general connection between the geographical distribution and color of birds. The species found in the arctics are, for the most part, white in color, those which take their origin in the north temperate zone are to a large extent plainly colored, while the brilliant species have apparently nearly always originated in the tropics, In the above lists of Nearctic genera another fact is noticeable, viz.: The large number of birds marked with streaks. Such, for example, are Harporhynchus, Certhia, Mniotilta, Passerella, Leucosticte, Melospiza, Ammodramus, Poœcetes, etc. Reasons have been given for considering this style of coloration more primitive than any other. Assuming this to be true, it is a curious circumstance that the oldest stock of birds should be the least specialized in their colors. This does not seem so surprising, however, when we consider the disadvantages under which they have lived as compared with their southern allies. One of the greatest has been an inauspicious climate. The cold of the glacial period in particular must have made food very scarce and competition very keen, so that all the energy of the bird was directed to making a living and maintaining the species, without any great regard to progress in respect to beauty. Looking at it broadly, the genial climate and abundance of food in the tropics has afforded a vast amount of surplus energy to be expended, or favored katabolism, while the cold climate and comparative scarcity of food in the north has demanded a constant effort to accumulate enough energy to preserve the vitality of the species, so an anabolic state of life has prevailed.

The birds of the tropics are, as Wallace has shown, by no means universally brilliantly colored.* Indeed, he questions if the proportion of brightly colored species is very much greater than in more temperate regions. This is due to the fact that bird life is so much more profuse in these regions and there are accordingly so many more brightly colored species here than in other parts of the earth, that we are accustomed to think of them all as being of variegated plumage. Notice the enormous family of Dendrocolaptidæ in South America, however, in which no bright tints are developed. Still, granting all this, the fact remains, that the greatest variety and brilliancy of color occurs in the tropics while forms characteristic of the north are seldom brightly colored, and perhaps never arrayed in the splendor of many tropical species.

Mr. Frank Beddard alludes to some more special instances of the relation between color and locality in his work on Animal Coloration.† He summarises Dr. L. Camerano's system of geographical colors,‡ as follows: "The Palæarctic region—that is, Europe and Northern Asia—has as prevailing tints grey, white, yellow, and black; in Africa yellow and brown are most abundant;

---

* cf. Tropical Nature.

† pp. 44–47.

‡ Zoologische Anzeiger, 1884, p. 341.

green and red are the prevailing tints of the Neotropical region (Central and South America), yellow and red of the Indian. Australia is to be distinguished from the rest by the great abundance of black animals."

Mr. Beddard adds: "A closer scrutiny of many of the above instances and of others which seem to indicate some connection between locality and colour, will probably show that other causes are probably responsible for the colour changes." He, however, gives a number of examples in which there appears to be some definite relation between a locality and a particular color. The most remarkable instance is that of a forest in southern Brazil, where "Dr. Seitz found a perfectly circumscribed region in which the insects were almost entirely blue; a few miles away from this locality the insects were red, yellow—any color but blue; but in the particular locality blue was so characteristic a tint, that out of twenty butterflies ten were entirely blue and the remaining ten partially blue." Another remarkable instance which he records is that of a butterfly found in South America, which is almost identical in color with an entirely distinct European form. Protective mimicry is in this case precluded by the fact that the two genera have always been restricted to the localities in which they are at present found. In commenting on this, Mr. Beddard says: "We see here a particular type recurring in regions widely separated, which may be reasonably supposed to be due to similar environmental conditions." Whether or not this easy explanation is sufficient to account for the phenomena, a parallel, but more remarkable case can be adduced which certainly cannot be so simply explained. The meadow lark of North America *(Sturnella magna)* is a very distinctively marked bird with its bright yellow breast, black crescentic throat patch, streaked flanks and brown streaked back, with a dark double line down the top of the head. Equally well marked is the South American *Sturnella defilippii*, in which the yellow is replaced by rose color. While at the National Museum, Mr. Ridgway handed me a bird which at first glance was unhesitatingly pronounced a meadow lark, so exactly did its colors match those of our bird. An inspection of the bill and feet, however, showed that it was structurally entirely unlike Sturnella. It was an African pipit *(Macronyx croceus)*. Still more remarkable is the fact that another African species *(Macronyx ameliæ)* is colored like the South American Sturnella.*

Surely no one would be rash enough to attribute this remarkable correspondence of colors and markings to environmental influences! It would be better to say that it was purely accidental or else confess complete ignorance on the point. To attribute such instances as this purely to environmental influences is to forget that, as Dr. Schurmann has said, every modification in an organism depends primarily upon the nature of the organism itself, which reacts upon its environment. Even if we granted, in this instance, that the environmental conditions in America which produced the two species of Sturnella were exactly reduplicated in the case of the two African species of Macronyx, still the same colors would not have been produced unless the two sets of species were also precisely alike in their respective constitutions—all of which is too great a tax upon our credulity. It would be far more easy to believe that, as Prof. Cope has suggested, a species might retain its specific character and yet change its generic type. It would then be merely necessary to assume that two species were evolved and afterwards separated in their distribution. A change in habits or environment might

---

* Recorded by Dr. L. Stejneger. Riverside Natural History, iv, p. 488.

then produce a divergence in the character of the bill and feet of the two species without altering their colors. Incomplete and unsatisfactory as this explanation certainly is, it is merely introduced to show that it is not absolutely necessary to assume so improbable an hypothesis as a definite complicated coloration being painted on, so to speak, by the environment.

Mr. Ridgway, in 1873, called attention to the relation between color and geographical distribution in North American birds.* He showed that certain species having a wide geographical range varied in one of two ways, either in a tendency towards melanism "which may be either an increase in the intensity of color or in the extent, of the black parts of the plumage," or in a tendency towards greater brightness or increase in the extent (hyperchromism), of one of the three primary colors, red, blue, or yellow. This tendency towards melanism and hyperchromism increases towards the equator and towards the Pacific Coast, but with red the color increases in intensity towards the tropics and in amount towards the Pacific. Mr. Ridgway calls especial attention to the different races of the Arizona goldfinch *(Spinus psaltria)*, as illustrating the principle of a tendency toward melanism as the tropics are approached. As this is an instance of unusual interest from the completeness and uniformity in the links of progression, I have figured three of the races (Plate VII). The typical race of the species *(S. psaltria)*, is the one occupying the northern-most limit of the range, north to about latitude 40° The back is in this form plain olive green with a cap of black confined to the top of the head, and with the wings and tail a dark brownish. This race shades

---

* Am. Journ. Science and Arts, iii, Ser., Vol. iv, pp. 454–460, Vol. v, pp. 39–44.

by insensible gradations into the one next south of it *(S. psaltria arizonæ)*, found in New Nexico, Arizona and northern Mexico in which the black on the head is somewhat extended, the shoulders have become black and mottlings of black have appeared in the back. Continuing south through Mexico the amount of black on the back steadily increases, the rump patch being the last to relinquish the olive color; "the bird now is var. *Mexicana*, and continues with nearly the same characteristics south to Costa Rica and Panama, from which latter countries we find specimens in which the black is often appreciably more intense and lustrous than in those from Mexico. These three forms all have white on the tail; but in specimens from New Granada, and occasionally in those from Panama, there is usually a total absence of white marks on the tail, or else they are greatly reduced in size." Perhaps the most remarkable thing about this variation towards black, which bears such a direct and obvious relation to the changes in latitude, and hence of climate, is the fact that the female remains almost or quite the same through all the changes of the male.

The following is a possible line of explanation of this state of affairs: the black pigment was first present in the system of the bird in conjunction with the yellow, giving rise to an olive green color. It was set apart in a limited area upon the head by the action of sexual selection or for sexual recognition. Then, the tendency to the production of pure black pigment having once been originated, would be favored by katabolism, which would increase under the more abundant food and higher temperature of the tropics. A specimen of *S. psaltria arizonæ* was taken by Mr. W. Otto Emerson at Haywards, Alameda County, some years since, while last summer I saw in Berkeley, Alameda County, a goldfinch in company with a flock of *S. psaltria*, which had the back almost, if not entirely, black. It is probable that these exceptional instances are not stragglers from the south, for the bird is generally a resident wherever found, but rather an unusual manifestation of the melanism which normally only asserts itself in a warmer climate.

Mr. Ridgway also mentions the following instances of melanism toward the south: "*Myiarchus Lawrencii*, which, starting with a grayish brown crown in the northern examples (var. *Lawrencii)* gradually assumes a blacker and blacker crown, as we trace it southward, first through var. *nigricapillus* (Costa Rica and Panama), and finally ending in var. *nigriceps* (Ecuador), which has the crown deep black. *Sayornis nigricans* from California and Northern Mexico, has the crissum pure white; Mirador specimens have it clouded with dusky, while in Costa Rica specimens (var. *aquaticus)*, it is entirely blackish, only the middle of the abdomen being white. * * * The same law as regards the Pacific province of North America is made evident by the well-known cases of *Picus villosus* var. *Harrisii*, *P. pubescens* var. *Gairdneri*, *Sphyrapicus varius* var. *ruber*, the Northwest coast forms of *Falco peregrinus*, *F. Columbarius*, *Bubo Virginianus*, *Scops asio*, and numerous other similarly affected species."

Mr. Ridgway mentions *Xanthoura luxuosa* and var. *guatemalensis*, and the different races of *Geothlypis* as examples of intensification in yellow toward the tropics. In Geothlypis the yellow not only becomes intensified but extended upon the white of the belly both in the warm moist climate of the Mississippi Valley and Gulf States and in Mexico. *Sylvania pusilla pileolata* and *Helminthophila celata lutescens* are illustrations of the intensification of yellow in the Pacific provinces.

Cardinalis virginianus and *Piranga æstiva* become much more intensely red toward Mexico and Central America. The house finch *(Carpodacus mexicanus frontalis)* is an especially instructive instance with respect to the spreading and intensification of the red color. Toward the south *(C. mexicanus)* the red becomes intense, but sharply restricted in extent. In the western United States it is less intense but more diffused, while upon Guadalupe Island *(C. amplus)* it is both more intense and more diffused, but the most deeply colored portion is restricted to the same areas as in *C. mexicanus*.

The transformations in the genus Sphyrapicus are of so much interest that I have figured the heads of the three forms, arranging them in a regular series of increasing red (Plate XV). It is to be observed that the series is a double one—from young to adult female, to adult male, increasing in redness, and from east to west the same. The upper map in Plate IX. indicates roughly the areas occupied by the three forms, A being the distribution of the *S. varius* group and B of *S. ruber*. In spite of the fact that these two forms are classed as distinct species, there can be no doubt that they are climatic modifications of the same stock. The young of *S. varius* and *S. varius nuchalis* are mottled brown, and with the colored areas of the adult male white. This is doubtless the plumage of the primitive bird from which the genus arose. The next stage of differentiation is shown in fig. 2 of the adult female in winter. The acquisition of a black plumage, not very different from the present coloration of Dryobates, may have been due to sexual selection, to a surplus of pigment in the system, to direct climatic influence, or to the need of recognition markings. However this may be, the brown color of the young would seem to indicate the presence of red pigment in the system in conjunction with the black. This is deposited, in small quantities at first, upon the white throat and upon the head, being increased by sexual selection to the stage now shown by the adult female of *S. varius* in breeding plumage (fig. 3). The element of climate is next brought in conpicuously to supplement the work of sexual selection. The birds in the Rocky Mountain district have the red considerably extended. Thus fig. 4 shows the female of *S. varius nuchalis*, in which the red has spread very considerably. On comparing the breeding plumage of the adult males of the two races (figs. 5 and 6), it will be found that a corresponding difference in the amount of red exists in them also. The climax is reached in the Pacific Coast form, in which the red has become almost complete upon the head and breast.

As an instance of an increase in blue from north to south, Mr. Ridgway cites the blue jays of the genus Cyanocitta. The modifications of this genus in North America are so interesting as regards the relation of color to geographical distribution, that they must be considered in some detail. The lower map on Plate X. is a conventional representation of the areas occupied by the different forms of the group. There are but two species, *C. cristata* (A) and *C. stelleri* (B), occupying respectively the eastern and western half of the North American continent. Coming from the same stock, the eastern bird early developed conspicuous white recognition marks on the wing and tail, which are lacking in *C. stelleri* in all its forms. It remained very homogeneous throughout its range, only varying slightly in Florida, where the white on the wings and tail is reduced, probably by direct climatic influence. In the western provinces *C. stelleri* is as variable as *C. cristata* in the east is constant. In the first place, there are two general forms, one occupying the region upon the Pacific Coast, and the other the Rocky Mountains south into

Central America. This latter form is distinguished by the presence of a white spot above the eye, which is wanting in the coast races. It is difficult to understand how climate could have produced this marking, and it seems more proper to regard it as a discriminative character. Toward the north the ranges of the two forms come together, and specimens from this region are intermediate in character. The farther we get away from this neutral ground the more distinctly marked do the characters become, showing the part isolation must play in the matter. Toward the south the white spot becomes successively larger and more distinct, until it reaches its maximum at the southern limit of the species. It is a remarkable fact that this bird is increasing the extent of white in the very region in which *Spinus psaltria* is growing melanistic. Furthermore, the eastern representative of the genus, *C. frontalis*, has the amount of white reduced toward the south, as would be expected. It seems inconsistent to maintain that the increase in the white spot of *C. stelleri* toward the south can be due to the same climatic influence which generally tends to intensify the plumage, and I think some other explanation must be sought. From the map it will be seen that the interior and coast forms intergrade only at their northern limit, and here the distinctive white marking probably originated before the species spread to the south. As it extended southward, it would become successively farther and farther separated from the coast form, and, like the land mollusks of the Hawaiian Islands, would become more and more modified, without regard to climatic influence. There are other changes taking place in these two forms besides the transformation of the white spot. The northern forms, both coast and interior, are darker, with more of black and brown, while the tendency toward the south is to assume a completely blue plumage. This may be accounted for by supposing that the rainy northwest coast region was the original home of the species. The pigment would there be darkened, but as the species spread toward the south the tendency would be not towards darkness so much as intensification and purity, which would result in a complete intense blue plumage at the southern limit of its range. The differences in color between the various forms may be tabulated as follows:

	Variety.	*Forehead.*	*Head.*	*Back.*	*Secondaries and Tail.*
Coast form. No white spot	1. Stelleri	Inconspicuous blue streaks.	Black	Deep black.	Deep Berlin blue.
	2. Frontalis	Conspicuous blue streaks.	Brownish slaty	Brownish slaty.	Deep azure, lighter than above.
Interior form. Post ocular spot present	3. Annectens	Indistinct light blue	Black	Dusky	Very deep Berlin blue.
	4. Macrolopha.	Bluish white	Bluish black	Dark ashy.	Bright blue.
	5. Diademata	Pure white	Bluish black	Dark'r than above, more bluish	Bright blue.
	6. Coronata	Deep blue	Deep blue	Deep blue.	Deep blue.

Mr. J. A. Allen has drawn particular attention to the relation between climate and geographical races, both as to the modifications in the bill, feet and tail, and of color.* He calls attention to the increase in the intensity of color to the southward and also to the "increase in the extent of dusky or black markings at the expense of the intervening lighter or white ones; or conversely; the reduction in size of white spots and bars." He draws attention to the extreme pallor of desert forms as contrasted with the same species in a moist climate, and says: "This coincidence of bright and pale tints, with the relative humidity of the locality, is certainly suggestive, if not demonstrative, of the relation of cause and effect between these two phenomena, since the same

---

* cf. Boston Soc. Proc., 1872, pp. 15, 212, 219.
Bull. Mus. Comp. Zool. ii, pp. 229, 247.
Am. Jour. Sci. and Arts, xii, 1866. Baird on Geographical races.

rule is traceable over large portions, at least, of the Old World."

One of the very best illustrations of the influence of climate upon color is illustrated in Plate XIII. The song sparrow *(Melospiza fasciata)* is a resident of all the temperate portions of the North American continent. The plate shows the general color effect of the back of each of the various forms into which it divides in the various portions of its range. In the Eastern States the color is normal, being neither excessively dark nor light. In the arid regions of the great plains and Rocky Mountains it is pale *(M. fasciata montana)*, while in the Colorado desert region of Arizona it is very small, and the colors peculiarly light *(M. fasciata fallax)*. Coming to the Pacific Coast, the darkest forms are found, *M. fasciata samuelis* and *heermanni* in California, the dark rusty form *M. fasciata guttata* in Oregon and Washington, and the darkest of all, *M. fasciata rufina*, along the northwest coast of British America. It will be noted that these various races coincide perfectly with the regions of greatest and least rainfall, the palest forms being found on the hot arid deserts and the darkest in the region of most constant rains. It may be thought a singular contradiction that in the genus Sphyrapicus the bird of the Rocky Mountain district is darker than the eastern form, while in the genus Melospiza, the variety inhabiting this district is paler. This may be understood, I think, by taking into account the difference in habits of the two species. Sphyrapicus inhabits the forests exclusively, and in the mountainous districts would resort to the groves of pine, etc. Melospiza, on the contrary, is confined to underbrush, and in the Rocky Mountain district would most frequently live in the sagebrush country, which is dry and comparatively exposed to the sun's rays.

In the Aleutian Islands a distinct species of song-sparrow *(M. cinerea)* is found, which is larger and grayer than any of the others. Mr. Ridgway thinks that if material could be had from the intervening district it would prove to intergrade with *M. fasciata rufina*, but whether this be so or not, it is perfectly evident that the form is a comparatively recent off-shoot from the same stock as the others. On comparing the extreme forms of this species it is difficult to believe them so closely related, yet every stage of intergradation between them can be shown.

On Plates IX to XII, inclusive, I have represented in a conventional manner the distribution of a number of forms, which are of interest as showing the effect of environmental influences. As a general rule, a closely related group, resident over the North American continent, divides into two species, and then subdivides into several races. Mr. Seebohm, in his "Geographical Distribution of the Charadriidæ," makes the isolation incident to the successive glacial epochs an important factor in the establishment of generic, specific and varietal characters. The fact that in a number of instances two tolerably distinct species of the same genus are found upon this continent, one to the east and the other to the west of the Rocky Mountains, would seem to argue that the genus was originally one homogeneous species found in the northern part of the continent, which was pushed south by the invasion of the ice, and kept apart by an ice cap following south along the highest mountain range of the continent. This may be the explanation of the two species of Cyanocitta and of Pipilo, for instance. The western country is much more diversified in topography and climate than the eastern, so it is but natural that the western species would become modified into more races than the eastern.

The screech owl (*Megascops asio*) is a form of especial interest, from the fact that it is intermediate between such groups as the song-sparrows (Melospiza) and horned larks (Otocoris), in which there is but one species in the east and west, and such as the blue jays (Cyanocitta) in which the Rocky Mountains divide the group into two species. In the *Megascops asio* group there is but the one species, but east of the Rocky Mountains it is dichromatic, and west of them monochromatic. If, either from the action of natural selection or from some constitutional weakness, the gray phase should die out in the east, it is obvious what very different species would be found on the two sides of the mountains. The following table, based on Ridgway's Manual, shows the influence climate has had on the different forms. It is to be used in connection with Plate X.

Eastern (dichromatic)	1. *M. asio*, normal.
	2. *floridanus*, darker, markings more numerous and extended.
	3. *maccallii*, darker than 1, light mottlings coarser and more conspicuous.
Western (monochromatic)	4. *trichopsis*, nearly pure ash gray and black. Bars on lower parts numerous and narrow.
	5. *bendirei* mostly grayish brown, marks below fewer and coarser than in 4.
	6. *kennicottii*, plumage tending toward a deep umber brownish.
	7. *maxwelliæ*, "very light colored, white largely predominating on lower parts."

The towhees (Pipilo), are of peculiar interest in the study of the evolution of color, but at present I will only allude to two species which are influenced by climatic agencies—*P. erythrophthalmus* and *P. maculatus*. These two species are so very much alike in their general colors that at first sight they hardly seem separable as distinct species. The females, however, are unlike in color, in the former species being black where the latter are brown. In the latter species, moreover, the wing coverts, scapulars and back are streaked with white which is wanting in the former. In spite of these constant specific distinctions, certain characters vary from one species to the other in an unbroken succession. Thus Plate VIII shows the outer tail feathers of three forms, and the uniformity of the reduction in the white from the eastern species through the two varieties of the western is very noticeable. This reduction in white is most pronounced on the northwest coast and is undoubtedly due to the direct action of the environment, being paralleled to a certain extent by the Florida race *(P. erythrophthalmus alleni)*. Reference to the lower map on Plate IX will show how the two species were probably marked off by the Rocky Mountain ice cap, so that the white streaks on the back of the western species may be due solely to the influences of geographical isolation and the indirect effects of a different environment. They would be of use as recognition marks and so be encouraged by natural selection.

The different races of the two species have been modified principally by climatic influences, *P. maculatus arcticus* (B 2) of the Great Plains being the form with the maximum of white markings, *P. maculatus megalonyx* (3) having the white markings much restricted, and *P. maculatus oregonus* (4) of the Northwest Coast region with the white markings lacking or much restricted. The fact that the Mexican form of the genus is so light colored is not easy to explain. The following hypothesis may throw some light upon it, however. The Pipilos were a northerly genus probably with no white on the back, and simply with the white recognition marks at the tip of the tail. They were crowded south by the ice into two districts, one to the east, the other to the west of the Rocky Mountains. Those on the western side developed into a new race, the dryness of the climate encouraging the production of white markings. Later this new species *(P. maculatus arcticus)*, spread to the south and west. Toward the west it became successively darker as it approached the moist coast district, or if there was free intercrossing for a time the coast birds would mingle with the interior race tending to make it darker. In the interior of Mexico, however, the birds probably inhabit a dry arid region and have consequently not become conspicuously darker than the form from which they were descended.

In the species so far considered there has been a tolerably uniform east and west isolation, but in many instances the segregation is far more complex, there being an east and west isolation of species and a north and south isolation of varieties, or, conversely, a north and south isolation of species and an east and west of varieties. Both these forms are illustrated in the genus Dryobates as shown in Plate XI. The different races of the *D. villosus* group all belong to the same species but the forms east of the Rocky Mountains have the wing coverts and tertials conspicuously spotted with white, these marks being largely or wholly lacking in the western and Central American races. It will be noted that this is the converse of the relations in the genus Pipilo, tending to show apparently that isolation, together with various indirect effects rather than the direct influence of the environment has been instrumental in producing the difference. The eastern and western forms bear a relation to one another midway between species, such as in Pipilo, and varieties such as *Sphyrapicus varius* and *nuchalis*, being much more distinctly differentiated than the north and south races. Indeed, in group A the differences appear to be in size rather than in color, with the exception of the insular form *D. villosus maynardi* which differs in having the lores white instead of black—the result of isolation. The Central American form, *D. villosus jardinii*, is characterized by the smoky brown color of the under parts which replaces the white or gray of the northern race. This is probably a climatic influence corresponding to the tropical tendency towards melanism in other species.

The lower map of Plate XII shows the distribution of the barred members of the genus Dryobates—the "ladder backs." They are all apparently forms of Sonoran origin, dividing into three species and a number of races. The distinctions, both specific and racial, it would seem, are due to isolation rather than to any direct environmental influence. The forms thus far considered have been such as display trifling varietal or specific distinctions which are due wholly or in large measure to their geographical distribution—either to the direct influence of the environment or to the indirect influence of environment together with segregation. There are certain closely related species or varieties, on the other hand, whose ranges are to a greater or less degree coincident, or overlap. Sometimes, as with *Ammodramus sandwichensis bryanti* and *alaudinus* it is simply in the winter distribution that they are together, but in a number of cases it is the breeding range which coincides. If the forms are tolerably distinct species it is not impossible that they have been differentiated through geographical segregation and afterwards come together, but when the races are not very strongly marked, or occupy a large territory in common this hypothesis will hardly be a satisfactory one. The following is a list of such species and varieties which occupy territory in common:

Bubo virginianus and *B. mexicanus.*
Chordeiles virginianus henryi and *C. texensis.*

Dryobates scalaris and *D. stricklandi.*
Dryobates scalaris bairdi and *D. arizonæ.*
Dryobates villosus leucomelas and *D. pubescens.*
Dryobates villosus harrisii and *D. pubescens gairdnerii.*
Tyrannus verticalis and *T. vociferans.*
Aphelocoma sumichrasti and *A. sieberii.*
Agelaius gubernator, A. phœniceus and *A. tricolor.*
Carpodacus purpureus californicus and *C. cassini.*
Calcarius lapponicus and *C. pictus.*
Zonotrichia leucophrys and *Z. leucophrys gambeli.*
Spizella pallida and *S. breweri.*
Junco caniceps and *J. cinereus dorsalis.*
Junco caniceps and *J. annectens.*
Amphispiza bilineata, A. belli and *A. belli nevadensis.*
Peucæa mexicana and *P. cassini.*
Passerella iliaca unalaschcensis and *P. iliaca megarhyncha.*
Pipilo fuscus mesoleucus and *P. aberti.*
Megascops flammeolus, M. asio maccallii and *M. trichopsis.*
Thryothorus ludovicianus and *T. bewickii.*

Plate XII shows the distribution of two of these overlapping groups. The different races of the great-horned owl *(Bubo virginianus)* follow the usual lines of climatic modification—normal in the eastern states, grayer in the west, very dark on the northwest coast, and almost white in the Arctic regions. *Bubo mexicanus,* a tropical offshoot of the genus, is marked with black stripes instead of dusky bars. It is quite evident that these two species were developed in separate districts and afterwards encroached to a slight degree upon each other's territory. It may be well to point here to an exemplification of the inefficiency of climatic influences as the sole cause of a modification. The ladder-backed group of Dryobates are southern forms of the same stock as the striped species. In the genus Bubo, on the other hand, the northern forms are barred and the southern striped, yet in both these instances geographical distribution must have had a part in the differentiation.

The lower map on Plate XII shows the distribution of the different forms of the nighthawk (Chordeiles). The eastern variety extends northwest to the Pacific Coast, as is the case with a number of eastern species. The western race is, as would be expected, paler, and the Florida and Cuba bird darker—both due to direct environmental influence. The differences between *C. virginianus* and the southern species (B) *C. texensis*, may be due to climatic influence entirely, the overlapping of the ranges being subsequent; but it seems more probable that the characteristic wing markings of this latter species are discriminative marks developed to distinguish two diverging forms occupying the same district.

The difference between the hairy and downy woodpecker groups *(Dryobates villosus* and *D. pubescens)* cannot, it would seem, have been causedby geographical isolation. To determine positively which of the other forms of isolation as tabulated by Gulick has been operative in any particular instance is, in the present state of our knowledge, impossible. The red-winged black birds (Agelaius) afford another instance of closely related species which do not owe their differentiation to climatic or geographical influences. *A. phœniceus*, *A. gubernator* and *A. tricolor*, all occur in California, the two latter species being confined to the Pacific Coast. Plate XIV shows the principal mark of distinction between these three species in the adult male. These differences are hardly striking enough to be of great use as discriminative marks, particularly between *A. phœniceus* and *A. gubernator*, and would seem to be the result of some form of isolation, rather than of selection. In the case of the king birds, *Tyrannus verticalis* and *T. vociferans*, the differences appear to be in general climatic, the southern form being darker than the northern, but the ranges of the two species overlap. The distinct white edge to the outer tail feather is an excellent example of a discriminative mark for distinguishing the two very similar races.

In the preceding discussion forms have been considered which are on the very threshold of divergence—species which are either still forming or barely formed. It is seen that in a large number of instances the cause of the first divergence has been the direct action of the environment. In some cases, however, it was impossible to see how the environment could have produced the change, and in these instances the new character was ascribed to spatial segregation, or some other form of geographical isolation. In still other species the geographical environment seems to have little or nothing to do with the variation, since the diverging forms occupy the same territory. Here the factor of sexual isolation and discriminative marks may be called into play, or some other mode of segregation too intricate to be unraveled may be at the bottom of it.

Before taking leave of this branch of our inquiry, one interesting case of direct enviromental influence must be noted. It is of special interest because the direct climatic influence, instead of merely producing varieties, seems to have pushed on, and been the principal, if not the sole, factor in the establishment of species. I refer to the three North American species of crested flycatchers (Myiarchus), the colors of which are shown on Plate VI. The darkest species is found in the Eastern States *(M. crinitus)*, while the palest species, which is nearly identical with it except that the colors are almost completely bleached out *(M. cinerascens)*, inhabits the arid regions of the West. Exactly intermediate in color between these two species is *M. mexicanus* of eastern Mexico.

Having now considered all the factors, which seem to have an influence upon the evolution of the colors of North American birds, a brief application of these principles to the various families and genera must next be attempted.

ORDER GALLINÆ. THE GALLINACEOUS BIRDS.

FAMILY TETRAONIDÆ. The Grouse, Partridges and Quail.

The colors of the North American representatives of this family are in general protective in their nature, although sexual characters are present in certain genera, while some form of recognition marking is almost always found. Black and white are found in every genus, while brown and gray are the principal colors of the group. Red and yellow in an impure form, as reddish brown and ochraceous, occur in nearly all genera, and blue in combination with black or gray in two of them. There are no genera in which bright colors occur.

Genus Colinus. The Bobwhites.

(8)* Adult male more conspicuously colored than female; young with peculiar first plumage.

Colors—Black, white, brown, rufous, ochraceous.

The colors are in the main protective, the black and white markings of the head being characteristic of the group, and probably directive recognition marks. They may very probably be for sexual recognition also, the colors of the female being much less distinctly indicated, the black being replaced by brown, and the white by buff.

Several forms, mostly races; the colors due largely if not

---

*These numbers refer to the table on p. 214.

exclusively to the direct influence of the environment, and varying characteristically from the dark races of Florida and Mexico *(C. virginianus floridanus* and *C. graysoni),* to the pale desert form of southern Arizona *(C. ridgwayi).*

GENUS OREORTYX. MOUNTAIN PARTRIDGES.

(2) Adult male like female; young like some ancestral stage of the adult.

Colors—Black, white, gray, plumbeous, chestnut, ochraceous.

The varied and beautiful markings of this bird were doubtless acquired by the male first, by sexual selection (Epigamic) and afterwards transferred to the female. They may also have been of use as recognition marks. This is particularly the case with the distinct buffy or ochraceous stripe on the inner web of the tertials, which is characteristic not only of this genus but also of Callipepla. The young are much spotted, representing an ancestral stage of plumage which may still be protective, blending with the lights and shadows of the forest.

Two races, darker in the Coast Range, lighter in the Sierra Nevada Mountains, from climatic influence.

GENUS CALLIPEPLA. VALLEY QUAIL.

(8) Adult male more conspicuously colored than female (usually); young with peculiar first plumage.

Colors—Black, white, gray, brown, chestnut, buffy.

The colors in this group are obviously sexual in their nature, being partly for recognition and partly for adornment. The genus is of special interest as showing different stages of differentiation of the sexes. The sexes are alike in *C. squamata*, the degree of specialization of colors being slight, and the general tendency being protective. In fact, both sexes are at about the degree of development of the female *C. californica*, the colors of the male of this form being sexual. Young protectively colored.

GENUS CYRTONYX. MASSENA PARTRIDGE.

(7) Adult male more conspicuously colored than female; young similar to adult female, but colors duller.

Colors—Black, White, brown, rufous, buff, plumbeous.

The colors of the female are protective, of the male for recognition. The Mexican forms, *C. ocellatus* and *C. sallæi*, in which the flanks of the male are respectively rich chestnut varied with black and plumbeous, and "plumbeous, barred and spotted with chestnut," in distinction from *C. montezumæ*, which has no chestnut on the flanks, are probably thus marked for sexual recognition, in distinguishing the three races. The pattern of markings on the head of the male is one of the most unusual and complex among North American birds, and may very probably have originated at the time when Cyrtonyx first separated from Callipepla. It was quite likely a recognition mark exclusively at first, but may have afterwards been accentuated and modified by sexual selection from the mere attractiveness of something odd and grotesque, as Weismann has suggested in commenting on tailless cats. (See *ante*, pp. 96–97.)

GENUS DENDRAGAPAS. THE GROUSE.

(2) Male differing only slightly from female; young with a peculiar first plumage.

Colors—Black, white, slate-gray predominating—some brownish, buffy, etc.

An apparent tendency towards melanism by way of cross barrings is present in this group. Retiring in its habits, this genus has probably had little need for protection, and has in past times had few enemies as shown by its "stolidity or indifference to the presence of man," and the ease with which it may be killed (see Coues' Key, p. 578). Natural selection has consequently had comparatively little to do with modifying its colors, except in supplying the recognition marks of the tail (see *ante*, page 204). Nor has sexual selection had a very important part in modifying the colors, for although the colors of the male are somewhat darker and more sharply cut than in the female, this may be the simple result of katabolism. The colored comb over the eye is, however, unquestionably the result of sexual selection. The cross barrings, however, were probably originally protective in their nature, harmonizing with the lights in the forest or the bark of trees, but they are fast becoming obliterated by the increase in black. This increase would naturally be most marked on the back where the greatest amount of light falls. Young, brown, spotted—protectively marked. The different races are geographically isolated, and have become distinguished by discriminative marks on the tail.

GENUS BONASA. RUFFED GROUSE.

(2) Adult male like female; young like some ancestral stage of adult.

Prevailing colors, brown, reddish, gray, white, black. Colors protective, blending with the ground. Ruff of male sexual. Black and light bars of the tail probably directive marks, assisting in recognition in close flight. Young, spotted, mottled and barred, the latter an inheritance from the adult, the former a retention of an earlier form of plumage. The different races are due to environmental influences, being darkest in the Northwest Coast region and lightest in the Rocky Mountain district.

GENUS LAGOPUS. PTARMIGANS.

(4) Both sexes change with the seasons, in summer plumage differing slightly; young differ slightly from summer plumage of adults.

Prevailing colors, black, white, chestnut, brown.

The remarkable adaptations of this species to a summer and winter environment, brown at the former and pure white at the latter season, are too universally known to need mention. The winter plumage, however, may not be exclusively intended for protection. White feathers are much denser and warmer than colored ones, and, moreover, it is claimed by some, that the intense cold has a direct effect in causing the feathers to turn white. Nevertheless there can be no doubt that protection is one of the chief if not the exclusive object of the white plumage. The different races, and even species, have become modified by geographical isolation. *L. rupestris* is the stock form inhabiting Arctic America in general; *L. rupestris reinhardti*, is found only in Greenland, northern Labrador, etc.; *L. rupestris nelsoni* is restricted to the island of Unalaska, in the Aleutian chain, and *L. rupestris atkensis* to the island of Atkha in the same group, while *L. welchi* is confined to Newfoundland. *L. leucurus* is found upon the Alpine summits of the Rocky Mountains, where it also is effectually isolated, for the birds are resident wherever found. Little differences have thus originated which are of no particular utility, and may not be due even to the action of the environment, but simply to geographical isolation.

GENUS TYMPANUCHUS. PRAIRIE HENS.

(2) Male like female; young like some ancestral stage of the adult.

Prevailing colors, brown, dusky, buff, white.

The colors in this genus are almost entirely protective, the brown stripe below the eye being the only recognition mark. The ruffs and inflatable sacks on sides of neck of male are the only sexual characters, the former having been imperfectly inherited by the female. The colors of the young would seem to indicate that the ancestral form was much more diversified in its markings. The plumage of the young is much spotted with black and white on a ground of light brown, and with a medium stripe of black on the head and patches of dusky on the ear coverts. Three species, formed by geographical isolation.

GENUS PEDIOCÆTES. SHARP-TAILED GROUSE.

(3) Male like female; young like some ancestral stage of the adult.

Prevailing colors, black, white, brown, gray.

Colors protective, the round white spots on the wings for recognition. The sexual characters are in a very undeveloped state, there being no very obvious difference in the colors of the sexes. The young are much spotted, but also barred with black and streaked with white.

GENUS CENTROCERCUS. SAGE GROUSE.

(7) Male differing slightly from female, young like female but with markings less sharply defined.

Prevailing colors, black, white, gray, buffy, brown.

It is difficult to say whether the colors of this bird are of any great utilitarian significance or not. The only recognition mark is an imperfectly defined white crescent on the throat surrounding a patch of black, which is replaced by white in the female. The general colors may be protective, but are not peculiarly so, and this may be another bird which is on the road to the assumption of a melanistic plumage. The young lack the spotted plumage characteristic of so many of the family.

FAMILY PHASIANIDÆ. THE PHEASANTS, TURKEYS, ETC.

This is the family upon which Darwin relied more than any other as a demonstration of the validity of sexual selection in the origination of the ornamental colors of birds. The only genus indigenous to North America, however, is not so peculiarly notable as an ex-example of this principle, although the rich bronzy colors and elaborate appendages of the turkey are not to be despised because they cannot vie with the gorgeous hues of the pheasants of Asia.

GENUS MELEAGRIS. THE TURKEYS.

(7) Male colored like female but tints brighter; young like adult female.

Prevailing colors, brown (metallic), black, white.

Colors largely sexual, but transferred to the female in great measure. The black and white bars on the wing feathers are probably recognition marks. The account of the habits of the turkey given in Wilson's Ornithology, shows many uses for recognition marks. The birds are eminently social in their habits, and from their large size and savory flesh are especially subject to persecution by hawks, owls, lynxes, etc. The young are peculiarly subject to the persecution of the male bird and recognition marks might even be of use to enable the female to keep her brood out of the way of her fierce mate. How well Wilson understood the significance of the colors in sexual selection, and how near he came to anticipating this hypothesis of Darwin is shown in his account of the courtship of turkeys. He says: *" Where the turkeys are numerous, the woods from one end to the other, sometimes for hundreds of miles, resound with this remarkable voice of their wooing, uttered re-

---

* American Ornithology. Jardine's Edition, iii, pp. 238–239.

sponsively from their roosting places. This is continued for about an hour; and, on the rising of the sun, they silently descend from their perches, and the males begin to strut, for the purpose of winning the admiration of their mates.

If the call be given from the ground, the males in the vicinity fly toward the individual, and, whether they perceive her or not, erect and spread their tails, throw the head backwards, distend the comb and wattles, strut pompously, and rustle their wings and body feathers, at the same moment ejecting a puff of air from the lungs. Whilst thus occupied, they occasionally halt to look out for the female, and then resume their strutting and puffing, moving with as much rapidity as the nature of their gait will admit. During this ceremonious approach, the males often encounter each other, and desperate battles ensue, when the conflict is only terminated by the flight or death of the vanquished.

This pugnacious disposition is not to be regarded as accidental, but as resulting from a wise and excellent law of nature, which always studies the good of the species, without regard to the individuals. Did not females prefer the most perfect of their species, and were not the favours of beauty most willingly dispensed to the victorious, feebleness and degeneracy would soon mark the animal creation; but, in consequence of this general rule, the various races of animals are propagated by those individuals who are not only most to be admired for external appearance, but most to be valued for their intrinsic spirit and energy."

The characters separating the different forms appear to be discriminative marks.

FAMILY CRACIDÆ. The Curassows and Guans.

Genus Ortalis. The Chachalacas.

Only one species of this genus comes within our limits, and it has the appearance of being a form which has deteriorated from some more brilliant phase of plumage.

ORDER COLUMBÆ. THE PIGEONS.

FAMILY COLUMBIDÆ. The Pigeons or Doves.

The North American representatives of this family are not so remarkable for the brilliancy of the plumage as is the case with many extralimital species, but the tints are beautifully soft and pleasing, with metallic tints of the less pronounced sort. All the genera, and frequently different species of the same genus, are distinguished by characteristic white and black recognition marks, principally on the wings or tail (see *ante* p. 205), or frequently on both—these being especially important in this family from the fact that the birds generally associate in flocks, often of immense size. I do not think it can be held that the other colors of the family are of any utility whatever. In an old cosmopolitan group of birds like this hereditary tendencies have been fixed for indefinitely long periods, and it may well be that all the North American genera are mere side shoots from the main stem, colored in the prevailing hues of the type—plumbeous, bluish gray, reddish or chestnut, with black and white, and varied with some mild iridescent tints. These colors may doubtless have first been acquired by sexual selection, but what factors may have come into play in the establishment of the colors of the genera found within our limits is far too complex a question to discuss without a knowledge of the entire order. It need only be remarked here that sexual selection in conjunction with isolation, has undoubtedly had a more important role to play than any utilitarian principle. As is generally the case with long established groups, the characters of the male have been generally either completely or almost entirely transferred to the female, while even the young vary little or not at all from the adult.

ORDER RAPTORES. BIRDS OF PREY.

The birds of prey are eminently the despots of the feathered realm. Having no formidable rivals outside their own ranks, they have no need of protective colors, these being absent in the entire group. Some species are marked with agressive (anticryptic) colors, however, enabling them to steal upon their prey unawares, but the majority of them trust rather to the sharpness of their eye and the fleetness of wing for their food. What good would agressive colors be to an eagle swooping upon a lamb, or a Cooper's hawk falling upon some luckless chicken or rabbit? Nor would directive marks be of any use, as a general rule, for these birds have no enemies to escape from. It is a notable fact that bright colors are wholly wanting in the order, and that there are but few species in which an elaborate pattern of coloration exists. A tendency towards melanism is everywhere present, or else the color of the back is some uniform shade of brown or gray, and the breast streaked or barred with the same color. All this points to the independence of these birds, so far as the color is concerned, of utilitarian influences. The colors seem to have been, for the most part, developed without the interposition of natural selection, and simply in accordance with the general principles of growth. The tail is generally, and the head occasionally, colored with recognition marks of some sort, discriminative, sexual, socialistic, and possibly to a less extent directive. The barrings on the tail, probably in accordance with the principle of repetitive marks rather than for any principle of utility, have in many species extended up on the body, especially upon the flanks, but in some instances over the back as well.

FAMILY CATHARTIDÆ. The American Vultures.

(1) Male like female (except for the fleshy comb on the cere); young but little different from adult.

Prevailing colors, black, dark brown, white.

In the three North American genera, Pseudogryphus, Cathartes and Catharista, the colors are of no utilitarian significance whatever, except that a black bird may be seen at a great distance in the sky, and they might thus assist one another in congregating at a place where food had been discovered. Natural selection would thus encourage this general tendency towards the assumption of a melanistic plumage.

FAMILY FALCONIDÆ. Vultures, Falcons, Hawks, Eagles, etc.

Genera Elanoides, Elanus, Ictinia and Rostrhamus. The Kites.

(2) Male like female; young with peculiar first plumage.

Prevailing colors, black, white, plumbeous, bluish gray, brown (in young).

It is not easy to see how the beautiful uniform white and bluish gray marks, relieved by patches of black in the kites, can be of any more utility than a similar style of plumage is among the gulls. In both instances the colors may be in general, of use for recognition, although such pleasing tints would hardly be necessary for this purpose. There is a great temptation in this instance to fall back on the theory of a tendency towards a uniform coloration, white in this case, varied by sexual selection which may have produced the beautiful clearness and softness of effect, and by the need for discriminative marks to distinguish between closely allied forms. The plumage of the young is much less uniform, inclining to be mottled and streaked, and indicating the coloration from which the species of to-day have been evolved.

GENUS CIRCUS. MARSH HAWK.

(7) Male unlike female; young like female.

Prevailing colors (of male) bluish gray, and white; (of female) dark brown, tawny and white.

How to explain the difference in the colors of the sexes in this bird, except by an appeal to sexual selection, I am unable to suggest, for the colors of the male are not darker than those of the female, so that the law of katabolism could not be resorted to. The white rump-patch and barred tail are excellent recognition marks, but of what sort is difficult to determine. In reading the life history of this species the use of so pronounced a recognition mark is not made apparent.

GENUS ACCIPITER. GOSHAWKS, ETC.

(2) Adult male similar to female; young like some ancestral stage of adult.

Prevailing colors, bluish gray, ashy, brown, rusty, white.

The difficulty of ascribing the colors of the birds of prey to any form of utilitarian cause is again exhibited in this genus. Can it be said that the bluish gray of the back in adult birds is due to sexual selection, transferred by inheritance to the female? If not it seems that an explanation must be despaired of for the present, since for either protective or agressive resemblance the brown plumage of the young would seem the best suited. Neither can it be attributed to any known general laws of growth, for why should these produce first a brown plumage and afterwards transform it into a bluish gray one?

GENUS PARABUTEO. HARRIS'S HAWK.

(2) Adult male like female; young with a peculiar first plumage.

Prevailing colors, dark brown, black, white.

This is one of the genera which is comparatively free from the workings of natural selection and is fast becoming melanistic. The white base and tip of the tail in contrast to the black middle portion affords an excellent recognition mark, which was perhaps originally discriminative in its nature. The young are irregularly marked as would be expected if the pigment was deposited without the guidance of natural selection.

GENERA BUTEO AND ARCHIBUTEO. THE BUZZARDS.

(2) Adult male generally like female; young with a peculiar first plumage.

Prevailing colors, brown, rusty, gray, black, white.

There is a general tendency throughout this group of large and powerful birds, so well able to take care of themselves, to become melanistic. Some species, indeed, have two phases of plumage, a lighter normal one, and a melanistic one, which shade into one another through every possible stage of transition. The red color of the tail in *B. borealis* is a striking recognition mark which can be seen at surprisingly long distances, and may have been at first discriminative and afterwards directive or socialistic in nature. The different geographical races of this species are largely the result of the direct influence of the environment, together with isolation. The same is true of the races of *B. lineatus*, these two species being exceptional among hawks for their susceptibility to environmental changes.

GENUS URUBITINGA. MEXICAN BLACK HAWK, ETC.

(2) Adult male like female; young with a peculiar first plumage.

Prevailing colors (adult) black, white; (young) brown, ochraceous.

The adults in this genus have completely attained the black plumage with the exception of the white recognition marks of the tail. The plumage of the young probably has no reference to utility but is simply at a less advanced stage of pigmentation. The different species are distinguished by the distribution of white marks on the tail, which afford an excellent illustration of discriminative marks.

GENUS ASTURINA. MEXICAN GOSHAWKS.

(2) Adult male like female; young with peculiar first plumage.

The remarks made concerning the genus Accipiter would apply equally to the present bird, the general features of coloration being about the same.

GENERA AQUILA, THRASÆËTUS, HALIÆËTUS. THE EAGLES.

(2) Adult male like female; young with peculiar first plumage.

Prevailing colors, black, white, gray, brown.

The markings of the eagles, perhaps, more than of any other land birds, are to be explained almost exclusive by the general laws of growth. Very possibly such marks as the white thighs with black bars in Thrasæëtus, the white tail of Haliæëtus, and the white head of *H. leucocephalus*, were developed as discriminative, or possibly to some extent as socialistic, marks. The plumage of the young is simply less pigmented than that of the adult.

GENUS FALCO. THE FALCONS.

(2) Adult male generally like female; young with peculiar first plumage. In some species (7) male unlike female; young resembling the latter.

Prevailing colors, black, white, brown, rusty, bluish, gray.

The colors in this widely dispersed genus are partly in accordance with the general laws of growth, in nearly all species enhanced by sexual selection (?), and with recognition marks, sometimes as is *F. sparverius* in the form of characteristic head markings, but more often in variations of the tail bars. The markings of *F. sparverius* are peculiarly pronounced, for, besides the head markings which would alone serve to distinguish it, the flanks have large circular spots of black, the wing feathers are barred, and the tail markings are peculiar. The distinction between *F. sparverius* and *F. sparverioides* is a peculiarly interesting one. In the females of both the back is rufous, but in the former the male is similarly colored, while the back of the latter is plumbeous or dark bluish gray. No appeal to the laws of growth would explain this, and it is evidently to be accounted for either as a discriminative mark, or as due to sexual selection. Probably both factors were instrumental in its development for in many instances characters which at first were only useful for sexual recognition, in leading the female to select a mate of her own kind, afterwards became attractive to her and were still further developed by sexual selection. Certain species have been directly influenced by their environment and divided into geographical races, as for instance, *F. columbarius suckleyi*, the dark form of the Northwest coast region.

GENUS POLYBORUS. CARACARA.

(2) Adult male like female; young with peculiar first plumage.

Prevailing colors, black, white, brown.

It is difficult to suggest any use for the striking distribution of color marks in this genus. There are three species, in general much alike. The Guadalupe Island form *(P. lutosus)* is of peculiar interest from an evolutionary point of view. Left stranded upon this island without any more powerful rival, and from its habits of feeding on carrion, without any need of agressive resemblance, it has been perfectly free to develop its own life history independent of the bulk of its own species or of natural selection (so far as its colors are concerned). Some of the points in which the island species has varied from the parent form may be tabulated as follows from the description in Ridgway's Manual:

cheriway.	*lutosus.*
Rump white (with or without bars).	Rump dull brownish buff, broadly barred with dull brown.
Tail white, the narrow bars grayish.	Tail brownish buff, broad bars of grayish brown, bordered by narrower zigzaggy lines of dusky.
Terminal dark band 2-in. or more wide.	Terminal dark band less than 2-in. wide.

GENUS PANDION. OSPREY.

(2) Adult male similar to female; young somewhat different from adult.

Prevailing colors, brown, gray, white.

The young differ from the adult simply in having the dark feathers of the back tipped with white or buffy. The coloration does not apparently serve any useful purpose.

FAMILY STRIGIDÆ. The Barn Owls.

Genus Strix. The Barn Owls.

(1) Male like female; young like adult.

Prevailing colors, ochraceous yellow, grayish, white. The snowy whiteness of the face, and sometimes the breast, of this bird I take to be a socialistic recognition mark, which would be useful in their social intercourse at night, in the darkness of their nesting place, etc. What the use of the mottlings may be, or the general color of the back, I am unable to suggest.

FAMILY BUBONIDÆ. The Horned Owls, etc.

The color markings of this family are of a very unmodified order of development, as might be expected in a group of nocturnal birds. Two features are noticeable with regard to the coloration: (1) the absence of any tendency towards melanism as among the hawks, but rather the reverse tendency towards albinism; (2) the absence of a tendency towards a uniform color as among the hawks, but rather an inclination towards a retention of the mottled plumage. Glaucidium is an exception to this latter rule, however. This tendency towards albinism in a group of birds habitually living in the dark, and towards melanism in an allied group which live in the light and with little selective influence to restrain the deposition of pigment, would seem to be in accordance with the influence of light upon the development of pigment. Still, other causes have doubtless been instrumental in bringing about this result, for the whiteness becomes most pronounced towards the arctics where it would be most needed for protection, whereas in more southern latitudes it is a useful form of recognition mark.

The different genera present some interesting features of color modification. The adults are generally exactly alike in color and the young frequently do not differ greatly from them, but are sometimes distinctly barred instead of mottled. Brown, gray, and white are the usual colors, together with some buffy, tawny or ochraceous. The genus Megascops is peculiarly susceptible to the direct influence of the environment, and as has been already mentioned under the head of geographical distribution, breaks up into a great variety of forms in different parts of the country. The *Bubo virginianus* group is also interesting from the manner in which it becomes pale toward the Arctics, being almost pure white at the northern limit of its range. The general mottled appearance of most owls blends very well with the tree trunks, and they are thus protected during the day at which time they are so comparatively helpless when attacked. The color of the burrowing owl *(Speotyto cunicularia hypogœa)* blends very well with the ground of the fields in which it is generally found, and its white throat has already been mentioned as a socialistic marking which would be useful in the darkness of its burrow.

ORDER PSITTACI. THE PARROTS, MACAWS, PAROQUETS, ETC.

FAMILY PSITTACIDÆ. PARROTS.

Like the pigeons, this cosmopolitan and long established group should be considered as a whole in attempting to arrive at any conclusions with regard to the evolution of the colors. These birds are eminently denizens of the tropics, and their colors have all the diversity and brilliancy which we naturally associate with that region. The green colors are probably in the main protective in their nature, blending with the leaves, while the blues and yellows are doubtless the result of sexual selection. The red appears to be generally a mere intensification of the yellow, in accordance with the principle of correlative colors. The adults are alike and the young similar to them, but with the more special color marks absent.

ORDER COCCYGES. THE CUCKOOS, TROGONS, KINGFISHERS, ETC.

FAMILY CUCULIDÆ. THE CUCKOOS, ANIS, ETC.

The three North American genera of this family are entirely unrelated so far as their colors are concerned, and accordingly must be considered singly. With regard to protective mimicry in this group, Dr. Stejneger says:* "The cuckoo *(Cuculus canorus)*, in different local forms, occurring all over the Palæarctic region, and wandering south in winter, is astonishingly like, in external appearance, some of the smaller hawks, not only in color, but also in its manner of flight, a resemblance which in Europe caused the superstition that the young cuckoo in the autumn turns into a hawk. * * * * Some Oriental cuckoos belonging to the nearly allied genus Hierococcyx carry the Accipitrine resemblance still further, as the young birds have the dusky markings on the lower surface longitudinal, as in many hawks and falcons, later on, like them, changing into a plumage transversely barred. This similarity is not accidental, but evidently a case of protective mimicry, a supposition greatly strengthened by the fact that we know of some small Malaccan cuckoos (Penthoceryx), rusty brown above, and white beneath, barred with dusky, which, in size, color, and general habits most

---

* Riverside Natural History, p. 374.

closely ape the appearance of certain diminutive shrikes inhabiting the same country."

GENUS CROTOPHAGA. THE ANIS.

(1) Adult male like female; young like adult (but colors lacking the metallic lustre).

Color entirely black, with dull bluish, greenish, or bronzy reflections.

This is probably a very old and highly specialized genus of birds, which has reached the limit of pigmentation. Sexual selection has probably been a factor in the development of its present plumage, and the black may be a form of directive marking, for the birds are gregarious.

GENUS GEOCOCCYX. THE ROADRUNNERS.

(1) Adult male like female; young like adult.

Prevailing colors brownish, buffy, white, bronze and greenish.

There seems to be little doubt that this genus has been in past times a brilliantly attired bird, the colors having been developed by sexual selection. These have been lost, either for the sake of protection in the comparatively open desert country in which the bird is now found, or because the genus is degenerating, or possibly the direct influence of the desert climate may have affected the plumage. The principal reason for holding that the group is a degenerate one in its coloration is that while the exposed edges of the feathers are apt to be dull brownish or buffy, the basal portion and interior of the feather which is largely concealed has the most iridescent bronzy and green colors.

GENUS COCCYZUS. AMERICAN CUCKOOS.

(1) Adult male like female; young like adult, but colors slightly duller, and tail markings less distinct.

Prevailing colors, brownish, grayish and white.

It is difficult to find any use for the general markings of this group, but with what is known of the remarkable tendency toward protective mimicry of the cuckoos in all parts of the world, it is not impossible that the plumage of this genus may be an imitation of the markings of some extinct species of hawk, some form allied to *Accipiter velox*, for instance. However this may be, the differences between *C. americana* and *C. erythrophthalmus* are doubtless discriminative in nature, the yellow bill and distinct white spots on the tail of the former serving to distinguish it very readily from the latter. *C. minor* and *C. maynardi* have been differentiated by isolation upon groups of islands, the direct influence in the environment perhaps aiding in the changes of their plumage.

FAMILY TROGONIDÆ. THE TROGONS.

GENUS TROGON. THE TROGONS.

(8) Male more conspicuously colored than female; young with a peculiar first plumage.

Prevailing colors, metallic green, black, red, yellow, gray, white.

This tropical genus is represented by but one species along our southern border, and the colors may be accounted for by the action of sexual selection, together with a tropical climate. The areas of color are the same in the female as in the male, but the bright metallic shades are replaced by brownish or grayish. The plumage of the young is still less specialized than that of the female, the species thus exhibiting three stages of evolutionary progression.

FAMILY ALCEDINIDÆ. THE KINGFISHERS.

GENUS CERYLE. THE KINGFISHERS.

(7) Adult male unlike female; young similar to female.

Prevailing colors, plumbeous blue, bottle-green, rufous, white.

The colors of *C. alcyon* are probably a form of aggressive resemblance, making the bird inconspicuous from the point of view of the fish. The white throat is doubtless also a socialistic recognition mark of use in the darkness of the burrow where the nest is always placed. The different American species are closely related in spite of the great discrepancy in size and colors. Mr. Ridgway, in a paper entitled "On some Remarkable Points of Relationship between the American Kingfishers,"* has called attention to this fact. Each of the large species is duplicated in miniature more or less by an allied species or fratercule. There must be some utility in the colors for them to have remained so constant in spite of a reduction in size of the species in one case to a half. It seems quite possible that the reddish and green colors would be as invisible to a fish in muddy water as white and blue to a fish in a clear stream, and it is not impossible that the first differentiation in color was dependent upon the clearness of the water in the districts in which the different forms arose. It may also be possible that green and blue are correlative colors just as yellow and red are. Such birds as the green jay *(Xanthoura luxuosa)*, and some of the parrots would seem to give an air of plausibility to this view. In the kingfishers the combination of rufous and green is apparently a more primitive one than of white and blue.

The following facts will prove this: *C. superciliosa* is

---

* Bull. Nutt. Orn. Club, viii, pp. 59–60.

the smallest species and the fratercule of *C. inda* the next larger in the group. These two are green above and rufous below, but the male has a pectoral band of white and dark green bars. The next in size is *C. cabanisi*, the fratercule of *C. amazona*. In these two the back is green but the under parts of the male are white with a pectoral band of green. In the female the rufous persists posterior to the green band. In *C. alcyon* the fratercule of *C. torquatus* the green is replaced by blue while in the female the rufous still persists, but to a less degree than in *C. cabanisi*, posterior to the blue pectoral band.

If, as suggested, the red and green colors are aggressive resemblance marks, concealing the bird from fish in muddy water, they would naturally be the primitive color because streams were more universally muddy in earlier geological ages when erosion was greater. Furthermore, the rufous color would naturally persist the longest on the posterior parts of the body, for there it would be invisible to the fish as the bird plunged from above.

ORDER PICI. THE WOODPECKERS, WRYNECKS, ETC.

FAMILY PICIDÆ. THE WOODPECKERS.

This cosmopolitan group is especially interesting in connection with the evolution of colors. Tropical species are frequently very brilliantly colored, while all the species found in North America show at least some traces of a bright plumage. The different genera may be divided into two groups—those which appear to have lost much of the former brilliancy of their markings, either from degeneration or the need for protection, and those which are to-day either becoming more brilliant, or are now at the climax of their development. Dryobates, Xenopicus and Picoides belong to the former class and Sphyrapicus, Melanerpes, and Colaptes to the latter. It is doubtful where Campephilus and Ceophlœus should be placed in this scale. This loss of brilliant color in certain genera is demonstrated by the fact that the young are more brightly colored than the adult—a very unusual state of affairs. This is particularly noticeable in Dryobates where the young male has the entire top of the head scarlet, this color being restricted in the adult to a narrow-patch on the nape. As this excess of red in the young cannot be of any conceivable utility it seems to afford a perfect demonstration of the former plumage of the adult. Furthermore, in certain forms, particularly in the genus Melanerpes, an excess of red or yellow, or both, very frequently occurs on the breast and belly. If the amount were very slight and occasional, it might be looked upon as an excess of pigmentation along the line of future color development. From the frequency with which it occurs, however, and its intensity in some instances, it seems more probable that it is a character which is being rapidly lost at the present time. It seems probable that the American species of Dryobates also had the belly colored red in past times, for in certain Asiatic species which have the red head like the young of American forms, the belly is also more or less strongly tinged with red. It would seem then that Melanerpes had but recently passed the climax of its most brilliant coloration, while Dryobates must have long since donned the garb of old age. It seems a rather curious circumstance that birds such as the woodpeckers, which habitually cling close to the trunks of trees, should have a bright color upon the abdomen. May it not be possible that this plumage was assumed before the tree climbing habit was acquired, and is now being lost because it is so inconspicuous as to be of no particular use? I fail to see that the bright markings in this family can have been developed otherwise than by sexual selection. In most cases the colors have been transferred by inheritance to the female, but generally in a more or less imperfect manner. Why the bright colors, particularly of the crown patch, should be lost, is even a more difficult question than how they were acquired. Woodpeckers are not peculiarly exposed to the attacks of rapacious birds or mammals, so the suppression of red could hardly have been due to the need for protection.

The white-headed woodpecker *(Xenopicus albolarvatus)* is remarkable from the fact that there are no hybrid feathers along the edge of the white marking. This would seem to argue that the white head is due to some constitutional weakness, rather than to the operation of natural selection. It is probably a step in degeneration, which may have been pressed into service by natural selection as a recognition mark. Picoides, on the other hand, together with Ceophlœus and Campephilus and *Sphyrapicus thyroideus* are rapidly tending towards melanism.

Characteristic recognition markings are very prevalent in the family, particular attention having already been called to a number of examples in preceding pages. The flickers (Colaptes) afford the best possible illustration of these marks. As the flicker flies the first thing to arrest the attention is the white rump patch, and in connection with this the flash of yellow or scarlet from the wings. Whether the characteristic round black spots on the sides are a form of recognition mark or due to some other cause is a very difficult matter to decide. The black and red malar streaks in the eastern and western races, respectively, might be held to be discriminative marks were it not for the remarkable indiscriminate breeding between the two species, apparently with no deleterious result to the species.* The red of the western species is apparently the correlative of the yellow of *C. auratus*, and is due to some form of pigment intensification more than to selection. Mr. Frank M. Chapman has published a note On the Color-Pattern of the Upper Tail-Coverts in *Colaptes auratus*,† illustrated with cuts of the feather, in which he shows that the barred pattern is the earliest form of marking, culminating in a solid black feather, rimmed with light. It is an interesting fact that the circular spots on the side are modifications of the barred feather, as is shown by a study of the successional taxology of the feathers on the lower part of the body, the barred type being posterior to the circular. The fact that although Colaptes does not present an obviously barred plumage the specialized markings have all been developed from the bar, taken in connection with the frequency of barred markings throughout the woodpecker family would seem to indicate that the common ancestor of the group had been a strongly barred form, these markings having continued to the species of to-day with greater or less persistence.

Figs. 4 and 5 of Plate I show the typical markings of the *Dryobates villosus* and *D. scalaris* groups, the striped and barred forms. In this instance the difference between a streak and a stripe may be illustrated. In a streaked plumage the pigmentation is generally along the line of the shaft, and is the most primitive style of marking. A striped plumage is produced in a much bolder manner and is not necessarily a primitive form.

---

* cf. The North American Species of the Genus Colaptes, considered with Special Reference to the Relationship of *C. auratus* and *C. Cafer*. J. A. Allen. Bull. Am. Mus. Nat. Hist., iv, pp. 21–44.

† Bull. Am. Mus. Nat. Hist., iii, pp. 311-314.

In the feather here shown (fig. 4) the pigment is along one side only, it being in fact a lateral hybrid, producing a line of demarkation for a definite color patch.

The prevailing colors of the family are black, white, brown, red and yellow. The relation of the plumage of the sexes and young has already been discussed (see *ante*, p. 224).

ORDER MACROCHIRES. THE GOATSUCKERS, SWIFTS, ETC.

FAMILY CAPRIMULGIDÆ. THE GOATSUCKERS.

The colors of this family are remarkably homogeneous in general style, being mottled brown, gray, ochraceous and white. There are no marks of sexual adornment among North American forms, the general colors being very perfect protective marks, and the variously distributed white marks affording a beautiful illustration of several classes of recognition marks. As these were discussed somewhat fully in the preceding pages (see *ante*, pp. 207–209) it is unnecessary to repeat what was there stated. It need only be added that there is no group which appears to present less difficulty in the elucidation of color marks.

FAMILY MICROPODIDÆ. THE SWIFTS.

(1) Adult male like female; young similar to adult.
Prevailing colors, blackish, grayish, brown, white.

Like the hawks, the colors of this family do not seem to have been greatly influenced by natural selection. From their crepuscular habits and swift flight, they can can hardly have any enemies, nor do they need aggressive colors for the capture of their prey. Cypseloides and Chætura have not even a suggestion of a recognition mark, apparently, and their colors do not appear to be of any significance whatever, but the white under parts of Micropus may be a form of recognition mark, possibly socialistic in nature. There seems to be a discrepancy between the view that light favors the deposition of pigment and the fact that Cypseloides, which is abroad only in the twilight or in cloudy weather, is almost black in color. There is not an inevitable contradiction in this, however, because although light may undoubtedly accelerate the production of pigment, or intensify and make more brilliant the colors, nevertheless, if pigment be a waste product, it must necessarily be thrown off after enough has been accumulated in the system, light or no light. Accordingly, if an animal were in a state of increasing vigor and vitality, we should look for an increase in pigmentation and a darkening, but not an increasing brilliancy of color, in the absence of sunlight. The direct action of the sunlight would, however, tend to guide the pigment to particular parts of the body. In most of the swifts it is almost evenly distributed, but in Micropus, which is more diurnal than the rest, it is nearly all on the back, the under parts being left white.

FAMILY TROCHILIDÆ. The Hummingbirds.

(7) Adult male more conspicuously colored than female; young similar to adult female.

Prevailing colors, white, black, metallic reds, greens and blues.

This genus appears to afford one of the most striking illustrations in the entire bird world of the operation of sexual selection. Mr. Wallace has argued that the unparalleled beauty and diversity of color and ornamentation among these feathered gems is due solely or chiefly to the operation of the general laws of growth. To me, however, it seems a significant fact that the beautiful metallic colors are as, a rule, confined to the head and throat, in the form of a coronet and gorget of the most beautiful iridescent hues conceivable. Why, it may be asked, have not the general laws of growth placed some of these colors on the abdomen and sides, leaving the throat and head some plain, dull hue? If Mr. Wallace can suggest any single law of growth which can throw even a glimmer of light upon the reason for the production of not merely the greatest amount of pigment, but rather the most beautiful modulations of color, dependent more on the structure of the feather than on pigmentation, upon the most conspicuous parts of the body, and upon no other part—if he can indicate even a possible line of investigation of any law of growth explaining this, it will be time enough to concede that it is an open question whether or not sexual selection has been the agent. It the meantime, it may be remarked that recognition markings cannot be resorted to as an explanation, because the metallic colors are only visible when the bird is facing the observer, and recognition markings could never be more useful from being invisible from all but one point of view.

FAMILY TYRANNIDÆ. The Tyrant Flycatchers.

So far as the significance of its colors is concerned, this family may be divided into two divisions—the one in which the red or orange crown patch is present and that in which it is wanting. As has already been shown (see *ante*, p. 199), this crown patch is unquestionably a form of alluring color (pseudepisematic) in certain species, and in all probability this is its function in all forms, as it is present in both sexes, although generally slightly restricted in the female. The genera in which it is present are Milvulus, Tyrannus, Pitangus and Myiodynastes. The colors of these forms can be explained, it seems to me, by the application of two principles already enunciated—the law of the assortment of pigments, and the bleaching and intensifying of colors by environmental influences. The original pigments of the ancestral form were probably black and yellow. These combined produced the olive green and brown so common in this family, as in *Tyrannus verticalis*, for instance. By selection the pigments were separated to a greater or less extent producing such specialized marks as the black cap of *Milvulus tyrannus*, the black tail of *Tyrannus verticalis*, the yellow crown patch of *Tyrannus tyrannus*, etc., or in more diffused form the yellow appeared on the belly as in *Pitangus derbianus*, or even extended over the entire breast in a much richer shade, as in *Tyrannus melancholicus couchii*, and other tropical species. The yellow has been both extended and intensified by the influence of a tropical climate, while from less determinate causes of intensification it has been modified into its correlative red. As has been previously pointed out, the stages of intensification of the yellow into red through orange, are shown in the crown patch of the genus Tyrannus. A more complete transition of the yellow into red has occurred in the vermilion flycatcher *(Pyrocephalus rubineus mexicanus)*, in which species it is to be noted that the red color occurs in the same parts of the body that have a tendency to be colored yellow in other genera, viz., on the top of the head and under parts.

Attention has already been called to Plate VI, as showing the bleaching influences of an arid environment on different species of the genus Myiarchus. In the same manner, probably, the light gray and white of the genus Milvulus has been largely produced.

All the smaller flycatchers are to be regarded, it seems to me, as degenerate descendants from some more brightly colored race. They have been enabled to survive by becoming insignificant. Thus, in the phœbe and black pewee *(Sayornis phœbe* and *S. nigricans)* the wing bands are distinct rusty, but obscured in the adult. In Say's pewee *(S. saya)* the young has the reddish tinge much brighter than the adult, and suffused over the back as well as the breast. The young of the olive-sided flycatcher has the breast clear white, the streaks being more restricted to the sides, while in the adult the breast is buffy and heavily streaked. It seems from this as if the bird of to-day had reverted from a brighter or more specialized color, to the primitive streaked style of marking. In the genus Empidonax the different species were apparently more specialized in former times, but through reversion have become very closely alike in color, and have lost even their distinctive recognition marks, except the obscure wing bands.

FAMILY ALAUDIDÆ. The Larks.

The members of this family are generally dull colored birds not very highly specialized in respect to their markings. Living almost exclusively on the ground, when not in flight, the need for protective colors harmonizing with the ground is particularly manifest.

Genus Otocoris. The Horned Larks.

(8) Male more conspicuously colored than female; young with a peculiar first plumage.

Prevailing colors, brown, white, black, yellow, buffy, etc.

Unlike most of the family, the species of this genus appear to be the descendants of a much more darkly colored form. They have been modified largely by the direct influences of the environment, probably in comparatively recent times, as the distinctions are in the main only varietal and not specific. As usual, the darkest form is found in the northwest coast region and the palest varieties in the western desert region, particularly of Lower California.

The young are strikingly different from the adult in colors and markings. The plumage is generally very much darker, sometimes being almost black and the feathers are tipped with white. From the darker and more closely spotted head of the young it seems probable that the ancestral bird had a black head. This has become modified in the adult into a very unusual pattern on the side of the head, which is doubtless a recognition mark of some sort. It should be pointed out that the colors of this genus hardly appear to harmonize with the law of the assortment of pigment, for the special colors being black and yellow we should expect the generalized colors to be olive green instead of brown tending toward rusty or vinaceous.

FAMILY CORVIDÆ. The Crows, Jays, Magpies, etc.

(1) Male like female; young like adult, but colors sometimes less distinct.

Black, white and blue are the characteristic colors of this specialized family. Gray is also present as a generalized color, and much more prevalent than brown. Yellow and green occur only in one tropical genus, Xanthoura.

There is a strong melanistic tendency in this group, due to the high specialization and the fact that from their powerful size and gregarious habits these birds have few enemies to contend with. The generalized gray is due to the combination of the specialized blue and black. Sexual selection has apparently been instrumental in the development of the blue pigment among the jays, although it has become completely transferred to the female and young. The influences of isolation and environment upon the genus Cyanocitta has been already discussed (see *ante*, p. 245). Isolation and environmental influences have also been responsible for most if not all of the forms of Aphelocoma. The unusual number of closely allied species or varieties inhabiting the different parts of southern North America is to be accounted for by the fact that the bird is generally resident wherever found, and not much given to wandering, except in a local manner when food is scarce in a particular locality.

The colors of the magpies (Pica) were probably first developed as recognition marks and afterwards enhanced by sexual selection. The habits of the magpies are such that recognition marks would be of great service, particularly in their social relations. The yellow bill and smaller size of *P. nuttalli* is doubtless the result of geographical isolation, and not a character to which any utility can be ascribed. Perisoreus from the somber forests of the north has simply never acquired a specialized plumage, since the labor of gaining a living must have quite monopolized the bird's attention, and entirely driven any æsthetic tendencies out of its head. The different species and varieties are largely the result of climatic influences. Clarke's nutcracker *(Picicorvus columbianus)* is marked with conspicuous black and white recognition characters on the wings and tail, the rest of the body being of the generalized gray of the family. The piñon jay *(Cyanocephalus cyanocephalus)* is without decided recognition marks, but has the ground color a pale blue, not unlike that of Aphelocoma. The black of the crows and ravens is simply the completion of color specialization, but it is doubtless also useful as a general recognition mark. There can apparently be no possible utilitarian significance in the white basal portion of the feathers of the neck of *Corvus cryptoleucus*, and no way of accounting for it can be suggested.

FAMILY ICTERIDÆ. The Blackbirds, Orioles, etc.

Yellow, red and black are emphatically the colors of this family, with brown as the generalized shade. White is almost completely excluded except in the bobolink (Dolichonyx), which, in respect to its colors, is more closely allied to the Fringillidæ than to this group. Nearly all the genera are very highly developed in their colors, in most instances the specialized colors covering the entire body.

Genus Dolichonyx. The Bobolinks.

(5) Male in breeding plumage differs from female; young with peculiar first plumage, but similar to that of adult female.

Prevailing colors, black, white, buffy, gray, brown.

I am utterly at a loss for any explanation of the colors of this bird either in accordance with the general laws of growth or any principle of utility. The only resort is to suppose the breeding plumage of the male to be wholly the result of sexual selection, but this seems to be a very unsatisfactory means of accounting for it. Mr. Frank M. Chapman* has described the manner in which the breeding plumage of the male is assumed, partly by a moult and partly by the wearing away of the tips of the feathers.

Genus Molothrus. The Cowbirds.

(8) Adult male more conspicuously colored than female; young with a peculiar first plumage.

Prevailing colors, black, brown, gray, buffy.

The young plumage with the breast lighter colored

---

* Auk, vii, pp. 120–124.

and indistinctly streaked indicates the style of coloring of the bird from which this genus, in common with Agelaius and others, was derived. The black color of the male is to be regarded as an indication of specialization, accelerated by sexual selection, utility as a recognition mark, and by the principle of sexual intensification. The only explanation which occurs to me of the brown color of the head and neck of the male is that the specialization has progressed, in accordance with Eimer's law, from posterior to anterior. The bronzed cowbird *(M. æneas)*, would then be a more specialized form, the black having finally spread over the entire body. The metallic colors are to be regarded as the result of sexual selection.

GENUS XANTHOCEPHALUS. YELLOW-HEADED BLACKBIRD.

(6) Plumage of male in summer different from winter plumage; female different from either; young similar to female.

Prevailing colors, black, white, yellow, brown.

The yellow color of the head of the male can hardly be explained except as the result of sexual selection, incompletely transferred to the female by inheritance. The white bars on the wing-coverts are undoubtedly recognition marks, and the general black color the result of pigment intensification. That the ancestral bird had a white breast (probably streaked like Molothrus), is indicated by the white mottlings on the breast of the female. There is a marked similarity between the colors, and even the distribution of colors in this genus and in the Arizona hooded oriole *(Icterus cucullatus nelsoni)*, which may be a mere coincidence, but may well have some significance as pointing to an affinity in origin. In both the head is yellow, the back black and the wing bars white. Intense examples of Xanthocephalus have the head orange or more rarely pinkish saffron, while the intense races of the *Icterus cucullatus* group have the head varying from orange to red. The principal difference in color distribution is that in the former bird the black is on the posterior portion of the under parts of the body, while in the latter it is upon the anterior portion.

GENUS AGELAIUS. THE RED-WINGED BLACKBIRDS.

(6) Plumage of male in summer different from winter plumage; female different from either; young similar to female.

Prevailing colors, black, brown, buff, white, scarlet.

The adult males of this genus are highly specialized, no generalized color being left, in fact. Like most birds with black plumage, the members of this genus are gregarious. Gregarious birds, from their very habits, would hardly be benefited by protective colors, and, accordingly, instead of acquiring a protective plumage with some distinctive markings, the black color itself becomes a recognition mark. Whether the red shoulder patch is primarily a recognition mark or a character developed by sexual selection is difficult to determine. From the fact that it is so inconspicuous in the female, it seems that it cannot be a directive mark, and was probably developed primarily by sexual selection upon the wings where it would attract the most attention. Plate XIV shows the different phases in the development of the wing patch. The differences between the adult males of the three species, *A. phœniceus*, *gubernator* and *tricolor*, may have been developed by sexual selection, or else are discriminative marks as a result of physiological selection. They certainly do not appear to have been produced by geographical isolation. That these wing markings are associated with the breeding habits, is shown by their incomplete development in winter, when the color is yellow and much broken. Sexual intensification has, in this instance, been an important factor in the development of the specialized colors of the male, the red of summer being merely an intensification of the yellow, which still persists in winter, and the black an intensification of the brown.

The ancestral bird was a brown streaked bird, lighter or white on the breast.

GENUS STURNELLA. THE MEADOW LARKS.

(1) Male similar to female (the latter duller); young similar to adult, but duller.

Prevailing colors, black, white, brownish, grayish, yellow.

The colors of this genus suggest somewhat an affinity with the orioles (Icterus). The browns and grays of the back are protective in nature, harmonizing with the ground, and the yellow breast and black crescent are probably due, in some measure at least, to sexual selection, partly transferred to the female by heredity. There are slight seasonal as well as sexual differences, the full breeding plumage being produced by the wearing away of the tips of the feathers, but the change is not a very marked one. The intensification of the yellow into its correlative red in the tropical representative of the genus has already been mentioned (see *ante*, p. 156).

GENUS ICTERUS. THE ORIOLES.

(7) Adult males more conspicuously colored than females; young generally similar to female; young male (second year) intermediate between adult male and female.

Prevailing colors, black, white, yellow, orange, red, brown, olive green, gray.

This genus affords an especially good illustration of the working of sexual selection in accordance with the law of the assortment of pigments. Plate XVI shows the generalized plumage of the group. It will be noticed that the Arizona hooded oriole *(I. cucullatus nelsoni)* in female plumage is a dull-colored greenish olive bird without any special markings, except the partial band of white on the wings. The young male is similarly colored the first year. Upon the second year the young male acquires a brownish black throat patch, as shown in the plate. In these two phases of plumage, the orchard oriole *(I. spurius)* is colored almost exactly the same, although in both species there is a large amount of individual variation.

In the adult female of Bullock's oriole *(I. bullocki)*, the colors of the male are indicated on a much duller key. In the figure of the immature plumage of this species it will be noticed that already the superciliary stripe has appeared. The immature plumage of *I. spurius* seems to have even more yellow than later stages, and indicates the relation of the colors of the adult of this species to the other orioles which are so differently colored. The female Baltimore oriole *(I. galbula)* is rapidly acquiring the plumage of the male, although the colors are much duller and broken.

While the general tone of color in this plate is olive greenish and brownish, the effect of Plate XVII, showing the heads of the adult males, is black and yellow or orange. The separation of the component pigments of the undeveloped phases of coloration would produce the colors of the specialized males. And what factor can be suggested to account for this better than sexual selection, which explains at once the similarity of colors and the difference in their distribution? The colors would first be black and yellow, but by intensification of the latter orange and crimson would be developed. This is especially well illustrated in the *I. cucullatus* group which becomes intensified from a yellow at its northern limit to an intense flame in the tropics. In *I. bullocki* the black has extended over the head, leaving a superciliary stripe, however. In *I. galbula* the black has spread over the sides of the head connecting the throat patch and back. In *I. parisorum* and *I. spurius* it has extended still farther down on the breast. There is apparently here a tendency towards the assumption of a completely black plumage as the bird becomes more and more specialized. The reddish brown color of *I. spurius* seems very different from the rest of the group, but I do not think it has been produced by the introduction of a new pigment but rather by a modification of the yellow. It is apparent that the color of the ancestral form is yellow, from the persistence of this color in the young. By intensification this yellow becomes red as in the analogous case of *I. cucullatus*, and it is perfectly conceivable that by further intensification, even by the simple increase in the amount of the pigment, the red would become darker instead of more brilliant.

GENUS SCOLECOPHAGUS } THE BLACKBIRDS AND
GENUS QUISCALUS } GRACKLES.

(7) Adult male more conspicuously colored than female; young similar to adult female. In some species a seasonal difference (6) in which the male differs from the female in both summer and winter plumage.

Prevailing colors, black, brownish, various metallic hues.

General pigment intensification, sexual selection, and the advantage of conspicuous colors for gregarious birds serve to explain the colors of these two genera.

FAMILY FRINGILLIDÆ. THE FINCHES, SPARROWS, ETC.

This large family has comparatively few genera within our limits which are highly specialized in coloration, a large proportion of them being colored in a decidedly primitive fashion. Brownish and buff colors prevail, although red here reaches its maximum development. The lack of more fully developed color markings is to be explained partly by the terrestrial habits of so many of the family, making dull protective markings a matter of necessity, and partly by the severe climate, comparatively speaking, in which a large proportion of the group reside.

GENUS COCCOTHRAUSTES. THE EVENING GROSBEAKS.

(7) Adult male more conspicuously colored than adult female; young similar to adult female (but duller).

Prevailing colors, black, white, yellow, brown, olive, gray.

The colors of the male are probably in the main, if not exclusively, the result of sexual selection, incompletely transferred to the female and young. The black wings with white bars are doubtless recognition marks which would be of especial use to this bird on account its gregarious habit.

The ancestral form, as shown by the unspecialized plumage of the females and young, was dull brownish gray and streaked, probably not unlike that of Pinicola, Carpodacus, etc.

GENUS PINICOLA. THE PINE GROSBEAKS.

(7) Adult male more conspicuously colored than female; young similar to female, but colors duller.

Prevailing colors, red, gray, white, brown (abnormal).

The colors of the male have apparently been developed from the dull gray plumage of the female by sexual selection. White wing-bars, directive recognition marks.

GENUS CARPODACUS. THE PURPLE FINCHES, ETC.

It will be remembered that each of the larger American kingfishers (Ceryle) had a corresponding allied smaller species (see *ante*, p. 278). The relation between the colors of Pinicola and Carpodacus seems to be a similar one, although less direct. The relative colors of the sexes and young, as well as the absolute colors of these two genera, are very similar, and undoubtedly had a common origin and were developed by the same agencies. In speaking of the scarlet rose finch *(C. erythrinus grebnitskii)*, Dr. Stejneger says:* "There can be no doubt that males of this species breed in the gray plumage. I found these breeding gray males almost as common in Petropaulski as the red ones, their conduct and song being exactly the same as that of the latter, and dissection showed that the genital organs were well developed and fully matured. It seems to be a question whether these mature gray birds will ever assume the red plumage, and I should be most inclined to believe that we have here to do with a kind of dichromatism." May not this tendency towards dichromatism in Carpodacus be parallel to the phases of coloration in Pinicola noticed by Mr. Ridgway in the following note in the Manual of North American Birds:† "Apparently adult males are occasionally found in which the plumage is not distinguishable from that of the female; in others the general plumage is that of the female, except that the olivaceous or tawny color on head, etc., is replaced by a more reddish tint (varying from light dull orange-red to deep madder-brown)."

---

* Bull. U. S. Nat. Mus. 29, p. 266.

† pp. 387-388.

GENUS LOXIA. THE CROSSBILLS.

(8) Adult male more conspicuously colored than female; young with a peculiar first plumage, but more or less similar to adult female.

Prevailing colors, red, yellowish green, olivaceous, grayish, white.

Like the preceding, these birds have descended from a gray streaked ancestor, in fact, probably from the same species. The colors are the result of sexual selection, apparently, the yellow correlative of the red having been transmitted more or less to the females and young males. It is probable that Coccothraustes, Pinicola, Carpodacus and Loxia all have originated from the same stock, the first genus alone retaining the yellow color in the adult male plumage, the others acquiring the red correlative.

The white wing bands of *L. leucoptera* are apparently discriminative recognition marks.

GENUS LEUCOSTICTE. THE LEUCOSTICTES.

(4) Sexes alike, changing color with the season; young differ from adults at any season.

Prevailing colors, black, brown, gray, white, red (generally rose).

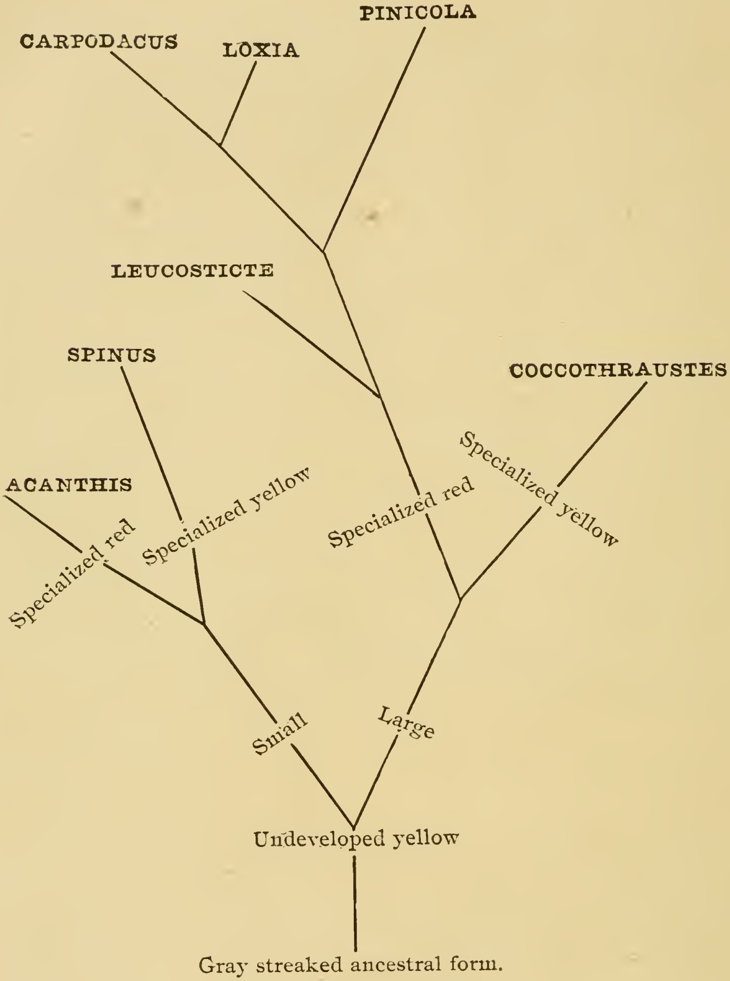
The structural affinity and general character of the colors of this genus ally it with Pinicola, etc., although the sexes do not differ in plumage, and the young are plain brown, less conspicuously streaked, thus differing from the genera previously considered. It is difficult to determine what factors besides sexual selection have produced the colors of this genus. Geographical isolation has had some influence in the origination of specific differences, although probably not the only factor.

GENUS ACANTHIS. THE REDPOLLS.

(8) Adult male more conspicuously colored than adult female; young with a peculiar first plumage.

Prevailing colors, brown, white, gray, red, pink.

The colors of the young, female and adult, represent three stages in the assumption of the red color, first the plain streaked bird, not unlike the pine goldfinch *(Spinus pinus)*, next with the red cap (acquired first by the male as a sexual charm, and afterwards transmitted to the female by heredity), and lastly the red on the rump and under parts. There is a tendency towards the assumption of an albinistic plumage in the northern forms of this genus. Just as the two large forms, Pinicola and Coccothraustes, seem to have come from the same stock, and developed, one the red and the other the yellow color, so also even more intimately the small forms Acanthis and Spinus appear to be related. The probable genealogical connections of the genera thus far considered, which seem to constitute a group by themselves, may be indicated by the following diagram:



GENUS SPINUS. THE GOLDFINCHES.

(7) Adult male more conspicuously colored than female; young similar to female, but duller; or (5) Male in breeding plumage differs from female; young with a peculiar first plumage, but similar to winter adults.

Prevailing colors, black, white, yellow, olive green, brown.

As the male is uniformly more brightly colored and has more special markings than the female, the coloration has undoubtedly been acquired by sexual selection in accordance with the law of the assortment of pigments. Reference has already been made to the supposition that this golden color which was acquired for adornment may have been utilized for protection since the Compositæ to which they so commonly resort are colored thus (see *ante*, p. 195). The pine finch *(S. pinus)* retains a plumage but little modified from the bird which was the common ancestor of the entire group.

GENUS PLECTROPHENAX. THE SNOWFLAKES.

(6) Plumage of male and female changes with the season; male unlike female in both plumages; young similar to female, but duller and more streaked.

Prevailing colors, white, black, gray, brown, buffy.

There is a strong tendency in this genus towards the assumption of a completely white plumage. The ancestral form was a streaked bird, as shown by the present condition of the young. Next a black and white plumage was assumed, which still persists to a certain degree, although the black is becoming eliminated. Thus Mr. E. W. Nelson writes as follows concerning an abnormal *P. nivalis*:* "One specimen, a female, obtained at Saint Michaels, April, 1879, is pure white over the entire body, with the exception only of the tips of the primaries for an inch from their ends. This part of the primaries is jet black, mainly on the inner web, with a narrow edge of white at the tip, but the shaft and most of the outer web are white. The tail is pure white without a trace of black. The bases of the feathers are not black, as is usually the case with this bird, but are dark

---

* Report upon Natural History Collections made in Alaska. Arctic Series of Pub. Issued in Connection with Sig. Service, U. S. Army, p. 182.

sooty plumbeous. Feet black, bill pale. This bird is not an albino, as is shown by the black wing tips, which have much the same color arrangement as is exhibited in the gulls." As Mr. Nelson also found other specimens which were abnormally white, though not albinos, it appears that these must be individuals which have advanced beyond the species. The utility of a white plumage to an Arctic bird like the snow bunting would at first sight appear to be very manifest, yet, on further consideration, it is found that the nest is not built in the immediate vicinity of snow, and that accordingly a white plumage would not be protective during the breeding season. That the black is the earlier plumage and the white a later phase, is proved by the fact that the base of the feather is nearly always black, the tip alone being white. This might be suggestive of a direct influence of arctic cold in whitening the plumage, regardless of utility. This view is strengthened by the fact that it is during the winter months that the back is white, this white edge of the feather wearing away at the approach of spring (see Plate I, fig. 9). The back of McKay's snowflake *(P. hyperboreus)* does not become black in the breeding season, the white feathers remaining unworn (Plate I, fig. 10); and this is to be expected from the fact that the bird is more exclusively a resident of the Arctic regions. Another factor which may have aided in the production of the white plumage is that white feathers containing gas bubbles are much denser and warmer. The wings and tail, which do not form part of the bird's clothing, would thus not need to change to white, but would rather be of use as recognition markings by retaining their black hue.

GENUS CALCARIUS
GENUS RHYNCHOPHANES } THE LONGSPURS.

(5) Adult male in breeding plumage differs from female; young with a peculiar first plumage.

Prevailing colors, white, black, gray, brown. chestnut, buffy.

This genus is closely allied to the preceding in regard to its colors, but has not resided so long or been so much confined to the Arctic regions, and hence has not acquired the same amount of white. It is a significant fact in this connection, I think, that in this genus although the plumage does not become white in winter the black markings are largely obscured either by white or buffy tips to the feathers. This might well be interpreted as the commencement of a climatic influence which will culminate in a white plumage. Natural selection would favor this change as resulting in a warmer winter dress. The characteristic marks of the different species are apparently directive and discriminative recognition marks.

GENUS POOCÆTES. THE VESPER SPARROWS.

(1) Adult male like female; young like adult, but markings duller.

Prevailing colors, brown, rufous, gray, white.

This is one of the plainly attired ground birds in which very little specialization of marking has been attained, the colors being protective in nature. The only recognition mark is the white outer tail feathers, unless the rufous patch on the wing coverts be considered as such. This latter may be a discriminative mark, although it seems hardly conspicuous enough. On the other hand it cannot well be looked upon as the result of sexual selection, for it is not highly enough developed to have been completely transmitted to the female.

GENUS AMMODRAMUS. THE SAVANNA SPARROWS, ETC.

(1) Adult male like female; young more or less closely resembling adult.

Prevailing colors, black, white, brown, gray, buff, yellow.

This genus consists mainly of unspecialized streaked species, although a greater degree of development is exhibited in a few forms. Most of the species show yellow either on the face and superciliary stripe or on the edge of the wing, or sometimes in both places. What its significance may be I will not attempt to suggest, for although it may be the result of sexual selection it is present equally in both sexes. Climatic influence has played an important part in the differentiation of the various races, particularly of the *A. sandwichensis* group. The seaside sparrow *(A. maritimus)* has assumed a uniform coloration above, but the young are streaked like typical members of the group.

GENUS CHONDESTES. THE LARK SPARROWS.

(2) Adult male like female; young like some ancestral stage of the adult.

Prevailing colors, black, white, brown, chestnut, gray.

Although not highly developed in color, the markings of this genus are more specialized than any of the family thus far considered. The complicated black pattern of the head is to be looked upon as the combination of the streakings of the primitive plumage into certain well defined areas. These head stripes are probably recognition markings of some sort, but whether directive or discriminative, is uncertain. The little spot of black on the breast is of interest, being apparently the incipient stage of a new character. The plumage of the young points directly to a streaked ancestor in common with most of the group.

GENUS ZONOTRICHIA. THE WHITE-CROWNED SPARROWS, ETC.

(2) Adult male like female; young like some ancestral stage of the adult.

Prevailing colors, black, white, brown, gray, yellow

This genus has become modified from the primitive bird by losing the streaks on the breast, a corresponding darkening of the back, and by the acquisition of highly characteristic recognition marks about the head. These marks were probably primarily of use as discriminative characters. They would then be most necessary during the breeding season, at which time they reach their maximum development. Without the introduction of any new colors, such striking differences are produced as between *Z. querula*, with its black head and throat, *Z. albicollis*, with its pure white sharply defined patch of white on the throat, and *Z. leucophrys*, with the characteristic black lines on the head. Still different and equally well marked is *Z. coronata* in breeding plumage, although in winter these last two birds are not so readily distinguished at a distance. It is a noteworthy fact that *Z. albicollis*, although so differently marked, has the same shade of yellow on the head as *Z. coronata*, but located on the superciliary stripe, instead of on the median line, as in the latter. This is a fact of some significance with regard to the law of the assortment of pigments. It is also worthy of note that the yellow of *Z. albicollis* is distributed as in Ammodramus, for this may indicate either a genetic relationship or a common cause at work.

GENUS SPIZELLA. THE TREE SPARROWS, CHIPPING SPARROWS, ETC.

(2) Adult male like female; young like some ancestral stage of the adult.

Prevailing colors, black, white, brown, chestnut, gray.

The birds of this genus, like the preceding, have developed from a form streaked above and below, this style being preserved in the young of all the living forms except *S. atrigularis*, in which the streaks are but very faintly indicated. The only specialization has been the loss of the streaks on the breast, which has become uniform whitish, and the acquisition of a chestnut colored cap in some species, and a black throat-patch in *S. atrigularis*. *S. pallida* has the head striped in brown, black and gray, while *S. breweri* seems to be without any form of recognition marking. Recognition markings, when present, are rather discriminative than directive in their nature, the habits of the birds rendering the latter unnecessary.

GENUS JUNCO. THE JUNCOS.

(2) Adult male like female; young like some ancestral stage of the adult.

Prevailing colors, dark slate, gray, rufous, white.

Although plainly enough deriving their origin from the same stock as the other sparrows, the significance of the colors of this genus seems peculiarly difficult to determine. The white tail feathers form an excellent directive mark, while the wing bands of *J. aikeni* may well be discriminative marks, but why some species should have the breast white and some vinaceous pink, or why the back should be gray in some species and reddish brown in others, I do not feel able to give an opinion. The general distribution of markings in the genus may be due to the working of laws of wide application—especially to the effect of light in controlling the deposition of pigment, as previously suggested (see *ante*, p. 230).

GENUS AMPHISPIZA. BLACK-THROATED SPARROW, ETC.

(2) Adult male like female; young like some ancestral stage of the adult.

Prevailing colors, black, white, gray, brown.

Although the colors of this genus are decidedly plain the markings are considerably specialized, the general tendency of coloration being solid rather than streaked, and the special markings being strongly developed. The white superciliary stripe of the black-throated sparrow *(A. bilineata)* as distinguished from the the supraloral white spot in other species, is a discriminative mark apparently. The evolution of the black throat-patch may be traced from the sage sparrow *(A. belli nevadensis)* where the "sides of throat [are] marked with a series of narrow dusky grayish streaks, but no continuous stripe," through Bell's sparrow *(A. belli)* which has the "sides of throat marked with a broad continuous stripe of blackish," to the Mexican forms in which we find the "upper part of throat black, the point of the chin white; fore-neck and lower part of throat uniform ash gray;"* and finally *A. bilineata* is reached with the throat completely black in the adult but white in the young. It is doubtless a directive mark, although possibly discriminative in function.

GENUS PEUCÆA. RUFOUS-CROWNED SPARROW, ETC.

(2) Adult male like female; young like some ancestral stage of the adult.

Prevailing colors, blackish, white, ashy, rufous, brown.

The plan of coloration in this genus reminds one greatly of Spizella, particularly in the presence of a rufous crown patch in some species and the substitution of streaks on the top of the head in others. The young are much more decidedly streaked than the adult, there

---

* Ridgway's Manual, pp. 425–426.

being a tendency towards the assumption of a uniform coloration. Climatic influences and isolation appear to have played an important part in the origination of specific and varietal differences.

GENUS MELOSPIZA. THE SONG SPARROWS, ETC.

(1) Adult male like female; young similar to adult.

Prevailing colors, brown, rufous, gray, ashy, white.

This genus is comparatively little modified from the streaked ancestral plumage. The general effect of sunlight upon pigmentation is shown by the tendency of the breast to be white and the back dark, although the bird is streaked both above and below. The special influence of the environment upon the colors is shown in Plate XIII where the color of the back of each race is marked in the locality inhabited by the respective form.

GENUS PASSERELLA. THE FOX SPARROW, ETC.

(1) Adult male like female; young like adult.

Prevailing colors, brown, rufous, gray, white.

The transition from a streaked to a uniform mode of coloration is shown by the backs of *P. iliaca* and *P. iliaca unalaschcensis,* which are races of the same species probably largely due to climatic influences. Upon the breast the primitive streaked plumage is replaced by the second type of marking, the spot. The markings of this genus are surprisingly like those of the thrush family, and may well have been produced by the same or similar influences.

GENUS EMBERNAGRA. TEXAS SPARROW, ETC.

(1) Adult male like female; young like adult (?).

Prevailing colors, olive-green, brown, gray, buffy, white, yellow.

This genus appears as if it had been more brilliantly colored in past time, but had lost most of its characteristic marks. It is specialized beyond the streaked plumage, and the head has distinctive although very dull marks. The only conspicuous character which has persisted is the yellow edge of the wing, which is apparently either a sexual or recognition marking, developed upon this conspicuous place (see *ante*, p. 184).

GENUS PIPILO. THE TOWHEES.

(2) Adult male like female, or (8) more conspicuously colored than female; young like some ancestral stage of the adult.

Prevailing colors, black, white, brown, rufous, olive green.

This genus is of particular interest in the study of the evolution of color. In the first place, the relation of the sexes in such very closely allied species as *P. erythrophthalmus* and *P. maculatus*, changes in regard to the correspondence of color. Again, there are three groups of species in the genus, and they seem at first glance to be hopelessly different in point of color origin. An examination discloses the interesting fact, however, that there are more points of similarity than would at first appear. The first group includes *P. erythrophthalmus*, *P. maculatus*, etc., the second *P. chlorurus*, and the third *P. fuscus*. The differences between the first and second are peculiarly striking, yet it will be noticed that the color of the flanks of the first is the same as the crown of the head of the second, and accordingly might be explained in accordance with the law of assortment of pigments, the color being distributed to different parts of the body in different species. *P. maculatus* has the feathers of the throat subterminally marked with with white, showing that it formerly had a white throat, such as *P. chlorurus* has at present. The only part about which there appears to be some difficulty of explanation is the olive green color of the back in *P. chlorurus*. The following attempt to explain it according to the law of pigment assortment may seem forced, but is suggested for what it is worth. There can be no doubt that the orchard oriole *(Icterus spurius)* was originated from the same stock as the other orioles, from the fact that the young plumage is almost identical in color with corresponding stages of other species. Here it seems that an intensification of yellow has produced a reddish brown instead of scarlet or crimson. In the same way, it is not impossible that the rufous color of Pipilo has been produced by the intensification of yellow, which color is present in certain members of the genus, including *P. chlorurus*. The combination of the yellow with the black would produce the olive green of *P. chlorurus*. As showing the relationship of *P. fuscus*, it is to be noted that in this species the feathers of the belly are white, basally, indicating that this part was formerly as in *P. maculatus*.

These birds are all the descendants of a streaked ancestor, but what factors have produced the wide diversity at present exhibited we cannot well determine. Complete and long continued isolation of the original species into three sections may have started the different branches upon widely different courses of evolution. Sexual selection, recognition and protection have all played a part in this.

GENUS CARDINALIS } THE CARDINALS.
GENUS PYRRHULOXIA }

(7) Adult male more conspicuously colored than female; young similar to adult female, but duller.

Prevailing colors, vermilion, carmine, black, brown, buff, gray.

Sexual selection alone can account for the colors of this genus, the females having inherited a small portion of the bright colors of the male. The fact mentioned by Beddard (see *ante*, p. 228) that when food changes the color of the plumage certain parts are more readily affected than others may account for the color running down the breast in Pyrrhuloxia and not including the sides.

GENUS HABIA. THE GROSBEAKS.

(10) Adult male more conspicuously colored than female; young male (first autumn) unlike adult of either sex; young female like adult female.

Prevailing colors, black, white, rose, yellow, brown.

The two species constituting this genus are peculiarly interesting from the great difference in the adult males, and the different stages of specialization from the comparatively unmodified young plumage. As these different stages of transition were given previously they need not now be repeated (see *ante*, p. 223). Sexual selection has apparently been by far the most important factor in the evolution of the colors of the adult male, but the conspicuous white and black wing and tail markings are doubtless recognition marks, partly directive and partly discriminative. The striking example of correlative red and yellow in this genus has been sufficiently dwelt upon (see *ante*, p. 155).

GENUS PASSERINA. THE VARIED BUNTING, ETC.

(7) Adult male more conspicuously colored than female; young like female, but generally somewhat duller.

Prevailing colors, black, white, red, purple, blue, yellow, green, brown.

This genus belongs properly to the tropics, and the males have all the wealth and diversity of coloring of birds from that region. The colors appear to be principally due to sexual selection favored by a tropical environment, the females being dull brown in remarkable contrast to the males.

GENUS SPOROPHILA. THE SEEDEATERS.

(7) Adult male more conspicuously colored than female; young like female, but young male generally intermediate in plumage between female and male.

Prevailing colors, black, white, olive, brown; gray.

This genus is apparently becoming melanistic in accordance with the laws of growth and specialization. The colors are doubtless useful for purposes of recognition.

GENUS EUETHEIA. THE GRASSQUITS.

(7) Adult male more conspicuously colored than female; young like female, but young male generally intermediate in plumage between female and male.

Prevailing colors, black, white, gray, yellow, olive green, rufous.

The yellow and black of this genus are refined from the olive green of the back. The presence of black upon the breast instead of the back would seem to be in opposition to the rule that the excess of sunlight has caused the greater part of pigment to seek the back, but may perhaps be interpreted in harmony with this. Where black is the result of an intensified brown or blue it appears to be caused simply by the amount of pigment matter crowded into a given space. If, on the other hand, the system of a bird gives rise to definite black pigment, the color is not dependent quite so exclusively upon the amount. In the present instance two pigments, yellow and black, have apparently crowded together upon the back, producing the olive green color, while upon the breast they have been separated.

The tendency of the genus is towards the assumption of a completely melanistic plumage.

GENUS SPIZA. THE DICKCISSEL, ETC.

(8) Adult male more conspicuously colored than fe-

male; young with a peculiar first plumage, but similar to that of female.

Prevailing colors, black, white, gray, yellow, rufous.

This bird shows three well marked stages of evolutionary progress, from the young plumage through the adult female to the adult male. The colors of this genus are identical with the preceding, except the olive green, which is wanting in the present group. The distribution of color, however, appears to have been rather more controlled by sexual selection than in the previous instance.

GENUS CALAMOSPIZA. THE LARK BUNTING.

(5) Male in breeding plumage differs from female; young with peculiar first plumage.

Prevailing colors, black, white, brown, slaty, gray.

There is a strong tendency toward the assumption of a melanistic plumage in this genus, although worn only by the male during the summer. The conspicuous white wing patch is probably a directive mark.

FAMILY TANAGRIDÆ. THE TANAGERS.

This family consists of brilliant tropical genera, a few species of which have spread over the boreal province. The female are dull colored and the young generally represent a still earlier phase of developmental history. But two genera are present within our limits, Euphonia and Piranga. The prevailing colors of the male of the former are blue, black, and chestnut or rufous; of the latter scarlet, yellow and black. The female of Piranga is olive green and yellow, the colors of the male having been produced first by the assortment of pigments into yellow and black, and second by an intensification of the yellow into scarlet. The relationship of Euphonia to Piranga, so far as its colors are concerned, is shown by the plumage of the female which is colored an olive green, more yellowish below, but, unlike Piranga, with a blue patch on the head. What this blue was derived from is not apparent, unless it is separate pigment which is wanting in Piranga.

FAMILY HIRUNDINIDÆ. The Swallows.

All the members of this family are specialized beyond the streaked plumage, and the tendency is for the back to be darker than the breast, both being marked with solid colors instead of mottlings or streaks. All this is the result of specialization in accordance with the general laws of pigment deposition. The colors and markings which cannot be explained by these general laws appear to be the result of sexual selection.

Genus Progne. The Martins.

(7) Adult male more conspicuously colored than female; young like adult female.

Prevailing colors, black (metallic bluish), gray, white.

The male represents the culmination of specialization in a black plumage, enhanced, by sexual selection, by burnished blue lustre. The female has the underparts gray, becoming white posteriorly, showing the manner in which the black plumage was assumed, the abdomen probably having been affected last.

Genus Petrochelidon. The Cliff Swallows.

Genus Chelidon. The Barn Swallows.

(1) Adult male like female; young like adult but duller.

Prevailing colors, black, blue-black, white, chestnut, cinnamon, gray, brown.

The general tendency in these two genera, is, as in Progne, to have the back dark metallic black with greenish or bluish reflections, and the under parts more or less white or suffused with rusty more or less intensely.

The different characteristic marks were probably developed as discriminative characters first and afterwards modified by sexual selection.

GENUS TACHYCINETA. WHITE-BELLIED SWALLOW, ETC.

(8) Adult male more conspicuously colored than female; young with a peculiar first plumage, although similar to adults, the colors being duller.

Prevailing colors, steel blue, bronze green, purplish, violet, brown, white.

The beautiful colors of the adults of this genus are the result of sexual selection, the female, particularly of the exquisitely marked violet-green swallow *(T. thalassina),* being much duller than the male. This is an instance where Mr. Wallace's theory of the dull colors of female birds as the result of the supression of bright tints from need of protection appears to be utterly untenable. White, in contrast to some dark color is the most conspicuous marking in nature. The under parts of the female of this bird are pure white as in the male, but the violet-green colors of the male which are beautiful but in no way glaring or conspicuous, are much dulled in the female, conclusively showing that the need for protection is not the factor in this instance.

GENUS CLIVICOLA. THE BANK SWALLOW.

GENUS STELGIDOPTERYX. THE ROUGH-WINGED SWALLOW.

(2) Adult male like female; young similar to adult, but some of the feathers with lighter edgings.

Prevailing colors, brown, gray, white.

These are the two least specialized species in the group, being not unlike the young of the preceding genus.

The colors are to be accounted for almost wholly by the effect of environment and general laws of pigment development. It is a remarkable thing that two forms so much alike in respect to coloration as these genera are, should have no discriminative marks. It may be that the similarity of coloration is due to a retrogressive convergance, this view being strengthened by the similarity of the coloration of both genera to the young of Tachycineta.

FAMILY AMPELIDÆ. The Waxwings, etc.

Genus Ampelis. The Waxwings.

(2) Adult male like female; young like some ancestral stage of the adult.

Prevailing colors, black, white, brown, vinaceous, cinnamon, ashy, gray, yellow.

I see no possible way of accounting for the beautiful soft blended tints of these birds, except by sexual selection. The attainment of the goal of specialization by the male has permitted the female to acquire the complete plumage of the male, but the young still retains upon the under parts the streaks of the ancestral bird. The white wing markings so conspicuous in *A. garrulus* are recognition marks, probably both directive and discriminative in nature. The rufous under tail coverts of this species as contrasted with the white of *A. cedrorum*, appear to be a discriminative mark. An interesting example of correlation is to be found in the wax-like appendages to the wing feathers, which are also occasionally present, but in less pronounced degree, upon the tail. This genus also affords an instance of red as the correlative of yellow in the border of the tail, which is yellow in North American species, but red in the Japanese waxwing *(A. japonicus).*

Genus Phainopepla. The Phainopepla.

(7) Adult male more conspicuously colored than female; young like female.

Prevailing colors, bluish black, white, brownish gray.

The male has become completely glossy blue-black, with the exception of the white recognition mark on the wing, while the female is a brownish gray, not having yet acquired the specialization of pigmentation of the male.

FAMILY LANIIDÆ. The Shrikes.

Genus Lanius. The Shrikes.

(1) Adult male like female; young similar to adult.

Prevailing colors, black, white, gray, brownish.

I am unable to suggest any satisfactory explanation of the colors of this genus, although the black line through the sides of the head, and the black wings and tail with the contrasted white are excellent recognition markings. I fail to see any particular need for such markings, as the birds are not very social in their habits, and have no enemies to fear, in particular. Neither could these be discriminative marks, for they are shared in common by all the genera. Their origin must, accordingly, date back to some ancestral form in which such characters may have been of utility.

FAMILY VIREONIDÆ. The Vireos.

Genus Vireo. The Vireos.

(1) Adult male like female; young more or less closely like adult, or (8) male slightly more conspicuously colored than female; young with a plumage slightly duller than female.

Prevailing colors, black, white, olive green, brown, gray, yellow.

The vireos in their colors appear to be like undeveloped warblers. The olive green, black and yellow, so characteristic of that group is present here also, but has not yet obtained the mastery over the gray tints. I believe this genus shows us the effect of sexual selection which has, comparatively speaking, been in operation for a short time only. Although a number of species have one or more geographical races, differing but little from one another, the species themselves are for the most very distinct, even though few of them have any particularly striking individual characters. In some genera varieties merge into species in a gradual transition, as, for instance, in Melospiza, Sphyrapicus, Zonotrichia, etc., where the extreme varieties are almost or quite as different as the most closely allied species, but here, as a general rule, there is a considerable gap between the varieties of one species and the next most closely related form. This would seem to indicate that the different species had diverged quite widely before attaining their present distribution upon which the existing varieties depend. The isolation which produced the different species is difficult to determine, but it is a noteworthy fact that to the south certain mainland and insular forms pass by gradual stages from variety to species. This is notably the case with *V. crassirostris* and *V. crassirostris flavescens* of the Bahamas, and *V. ochraceus* of southern Mexico, which is intermediate in color between the two preceding. It would seem then that the differentiation of species may have been due to geographical isolation in a southern district.

FAMILY CŒREBIDÆ. The Honey Creepers.

Genus Certhiola. The Honey Creepers.

(2) Adult male like female; young like some ancestral stage of the adult.

Prevailing colors, black, white, olive, brown, gray, yellow.

The colors of this genus have been developed in accordance with the law of the assortment of pigments, but whether sexual selection or need for recognition has been the more important agent is not easily established. Both factors have apparently been operative.

FAMILY MNIOTILTIDÆ. THE WOOD WARBLERS.

This extensive family is particularly interesting from the almost uniform degree of specialization of color marks which it presents. They are to be explained principally by the influence of sexual selection supplemented by the advantage of recognition marks. The different genera, with some few exceptions, are closely related so far as their colors are concerned, making this family one of the best illustrations of the law of the assortment of pigments. The prevailing colors of the entire family are olive green, black and yellow. The gray which so often appears may be due to the bleaching of the olive green; the red, as in Setophaga, is obviously the result of intensification of the yellow, and the chestnut may be also a modification of the yellow, analagous to the change in *Icterus spurius*. This leaves the blue still unaccounted for, and it must be confessed that this is the most difficult color to explain in harmony with the law of pigment assortment. It is probably a modification of the black pigment, however. In the cærulean warbler *(Dendroica cærulea)*, the young is olive green, and the color of the adult is apparently produced by the loss of the yellow pigment.

The different species of a genus are as a rule sharply separate from one another, and do not blend through local races. Most species are not very widely spread over the country, and accordingly comparatively few are divisible into geographical varieties.

GENUS MNIOTILTA. BLACK AND WHITE WARBLER.

(7) Male more conspicuously colored than female; young similar to adult female.

Prevailing colors, black, white, brownish (in young).

This bird presents one of the best examples of black and white as cognate colors. The markings are modifications of the primitive streaked plumage, the streaks having simply been defined and accentuated, but whether chiefly by sexual selection or by other factors, I am unable to surmise.

GENUS PROTONOTARIA. PROTHONOTARY WARBLER.

(7) Adult male more conspicuously colored than female; young similar to adult female.

Prevailing colors, white, bluish gray, olive green, yellow.

The markings of this genus are probably due to sexual selection, which has not yet reached the end of its specializing influence. Individual variation in the head of the male throws considerable light upon the law of the assortment of pigments and correlative colors. In the young the top of the head is olive green, but with the assumption of a full plumage the tendency is for it to become more and more pure yellow in color. In full plumed individuals the yellow becomes an intense cadmium, sometimes tinted with orange.*

GENUS HELINAIA. SWAINSON'S WARBLER.

GENUS HELMITHERUS. WORM-EATING WARBLER.

(1) Adult male like female; young similar to adult.

Prevailing colors, black, white, brown, buff, yellowish.

These two genera may represent forms which have degenerated in respect to their color markings, but perhaps are species which have not yet attained the degree

---

* Ridgway's Manual, p. 484.

of specialization of the rest of the family. The fact which looks toward degeneration is that neither the adult nor the young show any tendency toward a streaked plumage (unless the specialized head stripes of Helmitherus be taken into account) which we would expect to find if the birds still retained a primitive coloration. The general aspect of both these species is that of forms which had been brightly colored and lost all but a vestige of their former splendor. They might be looked upon then as geratologous forms (see *ante*, p. 78).

GENUS HELMINTHOPHILA. GOLDEN-WINGED WARBLER, ETC.

(7) Adult male usually more conspicuously colored than female [(2) adults sometimes alike]; young usually similar to female, but sometimes (8) with a peculiar first plumage.

Prevailing colors, black, white, ash gray, brown, chestnut, olive green, yellow.

Sexual selection, aided by isolation, has doubtless been the chief factor in the origination of the markings of this genus. The colors may all be explained as suggested in speaking of the family in harmony with the law of the assortment of pigments. Geographical isolation has been an important, though probably not the only form of segregation. The different stages through which the genus has progressed are well shown by the forms of to-day. The young of the Tennessee warbler *(H. peregrina)* which is plain olive green, paler on the breast, represents the primitive plumage of the genus. Through pigment assortment by sexual selection a yellow crown patch was developed. Then the species was isolated in two districts, east and west of the Rocky Mountains, by the ice age, apparently. The eastern species developed white recognition markings upon the tail which have persisted through all its modifications, this character being lacking in western forms. Sexual selection, aided by further isolation of some sort, next produced one species with a yellow and one with a black throat. The latter by further isolation became subdivided into one species with the yellow crown persisting and another in which it is replaced by black, except on the forehead.

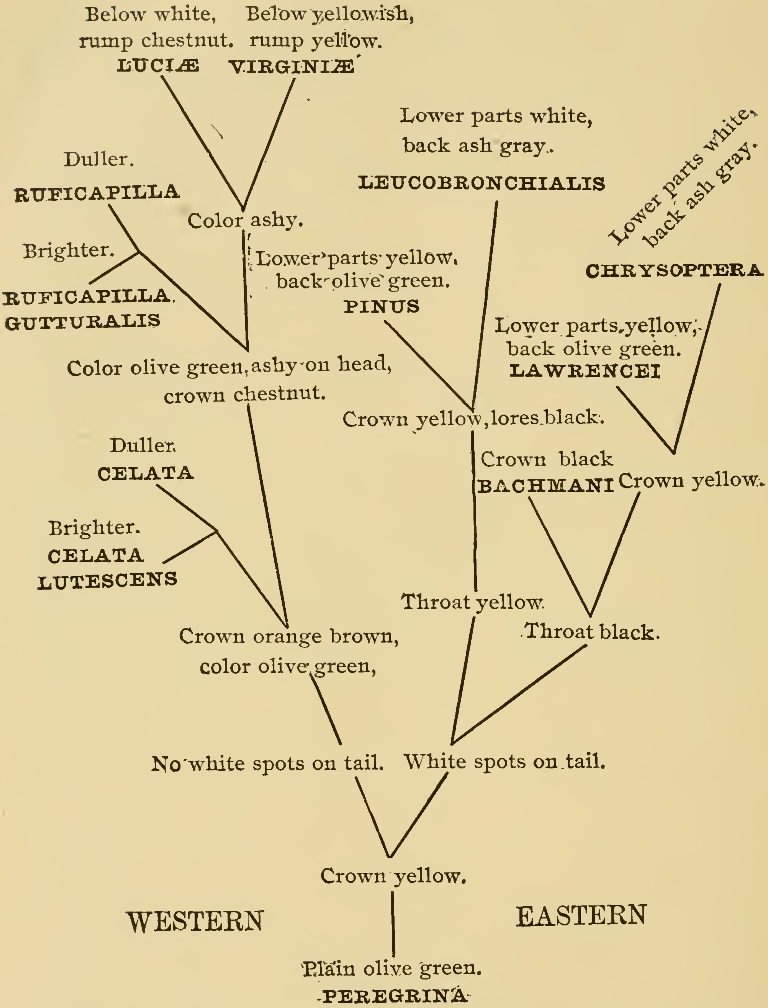
In the west the color of the crown patch became changed from the yellow to a chestnut brown apparently by a process of intensification. The orange-crowned warbler *(H. celata)* represents the stage intermediate between the yellow and the rufous crown. The general olive green color next became bleached out into an ash, the head being first affected, and at the same time the yellow of the under parts became bleached into white. Sexual selection, in conjunction with isolation, finally produced two species from this last one, one with the rump yellow, the other with the rump chestnut, corresponding to the changes of the crown patch. Two eastern species, *H. lawrencei* and *H. pinus*, seem to be dichromatic, having the normal olive green and yellow colors, and in the same locality being found with this color replaced by gray and white. The change here is similar to that from *H. ruficapilla* to *H. luciæ*, only the two forms have not become established as distinct species in the former instance. Mr. Ridgway, in a foot note in the Manual of North American Birds* suggests another explanation, as follows: "In a large series of specimens, every possible intermediate condition of plumage between typical *H. pinus* and *H. leucobronchialis* is seen, just as in the case of *H. chrysoptera* and *H. lawrencei*. If we assume, therefore, that these four forms represent

---

* p. 486.

merely two dichroic species, in one of which *(H. pinus)* the Xanthochroic (yellow) phase, and in the other *(H. chrysoptera)* the leucochroic (white) phase represents the normal plumage—and admitting that these two species, in their various conditions, hybridize (which seems to be an incontrovertible fact)—we have an easy and altogether plausible explanation of the origin of the almost interminably variable series of specimens which have found their way into the 'waste-basket' labelled '*H. leucobronchialis.*' "

Whatever view may prove to be the correct one, the important point to note in this connection is that olive green and yellow seem to be very closely related to gray and white, and that the latter has the appearance of being a bleached out phase of the former, due perhaps to the failure to deposit the pigment in sufficient quantities. The accompanying table shows the probable genealogy of the genus. I am largely indebted to Coues' Key for the specific characters, which are there stated in a particularly terse and comprehensive table.



Genus Compsothlypis. The Parula Warbler, etc.

(8) Adult male more conspicuously colored than female; young with a peculiar first plumage.

Prevailing colors, white, bluish gray, olive green, yellow, orange brown.

Sexual selection appears to have been the chief factor in the origination of the color markings of this genus. The orange brown of the breast is an intensification of yellow analogous to that of the crown of *Helminthophila celata*.

The young plumage shows the coloration of the primitive bird—dull olive and gray.

GENUS DENDROICA. THE WOOD WARBLERS.

(7) Adult male more conspicuously colored than female; young similar to female, or (8) with a peculiar first plumage; or, more rarely, (5) male differs from female in breeding plumage only; young with peculiar first plumage.

Prevailing colors, black, white, olive green, yellow, orange, bluish, chestnut.

There seems to be little doubt that the varied color markings of this extensive genus have been produced for the most part by the action of sexual selection. As this is a peculiarly favorable genus for the study of the effects of sexual selection I have prepared tables of the colors of the entire genus, one for the female or immature plumage and the other of the adult males (Plates XVIII and XIX). In order to get the colors of any one species read the colors in a line from right to left, while to compare the colors of the same part of the body in different species read the columns up and down. These two tables illustrate sexual selection, pigment assortment, environmental influences, and many less universal points. It will be noticed that although the colors in Plate XVIII are of dull monotonous tints, nearly all the specialized colors are suggested. The general effect of this plate is olive green on the left half and white or yellow on the right. The only conspicuous exceptions to the olive color are the three species in which the rump is yellow, and those in which the upper tail coverts are bluish gray. The white and yellow on the right hand side is considerably interrupted by streaks, but in general is fairly constant except in *D. æstiva* and its allies. From this it seems undoubted that the ancestor of the genus was an olive green bird, probably streaked both above and below. The olive green is a combination of black and yellow, which were apparently the original pigments of the genus. They were thrown off indiscriminately producing the olive green effect, and the bulk of the pigment following the shaft of the feather would give a streaked appearance to the bird. Excess of sunlight upon the back would cause the greater part of the pigment to lodge there, and the result would be a bird not unlike a composite of the females here represented.

Then sexual selection would step in as a factor in producing change. Occasionally a single feather or a particular spot on the bird would receive a trifle more of either the yellow or the black pigment than usual, from a cause which, for lack of a better name, we may call fortuitous, and this bird would be conspicuous among his fellows, and more easily gain a mate and leave offspring. In the course of time this character would become exaggerated, from the continual selection, into a specific character. Olive green, black and yellow would then be the three colors of the genus, the back being darker than the breast, and the black and yellow occurring upon the most conspicuous parts of the body. It will be noticed from the diagram that these colors occur most frequently upon the top of the head, rump, upper tail coverts, ear coverts, throat and breast, where they would be most noticeable. An intensification of the yellow would produce orange, as in *D. blackburniæ*, while a darkening of this, perhaps by reintroducing black, would result in the chestnut of *D. bryanti*, etc. This leaves only the blue as a doubtful color, although it appears to be related to the black through gray.

The following facts, shown by these plates, seem to be inexplicable in any way except by the law of the assortment of pigments, or else this law seems to account for them most satisfactorily: (1) the specialized colors of the males are generally the colors which, when combined, would produce the generalized colors of the females; (2) the specialized colors of the males when combined generally produce the generalized colors of the males; (3) exactly the same color appears in widely separated parts of the body of one species; (4) exactly the same color often appears on the same or on different parts of the body of different species; (5) in general, the same colors run through the entire genus, however differently they may be combined or modified in quantity or distribution.

The following details concerning the proportion and distribution of the different colors of the genus in the adult male plumage may be of interest in this connection: Black is present in nineteen out of the twenty-four species, being confined exclusively or mainly to the upper parts of the body in four, and to the lower parts in one species. The top of the head is solid black in four species, the back mainly or entirely so in two, the ear coverts in ten, throat in six, breast in three, and sides in one. Yellow appears in eighteen species, being confined to the upper parts of the body in two species and to the lower parts in eight. The top of the head is yellow in five species, the back never so. The rump is yellow in four, ear coverts in four, throat in nine, and breast in eleven. Olive or olive green occurs in thirteen species, being confined to the upper parts of the body in all of them. Blue is present in eight species, in all but one of them *(D. cærulea)* being excluded from the lower parts, while orange or chestnut are also represented in eight species. The following correlations of color may also be noted: When white appears on the throat or ear coverts it is the color of the breast and abdomen; when the rump is yellow the throat is yellow or white; when the top of the head is chestnut or orange, the throat is generally the same (one exception); when the top of the head is yellow the throat is generally yellow or white; when the back is streaked the sides are generally streaked.

GENUS SEIURUS. THE WATER THRUSHES, ETC.

(2) Adult male like female; young with a slightly less developed plumage.

Prevailing colors, black, white, brown, olive, orange, rufous.

The resemblance of Passerella to some of the thrushes has already been mentioned, but the present genus exhibits even more perfect similarity to the thrushes, both in color and markings. The orange crown of *S. aurocapillus* and the greenish olive color of the back in this species are of course exceptions. It would seem that the markings are to be explained largely by the general laws of pigment deposition, the greater amount of pigment going to the back has made it uniform in color, while the breast has retained the primitive spotted plumage, the markings having been defined and accentuated by sexual selection, perhaps. The superciliary stripe is a conspicuous recognition mark, and may have originally been discriminative in character, distinguishing the ancestral form of *S. noveboracensis* from the ancestral form of *S. aurocapillus* with a white orbital ring. The colors of this latter species are similar to the typical colors of the family—black, yellow (orange) and olive green, but the other species are all brown.

Genus Geothlypis. The Kentucky Warbler, etc.

(7) Adult male similar to female (but more conspicuously colored); young similar to female, or (8) with a more simple plumage than the adult.

Prevailing colors, black, white, ashy, brown, olive green, yellow.

The characteristic colors of the family, black, yellow and olive green, are conspicuously present in this genus —the result of pigment assortment. This genus is a particularly good example of the combined action of isolation, sexual selection, and climatic influences in the production of different species. Geothlypis has more geographical races than is usual in the family, and these are clearly the result of environmental influences. This is conspicuously the case with the different varieties of *G. trichas*. Such species as *G. melanops* and *G. beldingi* are merely climatic races in which the modification has become extreme enough to establish them as distinct from *G. trichas*. The Mexican yellow throats are distinguished from the Guatemalan species by the eyelid being black in the latter and white in the former. This cannot be solely the result of climatic influence, but is due either to isolation alone or to isolation and selection. The specific distinctions between *G. formosa*, *G. agilis*, *G. philadelphia* and *G. macgillivrayi* are due to isolation and sexual selection. *G. macgillivrayi* appears to be a retarded form of *G. philadelphia*.

Genus Icteria. The Chats.

Genus Sylvania. The Hooded Warbler, etc.

(8) Adult male more conspicuously colored than female; young with a peculiar first plumage.

Prevailing colors, black, white, gray, olive green, yellow.

The colors of these two genera are typical of the family, and are to be explained by pigment assortment and sexual selection.

GENUS SETOPHAGA. THE REDSTARTS.

(7) Adult male more conspicuously colored than female; young similar to female, but duller, or (2) adult male like female, young with a peculiar first plumage.

Prevailing colors, black, white, yellow, red, chestnut, brown.

The colors in this genus are the result of sexual selection. By pigment assortment the olive green has become entirely replaced by its component black and yellow. The yellow has become intensified into the correlative orange or red, and by sexual selection has been located under the wings, where it will be most conspicuous when the bird is in motion. The female has inherited the yellow color in place of the intensified red, and the black is replaced by olive gray. As in the orioles where chestnut occurs apparently intimately connected with yellow and intensified red, so here also a species is found *(S. miniata)* with a crown-patch of chestnut, apparently intensified from yellow. In this species the red of the under parts is on the breast, extending down on the belly, instead of on the sides, and is much more intense than in *S. ruticilla*. The different species have doubtless been originated by sexual selection and isolation in a tropical climate. The fact that in some of the most brilliant species the female is colored like the male is an evidence of a high degree of specialization.

GENUS CARDELLINA. RED-FACED WARBLER.

GENUS ERGATICUS. RED WARBLER.

(2) Adult male like female; young with a peculiar first plumage.

Prevailing colors, black, white, gray, brown, red, vermilion.

Like Setophaga, these two genera of brilliant red warblers are tropical in their distribution, and the colors have been produced by sexual selection in a hot climate.

Genus Basileuterus. Brasher's Warbler, etc.

(1) Adult male like female; young like the adult (?).

Prevailing colors, black, yellow, olive green, chestnut, orange-rufous.

The colors in this genus are the conventional ones of the family, and are to be accounted for as in the preceding instances. The different species appear to be largely due to climatic influences.

FAMILY MOTACILLIDÆ. The Wagtails and Pipits.

(5) Male in breeding plumage differs from female; young with peculiar first plumage (Motacilla and Budytes), or (4) both sexes change with season; young differ from adults at any season (Anthus).

Prevailing colors, black, white, gray, bluish, brown, yellow, olive green.

In this family a certain similarity to the colors of the genus Dendroica is to be noted. The bluish ground color is present in some of the species of Motacilla, while in *M. melanope* and in the genus Budytes the ground color is olive green, thus presenting the two colors most often occurring in the generalized markings of Dendroica. In this family also black and yellow form the principal specialized marks. Sexual selection has evidently been the factor which has produced the markings in this group, although far less completely carried out than in Dendroica. The terrestrial habits of the members of the family may have had a tendency to suppress the bright colors, Anthus in particular being protectively colored. The gregarious disposition of these birds has rendered necessary the white recognition marks of the wing and tail.

FAMILY CINCLIDÆ. The Dippers.

Genus Cinclus. The Dippers.

(1) Adult male like female; young like adult (young and winter plumage slightly different).

Prevailing colors, grayish, brownish, white.

The colors are protective, harmonizing with the rocks along the mountain streams frequented by these birds. The white color of the edges of the feathers on the lower parts of the body in young and winter specimens points to an affinity to southern forms, in which the under parts are white. Thus in *C. leuconotus* of Colombia and Ecuador the entire under parts, head and middle of back are white. The adult of *C. ardesiacus* of Costa Rica is very similar to *C. mexicanus*, but the breast of the young is almost pure white. Why there should be an increase in pigment toward the north instead of the reverse, as is the rule, I cannot suggest.

FAMILY TROGLODYTIDÆ. The Wrens, Thrashers, etc.

(1) Adult male like female; young like adult, or (2) young with a peculiar first plumage.

Prevailing colors, black, white, slaty, gray, brown, rufous, chestnut.

These birds are, as a rule, not highly specialized, so far as their colors are concerned, reminding one of the general plan of color markings among many of the sparrows. As a rule, the back is some shade of brown or rufous, with the breast white, and either the breast alone, or sometimes both back and breast, profusely streaked or spotted. Sexual selection has had, it would seem, but a subordinate part in producing this plan of marking.. Allusion has already been made to the use of the chestnut color of the under tail coverts of Galeoscoptes as a recognition marking (see *ante*, p. 203), while the black cap of this genus may serve a similar purpose. The white wing and tail characters are either directive or discriminative marks, and are very generally present. When the adult are specialized beyond the streaked plumage, either by the assumption of a uniform dark color or of a dark back and light under parts, the young show, to a more or less marked degree, the streaked or spotted plumage of the ancestral form. I am unable to suggest any explanation of the barred markings so common on the posterior part of the body among the wrens.

FAMILY CERTHIIDÆ. THE CREEPERS.

GENUS CERTHIA. THE CREEPERS.

(1) Adult male like female; young like adult.

Prevailing colors, brown, grayish, white.

The colors of this genus are protective in nature, the back harmonizing perfectly with the trunks of the trees to which the bird clings. The breast is white in accordance with the general laws of growth.

FAMILY PARIDÆ. THE NUTHATCHES AND TITS.

(1) Adult male like female; young like adult (except in Auriparus).

Prevailing colors, black, white, brown, bluish, gray, yellow.

The birds of this family are highly specialized, although never brilliantly colored. The primitive streaked pattern is almost or completely wanting even in the young plumage, showing that the specialization has been carried very far. Auriparus is the only genus which displays any bright colors, and in this instance the yellow head is obviously the result of sexual selection, being much duller in the female and wanting in the young. How this color can be accounted for in accordance with the law of the assortment of pigments I do not see at present, for it would seem that some species in the family should be colored olive green. The different species of the genus Sitta are very distinctively marked. As the sexes are alike it is difficult to decide how important sexual selection may have been in originating these markings and the same is true of Parus. The latter genus has been especially susceptible to the influences of climate, a large number of the species breaking up into geographical races. Psaltriparus is equally influenced by climate. Little inconspicuous marks are generally the most difficult to explain, and this is notably the case with Psaltriparus. Of what possible utility can be the brown head as contrasted with the gray back? It is present in both sexes so could hardly be looked upon as the result of sexual selection, nor is it conspicuous enough to be of use as a recognition mark. If, however, some other bird inhabiting the same territory looked very much like Psaltriparus but without the brown cap, it might serve at close range as a discriminative mark.

FAMILY SYLVIIDAE. THE WARBLERS, KINGLETS, AND GNATCATCHERS.

(7) Adult male generally more conspicuously colored than female; young like adult female, or (8) with a peculiar first plumage.

Prevailing colors, black, white, olive green, yellow, orange, red, bluish gray.

The colors of this specialized family may be explained by sexual selection and the assortment of pigments. The similarity to the Mniotiltidæ and Motacillidæ in point of coloration is quite striking, the olive green, black, and yellow being present and also the bluish gray. Phyllopseustes has not progressed beyond the generalized stage of the warblers, no conspicuous sexual ornaments having been added, but the crown patch of Regulus is a highly developed character. In *R. calendula* the yellow has been completely intensified into scarlet, but in *R. satrapa* the intensification is less complete. This species exhibits the pure yellow and its intensification into orange in different parts of the crown. The bluish or black crown patch of Polioptila is probably the result of sexual selection, as it is confined to the male. A remarkably fine illustration of discriminative marks is shown in the outer tail feathers of *P. plumbea* and *P. californica*, the outer web being white in the former and black in the latter species.

FAMILY TURDIDÆ. The Thrushes, Solitaires, Stonechats, Bluebirds, etc.

(8) Adult male usually more conspicuously colored than female; young with a peculiar first plumage, or (2) male like female; young like some ancestral stage of adult.

Prevailing colors, black, white, brown, rufous, plumbeous, bluish gray, blue.

The ancestral form from which this family arose was a brown spotted or mottled bird, as shown by the young of to-day. The different genera have diverged very widely in point of color, however, but may all be explained in accordance with the law of the assortment of pigments. If the primitive pigments were blue and reddish brown their combination would produce Myadestes, the brown alone would serve for Turdus, while the blue deepened would produce the color of the back of Merula and Hesperocichla, in combination with brown, the back of Cyanecula and Saxicola, and intensified, the back of Sialia. Deepened still further it would become the black of Merula and other species. In the same manner variations of the brown would account for the color of the under parts of the body.

Sexual selection with isolation has doubtless been an important, though by no means the only agent in the production of generic and specific characters. Recognition markings, both directive and discriminative have been developed by natural selection, and direct environmental influences have done their share in modifying species, as with *Merula confinis*.

BIBLIOGRAPHY.

The following list includes principally such titles as have been consulted in the preparation of this paper, but certain works have been included which have a bearing on the subject, but were not available for reference.

Allen, Grant. Physiological Æsthetics.

Allen, Harrison. The Distribution of the Color-marks of the Mammalia. Proc. Acad. Nat. Sci. Phil., 1888, p. 84.

Allen, J. A. On the Mammals and Winter Birds of East Florida, with an Examination of certain assumed Specific Characters in Birds, and a Sketch of the Bird-Faunæ of Eastern North America. Bull. Mus. Comp. Zool., ii, 1871, pp. 161–450.

——— On Geographical Variation in North American Birds. Boston Soc. Proc., xv, 1872, pp. 15, 212, 219.

——— Laws of Geographical Variation in North American Mammals and Birds. Am. Nat., viii, 1874, pp. 227–229.

——— The Influence of Physical Conditions in the Genesis of Species. Radical Review, i, May, 1877, pp. 108–140.

——— The North American Species of the Genus Colaptes, considered with Special Reference to the Relationships of *C. auratus* and *C. cafer*. Bull. Am. Mus. Nat. Hist., iv, pp. 21–44.

Argyll, Duke of. Acquired Characters and Congenital Variation. Nature, xli, pp. 173–174, 294–295, 366–367.

——— Organic Evolution, Nature, xxxiv, pp. 335–336.

Baird, Brewer & Ridgway. A History of North American Birds. Land Birds.

Baird, S. F. The Distribution and Migration of North American Birds. Am. Journ. Sci. and Arts, xli, 1866, pp. 78, 184, 337.

Ball, W. P. Are the Effects of Use and Disuse Inherited?

Beccari, O., and Morselli, E. L'eredità conservativa e la trasmissione dei caratteri acquisiti nella teoria della evoluzione organica. Riv. Filos. Sci., x, pp. 47–53.

Beddard, Frank E. Animal Colouration. An account of the Principal Facts and Theories Relating to the Colours and Markings of Animals.

Blythe, Edward. On the Reconciliation of certain apparent Discrepancies observable in the mode in which the seasonable and progressive Changes of Colour are effected in the Fur of Mammalians and Feathers of Birds; with various Observations on Moulting. Charlesw. Mag. Nat. Hist., i, 1837, 259–263; 300–311.

Brewer, Wm. H. On the Disposition of Color-Markings of Domestic Animals. Proc. A. A. A. S., 1881, pp. 246–251.

Brooks, W. K. The Law of Heredity. A Study of the Cause of Variation and the Origin of Living Organisms.

Camerano, Dr. L. Zoologische Anzeiger, 1884, p. 341.

Carter, R. Brudenell Colour-Vision and Colour-Blindness. Nature, xlii, pp. 55–61.

Chapman, A. C. On the Seasonable Changes in Plumage in Birds. O. & O., July, 1885, x, pp. 97–98.

Chapman, Frank M. On the Changes of Plumage in the Bobolink *(Dolichonyx oryzivorus).* Auk, vii, pp. 120–124.

——— On the Color-Pattern of the Upper Tail-Coverts in *Colaptes auratus.* Bull. Am. Mus. Nat. Hist., iii, pp. 311–314.

Cope, E. D. Origin of the Fittest. Essays on Evolution.

Coues, Elliott. Key to North American Birds.

——— Color-variation in Birds Dependent upon Climatic Influences. Am. Nat., vii, 1873, pp. 415–418.

Cunningham, J. T. The New Darwinism. The Westminster Review, July, 1891, pp. 14–28.

——— An Experiment concerning the Absence of Colour from the Lower Sides of Flat Fishes. Zool. Anz., xiv, pp. 27–32.

Dall, W. H. Dynamic Influences in Evolution. Proc. Biol. Soc. Wash., vi, pp. 1–10.

Darwin, Charles. The Descent of Man and Selection in Relation to Sex.

——— The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.

Darwin, Francis. Physiological Selection and the Origin of Species, Nature, xxxiv, pp. 407, 468.

Deane, Ruthven. Albinism and Melanism among North American birds. Bull. Nutt. Ornith. Club, i, 1876, pp. 20-24.

Dixon, Chas. Evolution without Natural Selection.

——— "Evolution Without Natural Selection." Reply to Review by Romanes. Nature, vol. xxxiii, p. 100.

Dyer, W. T. Thiselton. Mr. Romanes' Paradox. Nature, xxxi, pp. 7–9.

——— Mr. Romanes on the Origin of Species, Nature, xxxix, p. 126.

——— The Duke of Argyll and the Neo-Darwinians, Nature, xli, pp. 247–248.

——— Acquired Characters and Congenital Variation, Nature, xli, pp. 315–316.

Eimer, G. H. T. Organic Evolution as the Result of the Inheritance of Acquired Characters According to the Laws of Organic Growth. (Translation by J. T. Cunningham.)

——— Untersuchungen über das varriren der Mauereidechse, etc., 1881. Ueber die Zeichnung der Vögel und Säugethiere. Jahreshefte des Vereins fur vaterld. Naturk. in Wurttemberg, 1883, p. 556. Zoolog. Anzeiger, 1882-83. Humboldt, 1885-1887.

Eimer, G. H. T. Die Streifung der Thiere. Humboldt, vii, pp. 1–9.

——— Streifung der Thiere. Biol. Centralbl. vi, pp. 285–286. Ber. Vers. Naturf., Strassburg, 1885.

Elliot, D. G. Inheritance of Acquired Characters. Auk, ix, Jan. 1892, pp. 77–104.

Gadow, Hs. Description of the Modifications of certain Organs which seem to be Illustrations of the Inheritance of Acquired Characters in Mammals and Birds. Zool. Jahrb. v, pp. 629–646.

Galton, Francis. Origin of Varieties. Nature xxxiv, pp. 395-396.

——— On Blood Relationship. Proc. Roy. Soc., 1872.

Garman, S. W. Variation in the Colors of Animals. Proc. Am. Ass. Adv. Sci., xxv, pp. 187–204.

Gautier, A. Du Mecanisme de la variation des êtres vivants. Hommage à M. Chêvreul. Paris: Alcan, pp. 29–52.

Geddes, P. Proposed Contributions to the Theory of Variation. Rep. Brit. Ass., 1887, p. 735.

——— Theory of Growth, Reproduction, Sex and Heredity. Proc. Roy. Soc. Edinb., 1886, pp. 911–931.

Geddes and Thomson. The Evolution of Sex.

Giard, A. The Principle of Lamarck and the Inheritance of Somatic Modifications. (Trans.) Nature, xliii, pp. 328–332.

Gulick, J. T. The Variation of Species as related to their Geographical Distribution, illustrated by the Achatinellinæ. Nature, July 18, 1872.

——— Diversity of Evolution under one Set of External Conditions. Journ. Linn. Soc., xi, pp. 496–505.

——— Divergent Evolution through Cumulative Segregation. Jour. Linn. Soc. xx, pp. 189–274.

——— "Like to Like"—a Fundamental Principle in Binomics. Nature, xli, pp. 535–537.

——— Unstable Adjustments as effected by Isolation. Nature, xlii. pp. 28–29.

——— Indiscriminate Separation, under the Same Environment, a Cause of Divergence. Nature, xlii, pp. 369–370.

——— Divergent Evolution and the Darwinian Theory. Am. Journ. Sci., ser. 3, xxxlx, pp. 21–30.

——— The Inconsistencies of Utilitarianism as the Exclusive Theory of Organic Evolution. Am. Journ. Sci., xl, pp. 1–14.

——— The Preservation and Accumulation of Cross Infertility. Am. Journ. Sci., xl, pp. 437–442.

——— Intensive Segregation or Divergence through Independent Transformation. Journ. Linn. Soc. xxiii, pp. 312–380.

Hacker, V. Unter nichungen über die Zeichnung de Vogelfedern. Zool. Jabrb. iii, Jan. 15, 1888, pp. 309–316.

Haeckel, Ernest. The History of Creation, or the Development of the Earth and its Inhabitants by the Action of Natural Causes. A popular exposition of the doctrine of evolution in general, and of that of Darwin, Goethe and Lamarck in particular. The translation revised by Prof. E. Ray Lankester, M. A., F. R. S.

Hartog, Marcus. A difficulty in Weismann. Nature, xliv, p. 613.

Hodgkinson, Alexander. Colour and its relation to the Structure of Coloured Bodies; being an investigation into the Physical Cause of Colour in natural and artificial bodies, and the Nature of the Structure producing it. Proc. Manchester Literary and Phil. Soc., vol. ii, ser. 4 (vol. xxxii, old ser.), pp. 193–212.

Hurst, C. H. Heredity and Variation. Rep. from Tr. Manch. Micr. Soc., 1891, p. 9.

Hyatt, Alpheus. Fossil Cephalopoda in the Museum of Comparative Zoology. Proc. A. A. A. S., 1883, xxxii, p. 360.

Jeffries, J. A. Lamarckianism *v.* Darwinism. Am. Nat., xxv, pp. 42–49.

Keeler, C. A. The Colors of West Coast Mammals. Zoe, ii, pp. 203–216.

Kerschner, Dr. Zur Zeichnung der Vogelfedern. Arbeiten aus dem Zoologischen Institut zu Graz, i. Band, Nr. 4, Leipzig, 1886.

Lankester, Ray. Darwin *versus* Lamarck. Nature, xxxix, pp. 428–429.

Le Conte, Joseph. The Factors of Evolution. Their Grades and the Order of their Introduction. The Monist, i, pp. 321–335.

M'Aldowie, A. M. Development and decay of pigment layer on birds' eggs. Journ. Anat. Phys., xx, pp. 225–237.

MacMunn, C. A. Notes on some Animal Colouring Matters examined at the Plymouth Marine Biological Labratory. Journ. Mar. Biol. Assn., i, pp. 55–62.

McKendrick, J. G. On the Modern Cell Theory, and Theories as to the Physiological Basis of Heredity. Proc. Phil. Soc. Glasg., xix.

Meehan, T. On Parallelism in Distinct Lines of Evolution. Proc. Acad. Phil., 1886, pp. 294–295.

Meldola, R. Physiological Selection and the Origin of Species. Nature, xxxiv, pp. 384–385.

——— Lamarckianism *versus* Darwinism. Nature, xxxviii, pp. 388–389.

Merriam, C. Hart. Change of Color in the Wing-feathers of the Willow Grouse. Auk. ii, pp. 201–203.

——— North American Fauna, No. 3.

——— The Geographic Distribution of Life in North America. Proc. Biol. Soc. Wash., vii.

Merrifield, F. On the Conspicuous Changes in the Markings and Colouring of Lepidoptera caused by Subjecting the Pupa to different Temperature Conditions. Trans. Ent. Soc. Lond., 1891, pp. 155–168.

Mitra, S. B. Reply to Argyll. Nature, xxxiv, pp. 385–386.

Mivart, St. George. Natural Selection and Useless Structures. Nature, xxxix, 127.

——— Prof. Weismann's Essays. Nature, xli, pp. 38–41.

MORGAN, LLOYD. Animal Life and Intelligence.

——— Nature and Origin of Variations. Proc. Bristol Soc., vi, pp. 249–273.

MOSELY, H. N. Dr. August Weismann on the Importance of Sexual Reproduction for the Theory of Selection. Nature, xxxiv, pp. 629–632.

NELSON E. W. Report upon Natural History Collections Made in Alaska between the Years 1877 and 1881. No. iii, Arctic Series of Publications Issued in Connection with the Signal Service, U. S. Army.

OSBORN, HENRY F. Are Acquired Variations Inherited? Am. Nat., xxv, p. 191.

——— The Paleontological Evidence for the Transmission of Acquired Characters. Proc. Am. Ass. Adv. Sci. xxxviii, 1889, pp. 273–276.

——— Heredity: its Part in Organic Evolution. Am. Micros. Journ. xii, pp. 109–111.

PECKHAM, GEO. W. AND ELIZABETH G. Observations on Sexual Selection in Spiders of the Family Attidæ. Natural History Society of Wisconsin.

POULTON, E. B. The Colours of Animals, their meaning and use, especially considered in the case of Insects.

——— Lamarckianism *versus* Darwinism. Nature, xxxviii, p. 388.

——— A Difficulty in Weismann. Reply to Hartog. Nature, xlv, p. 52.

PRAEGER, WM. V. On Protective Coloration in the Genus Ægialitis. Auk. viii, p. 236.

RIDGWAY, ROBERT. The Grouse and Quail of North America Discussed in Relation to their Variation with Habitat. Forest and Stream, i, 1873, p. 289.

——— On the relation between Color and Geographical Distribution in Birds, as exhibited in Melanism and Hyperchromism. Am. Journ. Science and Arts, ser. 3, vol. iv, pp. 454–460; vol. v, pp. 39–44.

——— On some Remarkable Points of Relationship between the American Kingfishers. Bull. Nutt. Orn. Club, viii, pp. 59–60.

——— Manual of North American Birds.

——— A Nomenclature of Colors for Naturalists, and Compendium of Useful Knowledge for Ornithologists.

RILEY, CHARLES V. On the Causes of Variation of Organic Forms. Am. Ass. Adv. Sci., 1888, pp. 225–273.

ROMANES, GEO. J. Darwin and After Darwin. I. The Darwinian Theory.

——— Physiological Selection; An Additional Suggestion on the Origin of Species. Journal of the Linnean Society, xix, pp. 337–411.

——— "Evolution Without Natural Selection." [Review of book by Chas. Dixon.] Nature, xxxiii, pp. 26–27.

——— Physiological Selection; An Additional Suggestion on the Origin of Species (Abstract). Nature, xxxiv, 314–316, 336–340, 362–365.

——— Reply to Galton and Meldola. Nature, xxxiv, pp. 407–408.

Romanes, Geo. J. Physiological Selection and the Origin of Species. Nature, xxxiv, pp. 439, 545.

——— Physiological Selection; Nineteenth Century, xxi, pp. 59–80.

——— The Factors of Organic Evolution. Nature, xxxvi, pp. 401–407.

——— Mr. Seebohm on Physiological Selection, Nature, xxxviii, p. 246.

——— Lamarckianism *versus* Darwinism, Nature, xxxviii, pp. 413–490.

——— Definition of the Theory of Natural Selection, Nature, xxxviii, pp. 616–618.

——— Mr. Dyer on Physiological Selection. Nature, xxxix, pp. 103–104.

——— Natural Selection and the Origin of Species. Nature, xxxix, pp. 173–175.

——— Darwinism. Nature, xxxix, p. 645.

——— Weismann's Theory of Heredity. Contemporary Review, May, 1890, pp. 686–699.

Ryder, J. A. A Physiological Hypothesis of Heredity and Variation. American Naturalist, xxiv, p. 85.

——— An Attempt to Illustrate some of the Primary Laws of Mechanical Evolution. Proc. Phil. Acad. Nat. Sci., 1891, pp. 62–70.

Sauermann. Archiv. Anatomie und Physiol., 1889, Physiol. Abtheil., 543.

Schurmann, J. G. The Ethical Import of Darwinism.

Seebohm, Henry. The Geographical Distribution of the Family Charadriidæ, or the Plovers, Sandpipers, Snipes and their Allies. London, 1888.

Semper, Karl. Animal Life as affected by the Natural Conditions of Existence.

Spencer, Herbert. The Factors of Organic Evolution.

——— Principles of Biology.

Stejneger, Leonhard. Riverside Natural History. Vol. iv. The Birds.

——— Results of Ornithological Explorations in the Commander Islands and in Kamtschatka. Bull. U. S. Nat. Mus., 29.

Sutton, J. B. On Atavism. Proc. Zool. Soc., 1886, pp. 551–558.

Thomson, J. A. Synthetic Summary of the Influence of the Environment upon the Organism. Proc. Roy. Physical Soc. of Edinburg, vol. ix, p. 446.

Todd, J. E. Directive Coloration. Am. Nat., xxii, pp. 201–207.

Trotter, S. Effect of Environment in the modification of the bill and tail of birds. Proc. Phil. Acad. Nat. Sci., 1891, pp. 118–119.

Trow, A. H. A Difficulty in Weismann. Nature, xxiv, pp. 102, 175.

Vines, S. H. An Examination of Some Points in Prof. Weismann's Theory of Heredity. Nature, Oct. 24, 1889, pp. 621–626.

Virchow, R. Descendenz und Pathologie. Virchow's Archiv., ciii, pp. 1–15, 205–215, 413–437.

——— Ueber den Transformismus. Tag. Deutcsh. Nat. Vers. No. 6, pp. 136–144; Biol. Centralbl. vii, pp. 545–561.

WALLACE, A. R. Geographical Distribution of Animals.

——— Darwinism. An Exposition of the Theory of Natural Selection, with Some of its Applications.

——— Natural Selection and Tropical Nature. Essays on Descriptive and Theoretical Biology.

——— Criticism of Gulick. Nature, xxxviii, pp. 490–491.

——— Origin of Species and Genera. Nineteenth Century, vii, p. 93, 1880.

——— Episode in the History of the Evolution Theory. Fortnightly Review, xlvi, pp. 300-316.

WALLACE, W. An Inquiry into the Nature of Heredity. Proc. Phil. Soc. Glasgow, xxii, pp. 227–239.

WARD, LESTER F. Neo-Darwinism and Neo-Lamarckism. Proc. Biol. Soc. Wash., vi, pp. 11–71.

WEISMANN, AUGUST. Essays upon Heredity and Kindred Biological Problems. Edited by E. B. Poulton, Selmar Schönland and A. E. Shipley.

——— Prof. Weismann's Theory of Heredity. [A reply to Prof. Vines.] Nature, February 6, 1890, pp. 317–323.

WILSON, ALEXANDER. American Ornithology, Jardine's Edition.

WINDLE, B. C. A. Teratological Evidence as to the Heredity of Acquired Conditions. Journ. Linn. Soc., London, xxiii, p. 448.

YARRELL, WILLIAM. Observations on the Laws which appear to influence the Assumption and Changes of Plumage in Birds. Trans. Zool. Soc. of London, vol. i, pp. 13–21, 1835.

EXPLANATION OF PLATES.

PLATE I.

Figs. 1, 2, 3. Three outer tail feathers of *Dryobates pubescens*, showing individual variation in color marks.

Figs. 4, 5. Feathers from the back of *Dryobates villosus* and *D. scalaris*, respectively, illustrating the striped and barred pattern.

Fig. 6. Frontal feather of *Geothlypis trichas occidentalis* in winter plumage, illustrating acraptosis. The dark edge wears off in spring, leaving the yellow base exposed. Four times natural size.

Fig. 7. Feather from back of head of *Dendroica occidentalis* in winter plumage. The dark edge wears off in spring, exposing the yellow beneath. Three times natural size.

Fig. 8. Feather from breast of *Scolecophagus carolinus* in winter plumage. The light rusty edge wears off in spring, leaving the black exposed. Natural size.

Fig. 9. Feather from the back of *Plectrophenax nivalis* in spring plumage, the white having worn down and left the black base remaining.

Fig. 10. Feather from the back of *Plectrophenax hyperboreus* in spring plumage, the white tip remaining unworn.

Fig. 11. Feather from the throat of *Icterus cucullatus nelsoni*, changing from yellow to black by the accession of pigment without moult. Twice natural size.

Fig. 12. Feather from the back of the head of *Icterus bullocki*, showing the change from yellow to black by the accession of black pigment. Twice natural size.

PLATE II.

Feathers illustrating the stages of transition to a completely black mode of pigmentation. Natural size.

Figs. 1–6, inclusive. Changes from a streaked plumage. From the under parts of *Melanerpes formicivorus bairdi*.

Figs. 7–13, inclusive. Changes from a streaked to a barred, and from a barred to a completely black feather. From the under parts of *Sphyrapicus varius*.

Figs. 14–17, inclusive. Changes from a barred to a black stage. From the edge of the throat-patch of the female *Sphyrapicus thyroideus*.

PLATE III.

Feathers of the wing of *Falco sparverius*, showing transition of pattern according to successional taxology. Natural size.

PLATE IV.

Heads of various North American birds, showing types of black markings, with their combinations and modifications.

Fig. 1. *Polioptila plumbea;* a, *Leucosticte griseonucha;* b, *Melospiza georgiana;* c, *Petrochelidon lunifrons;* d, *Coccothraustes vespertinus.*

Fig. 2. *Zonotrichia coronata;* a, *Cyanocephalus cyanocephalus;* b, *Spizella socialis;* c, *Ceophlœus pileatus* ♂ ; d, *Cyanocitta cristata.*

Fig. 3. *Saxicola œnanthe;* a, *Geothlypis trichas;* b, *Dendroica dominica;* c, *Dendroica castanea;* d, *Dendroica pensylvanica;* e, *Hesperocichla nævia.*

Fig. 4. *Colaptes auratus;* a, *Passerina cyanea;* b, *Icteria virens;* c, *Ceophlœus pileatus* ♀ ; d, *Sphyrapicus varius.*

Fig. 5. *Dendroica virens;* a, *Helminthophila bachmani;* b, *Xanthocephalus xanthocephalus;* c, *Guiraca cœrulea;* d, *Cardinalis virginianus;* e, *Cardinalis cardinalis igneus.*

Fig. 6. *Dendroica tigrina;* a, *Zonotrichia leucophrys;* b, *Zonotrichia leucophrys intermedia;* c, *Campephilus principalis* ♂ ; d, *Dendroica cœrulescens.*

Fig. 7. *Dendroica blackburniæ;* a, *Sitta canadensis;* b, *Dryobates pubescens;* c, *Vireo atricapillus;* d, *Dendroica maculosa;* e, *Spinus psaltria mexicana.*

Fig. 8. *Dendroica striata;* a, *Dryobates borealis;* b, *Dendroica chrysoparia;* c, *Campephilus principalis* ♀ ; d, *Calcarius lapponicus.*

Fig. 9. *Parus atricapillus;* a, *Spinus lawrencei;* b, *Motacilla alba;* c, *Sylvania mitrata;* d, *Calcarius ornatus;* e, *Calcarius pictus.*

Fig. 10. *Ampelis garrulus;* a, *Parus gambeli;* b, *Melanerpes formicivorus bairdi* ♀ ; c, *Melanerpes formicivorus bairdi* ♂ ; d, *Xanthoura luxuosa;* e, *Otocoris alpestris.*

Fig. 11. *Helminthophila chrysoptera;* a, *Mniotilta varia;* b, *Picus villosus;* c, *Colinus virginianus texanus;* d, *Callipepla californica;* e, *Cyrtonyx montezumæ.*

PLATE V.

Examples of yellow and red as correlative colors. [The names *Icterus cucullatus* and *I. cucullatus nelsoni* should be transposed.]

PLATE VI.

The upper figure shows the effect of environment in bleaching color in the genus Myiarchus.

The lower figure shows a tail of an immature male *Icterus cucullatus nelsoni* changing from yellow to black by the accession of pigment without moult. Natural size.

PLATE VII.

Three races of *Spinus psaltria*, showing the change from a greenish olive to a black plumage. Natural size.

PLATE VIII.

Three outer tail feathers of Pipilo, showing decrease in size of white markings toward the west and northwest.

PLATE IX.

Geographical distribution of Sphyrapicus. A.—1, *S. varius*; 2, *S. varius nuchalis*. B.—*S. ruber*.

Geographical distribution of Pipilo. A.—1, *Pipilo erythrophthalmus*; 2, *P. erythrophthalmus alleni*. B.—1, *P. maculatus;* 2, *P. maculatus arcticus;* 3, *P. maculatus megalonyx;* 4, *P. maculatus oregonus*.

PLATE X.

Geographical distribution of the races of *Megascops asio*. 1, *asio;* 2, *floridanus;* 3, *maccallii;* 4, *trichopsis;* 5, *bendirei;* 6, *kennicottii;* 7, *maxwelliæ*.

Geographical distribution of Cyanocitta. A.—1, *C. cristata;* 2, *C. cristata florincola*. B.—1, *C. stelleri;* 2, *C. stelleri frontalis;* 3, *C. stelleri annectens;* 4, *C. stelleri macrolopha;* 5, *C. stelleri diademata;* 6, *C. stelleri coronata*.

PLATE XI.

Geographical distribution of the races of *Dryobates villosus*. A. 1, *leucomelas;* 2, *villosus;* 3, *audubonii;* 4, *maynardi*. B.—1, *harrisii;* 2, *jardinii*.

Geographical distribution of the ladder-backed forms of Dryobates. A.—1, *D. scalaris;* 2, *D. scalaris parvus:* 3, *D. scalaris bairdi;* 4, *D. scalaris lucasanus;* 5, *D. scalaris sinaloensis;* 6, *D. scalaris graysoni*. B.—*D. nuttallii*. C.—*D. borealis*.

PLATE XII.

Geographical distribution of Bubo. A.—1, *B. virginianus;* 2, *B. virginianus saturatus;* 3, *B. virginianus arcticus;* 4, *B. virginianus subarcticus*. B.—*B. mexicanus*.

Geographical distribution of Chordeiles. A.—1, *C. virginianus;* 2, *C. virginianus minor;* 3, *C. virginianus henryi*. B.—*C. texensis*.

PLATE XIII.

Map of North America, showing the influence of climate upon the color of *Melospiza fasciata*. The breeding range of each race is indicated, the territory occupied by each variety being colored as nearly as possible in harmony with the markings of the back.

PLATE XIV.

The shoulders of the different species of Agelaius, showing the transition from the unmodified brown of the female in winter to the adult male plumage in summer. Natural size.

PLATE XV.

Heads of the different species of Sphyrapicus, showing the transition from the brown plumage of the young, through successive stages of increasing red, to the adult male of *S. ruber*.

PLATE XVI.

Heads of the female and young of the genus Icterus.

PLATE XVII.

Heads of the adult males of the genus Icterus.

PLATE XVIII.

Color chart of the undifferentiated plumage, female or young, of the genus Dendroica. For description of a single species, read the lines from right to left; for comparison of the same part of the body, read the columns.

PLATE XIX.

Color chart of the specialized plumage, adult male in spring, of the genus Dendroica.

[NOTE.—In one or two instances the colors in the above charts were supplied from descriptions; otherwise, from specimens.]

INDEX.

- Acanthis, 153, 218, 299
- Acceleration, Cope on, 73; instance of Cope's law of, 169, 219
- Accipiter, 268
  - velox, 277
- Acquired characters, on the inheritance of, 2-50; Galton on inheritance of. 5; Ryder on inheritance of, 19; consequences of dispensing with inheritance of, shown by Cunningham, 27; inheritance of, by protozoa admitted, 28; Morgan on inheritance of, 29; Elliot on inheritance of, 38; three evidences of inheritance of, as given by Spencer, 43; inheritance of, 1st and 3d evidences in proof of, as given by Spencer, criticized by Romanes and Ball, 43-44; transmission of discussed, 29: transmission of, divided into two classes, 34; Japanese goldfish experimented with by Dr. Wahle, 34.
- Acquired habits; inheritance of, believed in by Darwin, 40; inheritance of, criticized by Ball, 40; inheritance of, supported by Romanes, 41-42.
- Acraptosis, definition of, 135; instances of acraptotic feathers, 135, 136, 137
- Acroptosis, definition of, 135, 137
- Ægialitis, 197
  - semipalmata, 197
- Æsthetic taste in birds, explanation of, 93-95; Poulton's views on, 93-95; opposed by Morgan, 95-96; Romanes on, 97-98; Allen on, 100; Morgan on, 101.
- Agelaius, 143, 146, 218, 220, 255, 292
  - gubernator, 178, 220, 254, 255, 292
  - phœniceus, 185, 220, 254, 255, 292
  - tricolor, 178, 220, 254, 255, 292
- Alaudidæ, 287
- Albinism, theory of, suggested by Stejneger, 226
- Alcedinidæ, 278
- Allen, Grant, on æsthetics, 100
- Allen, Harrison, on pigment, 182
- Allen, J. A., on geographical distribution as factor in evolution of colors, 247
- Ammodramus, 215, 233, 304
  - maritimus, 304
  - nigrescens, 151
  - sandwichensis, 304
    - alaudinus, 184, 253
    - bryanti, 253
  - savannarum passerinus, 184
- Ampelidæ, 316
- Ampelis, 216, 217, 236, 316
  - cedrorum, 188, 190, 316
  - garrulus, 190, 316
  - japonicus, 316
- Amphispiza, 180, 216, 307
  - belli, 254, 307
    - nevadensis, 254, 307
  - bilineata, 188, 254, 307
- Anabolism definition of, 68; as factor in pigmentation, 163
- Anis, 276
- Anthus, 204
- Anticryptic colors, defined, 194, 197, 198
- Antrostomus, 207
  - carolinensis, 186, 208
  - cubanensis, 208
  - macromystax, 208
  - vociferus, 208
    - arizonæ, 208
- Aphelocoma, 158, 215, 289
  - californica, 186
  - sieberii, 254
  - sumichrasti, 254
- Aposematic colors, defined, 194, 200
- Aptatic colors, defined, 194
- Aptosochromatism, definition of, 135, 137
- Aquila, 270
- Archibuteo, 236, 269
  - lagopus sanctijohannis, 147
- Aristotle, originator of doctrine of evolution, 2
- Asturina, 270

Atthis....... 236
Attidæ, habits of, as proof of sexual selection....... 88
Auriparus....... 236
Ball, criticism of Darwin's instances of acquired habits, 40; criticism of Spencer's evidences of inheritance of acquired characters, 43-44.
Basileuterus....... 331
Bathmism, definition of....... 65
Becards....... 157
Beckham, on pseudepisematic colors.. 199
Beddard, opposed to sexual selection, 88; on sexual coloration, 89-90; on color in birds, 138; on effects of food on color, 226; on influence of light on pigmentation, 230; summary of Camerano's system of geographical colors, 238; on protective mimicry, 239.
Belt, suggestions on natural selection as originator of species....... 114
Bernicla magellanica, instance of high coloration in female....... 90
Bilateral symmetry, explanation of.... 79
Blackbirds.......203, 295
  red-winged....143, 154, 178, 185, 220, 292
  rusty....... 136
  yellow-headed.......155, 291
Bluebirds.......203, 213, 222, 229, 335
  arctic....... 157
Bobolink.......149, 152, 185, 290
Bobwhite.......185, 257
Bonasa....... 260
Boreal genera, Wallace's list of....... 236
Brooks, modification of doctrine of pangenesis, 5; secondary laws of variation, 62; laws of variation criticized by Gulick....... 72
Brown birds, colors of, protective..... 196
Brown creeper, protective coloration of....... 197
Bubonidæ....... 273
Bubo mexicanus.......253, 254
  virginianus.......243, 253, 254, 274
    arcticus....... 152
    subarcticus....... 210
Bunting, lark.......152, 179, 313
  indigo.......157, 222
  varied....... 311
Butcher-birds....... 216
Buteo....... 269
  abbreviatus....... 147
  albicaudatus....... 206
  borealis.......150, 206, 269
    calurus....... 179
Buteo fuliginosus....... 147
  harlani....... 147
  latissima....... 206
  lineatus....... 269
  swainsoni.......147, 150, 206
Calamospiza.......236, 313
  melanocorys.......146, 152, 179, 218
Calcarius.......218, 303
  lapponicus....... 254
  ornatus....... 149
  pictus....... 254
Callipepla.......236, 258
  californica....... 258
  squamata....... 258
Camerano, system of geographical colors summarized by Beddard....238, 239
Campephilus....... 280
  principalis....... 146
Canaries, color of, changed by food.... 228
Caprimulgidæ.......207, 283
Caracara....... 272
Cardinalis.......153, 221, 310
  virginianus.......157, 243
Cardinella....... 330
Carpodacus.......153, 297
  cassini....... 254
  erythrinus grebnitskii....... 297
  mexicanus....... 244
    frontalis..136, 156, 184, 195, 229, 244
  purpureus californicus....... 254
Catbird....... 182
Catharista atrata....... 146
Cathartidæ....... 267
Cathartes aura....... 146
Catherpes....... 236
Cellular continuity, upheld by Morgan, 19-20; upheld by Eimer, 20.
Centrocercus.......236, 262
Centronyx....... 236
Ceophlœus....... 280
  pileatus....... 147
Certhia.......236, 333
  familiaris americana....... 197
Certhiidæ....... 333
Certhiola....... 318
  bahamensis....... 188
Ceryle....... 278
  alcyon.......175, 192, 198, 210, 278
  amazona....... 279
  cabanisi....... 279
  inda....... 279
  superciliosa....... 278
  torquatus....... 279
Chachalacas....... 265
Chætura.......215, 283
Chamæa....... 236

Chats 329
  yellow-breasted 215
Chelidon 314
  erythrogaster 216, 218
Chondestes 180, 216, 236, 304
  grammacus 217
Chordeiles 207, 210
  texensis 253, 255
  virginianus 255
    henryi 185, 253
Chuckwill's widow 186
Cinclidæ 332
Cinclus 332
  ardesiacus 332
  leuconotus 332
  mexicanus 218, 219, 332
Circus 268
  hudsonicus 206
Clivicola 315
  riparia 215
Coccothraustes 296
  vespertinus 157, 221
Coccyges 275
Coccyzus 276, 277
  americana 277
  erythrophthalmus 277
  maynardi 277
  minor 277
Cœrebidæ 318
Coues' Key, table of characters of Helminthophila 324
Cognate colors, definition of 152
Colaptes 280, 281
  auratus 282, 155, 156, 182
  cafer 155, 156, 173, 176, 203
Colinus 257
  graysoni 258
  ridgwayi 185
  virginianus 185
    cubanensis 146
    floridanus 258
Colors, classification of, by Poulton, 194; definition of aptatic, cryptic, procryptic, anticryptic, pseudosematic, puesdaposematic, pseudepisematic, sematic, aposematic, episematic, directive, discriminative, sexual, socialistic, epigamic, 194–210.
Colors, geographical distribution as factor in evolution of, 234: Beddard summarizes Camerano's system of geographical, 238-239; J. A. Allen on, 247,
Color in birds, general principles of, 137; Beddard on, 138; theory of, 138–139.
Colors in North American Genera, proportion and distribution of, 143–144; black contrasting with white breasts, 148; black with yellow or brown under parts, 148; black with rose patch on breast, 148; upper parts black, under parts light colored, 148; lower parts and top of head, black, 149; on ways of assuming a black plumage, 150, 151.
Color, Garman on variation in colors of animals, 231
Color, variation of, with sex, age or season, 211; Darwin on, 212, 213. 215; effects of food on, 226, 227, 228.
Columbæ 265
Columba fasciata 205
Compsothlypis 324
Concentration, law of, 64; definition of, 77.
Contopus 215
Cope on retardation, 25-26; definition of Bathmism, 65; on law of extent and density, 66; on laws of acceleration and retardation, 73; on four laws of structure, 77-78; instance of law of retardation, 169.
Correlation of growth, definition of 79
Correlative colors, definition of 154; instances of, 155-157; exceptions to, 157.
Corvidæ 288
Corvus 146, 215, 236
  cryptoleucus 152, 290
Cowbirds 290
Cracidæ 265
Creepers 333
  brown 197
  honey 318
Crossbills 156 298, 219
Crotophaga 276
  ani 146
  sulcirostris 146
Crows 203, 212, 215, 288
Cryptic colors defined 194
Cuckoo 198
  American 277
Cuculidæ 275
Cuculus canorus 275

- Cunningham, criticism of pammixis, 23; consequences of dispensing with inheritance of acquired characters, 27; on natural selection, 28; criticism of Weismann's observation on feet of Chinese ladies, 31; environment discussed by, 37; experiments on effect of light on pigmentation, 230.
- Cupidonia........................... 236
- Cusp growth, Osborn on, as evidence of the inheritance of acquired characters, 47.
- Cyanecula........................... 335
- Cyanocephalus........................ 215
  - cyanocephalus..................158, 289
- Cyanocitta..............158, 215, 245, 250
  - cristata....................182, 191, 245
  - stelleri........................245, 246
    - frontalis.......................... 246
  - table of specific and varietal characters of........................ 247
- Cyanospiza........................... 236
- Cypseloides.....................283, 284
- Cyrtonyx.......................236, 259
  - montezumæ.......................... 259
  - ocellatus........................... 259
  - sallæi.............................. 259
- Darwin, acceptance of principles of use and disuse and environmental influences, 3; hypothesis of pangenesis, 3; on disuse, 25; on acquired habits, 40; instances of inheritance of acquired habits criticised by Ball, 40-41; acquired habits supported by Romanes, 41; originator of theory of sexual selection, 80; description of preferential mating, 81–82; theory of sexual selection, 82: Wallace opposed to his theory of sexual selection, 82-83; on physiological selection, 112; on color variations, with sex, age or season, 212.
- Death, Weismann's explanation of, 8–9; Morgan's criticism of Weismann's explanation, 9.
- Dendragapus..................204, 205, 259
  - canadensis.......................... 204
  - franklinii.......................... 204
  - obscurus............................ 204
    - fuliginosus...................... 204
    - richardsonii..................... 204
- Dendroica.......................232, 325
  - æstiva...................157, 221, 326
  - auduboni.................203, 218, 219
- Dendroica blackburniæ...148, 188, 221, 326
  - bryanti............................. 327
  - cærulea..................158, 221, 319, 327
  - cærulescens......................... 221
  - castanea.........................185, 222
  - coronata.158, 182, 184, 187, 203, 218, 219
  - dominica.........................182, 215
  - maculosa...................148, 218, 219
  - nigrescens.................216, 217, 218
  - occidentalis...............136, 188, 221
  - olivacea............................ 187
  - palmarum.........................218, 219
  - pensylvanica........................ 222
  - striata....................187, 188, 222
  - tigrina..........................188, 222
  - townsendi........................... 221
  - vigorsii............................ 221
  - virens...........................188, 221
- Dickcissel........................... 312
- Dicrurus............................. 198
- Dippers.............................. 332
- Directive colors, definition of, 194, 201; classification of by Todd, 201; new classification of, 202.
- Discriminative colors, defined.....204, 205
- Dolichonyx........................... 290
  - oryzivorus...142, 152, 181, 182, 185, 218
- Doves, mourning...................... 205
  - white-fronted....................... 205
  - white-winged........................ 205
- Drongo cuckoo........................ 198
- Dryobates..............179, 224, 244, 252, 280
  - arizonæ............................. 254
  - pubescens...............175, 181, 211, 254
    - gairdnerii....................... 254
  - scalaris.........................254, 282
    - bairdi........................... 254
  - stricklandi......................... 254
  - villosus.........................252, 282
    - harrisii......................... 254
    - jardinii......................... 253
    - leucomelas....................... 254
    - maynardi......................... 252
- Dyer, objections to physiological selection, 123; objections to the term segregation of the fit, 123.
- Eagles............................... 270
- Ectopistes........................... 236
  - migratorius......................... 205
- Eimer, on continuity of body cells, 20; instances of observed cases of transmission of mutilations, 32; on pigmentation, 162; on general patterns of bird colors, 179; on environment in evolution of colors, 226.

- Elanoides 267
  - forficatus 152
- Elanus 267
  - leucurus 152
- Elliot, address on inheritance of acquired characters, 38–40.
- Embernagra 308
- Embryogenesis, definition of by Weismann 16
- Empidias 236
- Empidonax 215
- Engyptila albifrons 205
- Environmental influences, first recognized by Hilaire, 2. Morgan's instances of, 35; discussed by Cunningham, 37; direct influences of on colors of birds and insects, 238 et seq.
- Environment in evolution of colors, direct influence of, 225; Eimer on, 226.
- Epigamic colors defined 194, 211
- Episematic colors defined 194, 200
- Ergaticus 330
  - ruber 153, 157
- Euetheia 312
  - bicolor 146, 149
- Euphonia elegantissima 158
- Euspiza 236
- Evolution, history of the doctrine of, 2; laws governing, 64-65; relation of to species, 106.
- Falco 271
  - columbarius 243
    - suckleyi 147, 271
  - islandus 152
  - peregrinus 243
  - sparverioides 271
  - sparverius 206, 271
- Falconidæ 267
- Falcons 271
- Fecundity, segregate, definition of 131
- Finch, pine 145, 301
  - purple 297
  - scarlet rose 297
- Flickers 155
  - red-shafted 173, 176, 203
- Flute bird 152
- Flycatchers, crested 256
  - fork-tailed 155
  - scissor-tailed 155
  - shiny-crested 152, 196, 204
  - tyrant 285
  - vermilion 157, 177
- Fringillidæ 296
- Galeoscoptes carolinensis 182, 187
- Gallinæ 257
- Galton, on the continuity of the germ plasm and the inheritance of acquired characters, 5; on physiological selection, 115.
- Garman, on the influence of light upon the colors of animals 231
- Geddes and Thomson on katabolism and anabolism 68
- Genealogical table of Spinus and its allies, 300; of Helminthophila, 324.
- Geococcyx 215, 276
- Geothlypis 243, 329
  - agilis 221, 329
  - beldingi 329
  - formosa 329
  - macgillivrayi 221, 329
  - melanops 329
  - philadelphia 221, 329
  - trichas 157, 182, 218, 329
    - occidentalis 135
- Geratology, definition of, 78; example of, 227.
- Germ-plasm, continuity of, criticized Vines, 13–14; Weismann's reply to Vines, 15; Ryder on, 18.
- Gnatcatchers 334
  - blue-gray 158
- Goatsuckers 283
- Gold-finches 145, 195, 300
  - green-backed 150, 195
  - pine 299
- Goose, Upland 90
- Goshawks 268
  - Mexican 270
- Grackles 229, 295
- Grassquit 149, 312
- Greenjay 158
- Grosbeaks 311
  - blackheaded 155
  - cardinal 157
  - evening 296
  - pine 296
  - rosebreasted 148, 155, 176, 184, 191, 222
- Grouse 204, 259
  - Canada 204
  - dusky 204
  - Franklin's 204
  - Richardson's 204
  - ruffed 260
  - sage 262
  - sharp-tailed 262
  - sooty 204
- Guiraca cærulea 158, 218
- Gulick, criticism of Brooks' laws of variation, 72; on isolation, 125–128.

- Gymnokitta 236
- Habia 221, 311
  - ludoviciana 148, 154, 155, 176, 223
  - melanocephala 155
- Haeckel, explanation of views of Lamarck and Hilaire, 2-3; plastidule theory, 6; laws of heredity, 69, 79.
- Haliæetus 236, 270
- Harporhynchus 236
- Hartog, difficulty in Weismann's theory of variation 56, 57
- Hawk, broad-winged 206
  - Harris's 269
  - marsh 268
  - Mexican black 270
  - red-tailed 206
  - sparrow 165, 206
  - Swainson's 206
  - western red-tailed 179
  - white-tailed 206
- Helinaia 320
- Helmintherus 236
- Helminthophaga 236
- Helminthophila 321
  - celata 322
    - lutescens 243
  - chrysoptera 188, 221, 322
  - lawrencei 322
  - leucobronchialis 322
  - luciæ 217, 322
  - peregrina 321
  - pinus 221, 322
  - ruficapilla 221, 322
  - swainsoni 218
- Helmitherus 320
- Heredity, influence of, 25; laws of 79
- Hesperocichla 335
  - nævia 182, 186, 203
- Hilaire, originator of the doctrine of environmental influences 2
- Hirundinidæ 314
- Homology, explanation of by Cope 77
- House-finch 86, 136, 156, 195, 229, 244
- Humming-birds 221, 284
- Hyatt on geratology 78
- Hybrids, asymmetrical 174
  - lateral 174
  - symmetrical 174
- Hybrid feathers, use of, 172; classification of, 174.
- Hylatomus 236
- Hyperchromism, from environmental influences 241
- Icteria 236, 329
  - virens 215
- Icteridæ 290
- Icterus 157, 221
  - bullocki 149, 294
  - cucullatus 156, 292, 293, 295
    - igneus 156
    - nelsoni 133, 156, 291, 294
  - galbula 149, 294
  - parisorum 148, 295
  - spurius 148, 294, 295, 310, 319
- Ictinia 267
- Idioplasma, distinctions concerning made by Weismann 16
- Immortality of protozoa, explanation of by Weismann, 8-9; admitted by Vines, 11.
- Isolation, Gulick on 125-128
- Jackrabbit, black 71
- Jay, blue 141, 191, 245, 250, 288
  - california 186
- Johnson, on plumage changes in Icterus 133
- Junco 180, 204, 216, 217, 191, 236, 306
  - annectens 254
  - caniceps 254
  - cinereus dorsalis 254
  - hyemalis 147, 148, 177, 191
- Katabolism, definition of, 68; as factor in pigmentation, 163.
- Kingbird 143, 155, 199, 217, 255
  - gray 155
  - thick-billed 155
- King-crow 198
- Kingfishers 212, 278, 279
  - belted 175, 192, 198, 210
- Kinglets 334, 199
  - golden-crowned 156
  - ruby-crowned 143, 156
- Kites 267
- Ladder-backs 253
- Lagopus 236, 260
  - lagopus alleni 134
  - leucurus 261
  - rupestris 261
    - atkensis 261
    - nelsoni 261
    - reinhardti 261
  - welchi, 261
- Lamarck, originator of the principle of use and disuse 2
- Lanidæ 317
- Lanius 187, 216, 218, 236
- Lark-finch 216, 217
- Larks 287
  - horned; 196, 250, 287
- Leucosticte 153, 218, 236, 298
  - atrata 147
- Linota 236

Longspurs 303
  chestnut-colored 149
Lophophanes 236
Lophortyx 236
Loxia 218, 219, 236, 298
  leucoptera 298
Lunda cirrhata 200
Macrochires 283
Macronyx ameliæ 240
  croceus 240
Magpies 152, 215, 288
Melanerpes torquatus 216
Markings, classification of patterns of, 159; Eimer on patterns of bird colors, 179.
Martins 314
  purple 149
Meadowlark..156, 175, 178, 203, 211, 240, 293
Megoscops asio, 250; table of races of, showing relation of color, 250.
  asio maccallii 254
  flammeolus 254
  trichopsis 254
Melanerpes 280
  aurifrons 223
  carolinus 222
  erythrocephalus..145, 153, 216, 217, 218
  formicivorus bairdi..143, 170, 173, 175, 181, 191
Melanistic plumage, methods of, assuming, 151; theory of, suggested by Stejneger, 226; Spinus psaltria as an instance of the assumption of, 241; instances of noted by Ridgway, 243.
Meldola, criticism of Romanes theory of physiological selection, 115; Romanes' reply to, 115-116.
Meleagris 236, 263, 264
Melopelia leucoptera 206
Melospiza 196, 215, 225, 236, 250, 308
  cineria 249
  fasciata 248
    fallax 248
    heermanni 248
    montana 248
    rufina 248, 249
    samuelis 248
Merriam, on plumage changes, 134; on geographical distribution and North American faunal areas, 234, 235.
Merula 335, 336
  confinis 336
  migratoria propinqua 217
Metabolism, explanation of, 67-68; as explanation of pigmentation, 163.
Micrathene 236
Micropodidæ 283
Micropus 284
Milvulus 285
  forficatus 153, 155
  tyrannus 155, 286
Mimicry, Stejneger on, 198; Beddard on protective, 239.
Mimus polyglottos 183
Mniotilta 236, 320
  varia 151, 152, 221, 188
Mniotiltidæ 157, 319
Mockingbird 183
Molothrus 290
  æneus 146, 291
  ater 146, 222
Morgan, criticism of hypothesis of pangenesis, 5-6; criticism of Weismann's explanation of death, 9; Weismann's theory of heredity opposed by, 17; on cellular continuity, 19-20; criticism of panmixis, 22; on inheritance of acquired characters, 29-30; transmission of mutilations discussed by, 30; instances of environmental influences, 35; suggests modification of Spencer's theory of physiological units, 58; explanation of preferential mating, 81; opposed to Poulton's views of the æsthetic tastes of birds, 95-96.
Motacilla melanope 331
Motacillidæ 331
Muscivora mexicana 199
Mutilations, transmission of discussed by Morgan, 29-30; transmission of discussed by Weismann, 30-31; Eimer on observed instances of, 32.
Myadestes 335
  townsendii 204, 217
Myiarchus 256
  cinerascens 256
  crinitus 256
  lawrenceii 243
  mexicanus 256
  nigricapillus 243
Myiodioctes 236
Myiodynastes 285
Naegeli, on the existence of a nucleoplasm first developing into body cells, then becoming simplified into reproductive cells, 10.

- Natural selection, discussion of by Cunningham, 27–28; argued against as not creative, by Schurmann, 51; conditioned by variation, 52–53; further discussion of, 106–107, 110; Romanes on, as originator of species, 113-114; suggestions on as originator of species. by Belts, 114; as originator of species upheld by Meldola, 115.
- Nelson, E. W., on Plectrophenax nivalis, 301
- Neocorys, 236
- Nighthawk, western, 185, 196, 207, 210, 254
- Nuthatches, 333
- Nyctala, 236
- Nyctea nyctea, 152, 198
- Nyctidromus, 207
- Oporornis, 236
  - formosa, 187
- Oreortyx, 236, 258
- Oriole, 293
  - Arizona hooded, 133, 156
  - fiery, 156
  - hooded, 156
- Oroscoptes, 236
- Ortalis, 265
- Ortyx, 236
- Osborn, on laws of cusp growth, 47; criticised by Poulton, 47; reply to Poulton's criticisms, 48.
- Osprey, 272
- Otocoris, 218, 250
- Owl, barn, 273
  - burrowing, 197, 210
  - great horned, 254
  - horned, 273
  - screech, 250
  - snowy, 198
  - western horned, 210
- Pammixis, Weismann's explanation of, 22; criticism of by Morgan, 22; criticism of by Cunningham, 23; Romanes' explanation of, 23; Romanes' theories on, 24-25; Cope views in regard to, 25.
- Pandion, 272
- Pangenesis, Darwin's doctrine of, 3; explanation of by Romanes, 3-5; modification of by Brooks, Galton. Herdman, etc., 5; criticism of by Morgan, 5–6.
- Parabuteo, 269
  - unicinctus harrisi, 147
- Parallelism, Cope on laws of, 78
- Parauque, 207
- Paridæ, 333
- Parrots, 212, 274
- Partridges, 237
- Partridge, massena, 259
  - mountain, 258
- Parula americana, 221
- Parus, 236
  - atricapillus, 188
  - hudsonicus, 188
- Passerculus, 236
- Passer domesticus, 209
- Passerella, 196, 215, 236, 308
  - iliaca, 308
    - megarhyncha, 254
    - unalaschcensis, 254, 308
- Passerina, 222, 311
  - cyanea, 157, 187, 222
  - versicolor, 153
- Peckham, Prof. and Mrs., description of sexual selection among the Attidæ, 88
- Pediocætes, 236, 262
- Perisoreus, 215, 236, 289
- Petrochelidon, 314
  - lunifrons, 216, 218
- Peucæa, 180, 196, 216, 307
  - cassini, 254
  - mexicana, 254
- Phænopepla, 236
- Phainopepla, 317
  - nitens, 146, 152, 204, 221
- Phalænoptilus, 207
- Phalaropes, 220
- Phasianidæ, 263
- Phylogenic extent and density, explanation of, 66
- Physiological units, Spencer's theory of, 6-7
- Physiological selection, 110; Romanes on, 110–112; Darwin on, 112; suggestions on by Galton, 115; objections by Wallace, 116-117; objections by Wallace answered by Romanes, 118–119; further discussion of, 120; Seebohm's criticism of, 120-123; summary of, 124-125.
- Pica, 215, 236
  - nuttalli, 289
  - pica hudsonica, 146
- Pici, 279
- Picicorvus, 215, 236
  - columbianus, 289
- Picidæ, 279
- Picoides, 179, 223, 280
- Picus pubescens gairdneri, 243
  - villosus harrisii, 243

Pigmentation, definition of, 139; Eimer on, 162; Beddard on influence of light on, 230; influence of light on, experiments by Cunningham, 230; experiments by Poulton on effect of light on, 230, 231.

Pigment, definition of, 139; law of assortment of, 139–142, 145; law of growth force in regard to distribution of, 159–160; Eimer on distribution of, 162; Dr. Harrison Allen on, 182; metabolism as factor in distribution of, 163.

Pigeons 204, 265
  band-tailed 205
  passenger 205
Pinicola 153, 236, 296
  enucleator 154, 221
Pipilo 180, 216, 236, 309
  chlorurus 309
  erythrophthalmus 147, 148, 216, 222, 250, 309
    alleni 251
  aberti 254
  fuscus 309
    crissalis 182, 203
  maculatus 147, 148, 216, 250, 309
    arcticus 251, 252
    megalonyx 251
    mesoleucus 254
    oregonus 251
Pipit 240, 331
  African 240
Piranga æstiva 221, 243
  erythromelas 143, 150, 153, 180, 222
  hepatica 153
  ludoviciana 180, 222, 150, 157
  rubra 153, 222
Pitangus 285
  derbianus 188
Platypsaris, exceptions to correlative coloration 157
Plectrophenax 218, 301
  hyperboreus 152, 302
  nivalis 136, 152, 301
Plectrophanes 236
Plover, golden 133
Plumage changes, explained by Yarrell, 132, 136; Merriam on, without moult, 134; in breeding season, 136; classification of, 137.
Polioptila 209
  cærulea 158
  californica 353
  plumbea 187, 335
Polyborus 272
  cheriway 272
  lutosus 272
Poocætes 303
Poœcetes 236
Poulton, criticism of Osborn's evidence of the inheritance of acquired characters, 47; Osborn's reply to Poulton, 48; criticism of Wallace on sexual selection, 84; on æsthetic taste in birds, 93–95; criticized by Morgan, 95–96; on general principles of color, 137–138; classification of color marks, 194; on effect of light on pigmentation, 230–231.
Praeger, instance of procryptic colors 197
Prairie hens 261
Preferential mating, Darwin on 81, 82
Procryptic colors defined, 194, 195; Praeger's example of, 197.
Procyon lotor 210
Progne 314
  subis 146, 150, 221
Protonotaria 320
  citrea 221
Psaltriparus 236, 334
  melanotis 187
Pseudaposematic colors 194, 199
Pseudepisematic colors, 194–199; Beckham on, 199.
Pseudogryphus californianus 146
Pseudohybrids, definition of, 174, 177.
Pseudosematic colors 194, 198
Pseudozoorubin 138
Psitacidæ 274
Ptarmigan 134, 195, 260
Puffin, tufted 200
Pyrocephalus rubineus 153, 222
    mexicanus 141, 157, 177, 286
Pyrrhuloxia 236, 310
  sinuata 154, 181 221
Quail, valley 258
Quiscalus 146, 221, 229, 295
Raptores 266
Raven, white-necked 152
Recognition marks, 193; classification of, 194; Wallace on, 200–201.
Redpolls 299
Redstart 330
  American 147
Regulus 236
  calendula 153 335
  satrapa 182, 187, 335
    olivacea 143

Repetitive marks...................... 171

Reproductive cells, immortality of among matazoa, 10; simplicity of confirmed by Spencer, 17.

Retardation, explanation of by Cope, 25–26; definition of, 73; instance of Cope's law of, 169,

Rhynchophanes......... 303

Ridgway on relation between color and geographical distribution in North American birds, 241; instances of melanism 243.

Roadrunners.......................... 276

Robin varied......................203, 217

Rock-thrush.......................... 81

Romanes, explanation of Darwin's hopothesis of pangenesis, 3–5; on cessation of selection, 23: theories on pammixis, 24–25; on inheritence of acquired characters, 28; examples of instinct due to transmission of acquired characters, 41; supports Darwin's theory of acquired habits, 41; criticises Spencer's 1st and 3d form in evidence of proof of acquired characters, 43–44; supports Darwin's theory of sexual selection, 88; criticises Wallace's ideas on sexual selection, 92-93; on æsthetic taste of animals, 97–98; on species, 106-107; on physnatural iological selection, 110-112; opposes selection as originator of species, 113-115; reply to Meldola, 115-116; reply to Galton, 115; physiological selection opposed by Wallace, 116-117; reply to Wallace's criticism on physiological selection, 118-119; controversy with Dyer, 123-124.

Rostrhamus........................... 267

Ryder, theory of heredity opposed to Weismann, 17; on inheritance of acquired characters, 19; experiments on Japanese goldfish recorded by, 34.

Salpinctes...... 236

Sandpipers........................... 202

Sapsucker........................150, 165
    yellow-breasted..... 154

Sauermann, experiments on the influence of food on color............. 227

Saxicola............................. 335
    œnanthe........................... 187

Sayornis........ 215
    aquaticus 243
    nigricans.............147, 148, 152, 243

Schurmann, natural selection not creative, 51; discussion of origin of variations, 63.

Scolecophagus............146, 218, 236, 295
    carolinus, acraptotic feathers of... 136

Scotiaptex cinereum lapponicum...... 152

Scops asio.......................... 243

Seebohm, criticism of physiological selection, 120-123; glacial epoch as a factor in isolation, 249.

Seedeaters.......................... 312

Segregation, definition of environal, industrial, sustentational, defensive, nidificational, chronal, cyclical, seasonal, spatial, geographical, local, migrational, transportational, geological, fertilizational, artifical, reflexive, conjugational, social, sexual, germinal, floral, impregnational, 128–130; institutional, intensive, 131.

Segregation of the fit, 116, 120; objections to, by Dyer, 123.

Segregation, potential and prepotentional............................ 130

Seiurus.... ....216 217, 328
    aurocapillus................. .187, 328
    noveboracensis..................... 328

Sematic colors, definition of.......194, 200

Setophaga........................... 330
    miniata........................... 330
    picta, distribution of black on.147, 148
    ruticilla, distribution of black on, 147–148; instance of correlative colors, 156, 221.

Sexual Coloration, Beddard on......89, 90

Sexual intensification, explanation of. 68, 69

Sexual recognition, law of..... 209

Sexual selection, Darwin on, 80; criticized by Wallace, 82–83; discussed by Wallace, 85–86; Stolzmann's view of, 91; Peckham on, 88; Beddard opposed to, 88; Romanes supports theory of, 88; Wallace's objections criticised by Romanes, 92–93; Weismann on, 97; summary of 101, 102.

Shrikes......... ....218, 317

Sialia...... ....222, 229, 236, 336
    arctica.... 158
    sialis...................... ....213, 222

Sitta...........................236, 334
    canadensis 188
    carolinensis....................... 187

Siskin, pine.......................... 180

Size, segregate, definition of.......... 180

Snow-bunting 136
Snowflake 301
  McKay's 302
Socialistic colors, definition of 209
Solitaire 335
  Townsend's 204, 217
Somatoplasm, explanation of 11, 12, 13
Sparrow, Bell's 307
  black-throated 307
  chipping 217. 305
  dusky seaside 151
  fox 308
  Gambel's 184
  golden-crowned 176, 209
  grasshopper 184
  Harris's 183
  house 209
  lark 304
  rufous-crowned 307
  sage 307
  savanna 233, 304
  seaside 304
  song 248, 249, 250, 308
  Texas 308
  tree 305
  vesper 303
  white-crowned 209, 305
  white-throated 183
  western savanna 184
Specialized colors, classification of, 143-145; with or without loss of protection, 145.
Species, nature of, 103-106; Romanes on, 106-107.
Spencer, theory of physiological units, 6; on simplicity of reproductive cells, 17; three forms of evidence in proof of inheritance of acquired characters, 42; first and third form in proof of inheritance of acquired characters criticised by Ball and Romanes, 43-44; discussion of use and disuse, 44-45.
Speotyto cunicularia hypogæa 197, 210, 274
Sphyrapicus 236, 244, 248, 280
  ruber 243, 244
  thyroideus 146, 150, 165, 223, 281
  varius 164, 192, 222, 244, 252
    nuchalis 244, 245
Spinus 157, 218, 300
  lawrencei 177, 222
  pinus 145, 180, 215, 299
  psaltria 150, 177, 195, 241, 246
    arizonæ 150, 151, 242
    mexicana 146, 242
  tristis, specialization of without loss of protection 145
Spiza 321
  americana 222
Spizella 180, 196, 216, 217, 236, 305
  artigularis 306
  breweri 254, 306
  pallida 254, 306
Sporophila 312
  morelletti 146
Squirrel, black headed ground 68
Stejneger on mimicry, 198; on albinism and melanism, 226.
Stelgidopteryx 315
  serripennis 215
Stolzmann, views on sexual selection 91
Stone on plumage changes without moult 134
Stonechats 335
Strigidæ 273
Strix 273
Structure, law of, 64; definition of, 77; by Cope, 77; segregate, definition of, 130.
Sturnella 293
  defilippii 156, 240
  magna 156, 157, 175, 178, 182, 203, 211, 239
Successional relation, definition of by Cope 77
Surniculus dicruroides 198
Swallow 314
  bank 315
  barn 218, 314
  cliff 218, 314
  rough-winged 315
  violet-green 210, 215, 216, 218
  white-bellied 315
  white-breasted 210, 218
Swifts 283
Sylvania 329
  canadensis 221
  mitrata 222
  pusilla 157, 221
    pileolata 243
Sylviidæ 334
Tachycineta 216, 315
  bicolor 210, 218
  thalassina 210, 216, 218, 315
Tanager 150, 313
  Louisiana 150, 180
  scarlet 143, 155, 180
  summer 152, 222
  western 155, 222
Tanagridæ 313
Taxology, successional 164
Teleology, explanation of by Cope 78
Terpsiphone cristata, as instance of plumage change from dark to light without moult 134

Tetraonidæ........................... 257
Tetro................................ 236
Thomson, explanation of anabolism and katabolism, 68; with Geddes places sexual intensification upon firm basis, 73.
Thrasæetus........................... 270
Thrashers.........................196, 332
Thrushes, water...................... 328
Thrush, wood......................... 185
  varied............................. 186
Thryothorus bewickii................. 254
  ludovicianus....................... 254
Titmice.............................. 196
Tits................................. 333
Todd, J. E., on directive colors..... 201
Towhee........................212, 230, 309
  california......................182, 203
Transmission, abridged or simplified, definition of.................. 80
  interrupted or latent, definition of. 79
  mutual and amphigonous, definition of......................... 79
  sexual, definition of.............. 79
  uninterrupted or continuous, definition of...................... 79
Trochilidæ........................... 284
Trochilus.........................221, 236
Troglodytidæ......................... 332
Trogon............................... 277
Trogonidæ............................ 277
Turdidæ.............................. 335
Turdus mustelinus.................... 185
Turkeys...........................263, 264
Tympanuchus.......................... 261
Tyrannidæ............................ 285
Tyrannus...................216, 217, 218, 285
  crassirostris, instance of correlative colors...................... 155
  dominicensis, instance of correlative colors...................... 155
  melancholicus couchii.............. 286
  tyrannus...............155, 182, 199, 286
  verticalis.............153, 254, 255, 286
  vociferans......................254, 255
Urubitinga........................... 270
  anthracina......................... 146
Use and disuse, principle first suggested by Lamarck, 2; principle accepted by Darwin, 3; explanation of, by Darwin, 25; discussion of, by Spencer, 44-45; criticized by Poulton, 47.
Vines, an examination of some points in Prof. Weismann's theory of heredity, 11; admits the immortality of protoza, 11; questions explanations of evolution of immortal protoza into mortal metazoa, 11; criticism of Weismann's theory of heredity, 12; criticism of Weismann's theory of continuity of germ-plasm, 13; Weismann's reply to, 15.
Vireonidæ............................ 317
Vigor, segregate definition of....... 131
Vultures, American................... 267
Vireo......................157, 196, 215, 317
  atricapillus....................... 221
  crassirostris...................... 318
  flavescens......................... 318
  flavifrons......................... 157
  flavoviridis....................... 157
  ochraceus.......................... 318
Variations, Weismann's theory of, 55, 56; Weismann's theory of, argued against by Hartog, 56-57; explanation of, 59-60; explanation of conservative variations, 61; explanation of progressive, 61-62; secondary laws of, Brooks, 62; Schurmann's discussion of the origin of, 63; further discussion of, 71; Gulick's criticism of Brooks' theory of, 72.
Wag-tail.......................216, 217, 331
  water.............................. 217
Wallace, criticized on account of argument on variations, 52-53; opposed to Darwin's theory of sexual selection, 82-83; criticism of sexual selection opposed by Poulton, 84; on sexual selection, 85-86; Romanes' objections to his views on sexual selection, 92-93; objections to physiological selection, 116-117; Romanes' reply to criticism, 118-119; on recognition markings, 200-201; on geographical distribution, 234.
Wax-wings......................216, 217, 316
  Bohemian........................... 190
  cedar.............................. 190
  Japanese........................... 316
Warbler, Audubon's................... 219
  bay-breasted....................... 185

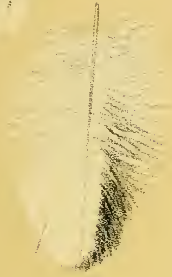
Warbler, black 151
black and white 320
Blackburnian 148
Brasher's 331
cærulean 319
golden-winged 321
gray 217
hedge 212
hooded 329
Kentucky 329
Lucy's 217
magnolia 118, 219
Nashville 217
palm 219
parula 324
prothonotary 320
red 157, 330
red-faced 330
Swainson's 218, 320
western 136
white 151
wood 319, 325
worm-eating 320
yellow-rumped 158, 182, 203, 219
yellow-throated 215
Water-ouzel 219
Weismann, value of his work, 8; on death, 8; immortality of protozoa, 9; against existence of neucleoplasm as advocated by Naegeli, 10; reply to the objections of Vines, 13; on embryogenesis, 16; theory of heredity opposed by Ryder, 17; summary of arguments between Weismann and opponents, 21; explanation of pammixis, 22, on transmission of mutilations, 30; experiments on tails of white mice, 31: criticism of observations on feet of Chinese ladies by Cunningham, 31: inheritance of artificially induced epilepsy in guinea pigs, 33-34; theory of variation, 55-56; theory of variation criticized by Hartog, 56-57; on sexual selection, 97.
Whip-poor-wills 196, 207
Woodpecker 203, 210, 213, 279, 280
Californian .. 143, 163, 170, 173, 178, 191
downy 175, 211, 255
golden-fronted 222
hairy 255
red-headed 145, 217
three-toed 155, 222
Williamson's 222
Wrens 196, 332
Wrynecks 279, 280
Xanthocephalus 218, 236 291
xanthocephalus, instance of correlation between red and yellow, 155, 157
Xanthoura luxuosa 158, 243
guatemalensis 243
Xenopicus 224, 280
albolarvatus 146, 281
Yarrell, on changes of plumage .. 132, 133, 136
Zenaidura macroura 205
Zonotrichia 180, 196, 305
albicollis 183, 305
coronata 187, 176, 209, 305
leucophrys 209, 254, 305
gambeli 184, 254
querula 183, 305
Zoorubin 138

PLATE I.


1


2


3


4


5


6


7


8


9


10

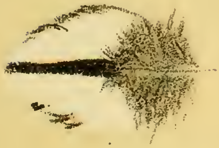

11


12

del. C.A.K.

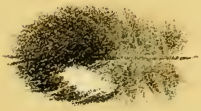
PLATE II.

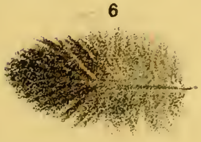
1


2


3


4


5


6


Melanerpes
formicivorus bairdi

7


8


9

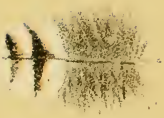

10


11


12

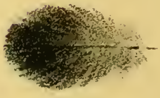

13


Sphyrapicus
varius

14


15


16


17


Sphyrapicus
thyroides

del. C A K

LITH H. BRITTON & REY, S.F.

PLATE III.

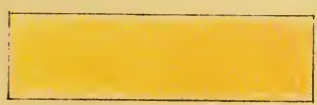

del. C.A.K.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44

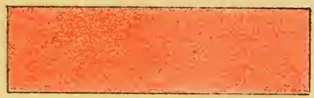
PLATE IV.

PLATE V.


Xanthocephalus xanthocephalus

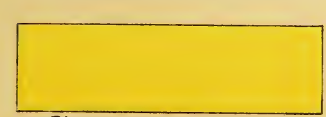

Agelaius


Habia melanocephala


Habia ludoviciana

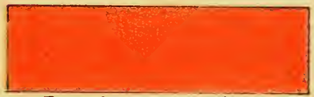

Colaptes auratus


Colaptes cafer


Piranga ludoviciana


Piranga erythromelas


Regulus satrapa


Regulus calendula


Icterus cucullatus


Icterus cucullatus nelsoni


Setophaga ruticilla ♀


Setophaga ruticilla ♂

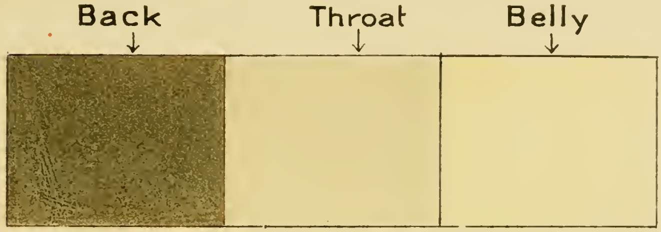

Sphyrapicus varius


Sphyrapicus varius


Agelaius phœniceus juv. ♂


Agelaius phœniceus ad. ♂

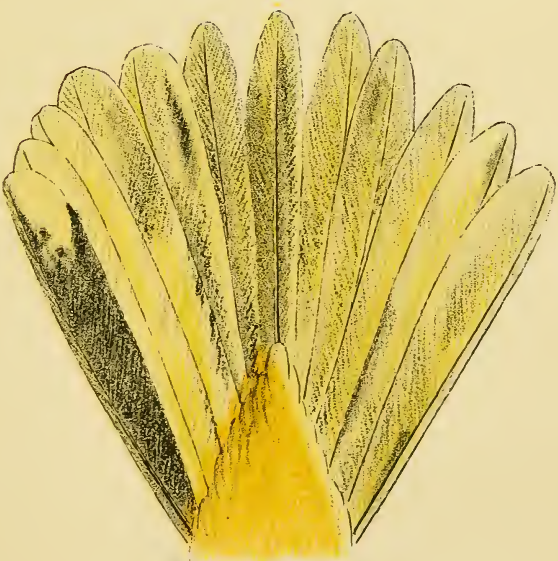
del. C.A.K.
LITH. BRITTON & REY, S.F.



Myiarchus cinerascens

Myiarchus mexicanus

Myiarchus crinitus

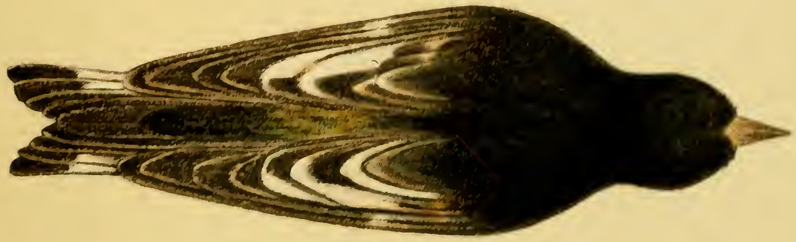


Icterus cucullatus nelsoni

LITH. BRITTON & REY S.F.
C.A.K. DEL

Spinus psaltria

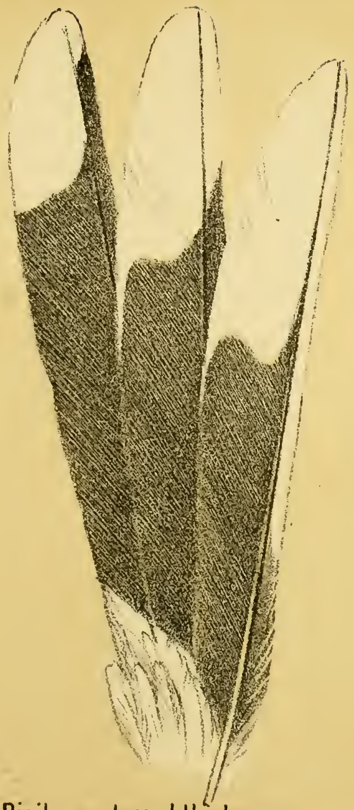
Spinus psaltria arizonae



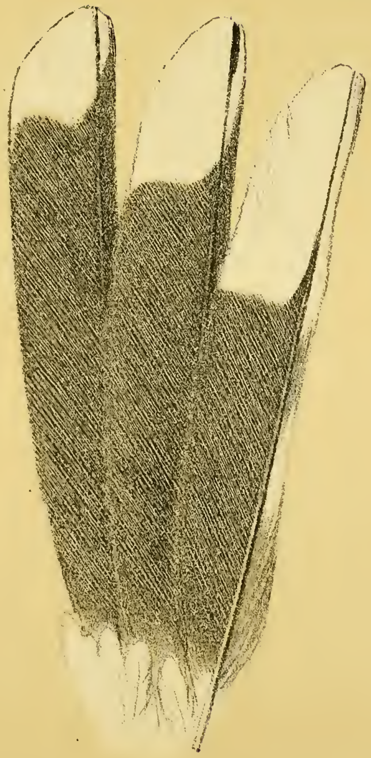
Spinus psaltria mexicana

[illegible] C. A. R. DEL.

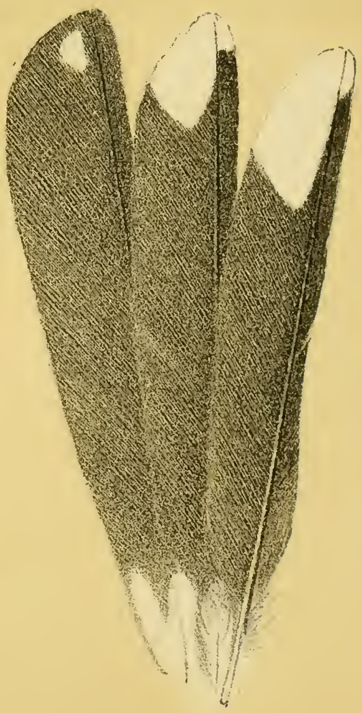
PLATE VIII.



Pipilo eryhrophthalmus

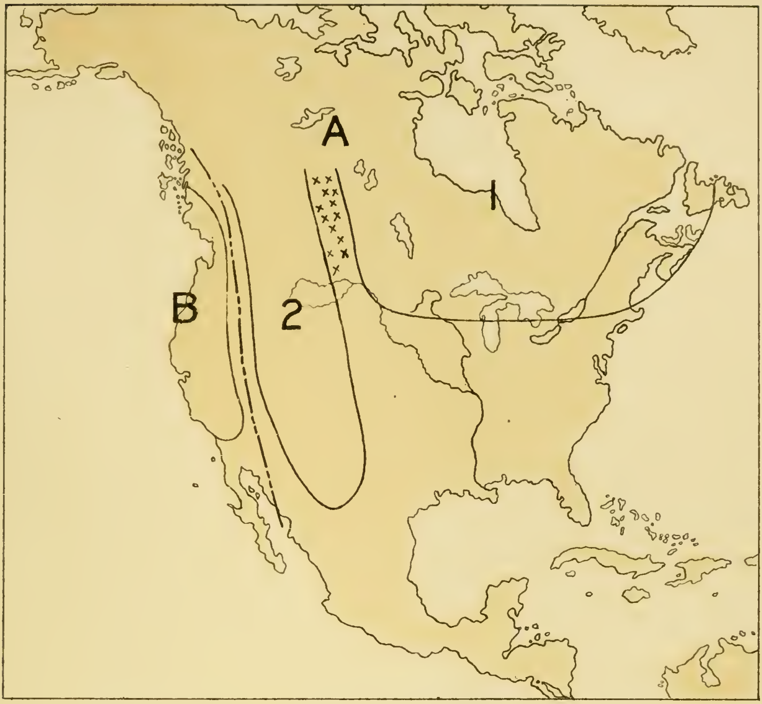


Pipilo maculatus megalonyx

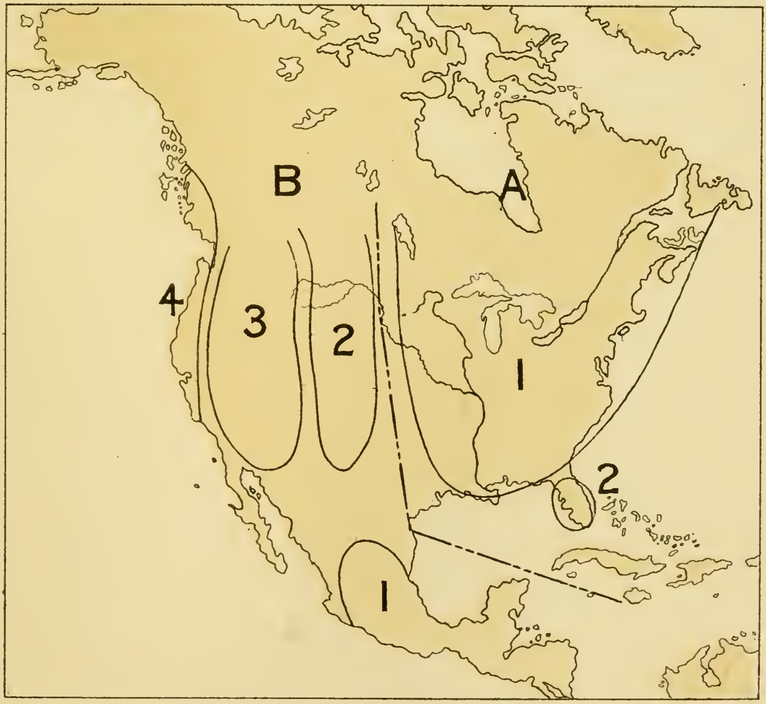


Pipilo maculatus oregonus

del. C.A.K.

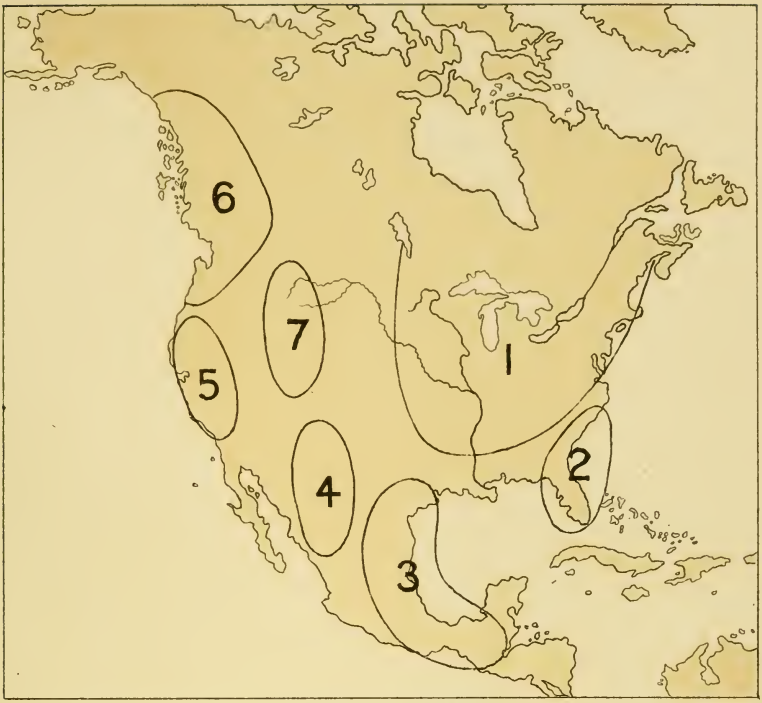


SPHYRAPICUS.

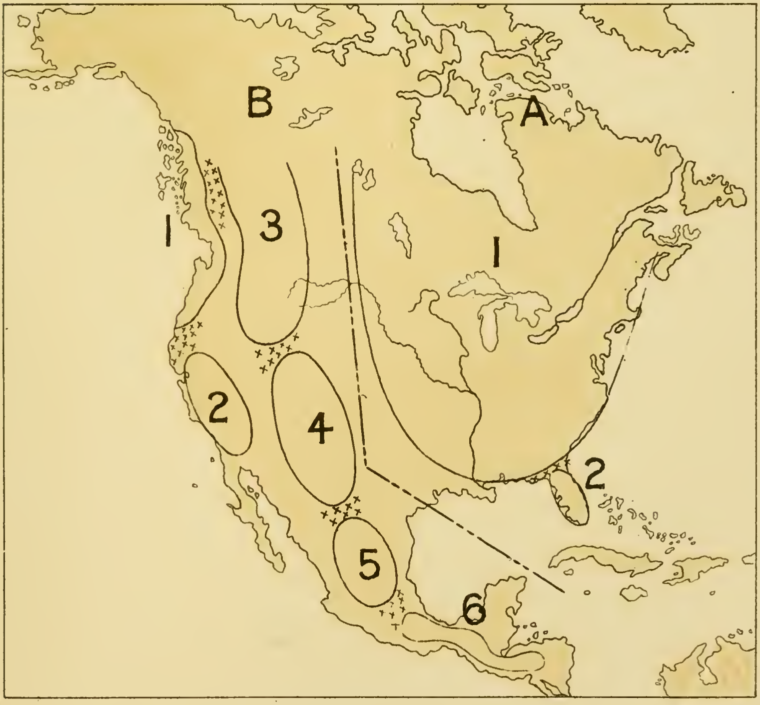


PIPILO.

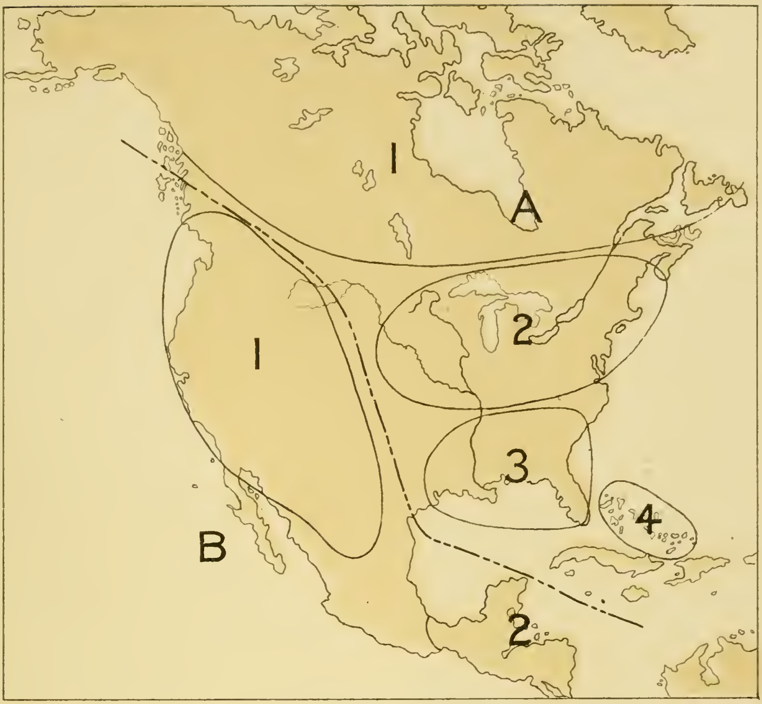
PLATE X.



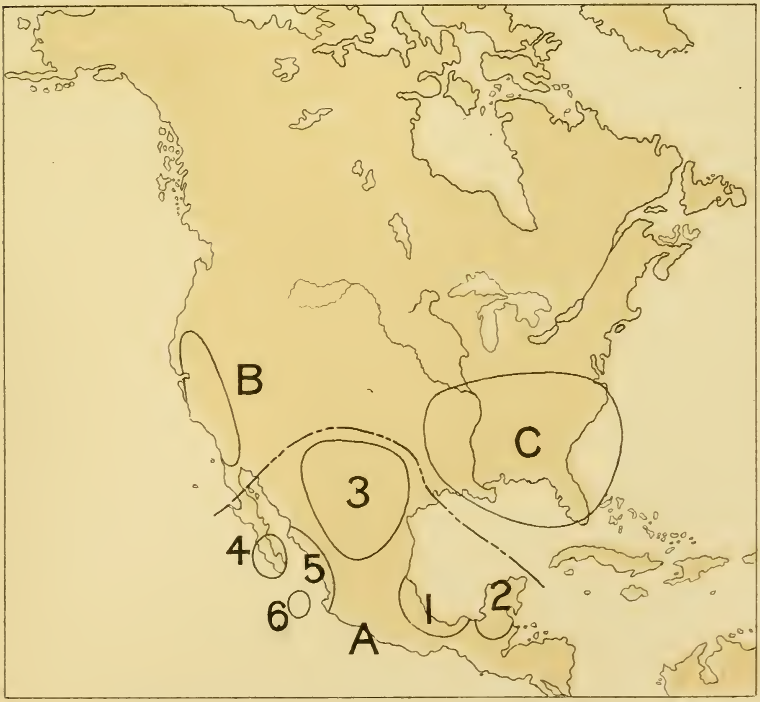
MEGASCOPS ASIO.



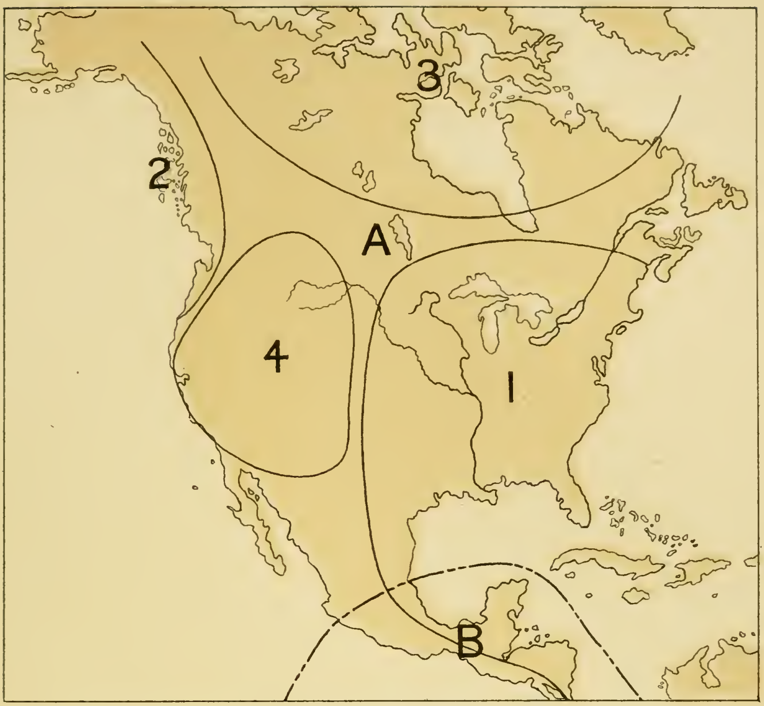
CYANOCITTA.



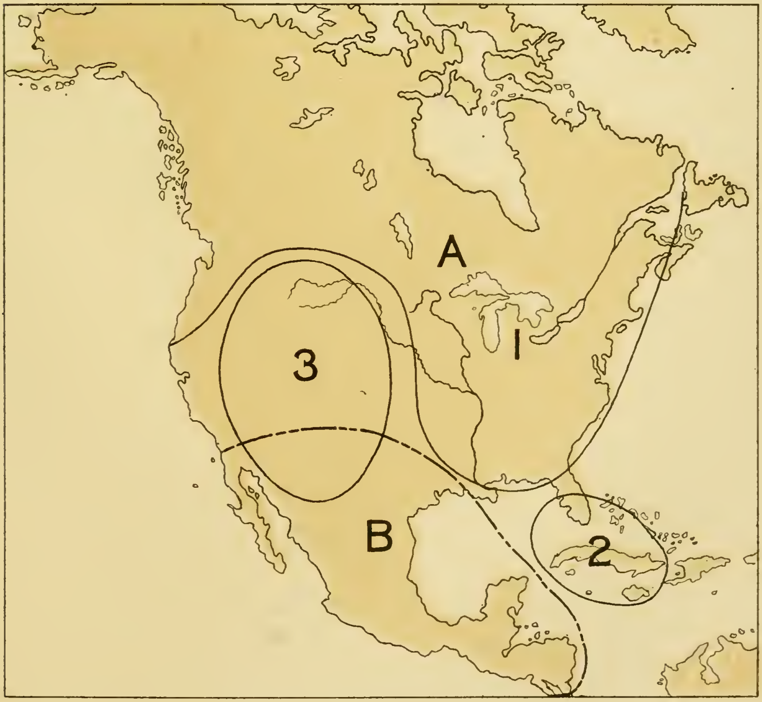
DRYOBATES HARRISI.



DRYOBATES SCALARIS NUTTALI & BOREALIS.



BUBO VIRGINIANUS.



CHORDEILES.

del. C. A K.
LITH. BRITTON & REY, S.F.

PLATE XIV.

Agelaius phœniceus ♂

Agelaius gubernator ♂

Agelaius tricolor ♂

Agelaius phœniceus ♂
winter

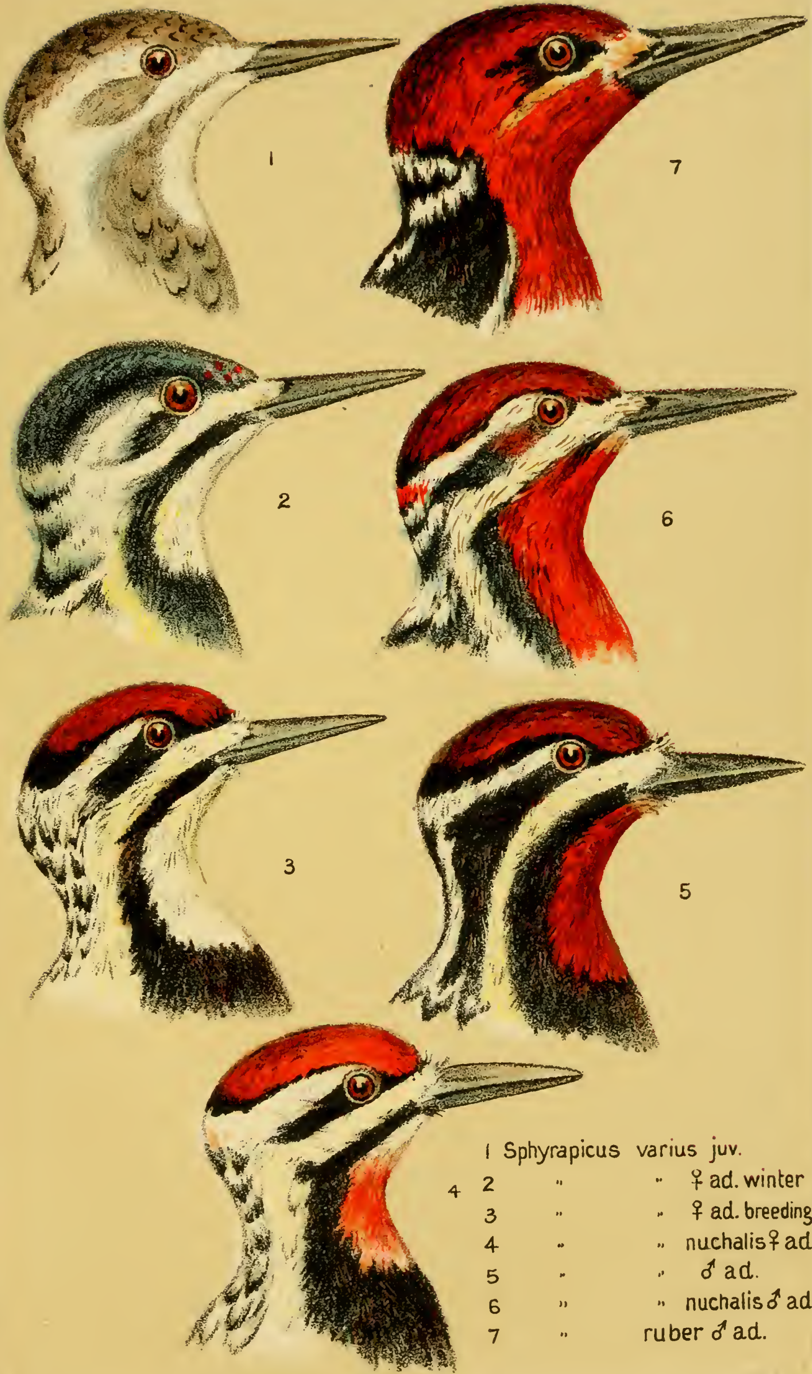
Agelaius gubernator ♀
summer

Agelaius tricolor ♀ summer

Agelaius gubernator ♀ winter

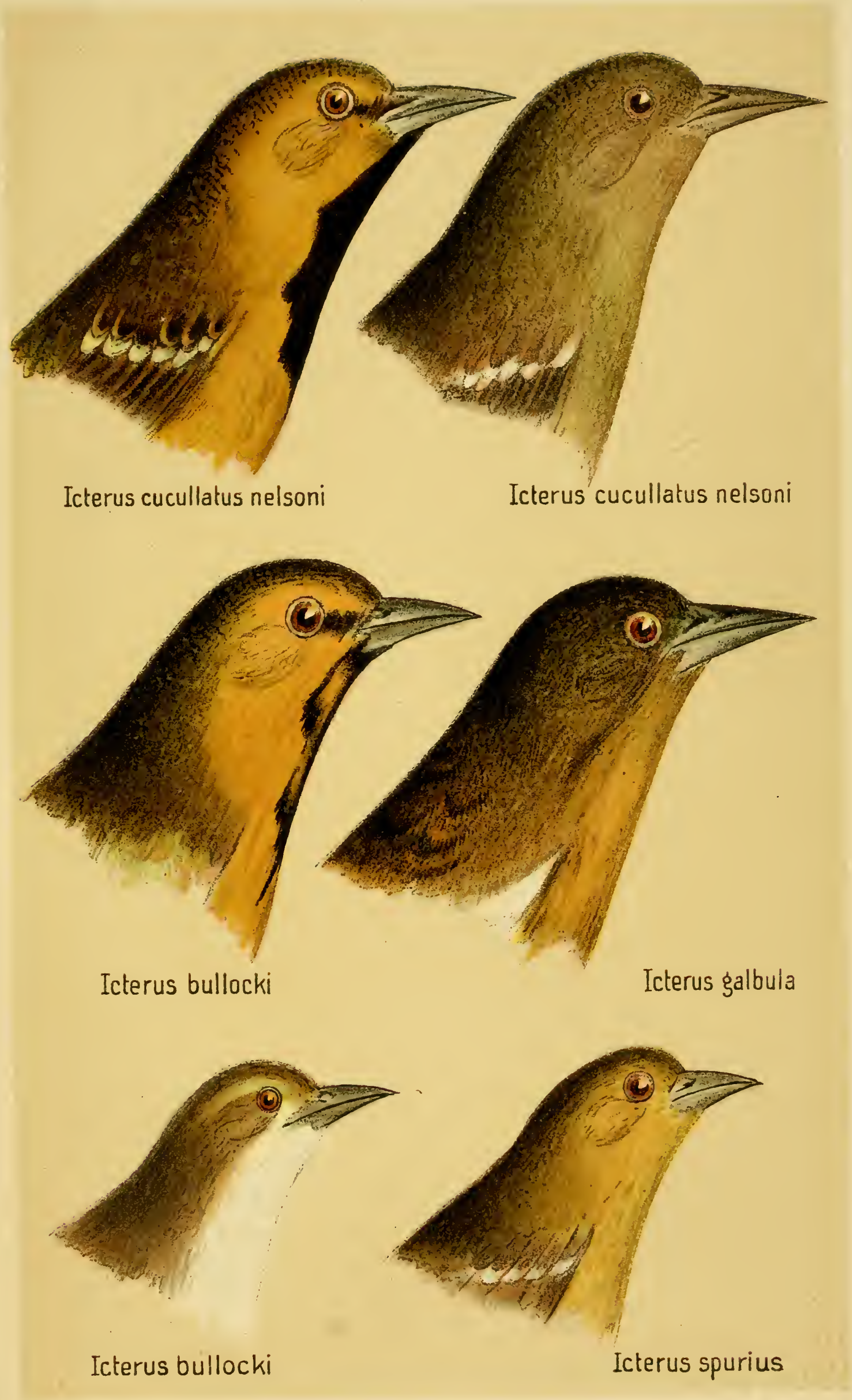
del. C.A.K.
LITH. BRITTON & REY S.F.

PLATE XV.



1 Sphyrapicus varius juv.
2 " " ♀ ad. winter
3 " " ♀ ad. breeding
4 " " nuchalis ♀ ad.
5 " " ♂ ad.
6 " " nuchalis ♂ ad.
7 " ruber ♂ ad.

del. C.A.K.
LITH. BRITTON & REY, S.F.



Icterus cucullatus nelsoni

Icterus cucullatus nelsoni

Icterus bullocki

Icterus galbula

Icterus bullocki

Icterus spurius

[illegible] & REY S. F.

C.A.K. DEL.

Icterus cucullatus

Icterus cucullatus nelsoni

Icterus bullocki

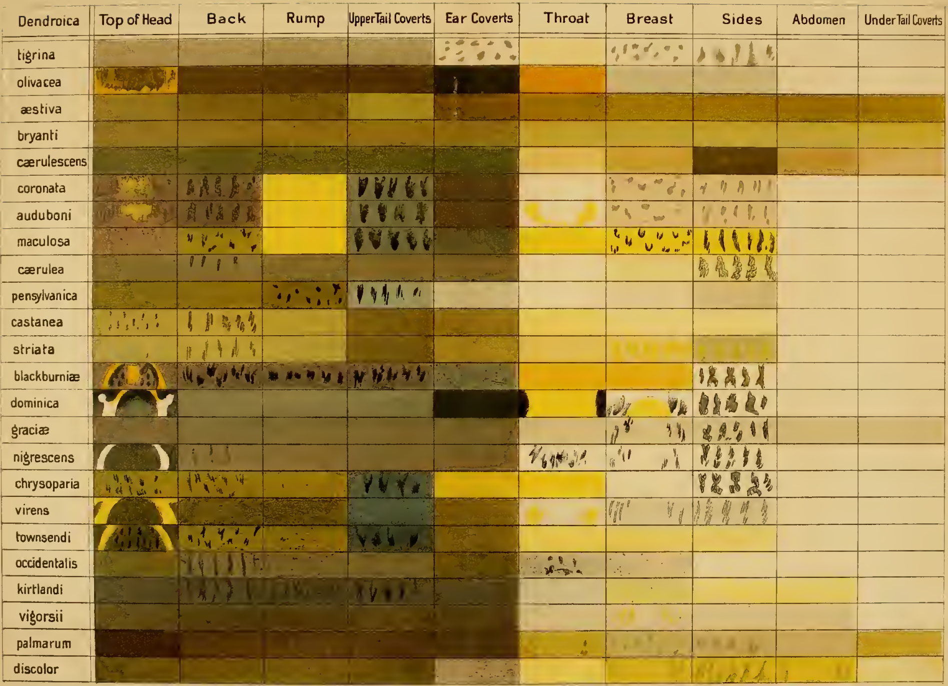
Icterus galbula

Icterus parisorum

Icterus spurius

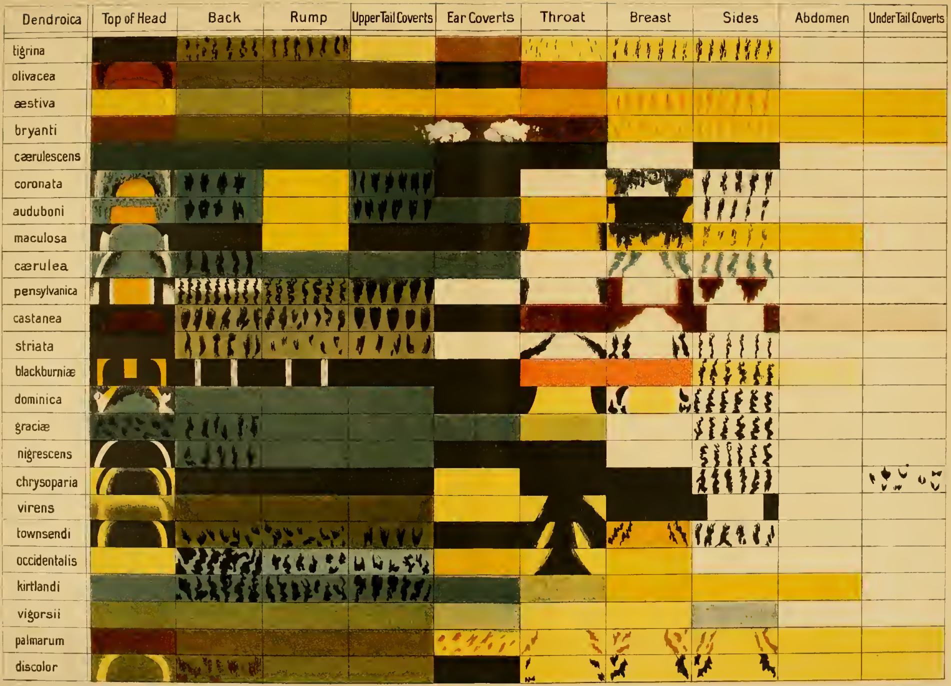
[illegible] BRITTON & REY S.F.

C. A. K. DEL.



Dendroica	Top of Head	Back	Rump	Upper Tail Coverts	Ear Coverts	Throat	Breast	Sides	Abdomen	Under Tail Coverts
tigrina										
olivacea										
æstiva										
bryanti										
cærulescens										
coronata										
auduboni										
maculosa										
cærulea										
pensylvanica										
castanea										
striata										
blackburniæ										
dominica										
graciæ										
nigrescens										
chrysoparia										
virens										
townsendi										
occidentalis										
kirtlandi										
vigorsii										
palmarum										
discolor										

PLATE XIX.



BRITTON & REY