Charles Otis Whitman
1901
Age 60 years

# ORTHOGENETIC EVOLUTION IN PIGEONS

POSTHUMOUS WORKS OF CHARLES OTIS WHITMAN

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EDITED BY

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VOLUME I
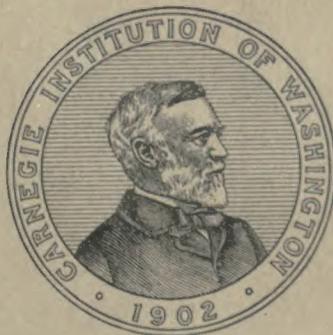
PREFACE BY THE EDITOR.

At the mature age of 50 years Professor Charles Otis Whitman began the work now presented in these volumes, and the long task was still incomplete when, 18 years later, on December 6, 1910, a brief illness terminated the work and life of this investigator, to whom biology and many American biologists especially are so much indebted.

After six years, the efforts of some of his friends to make the results of his long labors available to others are nearly concluded. This task has been necessarily shared by a number of persons and organizations, and the demands upon some of them have been so considerable and unusual that the nature of their endeavors is here most gratefully acknowledged.

The continued maintenance of the large collection of pigeons upon which this series of studies was based was essential to a presentation of anything more than a fragment of the results; it was necessary to learn the term of life and the sex of all the surviving individuals; and further breeding or testing of certain "mutants" among them was scarcely less urgent. This formed one of a number of heavy exactions upon those who have felt the necessity of presenting the largest possible portion of the author's results. The whole of these and other obligations, during the first year, was shared by Mrs. C. O. Whitman and by the editor, who was generously assisted by unasked grants from the A. A. Sprague Institute of Chicago and from the Laboratory of Experimental Therapeutics of the University of Chicago. During the five following years the Carnegie Institution of Washington has fully maintained the work—during two years at Chicago and for the succeeding three years at the Station for Experimental Evolution at Cold Spring Harbor, New York; that Institution has also assumed the entire expenditures incident to the publication of these volumes. For all this generous assistance the editor expresses enduring obligations.

Not more than one-fifth of the matter herewith presented was found to approach a stage of readiness for publication; it has required some years to bring the results to their present form. Even now we have been unable to utilize all of the records and data, and many of the carefully prepared illustrations are also omitted. If our progress in the preparation of these materials has seemed lingering and slow, it should be said that much time has been given to all those materials which proved impracticable for use as well as to those which are now incorporated in the work. It was, however, in some cases found obligatory to become familiar with a subject as to which only records and raw data were available. Again, other and nameless difficulties have sometimes attended our efforts.

In the task of preparing the various materials for publication the editor found himself wholly unprepared to deal with the manuscripts on Behavior in Pigeons. Professor Harvey A. Carr has most generously carried that work to completion and these studies are grouped to form Volume III. The special materials on voice were

assigned to Professor Wallace Craig, who was able to arrange for publication only a small part of them; these also will be found in Volume III.

The dominant feature of Professor Whitman's prolonged study of inheritance and evolution lies in its intensive and diversified attack upon the nature of a specific character. As early as 1897 he wrote:

> It is to a comparative and experimental analysis of *specific characters* that we must look for a knowledge of the phenomena of heredity and variation.

As Whitman was a contemporary of de Vries, who likewise avowed that the study of the origin of species is to be accomplished through a study of specific characters, it is truly remarkable that the results of the two investigators should be so strongly opposed. The reasons for these divergent conclusions may be demonstrated at some time in the future, but something can now be said as to *differences in method and material*, which certainly have accompanied the two decisions which now seem to stand in strong disagreement. It is clear, for example:

(1) That de Vries worked with much larger numbers of individuals than did Whitman. A corollary of this is—though it may not at first be entirely evident to all—that Whitman was able to and did more closely study and observe the specific characters with which he worked, and for longer periods of time, in the same individual. The one study was expansive, the other intensive.

(2) The purity of the greater part of Whitman's breeding material is beyond question. Can the same be said for de Vries's material of chief reliance?

(3) The phylogenetic relationships of Whitman's most studied species were known and the direction taken by evolution in the past had been ascertained. Does the want of this orientation in de Vries's material at all qualify his results?

(4) The observations and resultant theory of de Vries nowhere touch or are concerned with *recapitulation*. Whitman finds this to be the central fact of heredity and organic development, and the specific characters most carefully studied by him reveal it abundantly. Does this difference lend weight to the conclusions of the one or of the other?

Professor Whitman's devotion to the task of mastering a specific character was not limited by the conventions of any particular line of study; it heeded neither time, personal sacrifice, nor the knotty and thorny interpolations which the ensemble of life-processes is continually throwing upon the path of the biologist when he would isolate and examine a particular vital process; and, surely, these latter difficulties especially beset all studies on the origin and establishment of *new forms* of organisms. But Whitman was ready and eager to attend to each and every intercalated phenomenon, from whatever foreign or extrinsic source, if its analysis and meaning might lead to a better, surer, or closer measure of realities in his own main sphere of study. It thus happens that along the pathway which he has blazed into the central problems of evolution are to be found other landmarks of discovery—some mere sign-posts and some wide and well-done surveys of regions which lead well into the territory of such other and diverse subjects, as instinct, fertility, animal behavior, correlative variation, and the nature of sex.

Having selected color-pattern in pigeons as supplying a relatively small group of specific characters easily accessible to study, he first set about determining which patterns are the more primitive and which the higher and more recent, each bit of evidence being retested by search for the convergent testimony of various kinds of evidence. A general survey was made of the color-patterns of the wild species of pigeons, a group that includes nearly 600 species, besides nearly 200 domestic races that have been derived from one or a few wild species. Large numbers of genera and species from all parts of the world were brought to the breeding-pens of his yard. There with much patience the patterns were studied from the living birds; male and female were compared; the sequence of pattern in the plumages from young to old was accurately observed; thoughtful experiments were devised to bridge the gap between the molts and thus displace apparent discontinuities with evident continuities; the behavior of many characters in hybridization was extensively studied; and the primitive pattern of several diverse orders of birds was ascertained.

The direction of the evolution of pattern as it was indicated by all these studies was, moreover, further tested by evidence of an entirely different sort. Such characters as voice, behavior, and fertility were separately subjected to similar appropriate, comparative, and breeding tests to learn whether the resulting data would parallel each other and whether all would parallel the data furnished by the extensive study of the color-pattern. Only when Dr. Whitman had accumulated a vast amount of consistent and convergent testimony as to where the various genera stand in the phylogenetic series did he permit himself to feel that he was reading aright the history of the specific characters of the pattern.

In consequence, Whitman's work presents a large body of searchingly self-critical conclusions; and these conclusions unquestionably lead far into constructive evolutionary theory. For his material, he was convinced that he had demonstrated the reality and regnancy of definitely directed variation—*i.e.*, of *orthogenesis*—as the method of evolution. He has accumulated the most weighty evidences for continuity as against discontinuity in the phenomena of variation, inheritance, and evolution. He has thrown new and extraordinary light on the nature and meaning of "mutants"—such "mutants," at any rate, as occur among pigeons; and he has made a brilliant and comprehensive analysis of the phylogeny of pigeons.

Chapters I, II, III, IV, and X of the present volume were practically finished by Dr. Whitman, and except for the addition of references to the illustrations and the occasional insertion of a page or a few pages of supplementary matter—often written later by him on the same subject—these remain practically unchanged. The illustrations of Chapter X were descriptively united to the text by Dr. Whitman. Nearly all of the other illustrations have been placed by the editor at those points in the text which to him seemed necessary or appropriate. Chapters V to IX inclusive required a complete rearrangement by the editor. The sources of this material were quite scattered, as is indicated in connection with each chapter, and some topics were not sufficiently treated. In other cases the subjects were studied in the earlier years and it was found that later and more searching study had

thrown other or additional light on these topics. Several complete addresses by Dr. Whitman were found to repeat statements elsewhere given; these have been either entirely omitted or certain paragraphs have been transferred to a position in one or another of the present chapters where the same topic is discussed.

In some instances the editor has added statements of his own, but it is thought that the reader will never be in doubt as to the source of a statement. In all those chapters in which the present arrangement is wholly that of the editor, and where he has drawn material from manuscripts or folders variously designated by the author, references to those original folders are made at various points within the chapter or at its close. All of these original folders will be permanently filed with the Carnegie Institution of Washington, either in Washington or at the Station for Experimental Evolution at Cold Spring Harbor, where they will at all times be easily accessible to all interested parties.

The reader will find that the literature of some of the subjects considered here is not adequately treated. It will be easily granted, however, that since the author did not arrange these parts of the manuscript for publication, it would be unwise or impossible for another to go far in an attempt to do so.

To the two artists, Mr. K. Hayashi and Mr. Kenji Toda, whose skilful and numerous productions assist so much in the presentation of these studies, the author would, I am sure, have recorded his warmest gratitude.

The editor readily acknowledges that the imperfections of form of the work as it now appears are assignable to him, and not to the author; but if what he has done lacks the finish and completeness of all that which the author had made ready for publication, it is hoped that a full measure of indulgence may be granted for imperfect results in the rather difficult endeavor to make available material that otherwise must have been wholly lost. But even while deploring the imperfections of his work, he avows it—under the circumstances—the great pleasure of his life to have been able to assist in presenting the message of his colleague and master to those for whom the labors of many years had pledged it.

OSCAR RIDDLE.

STATION FOR EXPERIMENTAL EVOLUTION,
          Cold Spring Harbor, December 1916.

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ILLUSTRATIONS.

PLATES.

TEXT FIGURES.

ERRATA.

Page 73, line 36, for "pls. 16 and 17, Vol. II," read "pl. 8, Vol. II."
Page 76, line 5, for "Fig. B. 5, 6, 7, 8," read "Fig. B. 1, 2, 3, 4."
Page 76, line 11, for "Fig. D. 4, 5, 6," read "Fig. D. 1, 2, 3."
Page 80, line 3, for "*C. piqui*" read "*C. picui*"; also on page 84.
Page 84, under explanation of Plate 32, Fig. B. For "× 0. 5" read "natural size."
Page 94, explanation of Plate 40, under Figs. A and C, instead of "× 0.7" read "× 1.4."
Page 107, line 23. for "pl. 57, Vol. II," read "pl 35, Vol. II."
Page 128, near foot of page, for "× 0.75," read "× 0.35 (about)."
Plates 76 and 80, periorbital is misspelled.

ORTHOGENETIC EVOLUTION IN PIGEONS

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VOLUME I

CHAPTER I.

INTRODUCTORY.[1]

Progress in science is better indicated by the viewpoints we attain than by massive accumulation of facts. Darwin's perspective made him a prodigy in the assimilation of facts and an easy victor in the greatest conflict that science has thus far had to meet. His triumph has won for us a common height from which we see the whole world of living beings as well as all inorganic nature; phenomena of every order we now regard as expressions of *natural* causes. The supernatural has no longer a standing in science; it has vanished like a dream, and the halls consecrated to its thraldom of the intellect are becoming radiant with a more cheerful faith.

In no other field of science is the viewpoint of such ever-present importance as in biology. It means orientation of the field, clear vision in directing research, and insight in the interpretation of phenomena. It may be well, therefore, to prepare the ground a little in advance of the facts to be presented, and this can be done to best advantage by taking our bearings from two of our foremost guides—Darwin and de Vries.

The great problem in biology, as it presented itself to these leaders, was to account for progressive evolution by natural means. Supernaturalism had declared the living world a stupendous miracle, a creation by fiat. Science had already made good its claim to the physical world, but the animate sphere was still supposed to rise supreme above natural law. Darwin was taught the creation dogma, and all through the memorable voyage of the *Beagle* he was predisposed to regard species as immutable. He stated in a letter to Dr. Otto Zacharias, in 1877:[2]

When I was on board the *Beagle* I believed in the permanence of species, but, as far as I can remember, vague doubts occasionally flitted across my mind. On my return home in the autumn of 1836, I immediately began to prepare my journal for publication, and then saw how many facts indicated the common descent of species, so that in July, 1837, I opened a note-book to record any facts which might bear on the question. But I did not become convinced that species were mutable until, I think, two or three years had elapsed.

The five-year voyage on the *Beagle*, during which facts were collected with no definite theory but with a haunting doubt as to the immutability of species, was the foundation or germ-stage in the development of Darwin's great generalization. It is still a notable fact that the germ of Darwin's views at this inceptional stage was already a logical whole so far as fundamentals were concerned. The problem embraced the entire organic kingdom, from lowest to highest.

The great difficulty, then, was to find out how nature could be self-regulating in bringing forth such nice adaptations as are everywhere patent in the organic

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[1] The manuscript here selected as introductory to this volume was written in 1909, and formed part of a lecture at Clark University, entitled "A study in evolution, based on color-characters in pigeons, and bearing on moot questions." A few phrases of that address are omitted. The data presented in connection with this lecture were not reduced to writing, but accompanying lists of topics, illustrations, etc., show that many of the subjects which are fully treated in the several chapters of this volume were discussed.—EDITOR.

[2] Cited by Huxley in his Darwiniana Essays, p. 275.

realm. How could teleological results flow from non-teleological causes? That was the staggering problem that confronted Darwin and kept him from feeling entirely convinced "two or three years" longer of the mutability of species. Already he had "perceived that selection was the keystone of man's success in making useful races of animals and plants; but how selection could be applied to organisms living in a state of nature remained for some time a mystery."[3] For clearing up this mystery the credit still belongs to Darwin, for he alone knew there was such a mystery and made the application that dissolved it. As Huxley remarks:[4]

Variation occurs under natural, no less than under artificial, conditions. Unrestricted multiplication implies the competition of varieties and the selection of those which are relatively best adapted to these conditions.

This is a concise statement of the theory of natural selection, so simple and self-evident that it at once carries conviction. The theory tells us that nature is self-regulating in the living as in the non-living world. It tells us that the more useful variations have the best chance of survival in the struggle for existence, and thus shows that, variation being given, progressive evolution is inevitable.

The theory does not undertake to explain the first appearance of life or to state the causes of variation, but it does show how nature sifts out the fit from the unfit and builds upon such variations as have a winning value in the battle of life.

For this all-embracing viewpoint, which completes and crowns the advances by Newton and Lyell, the world is indebted to Charles Darwin.

The theory of de Vries, the distinguished author of the mutation theory, coincides in the main with that of Darwin; but he introduces a distinction in regard to variations which he regards as fundamental, dividing them into two classes: (1) ordinary or fluctuating variations, and (2) mutations. All species exhibit "fluctuations," but these obey Quételet's law of probability and never transgress the limits of the type. From them improved races may result, but never new species.

Mutations, on the other hand, are those variations which remain constant, and these are the sole source of new species and new varieties. Fluctuations are regarded as merely quantitative, while mutations stand for qualitative changes. However small or large, mutations are always sudden in appearance; that is, they do not arise by slow and transitional degrees, but come ready-made; and although they are subject to fluctuations, they are essentially immutable units—the so-called "unit-characters." A species thus consists in some definite number of these fixed units, from the germ onward to the full adult stage, and this number remains constant. The loss or addition of a single unit would make at once a new species.

The fundamentals in the mutation theory are:

1. Every species consists of a fixed number of unit-characters.
2. The species and the component units are alike sudden in origin and unchanging in type.
3. Old characters may be suddenly transmuted into new ones, but between the two there is always a gulf of absolute discontinuity, with no possible bridge of modification.
4. Continuous intergradations may connect a species with an improved race, but never one species with another species.

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[3] Life and Letters, I, p. 68.   [4] Darwiniana Essays, p. 279.

5. Species-formation is chancewise in direction, never resulting from a tendency to vary in any one determinate direction.
6. Natural selection can not give origin to new species; it can only weed out from those already in existence such as are incapable of sustaining themselves.

The central conception of this whole theory of mutation is that of fixed unit-characters. Specific characters are called units, because they are supposed to be individualities and to remain such in all stages of development and evolution. If such a character undergoes change, it ceases to be the same character and by sudden transformation becomes an entirely new unit, or unit-character. Transform one of these units, add one, or remove one, in each case the old species becomes a new species per saltum. These units are imagined to have the clean-cut individuality of a chemical molecule, and any real change is likened to a chemical substitution.

Such views are captivating, for they offer definiteness in place of the vague and mysterious. The problem of the origin of species hangs on the nature and meaning of specific characters. Reveal the secrets in the development and evolution of a single specific character, and you will furnish the key for understanding all characters and all species. Right or wrong, de Vries has done well to direct attention to the all-important point, the specific character. Here, I believe, lies the whole problem of evolution, and de Vries is right in trying to draw a line between specific and non-specific variations.

It should not be overlooked, however, that Weismann has already set us far along in this task; for not long ago he convinced most of us that only germinal variations are hereditary and that all so-called "acquired characters" of somatic origin are non-transmissible and therefore without specific significance.

Do we not have, then, in germinal variation, a better criterion of what is specific than we get in sudden appearance? Indeed, is it not here that the seeming suddenness of first appearance finds its explanation, and likewise the fact that so-called mutations involve the whole organism? If we are to accept the physiological conception of development, as is inevitable in my opinion, it is easy to see that a change, however slight, in the primordial constitution of the germ would tend to correlate itself with every part of the whole germ-system, so that the end-stage of development would present a new facies and appear as a total modification, answering to what de Vries would call a mutation. That something of this order does sometimes occur I have indubitable evidence, and in such form as to dispel the idea of discontinuity and sudden gaps in transformation.

The idea of unit-characters, however, as distinct elements that can be removed or introduced bodily into the germ does not appeal to me as removing difficulties, but rather as hiding them; in short, as a return to the old pangenesis view of preformed characters. In this theory, as is well known, we had two miracles involved. The first consisted in a centripetal migration of preformed gemmules and the second in the centrifugal distribution of the same elements. De Vries dismisses the first of these, but accepts the second, and on it rears the superstructure of his theory of mutable-immutable unit-characters. With all due respect to the distinguished author of this theory, and with abounding admiration for his great work and model methods, which have aroused universal interest and stimulated enormously experimental bionomics, I am strongly persuaded that his hypothesis of unit-characters fails as a guide to the interpretation of the species and its characters.

It is true that a great amount of work on Mendelian heredity seems strongly to support the unit-character hypothesis, and that cytology offers some further support. Nevertheless, I have to confess to wholesale skepticism. The germ, as I believe and have long maintained, stands for an organized whole. It is a unit organism, not an organism of units; all the features that arise in course of development are within the sphere of the individual unity and integral parts of it, and whatever specificity they possess is completely determined and not of independent origin.

The strongest suggestion of unit-characters is found in the Mendelian phenomenon known as segregation. I do not underestimate the importance of this striking behavior of so-called alternative unit-characters. I am familiar with them, and deeply interested; but I am unable to see in them the sum total of all we know about heredity. What I have said in regard to unit-characters applies to the Mendelian doctrine. Mendelism, like mutation, neglects the natural history of the characters it experiments with and is not primarily concerned to know how characters have originated and multiplied.

It seems to me a great error for the mutationist and the Mendelian to construe characters as disconnected entities rather than as modifications slowly and gradually evolved, in genetic continuity from stage to stage, as we see so well illustrated in normal development. De Vries attaches considerable weight to the fact that he has actually seen mutations and knows their pedigree for one or a few generations. Since the publication of his remarkable work, other investigators have reported numerous mutations, and I must join this group to the extent of admitting that I have witnessed phenomena that a mutationist would probably claim as confirmations of his theory. Some of these phenomena require a very detailed and specific treatment; but let us here define the nature of the field we are to enter and make clear the way of approach.

The ability to interpret evolutional phenomena, or even fully to understand a given interpretation, implies not only concentrated attention but also a prepared state of mind. I wish, therefore, first of all, briefly to discuss a query that may obtrude itself at the outset. The simple lifeless color-mark of a feather may, at first thought, appear to be artificial, too extremely variable, to deserve serious attention. But is not variation the foundation of all evolution? and is it not a great advantage to have our subject-matter where it can be easily seen? If the very exuberance of these colors and color-patterns be somewhat appalling on first approach, it costs but little effort to see that it all counts in favor of the investigator. The greater the variability, the closer, in general, will be the connections between stages, and the easier it will be to catch the trend of derivation, and to discover the common points of departure for whole groups of related color-patterns, and, possibly, to reduce these points to a single point of departure for the whole bird kingdom. Such a vista once opened would orient the whole field, disclose the direction or directions of evolution, provide the investigator with a key to the natural order of sequence in color-patterns, enable him to detect and to demonstrate orthogenetic evolution, if such there be, and to discriminate nicely between this and the results to be ascribed to natural selection and other intervening factors. From such a vantage-ground, juvenile stages of color-patterns would become luminous as recapitulations, in the sense of the biogenetic law, and not stand as isolated prodigies of mutation.

Nature has a long memory in that as she has built slowly through the ages, so she now rebuilds in each individual development, repeating, over and over, in each generation, the essential steps taken in the preceding generation. This drama of recapitulation, in every stage a *tableau vivant*, condensed and modified as of necessity it must be, since every stage is to some extent a remolding of the earlier, is nature's silent rehearsal of past history, or what is commonly called *heredity*.

This is unquestionably the greatest wonder that biology has yet disclosed. Its fundamental significance has scarcely yet found general appreciation even among students of evolution. A few—Hering, Haeckel, Semon, Francis Darwin, and especially Rignano—have grasped and treated its deeper meaning as a universal mnemonic law, a law that underlies all intelligence as well as all development. The disputations hitherto held over Haeckel's biogenetic law do not as a rule touch the essential phenomenon; indeed, they obscure the marvelous accuracy of hereditary recapitulation.

This uniformity of nature's laws and the perpetual repetition of her building processes are the two basal facts on which rests the hope of all cumulative science and of our ultimate triumph in reading the secrets of evolutionary history. These remarkable phenomena, which in normal development furnish, as a rule, only fragmentary and disconnected parts of past evolutional history, may be so expanded, by suitable experiments, as to demonstrate complete continuity of stages in the passage to the adult pattern.

This crucial experiment consists in plucking a few juvenal feathers at such points and time-intervals that the new feathers developing in the places of those removed will appear at successively later ages, each unfolding a pattern in a stage of evolution corresponding to its age. The result is that we get an ascending series of stages rising gradually from the juvenile to the adult pattern, so that we have pictured before our eyes the progressive transformation by which the earlier is converted into the later and final pattern. One such experiment as this reveals a law that must hold, in principle at least, for the pigeon phylum and all its branches; and not only for this group of birds, but also for the entire bird world.

Of course it is not to be expected that such an experiment would give equally conclusive results in all cases, for different species have run different courses and the length and fulness of the recapitulative phases vary greatly. But all development, it must be remembered, is essentially a repeating or recapitulating process. This is the central fact of heredity and the doctrine of descent. The first or germ stage is, of course, the oldest in the phyletic series, and the adult stage, which we commonly call the older stage, considering the age of the individual, is really the youngest of the phylum. From this point of view it is readily seen that we are to expect the fullest recapitulation in the final stages and the most condensed or abbreviated recapitulation in the initial stages. The development of the individual is everywhere a confirmation of this anticipation, if we allow for the fact that certain stages have greater physiological value than others, and consequently have been favored and kept at the level of need.[5] The cell-stage of the germ is an instance.

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[5] This is the work of natural selection, which is omnipresent and efficient in every part of the organic universe. To call for proof of the action of selection is to call for proof of such obvious facts as the struggle for existence and the survival of the fittest.

When, then, an evolution of millions of years has to be repeated in a few days or weeks, there must be enormous abbreviation in earlier stages, relieved here and there by a few essential landmarks, and only in the later stages relatively fuller exhibition of details. If we are fortunate enough to find a case here and there where lost history can be recalled and actually pictured forth in the living bird, we have, as I have said, a demonstration of a physiological law in development that must have universal validity. The process is not less one of recapitulation or repetition for being condensed or abbreviated.

These surface-characters, then, that at first sight seem so bewildering in their profusion, so baffling in their sudden seasonal and nuptial transmutations, so puzzling in their age-sequences, turn out to have quite peculiar advantages for the student of evolution. Their perfection as specific marks, delicacy as tests of variability, accessibility in breeding and hybridizing experiments, the convenient serial disposition of their intergradations in rows of feathers, the phyletic sequences they reveal in successive plumages, the ease with which we can force them to bridge gaps in normal development and reproduce lost stages, all these are advantages that speak for themselves.

In some birds there are several successive patterns graduating up to the adult pattern through as many molts, partial or total. In such cases it is often possible to find practically all the transitional phases that connect the earlier with the later pattern. Here nature turns the molting process into an experiment essentially the same as that I have tried on the diamond-dove and other geopelias. Whenever a bird develops its feathers slowly, so that they appear at different ages in different regions, as in the jungle-fowl, quails, pheasants, etc., it is easy to see that the passage from stage to stage is not by mutations, but by continuous development.

The testimony from the avian world in respect to the evolution of color-patterns is, as I have said, often fragmentary, and herein is to be found the only apology for an appeal to the theory of mutation. Wherever the evidence is fairly complete and wherever we find it possible to bring the apparent breaks in continuity of development to a crucial test, there we find positive confutation of the mutation hypothesis.

The evidence for mutation is mainly of a negative character. New species arise, and we discover them when it is too late to learn the history of their genesis. We search through the biological world for discontinuities, and we find them so numerous that ponderous volumes can not approach a full record of them. In our breeding-experiments, with both animals and plants, we not infrequently get departures from the parent type, and these unexpected novelties, seemingly in contradiction to the law of hereditary continuity, are then declared to have come suddenly into existence, to have slipped the bonds of parentage, to have hoisted themselves into existence inconsequentially, per saltum. Shall we assume a break in the chain at every point where our knowledge fails? or is it more rational to abide by the law of genetic continuity so long as we fail to discover evidence of an exception?

CHAPTER II.

THE PROBLEM OF THE ORIGIN OF SPECIES.[1]

Among the rival theories of natural selection two are especially noteworthy. One of these is now generally known as *orthogenesis*.[2] Theodore Eimer was one of the early champions of this theory, basing his arguments primarily upon his researches on the variation of the wall-lizard (1874–81). Eimer boldly announced his later works on The Origin of Species (1888) and the Orthogenesis of the Butterflies (1897) as furnishing "complete proof of definitely directed variation, as the result of the inheritance of acquired characters, and as showing the utter impotence of natural selection." Eimer's intemperate ferocity toward the views of Darwin and Weismann, coupled with an equally intemperate advocacy of the notion that organic evolution depends upon the inheritance of acquired characters, was enough to prejudice the whole case of orthogenesis. Moreover, the controversial setting given to the idea of definitely directed variation, without the aid of utility and natural selection, made it difficult to escape the conclusion that orthogenesis was only a new form of the old teleology, from the paralyzing domination of which Darwin and Lyell and their followers had rescued science. Thus handicapped, the theory of orthogenesis has found little favor outside the circle of Eimer's pupils.

The second of the two theories alluded to is the mutation theory of Hugo de Vries. The distinguished author of this theory maintains, on the basis of long-continued experimental research, that species originate, not by slow, gradual variation, as held by Darwin and Wallace, but by sudden saltations or sport-like mutations. According to this theory, two fundamentally distinct phenomena have hitherto been confounded under the term "variation." In other words, variation, as used by Darwin and others, covers two classes of phenomena, totally distinct in nature, action, and effect. Variation proper is defined as the ordinary, fluctuating, or individual variation, and this is held to be absolutely impotent to form new species.

It is claimed that no amount of either natural or artificial selection can by any possibility lead this variation up to the birth of a new species. The utmost that could be attained would be an improved race that would inevitably revert to the original state as soon as left to itself. Mutation, on the other hand, never advances by slow and minute modifications, which are continuous and cumulative, but by single, sudden jumps. In the words of de Vries (vol. 1, page 150):

Species have not arisen through gradual selection, continued for hundreds or thousands of years, but by jumps [*stufenweise*] through sudden, though small, transformations. In contrast with variations which are changes advancing in a linear direction, the transformations to be called mutations diverge in new directions. They take place, then, so far as experience goes, without definite direction.

[1] An address before the Section of Phylogeny and reprinted from "Congress of Arts and Science, Universal Exposition, St. Louis, 1904," Vol. V. A few introductory paragraphs have been omitted, and a very few minor additional changes have been made by the editor in adapting the address to this position in this volume.

[2] A name introduced by Wilhelm Haacke (Gestaltung und Vererbung, p. 31).

The new species arises from the old, but without any visible preparatory steps and without intermediate connecting stages. Like the old, it is subject to variation, but as a type it is essentially immutable. De Vries does not deny that variation produces what may appear to be transitional forms, but he maintains that these forms in reality have no such meaning. They are to be regarded as phenomena of "transgressive variability," which may obscure but not obliterate the specific limits. De Vries states (vol. 1, page 362):

The transitions do not appear before the new species, at most only simultaneously with this, and generally only after this is already in existence. The transitions are therefore not intermediates or preparations for the appearance of the new forms. The origin takes place, not through them, but wholly independently of them.

Granting that the position with respect to the mutants obtained from the evening-primrose (*Œnothera lamarckiana*) is unassailable, does it follow that *all* new species have arisen by mutation and that continuous variation has never had, and never can have, anything to do with the origin of species? Plausible as is the argument and impressive as is the array of evidence presented, I can but feel that there are reasons which compel us to suspend judgment for a while on this pivotal point of the mutation theory. America is the original home of the evening-primroses, and it is here that the natural history of the group remains to be worked out in the light of the experimental results obtained in Holland.

What does it mean that a few mutants keep on reappearing year after year, and that even the mutants themselves mutate, not in new lines, but in the same old ones? Persuaded as deeply as I am that we can never draw from a species anything for which no ancestral foundations preëxist, I anticipate that our wild evening-primroses have revelations to make.[3] Whatever revelations may await future investigation in this field, the work done in the primrose garden of Amsterdam will stand as a classical contribution to the new biology and as one of the very best models in method of research that we have yet seen.

Natural selection, orthogenesis, and mutation appear to present fundamental contradictions, but I believe that each stands for truth, and that reconciliation is not distant.

The so-called mutations of *Œnothera* are indubitable facts; but two leading questions remain to be answered: First, are these mutations, now appearing, as is claimed, independently of variation, nevertheless the product of variations that took place at an earlier period in the history of these plants? Secondly, if species can spring into existence at a single leap, without the assistance of cumulative variations, may they not also originate with such assistance? That variation does issue in new species, and that natural selection is a factor, though not the only factor, in determining results, is, in my opinion, as certain as that grass grows, although we can not see it grow.

Furthermore, I believe I have found indubitable evidence of species-forming variation advancing in a definite direction (orthogenesis), and likewise of variations in various directions (amphigenesis). If I am not mistaken in this, the reconciliation for natural selection and orthogenesis is at hand.

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[3] This was written (1904) before the publications of Davis and of Jeffrey on the *Œnothera.*—ED.

I am aware that orthogenesis is held by many to be utterly incompatible with both natural selection and mutation. De Vries says (vol. 1, page 40):

The Darwinian principle demands that species-forming variability and mutability be *indeterminate in direction*. Deviation in all senses must arise, without favor to any particular direction, and especially without partiality for the direction proceeding from the theory to be explained. Every hypothesis which departs from this principle must be rejected as teleological, and therefore unscientific.

Again (page 180) the same point is amplified:

Again and again, and by authors of different aims, it has been insisted upon that species-forming variability must be orderless. The assumption of a definite variation-tendency which would condition, or even favor, the appearance of adaptive modifications lies outside the pale of the natural science of to-day. In fact, the great advantage of Darwin's doctrine of selection lies in this, that it strives to explain the whole evolution of the animal and plant kingdoms without the aid of supernatural presuppositions. According to this doctrine, species-forming variability goes on without regard to the qualification of the new species for maintaining themselves in life. It simply supplies the struggle for existence with the material for natural selection. Whether this selection takes place between individuals, as Darwin and Wallace supposed, or decides between whole species, as the mutation-theory demands, ultimately it is, in either case, simply the ability for existence under given external conditions that decides upon the permanence of the new form.

I take exception here only to the implication that a definite variation-tendency must be considered to be teleological because it is not "orderless." I venture to assert that variation is sometimes orderly and at other times rather disorderly, and that the one is just as free from teleology as the other. In our aversion to the old teleology, so effectually banished from science by Darwin, we should not forget that the world is full of order, the organic no less than the inorganic. Indeed, what is the whole development of an organism if not strictly and marvelously orderly? Is not every stage, from the primordial germ onward, and the whole sequence of stages, rigidly orthogenetic? If variations are deviations in the directions of the developmental processes, what wonder is there if in some directions there is less resistance to variation than in others? What wonder if the organism is so balanced as to permit of both unifarious and multifarious variations? If a developmental process may run on throughout life (*e.g.*, the lifelong multiplication of the surface-pores of the lateral-line system in *Amia*), what wonder if we find a whole species gravitating slowly in one or a few directions? And if we find large groups of species all affected by a like variation, moving in the same general direction, are we compelled to regard such "a definite variation-tendency" as teleological, and hence out of the pale of science? If a designer sets limits to variation in order to reach a definite end, the direction of events is teleological; but if organization and the laws of development exclude some lines of variation and favor others, there is certainly nothing supernatural in this, and nothing which is incompatible with natural selection. Natural selection may enter at any stage of orthogenetic variation, preserve and modify in various directions the results over which it may have had no previous control.

It should be noted in this connection that the difficulty of incipient stages is not what it is so generally presumed to be. The advocates of natural selection

habitually assume that the evolution of an organ or character begins with an "infinitesimal rudiment," which has no way of emerging from its functionless state except through minute chance variations in various directions. In this assumption the problem is misconceived. The characters we meet with to-day have rarely, if ever, arisen by direct evolution from useless rudiments. When we know enough about a character to undertake to trace its genesis, the "rudiment" imagined to lie so near recedes, and we are led on, not to a "beginning," but to an antecedent, and if we are fortunate enough to be able to advance farther, we come to another antecedent, and so on. The series of antecedents stretches ever as far as we can see. As we repeat this experience with different characters, looking always for the primordial rudiment, our childish faith in such "beginnings" gives way to the conviction that the chase is led by a phantom.

No one of our sense-organs, for example, can be traced to a rudiment, except in the embryological sense. The eye of the vertebrate may appear as a rudiment in the embryo, but no one can doubt that it has had a phylogenetic history, the first term of which—if first there be—must have been very different from its present embryonic rudiment. To assume that the eye began in some different variation that fluctuated or mutated, chance-wise, into a state of incipient utility, and was then developed in a direct line to its present stage of complex adaptations, either gradually or per saltum, would be hardly more satisfactory than appealing to a miraculous succession of miracles. It is impossible to believe that such a system of harmonious coadaptations could ever arise by mutation;[4] and selection, although playing a very important part in such achievements, is probably never equal to the whole task. Without the assistance of some factor having more continuous direct-ive efficiency, selection would fail to bring out of the chaos of chance variation, or kaleidoscopic mutation, such progressive evolution as the organic world reveals.

In order to show that such a factor is essential, and that it is actually present, supplying the indispensable initial stages and holding the master hand in the general direction of evolution, demonstrative evidence is, of course, required. Such evidence lies in the history of specific characters. But how shall we approach such a task, if no near-by rudiment is to be found as a starting-point? Rudiments and premutations are alike illusory in this regard, for their beginning is always and necessarily assumed to lie in the realm of the invisible and unknowable. If we are to keep always on ground that is open to investigation, we must find our starting-points in known stages. As the laws of nature are constant, it is not essential to trace entire histories. If some chapters are sufficiently open to observation and experiment to permit close study, we may hope, in some of the more favorable cases, to read the phenomena in their natural order and to learn from what goes on in one part of the history the factors that govern in all parts.

The study of the problem of the origin of species resolves itself, therefore, ever more clearly into exhaustive studies of single favorable characters, in the more accessible portions of their history. For decisive evidence we must have characters of a comparatively simple nature, the evolutional records of which, in every case, are to be read in a considerable number of species of known common origin.

[4] Darwin frequently emphasized the same objection. In a letter to Asa Gray, referring to the orchids, he remarks: "It is impossible to imagine so many coadaptations being formed, all by a chance blow." Weismann has shown in a masterly manner how inadequate is the mutation theory to account for such phenomena.

PLATE 1

A. Adult male two-barred rock-pigeon, *Columba livia*. × 0.4. Nov. 1909. From the Caves of Cromarty, Scotland, 1908. This bird has a few concealed chequers of a third wing-bar.

B. Adult male chequered wild rock-pigeon, *C. affinis*. × 0.4. According to some authors only a variety of *C. livia*. Nov. 1909. From Caves of Cromarty, Scotland, (1908).

It is a great mistake to resort exclusively to domestic races, for here the ancestry contains so many unknown elements that it is often impossible to refer phenomena to their proper sources. Even the so-called "pure breeds" are decidedly impure as compared with pure wild species. The ideal situation, as regards material, is to have pure wild species in abundance as the chief reliance, and allied domestic races for subsidiary purposes.

The pigeon amply fulfils all these prerequisites. A simple and convenient character, presenting divergent courses of evolution in some species and parallel courses in others, is to be found in the wing-bars and their homologues. It is to some chapters in the history of this character that we may now turn for evidence that natural selection waits for opportunities, to be supplied, not by multifarious variation or orderless mutation, but by continuous evolutional processes advancing in definite directions.

The rock-pigeons (*Columba livia*) present two very distinct color-patterns, one of which consists of black chequers (pl. 1) uniformly distributed to the feathers of the wing and the back, the other of two black wing-bars on a slate-gray ground (pl. 1). These two patterns may be seen in almost any flock of domestic pigeons. The inquiry as to the origin of these patterns involves the main problem of the origin of species, for the general principles that account for one character must hold for others, and so for the species as a whole. Darwin raised the same question, but did not pursue it beyond the point of trying to determine which pattern was to be considered original and how the derivation of the other was to be understood. Darwin's explanation was so simple and captivating that naturalists generally accepted it as final. It is but fair to state that Darwin's conclusions did not rest on a comparative study of the color-patterns displayed in the many wild species of pigeons. Accepting the view generally held by naturalists, that the rock-pigeons must be regarded as the ancestors of domestic races, the question was limited to the point just stated.

It was known that the two types interbreed freely under domestication, and it had been reported that chequered pigeons sometimes appeared as the offspring of two-barred pigeons. Moreover, Darwin discovered that the chequers were homologous with the spots composing the bars. As the main purpose was to show that variation was present to any extent required for the origin of new species, rather than to trace its course in any specific case, and as variation was supposed to be multifarious and progress to be guided by natural selection of the "fittest," it is not strange that Darwin failed to get the direction of variation or to realize that in *direction* is given the key to one of the fundamental laws of evolution.

As the two color-patterns are alike in having a common element, and differ chiefly in the number of elements, it was natural enough to take the smaller number as the point of departure and to view the larger number as "an extension of these marks to other parts of the plumage" (*Animals and Plants*, vol. 1, p. 225). With the ancestral type thus determined, and a simple mode of variation pointed out, Darwin could dismiss the problem with these words: "No importance can be attached to this natural variation in the plumage."

Whence and how the two bars arose was not explained. The mode of departure assumed to account for the chequered variety would, however, suggest that the bars themselves originated in the same manner; that is, from one or two spots

EXPLANATION OF PLATE 2.

Adult *Columba livia*, uniform gray, third bar.   Photographed and spots measured Nov. 1898.

There are 14 secondary and tertial coverts (primaries, 10).

Left third bar (wholly concealed); measurements in millimeters.

Feather 14. A blackish spot on upper edge and just a last trace of one on lower edge.   Spots dusky gray; greatest width of spot, 6 mm. long by 1.5 mm.

   13. Upper spot, 6 mm. by 1.5, about same as in 14; lower spot so reduced that a magnifying glass is necessary in order to see the slight touch of dusky at lower edge.

   12. Upper spot reduced to last touch, recognizable only by aid of magnifying glass; lower spot absent.

   11. None on either side.

   10. No upper; lower spot, 3 by 1.

    9. Spot (lower), 3 by 1.5.

    8. Spot (lower), 3 by 1.75.

    7. Spot (lower), 5.5 by 3.25 (widest and most conspicuous of all).

    6. Spot (lower), just a dusky trace.

    5. Spot (lower), 5.5 by 1.5.

    4. Spot (lower), 7.5 by 1.5.

    3. Spot (lower), just a trace.

    2. Spot (lower), no trace.

    1. No trace.

A third bar, wholly concealed, in this pigeon is suggestive. It is much the same as I have several times found in the first plumage of some young domestic pigeons. The rock-pigeon of (uniform gray wing) then exhibits in adult plumage the juvenile condition of domestic pigeons.

Note, too, that two upper feathers exhibit double spots, at least in traces. The upper spot diminishes downward—is lost on No. 11. Of the lower spot there is only the minutest trace on two upper feathers; it is absent on the next two; and then, as the only spot, it increases downward, with a maximum on No. 7.

The larger spots are in lower half of series, and this agrees in a general way with the young domestic.

Notice for comparison chequered domestic (pl. 5), where the feathers of the third bar all have two spots instead of one.

Feather No.	Measurements.	Remarks.
17. Upper, lower......	12 long by 7.5	End notch of gray, 2.5 deep (long) by 3.5 wide.
16. Upper, lower......	14.5 long by 9.5	Gray tip, 4 mm. long, whole width of feather, nearly straight across.
15. Upper, lower......	16 long by 10	Upper runs a little obliquely outward; gray tip, 6 mm. long, whole width of feather.
14. { Upper.......... / Lower..........	}16 long by 10	{ Upper projects 1.5 mm. beyond lower. / Gray tip, 8 long, whole width of feather.
13. { Upper.......... / Lower..........	.... / 17 long by 12	Gray tip (upper), 10 mm.; upper spot paler, basal half largely gray. / Gray tip (lower), 13 mm.; lower obliquely cut on proximal part.
12. { Upper absent.. / Lower..........	}16 long by 12	{ Gray tip, 16.5 mm.; obliquely cut on proximal part.
11. Lower..........	17 long by 12	Gray tip, 17 mm.; less obliquely cut on proximal part.
10. Lower..........	17.5 long by 12	Gray tip, 17 mm.; about same as No. 11.
9. Lower..........	18.5 long by 12	Gray tip, 17 mm.; about same as No. 11.
8. Lower..........	18 long by 12	Gray tip, 17.5 mm.; spot begins to pale.
7. Lower..........	17 long by 11	Gray tip, 19 mm.; spot paler, more diffuse on proximal part.
6. Lower..........	14.5 long by 10.5	Gray tip, 19 mm.; spot diffuse on both ends; longest on lower edge; inclines to point as it begins to do in No. 7, and does more and more below.
5. Lower..........	14 long by 8.5	Gray tip, 20 mm.; spot begins to retreat from shaft in No. 7, and retreats more and more downward. Spot is now considerably freckled with gray, and obliquely in both directions; more pointed.
4. Lower..........	11 long by 6.5	Gray tip, 20 mm.; freckled triangle.
3. Lower..........	7 long by 2.5	A freckled trace.
2. Lower..........	3 long by 1.5	Still more diffusely freckled.
1. Lower..........	No trace left.	

PLATE 2
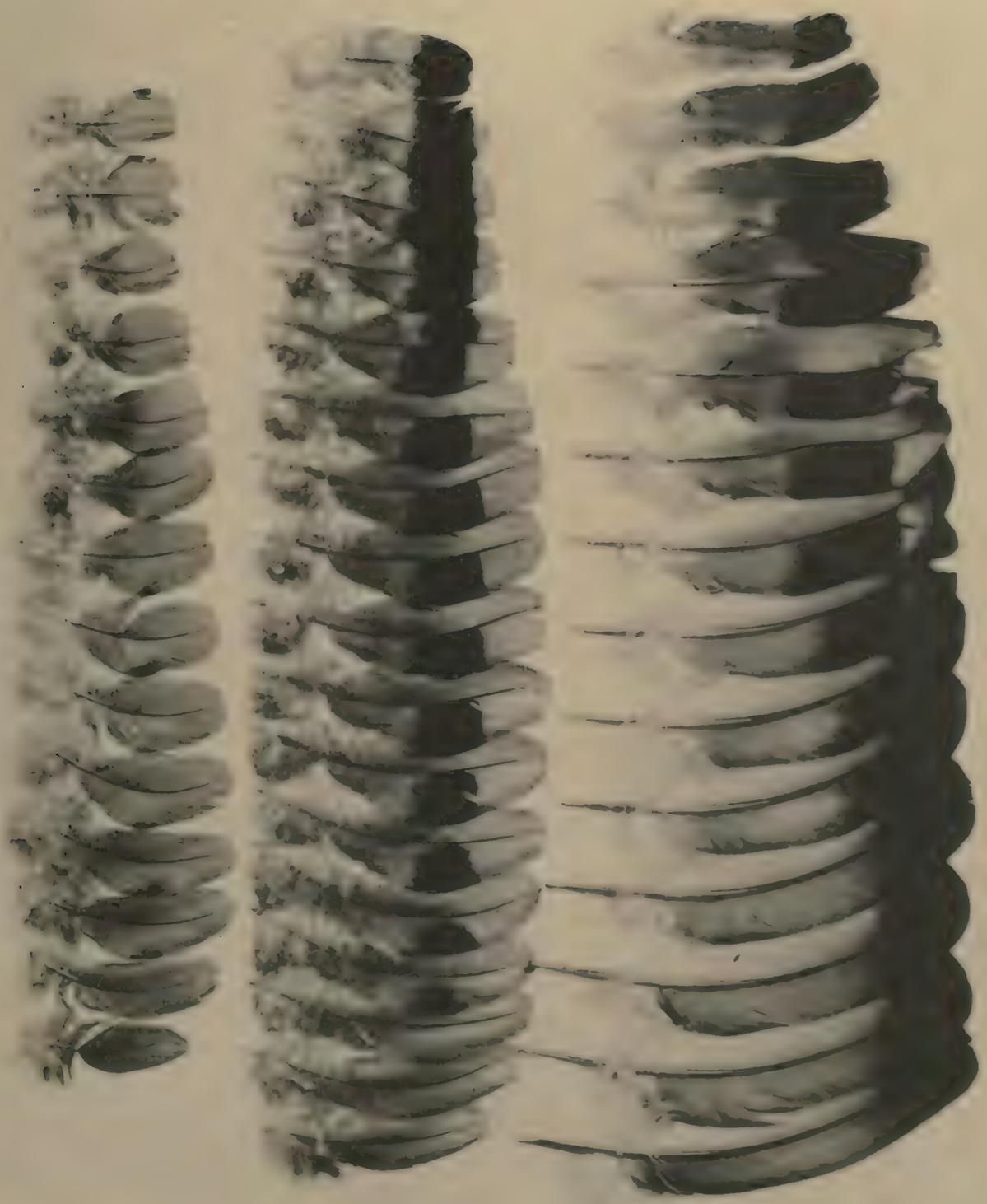
Adult *Columba livia*, uniform gray, third bar.   Photographed and spots measured Nov. 1898.

arising *de novo*, as chance variations, and the gradual extension of like spots in two rows of feathers. The one or more original spots, according to the general theory, would first appear as minute rudiments, and then be gradually enlarged and intensified by the aid of natural selection, guided by their utility as recognition marks.

Such a mode of origin would presuppose a plain, uniform gray ancestor, without any spots or bars in the wings, and would raise many puzzling questions that would be beyond the reach of investigation. For example: Why two bars? Why at the posterior end of the wing? Why do the spots taper backwards to a more or less sharp point in the chequered variety, while presenting a nearly square form in typical bars? Why should they have first extended upward, or downward, and in *two* rather than any other number of rows of feathers? If two rows of feathers were favored long enough to establish the bars for ornamental or other purposes, what freak of natural selection could have then interposed to turn a long-favored, definitely directed extension into a diffuse general extension, and thus to neutralize completely the very effects it was invoked to explain?

Natural selection could not be supposed to originate or to guide the first indiffer-

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EXPLANATION OF PLATE 2—*Continued.*

NOTICE.—(1) Double spots on 5 feathers. The upper spot disappears from the proximal end most rapidly on mesial or shaft side. Asymmetry on Nos. 14 and 13.

(2) The lower spot follows the upper in losing ground on its proximal end, and mainly on mesial side, and thus keeps up a certain sympathetic change of form. But as soon as the upper disappears the lower fills up again on its near end and becomes nearly square.

(3) The lower spot is most perfect on 5 feathers (Nos. 12 to 8), pales gradually from No. 9 downward, and loses in size rapidly from No. 7 downward.

(4) The upper feathers have highest development, as shown in double spots, but the lower spot is best developed in the middle feathers—from No. 12 to No. 8. From No. 7 to No. 2 the spot wanes and disappears.

Left first bar.—Spots of 14 tertials and secondaries.

Feather No.		Measurements.			Remarks.
14.	Upper	12.5	by	6.25	Equal and symmetrical.
	Lower				Gray tip; broad notch, 2 mm. deep.
13.	Upper	19	by	6	Gray tip; broad notch; equal both sides.
	Lower	22	by	9	
12.	Upper	23	by	8	Gray tip; 2 mm. above, 3 mm. below; retreat from tip
	Lower	24	by	9.5	greatest in lower spot; no notch.
11.	Upper	24	by	11	Gray tip; 4 mm. above, 6.5 mm. below (retreats as in
	Lower	31	by	11	No. 12).
10.	Upper				Just a slight intersprinkling of black; terminal bar has a shade of a beginning.
	Lower	25	by	13	Gray tip, 12.5 mm.
9.	Terminal	8			Whole width and slightly over shaft to lower web.
	Lower	24	by	13	Gray tip, 16 mm.
8.	Terminal	15			Whole width.
	Lower	26	by	13	Gray tip, 17 mm. terminal encroaches, advancing from shaft 4 mm.
7.	Terminal	18			Whole width plus an advance on lower web, where only
	Lower	19	by	14	a central triangular remnant of gray is left.
6.	Terminal	19			Full width of both webs.
	Lower	15	by	13	A freckled patch blending with terminal, but differing in hue.
5.	Terminal	17			Whole width, equal on both webs.
	Lower	13	by	12	A freckled blotch; a little less dense than No 6.
4.	Terminal	23.5			Whole width.
	No lower spot.				
3.					
2.	All with terminal	23.5			
1.					

Terminal increases downward; subterminal increases upward. (A fuller textual reference to this plate in Chapter IV.—ED.)

ent stages of new characters. Mutation would be equally helpless, and each step would leave a gulf of discontinuity—something that nature seems to abhor.

Turning from theoretical *impasses* to the facts, let us compare the two patterns.

In the chequered pattern all the feathers are marked alike—no regional differentiation. In the other type we have a conspicuous local differentiation (pl. 2 and text-figs. 1 and 2), suggesting at once a higher stage of evolution.[5] Chequered wings are to be found which vary all the way between a uniform marking and the barred type. If we arrange a number of unequally chequered wings in a series, running from the most to the least chequered, we shall see (pl. 3) that the pattern approaches more and more nearly to that of two bars, as the chequers diminish in size and number. We shall notice that the pigment is reduced more rapidly in the anterior than in the posterior part of the wing.

As chequers are reduced, they gradually lose their sharp ends and approximate the square or rounded form seen in the elements of the typical bars. The series shows a flowing gradation, that may be read forward or backward with equal facility. Darwin's view takes the bars as the starting-point and reads forward. Taking the chequered condition as the point of departure, the variation runs just as smoothly in the opposite direction. We here meet an ambiguity that is everywhere present in color-pattern problems—an ambiguity that is frequently overlooked with disastrous consequences. The only way to eliminate the difficulty is to take our evidence from several different sources, and when agreement is found for one direction and disagreement for the other, the way is clear.

As an experiment, we may take one or more pairs of pure-bred, typically barred pigeons and keep them isolated from chequered birds for several years, in order to see if the young ever advance toward the chequered type.

Another experiment should be tried for the purpose of seeing what can be done by working in just the opposite direction. In this case we take chequered birds, selecting in each generation birds with fewer and smaller chequers, and rejecting the others, in order to see if the process of reduction can be carried to the condition of three, two, and one bar, and finally to complete obliteration of both chequers and bars, leaving the wing a *tabula rasa* of uniform gray color.

If these experiments are continued sufficiently far, it will be found from the second experiment that a gradual reduction of pigment to the extreme conditions named can be comparatively easily effected, and that the direction of reduction will always be the same, from before backward; while, from the first experiment, it will be seen that it is hopeless to try to advance in the opposite direction, from the bars forward to the chequered condition. No variations will appear in that direction, but such as do appear will take the opposite direction, tending to diminish the width of the bars and to weaken their color. It is in this way that we must account for the existence of some fancy breeds in which the bars have been wholly obliterated. The direction of evolution can never be reversed. I have tried both experiments for eight years, and as both tell the same story as to the direction of variation, I am satisfied that further experiments will not essentially modify the results. Plates 4 and 5 indicate some of the results[6] in the reduction of the chequers.

[5] This situation is dealt with more fully in the explanations of plates 2 and 3.—Ed.

[6] Most of the available illustrations for these results exist only in a series of small lantern-slides. The breeding data for the birds illustrated in plates 4 and 5 are given in table 76, Vol. II; some further breeding data are also given in Chapter IX, and another illustration in plate 16 of Vol. II.—Ed.

PLATE 3

A. Fully chequered wing of domestic pigeon about 6 weeks old. Natural size. Hayashi del., 1896.

B. Chequers more strongly reduced in the anterior part of the wing of an adult homer. Natural size. Hayashi del., 1896.

Text-figure 1.—Adult barred rock-pigeon (*Columba livia*), male No. 0. × 0.75. Hayashi del., Oct. 1904.

Description of Bars and Size of Spots, October 1904.

Second bar.	Exposed (spot).	Total.	Covered.	Distance to tip.	Remarks.
First feather .	Upper= 8 mm.	10 mm.	2 mm.	4 mm.	Not shown in drawing.
	Lower= 8	10	2	5	
Second......	Upper=11	14	3	7	
	Lower=10	14	3	10	
Third.......	Upper =12	13	1	10	
	Lower= 9	13	4	14	
Fourth......	No upper, faintest dots.				
	6	12	4	17	
Fifth	7.5	12	4.5	20	
Sixth	8	14	6	22	
Seventh.....	7	14	7	22	
Eighth......	7	14	7	22	
Ninth	6	12	6	23	
Tenth	0	8	8	25	Spot is round and flecky.
Eleventh....	0	8	8	83	Scattered flecks only.
Twelfth.....	0	6	6	25	Spot so thin as to be barely visible.
Thirteenth ..	0	2	2	26	Spot; single fleck.
Fourteenth ..	0	0	0	0	No spot.
Fifteenth....	0	0	0	0	No spot.
Sixteenth....	0	0	0	0	No spot.

First bar.	Total length of spot.	Exposed.	Covered.	Distance to tip.	Remarks.
Tertials:					
First feather .	Upper=21 mm.	11 mm.	10 mm.	2.5 mm.	
	Lower=23	15	8	2.5	
Second......	Upper=25	1	24	3	
	Lower=26	16	10	4	
Third.......	30	3	27	1	
	25	13	12	15	
Fourth......	Upper=13	2	11	5	
	Lower=17	13	4	20	
Fifth	No upper; terminal; begins and expands over shaft at tip a little.				
	Lower=20	11	9	20	Term. above=ca. 12 mm.
Sixth	Term.=18				
	Lower=18	10	8	23	Lower term.= 8
Secondaries:	15	0	15	24	Term. upper=24
Seventh.....	Spot=thin flecks.				Term. lower=15
Eighth to the Fourteenth ..	No spot.				

(As I do not find 14, and as there seem to be no missing secondaries, I think that the first upper tertial is the missing feather. No. 7 can be reckoned either to tertials or to secondaries.

TEXT-FIGURE 2.—Adult male barred rock (*C. livia*), No. 7. × 0.75. Hayashi del., Oct. 28, 1904.   In this bird the bars have greatest width above and grow narrow downward (outward).

DESCRIPTION OF BARS AND SPOTS, OCTOBER 1904.

Second bar.	Length, exposed.	Total.	Covered.	Distance to tip.	Remarks.
First feather.	Upper=15 mm.	17½ mm.	2½ mm.	1½ mm.	
	Lower=15	17½	2½	3	
Second......	Upper=16	18½	2½	4	
	Lower=13	17½	4½	6	
Third.......	Upper=13½	16	2½	8	
	Lower=11	15	4	10½	
Fourth......	Upper=12	14	2	11	Upper spot triangular and reaches from
	Lower= 9	13½	4½	15½	shaft about two-thirds width of vein.
Fifth	No upper.				
	Lower= 8	13½	5½	19	
Sixth.......	Lower= 6	12	6	22	
Seventh.....	Lower= 6.5	14	7½	20	
Eighth......	Lower= 5.5	11	5½	21	
Ninth	Lower= 4	10	6	22½	Spot begins to be flecky.
Tenth	Lower= 2	8	6	22	Thin, flecky.
Eleventh....	Lower= ½	8½	8	20	Thin, flecky.
Twelfth.....	Lower= 0	7	7	22	Thinner and flecky.
Thirteenth ..	Few pale flecks				
14th to 16th .	0		0		

First bar.	Total length.	Exposed.	Covered.	Distance to tip.	Remarks.
First feather.	Upper=11	3	9	2	
	Lower=16	3	13	½	
Second......	Upper=21	12	9	2	
	Lower=27	15	12	2	
Third.......	Upper=25.5	3	22½	2½	
	Lower=29	18	11	2½	
Fourth	Upper=30	4½	25½	2½	
	Lower=37	23	14	4	
Fifth.......	Upper=17	3	14	3½	
	Lower=39	29	10	3½	At shaft (and)
				15	At outer edge of web.
Sixth	Upper nearly gone				
	Lower=24	10	14	18	
Seventh	Lower=16	5½	11½	18	
Eighth	Lower=16	5½	11½	20	Thinner, but present, though not drawn as black, and limits not seen in figure.
Ninth	=14	3	11	29	Thinner still; scattered flecks; terminal began on eighth, but first becomes plain here on ninth term.
					Term.=about 15 mm.
10th to 13th .	No spot	....	....	....	Term.=20 mm.

I do not find more than 13 feathers. The last 6 are secondaries (8–13). The others (1–7) are tertials.
I have examined this bird once before, but could find only 13 feathers. I think now that this is the true number, as No. (0) (=fig. 2, this figure.—ED.) agrees in this respect.

With reduction traveling from before backward, in the manner described, we get the bars in their typical number, form, and position, as one of the necessary stages of the process, and without appealing to *de novo* origin, incipient rudiments, etc. But if bars originated in such simple fashion—the direction of evolution being precisely the same as that of embryological development—if the theory of rudiments must be abandoned in this case, do we not meet the same theory again in any attempt to account for the chequers? What kind of rudiments could be imagined? We might assume that minute flecks of pigment first appeared, one in each feather; and then, further, imagine that these purely chance originations
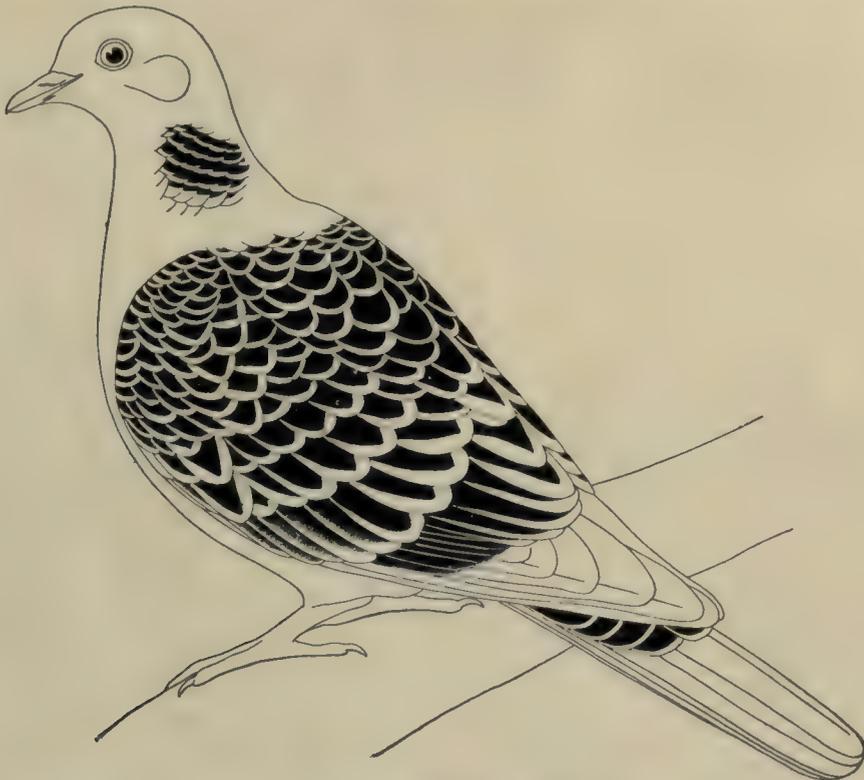
TEXT-FIGURE 3.—Oriental or Japanese turtle-dove, *Turtur orientalis.* × 0.5. Toda del., 1903. The color-pattern in black and white. The light-brownish or bronzed edges of the feathers given in white, the dark centers in black. This pattern is preserved in the feathers of the neck-mark.

happened to have some slight utility, and that natural selection did the rest. But it is just as difficult to account for a small as a large origin *de novo*, and the smaller it is the more unfortunate it is for the theory of natural selection.

If we seek refuge in the doctrine of mutation, are we better off? Mutation hides itself in the undiscoverable premutation, and so we have all the difficulty of an incipient stage, and no means of advancing by ordinary variation. Fortunately we are not driven to either alternative, for the chequers arise neither as mutations nor as rudiments, but by direct and gradual modifications of an earlier ancestral mark, which came with the birth of the pigeon phylum as a heritage from still more distant avian ancestors.

<center>EXPLANATION OF PLATE 4.</center>

A. Male homer, No. 4, stray, 1900. Natural size Hayashi del., Nov. 1904.

The male of a pair reserved to see if I could reduce chequered pattern to 3 bars. Result: could reduce to 2 bars, or 2 bars plus a vestigial third; that is, reduction was even for the whole wing. The 2-barred young (frequently obtained) bred true—gave 2-barred offspring. Thus far (Dec. 26, 1904, 5 years) there have been 5 young with only 2 bars and pale gray; 5 young nearly like male. The majority were intermediate to the male and female parents.

The black (of drawings) is of course misleading, for bars vary all the way between almost black and dark gray. These many shades are ignored in ink drawings. But the size is given, and thin edges and very thin or pale spots by dots.

Seen at a little distance, this male appears to have only 2 dark bars. Within a few feet we notice a few obscure and small vestigial chequers in the third bar and a few scattered chequers of about the same thinness in the scapulars. Spots a little stronger behind and above; weaker before and below. The bars are dark gray, not so dark as in the female mate. The gray ground of this male is considerably lighter than in the female. That is, with reduction of chequers comes a paler gray ground as well as less dark (paler) spots.

<center>*Measurements of first bar (Dec. 28, 1904).*</center>

Feather No.	Length exposed.	Total length.	Length covered.	Remarks.
	mm.	mm.	mm.	
1	7	18	11	
2	18	24	11	
3	17	25	8	
4	20	27	7	
5	18	21	3	
6	15	19	4	
7	16	18	2	Rather thin and freckled, except mid-third.
8	13	17	4	Mostly thin freckled, except in lower half.
9	6	12	0	Wholly and very sparsely sprinkled with pale.
10	..	..	..	Has only 2 or 3 obscure dots.

From here on the tips of secondaries are darkened. Tips of upper web of sixth and seventh secondaries darkened; the dark tip of eight secondary includes a little of lower web; this goes on more and more for lower web of rest of secondaries.

<center>*Measurements of second bar.*</center>

Feather No.	Total length.	Length exposed.	Length covered.	Remarks.
	mm.	mm.	mm.	
1	10	0	1	Lower web; upper web few freckles.
2	17	16	1	Lower web; upper web about same as lower.
3	17	16	1	Lower web; upper web a little weaker than lower.
4	18	15	3	Lower web; upper web total length = 15 mm.
5	{12 18}	12	3	Lower shaft; upper web only few freckles; pale. Margin.
6	{10 19}	12	2.5	Lower shaft; upper web no freckles. Margin.
7	{10 18}	11	2.5	Lower shaft; upper web no freckles. Margin.
8	15	12	3	Flecked at both ends a little more than seventh feather.
9	13	10	3	Flecky throughout.
10	8	0	2	All thin-flecked.
11	..	..	..	Only a few thin, pale flecks.
12	..	..	..	Fewer and paler.
13	..	..	..	Vanishing.

<center>*Third bar.*</center>

<center>Wholly vestigial and visible as pale dots or flecks only on 5 or 6 upper feathers.</center>
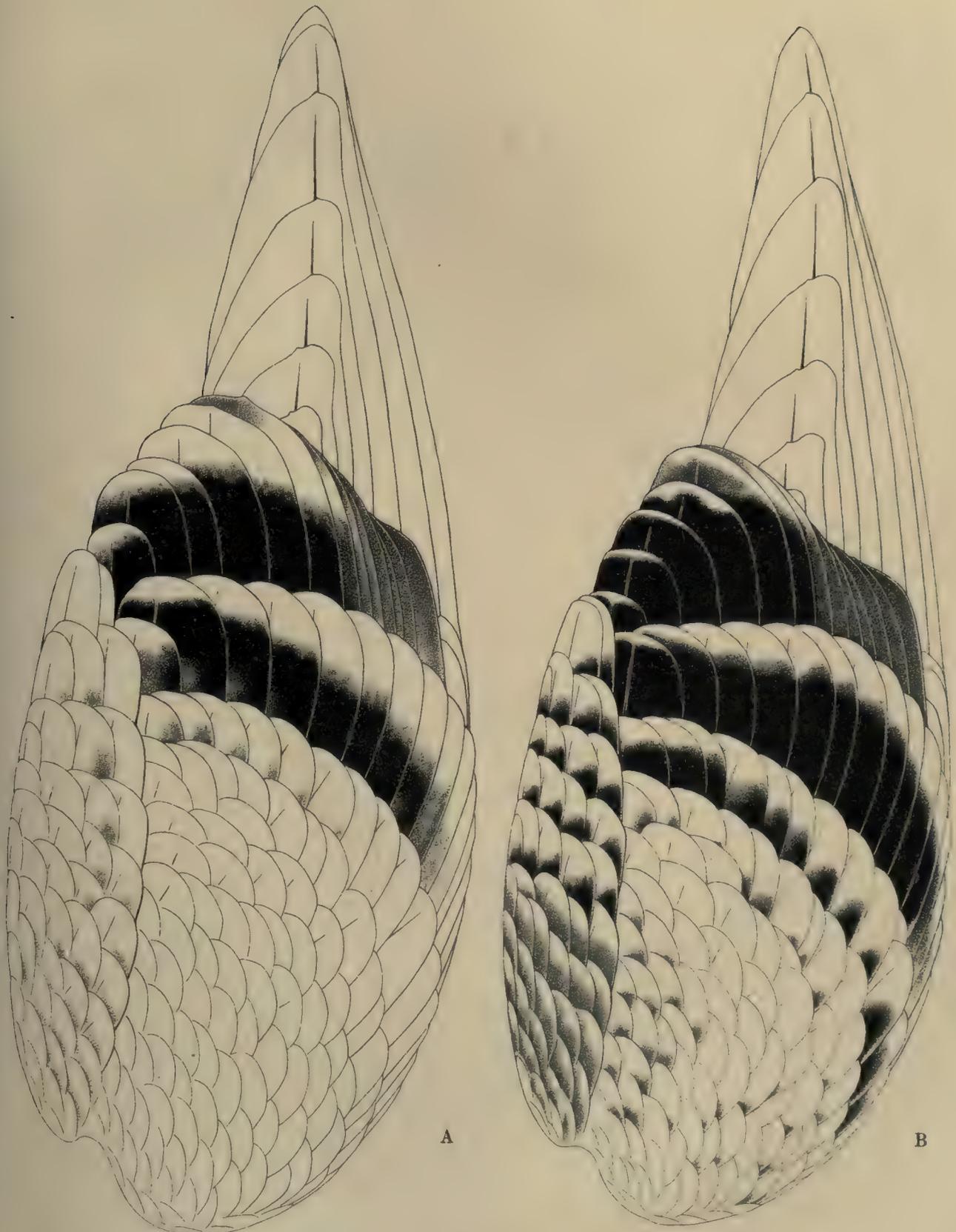
PLATE 4

A. Male homer, No. H4, stray, 1900.   Natural size.   Hayashi del., Nov. 1904.
B. Female homer, No. K2, mate of No. H4 above.   Natural size.   Hayashi del., Nov. 1904.

EXPLANATION OF PLATE 4—*Continued*.

B. Female homer, No. K2, mate of No. H4 above. Natural size. Hayashi del., Nov. 1904.

This female raised from a male bought February 1897. He was fairly thickly chequered, but there was some reduction manifest in the field of lesser coverts. The mother was a stray (1898), strongly and quite evenly chequered.

In K2 the scapulars are all double-chequered, but the spots are considerably reduced, paler in front than behind and more flecky-edged. The spots are fairly long behind, but the points are more or less rounded. There is a pretty well defined row of spots in the third bar, and a few spots of vestigial dimensions and paleness are visible in the fourth row of feathers. On lifting the feathers I find many spots that are wholly concealed. The rest of the small coverts are mostly without visible spots.

In the male the second bar is cut so straight that no points are seen, while in the female many of these spots are pointed, so as to give a serrate edge, particularly near the middle.

Measurements of first bar (Dec. 28, 1904).

Feather No.	Total Length.	Length exposed.	Length covered.	Remarks.
	mm.	*mm.*	*mm.*	
1	16	6	10	
2	26	15	11	
3	31	19	12	
4	35	20	15	
5	38	25	13	Has only a little black on upper web at tip.
6	35	25	13	Begins to be black on lower tip, and has more black on upper tip.
7	36	25	11	Black of tip increased in both webs.
8	38	27	11	Black of tip increased on upper web and on lower web it coalesces with spots.
	32	17	..	Original spot still distinguishable, although tip is all black. Nos. 38 and 27 apply to only the proper bar-spot, which is subterminal, as in the tertials
9	45	15		
10	45	15		
11	45	15		
12	45	15		Secondaries.
13	43	15		
14	40	15		

Measurements of second bar.

Feather No.	Total length.	Length exposed.	Length covered.	Feather No.	Total length.	Length exposed.	Length covered.
	mm.	*mm.*	*mm.*		*mm.*	*mm.*	*mm.*
1	19	13	6	9	23	18	5
2	20	14	6	10	22	16	6
3	22	17	5	11	21	15	6
4	25	20	5	12	21	14	7
5	27	20	7	13	21	13	8
6	27	20	7	14	20	11	9
7	26	20	6	15	20	11	9
8	25	19	6	16	15	10	5

The spot of the sixteenth feather is thin, but still quite a spot except for wide, flecky margins. Gradually, as we pass upward, the spots become darker and fuller (*i.e.*, the flecky parts are less in extent), until at the ninth feather we have a well-developed spot which is pointed but ragged-edged distally and proximally.

Third bar.

Most of spots have 6 to 8 mm. uncovered. Total length, 10 to 12 mm. In central part of field, where no spots are to be seen, there are many spots entirely concealed which are only seen when feathers overlapping are lifted.

22   ORTHOGENETIC EVOLUTION IN PIGEONS.

<div align="center">EXPLANATION OF PLATE 5.</div>

A. Female homer, No. 3, hatched Mar. 31, 1901. × 0.8. Hayashi del., Nov. 1904. Parents of the three birds of this plate are shown in plate 4.

Wing from a large bird of fine form; very pale; primaries inclining to whitish.

The bars in this bird are obscurely subdivided by lines (alternating light and dark narrow bands) or bands that are not perfectly transverse, but inclined so that those of two sides meet at a very obtuse angle (*i.e.*, they are what were later called "fundamental bars."—ED.).

Third bar.—First, second, and third feathers each have two spots—both weak and pale, and plainly obsolescent (ragged edges and light lines crossing them). Lower down only one spot to the feather (lower web), pale and increasingly thin and roughly outlined. Elsewhere in front of this bar the color is pure—very pale gray; no spots to be seen. A few vestiges found on lifting feathers.

Scapulars: In front no spots; in middle spots are pale reduced vestiges; behind they become more distinct, but they are everywhere weak and without clear outlines.

Second bar.—On right side some of middle spots are pointed, but on left side corresponding feathers show spots with points disappearing.

Feather 2. Length of spot, 13, exposed; total length, 20 mm.
          3 and 4. Length of spot, 13, exposed.
          5. Length of spot, 11, exposed; point obsolescent.
          6. Length of spot, 21, exposed; point intact but distal edge flecky.
          7. Length of spot, 12, exposed; point cut off as an island.
          8. About same, but island thinner.
          9. About same, but thinner.
          10. Shorter and still thinner.
          11. Length 8 mm., pale and flecky throughout.
          12 to 15. Thinner and vanishing on last.

About 4 mm. of the mid-spots are covered.

<div align="center">*Measurements of first bar.*</div>

Feather No.	Total length.	Length exposed.	Length covered.	Remarks.
	mm.	*mm.*	*mm.*	
1	23	16	7	Lower web; spot on upper web about half as long, terminal reduction from proximal side.
2	27	21	6	Upper web; spot; terminal 16 mm.
3	30	19	11	Upper web; spot; terminal 20 mm.
4	36	20	16	Upper web; spot; terminal 18 mm., very thin.
5	31	20	11	Upper web; no spot.
6	31	20	11	Upper web; no spot, but faint shadow of a tip spot; spreads over onto lower web.
7	32	20	12	Terminal spot enlarges and creeps over to lower web more; length about 1.4 mm.
8	24	13	11	Whole tip (ca. 19 mm.) now dark, but original spot is darker, so its limits are plain; it is retreating from tip, being now 19 mm. against 14 mm. in seventh feather.
9	15	12	3	Whole tip (ca. 24 mm.) dark; original spot is flecky throughout.
10	14	10	4	Whole tip dark; original spot very pale flecky, almost gone.
11	..	..	..	Just a trace left; tip dark, 25 mm.
12	..	..	..	No traces; tip dark, 25 mm.
13	..	..	..	Tip dark, 24 mm.
14	..	..	..	Tip dark, 23 mm., about one-half as dark as preceding feathers.

Eighth spot is decidedly paler than in seventh feather. This sudden drop to pale spots at eighth seen again in figure B of plate 4.

This bird has made a decided advance over the dam, but she is not quite so far along as the sire. The second and third bars are narrower than in the dam. The first bar is wider than in the sire, but the second is about the same.
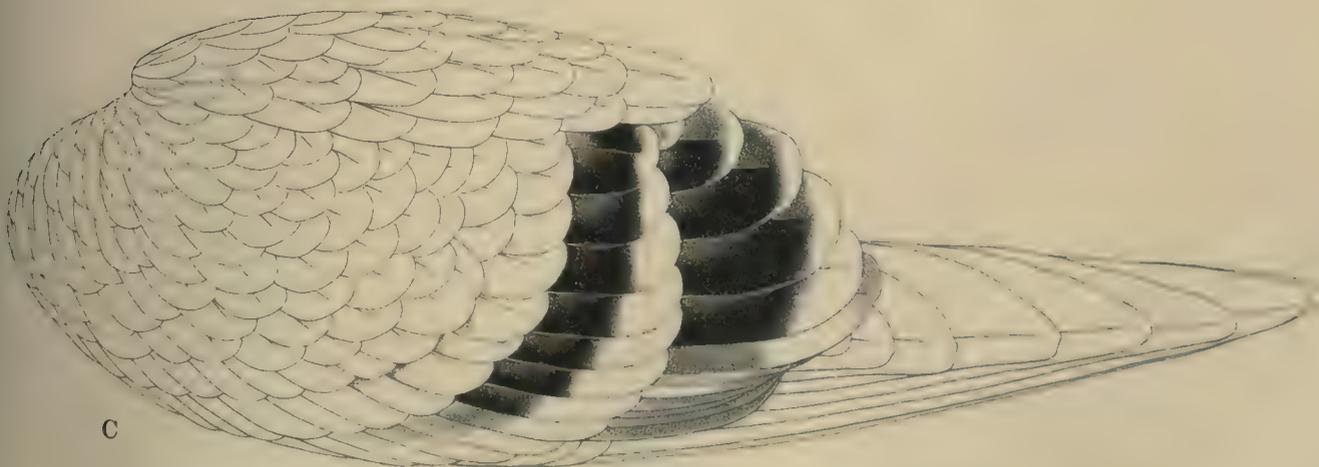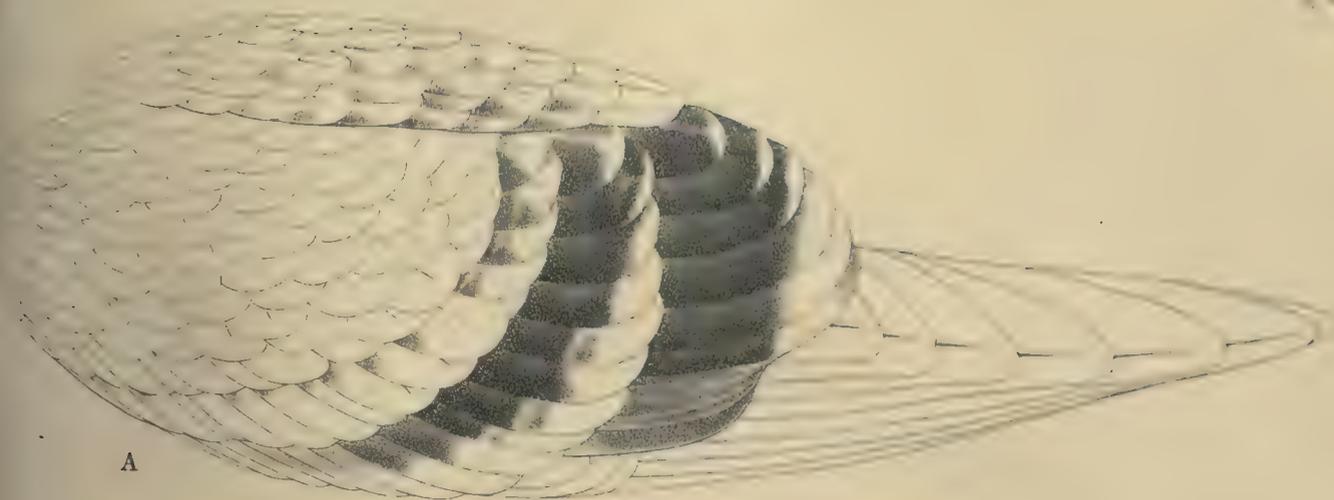
PLATE 5

A. Female homer, No. 3, hatched Mar. 31, 1901. × 0.8. Hayashi del., Nov. 1904. Parents of
   the three birds of this plate are shown in pl. 4.
B. Male homer, No. 7, hatched May 1, 1904. × 0.8. Hayashi del., Oct. 1904.
C. Female homer, No. 8, hatched May 1, 1904. × 0.8. Hayashi del., Oct. 1904.

This ancestral mark is a dark spot filling the whole central part of the feather, leaving only a narrow distal edge of a lighter color. This mark is still well preserved in some of the old-world turtle-doves—best in the Oriental turtle-dove of China and Japan. The chequer of *Columba livia* differs from the dark center of *Turtur orientalis* (text-fig. 3) only in form and in having a lateral position. Typically this spot appears in pairs, one on each side of the feather. The two spots represent the two halves of the old central spot, which becomes more or less deeply divided by the disappearance of pigment along the shaft of the feather. This change begins at the tip of the feather and advances inward, but usually more rapidly along the shaft than at the sides, thus resulting in two chequers with more or less pointed tips. The direction of change again coincides with that of embryonic development—the tips of the feather, where it begins, being first in order of development. In many chequered rock-pigeons we may find in the dorsal (inner) feathers of the bars undivided central spots, which pass gradually into the typical chequers as we pass towards the lower (outer) ends of the bars. Transitional stages of

EXPLANATION OF PLATE 5—*Continued.*

B. Male homer, No. 7, hatched May 1, 1904. × 0.8. Hayashi del., Oct. 1904.

The male bearing this wing resembles his sire in size and general form. The chequers on the scapulars are stronger and more numerous than in the sire, but fall far below the dam. The third bar has about the same number of spots, but these are here a little stronger.

The second bar inclines to red (red = light shading; black or rather dark gray = black). The shaft-line and the lower edge are also reddish gray in three or four of the upper (inner) tertials and long coverts.

Measurements.

Feather No.	Second bar.		First bar.	
	Length exposed.	Remarks.	Length exposed.	Remarks.
	mm.		*mm.*	
1	13	. . . .	. .	
2	13	. . . .	15	2 spots.
3	14	. . . .	20	2 spots.
4	15	. . . .	25	2 spots.
5	17	. . . .	24	1 spot; no upper spot.
6	21	. . . .	19	Spot on upper tip begins.
7	14	. . . .	17	Spot at tip spreads over to lower.
8	16	. . . .	17	Reduced to red-gray.
9	14	. . . .	15	Do.
10	10	Flecky.	11	Do.
11	8	More flecky and thinner.	(?)	See below.
12	8	Thinner.	(?)	
13	7	Thinner.	(?)	
14	6	Thinner.	(?)	
15	5	Few flecks.		

The eighth to fourteenth secondaries of the first bar have spots almost too indistinct to measure with certainty. (See preceding figure.)

C. Female homer, No. 8, hatched May 1, 1904. × 0.8. Hayashi del., Oct. 1904.

This female is pale, though not quite so pale as homer No. 3 (fig. A, this plate). The quills are whitish, but less so than in homer No. 3.

Third bar is here scarcely noticeable.

Second bar begins with 11 mm. width, increasing in second feather to 12 mm. and in third to 13 mm. It runs on nearly evenly to the seventh feather and then becomes gradually thinner.

First bar has its greatest width on fourth and fifth feathers—22 and 20 mm. respectively. The tip spot begins on both upper and lower webs of the sixth feather.

(The details of the breeding history of the three birds shown on this plate are given in table 76 of Vol. II.—ED.)

3

various degrees thus connect the derived with the ancestral type in one and the same individual, and so demonstrate that the two specific marks are not separated by impassable mutation-gaps. While it is not necessary to go beyond the wild rock-pigeons and the multitude of domestic races descended from them to learn that nature has here pursued one chief direction of color variation, always leaving an open door, however, to minor modifications and improvements through natural and artificial selection, it is nevertheless highly instructive to make a comparative study of the whole group of wild pigeons, in both adult and juvenal stages. It is in this field that we find the same lessons amplified and repeated in multitudinous
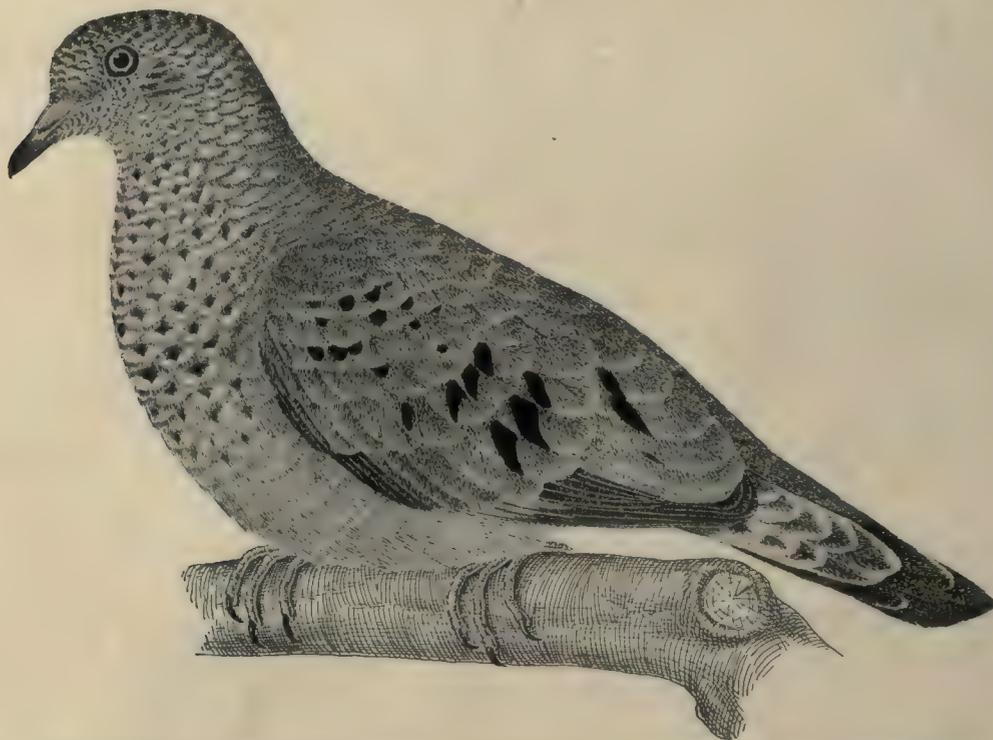
TEXT-FIGURE 4.—Adult female Florida ground-dove, *Chamœpelia passerina*. Natural size. Hayashi del., Apr. 1903. The feathers of head and neck are edged with pale dark edges, crescents not so strong as in *Scardafella inca*. Note the dark centers in feathers of breast and foreneck and the reduced spots of the wing. For fuller description of these feathers see pl. 28. In the anterior part of the wing—in the region of the oblique bar of some related forms (see under Peristerinæ, Chapter V.—ED.)—there is a noticeable persistence of spots.

ways, confirmation confirmed, convergence of testimony complete. It will be sufficient here to cite a few examples.

In the little ground-doves (*Chamœpelia passerina*) of Florida, Arizona, California, Central and South America, and the West Indies, we find the turtle-dove pattern preserved in the whole breast region (text-fig. 4) and in the anterior, smaller coverts of the wings, while in the posterior portion of the wings we meet with lateral spots or *chequers*, of higher finish than in the rock-pigeons. In many coverts of the wing we find the dark centers more or less reduced, with the distal ends of their remnants in various stages of conversion into lateral spots. Here again we find striking proof of gradual change from one specific type to another.

In the brilliant bronze-winged pigeon (*Phaps chalcoptera*) of Australia we have still another combination type, in which iridescent chequers coexist with the original dark centers (pl. 6, fig. A). Here the chequer seems to arise by direct differentiation of a lateral portion of the dark center (pl. 7, fig. B), the latter still occupying the original field and forming the ground within which the chequer appears as a more highly colored spot. While the dark center does not suffer any reduction in its field, it does lose considerably in intensity of color. The metallic spots are therefore probably built up by concentration of pigment at the expense of the dark

TEXT-FIGURE 5.—Chequers of wing of juvenal male passenger-pigeon, *Ectopistes migratorius*. × 0.8. Hayashi del., Apr. 1897.
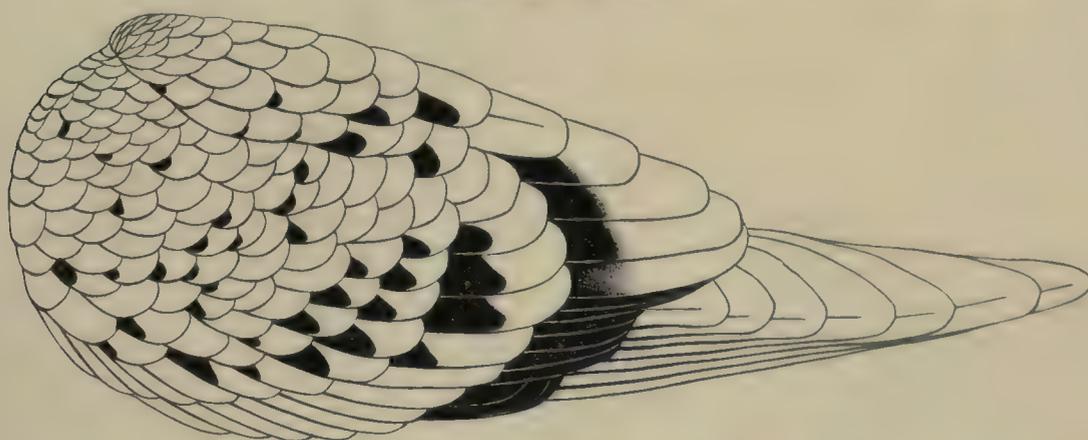
TEXT-FIGURE 6.—Chequers of wing of adult female passenger-pigeon. × 0.8. Hayashi del., Feb. 1897.

centers. As these birds make great display of their colors in the breeding-season,[7] this departure from the orthogenetic trend of development may be attributed to natural selection.[8]

The wild passenger-pigeon (*Ectopistes*) bears chequers closely resembling those of the chequered rock-pigeon, in form, color, and distribution. In this species the sexes are distinctly differentiated in color (see pls. 28 and 29, Vol. II); and we have

[7] This topic is treated in Vol. III.—ED.

[8] Soon after the above was written the author received and studied (and had illustrations made of) specimens of another bronze-wing (*Phaps elegans*), which bears a relation to the much-chequered species *chalcoptera*, quite similar to that borne by the two-barred rock-pigeon to the chequered rock. The figure for *Phaps elegans* is therefore also reproduced in plate 6, figure B.—ED.

for comparison three stages in an ascending series, namely, the juvenal (text-fig. 5), the adult female (text-fig. 6), and the adult male (text-fig. 7). As in so many other birds, the male makes the widest departure from original conditions; the female occupies a lower plane; the young are nearly alike in both sexes and may be said to recapitulate ancestral conditions with less modification than is seen in the adult of either sex.

<div style="text-align:center">

EXPLANATION OF PLATE 6.

</div>

A. Left wing of bronze-winged pigeon, *Phaps chalcoptera;* probably female No. S 1, red. Hayashi del., May 1899. × 0.75.

<div style="text-align:center">

Description, December 25, 1898.

</div>

First bar.—Some of the feathers are imperfect. This bar has four brilliant spots. There is a finish and definition here that excel anything I have seen thus far on the pigeons.

Feathers Nos. 14 and 13 have no spots.

No. 12 is darker in lower web, but no distinct spot.

Nos. 11 to 6, six feathers, which in closed wing are seen in upper part, are thus marked.

Nos. 11 to 8 have the four most brilliant spots. These spots have a rich purplish reflection, in some lights showing only black. The inner secondaries have in addition to the spots a steel-blue reflection on the outer web. In all these spots the fawn-color of the lower edge and tips of the feathers extends from the edge up into the web, forming a beautiful border on the terminal end of the spot, half converting the spot into an ocellate form. Notice that all these spots are more or less pointed posteriorly.

No. 11 spot is ovate in shape, with small end behind. It is bordered with a velvety black just within the light-fawn border behind.

No. 10 has a boot-shape with toe pointing backward; longest measure, 23 mm.; transverse, 8 mm.

No. 8 spot similar in shape, but more pointed at toe.

No. 6 spot is oval oblong and duller.

These four brilliant spots are placed where they can be seen to best advantage in the closed wing.

Second bar.—There are 6 brilliant spots. Here the lower 5 feathers have a metallic green reflection on the lower web, which becomes stronger upward, giving a spot on 5 that has an oval center of a bronze-green reflection. This becomes stronger in Nos. 6 and 7, and in No. 8 enlarges to an oblong form 16 by 11 m m., with a light-fawn streak as border behind.

In No. 9 we have the largest spot—squarish, measuring 16 × 11 mm. From here on to No. 13 the spots become smaller.

From No. 8 to No. 12 the spots show more or less obtuse points backward.

The spot on 13 is not pointed; it is the smallest, measuring 7 by 8 mm.

These spots, like those on the median and lesser coverts, are on a golden bronze-green, often reflecting a rich coppery red.

Here, as before, the spots are developed on the upper middle feathers, where they can be seen to best advantage.

Third bar.—Has 14 brilliant spots. This is the most highly developed bar, so far as number and brilliancy go. The 14 brilliant spots are all bluntly pointed behind. They increase in size and color from below up to the eighth (the largest) and then diminish gradually to the last or fourteenth. Here again it is the middle feathers that are richest. Sizes: Lower spot (1) 12 by 6 to 12 mm., largest (8) 16 by 9 mm., smallest (14) 2 by 3 to 12. The rounded posterior ends encircled with velvet-black and light fawn-color, giving the spots quite an eye-like appearance.

In Nos. 8 and 9 the spot extends a little above the shaft, reaching highest point in No. 11, where it has the bronze-green reflection. This seems to be a rudiment of an upper spot.

Fourth bar.—Has 11 brilliant spots, beginning in No. 3 (perhaps on No. 2), becoming largest on Nos. 5, 6, 7, and 8, then diminishing upward to a small circular spot of 3 by 4 mm. on No. 13. The spots are not quite so many nor quite so large on the average as in third bar. Most of them are bluntly pointed backward.

These spots begin to cross above shaft, slightly in Nos. 5, 6, 7, and more plainly in Nos. 8 and 9, and in No. 10 I notice the same bronze reflection in the small upper spot. This spot becomes black in No. 11, and is not seen above.

I find that the number of spots in a series, or row, differs in the two individuals I have. The specimen described has smaller spots than the other, and they are not so rich in color.

B. The bronze-wing, *Phaps elegans.* Adult male. × 0.75. Hayashi del., Sept. 1904. In first bar 3 spots.

<div style="text-align:center">

Note and description, Sept. 11, 1905.

</div>

I have two males that have just died. In one of these I find no distinct chequers in the tertials on the left side, but on the right side there are two obsolete chequers. The second and third bars are about as well developed as in specimen drawn. In the other I find two very obscure spots in the tertials of the left side and only one such spot on the right side. I find no spots in the second bar of the right side (some were lost on left side—presumably they were about the same). Thus while the first bar is almost obsolete, the second bar has two more spots than shown in the figure drawn.
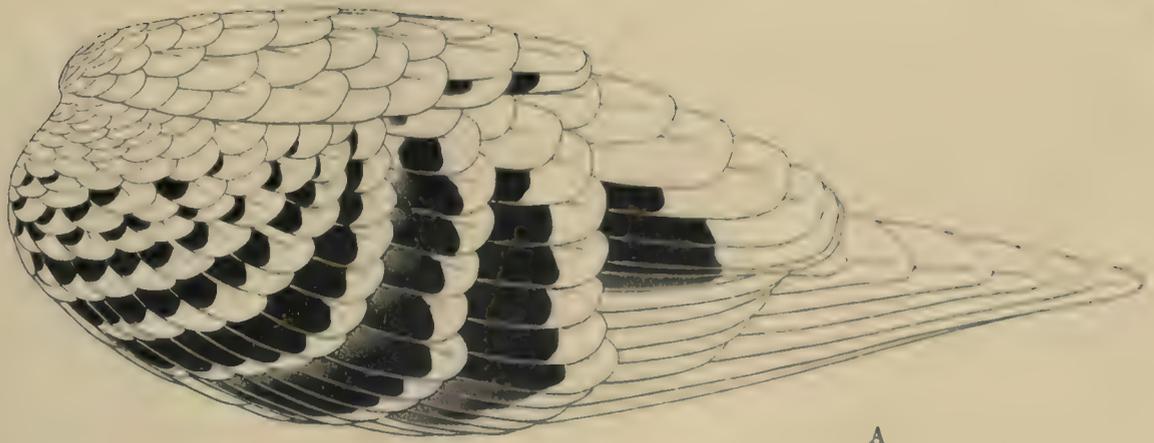
PLATE 6

A. Left wing of bronze-winged pigeon, *Phaps chalcoptera*; probably female No. 81, red. × 0.75.
  Hayashi del., May 1899.

B. The bronze-wing, *Phaps elegans*. Adult male. × 0.75. Hayashi del., Sept. 1904. In first
  bar 3 spots.

In birds taken at random, I count in the left wing and scapulars 90 chequers on a juvenal, 51 in an adult female, and 25 in an adult male. This is pretty conclusive evidence that chequers are, or have been, disappearing in the species. Not only the number but also the size of the chequers has been reduced. In the female the chequers are for the most part two or more times as large as in the male. The reduction in both respects has been greater in the anterior than in the posterior half of the wing, and greater along the lower edge than in the middle and back regions.

In this species we may recognize at first sight the homologues of the rock-pigeon bars. On the secondaries of the female we find the homologue of the posterior bar, and on the first row of long coverts the homologue of the anterior bar. The latter is scarcely recognizable as a bar, for we see only 5 or 6 chequers in the upper half of the row, the lower half being without chequers. Nevertheless, this row represents, so far as it goes, the elements of a bar which is already too far gone to have even a chance to attain the finish of a perfect bar.[9]

On the secondaries the chequers fall into juxtaposition, forming a continuous bar, with an irregular posterior outline, which indicates that the chequers have been unevenly reduced from behind. It is a rudely finished bar which has sunk below the horizon of utility, if it was ever above it, and is now facing ultimate effacement. The reduction has advanced further in the male, with no improvement towards regularity of outline. Here it becomes quite certain that effacement advances from all sides, leaving but a small remnant of a bar confined to two or three feathers.

Glancing at the wing as a whole, in both young and old, it is plain that the process of obliteration is in progress over the entire chequered area. The elongated, sharp-pointed marks of the earlier pattern have rounded tips in the adult; the posterior bar is roughly emarginated; the number of chequers is reduced by half or more; and some of the remaining ones are but little more than mere dots. It is also equally manifest that the process of reduction is making more rapid progress in the fore part of the wing and along its lower edge than elsewhere. There can be no mistake here as to the direction in which the phenomena are to be read.
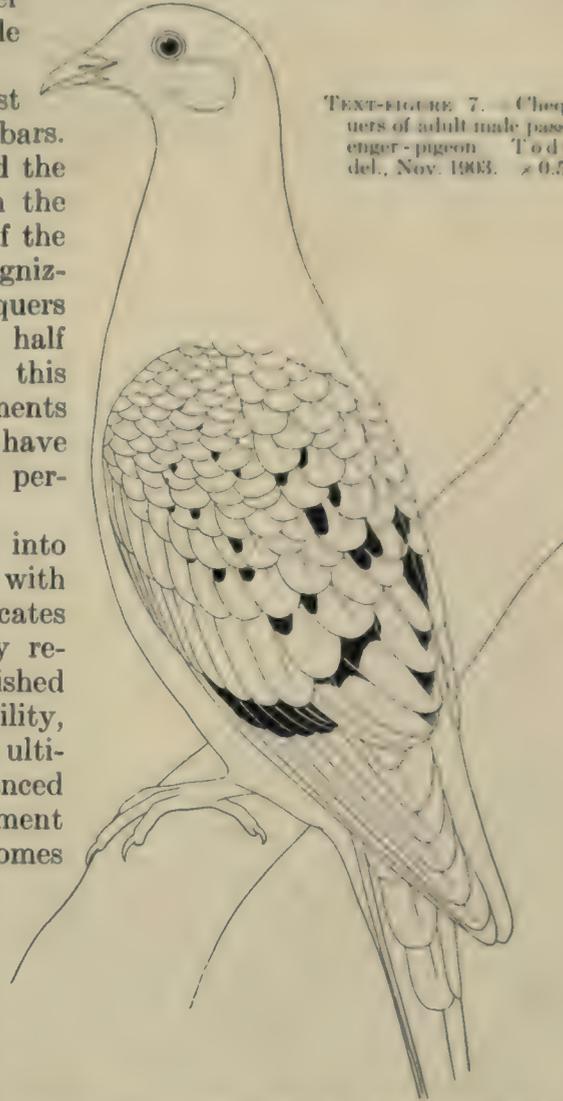
Text-figure 7. — Chequers of adult male passenger-pigeon. Toda del., Nov. 1903. × 0.5

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[9] In the young, the chequers of this row are more numerous and much more sharply pointed at the ends. In both respects the juvenal pattern approaches more nearly a condition of general uniformity.

The direction is as certain as that the adult male stands in advance of the adult female, and still more in advance of the young bird. The significance of the case lies mainly in the fact that it is not an isolated or exceptional one. Many other species tell more or less perfectly the same story.

A parallel case, only carried still farther in the same direction, is found in the mourning-dove (*Zenaidura carolinensis*). The adult male and female differ but slightly, each having only about a dozen chequers visible on each side. These are confined to the scapulars and to a few feathers at the posterior upper edge of the wing. In the young they are more numerous (pl. 7, fig. A), but less so than in the young passenger-pigeon. The middle and fore parts of the wing in the adult have no visible chequers, but a few concealed ones which may be seen on lifting the overlying feathers. These concealed chequers, and other differences between old and young, show that the species has its origin in a chequered stock, and that its history has been analogous to that of the passenger-pigeon.

The white-faced pigeon (*Melopelia leucoptera*) is a most instructive form. Although much more highly accomplished than the mourning-dove in the arts of display of form, feathers, and voice, it has suffered a complete effacement of the chequers it once possessed in common with other members of the family (see text-figs. 8 and 14). Indubitable proof of this is to be seen in the juvenal feathers, which in some cases exhibit a few pale vestigial spots in the last two rows of long coverts, at points where the chequers are usually best developed in chequered species. Another striking proof is to be found in the coverts and scapulars of the adult bird, where we find, on lifting the feathers, distinctly outlined areas, corresponding in shape and position with reduced chequers, but from which the black pigment has disappeared. These vestigial outlines, structurally defined, were first noticed in a female bird of a dark shade.[10] The outlines were more perfect than in lighter birds obtained from Arizona and California.

[10] Captured in Jamaica by Dr. Humphreys.

EXPLANATION OF PLATE 7.

A. Wing of juvenal mourning-dove, *Zenaidura carolinensis*; age 4 weeks. Natural size. Hayashi del., June 1897.

Left wing in first plumage. The tertials have 2 black spots, the dorsal one having no sharp bounding-line. The darker spots are at the upper part of the posterior bar. The next bar has 8 spots, and next 8.

Most of the scapulars have two spots, and many of the anterior lesser coverts bear indistinct spots. Spots grow darker backward. These spots are strikingly like those of the young *Ectopistes*.

Feathers edged with a dull buff-color. The quills are much like those of *Ectopistes*, but the edging is not of so rich and deep a color.

B. Wing of juvenal bronze-wing, female, *Phaps chalcoptera*. Natural size. Hayashi del., Dec. 1905.

Left wing at four weeks.

(1) Oblique streak which has about 10 feathers in one or two rows. These lie just in front of the fourth row in wing-coverts, counting from behind. The feathers of the streak have each one black spot on lower web, only slightly iridescent, and they are already long enough to reach over the tips of some feathers of the fourth row.

(2) On the tertials it can be seen plainly how the spots arise in or from the dark center of the turtle-dove pattern, a pale transverse band, running from the pale edge of the feather inward for all lengths, from a part of a millimeter to one-half or two-thirds of the width of the outer web. The cross-band is of same color as edge of feather. It means that pigment fails to appear here, and, as if in compensation, more pigment is laid down in front of the band, thus producing the spot or element of the bar; and this spot in adult feathers is built much more strongly—more black pigment and strong iridescence.

In another specimen of about the same age, also a female, I measured these cross-bands and found them to be from 2 to 3 mm. in width and 1 to 8 mm. in length. They stand 15 mm. distant from the tip of the feather. In the specimen drawn I see these bands in the row of long coverts, but not so well defined. Evidently these cross-bands or bars have had much to do in shaping spots and in giving eye-like borders (diamond-dove, adult bronze-wing, etc.).

The wing drawn was injured a little at outer edge.

PLATE 7
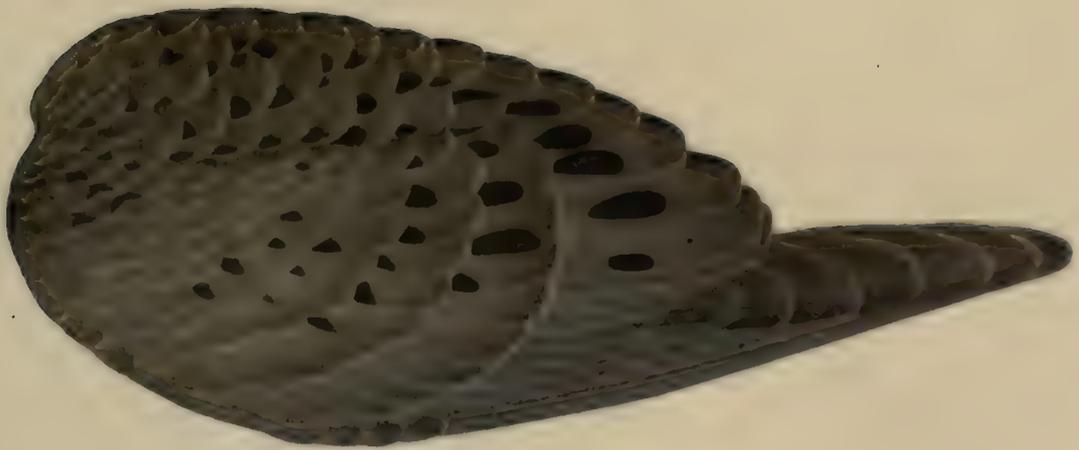
A

B

A. Wing of juvenal mourning-dove, *Zenaidura carolinensis*; age 4 weeks. Natural size. Hayashi del., June 1897.

B. Wing of juvenal bronze-wing female, *Phaps chalcoptera*. Natural size. Hayashi del., Dec. 1905.

Similar vestiges are present in the mourning-dove, and here their identification as marks formerly filled out with black pigment is freed from every shadow of doubt by chequers in all stages of obliteration. (The conditions presented by *Zenaidura* and *Melopelia* are fully discussed and illustrated in Chapter V.—ED.)

The large wood-pigeon (*Columba palumbus*) of Europe has departed still more widely from the turtle-dove type, having lost all its black spots except a few in the neck patches, which have retreated so far from the tips of the feathers as to be concealed (see text-fig. 6, Vol. II). The gray plumage and the white streak along

TEXT-FIGURE 8.—Adult white-winged pigeon, *Melopelia leucoptera*. × .77. The feathers at the lower outer edge of the wing are white. No chequers in the adult, but structural imprints of these in a few feathers of the wing.

the edge of the wing mark a plane in the evolution of this bird very nearly identical with that of the white-winged pigeon. A little higher plane has been reached by our band-tailed pigeon (*Columba fasciata*) of the Pacific coast, which is also a species of turtle-dove derivation,[11] as shown in the neck-markings (see text-fig. 5, Vol. II) and in the voice and behavior.

These illustrations, which could be extended into the hundreds, may be concluded with two cases, representing wide extremes, yet governed by the same law of progressive orthogenetic variation.

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[11] Minute blotches of black were found in the longer scapulars of a few individuals. These are probably atavistic reminiscences of lost spots.

The crested pigeon of Australia (*Ocyphaps lophotes*) stands at the uppermost limit[12] in the number of bands and in the perfection of finish. There are 11 or at most 12 parallel bands crossing the wing and scapulars transversely, each bend marking a single row of feathers with the regularity of zebra stripes (pl. 8, fig. A). The width of these bands increases from before backward, beginning with a width of about 0.5 mm. and reaching 4 to 5 mm. on the tenth band. The eleventh band, located on the long coverts, is especially interesting, as it begins above with narrow elements, like the preceding, but is continued, from the third or fourth feather onward, by elongated chequer-like spots. This band or bar is the homologue of the anterior bar in the rock-pigeon, and furnishes a standing picture of transitional continuity from one character to another, at the same time settling beyond dispute the direction variation has pursued. So clear and decisive is the case that one might safely predict that this entire bar is destined to be reduced to the narrow-band type seen in the fore part of the wing. We have only to turn to a closely allied species, the white-breasted crested pigeon[13] (*Lophophaps leucogaster*) to find that it has already realized the prediction to the full, having every chequer in this row converted into a typical band-element (text-fig. 9).

[12] The short statement on *Ocyphaps* given here is amplified by the whole of the following chapter.—ED.

[13] This bird is comparatively rare, and I have seen but a single pair that recently came to hand through the kindness of Mr. Frank M. Chapman.

EXPLANATION OF PLATE 8.

A. Wing of adult male crested pigeon, *Ocyphaps lophotes*. Natural size. Hayashi del., Dec. 1898.

This bird is nearly 2.5 years old.

First bar.—Comprises 6 secondaries and 8 tertials. The elements of the bar are long, broad spots on lower webs; iridescent; edged at tips with white.

The iridescence vanishes on fourth feather. The lower web is about equally dark on Nos. 1 to 4, darker on No. 5 and slightly iridescent; iridescence brilliant on Nos. 6 to 10; only a little purple iridescence on No. 11. No spots on Nos. 12 to 14.

Second bar.—Formed of 15 long coverts:
(1) Black narrow bar on No. 14; is of same character as on median and lesser coverts.
(2) Homologous with the broad iridescent spots of Nos. 13 to 5.
(3) Upper spot or bar appears on No. 14 and disappears on No. 8.
(4) Diminishes upward and downward, being strongest in mid-feathers, Nos. 12 to 8.

Third bar.—Formed of 12 median coverts.
(1) Bar consists of two parts, as seen on No. 12 and as shown in form on Nos. 10 to 2, and again on No. 1.
(2) Bar widens in mid-feathers, but does not expand as in second bar; does expand more than in the fourth bar.
(3) Bar of lower web on Nos. 10 to 2 is iridescent in some lights, but seen *en face* it appears deep black. Iridescence then diminishes from behind forward, and does not extend to upper web in third and first bars. It is interesting to find the iridescence of third bar invisible in most lights, and, when visible, sharply limited to lower web.

The double nature of the bars is evident on nearly all the lesser and median coverts, but the lower half becomes more pronounced than the upper in the second bar, and in the first bar no upper spots are seen. Here we have remarkable variations in the spots.

Fourth bar.—Formed of 11 feathers:
(1) The bar consists of two parts, best seen on upper feathers (No. 11).
(2) The lower half is iridescent, seen in favorable light.
(3) The width of the bar is quite even and plainly narrower than third bar.
(4) In form one can say with respect to these four bars that they become more perfect from behind forward; in color brilliancy they improve in the contrary direction.
(5) In first bar, iridescence runs from No. 11 to No. 5, Nos. 10 to 7 being the larger and more brilliant. In second bar, iridescence runs from No. 13 to No. 5, Nos. 13 to 6 being the larger and more brilliant. In third bar each feather is marked on both webs, except the first, and the last imperfectly on upper web. In fourth bar each feather has a bar crossing both webs. The iridescence in the lower web is stronger in third bar than in fourth.

B. Wing of juvenal female crested pigeon, *O. lophotes*. Age 19 days. Natural size. Hayashi del., Aug. 1905.

The ashen-gray ground-color contrasts strongly with the adult coloration (see above, fig. A). All feathers with pale or white tips; black pigment concentrated immediately in front of these.

PLATE 8

A. Wing of adult male crested pigeon, *Ocyphaps lophotes*. Natural size. Hayashi del., Dec. 1898.
B. Wing of juvenal female crested pigeon, *O. lophotes*. Age 19 days. Natural size. Hayashi del., Aug. 1905.

Moreover, the transformation has already begun in the first feather of the next and last row, so that the same prediction could be extended to this bar, which is the homologue of the posterior bar in the rock-pigeon.

Glancing again at *Ocyphaps*, and looking at the wing as a whole, the course of transformation, its mode, direction, and future termination are all very clearly defined. The wing-pattern, as shown especially in the light edges of the juvenal plumage (pl. 8, fig. B), takes us clear back to the turtle-dove type. Next came the chequered pattern (text-fig. 10), similar to that of the primitive rock-pigeon. Reduction of pigment, proceeding from before backward, fashioned the bilateral chequers from the unicentral spots. The reduction kept on in the same direction, shorten-
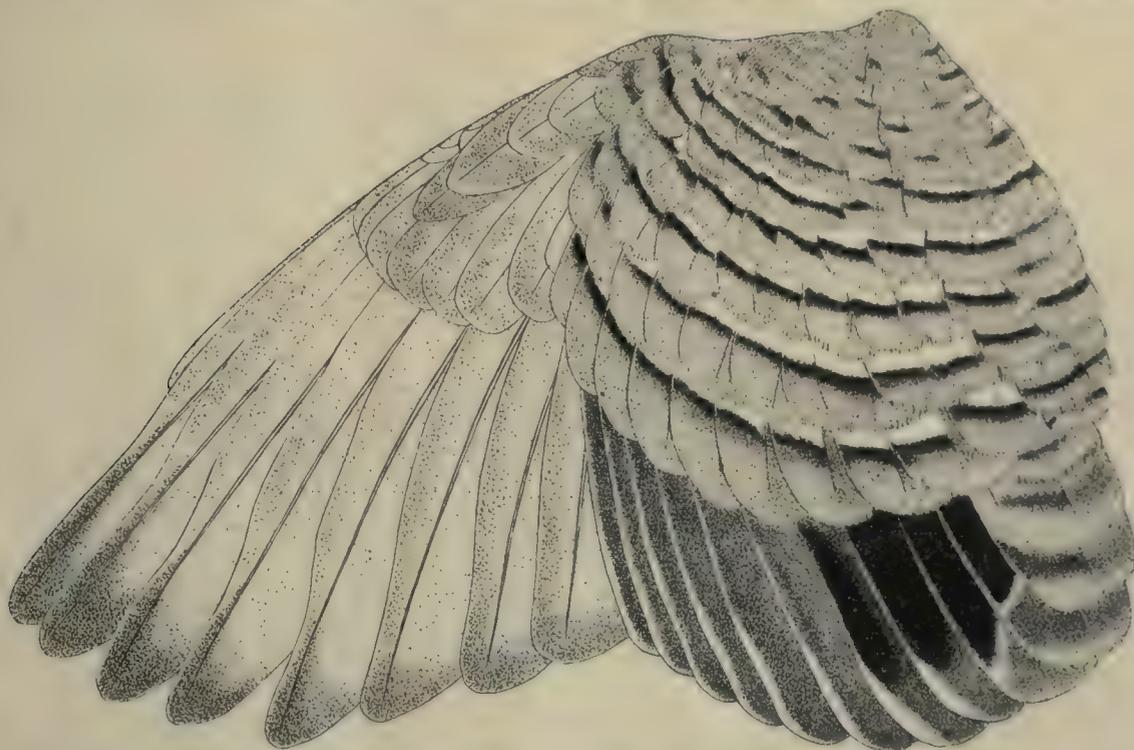
TEXT-FIGURE 9.—Adult white-breasted crested pigeon, *Lophophaps leucogaster*. Natural size. Hayashi del., Oct. 1902.

There are only four marks on tertials. The long tips of feathers are dotted for cinnamon color. The black bars are preceded by pale gray bars, not shaded. This bird stands in advance of the common crested pigeon, as shown by absence of elongated marks on the long coverts.

ing the chequers and transforming the rows successively into narrow bands, eventually reaching the eleventh row, where we find only one or two complete steps, followed by a graded series of four to six steps, less and less decided, until we lose every trace of them. So finely graded are these steps in some females that it is difficult to locate the vanishing-point.

Unless the process of transformation is arrested by the extinction of the species, or through the intervention of some more potent modifying influences than have thus far appeared, the fate of both posterior bars is irrevocably sealed. Granting that natural selection may be credited with strengthening the iridescent splendor of these bars, I believe that the orthogenetic influences are bound to prevail here as in the white-breasted species.

EXPLANATION OF PLATE 10.

Left wing of adult stock-dove, *Columba œnas*, No. 2. × 0.9. Hayashi del., Dec. 1904. The bars of both wings shown in figure B.

One of three adult stock-doves captured by Mr. Lane, of Cambridge, England.

In the figures the first of the tertials has been omitted. It is now present in the bird (Mar. 12, 1905) This feather reaches as far back as the longest scapulars, and hence to distal edge of the spot on the second feather, but it covers only the upper (inner) third of the spot.

Measurements of first bar, left wing.

Feather No.	Total length.	Exposed	Covered.	Distance to tip.	Remarks.
3	*mm.* No upper 0 Lower 9	*mm.* 0 0	Upper third Lower an- terior angle	*mm.* 0 11	Spots rhombic, with the lower (outer) distal and upper (middle) proximal acute.
4	15	14	1 mm......	12	Upper, smaller, and weaker; although rhombic, angles are rounded and outline is not sharp.
5	10	10	0 mm......	20	
6	No upper spots; upper edge of each spot is of course covered by the next feather above in all cases.				

The first bar is very pale—about half as dark as second bar; it appears too black in ink.

On the right side only two spots were found.

Second bar.

Feather No. 1, omitted in figure 1 (correct in fig. B).
    No. 2, shows mere trace of spot; would not be noticed.
    No. 3, spot middle of lower web, roundish, 9 mm. long, usually entirely covered; distance to tip, 13 mm.
    No. 4, spot about 14 mm. long, only 2 mm. exposed; distance to tip, 14 mm.
    No. 5, spot about 11 mm. diameter, only 2 mm. exposed; distance to tip, 18 mm.

Measurements of third bar.

Two minute rudiments, wholly covered; upper one occurs on fifth feather of row; distinct but not sharply out-lined, 5 mm. long by 2.5 mm. wide; 13 mm. distant from tip; lower one a very thin freckle of about same size as upper; would be overlooked if one were not guided by the upper spot.

EXPLANATION OF PLATE 11.

Left wing and bars of both wings of adult stock-dove, *Columba œnas*. No. 3. × 0.9. Hayashi del., Nov. 1904. One of three adult birds from Mr. Lane.

The first tertial is not shown in figure A; correctly shown in figure B. No upper spot in either bar. The distal side of all spots straight-slant in both bars; proximal end rounded in all spots of both bars. The first bar has three weak spots. Ink makes them too strong. They are so faded that at certain angles they almost vanish. In the fourth feather is found the strongest of the three spots.

Measurement of left wing shown in plate 11.

Feather No.	Total length.	Exposed.	Covered.	Distance to tip.
First bar:	*mm.*	*mm.*	*mm.*	*mm.*
3..............	12	0	3	10
4..............	17	10	7	15
5..............	14	11	0	19
Second bar (5 spots):				
3..............	9	3.5	5.5	9
4..............	11	5	6	13
5..............	13	6	7	15
6..............	13.5	0	7.5	15.5
7..............	0	0	5	19

Third bar has four spots, all concealed; they lie on fourth, fifth, sixth, and seventh feathers; are rounded remnants, with distance from tip varying from 14 to 20 mm.; second and third spots strongest, first and last much weaker.

PLATE 9

Adult female stock-dove, *Columba œnas*. ×0.5. Photographed 1902. by Mr. J. P. Hubbard. The relations of the general wing coloration to that of the two-barred *C. livia* are evident. The left wing shows 3 spots in first posterior bar. 4 spots in second posterior bar. 1 spot in third posterior bar. All spots in the third bar are concealed by overlying feathers. In the left wing there was only one of these spots, while there were 5 in the right wing. The feathers are pressed to one side to show the spots.
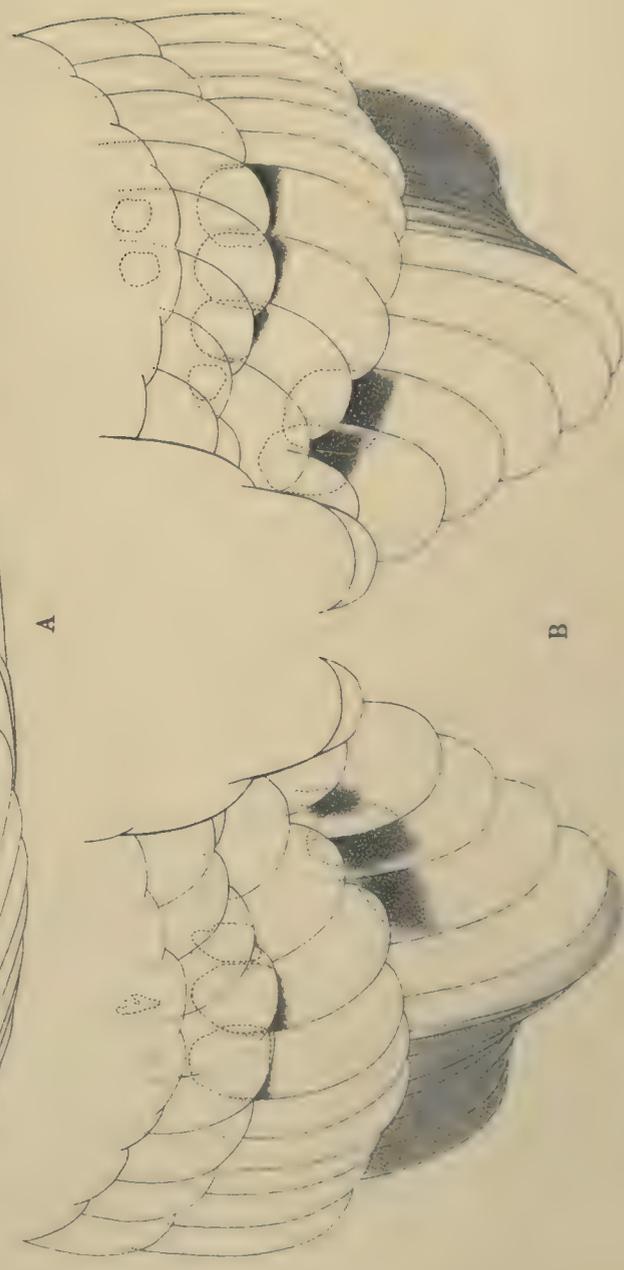
PLATE 10

Left wing of adult stock-dove; *Columba œnas*, No. 2. × 0.9. Hayashi del., Dec. 1904.
The bars of both wings shown in fig. B.

PLATE 11
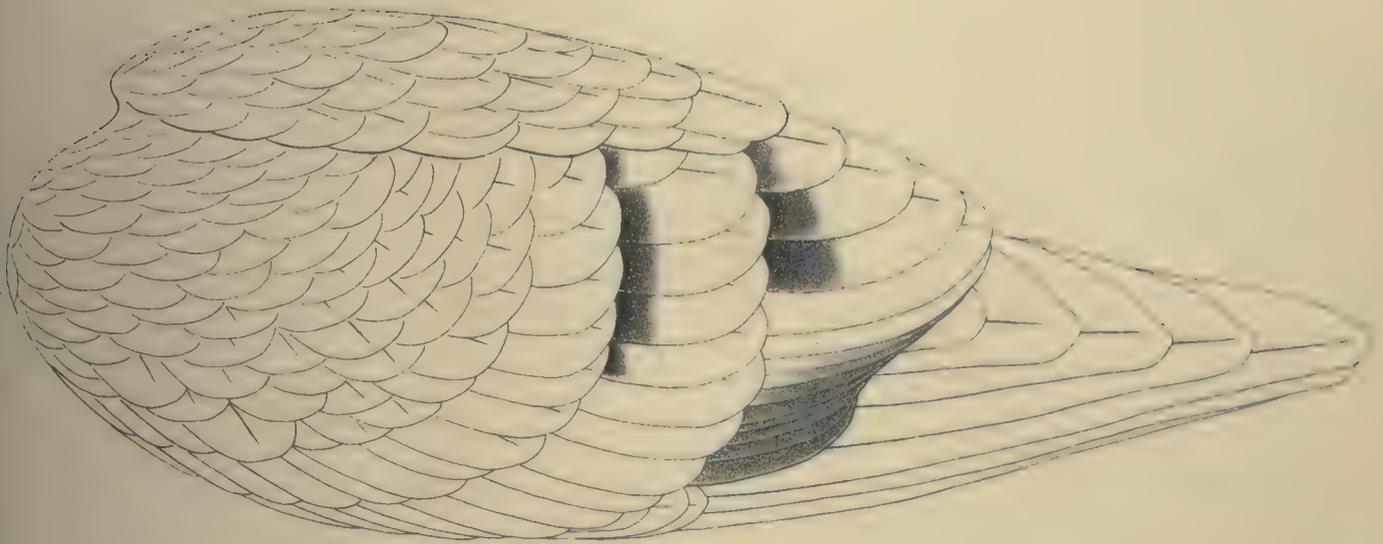
A
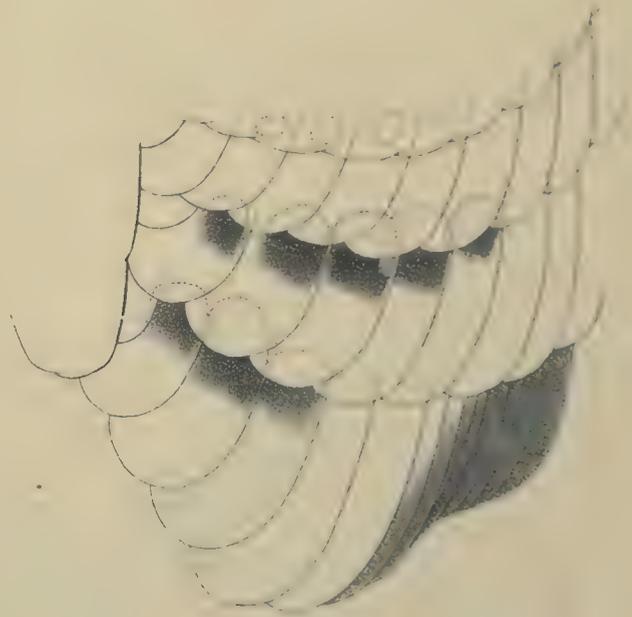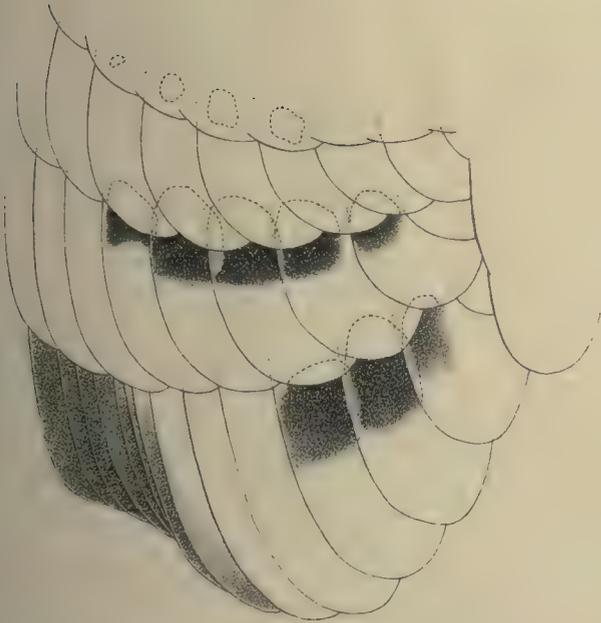
B

Left wing and bars of both wings of adult stock-dove, *Columba œnas*, No. 3.   × 0.9.   Hayashi del., Nov. 1904.   One of the
three adult birds from Mr. Lane.

The first tertial is not shown in fig. A; correctly shown in fig. B.   No upper spot in either bar.   The distal side of all spots
straight-slant in both bars; proximal end rounded in all spots of both bars.   The first bar has three weak spots.   Ink
makes them too strong.   They are so faded that at certain angles they almost vanish.   In the fourth feather is found
the strongest of the three spots.

But is there any direct proof that the transformation is actually making progress to-day? May not these transitional steps go on appearing generation after generation, without ever making any permanent progress?

We have to concede that we can not follow the processes that reveal themselves in steps. We can at most only see what is done, not the doing. We are entirely in the dark as to the time required to carry the change through a single row of feathers. But we know that this has been done in three other species of the same family. We see after it is done, not before, that the transitional steps appear in the next and last row. Moreover—and this is as close as we can hope to get to actual seeing—we find that progress of just the kind we are looking for is certainly made in passing from the juvenal to the adult plumage. This is an ontogenetic change of a few weeks, which we can easily demonstrate by experiment to be pro-
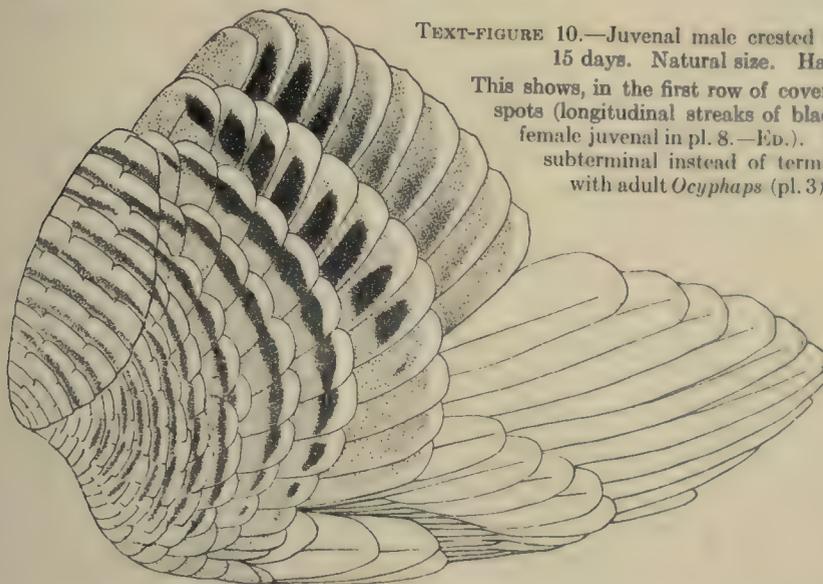
TEXT-FIGURE 10.—Juvenal male crested pigeon. *Ocyphaps lophotes*. Age 15 days. Natural size. Hayashi del., Dec. 1898.

This shows, in the first row of coverts, the transition between long spots (longitudinal streaks of black) and cross-bars (better than female juvenal in pl. 8.—ED.). In this species the cross-bars are subterminal instead of terminal (as in *Geopelia*). Compare with adult *Ocyphaps* (pl. 3) and *Lophophaps* (text-figure 8).

gressive and continuous. The corresponding phylogenetic advance has left no other record, and hence we only know that it took time—that it was not a momentary salt. In the adult plumage, one or two full steps are taken beyond the juvenal stage, and taken precisely at the points premarked by transitional steps. The number of transitional steps is increased at the same time.[14]

As the next and last illustration, I take a case in which the bars are verging to complete obliteration. The well-known wild stock-dove (*Columba œnas*) of Europe may serve as a convenient and instructive example. In this pigeon we find that reduction of the chequers has swept over the whole bar, leaving nothing except a few obsolete spots, which we recognize as vanishing elements of bars formerly more highly developed and homologous with those of the rock-pigeon.

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[14] One point here should not escape attention, namely, that the transitional steps in *Ocyphaps* form a linear series; but there is nothing artificial or arbitrary about it. It is a small-number series, each element of which stands in an appointed place and marks the height to which the transformation process rose at that point in its course. Such a series can not be open to the objections which de Vries has very justly made against large-number series, the elements of which are collected at random and then arranged arbitrarily to display transitional continuity. In the *Ocyphaps* series there is some fluctuation, the series varying in length, but always advancing in one predetermined direction, like a tidal flow guided along a prepared channel, and flowing to varying distances, according to the initial momentum.

Here we find what at first glance looks like extraordinary variability (pls. 9 to 13) suggesting mutations, incipient stages, bars *in statu nascendi*, etc. The selectionist and the mutationist could each find what he looks for. The first thing to decide is the direction in which the phenomena are to be read. Is it a positive, progressive upbuilding of new characters, or a negative, retrogressive weakening of old characters? I have already anticipated the answer and will now briefly show how the direction of variation is decisively settled.

(1) These spots have every outward appearance of being reduced remnants, such as we get in passing from the chequered to the barred condition in rock-pigeons. They are rounded or squarish in form, frequently irregular and thin at the edges, dull in color, as if fading, etc.

(2) The smallest stages are not found on the exposed surface of the feathers, but lie concealed beneath the overlapping feathers next above or in front. Concealed spots admit

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EXPLANATION OF PLATE 12.

A. Wing-bars of adult stock-dove, *Columba œnas*, No. 5.   × 0.9.   Hayashi del., Mar. 1905. A bird (young of 1904) captured by Mr. Lane.

Bars of both wings.—Measurements of left wing.

Feather No.	Total length.	Exposed.	Covered.	Distance to tip.	Remarks.
First bar, 4 spots:	mm.	mm.	mm.	mm.	
2..............	4	0	4	11	An extra spot on 2d
3..............	14	7	7	11	feather, small and
4..............	19	10	0	14	obsolete; not seen
5..............	9.5	7.5	2	23	on right side.
Second bar, 5 spots: *					
3..............	9.5	1	8.5	10	
4..............	13.5	2.5	11	14	
5..............	13	3.5	9.5	15	
6..............	12	4	8	18	
7..............	0	2	7	21	

* On right only 4 spots, none on fourth, leaving an interval.

Third bar, 6 spots, all concealed; lower two thin and flecky; found on third to eighth feathers; all rounded in form. Diameter of—First spot, 5 mm.; second spot, 8 mm.; third spot, 8 mm.; fourth spot, 6.5 mm.; fifth spot, 5.5 mm.; sixth spot, 3 mm.

7 spots on right side, 3 or 4 showing just at distal edge.

No trace of a fourth bar in any specimen examined. (Later, in 1909, a specimen with a trace of a fourth bar was found; see pl. 13.—ED.)

B. Wing-bars of adult stock-dove, *C. œnas*, No. 11.   × 0.9.   Hayashi del., Mar. 1905.   A bird (young of 1904) captured by Mr. Lane.

Bars of both wings.—Measurements of left wing.

Feather No.	Total length.	Exposed.	Covered.	Distance to tip.
First bar (3 spots):	mm.	mm.	mm.	mm.
3..............	9	2	7	14
4..............	19	7	12	15
5..............	14	8	6	20
Second bar (4 spots):				
3..............	2	2	0	10
4..............	8	0	8	14
5..............	13	1	12	17
6..............	10	2	8	20

In several specimens first and second bars are nearly concealed as in this bird.

Third bar (2 spots, rudimentary).—Concealed, thin, rounded, 4 to 5 mm. in diameter. Second spot, 4 mm. long by 2 mm. wide, both very weak. Three spots on right wing.

PLATE 12

A. Wing-bars of adult stock-dove, *Columba œnas*, No. 5. $\times 0.9$. Hayashi del., Mar. 1905.
   A bird (young of 1904) captured by Mr. Lane.
B. Wing-bars of adult stock-dove, *C. œnas*, No. 11. $\times 0.9$. Hayashi del., Mar. 1905. A bird
   (young of 1904) captured by Mr. Lane.

PLATE 13
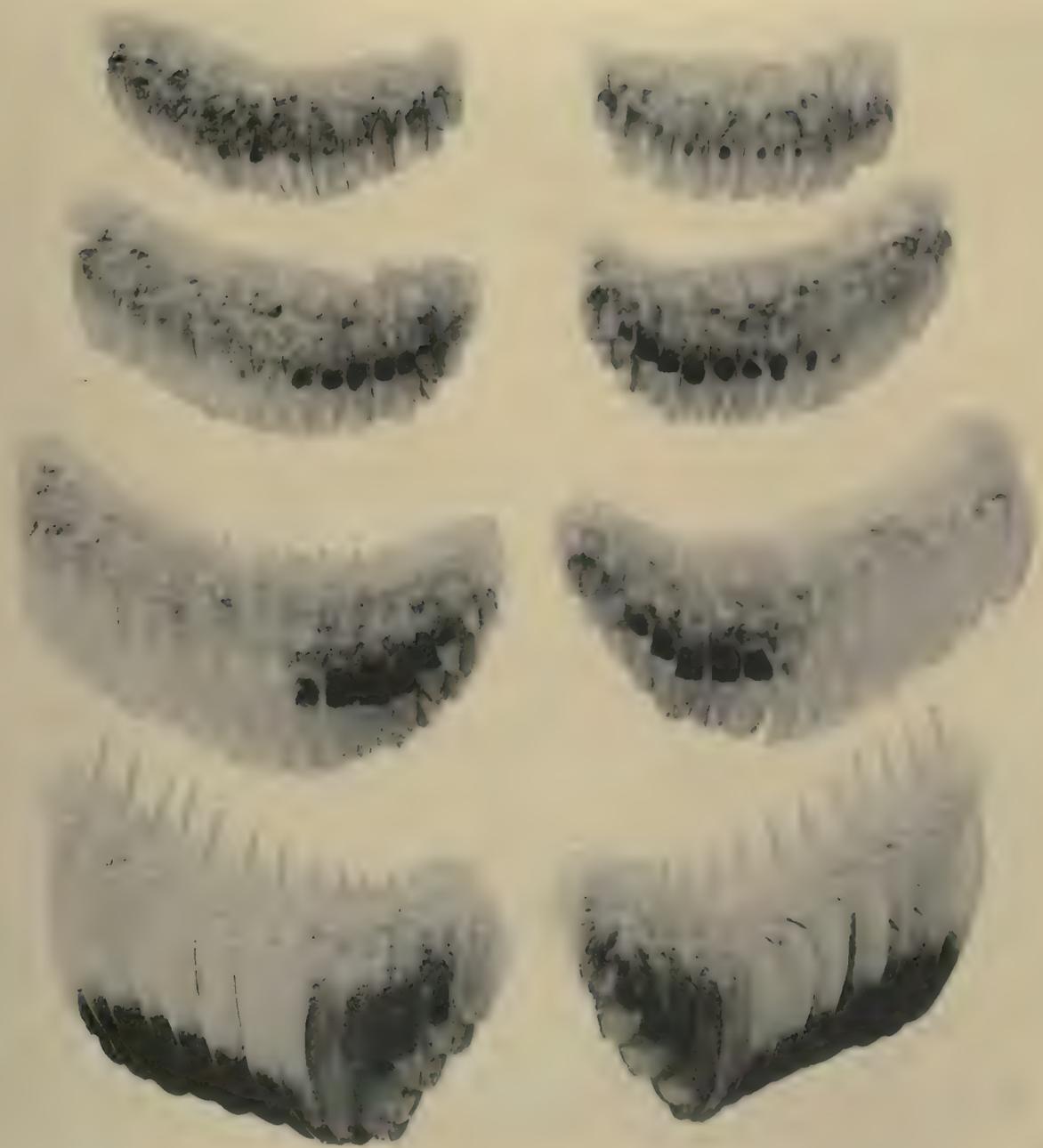
Rudimentary fourth wing-bar in adult female stock-dove, No. 24. Photographed Jan. 1909; hatched 1901 or 1902. The spots of the right wing were almost wholly concealed on the live bird; the second bar of the left wing was plainly displayed, its spots are plainly longer and stronger than in corresponding bar of right wing. A fourth bar (upper figures) is unmistakably present here.

of but one interpretation. This pigeon is a not-distant relative of the rock-pigeon, has a similar gray ground, and is therefore probably moving in a parallel direction, only more advanced.

(3) The spots are found at the posterior end of the wing, near the upper edge, on one to three tertials and on a few long coverts. In some cases they occur also on a few of the second row of long coverts,[15] but here they are always very small and completely concealed. They are thus in the position occupied by vanishing spots generally.

(4) The adult plumage makes no advance in the number of spots, and some spots (second row of long coverts), visible in the young, are completely concealed in the adult. This indicates degeneration unmistakably.

(5) The stock-dove, although sometimes having a concealed third bar of few spots, never appears in chequered dress. It seems to have moved so far in the opposite direction that no reversal of course is now open to it.

Taking the chequered pattern as the earlier one, the various conditions of chequers and bars in rock-pigeons, domestic races, and indeed in all the wild pigeons, become almost self-explanatory. We could not explain satisfactorily how just two bars could arise *de novo* in one species, three in another, twelve in another, and so on. The repetition of *de novo* origins would become ever more incredible. Making phylogeny our guide as to the starting-point, we find it comparatively easy to thread our way through the maze of patterns existing among 500 or more species of pigeons, and even to trace affinities farther back in the bird world.

The orthogenetic process is the primary and fundamental one. In its course we find unlimited opportunities for the play of natural selection, escape the great difficulty of incipient stages, and readily understand why we find so many conditions arising and persisting without any direct help of selection.

Charles Darwin:

As natural selection acts solely by accumulating slight, successive, favorable variations, it can produce no great or sudden modification. (*Origin of Species*, Chapter XIV, p. 421.)

Slight individual differences, however, suffice for the work, and are probably the sole differences which are effective in the production of new species. (*Animals and Plants*, Vol. II, Chapter XX, p. 233.)

As modern geology has almost banished such views as the excavation of a great valley by a single diluvial wave, so will natural selection, if it be a true principle, banish the belief of the continued creation of new organic beings, or of any great and sudden modification in their structure. (*Origin of Species*, Chapter IV, p. 98.)

August Weismann:

The simultaneous modification of numerous co-functioning parts, in essentially different ways, yet in harmonious functional relations, points conclusively to the fact that something is still wanting to the selection of Darwin and Wallace. (*Germinal Selection*, p. 22.)

We know of only one natural principle of explanation for adaptation, that of selection. (*Ibid.*, p. 61.)

The three principal stages of selection—that of personal selection, as held by Darwin and Wallace; that of historical selection as upheld by Wilhelm Roux in the form of a "Struggle of the Parts"; and, finally, that of germinal selection, the existence of which I have endeavored to establish—these are the factors that coöperate to maintain the forms of life constantly capable of life. (*Ibid.*, p. 60.)

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[15] Rudimentary spots on the third row of coverts—a fourth bar—were later found (1909); these are shown in plate 13.—ED.

The harmony of the direction of variation with the requirements of the conditions of life is the riddle to be solved. The degree of the adaptation which a part possesses itself determines the direction of variation of that part. (*Ibid.*, p. 54.)

When a determinant has assumed a certain variation-direction it will follow it up of itself, and selection can do nothing more than secure it a free course by setting aside variations in other directions by means of the elimination of those that exhibit them. (*Evolution Theory*, Vol. II, p. 123.)

Carl von Nägeli:

Between the theory of selection and that of direct causation, there is, apparently, only a little difference, since, according to the latter, the present condition of the organic world would likewise result from individual variation and elimination. But these two processes (selection and direct causation) differ fundamentally in their causal import. According to Darwin, variation is the germinating factor, selection the directing and regulating factor; according to my view, variation is at once both the germinating and the directing factor. According to Darwin, selection is indispensable; without it there could be no progression, and organisms would remain in the same condition as at the beginning. In my opinion, competition simply removes what is less capable of existence, but it is wholly without influence in bringing to pass anything more perfect or better adapted. (*Theorie der Abstammungslehre*, p. 285.)

The fortuitous or directionless variation of individuals would be conceivable, if it were conditioned by external influences (food, temperature, light, electricity, gravitation); for, as these causes obviously can not be brought into any definite relation to the more or less complex organization, they must effect sometimes a positive, sometimes a negative, step. If, however, the causes of variation are internal, in the constitution of the substance, then the matter stands otherwise. In this case the determinate organization of the substance must exercise a restricting influence upon its own variation; and this influence, as development begins at the lowest point, can only take effect in an upward direction. (*Abstammungslehre* p. 12.)

Individuals transmit to their offspring the tendency to be like themselves, but the offspring are not perfectly like the parents. The tendency to variation must therefore also be transmitted. A primordium, if all conditions are favorable, must be able to develop ever farther in a series of generations, as a capital enlarges to which interest is added annually; for each generation inherits from the preceding not only the possibility to realize the capital, but also the possibility to add the interest. (*Individuality in Nature*, 1856.)

Hugo de Vries:

According to the theory of mutation, species have not arisen through gradual selection continued for hundreds or thousands of years, but by steps, through sudden though small transmutations. In contrast with variations, which are changes advancing in a linear direction, the transformations to be called mutations diverge in new directions. They take place, then, so far as experience goes, without definite direction, *i.e.*, in various directions. (*Die Mutationstheorie*, Vol. I, p. 150.)

CHAPTER III.

THE PROBLEM OF THE ORIGIN OF SPECIES (CONTINUED).[1]

In the Australian crested pigeon (*Ocyphaps lophotes*) we find the homologues of the two bars of the rock-pigeon, the elemental spots having nearly the same form, but a much more brilliant color (pl. 8). Moreover, in front of the secondaries and the long coverts which bear these two bars, each row of the median and lesser coverts of the wing bears a narrow band of black (text-fig. 11), and these, nine to ten in number, gradually diminish in width until at the anterior end they become mere lines.

Between these bands and the two posterior bars there is the sharpest contrast in form as well as in color, the one being plain black and the other iridescent green and purple. Nevertheless, it can be shown that the two marks are serial homologues, two different forms, but one derived from the other. From the form and position of the bars, from the close resemblance they hold with the bars of the rock-pigeon, which resemblance is still closer in the juvenal feathers (pl. 8, fig. B, and text-fig. 10), and from the fact that bars among pigeons appear everywhere to be made up of like constituent elements, I feel certain of these homologues.

The longitudinal spots composing the bars are, then, safely identified with the so-called chequers in the wild rock-pigeon and its domestic descendants, and both have been derived from the same old mark, named the dark center, of the turtle-dove pattern.

There can be no doubt, therefore, as to which of the two marks found in the wing of the crested pigeon is the older element, and this relation furnishes the key to further orientation. The transformation of the longitudinal spots into the later transverse bands has already swept over a large portion of the field. Has the change been gradual and slow, or was it all accomplished suddenly, and in such a manner that no genetic continuity ever existed between the two marks? Were no intermediate steps or transitional phases required to pass from one extreme to the other? Was there no connection between them, and did one succeed the other as one picture replaces another by a turn of the kaleidoscope? Was there no predetermined direction of change manifest at any time before fulfilment? If orderless and directionless, then its appearance in the anterior rather than the posterior part of the wing, and its complete regularity in this part of the field, have no particular significance.

These questions answer themselves in a most decisive way in the present case. We shall see that the change is a progressive one, still moving on in a definite course, which is premarked by gradual transitional phases. If these bands and bars were not found in one and the same bird, but one in one bird, the other in another, no one could hesitate to pronounce them distinct specific characters, and the mutationist would undoubtedly claim at least one saltation between them. But nature has here put these characters in such relations, joined them by such indubitable connecting stages, and now repeats her steps in such gradual ways

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[1] This was written in 1905 as a continuation of the preceding address (Chapter II). It is here published for the first time.—Ed.

in successive plumages as to completely forestall the saltation hypothesis. Not only is the direction of the change hitherto discoverable, but its future course is predictable. In fact, a few allied species are found in which the change has been carried farther and in the direction plainly anticipated in the species we are considering. One species (*Lophophaps leucogaster*), also a crested pigeon and confined to Australia, shows this same variation carried through the whole row of long coverts (text-fig. 9), and already moving down the last row of feathers in the wing. Only 4 of the elongated metallic spots are left in this last row, while 5 to 7 are to be seen in *Ocyphaps*. The number falls to 3 in another species (*Lophophaps plumifera*).

For questions involving the vital principles of the prevailing theories of organic evolution, the usual difficulty is to find tests that are really conclusive. As the main question turns on the nature of the relation between two specifically distinct conditions of a character, one of which is known or conjectured to be a variation or a mutation from the other, it is generally assumed, as a matter of course, that
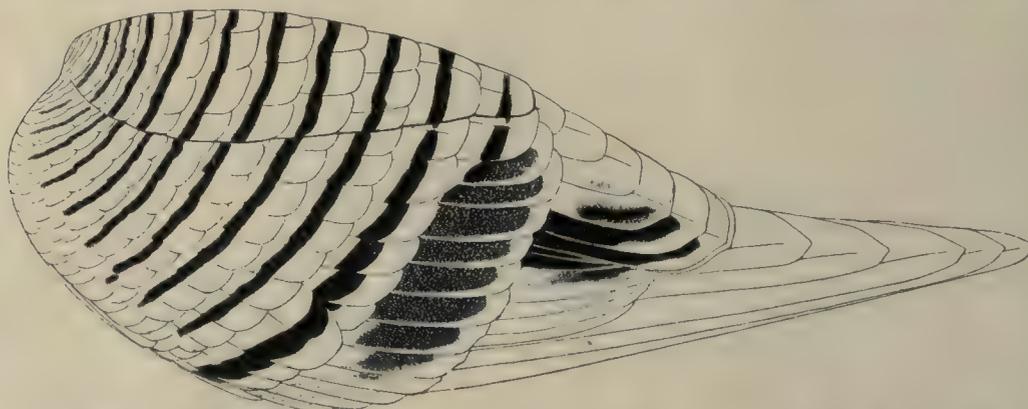
TEXT-FIGURE 11.—Adult female crested pigeon, *Ocyphaps lophotes*. × 0.8. Hayashi del., 1898. Spots and bars of left wing. Compare with juvenal crested (text-figure 10) and with examples of *Geopelia*.

we must go to two distinct but allied species for the two conditions to be compared. Variates are collected from both sides in order to see if they can be arranged in a single series running so continually from one species into the other that it will be impossible to find the dividing-line. Such series can be readily formed in numberless cases, but, as de Vries has so well shown, they supply no test. De Vries states:

> The overstepping of the limits occurs only in single and relatively rare individuals; the great majority belong to the mid-type of their species. If therefore we do not search for transitions, or if we do not seek merely to complete the series, but rather to make the measurements as numerous as possible, then the curves will come to light. Precisely that will come out which we noted in the consideration of the *Œnothera* flowers. The well-known multimodal curves studied by Bateson, Ludwig, and many other investigators will appear. Every modal summit corresponds to a group of individuals belonging together—a type, or an elementary species.
>
> The transition-forms are easily detected by their infrequency. It becomes evident at once that they only apparently obliterate the limits, and that they can not possibly bring into confusion the centers of greatest frequency. They prove nothing beyond the fact that neighboring curves on the same abscissa may overlap each other with their limbs.[2]

[2] Die Mutationstheorie, I, p. 307.

De Vries dwells at length and with effect on this "transgressive variability," as he terms it, endeavoring to make it abundantly clear that it is not really transitional, and hence can have no value as a support for natural selection.

The trouble with such series is that the sequence is always wholly artificial and of doubtful significance, as it holds only for the extremes of single characters. Moreover, if the extremes are taken from two distinct species, they can not of course be interpreted as transitions looking to the origin of a new species. Such prospective significance can not lie between two species already in separate existence.

It does not follow, however, that any sharp line of qualitative distinction is to be drawn between such variation and the variation (or mutation) which eventuates on new species. In statistical attire, individual variations may seem to be amenable to Quételet's law, and to merely oscillate about a center which sets limits to their excursions, but never follows them. Thus conceived, they may appear to be qualitatively different from variations that result in a shifting of the center of gravity to a new face of the polyhedron, to use the famous simile of Galton. If gathered at random and arranged arbitrarily, we may get as much chance out of them as we put into them. But is it safe to conclude that the mathematical theory of chance really covers all that is essential for a theory of such variations?

It is on this assumed distinction that the whole theory of mutation rests. If true, then natural selection is not directly concerned in the origin of new species. Neither is there any room in such work for definite and continuous variation advancing in one direction. No matter how small the difference between two allied species, that difference is absolute and unmediated. Neither natural nor artificial selection has any power to raise the species to a new specific level. The species may be improved within its sphere, but the limit of such improvement is soon reached, and retrogression to the original status is swift and inevitable if the species is left to shift for itself. In the same way all human endeavor and progress is tethered, with no possibility of escape through cumulative improvement. *Stare super antiquas vias* is the utmost hope of the species. As de Vries remarks:

A hard, a difficult, I should be inclined to say, a sad law. What is obtained with much trouble and care can be preserved only by as great care and trouble. And history is witness that this law is also true for mankind. Everywhere and always progress, but followed by regression as soon as the effort ceases.[3]

Conclusions of so far-reaching import, based upon twenty years of observational and experimental research that has not been equaled since Darwin's time, certainly challenge our deepest interest.

The distinction which threads this great work, binding it into one logical whole, is one not easily brought to a decisive test. The behavior of species in hybridization strongly suggests qualitative differences, such as are not apparent in ordinary individual variation. The usual aversion of one species for another, and the general infertility and instability of hybrids, seem to show that the behavior of species towards one another is influenced by something more deeply seated than habit.

Ordinary individual variability fluctuates in such an aimless way, and is so unstable even when nursed continually in a definite direction and for long periods,

[3] "Unity and Variability." Inaugural address, University of Amsterdam, Jan. 8, 1898. Also, The University Chronicle, Berkeley, Cal., Sept. 1898.

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that it seems to stand in sharp contrast with changes of a specific nature, which, according to de Vries, are fixed on their first appearance.

In biometric dress, individual variations present themselves as oscillations to and fro in a linear direction, while mutations appear to diverge in various directions. On the one side, every advance is sooner or later lost in regression; on the other, regression never appears. Variability seems to rise and fall with the food-supply, while mutation is not so affected.

Mutation appears with the suddenness and completeness of a chemical substitution, and it can no more pass into a new specific form through flowing variation than could a crystal be slowly transformed into another of a totally different nature. In such respects, variability is represented as always standing at the opposite pole; cumulative to a degree, but without permanency; plus or minus, but never qualitative.

The mutation theory puts the origin of species beyond the reach of investigation, shrouding it in the utter darkness of premutation stages. The idea of fixity as an essential characteristic of species bars the way to accounting for the origin of the most remarkable phenomena of the organic world, namely, adaptations. The characterization of variability as linear is too superficial to be of diagnostic value.

If fertility is a thing of all degrees, and that, too, within the limits of a single species, are not the qualitative distinctions inferred therefrom likewise things of degrees and variable within the same limits? If fertility may vary individually, as is certain, is there any reason to doubt that its physical bases are equally variable from individual to individual? But fertility varies also according to age and conditions of food, temperature, etc.[4] How then can qualitative differentiations be an infallible criterion of species?

But discussion of such questions is somewhat aside the main purpose here. It is more profitable to take the fundamental issue to the test of facts. This issue is found in the denial of transitional stages in the evolution of species. If indubitable transitional stages between indubitable specific characters can be found, even in a single case, the mutation theory falls. To catch a character in the very act of giving birth to a new character, through gradual transitional steps, to be able to see the genetic continuity before it is broken for the last time, that is the kind of evidence most to be desired. Such evidence can only be given in a natural series, which is presented in a field completely oriented. The extremes of the series must be two characters specifically distinct, but not yet completely separated. The transitional stages must lie between these extremes, and lead in a definite direction and continuously from the later into the older character. Such transitions will gradually descend in the same direction; i.e., they will depart less and less from the earlier mark as they approach and pass into it. Under such conditions chance is not the law, and probability curves lose their enchantment. All the bearings are given by direct inspection, and no dispute can arise as to the transitional nature of the connecting stages.

All these crucial advantages are placed in our hands in the species to be examined, and they are all the more decisive in that the transitional phases are to be seen in several consecutive stages of evolution in the young and adult birds.

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[4] The data which establish these facts are given in Vol. II.—ED.

The orientation of the field is given in all essentials by simple inspection of the wing, and hence I need not here go into the genealogy and the present status of the older character, beyond the incidental mention of one or two facts for the sake of perspective.

The elemental units of the two color-characters take, of course, the serial order of the feathers bearing them, and so fall in transverse rows. The sequence in each row is, again, that of the feathers, which run above downward. The sequence of the rows, as wholes, runs from before backward, and this antero-posterior sequence coincides, as will be seen, with the direction of the transformation of the color-pattern. As this direction is that of axial development in the embryo, it seems probable that it is determined by the same general laws in both cases.

The pathway of transformation to be followed in the future is already pre-delineated, in part, by transitional phases, and hence the nature and position of the goal may be forecast.

With the orientation indicated in a preliminary way, we may turn to the examination of the several plumage stages. The simplest stage for this species (Ocyphaps lophotes) is to be seen in the first or juvenal feathers. It is here that earlier ancestral features have not been entirely obliterated; and for the sake of a better perspective these may be briefly called to mind without citing evidences to be dealt with elsewhere. The ancestral pattern is that of the typical turtle-doves (Turtur turtur, pl. 2, Vol. II; wing, pl. 22, Vol. I) and T. orientalis (pl. 1, Vol. II, and text-fig. 3, this volume). It is everywhere among pigeons, as among many other birds, the point of departure in the evolution of color-patterns. The common element of this uniformly mottled pattern consists of a black spot occupying the center of the feather and a light border at the edge of the feather. The dark center has become pale in the young crested pigeon, and is indicated only by the dotted area in text-figure 10. The light edge is everywhere present, but it is also paler than the same part in the ancestral pattern.

To this pattern two quite distinct new patterns have here been superadded. One of these consists of longitudinal black spots, or chequers, placed on the two posterior rows of feathers. The other consists of transverse stripes or bands, seen in all the anterior rows. In these longitudinal spots and transverse bands we have the two distinct characters to which we have looked forward. They are so different that at first they appear to be quite independent of each other.

The two rows of chequer-like spots will readily be recognized as homologues of the two bars seen in rock-pigeons. Such spots are widely distributed among both wild and tame species, and although they have many specific forms they have everywhere the same origin from the dark central spots of the turtle-dove pattern. There can, then, be no doubt as to the specific value of these spots. That the bands are equally entitled to rank as specific marks will not, I believe, be questioned. Much smaller differences would pass as specific, if the marks stood alone, each in a species by itself.

If one of two marks contrasting as sharply as these do can be transformed gradually into the other, it is of no vital importance how we rank them. The proof of transitional variation remains the same. It would be but a specious quibble to maintain that two such different characters can not be regarded as specifically distinct because they stand side by side in the same species. It can be seen readily

that one of these characters differentiates from the other; and how far would such differentiation have to advance before becoming specific? If carried to the extent of turning the two bars into bands, would the specific rank of the bands then be indisputable? If so, the whole point is conceded, for the transforming process advances to the end by transitional stages, as is plainly to be seen in the few species that have reached a higher level than *Ocyphaps*.

Glancing now at the pattern as a whole, we notice first of all that the two characters are separately distributed, each in a field of its own. As the rows of feathers succeed one another in regular order, without a break, how does it happen that just two rows have been reserved for the older character, while all the others are monopolized by the later character? There must be some definitely directed process of transformation to account for such relations. Is it a process that operates progressively and with continuity, or is every advance a clean-cut jump? But a linear series of jumps running in one direction would leave no very certain distinction between mutation and orthogenetic variation. In the fore part of the wing the bands are very narrow and pale, and they completely vanish a little behind the front edge of the wing. As we pass backwards, they become wider from row to row, the last band being about twice as wide as the one just before it, and about one-third as wide as the bar that follows it. All this looks as if the transformation had moved along quite gradually, following the law of reduction of pigment, which I have demonstrated in other pigeons. If the nature and direction of the variation are what they seem to be, then the regional distribution of the two characters and the gradual increase of the width of the bands as they run backwards towards the bars begin to clear up.[5]

However, before all the features and relations in the pattern and the nature of the variation can become fully intelligible, the mode of origin of the bands must be precisely ascertained. In this matter we come squarely to the main issue: Is it mutation or transitional variation? At first sight the juvenal pattern suggests mutation. Although the bands vary by increasing width, the difference between the last band and the bar following it is manifestly greater than is the difference between any two successive bands. But observe that in the upper part of the bar the bridge of transitions is given in three spots. It is here that we see just how the longitudinal elements of the bar are converted into the transverse elements of the bands. This is done by reducing the length of the spot, chiefly from the proximal end, until nothing remains but a narrow band-like remnant, with its longer axis at right angles to that of the original spot.

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[5] It would be very interesting to know whether the process is one of continuous development or one that moves mutation-wise, jumping all at once from the juvenal to the adolescent stage. As feathers once formed are fixed structures, we can not of course expect to see one of these long spots reduced in length from day to day, and thus gradually turned into a transverse band. We can, however, demonstrate experimentally that the advance from the juvenal to the adolescent pattern is a progressive development that continues for at least several months and possibly for a year or more. Successive plumages and color-patterns seem like discontinuous phenomena, because they measure off at regular intervals the results of work that is done behind the scenes. The juvenal feathers show only how far the transforming process had advanced at the end of the first week or ten days of life. The next plumage reveals the progress made from that time to the time of the first molt. The proof that the process moves on gradually from one plumage stage to the next is easily obtained by plucking a feather or two in the region of transitional change at any time or times before the first molt. In this way we may make room for new feathers to appear at any desired ages intermediate between the juvenal and adolescent periods. In these new feathers we shall get the juvenal pattern more or less modified in the direction of the adolescent according to the ages represented by them. I have not made this test in the crested pigeon, but have made it in the young of *Geopelia cuneata* with such perfect success (see Chapter X) that I feel safe in assuming that similar results would follow the test in other cases.

PLATE 14
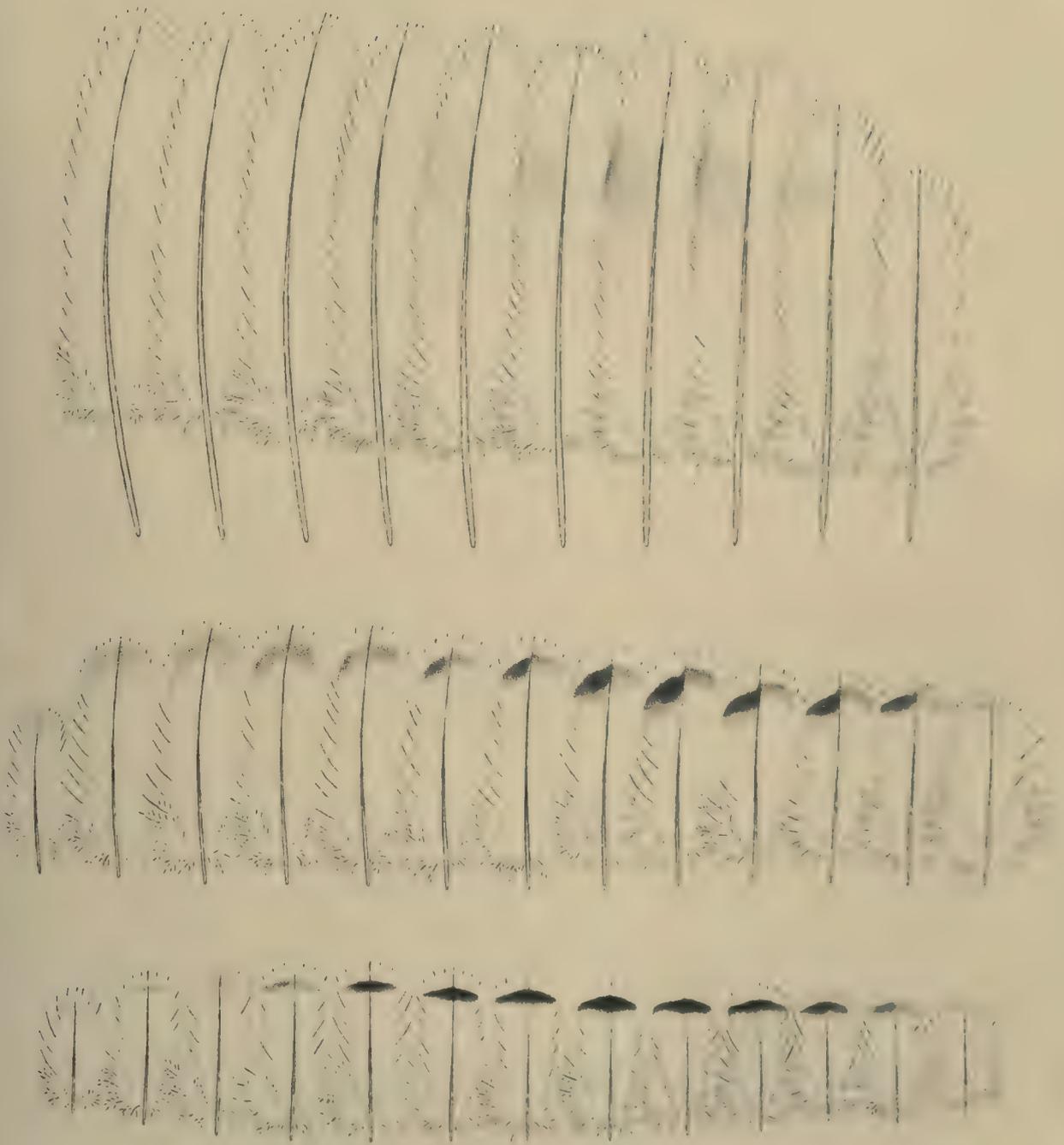
Juvenal female crested pigeon, *Ocyphaps lophotes*, age 32 days. Toda del., Aug. 1905. Last (posterior) three rows of feathers of left wing.

PLATE 15
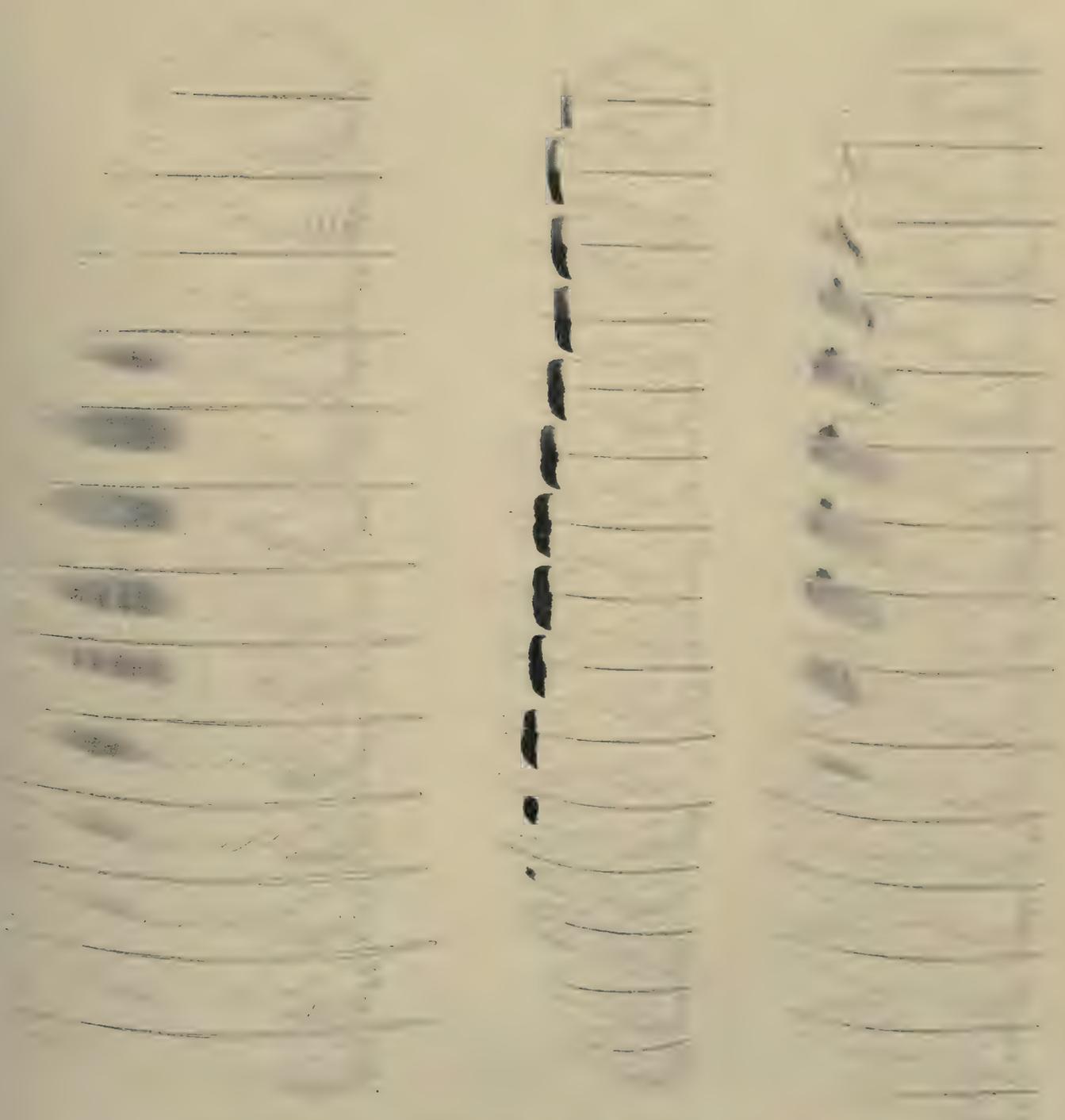
Adult female crested pigeon, *Ocyphaps lophotes*. Toda del., July 1906. Last three rows of feathers of left wing. Compare with juvenal female and three stages of male. The "fundamental bars" are to be seen in all these feathers.

This simple mode of transformation is about three-fourths completed in the upper feather of the row, about half completed in the second feather, and only just begun in the third feather. If the figure (text-fig. 10) tells the truth, there can be no mistake about the conclusion. The direction and the manner of change are what we might have anticipated (compare also wing of adult female, text-figure 11).

But is not this "bridge" a thing of chance that may appear once in a thousand times, more or less? And may we not find it next time in another place and telling a different story? Even the upper spot here is not quite reduced to a typical band, and may it not be a mistake to identify it as a stage of transitional significance? For certainty on this point we require a longer series, with the steps ending in a finished band. We should find the series invariably in the same place and running always in the same direction, in both sexes and at all ages. All these desiderata are amply fulfilled.

The color-pattern does not reach full development in the first plumage and the male carries the development somewhat farther than the female. The female presents two and the male presents three consecutive stages in this development. Although the stages run nearly parallel in the two sexes, the female not only has one stage less than the male, but her two stages represent somewhat lower grades than the corresponding stages of the male. Hence we have the transitional series in five stages, which ascend in the following order: (1) juvenal female (pl. 14); (2) juvenal male (text-fig. 10); (3) adult female (pl. 15); (4) adolescent male (first-row coverts compared in pl. 17); (5) adult male (pl. 16).[6]

Two different sequences are here to be distinguished. One of these falls within a single row of feathers in the individual plumage and is represented in the series of transitional steps leading from the new into the old character. Its closeness and length vary considerably from sex to sex and according to age, but only slightly in different individuals of the same sex and age. The second sequence runs parallel with the development of the bird, from the stage of the first plumage to that of full maturity. It is not a sequence of transitions, as presented in a single row of feathers of a single plumage, but a sequence of the stages of the same transitional series, as presented in successive plumages. The accompanying diagram (text-fig. 12) will illustrate the relations of the two sequences in the anterior bar in the three plumages of the male.

The single feather with its transitional mark is the unit of the first sequence; the transitional series as a whole is the unit of the second sequence. The first sequence has continuity serially stamped upon it by nature; the second sequence

[6] Before we go on with the examination of these stages we must take note of the new character which invades the field occupied by them. This new character is a brilliant metallic luster—a bronzy green in the long coverts, where we meet the transitional phases, and a metallic purple in the secondaries or last row of wing feathers. This iridescence, evidently one of the latest acquisitions of the species, is increasing, and spreads from the tip of the feather inward, in a direction precisely opposite to that of pigment reduction. It appears first of all in the field of the black spot, but spreads inward beyond the limits of the spot. The outline of the spot disappears in the full blaze of iridescence, but it may be readily brought into view by turning the feather until metallic reflections no longer reach the eye. This can be done most easily with feathers mounted in serial order on a card-board. Held at the proper angle, the outlines of the spots become clear, and we have before us a full series of transitional phases. The sequence of stages is likewise a continuous whole in which the stages are merely favored terms in a flowing series of intergrades. Iridescence thus appears to be a phenomenon tending to elevate the spots and bring them within the sphere of utility. It seems not only to put a check upon the reduction of pigment, but also to actually turn the tide in the opposite direction, for the reduction in this region is not carried so far in the old as in the young male and the female, as we shall presently see. As the acquisition of metallic brilliancy is accompanied by an exceptional love of display in the male, the chief directing factor in its development may well be natural selection.

is broken into stages that represent results in the progress of differential develop-
ment which are unfolded at successive epochs. The intervals between the stages
give no outward indications of steps connecting them. Are we to conclude that
this sequence is one of discontinuities?

Although the transitional series linking two characters in one and the same
plumage is the main theme in this paper, it will not be without interest to make
clear that mutation has just as little to do with the second sequence as with the
first. But first let us finish the examination of the stages individually, as this is
necessary to complete the story of the transitions actually realized in each of them.

The juvenal stage of the male, as we have seen, presents three transitional steps
or intergrades between the two characters. I have not thus far examined the
corresponding stage of the female, but it is safe to assume that the contrast between
the last band and the first bar is less than in the male.

The third stage in the order above named is that of the adult female (pl. 17,
third row). In the uppermost of the long coverts we find a weak transverse band
on the lower web. In the second feather we see just a shadow of a band on the upper
web, and on the lower web a rather dim spot, in a half-way condition between the
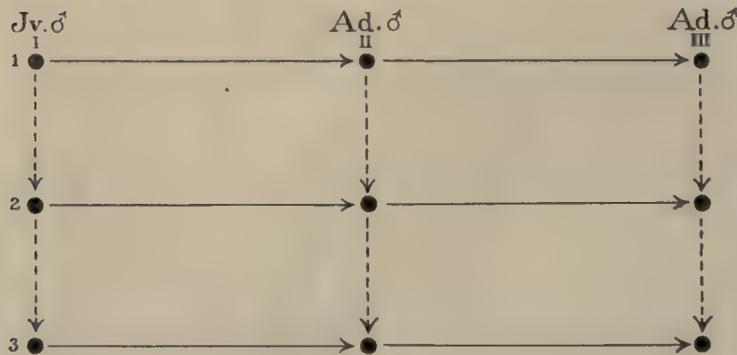
TEXT-FIGURE 12.

Diagram to illustrate pattern sequence in
the anterior wing-bar of male *Ocyphaps*.

1, 2, 3 represent 3 feathers of the an-
terior bar. I, II, III represent 3 plumage
stages of the bar in the male—juvenal,
adolescent, and adult. 1–3 show the first
or feather sequence of transitions. I–III
show the second or plumage sequence of
the transition series.

two characters. In the third feather the longitudinal spot comes to fuller develop-
ment on the lower web. If the feather be turned just enough to cause the irides-
cence to vanish, we see more plainly the shape of the spot and notice in its slanting
proximal border a first step in the transformation to the band condition. In the
next three feathers the spot elongates somewhat, but shows no sign of transforma-
tion. The bronzy iridescence is strongest in these mid-feathers of the row and
vanishes wholly on the tenth feather.

In the fourth stage, seen in the adolescent male (pl. 17, first row), the transi-
tional steps are extended through the whole row of spots, if we accept the last
trace of a spot seen in the ninth feather. The series then consists of no less than
eight steps in a single row of nine spots. No one can look at this series and fail to
see that each step is a demonstration of transition, and that the series, taken as a
whole, puts the genetic continuity of the two characters beyond a doubt. Here
nature, as if to forestall the indirections of biometric gymnastics, draws a straight
line between her two extremes, thus disclosing in a small number of steps a path-
way of variation essentially different from anything within the purview of the
large-number curve.

PLATE 16
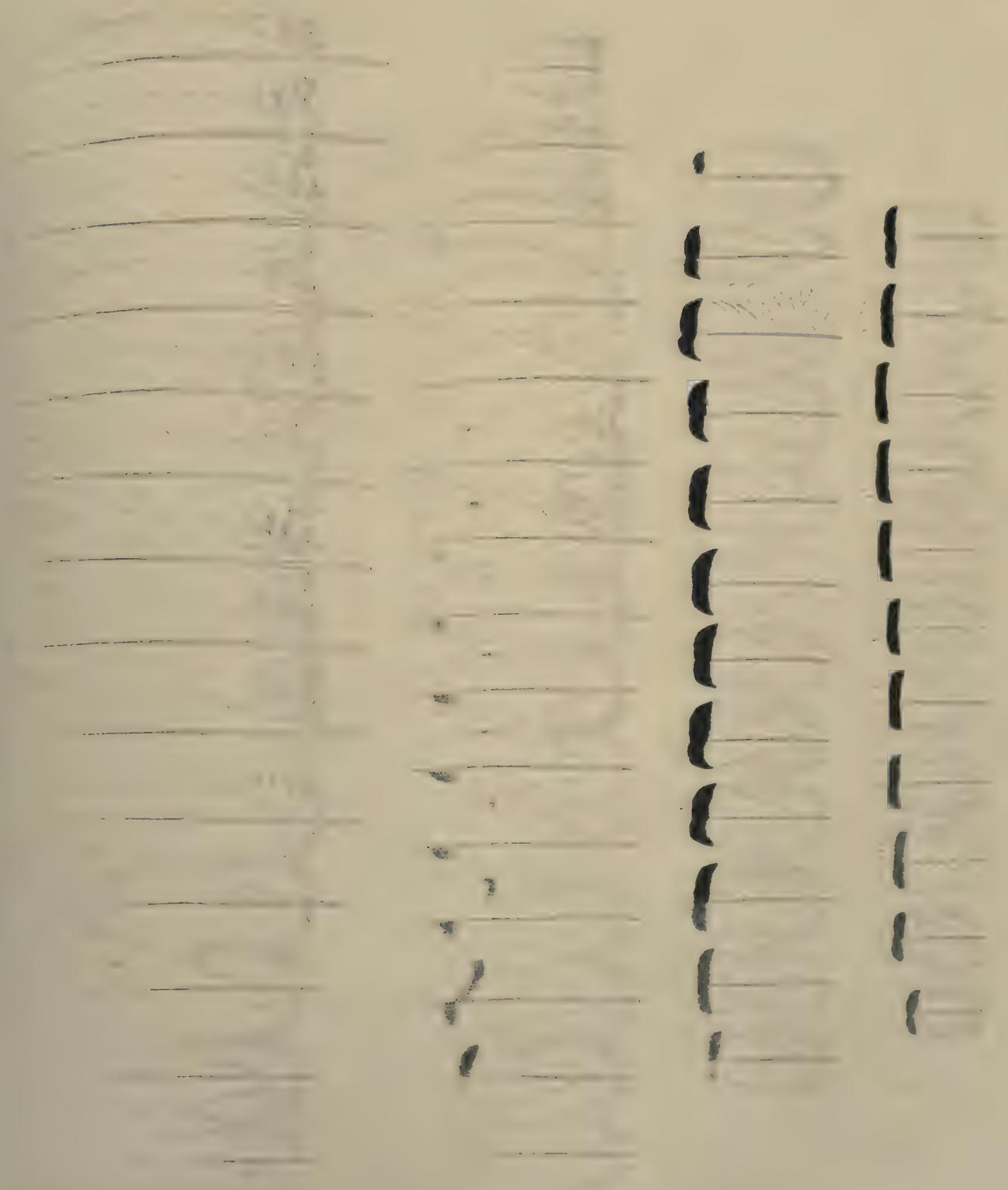
Adult male crested pigeon, *Ocyphaps lophotes*.   × 0.7.   Toda del., May 1906.   Last (posterior)
four rows of feathers of right wing.   The extent of iridescence is marked by dotted circles;
the presence and depth of pigment by stippling of various degrees.

Let us follow this series through, step by step, beginning with the uppermost feather of the row. In this feather we find a well-defined half-element of a band crossing the lower web a little obliquely. On the upper web only a mere shadow of a counter half-element is discernible; and this is not discoverable in the juvenal stage and is only slightly strengthened in the adult stage.

The half-element of the lower web deserves closer examination, as it represents a fully finished transformation. It has an even width of 1.5 mm. and sets off a light apical margin of the feather 5 mm. wide. In so far it comes fully up to the type. It falls a trifle short only in one particular, namely, its inclination from a transverse line is about 23°, which exceeds by at least 4° or 5° the slant of any corresponding part in front of it. Slight as this deviation may appear, it is significant in the last step of a series that approaches the type gradually in this as well as in all other respects.

This step is led up to, not only through the bar, at the upper limit of which it stands, but also through all the bands in front of it. To understand its peculiarity, we must therefore approach it from both directions—*i.e.*, from the typical band as well as from the typical element of the bar.

On the fore part of the wing, where the type is best realized, the two half-elements in each feather coalesce at the shaft-line and together form one straight mark crossing the feather at right angles. This rectilinear form prevails back to the last two or three bands, although a few elements may be found farther forward with a slight curvature; and in such cases the convex side of the element looks forward, and a minute notch is usually seen at the middle, making evident the double nature of the element.

As we pass backwards, the width of the bands increases very gradually, rising from about 0.5 to 3 or 4 mm. In one out of a dozen cases examined a maximal width of 5 mm. was reached in the fifth feather of the last row. It is in this row that we get the widest elements, the strongest indications of their double nature, and at the same time an inclination in the half-elements that almost reaches the condition seen at the upper extremity of the bar. But these modifications in the band are so small that, viewed as a whole, there is nothing, at first sight, to indicate departure from the type. In the closed wing only the lower web of each feather is visible, the upper web being covered always by the overlapping lower web of the next feather above. The whole band, as thus presented, consists only of the lower half-elements, which flow into each other with such regularity as to mask the slight deviations from the type. For a clear view of all parts of the band the feathers must be plucked and separately mounted in their proper sequence (as in pls. 14 to 17). Thus exposed, it will be seen that the width, shape, inequalities, etc., although considerable, are yet so closely graded that the conditions in any one feather flow into those of the next above or below, so that the series may be read in either direction with equal facility.

It is in the two upper feathers that the conditions approach more nearly those of the typical band, and it is here that we again meet with a slight inclination of the half-elements in the same sense, though not quite to the same degree as we noted in the half-element at the upper end of the bar. This inclination runs through the whole series and is most strongly expressed in the wider elements, which have a crescentic shape, with the horns following the outline of the feather and so curv-

ing forward. At the junction of the two halves of the crescent we have a broad re-entrant angle on the distal side, which vanishes as we run up to the series and sharpens into a minute notch as we go in the opposite direction. Throughout this row the lower half of the crescent is a little wider than the upper half, and this extra width (0.5 to 1 mm.) is added evenly to one side, namely, the proximal concave side. The result is that the lower half preserves its symmetry with the upper half on the distal side, while on the proximal side its curve is retained, but advanced by 0.5 to 1 mm. beyond that of the upper half, thus producing a sharp salient angle in the shaft-line, opposite the re-entrant angle of the distal side. The lower half differs also from the upper in having a slightly stronger inclination. This difference is quite small, but once recognized in this band it may readily be detected in lesser and vanishing degrees in the preceding band.

Now, every one of the peculiarities here pointed out—the greater width of the posterior band and of the lower half-elements in this band, the crescentic form of the elements, the distal notch and the proximal angle, the inclination of the half-elements increasing with their width—all these peculiarities are so many transitional phenomena, passing phases of a transformation still in progress. The process, although always flowing onward in one direction, advances more rapidly in the upper than in the lower part of the field, and hence the crest of the wave, if such a metaphor be allowable, sweeps over the feathers of each row in regular sequence from above downward. This accounts for the differences in width between the upper and lower half-elements, for the approximations to the typical band being closer in the upper than in the lower parts of the rows, for the obliquity of the band elements, and for the gradual rectification of the latter as the transformation comes nearer and nearer to completion.[7]

Having seen that the first step in the anterior bar has peculiarities which are partially intelligible when approached through the bands that lie in front of it, it remains to examine its relations in the bar itself.

In the second feather we find (pl. 17, first row), in the lower web, an oblique mark, strongly band-like in appearance, but in several respects falling short of the type to a slightly greater degree than the corresponding mark in the first feather. Its inclination is 29°, 6° greater than that of the first mark; its distance from the apex of the feather is 2 mm. greater; and its outline is not so sharply defined, the pigment spreading a little on either side. These differences, though small, are not to be credited to chance, for they are never reversed or wiped out in fluctuations from individual to individual. In the upper web is to be seen just a shadowy indication of the counter-mark, barely stronger than in the first feather. The proximal edge of this upper mark falls 2 mm. nearer the tip of the feather than the lower mark, and thus we get a lack of symmetry of the same nature but more

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[7] This change from an oblique to a transverse position, in which the rotation of the element follows the direction of the hands of a watch when we face the right wing, or the contrary direction when we face the left wing, is a phenomenon that would repay further study. Is the rotation towards a position of more perfect equilibrium, depending upon the ontogenetic distribution of pigment in a symmetrical structure? Why, then, in the fore part of the wing, is the rotation carried beyond the vertical or transverse line, so that the half-elements lean slightly forward? And why in so many birds, with essentially the same symmetry of feather, are the half-elements permanently inclined so as to form V-shaped figures pointing sometimes backward, sometimes forward? These are only a few of the great multitude of forms which take their departure from bars and bands. Feather structure may have much to do with the primary phenomenon of transverse bands; but certainly it can not be responsible for ornamental figures in which many feathers may coöperate, contributing very unlike parts to a single design, with a symmetry overriding that of the single feathers, and following lines that regard only the form of the bird as a whole.

PLATE 17
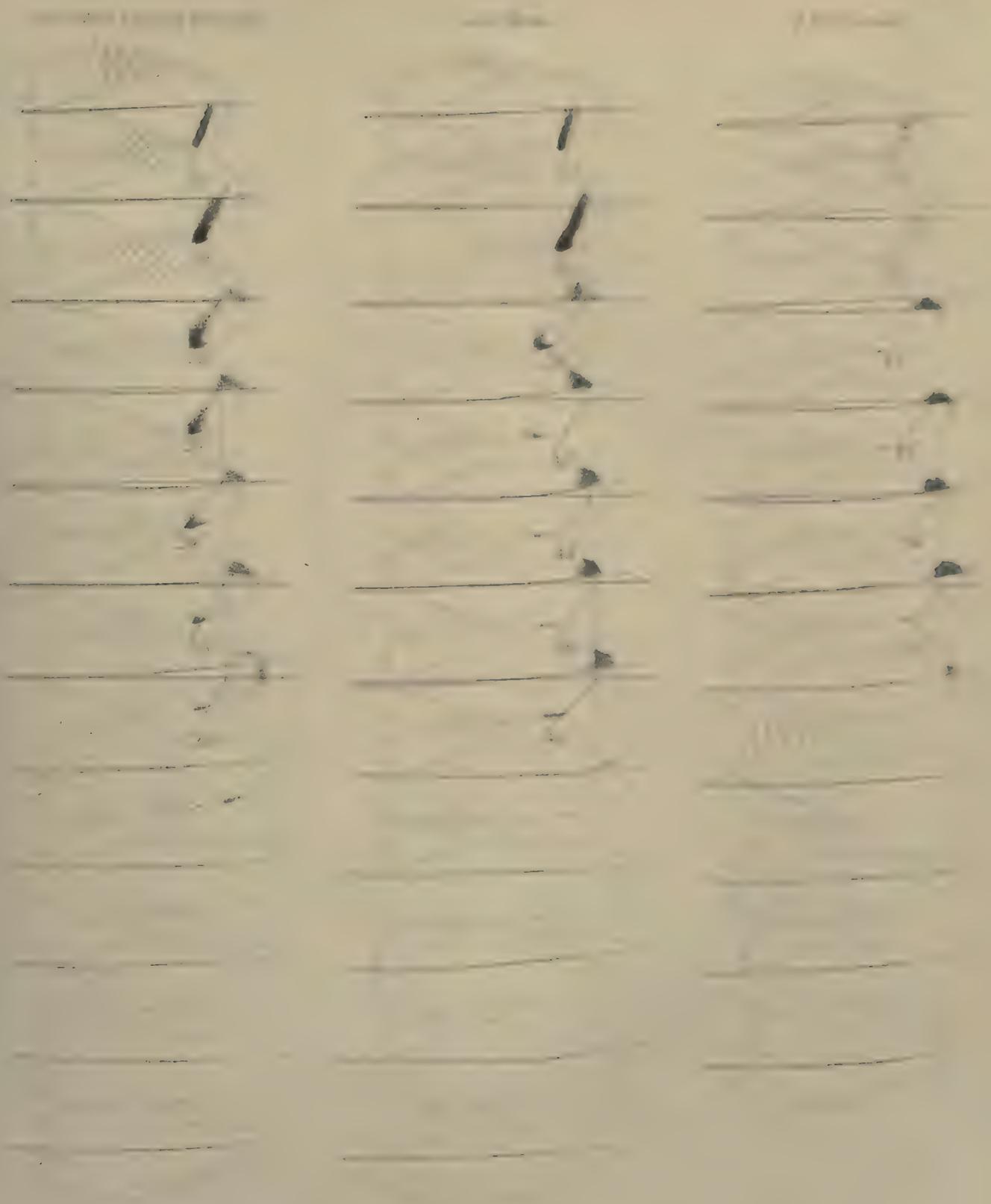
The longer left wing-coverts of adolescent (second plumage) male, adult male, and adult female crested pigeons. × 0.9. Toda del., Apr. 1906. For comparison, feather by feather, in the three forms. Depth of pigment and extent of iridescence indicated as in pl. 16. The blue color gives the angles formed by the proximal border of the band-elements and the spots with the feather shaft (see text).

strongly expressed than that before described in the crescentic marks of the posterior band. On the distal side of the lower mark, or half-element, there is a very thin sprinkling of dark pigment, the meaning of which becomes clear in the next feather below. There is also a very weak iridescence overlying this mark and extending over the surface to near the apex of the feather.

In the third feather the band-character falls still farther below the type, so far, in fact, that had we only this one feather to look at its identification would be somewhat doubtful. Close comparison with the first and second feathers, however, is all that is required to make the conditions here intelligible and to let us into their full transitional significance. It is in this feather that the two characters—the bar and the band—are presented in nearly even balance, the former being near the mid-stage of decline, the latter at about the same stage of its rise. What appeals most to our interest here is the union of the two characters within the field of the older one, the individuality of the latter being remolded directly into that of the new character. We can not, of course, see the remolding, but only the several steps in their natural order. Let us look at the picture in this feather, then, as a delineation of a single step in the series—as an image of a character caught by the feather at a moment when the transmutation was in actual progress.

We noticed that the inclination and width of the band-character and the distance from the tip increased in passing from the first to the second feather, while its sharpness of outline diminished, especially on the distal side, where a sprinkling of pigment appeared, spreading away to near the edge of the feather. These peculiarities are increased or diminished in the same respective senses in passing to the third feather. The sprinkling of pigment is strengthened to a degree that enables us to recognize in the picture as a whole the form of the longitudinal spot seen in the corresponding juvenal feather. In short, we see here our two characters blended into one; or, more accurately speaking, the new band-character arises from the proximal border of the original spot, or bar-character, and hence takes its inclination, outline, and distance from the tip of the feather directly from the spot itself.

The shape of the spot as a whole is given in plate 17 (first row). It is approximately fusiform and is set obliquely just within the white crescentic edge of the feather. Its long axis is 12 mm. and its short axis 6 mm. I's distal side is strongly rounded; the proximal side is but slightly curved and inclines 36°. In the upper web a small triangular area of pigment is seen, its longer side (4.5 mm.) resting on the shaft. This is a remnant (not a rudiment) of a spot; the proximal border of which shows an obscure band-like differentiation (compare adult condition).

The proximal border of the spot in the lower web represents the band-character rising into plain view in its lower third, but attaining only a shadowy outline in the upper part, where the pigment is sprinkled in only a little more closely than elsewhere in the spot. This border has a slight curvature, which becomes a little stronger towards the lateral edge of the feather, finally makes an abrupt bend, and runs out into a small and pointed extension, thus giving a rather sharp boundary to this angle of the spot. The extension reaches only 1.5 mm. beyond the border proper, and is therefore quite inconspicuous. It is constant, however, and becomes a convenient landmark for locating the band-character in the first and more obscure stages of its appearance. It sinks almost out of sight in the second feather, measuring here only 0.5 mm., and no trace of it is left in the first feather.

In the fourth feather we find at first glance no striking change in the general form and extent of the two spots. It is only by close inspection of the minute features that we discover that the trend of cumulative changes is still in the same direction, and that as the band fails more and more of its highest development, its individuality becomes less and less distinct from that of the bar. Both spots are a little more strongly and evenly pigmented than in the third feather. The proximal borders are less band-like, but fall only in fine degrees below the conditions seen in the third feather.

In the upper spot there is still a suggestion of the band in the slight preponderance of pigment in the proximal part of the triangle. There is also a very slight incurving of the upper side of the spot, corresponding to the deeper curve seen at the same place in the third feather.

In the lower spot the condition of the proximal border is particularly instructive. Although the spot as a whole is a little more strongly pigmented than in the third feather, the border takes a step in just the opposite direction; that is, it sinks plainly below its height in the third feather. The two characters are no longer in equipoise; the scales turn in favor of the spot.

Let us compare closely, in order to see with what nicety the transitional degrees are marked. As shown in the figure, the loss of pigment is so nearly even for the entire proximal border that it still looks as if it were the same thing before described, except as weakened in quantity of pigment. As before, the pigment is densest at the lower end, becoming gradually thinner towards the shaft, until in the upper third its individuality, if it have any here, is quite beyond recognition. The conditions in the two spots have changed so very little that we have no difficulty in seeing just where the pigment should lie if present; but I find that no border is here marked off; band and bar are one in this third.

The bend of the border around the lower angle of the spot and its pointed extension are still quite distinct, though not so sharp in outline as before. The distance of the bend from the tip of the feather is here 1.7 mm. greater than in the third feather.

In the feathers thus far examined, the inclination of the border and the distance of the bend from the tip of the feather run as shown in the accompanying table. From these measurements it will be seen that the distance from the tip is closely correlated with the inclination of the proximal side of the spot, every 1 mm. in one column corresponding to about 2° in the other. As we descend the series, the band gradually loses its transverse position and sinks out of sight in the proximal border of the enlarging spot. As we ascend, relations are reversed; the spot is reduced in length, its proximal border becomes less and less inclined and more and more band-like. In one direction the band merges in, in the other it emerges from, the bar. Evolution is here linear, and hence it can have but one direction.

Feather.	Inclination.[8]	Distance.
	°	mm.
First........	11	6
Second.....	18	10
Third......	27	13.5
Fourth.....	30	15.2

[8] The figures for *inclination* given here do not agree, except in the sense of an orderly increase, with those given in connection with plate 17.—ED.

CHAPTER IV.

THE ORIGIN AND RELATIONSHIPS OF THE ROCK-PIGEONS AS REVEALED IN THEIR COLOR-PATTERN.[1]

The wild rock-pigeons, universally regarded as the ancestral stock of all our domestic pigeons, exhibit two very distinct color-patterns, one consisting of black *chequers* uniformly distributed to the feathers of the wing and the back, the other consisting of two black wing-bars on a slate-gray ground. The latter was regarded by Darwin as the typical wing-pattern for *Columba livia;* the former was supposed to be a variation arising therefrom, of frequent occurrence but of no importance.

Just the contrary is true; the *chequered* pigeon represents the more ancient type, from which the two-barred type has been derived. From this standpoint the *chequered* type deserves the distinction of the specific name, *Columba affinis,* once accorded to it but subsequently abandoned by Mr. Blyth. *Columba livia* could well be reserved for the derived type.

The direction of evolution in pattern in the rock-pigeons has been from a condition of relative uniformity to one of regional differentiation. That seems reasonable enough, and yet Darwin's view to the contrary rested on plausible grounds. Indeed, the chequered wing might, at first sight, appear to be a departure from the more to the less uniform condition; and this would be true with respect to the gray surface, considered as a plain unadorned area, that originally included the entire wing. The appearance of two bars would be the first break in uniformity, and the extension of chequers, like those composing the bars, to all the coverts, might seem like turning uniformity into variformity. On the other hand, if we attend to the black chequers rather than to the gray ground, it is at once apparent that the chequered wing presents a condition of fairly uniform distribution of like spots, while the two-barred wing represents a long departure in the direction of regional differentiation.

It is quite natural to suppose that an unspotted stage preceded the spotted one, but general theory of this kind is often misleading. Uniformity in color is not always proof of simplicity. Some of the more highly developed colors, as green and blue, may be quite as uniform as the gray of the pigeon's wing. Even iridescence may sometimes extend more or less evenly to large surfaces and at times characterize the plumage as a whole. The gray of the pigeon is certainly not to be regarded as a primitive ancestral color. Its evolution has not been worked out, but it is known that it is not a pure pigmental color. It is an effect produced by the withdrawal of brown pigment from the superficial parts of the feather, and by a segmental arrangement of the pigment granules in the barbules (Häcker).

Gray in the pigeon is undoubtedly a relatively late acquisition, brown representing the simpler and more primitive color. Evidence of this is seen in the

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[1] An address read November 18, 1903, to the National Academy of Sciences at the University of Chicago. The slight amount of repetition of statements made in Chapter II will probably not prove a disadvantage to the reader. Two pages of a manuscript (Z 10), written in 1907, have been added to amplify the briefer statements of the earlier address. A detailed comparison of the individual spots or chequers in *Columba livia* and *Columba affinis* has been included. The address of 1903 was also delivered at Woods Hole, and a one-page abstract of it published in the Biological Bulletin, Volume VI (1904), p. 307. That abstract is used as a partial summary of this chapter. — ED.

prevalence of brown among the wild species of pigeons, and, further, in the fact that in all species with a gray plumage in the adult state the juvenal feathers are always suffused with brown.

The first ancestors of the pigeons, or of the pigeons together with all other birds, may have been of a single unspotted[2] brown color. But as color-patterns are found quite generally distributed among the lower orders of animals, it is hardly probable that the avian branch came into existence entirely unprepared for the decorative supremacy it was destined to enjoy.

Be this as it may, it can be made very clear that the rock-pigeons are not those first ancestors, nor yet their nearest relatives among the pigeons. The rock-pigeons represent a terminal twig in the avian genealogical tree. The main stem of the pigeon branch, if I read correctly the testimony of color-patterns, is represented most nearly by the turtle-doves (*Turtur orientalis* and *T. turtur*) of the Old World. The original turtle-dove pattern, in which all or most of the feathers were similarly differentiated into a dark center and a light edge, seems to have been a very general if not a universal avian pattern. This pattern certainly preceded the chequered type of the rock-pigeon (*Columba affinis*), and it is possible still to find connecting types—types in which the turtle pattern coexists with the chequered pattern— the latter coming in to replace or supersede the former. Examples are to be seen in the bronze-winged pigeon (*Phaps chalcoptera*) of Australia, the Florida ground-dove (*Chamæpelia passerina*), and some others. The genetic connections between these two patterns belonging to two distinct families have been considered in Chapter II.

The main problem to be dealt with in this paper concerns the closer relation of two patterns differing at most only in specific rank. That the two patterns are connected by direct lineal derivation is not questioned. But what is the direction and what the mode of derivation? The problem is only one of thousands of similar problems; but if it admits of a decisive solution it will furnish answers to a few questions of leading interest at the present time.

The wing-bars of the rock-pigeon represent a specific character with a history that can be clearly read in both the wild and the domesticated forms. The chief transitional phases are to be seen in almost any flock of mixed breeds. The direction of evolution can be determined in two ways: (1) by comparison of individuals, young and old, in each of the two species and in domestic races; and (2) by comparison of the different wild species that are marked with spots and bars in various stages of evolution or decline. The conclusions arrived at through comparative observation can then be tested by experiments in breeding, cross-breeding, etc.

In tracing the origin and genesis of a single character we meet the leading questions in the evolution of species. First and foremost, the question as to the nature of the initial stages. Did the character arise as a variation *de novo*, or as a progressive modification of a preëxisting character? If *de novo*, did it spring suddenly forth, with some decisive advantage in the struggle for existence? or did it appear as one of many minute changes, and by some happy chance get a start that gave it the lead in future development? In other words, did it begin as a discontinuous variation, sport, or mutation? or did it arise cumulatively, as a continuous development? If it originated by modification of an earlier character, was

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[2] Later Professor Whitman questioned this possibility much more seriously than is done here.—ED.

it at first a sudden, sport-like departure? or was it a slow and continuous transformation of a progressive or retrogressive nature?

Then we come inevitably to the deeper question, which natural selection only partially penetrates—the question how variation, multifarious and undirected, without the aid of design or a designer, can advance to such definite and wonderful achievements as specific characters.

As the bars and chequers represent the two known extremes of a lineal series of variations, if we could determine which came first in time, the problem would be fairly within grasp, for then the direction of modification would be clear, and the mode of progress or retrogression would be but a matter for simple observation to settle.

Such series can usually be read in either direction with about equal facility, and even if all the intermediate terms are before us, the direction of sequence is still ambiguous. This ambiguity infects many a biological problem, and in the field of color-patterns it is omnipresent.

In the present case it can be eliminated, or reduced to negligible limits, by taking bearings from a number of different vantage-grounds.

Which is more primitive in the rock-pigeons, the chequered or the uniform color? The following detailed description of the chequers and bars of a bird representing each of these two forms assist in supplying the answer.[3]

One of three chequered individuals received in 1898 from Mr. Chatwin, of Dover, was *less thickly chequered* than the two others, which were thickly so marked. I found in the least-chequered bird, which is here described, only eleven feathers, so that at least four or five are missing; probably in molt. The measurements are omitted, as the series is not complete.[4] One or two points, however, are worthy of notice:

(1) The spots here are *longer* than in the uniform gray individual (pl. 2), and *pointed* behind.

(2) The gray tips are here as much shorter than in plate 2 as the spots are longer— the spots being about twice as long and the tips about one-half as long. The spots being at near the mid-length of the feather in both sets, the gain in length in this set, or the loss in length in the other, is wholly an elongation towards, or retreat from, the tip.

Assuming, as I believe one must, that the *elongated pointed spot* is the more primitive, we have the means of judging whether the *uniform gray with two bars of more or less squarely cut spots*, or the chequered variety with its second bar always more or less serrate, stands nearer the original type. I do not hesitate to place the chequered variety as the earlier, for its spots are of the earlier pointed form which is so generally characteristic of the chequers on the anterior coverts. The *uniform gray with two bars is a derived, later pattern*, and not, as supposed by Darwin and others, the ancestral form, from which the chequered type is a secondarily derived form. This view is fully borne out by all the facts we can obtain:

(1) The most highly developed bar is the first (posterior). It is in this bar that we find the greatest width and the greatest depth of color. Passing from behind forward, we find the bar-spots less and less developed. This is true in all species with bars; *e.g.*, in crested pigeons the posterior bar is the most highly colored, the second bar is less brilliant, while the third is still less so, and those anterior to the third grow narrower and duller.

(2) The posterior bar seldom shows traces of a serrate edge; the second bar shows all stages of serration, from the long, sharp point to the obtuse, rounded, slightly convex, and

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[3] The following pages (MSS. A 50), in smaller type, have been inserted at this point by the editor.

[4] An illustration of the chequers and bars of this bird was prepared, but it is not available to the editor.

straight-cut outline. The less black in the wing as a whole, the more serrate this bar, as a rule; the more black, the more the long point fills up towards the straight-cut form.

(3) In the first plumage of young domestic doves I find that the second bar generally exhibits pointed spots, and more strongly pointed as we descend from the back—where the spots are most developed and most nearly straight—to the lower edge of the wing, where the spots disappear, or become much less developed and increasingly pointed. In the second plumage these spots become fuller and less pointed, often losing all marked serration.

(4) The first plumage of passenger-pigeons and the adult plumage of passenger females contains well-marked serrate bars, which are more or less lost in the adult males—the males having a more nearly uniform color than the females and young.

(5) The young of *Geopelia humeralis* have the long-pointed spots in the first plumage. In the second plumage they are wholly absent.

(6) The fact that the element of the bars is so generally distributed among wild species and that it generally takes the *pointed* form, or a form plainly derived from the pointed type, is a strong evidence that the pointed spot is the archaic form.

(7) On any other assumption, what explanation do we have for the pointed pattern in so many wild species, and especially in the first plumage of pigeons? Evidently we must have a view consistent with some sort of evolution of the bars. If the pointed spot is not the original element, then what is more so?

(8) *Two bars* are nowhere indicated to be the original number; on the contrary, the evidences are for more or less even distribution of the spots over the wing and scapulars. It is, in fact, easy to find many different species with *many* bars in progress of evolution, but no species where these marks are limited to two, as in some of the *Columba livia*.

In the other form—a barred wild rock with traces of a third bar—the tertials and secondaries (14 in number) graduate into one another in form and color-marks so that no dividing-line is possible (pl. 2). This (first) bar is' compounded of two distinct bars, one being terminal (secondaries), the other subterminal (tertials). The upper, *subterminal* bar continues from the fourteenth feather to the fifth; the terminal from tenth to the first. The two, therefore, are present together on the tenth to the fifth—*i.e.*, on 6 middle feathers—the lower 4 secondaries having only the terminal, while the upper four tertials have only the subterminal bar. On the middle six feathers (10 to 5), the terminal bar diminishes *upward*, while the subterminal diminishes *downward*.

In some of my domestic pigeons both bars extend farther, the terminal running up on the tips of the tertials, the subterminal running down across the lower secondaries and even across the primaries in *diffuse freckles*. The extension in opposite direction is the *later* development.

We have, in this (first) bar, double spots (upper and lower) on the upper four feathers and a trace on the tenth; the spots of the subterminal bar average about *twice the length* of the spots of the second bar.

The *subterminal* bar alone is the *serial homologue* of the anterior bars, while the terminal bar is not represented in the anterior feathers except for a bare trace, as seen in young domestics. This trace is very interesting, showing that there is a tendency to repeat the same pattern in each feather, and if the pattern is reduced it is the weaker position that suffers first; *e.g.*, the anterior bar disappears before the second or first; the lower parts fail of development sooner than the upper parts. Reduction of development leaves the pattern in a more ancient form—that is, in elongated spots, rather than square or rounded spots.

In looking at the first bar of a young domestic pigeon, I notice that in the folded wing only the upper ten feathers—secondaries and tertials—take part in forming the visible portion of the bar (*i.e.*, the subterminal bar). The lower four secondaries have the spots diminishing in extent and depth of color *downward* and each showing the *original pointed*

form; but in the closed wing these spots are entirely out of sight, and only the *terminal spots* of these feathers and portions of the "gray spots" are in sight, and these are so closely folded as to fall nearly in line with the subterminal bar, and thus appear at first sight to form a part of it. The part they appear to form, however, is very small, so closely are the feathers folded up under each other.

The whole length (from top to bottom) of the first bar in this specimen is 65 mm. and the part formed by the lower four secondaries is not over 8 mm.—*i.e.,* not over one-eighth of the whole bar.

Now, in the above-described *Columba livia* (pl. 2) these four secondaries have no trace of the subterminal bar, and the next two feathers have only freckled indications of the bar.

In a wild female passenger-pigeon the "terminal spots" of some six or more secondaries form the lower *half* of the bar, and the upper half of the bar (subterminal spots) is not longer or more conspicuous than the lower half. The second bar shows five spots belonging to the middle long coverts, the middle spots being the larger and longer, the upper and lower spots diminishing until only the tip of the spot is visible. The third bar consists of six or seven visible spots, and this bar comes mainly in the lower half of wing. The fourth bar shows two to four spots in the lower middle part of the wing. In front of the fourth bar I see from one to two or three spots at different points—elements of so many imperfect bars, extending up to the front end of the wing. This (female passenger) wing is a very instructive type, especially in a comparison with chequered homers.

The distribution of bars and chequers among wild species of pigeons may be trusted to give unequivocal indications as to the origin of bars. There are several kinds of bars, all compound, and all composed of similar elements. They are found in only a few of the more highly developed pigeons, such as the crested pigeons of Australia, the red-breasted pigeon of the Philippines (*Phlogœnas luzonica*), the stock-dove of Europe, and the rock-pigeon. The chequers composing the bars are everywhere the same, homologues of the chequers of the rest of the wing. These spots are very widely distributed, and in most cases there are no bars present to which their origin could be referred.

The conditions presented by the bars are everywhere indicative, not of a simple, primitive character, but of a character derived from simpler elements by various modifications in form. There is no evidence that bars are the incipient stages in the evolution of chequers. They appear rather to have already reached their highest stage of differentiation, and in some cases to be in decadence. This is most decidedly indicated in the much-reduced bars seen in the stock-dove (see pls. 9 to 13). Conditions have been noted even in the rock-pigeons looking towards disappearance of the bars.[5] "Occasionally," says Darwin (*Animals and Plants*, Vol. I, p. 225), "birds are seen in Faroe and the Hebrides with the black bars replaced by two or three black spots; this form has been named by Brehm *C. amaliæ.*" The bars have been completely obliterated in some races of domestic pigeons and more or less reduced in width in many others.

In comparing the juvenal with the adult plumage we get another class of evidences that are scarcely less than decisive in their bearing on this question. In some species chequers are present in the juvenal feathers and wholly absent in the adult plumage. This is the case in the small ground-doves[6] (*Geopelia*) of

[5] In a few individuals of our band-tailed pigeons (text-fig. 5, Vol. II) I have seen minute blotches of black on some feathers in the place of the bars; the affinities of this pigeon, as well as its high general finish, compel us to regard these flecks as the last vestiges or atavistic reminiscences of lost bars or chequers.

[6] The geopelias are illustrated and further described in the following chapter.—ED.

Australia. On the secondaries and the longer coverts these chequers fall into regular rows, conforming necessarily to the serial arrangement of the feathers bearing them. They are thus in a position and order corresponding precisely to the position and order of the elements of the bars in *Columba livia*. To convert them into typical bars it would be necessary only to enlarge them transversely until they coalesced by juxtaposition. These transient chequers, distributed to all the coverts of the wing, seem to tell us that the geopelias were descended from chequered ancestors, whose color-marks are now recapitulated, but soon superseded by the later pattern which characterizes the species in the adult stage. The barred condition of the adult plumage differs widely from that of *C. livia;* but the important point is that longitudinal chequers are first and transverse bars second in order of development.

While all species of *Geopelia* exhibit the same transitory chequers in the juvenal feathers, in the adult plumage two distinct patterns are presented. In *G. cuneata*[7] the ground-color is gray and each of the upper wing-coverts is marked with two small lateral, roundish, white spots, which fall into regular transverse rows on the longer coverts. These rows cross the wing in lines that would be followed by transverse bars, and development shows that the spots are differentiated remnants of bars.

In the other geopelias, narrow transverse bars are formed by the coalescence of the dark crescents at the tips of the feathers. As these bars follow the tips of the feathers, they are really composed of serially connected scallops that simulate bars only in a few of the longer rows of coverts, where the feathers overlap in a way to conceal the upper third of each crescent and leave the lower third exposed as component parts of nearly straight and continuous bars.

In the ontogeny of the geopelias we see the different species all taking departure from a common color-pattern, consisting of longitudinal spots or chequers distributed uniformly to all the feathers of the wing. We see this common and earlier pattern retained for only a few weeks, then exchanged for the specific patterns of the adult birds, the later patterns developing in two widely diverging directions, leading to two types of generic rank.

In the geopelias the chequers are completely lost with the juvenal feathers; in a distinct but allied genus (*Ocyphaps*), the crested pigeon, an interesting variation is presented.[8] Here typical chequers have been retained in two rows of feathers—the long coverts and the secondaries—and replaced in all the other upper wing-coverts and scapulars with narrow transverse bars, differing from those of *Geopelia* in being subterminal and straight and in being directly derived from the original chequers by simple reduction of the latter in length. In the second row of coverts—next in front of the long coverts—the reduction is less than in the anterior coverts, and consequently the bars are here more evidently shortened chequers. In the young bird the bars shorten gradually from behind forward, from chequers of full length to the narrowest anterior bars. The mode of transformation is demonstrated to perfection in the two inner feathers of the row of long coverts.

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[7] Reichenbach gave this unique species the generic name *Stictopelia*, and Bonaparte concurred in this. I think the development of the color-pattern warrants the separation from the other geopelias.

[8] This is fully described in the preceding chapter.—ED.

The two posterior rows of chequers, which have been preserved in this genus and raised to a state of brilliant iridescence, are the exact homologues of the two black bars of *Columba livia*. The starting-point is then again found in general chequers, and evolution has advanced by a definitely directed reduction of pigment, proceeding from before backward,[9] in the same direction as that of embryonic development. That this is the direction of evolution, and that there is no possibility of reading the conditions in the opposite direction, becomes still clearer when we discover that a closely allied genus (*Lophophaps*) has taken a step in advance of *Ocyphaps*, in that it has acquired the narrow bars in the place of chequers in the row of long coverts, leaving but a single row of chequers on the secondaries. That *Lophophaps* occupies the higher plane is obvious in other modifications seen in the head, breast, and wing-pattern.

If the testimony of juvenal patterns be extended to species having chequers so closely agreeing in form, color, and distribution with those of the chequered rock-pigeon that no shadow of doubt can remain as to their homology, we shall get only additional confirmatory evidence that the process of evolution in color-patterns has been a sweeping one, involving the whole surface and taking the same general direction. The stages reached are various, ranging all the way from the full-chequered to the wholly unchequered state; from chequers and bars combined in different proportions to bars alone; from many bars to three, two, one, a remnant, or none; and in all shades of brown, black, gray, red, to pure white. Nowhere in this field of variations do we find any indications that chequers originated in the form of bars at the posterior end of the wing and then spread from behind forward.

The wild passenger-pigeon (*Ectopistes*) bears chequers closely resembling those of the chequered rock-pigeon.[10] There can be no mistake here as to the direction in which the phenomena are to be read. The direction is as certain as that the adult male stands in advance of the adult female, and still more in advance of the young bird. The significance of the case lies mainly in the fact that it is not an isolated or exceptional one. Many other species tell more or less perfectly the same story.

A parallel case, only carried still farther in the same direction, is found in the mourning-dove (*Zenaidura*). The adult male (see pl. 19, Vol. II) and female differ but slightly, each having about a dozen chequers visible on each side. These are confined to the scapulars and to a few feathers at the posterior upper edge of the wing. In the young (pl. 7) they are more numerous, but less so than in the young passenger-pigeon. The middle and fore parts of the wing in the adult have no visible chequers, but a few concealed ones which may be seen on lifting the overlying feathers. These concealed chequers and other differences between old and young show that the species had its origin in a chequered stock and that its history has been analogous to that of the passenger-pigeon. The reduction has not been carried out in a way to leave bars, but the location and the clean-cut outlines of the spots, as well as their intensity of color, suggest that some influence may have operated to preserve and then intensify them in a region suited to their most effective display.

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[9] Just the reverse of the contention of Eimer and his school, that evolution in color-marks progresses in a *postero-anterior* direction.

[10] These have been described and illustrated in Chapter II.—ED.

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It is here that we may with some reason suspect the intervention of natural selection. It would, in this case, come in, not as a primary factor to originate a new character, but adventitiously, by invitation, as it were, of favoring predeterminations and environmental conditions. The process of deletion of the chequers, traveling backward and upward, would tend directly to clearing the field in a way to leave a few chequers just where we now find them. The ornamental value of these few chequers and their utility as recognition-marks would obviously be enhanced by their isolation in a plain ground, just as a few trees, concealed in a large forest, become conspicuous when left standing alone. These chequers, being on the larger feathers, would have the advantage of size, and so their preëminence,
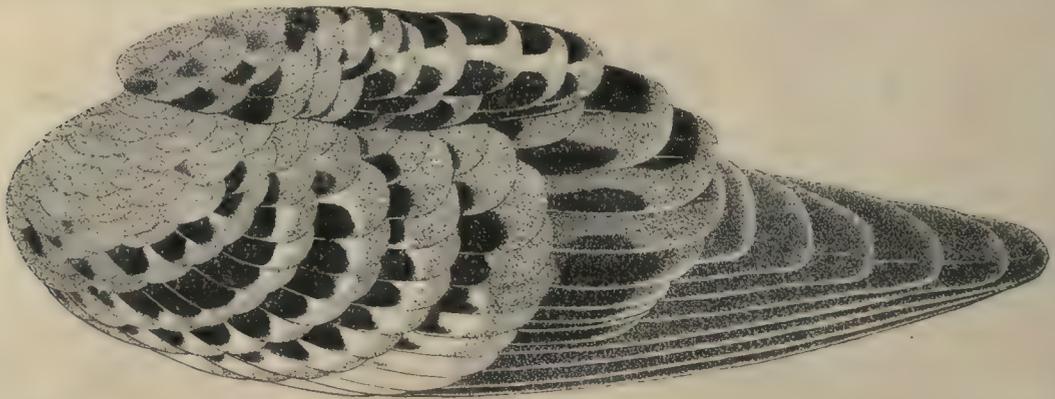
TEXT-FIGURE 13.—Adult male *Nesopelia galapagoensis*. Natural size. Hayashi del., June 1907, from a skin loaned by the U. S. National Museum.

    1. Three or four irregular rows of the anterior lesser coverts have lost the chequers.
    2. Following these are one or two rows of lesser coverts with vestigial chequers, mostly concealed.
    3. Then follow five rows of coverts bearing chequers. Of these five rows, one could be reckoned with the lesser coverts, three as median, and one as long or larger. Each feather usually bears two spots, the outer spot the larger; passing from the inside outward, the spot on the inner web becomes rapidly smaller until at least it is only a marginal streak, and then the outermost feathers bear only one chequer on the outer web. The chequers are mostly rounded distally. The dotted part of the feathers is brown, and the white spaces between spots and behind them are left as they appear.
    4. The scapulars are double-spotted.
    5. The tertials are double-spotted, but the outer spot becomes smaller passing downward.
    6. On the inner tertials there is asymmetry in position of the two spots, as in mourning-dove.
    7. The secondaries have black spots, so that here we get the essentials of a posterior wing-band.
    8. Many feathers of the back, between the scapulars, are spotted black. *Nesopelia* is more primitive than the mourning-dove in the number of spots, but has white between spots, which makes them much more conspicuous than in the mourning-dove.

attained without the aid of natural selection, would be an open door through which it might enter and contribute to their improvement. The part possibly taken, however, could at most be but a late and inconsiderable share of the total achievement summed up in these spots; and the course of events in at least one of the allied forms (*Melopelia*) indicates that these marks are destined to be washed out.

    The question here raised is one of general interest, and it could probably be settled by an extended study of the marks in the mourning-dove and a comparison of all the Zenaidinæ. *Nesopelia galapagoensis* is the only one of this family which is fairly evenly chequered over the whole wing and scapulars (text-fig. 13), and this condition stamps it as the oldest member. *Melopelia*, with its two species,

stands at the opposite extreme, with not a single black chequer left on the wings, and is therefore to be classed as the latest branch of the family. Intermediate stages, with few to fewer spots, are seen in the two genera, *Zenaida* (pls. 83 to 87) and *Zenaidura* (pl. 19, Vol. II).

The white-winged pigeon (*Melopelia leucoptera*) is a most instructive form. Although a much more highly accomplished bird in the arts of display of form, feathers, and voice than the mourning-dove, it has suffered a complete effacement of the chequers it once possessed in common with other members of the family. Indubitable proof of this is to be seen in the juvenal feathers, which, in some cases, exhibit a few pale vestigial chequers (text-fig. 14) in the last row of long coverts at points where the chequers are usually best developed in chequered species.

TEXT-FIGURE 14.—Left wing of juvenal white-winged pigeon, *Melopelia leucoptera*, age 25 days. Natural size. Hayashi del., May 1899.

Rudimentary (obsolescent) spots are shown, but so nearly faded out and so nearly covered that one would not notice them unless looking especially for them. Color dark gray; in shape they are pointed posteriorly. The spot is elongated along the lower margin of the feather. There are only a few of them; three or four of the longer tertials have long, narrow edge streaks, completely out of sight under the longer coverts. I found four spots on the upper longer coverts, the lower of which was covered and is not seen in figure. The next row of coverts has three or four spots, rather smaller and more obscure, at about the same level as spots in long coverts.

The secondaries are quite dark, with white edge and tip. This is the lower half of the first bar. The upper half of this bar is represented by the three or four covered spots of the tertials. I could find no other spots on the coverts or scapulars.

When the feathers are mounted on white board, one can scarcely make out even rudimentary spots, yet there are slight traces.

I predicted that the young of this species, which in the adult has no spots, might show traces of spots. This is a good demonstration of my theory that the ancestral pigeon had elongated pointed spots.

Another striking proof is to be found in the coverts and scapulars of the adult bird, where we find, on lifting the feathers, distinctly outlined impressions, corresponding in shape and position with reduced spots, but from which the black pigment has disappeared. These vestigial outlines, structurally defined, were first noticed in a female bird of a dark shade captured [11] in Jamaica. The outlines were here more perfect than in lighter birds obtained from Arizona and California.

Similar imprints are present in the mourning-dove, and here their identification as marks formerly filled out with black pigment is freed from every shadow of doubt by chequers in all stages of obliteration. They show us that chequers are

[11] By Dr. Humphreys.

not mere blotches of pigment added to an undifferentiated surface, but structurally defined areas, which are the skeleton outlines or blank forms once filled out with pigment. That they should persist for a time after the pigment has ceased to appear is not surprising.

The process underlying the evolution of color-patterns, so far as illustrated in the species referred to, only takes us back to the chequered condition as a starting-point. How pigeons came into possession of chequers is quite as interesting a question as how they are losing them. This I will briefly indicate, in order to make clear how the same process of evolution reaches far back to the primeval history of the pigeon group and, in fact, to that of the whole class of birds.

As before remarked, we find in the turtle-doves of the Old World a pattern which seems to have been the aboriginal pattern for the pigeons and other birds as well. With this pattern as an archetype it is possible to get an orientation of the whole field of avian patterns and to thread our way through what before seemed an impenetrable maze of multifarious variations, with no discoverable beginning or end or order.

The pattern is very simple, each feather having a dark center and a light edge. This simple unit or elementary pattern, repeating itself with little or no variation in each feather, results in a uniformly spotted pattern for the bird as a whole. This pattern is well-preserved in the oriental turtle-dove from Japan; but in the adult it has already suffered reduction in the head, neck, and breast regions, only a patch being left on each side of the neck. In the young (in color, pl. 2, Vol. II) the pattern is carried out on these regions, but less strongly than elsewhere, and without any distinct patch on the neck. On the wings and back the juvenal pattern is the same as the adult. The young bird, then, gives no intimation of an earlier pattern, but in striking directly into the general surface-pattern of the adult bears witness to its primeval character.

In birds that have made considerable departure from this type the young generally repeat the pattern in their first feathers and exchange it for the later-acquired pattern at the first molt. The adults may retain the original marking in some regions while advancing beyond it in other parts, and in such cases we get the clearest evidence in transitional phases of the direction of modification. Even in the widest departures, where every spot has vanished in the adult plumage, the young bird frequently exhibits more or less perfect traces of the old marking and sometimes requires several molts to reach its mature condition.

Without farther digressing into the general field of color-patterns, it remains to explain the genetic connection between the chequered and the spotted type, and to show how both types originated in and have been diversified by the same general process of reduction of pigment.

The light apical edge of the feather, by the presence of which the central field becomes defined as a spot, represents a first step in this direction. That this is the correct interpretation is conclusively shown in the turtle-doves and their nearer allies. Taking the oriental turtle-dove as the least modified in this direction, and comparing it with the European species *Turtur turtur* (color, pl. 2, Vol. II; wing, pl. 22, Chapter V), we see at once that a distinct advance has been made—the light edge is wider and the spot correspondingly reduced, becoming more sharply pointed. In another species, the Surate turtle-dove (*Spilopelia suratensis*), the reduction is carried still farther (pl. 24, Vol. II), having only a mesial streak. In

the Chinese turtle-dove (*Sp. chinensis*) the spots have been completely obliterated (pl. 23, fig. A). The neck-spots have been carried to higher and higher stages of differentiation in these four species, and in the order mentioned,[12] so that there can be no doubt as to the direction of modification.

The large wood-pigeon (*Columba palumbus*) of Europe has departed still more widely (text-fig. 6, Vol. II) and evidently from the same type, having lost all its black spots, except a few in the neck patches, which have retreated so far from the tips of the feathers as to be concealed. The gray plumage and the white streak along the edge of the wing mark a plane in the evolution of this bird very nearly identical with that of the white-winged pigeon. A little higher plane has been reached by our band-tailed pigeon (*Columba fasciata*) of the Pacific coast, which is also a species of turtle-dove derivation, as shown in the neck-marking and in the voice and behavior (text-fig. 5, Vol. II).

The ring-doves forming the large genus *Streptopelia*, embracing thirteen[13] species, are a branch arising directly from turtle-dove ancestors. They have all lost their dark spots everywhere except in the black collar, and the only remaining visible trace of the spots elsewhere is the narrow light edge shown at the tip of each feather in the juvenal plumage (pl. 8, Vol. II).

The little red ring-dove (*Streptopelia humilis*) stands nearest to the turtle-doves, both in color (pl. 21, Vol. II) and behavior. In this species the red is but an extension and intensification of the light edge of the turtle-dove feather. Lifting the scapulars and inner secondaries, we still find obsolete remnants of the dark centers, which have been so reduced as to be wholly concealed by the overlying feathers. The shaft of the feather still remains dark, while in the common cage ring-dove even this reminiscence of the dark spot has been bleached.

In the ring-dove species the reduction process has not only washed out the spots, but also advanced from the darker brown-red to gray, isabelline, and blond, and finally to pure white. Albinism is the finishing stage of the process we have been following. In the common domestic doves it advances through paler and paler shades of gray, the bars growing always narrower. The white rump in the rock-pigeon has followed the pale-gray rump, and this the darker gray. The white-edged wing seen in many wild species has succeeded the gray-edged wing, and this sequence is still often shown in passing from juvenal to adult plumage.

The spotted type originated in a marginal reduction of pigment, beginning at the apex of the feather and extending along both sides. Further reduction advanced in the same direction, and so evenly on both sides as to leave the longitudinal axis of the spot generally coinciding with the shaft of the feather. The main advance of the process as a whole was antero-posterior in direction, while in the individual feather it was primarily and predominantly in a postero-anterior direction—*i.e.*, from the apex towards the base. The opposition in direction is apparent rather than real; the free end of the feather is first in development, and hence the direction of reduction is here the same as that of development, as it is in the case of the body as a whole.

The chequered pattern of the rock-pigeon originated from the spotted type, by division of the single central spot into two lateral spots. The general course of

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[12] These neck-marks are fully illustrated and their behavior in hybridization is fully described in Chapter XVII, Vol. II.—Ed.

[13] Seventeen species were later recognized; see Chapter XV, Vol. II.—Ed.

reduction is the same for both types, but a slight difference in detail is superadded for the chequered type. The light edge, which is an important and permanent feature in the spotted type, is very narrow and transitory in the chequered type, disappearing with the molt of the juvenal feathers.

Within this narrow light (pale brown) edge appears a zone of gray that usually enlarges at the middle and extends inward in the form of a wedge, or as a mesial streak, dividing the dark spot more or less deeply into two lateral chequers with pointed tips. The gray area, which arises and enlarges at the expense of the black spot, varies greatly in form and extent in different feathers and in different individuals. It may be wholly absent in some feathers, the black spot remaining undivided, as in the turtle-dove; it may take the form of a narrow crescent more or less thickened at the middle; it may have the form of a triangular spot, as in the guinea-pigeon (*Columba guinea*) of Africa,[14] or be more obtusely pointed, as in the spotted pigeon (*Columba maculosa*) of South America (pl. 18); it may expand over the whole width of the feather and enlarge mesially so as to deeply or completely divide the black; the mesial streak may expand equally on both sides of the shaft until the two spots are left as edge streaks, or unequally, leaving more or less of one spot than of the other.

The mesial extension of the reduction process, which prevails in the chequered type and is its chief peculiarity, is not after all an exclusive distinction. A light mesial streak dividing a central dark spot may and actually does occur in the breast feathers of some of the young of the European turtle-dove; and thus we see that both primary characters—the single central spot and the two bilateral spots—may occur together in each type.

I have seen the same mesial streak in the juvenal upper wing-coverts of *Leptoptila* (pl. 43). It occurs also in the young robin (see pls. 56, 57), where it closely simulates conditions presented in domestic pigeons. It is a permanent condition in a large number of birds, the female jungle-fowl being an example.

We have seen that the process of reduction tends to sweep the whole surface and in the same general direction. The conclusion supported by comparative study admits of experimental confirmation. We may take pigeons of the two-barred type, and try to advance from this condition to that of the chequered type, by selecting in each generation birds with the widest bars, and especially any that may have a trace of a third bar. This I have tried[15] continuously for six years and with several different stocks. I have not been able to establish a third bar, or to extend chequers in front of the vestigial third bar, which is often found. With pure-bred birds, not allowed to mingle with chequered birds, I believe it is impossible to advance from bars to the chequered state. With chequered pigeons, on the other hand, it is fairly easy to advance in the opposite direction, gradually clearing the field and leaving two bars. The process has been carried to the point of completely eliminating the bars.

From these considerations we can readily understand why the stock-dove,[16] which has, at least in many cases, a vestigial third bar, quite like that in domestic

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[14] See Chapter IX and illustrations. The present discussion of the "guinea-mark"—or triangular white tip of the feather—may serve as an introduction to the "guinea-mark" *mutations*, which are described and illustrated in Chapter IX. It is partly for this reason that some of the illustrations dealing with this character are placed with the references to them in the present chapter.—ED.

[15] As noted in Chapter II.—ED.

[16] *Columba œnas*, discussed and figured in Chapter III.—ED.

PLATE 18

Adult spotted pigeon, *Columba maculosa*. Photographed July 21, 1910; colored by Hayashi. × 0.66. This South American species shows the "guinea-marks" (triangular white tip of wing-coverts) in a form slightly modified from that found in the African species, *C. guinea*, with which it should be compared (pl. 76)

pigeons, never appears in chequered dress. It is moving in the other direction, and no reversal of course is now open to it. Moreover, the various conditions of chequers and bars in rock-pigeons and domestic races are self-explanatory from the same point of view.

We could not explain how two bars could arise *de novo* in a clear gray wing-surface; but we can see how a sweeping reduction process, antero-posterior in direction, would leave two or more rows of chequers cut to dimensions that would coalesce in transverse bars at the posterior end of the wing. The great variations in the width of these bars, the serrate edge of the wider bars, the more evenly cut edge in narrow bars, the presence of one or two rudimentary bars, wholly concealed from view, in short, all the peculiarities of the wing-pattern, become intelligible as soon as we discover the nature and drift of variation.

To attempt to explain all this as the work of natural selection would lead into an endless tangle of conjecture that would leave even the simplest facts as unapproachable mysteries. Natural selection has probably had much to do with the end-stages in the evolution of characters, but little or no direct influence in originating them.

The two-barred condition has been reached in the simplest possible way, not by accidental variation of chance mutation, but by progressive modification of a chequered condition previously established. The long coverts and the secondaries, which are the larger of the chequered feathers, have the larger spots. In the course of a progressive reduction of pigment, affecting all parts of the chequered area, but advancing from before backward, the spots in the lesser and median coverts will reach the point of disappearance at a time when the spots on the long coverts and secondaries have only been cut down to a half or a third of the initial size. At that time we should have left these two rows of spots, reduced in number at the lower ends, where they are weak at the start, and shortened up by a more or less even cutting off of their ends to square or roundish chequers. The two bars, as wholes, would of course have the position and curvature prescribed in the arrangement of the feathers bearing them. Standing alone on a pale-gray ground, these bars would gain immensely in conspicuity and utility as ornamental recognition-marks. The advantage of all this to the species, whatever it be, would be merely an accident of the situation presented at this particular point in a progressive series of modifications. It is conceivable that the utility of the bars might be great enough to give natural selection a chance to step in and bar the way to further reduction. But the process of obliteration has certainly gone much farther in many other species. There may be stages in the process which suggest utility; but when we consider the whole series of stages and note that the process runs on, sweeping away the stages which we imagine to be most useful, we are left with the conviction that some general principle underlying the course of events has not yet been fathomed.

The mutationist is compelled to take his stand on immutable unit-characters. A character may fluctuate to and fro, but it never loses its balance, except by a sudden transformation that makes it a wholly new character and its bearer a new species. To the mutationist the bars of the *Columba livia*, both as a whole and in their component elements, would be viewed as essentially fixed units. As we look at the character in the mature state, it seems a perfect picture of immutability. To

reach such a definitely localized and apparently rigid character, it might seem that evolution had come to a halt, that the character was caught in a mutation-trap, from which there could be no escape. But even while we are looking at this picture the selfsame process that produced it may be preparing another picture to appear after a molt in more or less different guise. Can a single individual mutate from plumage to plumage, *i.e.*, become a new species?

When we look around among allied species and see these same bars reduced to about half dimensions in the rock-pigeon of Manchuria (*Columba rupestris*, text-fig. 23), reduced to mere remnants of two to six spots in the stock-dove (*Columba œnas*), carried to complete obsoletion or to a few shadowy reminiscences in the secondaries in *Columba rufina* of Brazil (pl. 46), gone past return in some of our domestic breeds and in many of the wild Columbæ[17]—when we see all these stages multiplied and varied through some 400 to 500 wild species and 100 to 200 domestic breeds, and in general tending to the same goal, we begin to realize that they are not to be regarded as permanent halts, but rather as slowly passing phases in the progress of an orthogenetic process of evolution, which seems to have no fixed goal this side of an immaculate monochrome—possibly none short of complete albinism.

Even in cases where natural selection has probably played a conspicuous part in modifying and beautifying these marks, *e.g.*, in the crested pigeon of Australia (*Ocyphaps lophotes*), we find that the reducing process has not been brought to a standstill. Indeed, a careful comparison of the juvenal and adult plumages in both sexes shows that differentiation has been gradual and continuous and that it is still in progress in the bar of the long coverts, the homologue of the anterior bar in the rock-pigeons. What we see now going on in this bar has been already achieved in the white-bellied plumed dove[18] (*Lophophaps leucogaster*) of the same country, and is now progressing down the next and last bar.[19] A most striking demonstration of progressive orthogenetic differentiation, still advancing and even cutting through the brilliant coloring, which, in part, we attribute to natural selection.

SUMMARY.[20]

The wild rock-pigeons present two very distinct color-patterns: (1) the chequered type and (2) the barred type.

Two black wing-bars on a gray ground have always been held to be the more primitive pattern, and birds of this pattern are supposed to represent the typical *Columba livia*.

The form with black chequers evenly distributed over the wing and back, although once named *Columba affinis*, as a distinct species, was regarded by Darwin as a variety derived from the two-barred rock, and his opinion has stood undisputed.

It appears from a comparative study of many species of wild pigeons, and from a study of the variations in domestic species, that the relationship is just the reverse: *C. affinis* is the original rock-dove and *C. livia* is the derived type. Domestic pigeons have come from both sources.

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[17] Illustrations of some of these are given in Chapter VII.—ED.

[18] A good picture of this dove was given by Mr. D. Seth-Smith, in the Avicultural Magazine, December 1906. (The wing-bars of this bird are here shown in text-fig. 9.—ED.)

[19] A detailed account of this case is now in preparation (the account was not completed.—ED.).

[20] The abstract of an address of 1903 (Biological Bulletin, 1904, Vol. VI, p. 307) is used as a summary for this chapter. The four final paragraphs have been substituted by the editor, from the manuscripts for the completed chapter, for the two final paragraphs of the author's abstracts.

Columba affinis, however, is not the most primitive form among the wild pigeons.[21] It was derived from a more ancient type, best preserved in the turtle-doves (*Turtur orientalis* and *T. turtur*). In the turtle-dove type each feather has a dark center and light edge.

The turtle-dove pattern is at the same time a general avian pattern.

The turtle type and the rock type coexist in some forms (*e.g., Phaps chalcoptera*).

The two-barred pattern of *Columba livia* was reached in the simplest way by an even reduction of the dark pigment, which would result, at one stage, in leaving remnant spots on the long coverts and the secondaries.

The process of reduction has run in one direction in many, if not all, pigeons, and present species have reached different stages, varying all the way from a uniformly spotted condition to four, three, two, one, or part of one bar, or no bars.

The light apical edge of the feather represents a first step in this direction (reduction).

The spotted type (many species) originated in a marginal reduction of pigment, beginning at the apex of the feather and extending along both sides. Further reduction advanced in the same direction, and so evenly on both sides as to leave the longitudinal axis of the spot generally coinciding with the shaft of the feather. The main advance of the process as a whole was anterior-posterior in direction.

The chequered pattern of the rock-pigeon originated from the (earlier) spotted type by division of the single central spot into two lateral spots. The general course of reduction is the same for both types, but a slight difference in detail is superadded for the chequered type. The light edge, which is an important and permanent feature in the spotted type, is very narrow and transitory in the chequered type, disappearing with the molt of the juvenal feathers.

Within this narrow light (pale-brown) edge appears a zone of gray that usually enlarges at the middle and extends inward in the form of a wedge or as a mesial streak, dividing the dark spot more or less deeply into two lateral chequers, with pointed tips. The gray area, which arises and enlarges at the expense of the black spot, varies greatly in form and extent. It may be wholly absent in some feathers; it may take the form of a narrow crescent more or less thickened at the middle; it may have the form of a triangular spot as in the guinea-pigeon (*C. guinea*) of Africa, or be more obtusely pointed as in the spotted pigeon (*C. maculosa*) of South America.

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[21] The succeeding chapters on the Turtle-Dove Pattern in the Phylogeny of Pigeons furnish much of the evidence for this and the several following conclusions.—ED.

CHAPTER V.

THE TURTLE-DOVE PATTERN IN THE PHYLOGENY OF PIGEONS.[1]

> But the causes and conditions of variation have yet to be thoroughly explored; and the importance of natural selection will not be impaired, even if further inquiries should prove that variability is definite and is determined in certain directions rather than in others, by conditions inherent in that which varies. It is quite conceivable that every species tends to produce varieties of a limited number and kind and that the effect of natural selection is to favor the development of some of these, while it opposes the development of others along their predetermined lines of modification. (Huxley, Darwiniana, p. 223.)

GENERAL STATEMENT.

Color and color-marks present a wide range of the most puzzling problems—the shades of the ground-color, the endless diversity of specific color-marks, the distribution of color and color-marks geographically, their age sequences, regional differentiations, form metamorphoses, sexual correlations, seasonal changes, protective adaptations, irregularity, lawlessness, non-amenability, non-conformity to laws of heredity.

What, at first thought, could appear more insignificant than a simple color-mark of a feather? Can such lifeless surface-characters lead us directly to central problems in evolution—problems which involve at once variability, adaptation, heredity, the genesis of species, and progressive development? Is not variation here too profuse, too multifarious, too lawless to serve as safe ground for fruitful comparative studies and reliable experimental tests? Such, very likely, might be one's first impressions. As we inquire into the subject more closely, we shall see room for a more favorable judgment.

Where and how shall we study variation, if not in that which exhibits it abundantly? Great variation in outward expression implies a correspondingly high grade of plasticity in the internal foundations of such manifestation. Whether we imagine that each mode and degree of expression has its special primordium, or prefer to refer all the various expressions to one common germ-substance, it is obvious enough that in these color-marks and the patterns which they form we have a wide-ranging variability to deal with, with endless opportunity for both natural and artificial selection and for experimentation.

If the very exuberance that confronts one in the feathered world be somewhat appalling on first approach, it costs but little effort to see that it all counts in favor of the investigator. The greater the variability, the closer, in general, will be the connections between stages, and the easier it will be to catch the trend of phyletic derivation and to discover the common points of departure for whole groups of related color-patterns, and possibly to reduce these points to a single point of departure for the whole bird kingdom. Such a vista, once opened, would orient the whole

[1] The arrangement of the several "groups" of materials of the chapters dealing with this subject is that of the editor. Little of these materials was put into finished form by the author, and it has not been thought advisable to make extensive changes in the record as found. The amount of textual matter is, at many points, more limited than is desirable. The statements here given—supplemented by the several very full considerations of previous chapters—will, however, doubtless prove sufficient to guide the reader through the great number of illustrations. Further, the legends accompanying the plates are often so full and complete as to render text less essential. The plates and figures, if given alone, would go far toward accomplishing the aim of these chapters, namely, to show that the most divergent forms—of pigeons, and of still other groups of birds—exhibit one or another stage or degree of transformation of an identified ancestral color-pattern.—Ed.

field, disclose the direction of evolution, provide the investigator with a key to the natural order of sequence in color-patterns, enable him to detect and to demonstrate orthogenetic evolution, if such there be, and to discriminate nicely between this and the results to be ascribed to natural selection and other intervening factors.

From such a vantage-ground one may proceed to work out details of evolutional progress by the aid of comparative study of patterns at all stages and ages of development. Juvenile phases of color-patterns become luminous as recapitulations in the sense of the biogenetic law and do not stand as isolated prodigies of natural selection or as meaningless exhibitions of mutations.[2]

In the 500 or more perfectly distinct wild species (see table 1) with phyletic relationships of easy determination in most cases; in the 200 or more domestic races, all springing primarily from a single known wild stock[3]—in all this abundance of natural and cultivated forms, with a multitude of comparatively simple characters, the evolutional history of which can be largely deciphered in many cases through comparative and experimental study, we find inexhaustible material for just such test-cases as we desire.

The more generally distributed patterns, such as occur only in the first plumage, or only in this and the adult female plumage, furnish the chief problems. The patterns of first interest are: (1) the *light-edged* feather; (2) the *dark-edged* feather; (3) the *dark-centered* feather; (4) the *transversely barred* feather; marginal bar alone dark and light, or light and dark repeated, V-shaped, vermiculate, wavy; (5) the *two-dotted* feather; (6) the *cross-barred wing;* (7) the relation of *black* and *iridescence.*

The *principles* found to obtain in plumage patterns are:

(1) *The juvenal plumage presents the earlier type.*

(2) *Females are less modified than males.*

(3) *The upper surface is more modified than the lower surface.*

(4) *Repetitive marks* (cross-bars) *are multiplied from the tip inward toward the base,* the tip bars being the stronger and best defined.

(5) *The tendency is sometimes (usually) to lose marks and gravitate to uni-color or whole-color;* other times to strengthen and extend (?) the marks as *ornamental* recognitional, warning marks.

(6) *The pale edge of the first feathers is partly directly continuous with the down,* and perhaps this relation accounts for its *pale color* (like the down). The tips of the barbs come nearest to the primitive color, because first formed. The pale edge varies in width—is wide in the turtle-doves, narrow in *Columba livia,* and obsolescent in young *inca* and others.

(7) *The more primitive the type of color the quicker it is reached;* e.g., the Japanese turtle-dove reaches it in the first plumage, while in other families the type of the species is not reached until the adult plumage appears. Again, the inca-dove is more primitive than the geopelias, and it is losing the light edge, which is so conspicuous in geopelias.

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[2] These remarkable phenomena, which, as a rule, in normal development, furnish only fragmentary and disconnected parts of past evolutional history, may be so extended by suitable experiments (as noted elsewhere. —ED.) as to demonstrate complete continuity of stages in the passage to the adult pattern.

[3] It is a great mistake to resort exclusively to domestic races, for here the ancestry contains so many unknown elements that it is often impossible to refer phenomena to their proper sources. Even the so-called "pure-breeds" are decidedly impure as compared with pure wild species. The ideal situation, as regards material, is to have pure wild species in abundance as the chief reliance and allied domestic races for subsidiary purposes.

(8) *The more the type is modified the longer it takes to reach it.* This is shown in highly bred domestic pigeons and in the males of many species of birds, where to reach the much-modified adult type several molts are sometimes necessary.

The biogenetic law certainly holds, and often in the most striking manner, in the sequence of color-patterns in individual development.

THE TURTLE-DOVE PATTERN IN THE PERISTERIDÆ (SEE TABLES 1 AND 2).

The Turturinæ.

The patterns of greatest interest are: (1) neck-marks; (2) dark centers and pale tips.

Attention may first be directed to the *neck-marks:* In the turtle-doves of Europe (*Turtur turtur*) and those of Japan (*T. orientalis*) there are to be seen in the first feathers no sign of the adult neck-mark, except that 3 to 5 rows are better defined *as rows* than the rest (see pl. 36 of Vol. II).[4] This much is precisely the case in the

TABLE 1.—*The Five Families of Columbæ according to Count Salvadori.*[5]

ORDER COLUMBÆ (5 families).				
I. Treronidæ.	II. Columbidæ.	III. Peristeridæ.	IV. Gouridæ.	V. Didunculidæ.
Asia, Malay Archipelago, Japan, Africa, Philippines, Australia, mainly tropical and green plumage and many fruit-eating. Tail, 14 feathers (12 in 2 genera; 16 in 1 genus).	Columba is universal. Tail, 12 feathers. Tarsus generally shorter than middle toe. Large, mostly tree-pigeons.	Widely distributed. Many genera and species. Mourning-dove, ground-doves, geopelias, geotrygons, Nicobar crested pigeons, turtle-doves. Tail, 12 feathers mostly; geopelias, 14 or 12 feathers; Zenaidura, 14; bronze-wing, 16; otidiphaps, 20 feathers. Tarsus equal to or longer than middle toe. Smaller, many ground-doves.	Papuan Islands; 6 species; head crest; tail feathers, 16.	Samoa Island; 1 species. Bill hooked. Lower mandible toothed or serrated.
			Isolated and distinct from true pigeons.	
			1 genus. 6 species.	1 genus. 1 species.

SUBFAMILIES UNDER FAMILIES I, II, AND III.

Family I.	Family II.	Family III.	
1. Treroninæ. 2. Ptilopodinæ. 3. Carpophaginæ.	1. Columbinæ. 2. Macropygiinæ. 3. Ectopistinæ.	1. Zenaidinæ. 2. Turturinæ. 3. Geopelinæ. 4. Peristerinæ.	5. Phabinæ. 6. Geotrygoninæ. 7. Caloenadinæ.

I. Treronidæ.......	1. Treroninæ.......... 7 genera,	43 species.
	2. Ptilopodinæ........17 genera,	100 species.
	3. Carpophaginæ......12 genera,	61 species.
	3 subfamilies.......36 genera,	204 species.
II. Columbidæ......	1. Columbinæ......... 4 genera,	65 species.
	2. Macropygiinæ...... 4 genera,	33 species.
	3. Ectopistinæ........ 1 genus,	1 species.
	3 subfamilies....... 9 genera,	99 species.
III. Peristeridæ......	1. Zenaidinæ.......... 4 genera,	13 species.
	2. Turturinæ.......... 5 genera,	28 species.
	3. Geopelinæ.......... 3 genera,	8 species.
	4. Peristerinæ......... 6 genera,	14 species.
	5. Phabinæ...........12 genera,	25 species.
	6. Geotrygoninæ...... 9 genera,	69 species.
	7. Caloenadinæ........ 1 genus,	2 species.
	7 subfamilies.......40 genera,	159 species.
IV. Gouridæ................................. 1 genus,	6 species.
V. Didunculidæ............................. 1 genus,	1 species.
Total......5 families, 13 subfamilies, 87 genera,	469 species.

[4] For the juvenal and adult neck-marks of various grades of *risoria* × *turtur* hybrids see plates 35 to 39 and text-fig. 11 of Vol. II.—Ed.

[5] Catalogue of Birds in the British Museum. Vol. XXI. 1893

TABLE 2.—*The family Peristeridæ according to Count Salvadori.*[a]

Family and subfamilies.[7]	Plumage distinctions.	Genera.	Habitat.
FAMILY PERISTERIDÆ.			
1. ZENAIDINÆ. (New World and Galapagos.)	a. Black spot below ear........ b. Sides of neck with metallic gloss. c. Scapulars and wing-coverts spotted, except in Melopelia. d. Tail, 14 feathers (12 in one).	1. Zenaidura... 2. Zenaida. 3. Nesopelia...... 4. Melopelia.....	North America to Central America and West Indies. Yucatan and Florida Keys to South America. Galapagos Islands. Southern United States, Mexico, Lower California, West Indies.
2. TURTURINÆ. (Old World.)	a. Side-neck spots or dark collar. b. Neck not metallic.......... c. Upper feathers fulvous or pale-edged; dark centers or plain. d. Tail, 12 feathers............	1. Turtur........ 2. Homopelia.... 3. Streptopelia.... 4. Spilopelia..... 5. Stigmatopelia..	Europe, Asia, Japan, Africa, India. Madagascar region. Africa, India, Oriental Malay Archipelago. Oriental Malay Archipelago. Africa, Turkey, West Asia to India.
3. GEOPELIINÆ. (India, Malay Archipelago, Australia, Southern United States, Central America to Brazil.)	a. Neck with bars—not metallic. b. Upper feathers black-edged in most species. c. Tail, 14 feathers (or 12)......	1. Geopelia...... 2. Scardafella..... 3. Gymnopelia....	Burma to Australia. Southern United States, Mexico, Central America, and Brazil. Peru, Bolivia, and Chile.
4. PERISTERINÆ. (Confined to America.)	a. Metallic spots on wing (except Metriopelia melanoptera). b. Tail, 12 feathers............	1. Columbula..... 2. Chamæpelia.... 3. Uropelia....... 4. Oxypelia....... 5. Peristera...... 6. Metriopelia....	South America. Southern United States, Mexico, Central America to South America. Brazil and Bolivia. Brazil. Mexico to Peru and Paraguay. South America.
5. PHABINÆ. (Africa, India, Malay Archipelago, Australia.)	a. Metallic spots on wing, transverse bars in some. b. Tail, 12, 14, or 16 feathers ...	1. Œna .... 2. Tympanistria.. 3. Chalcopelia.... 4. Chalcophaps... 5. Calopelia...... 6. Henicophaps... 7. Phaps......... 8. Histriophaps.. 9. Petrophassa.... 10. Geophaps...... 11. Lophophaps.... 12. Ocyphaps......	South America. Ethiopian region. Africa. India and Australia. Africa. New Guinea. Australia. Do. Do. Do. Do. Do.
6. GEOTRYGONINÆ. (Africa, America, Malay Archipelago, and Australia.)	a. No spots on wing (a violet patch on bend of wing in some). b. Tail 12, 14, 20 feathers......	1. Haplopelia..... 2. Leptoptila..... 3. Osculatia...... 4. Geotrygon..... 5. Phlogœnas ... 6. Leucosarcia.... 7. Eutrygon...... 8. Otidiphaps..... 9. Starnœnas.....	Ethiopian region. Texas to South America. Ecuador. Mexico to South America. Malay Archipelago and Polynesia. Australia. New Guinea. Do. Cuba and Florida Keys.
7. CALŒNADINÆ. (Malay Archipelago and Pelew Islands.)	a. Neck feathers hackled; very long. b. Plumage metallic green. c. Tail white.	1. Calœnas.......	Malay Archipelago and Pelew Islands.

[a] *Loc. cit.*, p. 372. This can not be a correct arrangement of the subfamilies.

common pigeon, indicating common parentage. In blond ring-doves (*Streptopelia risoria*), which have advanced beyond the turtle-dove, we find in all the young these rows not only better defined as rows in the first plumage, but in more than half the individuals there are plain lateral spots (see pl. 19, fig. B), generally extending over 3 rings, sometimes 4, at other times only 2. In many young, however, the

spots are absent in the first plumage, or so nearly so as not to be visible to surface examination.[8] In the related red ring (*St. humilis*) all of the young have these spots in the first plumage.[9] This species has more pigment, hence enough to appear in the first feathers. The Japanese ring (*St. douraca*) is darker than the common blond ring, and therefore more often—almost invariably—has spots in the first feathers. The Damar ring-dove (*St. damarensis*) is another form more pigmented than the blond ring; in this dove (pl. 19, fig. B) the mark is quite strong in the juvenal feathers and is plainly lateral.

In these neck-marks of the collared ring-doves we have, therefore, a good example of a character which appears earlier in the ontogeny than in the phylogeny— a tendency to appear earlier—what first came in second feathers now comes in the first feathers.[10]

The neck-marks of the five groups into which Salvadori[11] divided the former genus *Turtur* were somewhat inaccurately or inadequately described. These groups were designated: (1) *Turtur*, (2) *Homopelia*, (3) *Streptopelia*, (4) *Spilopelia*, (5) *Stigmatopelia*. Groups (4) and (5) are stated (p. 396) to have bifurcated neck-feathers.

Spilopelia: "Feathers of the hind neck *bifurcated*, black, with two *white* apical spots."
Stigmatopelia: "Feathers of the fore neck *bifurcated*, black, with two *rufous* apical spots."

It is strange that Salvadori should entirely overlook this feature in *Homopelia*. Mr. T. H. Newman[12] calls attention to this oversight, and also refers to Temminck[13] as having given a separate figure of one of the bifurcated feathers.

These homopelias are very interesting cases, as they have bifurcated neck-feathers, sometimes on the sides and back of the neck, and sometimes on both sides and front of the neck. The latter seems to me to be a departure from the rule that such marks are limited to the side and back of the neck.

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[8] The black ring or collar in the blond ring (*St. risoria*) is sometimes narrower at its middle, on the back of the neck, than at the ends. This fact, together with the complete interruption of the ring on the back of the neck in the first plumage, by which it is broken into two portions—one on each side of the neck, beginning a little below and behind the ear-coverts, and growing narrower backward—suggests that the half-ring has arisen by the extension of two spots like those seen in the turtle-dove. This ring is creamy white in the white ring (*St. alba*). It is often reduced to a mere shadow, or wholly absent, in the first plumage (see Chapter XVII, and plate 31, Vol. II).

[9] For the juvenal neck-marks of the *risoria* × *humilis* hybrids, see text-fig. 9 of Vol. II.—ED.

[10] Darwin (Descent of Man, Vol. II, p. 153) points out the fact, and makes frequent use of it, that "variations occurring at different ages are inherited at the same age." And, further: "Variations which occur late in life are commonly transmitted to the same sex in which they first appeared; while variations occurring early in life are apt to be transmitted to both sexes; not that all the cases of sexually-limited transmission can thus be accounted for."

From the standpoint of the present, all inheritable variations are in the germ. The order in which they come to sight is the order in which the germ has been modified—not the order in which a new *unit-character* was added, but the order in which the germ as a whole was modified.

Darwin's reasoning on the "*lopping* of the comb" in the *hen* of Spanish fowl (pp. 151-152) is characteristic of his viewpoint. My idea is that the difference here between the sexes is merely one of *strength*.

Darwin says, too (p. 148), that "characters which are limited in their development to one sex *are always latent in the other*." He had elsewhere written (Origin of Species, p. 12): "A much more important rule, which I think may be trusted, is that at whatever period of life a peculiarity first appears, it tends to reappear in the offspring at a corresponding age, though sometimes earlier. In many cases this could not be otherwise; thus the inherited peculiarities in the horns of cattle appear only in the offspring when nearly mature; peculiarities in the silkworm are known to appear at the corresponding caterpillar or cocoon stage. But the hereditary diseases and some other facts make me believe that the rule has a wider extension, and that, when there is no apparent reason why a peculiarity should appear at any particular age, yet that it does tend to appear in the offspring at the same period at which it first appeared in the parent. I believe this rule to be of the highest importance in explaining the laws of embryology."

[11] Catalogue of birds in the British Museum, Vol. XXI, 1893.

[12] Avicult. Mag., Jan. 1908, p. 80.

[13] Hist. Nat. Gen. des Pig. Pl. Col. 242, 1823.

PLATE 19

A

B

A. Juvenal, 6 weeks old, Damar ring-dove, *St. damarensis*. Shows strong neck-mark in first plumage. The neck-mark is (as in the adult turtle-dove) a *side* spot, not a half collar as in the adult Damar ring.

B. Juvenal blond ring, *St. risoria*, to compare with above. The first feathers show weaker neck-marks than the Damar ring. The mark in the blond ring (when present) is also a *side* spot instead of a half collar. The turtle-doves show no color in these feathers in the first plumage.

Newman figures the painted dove (*Homopelia picturatus*), commonly called the Mauritian turtle-dove, and proposes to call it the "Madagascar turtle-dove," as Madagascar is much the larger island and is perhaps the only true habitat of the species.

I have a number of the Senegal turtle-doves (*Stigmatopelia senegalensis*), and find that some of them have the whole front of the neck with bifurcated feathers; but one or two individuals show a narrow median front line,[14] in which the feathers are neither marked with black nor bifurcated. The Madagascar birds would be the more primitive type, while the Senegal birds would be the later form. These birds fly without noise, like young doves generally.

The *dark centers*—already described as an early or primitive avian character—most nearly fill out the feather and are least pointed in the Japanese turtle-dove (*Turtur orientalis*) (see pls. 1 and 2, Vol. II; and text-fig. 3, Vol. I). The position and extent of the black in the wing-coverts is best seen in a series of the separately drawn feathers (pl. 20). The black center blends with the reddish edge or feather tip; *i.e.*, at the boundary of the black we see an intermixture of red, with no sharp separation. The lowermost coverts of the wing show the red replaced by gray.

This black center can be regarded as consisting of an upper (inner) half and a lower (outer) half. On the upper tertials the upper half may fill more of the surface than the lower half; in other words, there is an asymmetry such as we see in the black spots of *Columba*.

In the young the centers of the coverts, scapulars, tertials, etc., are sometimes blackish, sometimes dark brown, as in some of the tertials. In the adult the spot is clearer black and more decidedly angular at the tip.[15]

In the European turtle-dove (*Turtur turtur*) the black center is more reduced and more pointed. This is made clear by a comparison of corresponding wing-coverts in the two forms (pls. 20 and 21). The drawings of the entire wings (*turtur*, pl. 22, fig. 1; *orientalis*, text-fig. 3) show the same distinction, and that of *turtur* further shows that it is the anterior part of the wing that has suffered relatively greatest reduction of the black.

The pale tips and lateral edges are characters of much interest in the young of turtle-doves. Old types reach adult conditions in their first feathers; *e.g.*, the turtle-dove gets its characteristic light edges in the juvenal plumage.[16]

The first young Japanese turtle-dove that I examined seemed to have its entire adult pattern in the first feathers. I have now seen other young as well as many young European turtles, and I find that it is necessary to distinguish in the first feathers the tips and the lateral edges. The tips (apical edges) in Japanese turtles have a decidedly paler color than the lateral edge, the lateral edge being here more nearly the equivalent of its adult color. This distinction is particularly evident in the European turtle, which is much lighter in color than the Japanese. I find, however, that the distinction also holds, though in a lesser degree, in *orientalis*. In this species the difference can not be seen on the scapulars, upper long coverts, and

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[14] It will later be seen, in the geopelias and other forms, that this midfront line and the parts immediately adjoining it are points that differentiate themselves from the rest of the body plumage.

[15] In the young a barred effect on the wing and scapulars is produced, owing to the fact that the crescentic rufous edges of adjacent feathers match so well (reminding of *Geopelia humeralis*). These rufous bars of course alternate with dark bars, which are broader than the reddish or fulvous bars. This is a very simple type of barring, and possibly the starting-point for bars repeated from the tip towards the base, centripetally or basipetally.

[16] The blue-jay gets the adult pattern in its first feathers, and even the head-crest is there but little less developed in the young than in the old.

tertials, all of which have about the same color at the tips and lateral edges as in the adult. But farther down on the body the feather-tips lighten up, more or less, and at least some few of the central barbs of the tip will show the lighter color.

The third long covert (counted downward) of *Turtur orientalis* is compared with the same feather of *T. turtur* in figures 2 and 3, plate 22. The rufous tip of *orientalis* is about 2 mm. wide, and it lightens up gradually, becoming cinnamon-brown only at the very edge. There is no well-defined tip distinct from margins in the particular feather drawn, but in the covert that grew next to it there is also a little of the apex that is pale. The dark center is here much broader than the same feather of *turtur*, but this center varies in extent and intensity in both species, although the maximum in *turtur* is less than the minimum in *orientalis*. The European turtle-dove is losing these spots.

In *orientalis* the primaries are also rather widely margined with rufous, and remind strongly of young *Ectopistes*, which is similarly marked, though to a little less degree.

Can we say, then, that the light edge seen in all the pigeons in the first feathers indicates a turtle-dove ancestry? I still think so, although it can not be said that

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EXPLANATION OF PLATE 20.

The original feather color-pattern, as shown in a female Japanese turtle-dove, *Turtur orientalis*. Figs. 1 to 18, × 1; figs. 19–24, × 2. Hayashi del., May 1903. All feathers from right side of bird.

Figs. 1 to 4.—A series running from before backward in the interscapular region of the back. All have a fulvous margin, duller than on wing-coverts and scapulars. Shafts of feathers dark and whole feather gray, darkening somewhat in distal half (this darkening is quite gradual, scarcely showing so strong a concentration as the artist represents).

Figs. 5 to 8.—A scapular series running from front to rear end. Black and pointed centers here become stronger, and red tips more clearly marked off.

Figs. 9 to 16.—Wing-coverts: second row long coverts, counting from behind forward, running from above downward, or from inner to outer to below middle of row. Here is the typical pattern for the turtle-dove well defined. The blackish centers pale into brown-gray on Nos. 15 and 16.

Fig. 17.—An upper long covert (first row).

Fig. 18.—The same from a female hybrid between a male chequered homer and female Japanese turtle. Here the fulvous turns into a dull cinnamon that blends with the gray-brown center, which is not sharply defined in any of the feathers.

Fig. 19.—First of second row of neck-spot, anterior end of row.

Fig. 20.—Fourth of third row of neck-spot.

Fig. 21.—Sixth of fourth row of neck-spot.

Fig. 22.—Fifth of fifth row of neck-spot.

Fig. 23.—Fourth of sixth row of neck-spot.

Fig. 24.—Third of seventh row of neck-spot.

The feathers of figures 19 to 24 have tips of gray. The black portion is seen but little if the feathers are drawn close. We have here the same dark center, obtusely pointed, and a gray tip instead of light or fulvous tip; this gray is a higher stage, and white is higher still.

EXPLANATION OF PLATE 21.

Feather pattern in the European turtle-dove, *Turtur turtur*. Figs. 1 to 17 × 1; figs. 18 to 23 × 2. Hayashi del., Apr. 1903.

Figs. 1 to 6. A series of back feathers (interscapulars).

7 to 10. A series of anterior scapulars.

11 to 16. Second row of long coverts, from above to below middle of row.

17. Upper feather of upper row in neck-spot.

18. Anterior feather of upper row in neck-spot.

19. Third feather of second row in neck-spot.

20. Fourth feather of third row in neck-spot.

21. Sixth feather of fourth row in neck-spot.

22. Fourth feather of fifth row in neck-spot.

23. From mid-back of second row in neck-spot.

In general this type stands above the Japanese turtle in (1) a reduction in area of the black center and in giving it a sharper definition; and (2) in the whitish or very pale gray edges of the feathers of the neck-spot.
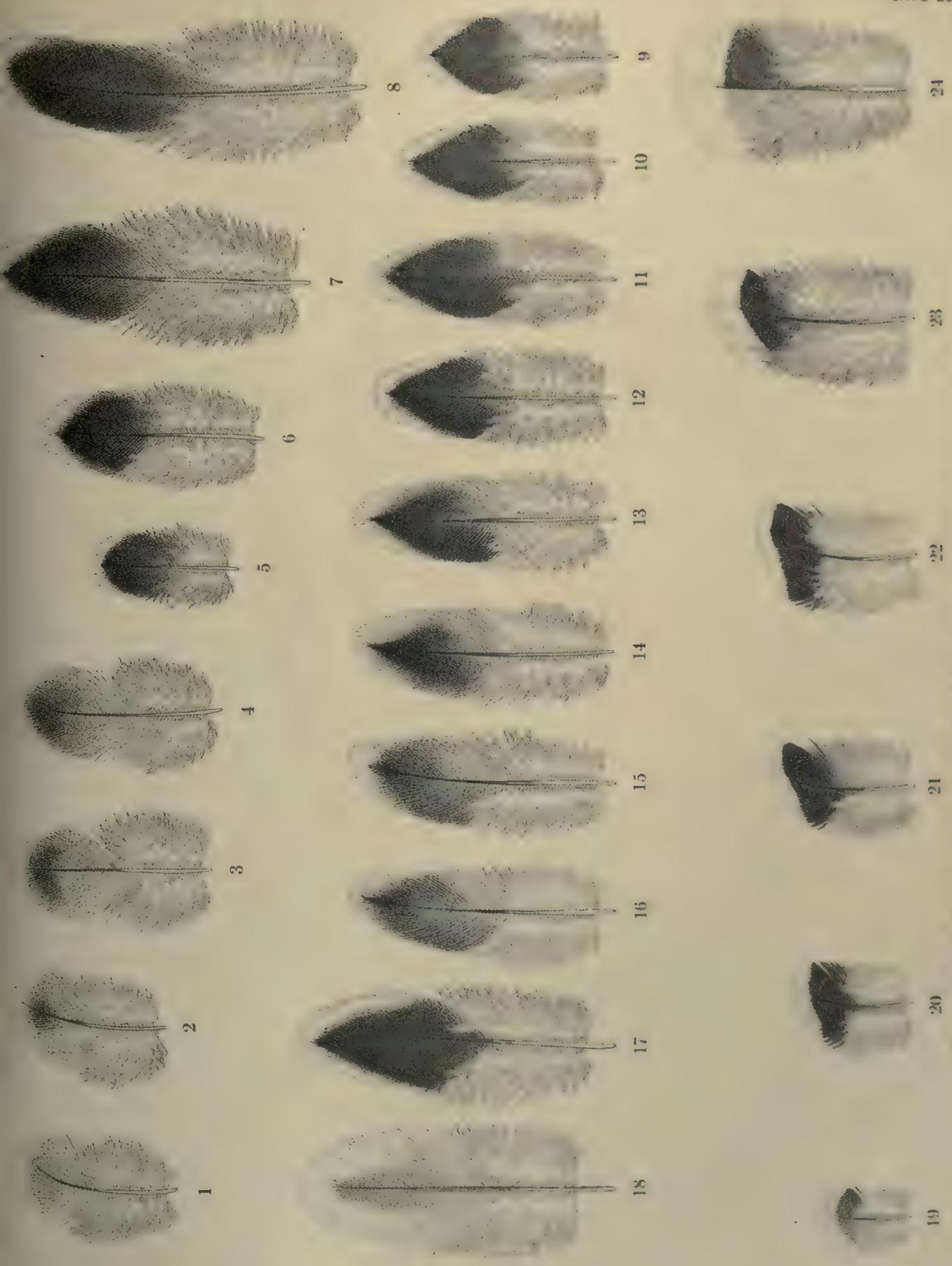
PLATE 20

The original feather color-pattern, as shown in a female Japanese turtle-dove, *Turtur orientalis*.
Figs. 1 to 18, × 1. Figs. 19-24, × 2. Hayashi del., May 1903.

PLATE 21

Feather pattern in the European turtle-dove, *Turtur turtur.* Figs. 1 to 17 × 1; Figs. 18 to 23 × 2.
Hayashi del., Apr. 1903.

this light edge is homologous with the whole fulvous margin. This margin has been widening and has now become much wider than it was originally.[17]

In the young of *turtur*, the dark center is reduced—*i.e.*, it retreats farther from the feather margin (fig. 3, pl. 22)—and here the rufous lateral edges are wider than in *orientalis*, the rufous seeming to take the place of the retreating black.

In these feathers the tip is cinnamon-brown, only a shade darker than the down itself, and is 1.3 mm. wide at the center, from which it narrows outward. There is no concentration of dark pigment bordering the proximal side of this tip—such as I see in *Streptopelia humilis, Stigmatopelia senegalensis, Streptopelia damarensis* (figs. 4 and 5, pl. 22), and other forms that have lost or much reduced the dark center.

The third long covert (counted downward) may be said to have the pattern in typical form for this European species. Here the feather's base is gray, becoming distally dark gray, and passes into black in the distal half of the center, the black becoming pointed and reduced to a shaft-line which reaches, but does not extend into, the light tip. The rufous margins are of very considerable width, easily attaining 5 mm. The rufous of the margin has a sprinkling of blackish beginning on its inner half and increasing towards the dark center, thus blending with the center, so that we have no sharp boundary.

In the breast-feathers of a juvenal *turtur* (about 2 weeks old), and in the same feather of its nest-mate, I find what I had not previously noticed in other young turtles—a pale, whitish shaft, or a narrow shaft-streak, expanding at the feather's tip into a *triangular cinnamon-brown spot*, comparable in shape and position with the apical spot seen in the robin and some other forms. (Later, I recognize in this mark of the turtle-dove an indication of the guinea-pigeon's apical mark of white.)

The breast-feathers are all tipped with the cinnamon-brown and the median spot forms part of the tip or pale edge; *i.e.*, the color of the spot and the edge are the same and continuous. In other specimens of European turtles I do not recognize this median streak and spot. Neither do I see it in the Japanese turtles.

Among the speckled-neck doves (*Spilopelia*) we find the black center further reduced. In the Surate turtle of Latham (*Sp. suratensis*) Salvadori (p. 445) notes that the "black contracts to a central streak," and that this reduction is accompanied by a modification (in the scapulars and upper back feathers) of the pale edge into "two pale vinous isabelline spots"[18] (pl. 24, Vol. II); in the tiger turtle-dove

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[17] The author later noted the neck-mark, dark center and pale tip of *orientalis* and *turtur* in *Turtur ferrago*. Salvadori's description (pp. 400 and 408) makes it clear that all these are also present in the two remaining species, *T. isabellinus* and *T. lugens* of the genus *Turtur.*—Ed.

[18] The Surate turtle of Latham (*Spilopelia suratensis*), in its juvenal stage, represents, in its color-pattern, quite closely *Sp. tigrina*. The female does this more closely than the male. I have a pair now (July 1910) in full juvenal plumage. The male shows in its scapulars a decided step towards the adult pattern—most of these feathers showing the "two pale vinous isabelline terminal spots, enlarging and spreading upon each side of the feather" (*vide* Salvadori, p. 445). The coverts of the whole wing exhibit the "dark mesial stripes" of the tiger turtle. The female shows less of the pale isabelline spots on the back, and its wing-pattern closely resembles that of the tiger turtle.

I have preserved three of the posterior scapulars of the right side of the young male in order to show the spots and at the same time to show that these spots are nothing but transverse bars in origin. Every feather in the juvenal stage of all pigeons has a more or less pale-brownish apical edge. This apical bar is followed in the Surate turtle by a dark bar, and this by another pale bar. It is this subterminal second pale bar out of which the pale-isabelline spots arise. The evidence of this is plainly seen in these plucked juvenal feathers; the identity of the spot with the second pale bar is well shown. The enlargement of the lateral elements of the bar takes place through the suppression of one to several of the subterminal dark bars, the light bars thus coalescing to form the two "terminal spots."

The case of the Surate turtle is not an isolated case. Out of these same transverse bars arise the pair of white dots on each of the wing-coverts in the little diamond-dove (*Geopelia cuneata*), as I have found out by studying the juvenal plumage. These transverse bars play a great rôle in giving rise by modification, fusion, etc., to specific color-types.

6

(*Sp. tigrina*) the dark center is reduced to a narrow mid-streak. In still another, the Chinese turtle (*Sp. chinensis*), it is absent (pl. 23, fig. A).

The evolution of the dark center in these forms, then, was as follows: We have to start with a form most nearly represented in *Turtur orientalis* of China and Japan. The centers of the wing-feathers have the black rounded out full behind, leaving only the apical reddish bar or tip.

In *Turtur turtur* of Europe the dark center becomes reduced, ending in an angular point behind.

In *Spilopelia suratensis* the black is still further reduced—to a *dark* mesial stripe (and has also bifurcated neck-feathers).

In *Spilopelia chinensis* even the mesial stripe has departed, and the neck-feathers, tipped with white, are bifurcated. In these two last-named species we have the neck-feathers not only bifurcated, but a large number of rows are differentiated.

EXPLANATION OF PLATE 22.

1. Left wing of an adult European turtle-dove, *Turtur turtur*. Natural size. Hayashi del., Sept. 1898. For comparison with wing of the Japanese turtle (text-fig. 3). (Figs. 2 to 5 × 2/1, Hayashi del., 1903–08).

Dark centers smaller in size and more pointed or angular at tip; the pale edges correspondingly increased in width. These modifications effect their most striking change in the appearance of the wing in its anterior part.

2. Third (inner) longer covert of juvenal (4 weeks) *T. orientalis*.

The pale tip is 2 mm. wide, and the dark center leaves only slender lateral edges.

3. Third (inner) longer covert of juvenal (2 weeks) *T. turtur*.

The pale tip is 1.3 mm. wide; the black rufous lateral margin is 5.5 mm. wide at its widest part. Practically only the shaft is black at the most narrowed posterior extremity of the black center; the black of the shaft reaches to but does not invade the pale tip.

A description and comparison of the posterior scapular in *orientalis* and *turtur* follows:

T. orientalis.—Posterior scapular. The black is more extended and the brown less extended than in *T. turtur*. The basal part shades into gray.

T. turtur.—Posterior scapular. Cinnamon-brown margin, black center arrow-pointed. Basal half gray, grading into black center, which fades into a trace of gray at its border.

The third tertials compare as follows:

T. orientalis.—Third tertial, *i.e.*, next above longest. The brown in these feathers is darker and richer than in *T turtur*.

T. turtur.—Third tertial. The black spot is arrow-pointed. Posteriorly the brown or dark center fades into gray at the basal half.

In both species the pointed black centers mark all of the feathers of the upper surface and wing, being larger and generally less pointed in *T. orientalis* than in the other species. There is not an indication anywhere that the black center represents a fusion of two spots.

4. Third (inner) longer covert of juvenal *St. damarensis*.

5. Third (inner) longer covert of juvenal *Stig. senegalensis*.

These four figures show that the dark center and pale edge of the *T. orientalis* pattern is present in all these species, and is most modified in the less closely related *Streptopelia* and *Stigmatopelia*.

EXPLANATION OF PLATE 23.

A. Adult Chinese turtle-dove, *Spilopelia chinensis*. × 0.7. Hayashi del., Dec. 1903.

No dark centers in the general plumage, present only in the neck-mark.

B. Fifth feather (natural size) third row (right side) of the neck-mark of Chinese turtle (same as fig. A). Shows strong bifurcation, white tip, and dark center.

C. Wing of juvenal mourning-dove and ring-dove (female parent—*alba-risoria* × *risoria-alba* hybrid) hybrid; hatched May 9, 1899. Natural size. Hayashi del., June 6, 1899. 4 weeks old.

There are three small pale gray spots visible on the upper long coverts, and a fourth spot on the next tertial below; the latter spot is entirely concealed.

On the next row of coverts, at the same level, are three smaller spots, similarly placed at the lower edge of feathers. On one or two of the upper tertials just a trace of a streak may be seen.

This picture should be compared with the juvenal *Melopelia leucoptera* (text-fig. 14). The influence of the ring-dove (chequers wholly lost from the wing) mother does not lead to a suppression of the chequers of *Zenaidura*, but to a reduction to a stage nearly that of *Melopelia*.

PLATE 22
7 2
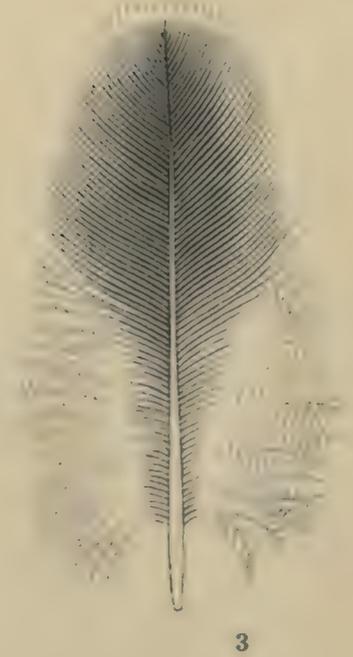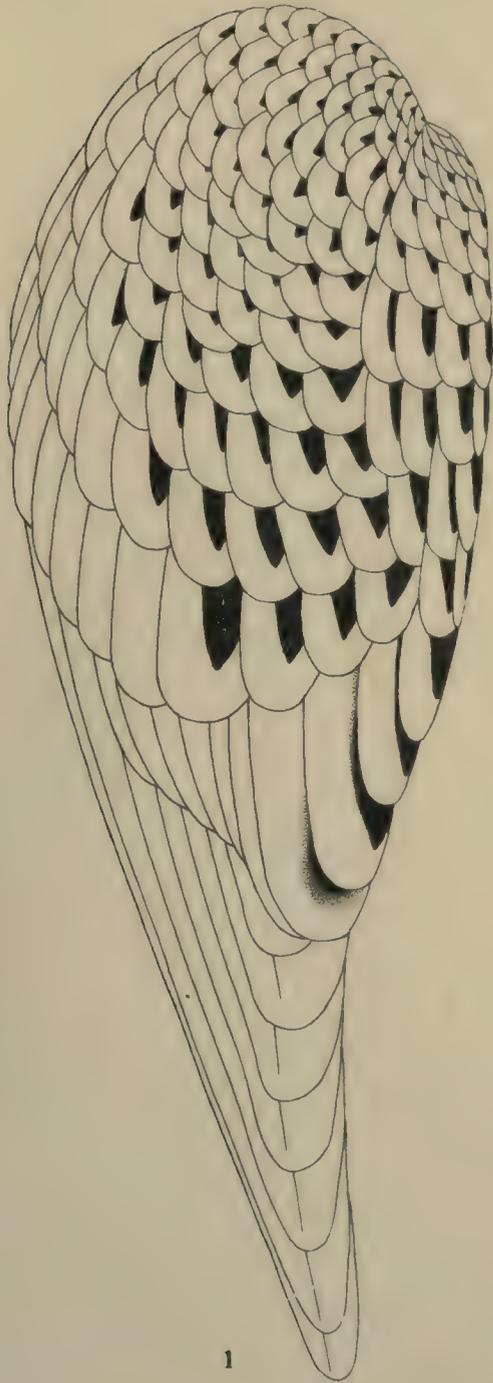
1. Left wing of an adult European turtle-dove, *T. turtur.* Natural size. Hayashi del., Sept. 1898.
2. Third (inner) longer covert of juvenal (4 weeks) *T. orientalis.* × 2.
3. Third (inner) longer covert of juvenal (2 weeks) *T. turtur.* × 2.
4. Third (inner) longer covert of juvenal *St. damarensis.* × 1.
5. Third (inner) larger covert of juvenal *Stig. senegalensis.* × 1.

PLATE 23

A. Adult Chinese turtle-dove, *Spilopelia chinensis*. × 0.7. Hayashi del., Dec. 1903.

B. Fifth feather (natural size) third row (right side) of the neck-mark of Chinese turtle (same as fig. A). Shows strong bifurcation, white tip, and dark center.

C. Wing of juvenal mourning-dove and ring-dove (female parent—*alba-risoria* × *risoria-alba* hybrid) hybrid; hatched May 9, 1899. Natural size. Hayashi del., June 6, 1899. 4 weeks old.

Running back to *Turtur orientalis*, we come to entire neck-feathers and fewer rows—six down to only three or four. An extension of differentiation towards the mid-back of the neck has occurred in the derived forms, the two spots here coalescing plainly for the upper three or four rows.[19]

It is clear that there are two modes of reducing the original black or brown centers: First, by the guinea-mark (the white or light-colored wedge-shaped extension of the light apical edge) splitting the center into paired chequers; second, by reducing the center through an extension of the whole of the pale feather border. It is this second method—or extension of method[20]—that has been effective in the Turturinæ. It is in this way that the somewhat narrowed and pointed centers of the European turtle, the narrow mesial stripes of the tiger and Surate turtles, and the dark shafts of the red ring were formed. Evidence for this latter conclusion, from an hitherto unmentioned source, is easily obtained by hybridization experiments. Crossing the Japanese turtle with, for example, the blond ring-dove, which has a whole color—no spots except in the collar—we obtain in the hybrids feathers whose indications of dark centers are confined wholly to their shafts, or to their shafts and the immediately adjoining parts.[21]

The *pale tip* or brownish edge of the feather varies in *orientalis* and *turtur* in a reverse direction to that of the dark center, the tip being relatively wider and more pronounced in *turtur*. Although the juvenal pattern in both of these species is identical in the main with the adult pattern, we may note some differences:

(1) The fulvous-edged feathers in the young include not only the wings, scapulars, back, and tail-coverts (as in the adult), but also the feathers of the neck, breast, and even those of the head, which in the adult are not so edged, but are uniform gray-brown.

(2) The fulvous edges are more nearly straight in the juvenal plumage, owing to the form of the feathers.

(3) The fulvous edges are, in general, paler in the young than in the adult. The tertials and posterior scapulars are practically the same as in the adult.

This light apical edge seems to be universal in birds.

Other features of the color-pattern of some of the collared doves (*Streptopelia*) than the neck-mark, already referred to, indicate the direct derivation of these species from a form like *Turtur orientalis*.

The 13 species[22] have all lost their dark spots everywhere except in the black collar, and the only remaining visible trace of the spots elsewhere is the narrow light edge shown at the tip of each feather in the juvenal plumage (pls. 16 and 17, Vol. II). The reduction process has not only washed out the spots, but has also advanced from the darker brown-red color to gray, isabelline, and blond, and finally to pure white (*Streptopelia alba*). Albinism is the finishing stage of this reduction process.

The little red ring-dove (*St. humilis*) stands nearest to the turtle-doves both in color (pl. 21, Vol. II) and behavior. In this species the red is but an extension and intensification of the light edge of the turtle-dove feather. In its adult feathers the light or pale edge is wholly wanting; but in the first feathers we have a neatly

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[19] The neck-marks of the several species here mentioned were separately drawn —much enlarged—and are shown and described in Chapter XVII of Vol. II.—Ed.

[20] The whole of the pale edge instead of the ontogenetically older part of it—the apical edge —here takes part in the invasion of the black.

[21] This median streak curiously appears in several of my young pouters (of this year—1910) which have fallen back from a very light gray with white bars to a much darker gray with red bars bordered with a narrow black.

[22] Later (see Chapter XV, Vol. II) Whitman recognized 17 species in this genus.—Ed.

marked edge—pale yellowish-brown crescents—on all the feathers; these, however, are best marked on the wing. The rest of the middle part of the feather (exposed part) is a uniform brown, darker in the male (pl. 21, Vol. II), lighter in the female.

I have frequently noticed further that the young birds, in many of the wing-coverts and scapulars, have the dark pigment more concentrated on the inner edge of the light margin, giving an appearance that reminds of the dark crescents within the pale margins in the young geopelias.[23] Proximally of this dark bar I usually see an irregular but plain light transverse band—a kind of imperfect or incipient bar.

Again, the vinous red of the adult seems to be an extension of the reddish edges of the turtle-dove's feathers. Lifting the feathers, we see that their basal portions are dark gray, the dark gray frequently extending farther on one web than on the other. The gray center has simply been reduced so that the uncovered part of the feather is all vinous red.

The juvenile feathers of this species give strong evidence of its turtle-dove ancestry (pl. 21, Vol. II):

(1) The pale yellowish-brown edges of the feathers incline more to red on the primaries.

(2) The neck-spots are always present, sometimes quite strong; but they never meet on the back of the neck.

(3) The mid-ribs of the feathers (coverts of wing) are distinctly dark—a final stage in the loss of dark centers, as shown in hybrids of ring-doves and turtle-doves.

(4) One feature is particularly significant. On the tertials (upper inner secondaries) and on the third or fourth posterior rows of coverts we see that the lateral edges as well as the tips are pale; but the lateral edges are decidedly more reddish than the tips, quite closely following the plan seen in the Japanese turtle-dove young. The color is here not so strong as in the turtle-dove, and it is not so well delimited towards the central field of the feather. In fact, it extends inward rather diffusely to or near the mid-rib on the lower web more than the upper (inner) web. There is a subterminal concentration of dark pigment following the light edge, as if light and dark alternated in the manner of transverse bars.[24]

The probable relationship of several genera of pigeons is indicated in the following diagrams:[25]

T. orientalis
T. turtur
St. humilis
St. douraca
St. risoria
St. alba
Spil. tigrina; Spil. suratensis
Spil. chinensis
Columbidae (e. g., C. palumbus)

Derivation of species of Turturinæ[26] and part of Family lu Combidæ.

Turtle-dove type
Nesopelia
Chamaepelia
Zenaidura
Zenaida
Columbidae (e. g., Ectopistes migratorius)
Melopelia

Derivation of genera of Zenaidinæ and part of Family Columbidæ.

[23] This appearance is also strikingly simulated in the dark borders to the red chequers borne by certain homers I have seen.

[24] Stigmatopelia senegalensis, not described here, is figured in plate 27, Vol. II.—Ed.

[25] These diagrams have been constructed by the editor. The materials used in their preparation are as follows: The statements already given in this chapter; data found elsewhere in this volume; data given in Vol. II—particularly in Chapters XII, XIII, XV, and XVII, and in the explanations of plates illustrating those chapters; data on behavior in Vol. III.—Ed.

[26] Professor Whitman was convinced that all doves having a "coo" of three syllables are derived from the Japanese turtle.—Ed.

THE ZENAIDINÆ.

The genus *Nesopelia*, represented by a single species (*galapagœnsis*), is the only member of this subfamily which is fairly evenly chequered over the whole wing (see text-fig. 13), and this condition stamps it as the oldest member. The single specimen which I have examined shows that the feathers of the wing bear, as a rule, each *two* spots. The outer spot is the larger, and as we pass from the inside outward the spot on the inner web becomes rapidly smaller until at last it is only a *marginal streak;* feathers beyond this point bear only one chequer, that on the outer web. The chequers are mostly rounded distally.

On the inner tertials there is a plain asymmetry in position of the two spots as in *Zenaidura*. The secondaries have black spots, so that here we get the essentials of a posterior wing-band, which is so pronounced a feature of the pattern in some *Columba* and in still other groups.

In the mourning-dove (*Zenaidura carolinensis*) the male (in color, pl. 19, Vol. II) and female differ but slightly, each having about a dozen chequers visible on each side. These are confined to the scapulars (see pl. 24) and to a few feathers at the posterior upper edge of the wing. In the young (pl. 7) the spots are more numerous, though weaker and not so well defined (pl. 25). The ground-color is also weaker in the young. The pale edge is present in the young and absent in the adult.

The middle and fore parts of the wing in the adult have no visible chequers, but a few concealed ones which may be seen on lifting the overlying feathers. These concealed chequers and the differences between old and young show that the species had its origin in a chequered stock and has suffered a reduction of dark spots.

In the genus *Zenaida* the reduction of the spots or chequers has been carried somewhat further. In this respect *Z. amabilis* (pl. 87) does not differ appreciably from *Z. vinaceo-rufa* (pl. 83). The young of this group also have a much greater number of chequers than the adults.[27] The scapulars and tertials have, moreover, smaller spots and fewer double spots (pl. 24) than do those of *Zenaidura*.

Some of the juvenal feathers, notably those of the breast, have a rufous mid-streak which near the tip of the feather gradually widens out to include or become continuous with the pale apical edge (this mark was the foundation for the sudden appearance of the broad white "guinea-mark" which appeared in a *Zenaida* of 1906. This mutation is described in Chapter IX. [The reader will find other references to this character in the pages which follow.—ED.]

The genus that stands highest in this group is *Melopelia*. Our white-winged pigeon (*M. leucoptera*) has practically completed the deletion of spots (text-figs. 8 and 14), only a few vestigial traces being discoverable in a single specimen obtained from Jamaica. I do not find such vestiges in white-wings from Mexico and Arizona. *Melopelia* is therefore to be classed as the latest branch of this subfamily.

The neck-mark of this species—and of all species of Zenaidinæ—presents an interesting and very considerable modification (pl. 26) of the turtle-dove neck-mark. The mark here extends farther upward (closer to the auriculars) and consists of two parts—an uppermost black spot and a structurally modified or iridescent area.

The young of *Melopelia* have been found to have rudimentary or obsolescent spots. These are so nearly faded out and so nearly covered that one would not notice them unless looking especially for them. Their color is dark gray, and they

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[27] For the pattern in a *Zenaida* × *Zenaidura* hybrid see plate 20, Vol. II; for a hybrid composed of these two genera and *St. risoria* see the same plate.—ED.

A and B. From adult female *Zenaidura carolinensis* (11). Natural size. Hayashi del., June 1907.

FIG. A. 1, 2, 3, 4, four inner longer scapulars (left side). On 1 and 2 a single inner marginal spot. Asymmetrical spots on 3 and 4.

FIG. B. 5, 6, 7, 8, four inner tertials (left side). All spots of the scapular series are strengthened here, and all are asymmetrical, with the inner spot the stronger of the pair.

Measurements are omitted by the editor. All spots stronger than in *Zenaida* (figs. 3 and 4). Compare with juvenal inner tertials, pl. 41, figs. D, E.

C and D. From adult male *Zenaida vinaceo-rufa* (11). Natural size. Hayashi del., Mar. 1907.

FIG. C. 1, 2, 3, inner longer scapulars (left side). All spots are weak, thin marginal streaks.

FIG. D. 4, 5, 6, three inner tertials (left side). The lower (outer) spots shorter (as in scapulars), oblong or elliptical. No. 6 not quite so strong and definite in outline as No. 5.

Measurements are omitted by the editor.

E. Third tertial from a hybrid (ZZ–A 1); the sire was a hybrid *Zenaida* × *Zenaidura*; the dam was a white ring-dove (*St. alba*).

The influence of the dam—a species that has gone far past dark centers and spots—is not sufficient completely to efface the spot, but levels it to its weakest form, mainly to a very thin marginal streak.

Selected feathers from the juvenal mourning-dove, *Zenaidura carolinensis*. Hayashi del., Feb. 1904.

Figs. 1 to 3. Three smaller coverts (right side, × 2). In Nos. 1 and 3 there is a tinge or trace of pigment on the right (lower) web—quite at the edge.

Figs. 4 to 7. Scapulars from before backward to about the middle of scapular region (× 2). Black gradually appears on the right (lower) web. This means that black in the center of the distal end of the feather has disappeared, leaving an increasing trace of a lateral spot.

The young feathers show that the clear-cut spots of the adult are probably derived from elongated patches, parts of a dark center.

Figs. 8 to 11. Tertials, or inner secondaries (right side).

Fig. 12. Second feather in right side of the tail.

The outlines of these spots are less distinct than in adult tertials (see pl. 24). The pale edge is scarcely differentiated in these figures.

A. Neck-mark of adult male white-winged pigeon, *Melopelia leucoptera*. Hayashi del., Dec. 1902.

This species has the black spot close under the auriculars; its position is the same as in the mourning-dove, but is larger in the white-wing. The iridescence here is bronzy.

The rows of feathers that are spotted in the turtle-dove are here iridescent (shown by lighter shading). It is remarkable that the ornamentation in color should here be carried higher up, and that the iridescence also moves up with it. The upper row of black is continued backward into iridescent feathers, and the iridescence can be seen for one to two or three rows higher still, to about the upper boundary of the ear-coverts. The iridescence extends downward from the uppermost black row over about 8 or 9 rows, to about the mid-height of the neck. None of these black feathers of the spot have any trace of white tips.

The feathers, through the black spot and the iridescent area, are not so sharply cut at the tips as in the turtle-dove and the ring-dove, but these feathers are cut a little shorter and the barbs are a little closer and more trim than feathers elsewhere. In other words, the differentiation is, though in lesser degree, similar to that of the turtle-dove (× 2/1).

FIG. 1. First feather of second row, left (× 2.75).

2. Mid-feather of third row, right (× 2.5).

3. Last feather of third row, left (× 3); right half is iridescent.

In this specimen there are only four rows of black feathers. A female that has just died shows five rows, and I think some birds have as many as six. These feathers in favorable light exhibit a greenish or purplish or in some cases an indigo iridescence.

B. Neck-mark of adult male mourning-dove, *Zenaidura carolinensis*. Hayashi del., Dec. 1902.

In this specimen I find only two rows of velvety black feathers, some of which show iridescence.

The iridescence is purplish-red and covers the area of the turtle-dove spot and extends up to the auriculars. It is represented by light shade. These feathers are not cut so short as in the ring region of ring-doves, but they exhibit some differentiation even in the structure.

FIG. 1 (3). Middle feather of second row.

2 (3). Last (lower) feather of second row.

3 (2). About four rows below the spot; shaded part is bright purplish-red.

PLATE 24

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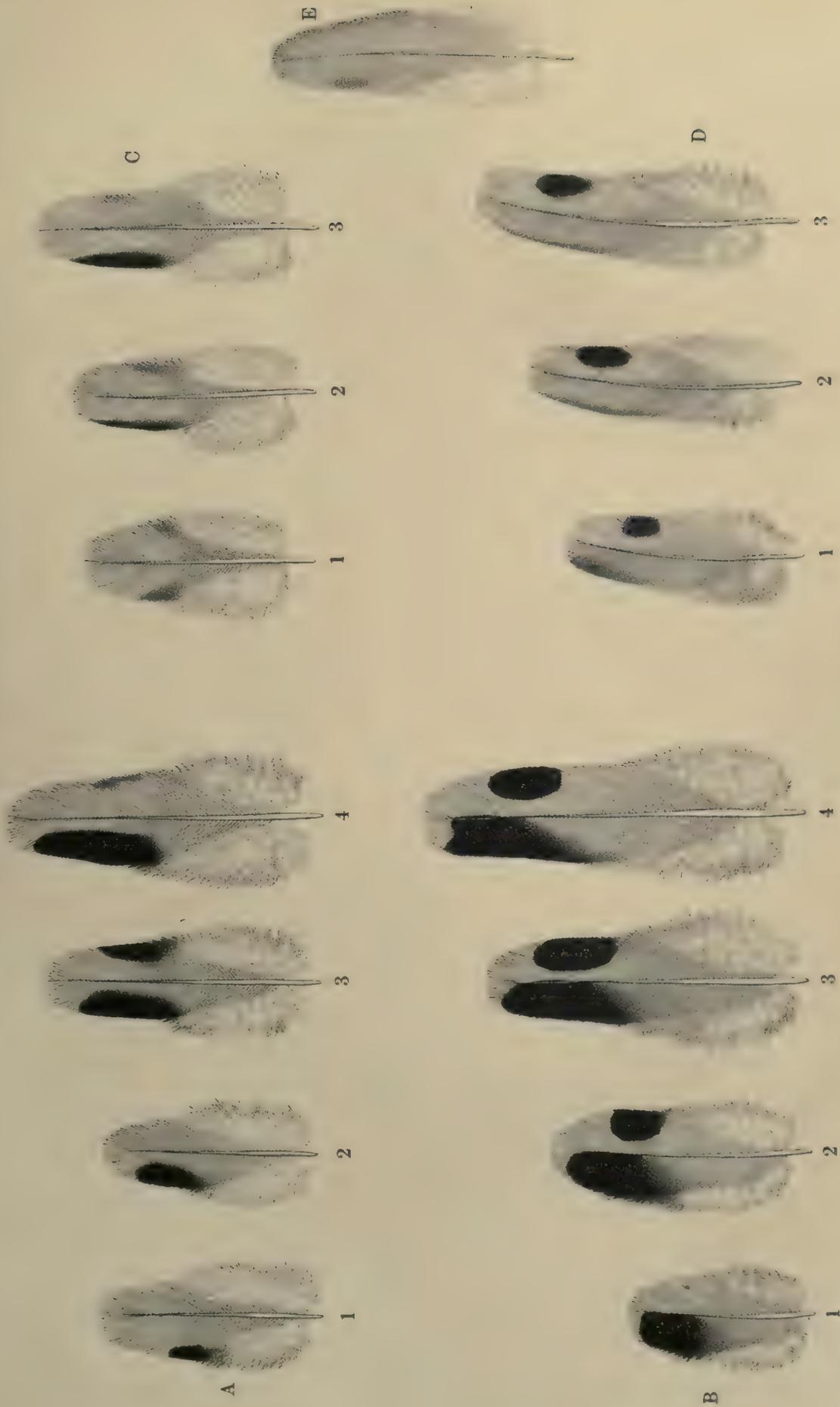
A and B. Scapulars and tertials from adult female *Zenaidura carolinensis* (11). Natural size. Hayashi del., June 1907.
C and D. Scapulars and tertials from adult male *Zenaida vinaceo-rufa* (11). Natural size. Hayashi del., Mar. 1907.
E. Third tertial from a hybrid (ZZ–A1); the sire was a hybrid *Zenaida* × *Zenaidura*; the dam was a white ring-dove (*St. alba*).

PLATE 25

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Selected feathers from juvenal mourning-dove, *Zenaidura carolinensis.* × 2. Hayashi del., Feb. 1904.

PLATE 26
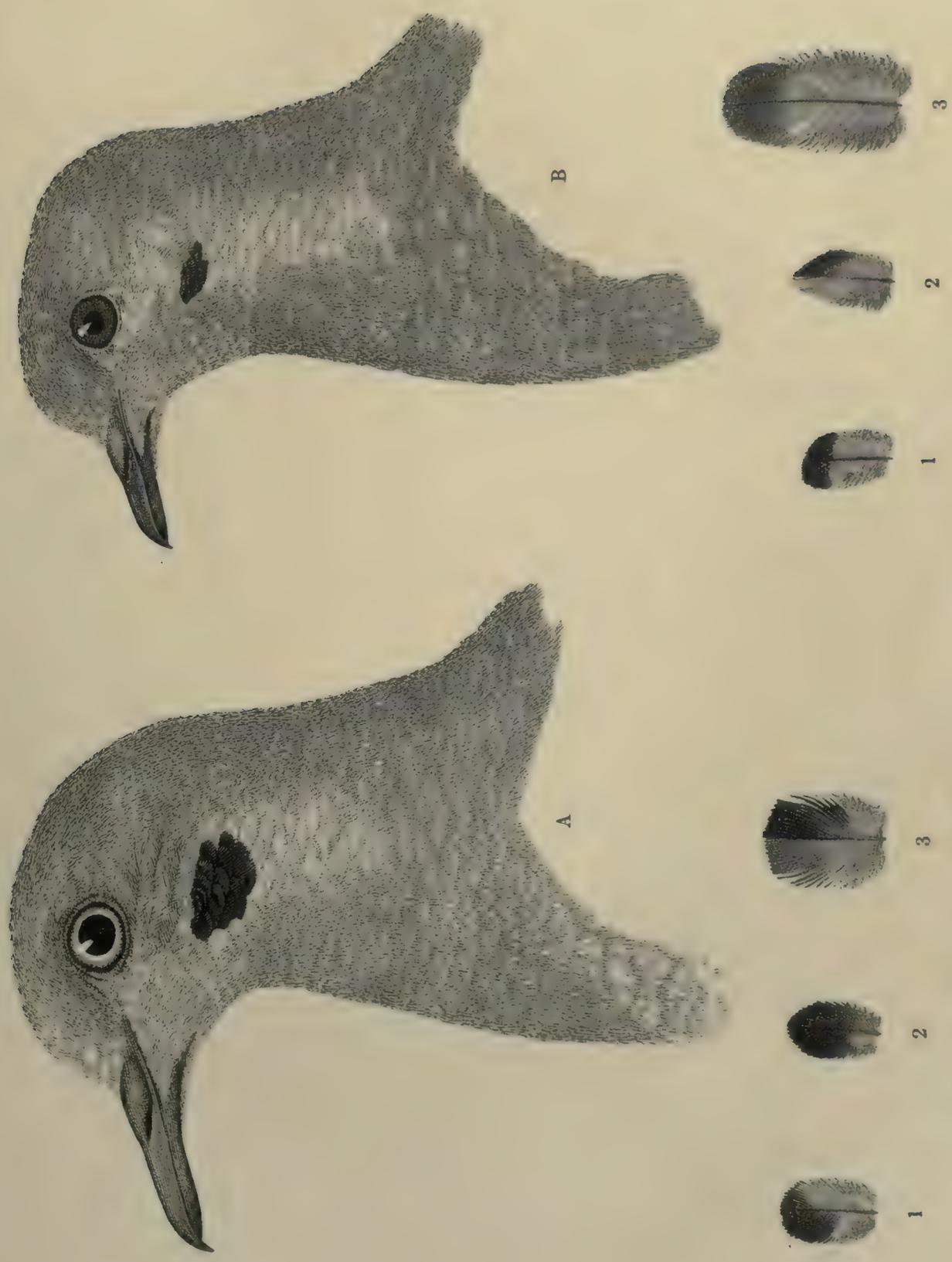
A. Neck-mark of adult male white-winged pigeon, *Melopelia leucoptera*.   × 1.5.   Hayashi del., Dec. 1902.
B. Neck-mark of adult male mourning-dove, *Zenaidura carolinensis*.   × 1.5.   Hayashi del., Dec. 1902.

are pointed posteriorly (text-fig. 14). There are only a few of them. A condition of wing-spots closely similar to this has been obtained (pl. 23, fig. C) by crossing *Zenaidura* (fairly strong spots) with ring-doves (no trace of spots).[28] I predicted that the young of this species (*M. leucoptera*), which in the adult has no spots, might show traces of spots. This is a good demonstration of my theory that the ancestral pigeon had elongated pointed spots.

THE PERISTERINÆ.

In some of the ground-doves (*Chamæpelia*) the turtle-dove pattern is preserved in the whole breast region and in the anterior, smaller coverts of the wings, while in the posterior portion of the wings spots or chequers are found. In many coverts of the wing we find the dark centers more or less reduced, with the distal ends of their remnants in various stages of conversion into lateral spots.

We may examine in detail the turtle-dove marks as seen in the Florida ground-dove (*Ch. passerina*). The forehead, sides of head, front and sides of neck, breast, and abdomen are bright purplish vinous in color (darker or more reddish than in the inca-dove). This vinous shade darkens to vinous-brown on the edges of the feathers, giving a scale-like appearance. The vinous lightens up on the sides of the neck and passes gradually into the darker color of the nape and hind-neck. These neck-feathers with their darker (not black) edges remind of *Scardafella inca* and of *Geopelia humeralis*.

The occiput and nape are light gray, edged with dusky—again similar to the inca-dove, though not quite so strong or dark. On the lower hind-neck I fail to see any crescentic dark edges to the feathers.

Aside from the resemblance to the inca-dove in color (dark edges of feathers) and behavior, this bird is especially interesting in that it preserves on its throat and breast, and to some extent on the sides of the neck, the old turtle-dove mark—the dark center of the feather pointed at the distal end (text-fig. 4). This same mark—obsolescent—may be seen on the wing-coverts, especially on the lesser coverts. On the scapulars, tertials, and long coverts the mark has wholly or nearly disappeared.

The next point of interest is that we find on the coverts and tertials the lateral spots seen in *Columba livia*, which are here "steel-blue with violet reflections," as shown in color, plate 29, figure B, and these spots coexist with the obsolescent dark (more or less dark-gray) centers.

Salvadori (page 477) has noted that this species is quite variable. In the wing of one male I find 26 spots; only 19 in another. On the lesser coverts I find, on lifting the feathers, that there is a plain, though pale, pointed central spot like the turtle-dove spot, and this spot fuses in some cases with the small black chequers.

I have selected a number of feathers from the left wing of the male having 26 spots to show the coexistence of the two forms of the mark in the same individual (pl. 27, fig. A).

There is no side-spot on the neck of this species, but the feathers run in very regular rows. The dark turtle-dove center is largest and most perfect on the front of the neck. On the breast the spots rather abruptly become narrower and cease

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[28] I find a dull reddish-brown mid-streak in most of the wing-coverts of juvenile white-wings. The color of this streak is the same as that I have seen in young geotrygons. (It seems probable that the author would later have identified this mid-streak with that (later found) in *Zenaida*. In the latter he has shown that the mid-streak arises as a median extension of the light apical edge to form an incipient "guinea-mark."—Ed.)

to be visible, except when the feathers are parted. The spots run into narrow and slender pointed streaks towards the abdomen, and then disappear wholly on the abdomen. The under tail-coverts show the same spots in brownish gray. The distribution of red on the primaries, and elsewhere on the wing, is best shown in plate 30.

The juvenal *Chamæpelia passerina* presents some interesting conditions. The coloration is weaker than that of the adult, but much more nearly approximates that of the female than that of the male. The spots or chequers resemble—more than do those of the adult—the posteriorly pointed chequers of the chequered rock-pigeons (*Columba affinis*). The feathers are all pale-edged (pl. 28, fig. B). The female plumage-pattern is in many respects an intermediate of the juvenal and the male (pl. 27, fig. B).

In these juvenal plumages one also finds convincing transitional stages, linking the central turtle-dove spot with the modified spots or chequers (pl. 28).

Still other species of *Chamæpelia* exhibit similar or more modified patterns. In *Ch. buckleyi*, according to Salvadori, brown and black largely replace vinous and cinnamon, respectively, of the *Ch. passerina* coloration. The breast-feathers have

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EXPLANATION OF PLATE 27.

A. Fifteen selected feathers from left wing, neck, and breast of an adult male *Chamæpelia passerina*. All figures × 2. Toda del., Mar. 1903.

FIG. 1. From mid-front neck. Shows turtle dark center in typical form—a dark-gray triangular area, with a broad vinous edge.
2. Mid lower front neck. The turtle center equally perfect in definition; color and shape same as above.
3. Mid-breast, between front angles of wings. Spot acuminate, pale gray.
4. From abdomen. Spot much reduced, pale gray.
5. Middle of side of neck, in ring region; central spot has vanished.
6. Small covert near front edge of left wing, next to scapulars. The turtle center is plain, though not quite so dark as in figure 1. Dusky gray and pointed.
7. From close behind figure 6. An obscure small dull-gray spot on left (lower) web, on which side the central spot retreats a little.
8. Nearer bend of wing. The dark chequer is here larger and stronger; the central spot retreats more on this, the side bearing the chequer.
9. From close beside figure 8.
10. From just behind bend of wing.
    Both 9 and 10 show the growth of the chequer and a one-sided reduction of the central spot. In all the chequers basal edge is less sharply marked than apical edge; the chequer seems to blend with the dark center.
11. From just behind bend of wing, shows plain fusion of chequer and center.
12. Middle of small coverts, fusion more complete.
13. From middle of third row of coverts, only a rudiment of a chequer, and an obscurely outlined center.
14. From middle of second row of coverts; dark center still perceptible.
15. The two uppermost long coverts; chequers more elongated.
    Some feathers corresponding (13 to 15) to these, from juvenal female and adult female, are shown in plate 28.

B. Five feathers corresponding to figures from male shown above. Toda del., Sept. 1903. × 2.

Figs. 1a to 5a from adult female *Ch. passerina*, same date.
Figs. 1a and 5a correspond to figs. 11 and 12 of the adult male (pl. 27).
Figs. 3a to 5a correspond to 2 to 4 of the juvenal female described and figured above, and to plate 27, figs. 14 to 16 (fig. 15 there represents two feathers).
The young have the distal third of the feather more brown. Adults have the distal third of feather more gray. The spots in the adults are less like typical chequers.
(1) The female is much nearer the young in general color than is the male.
(2) The spots point more directly backward—i. e., less transversely, and more like *C. affinis*.
(3) The edges of the feathers are more distinctly dark.
(4) In figure 5a a small spot is seen on right edge of feather—another more primitive feature not found in the male.
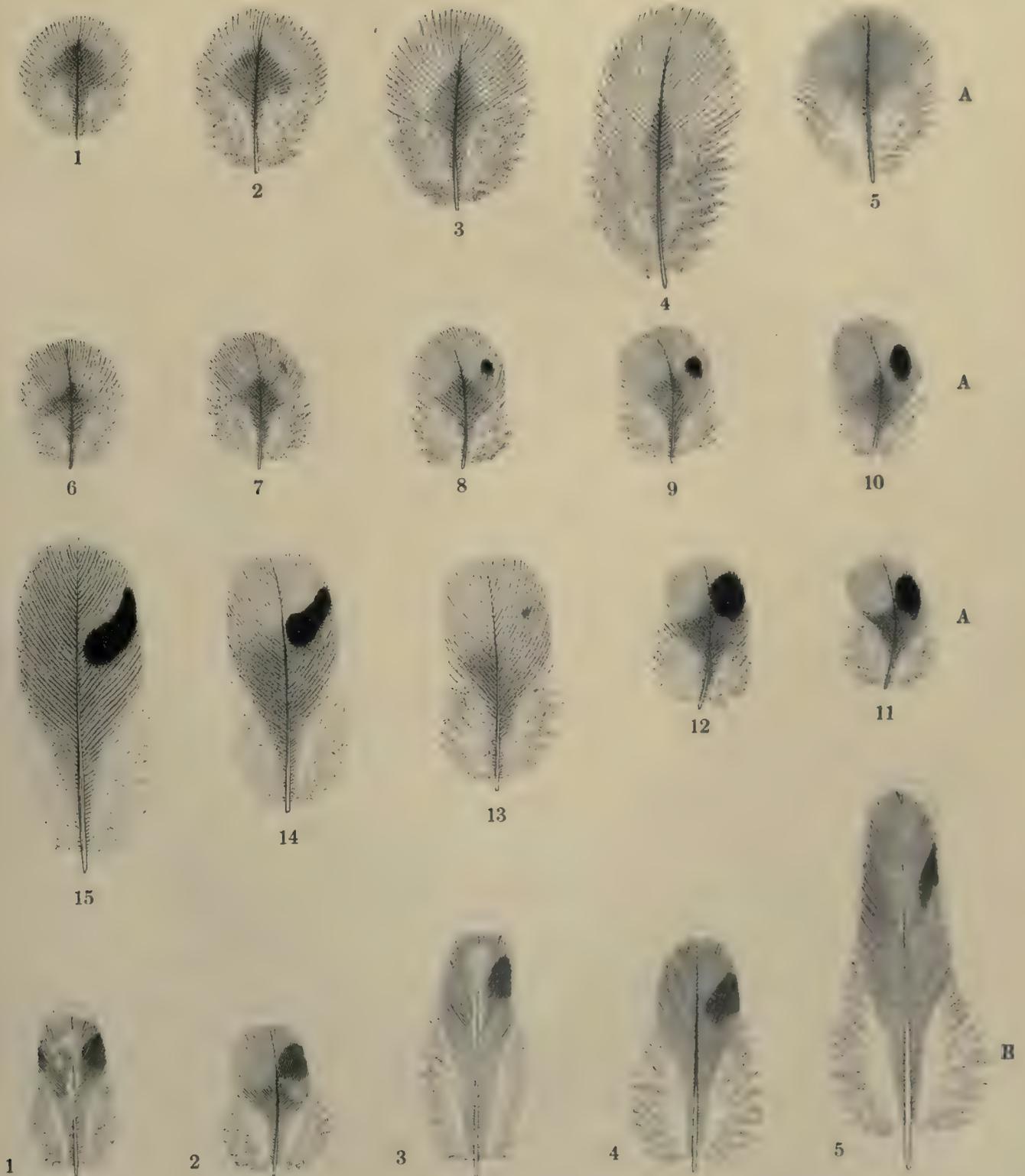
PLATE 27

A. Fifteen selected feathers from left wing, neck, and breast of an adult male *Chamæpelia passerina*. All figures × 2.   Toda del., Mar. 1903.

B. Five feathers from an adult female *Chamæpelia passerina*, corresponding to figures from male shown above.   Toda del., Sept. 1903.   × 2.

no dark centers (pl. 30, fig. B). In *Ch. pallescens* I find the pale edge, the median streak, and spots most nearly of the rock-pigeon type in the juvenal plumage. These are all absent in the adult pattern (pl. 30, fig. C).

Chamœpelia talpacoti lacks the dark center in the breast-feathers, and has a paler and more uniform coloration (pl. 29) than *Ch. passerina.* In the young[29] the upper parts are dusky reddish-brown. The scapulars and coverts have a *rufous* shaft-line, reminding of the mark of young zenaidas. It is noteworthy that the three inner tertials have black chequers on the outer margin, and that only the *innermost* one has in addition just a bare trace of a chequer on its inner edge—just where we should expect to find the trace or vestige if any remained. These chequers do not lie cross-wise or obliquely on the feather, but are pointed directly backward and follow along the feather's outer margin, leaving only a very narrow pale edge or boundary-line continuous with the apical mark. On the four inner long coverts the chequers are similar, though shorter, and wider at their anterior ends. These
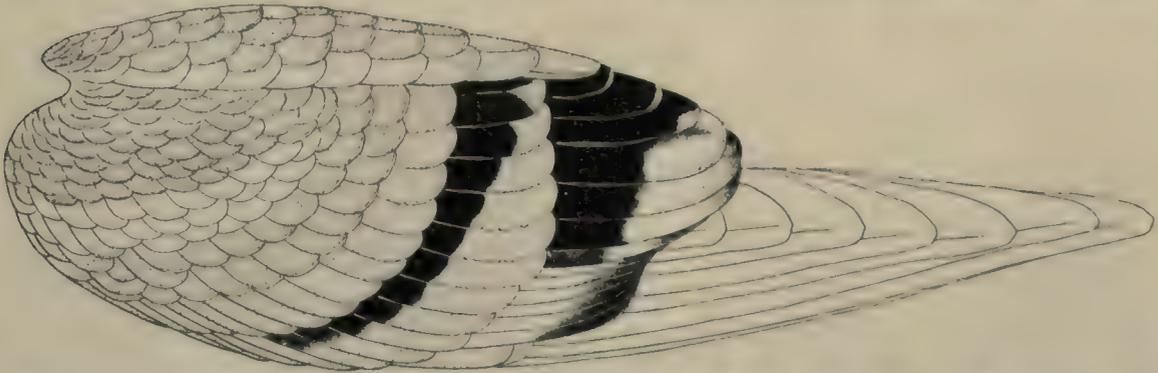
TEXT-FIGURE 15.—Showing the oblique streak in a common pigeon of 7 weeks and 2 days. This region—of the lower, anterior wing—is unshaded; the feathers of this area are gray, without the mixture of brown seen elsewhere. In this same region the adult color is quickly attained. × 0.7.

are again located on the outer web, and I fail to see any vestiges on the inner webs. The shape of all these spots or chequers of juvenal feathers is more like the typical rock-pigeon chequers than are the spots of adult feathers.

In the genus *Peristera* we find the wing of *P. cinerea* bearing numerous spots (pl. 31, fig. A), and some of the anterior lesser coverts showing the dark centers (pl. 31, figs. 1a–9), though these are less strong[30] than those of *Chamœpelia passerina.*

In the genus *Columbula* a wing-pattern of some interest is found. The wing of *C. piqui* bears *anteriorly*, in the oblique tract, only an isolated series of conspicuous chequers that might seem to suggest a character quite *new* in this field (pl. 32, fig. A). Glancing at conditions in some related genera—*Chamœpelia, Peristera, Geopelia*, and even in *Zenaidura*[31]—it becomes clear (pls. 32, 33) that these latter reveal

[29] The young described were out of a male from Brazil and a female supposed to have been trapped at Vera Cruz. See note to plate 29, figure A.—ED.

[30] Among a group of birds received from Brazil is one in juvenal plumage which I should call *Peristera cinerea.* The three inner tertials have each a pale spot on the outer web; the other tertials have no spot. The first four inner long coverts are spotted, with the fifth unspotted. The first five median coverts are spotted, with the sixth unspotted. One lesser covert from about the middle of the oblique streak has a fairly well defined spot. The spots in most of these feathers are remarkably shadow-like, especially on the median coverts and tertials. There is a median buff freckled streak in each of the median and long coverts. There are buff apical marks, and a faint trace of a subapical dark bar.

[31] It seems that no special illustration was prepared of the oblique bar in *Zenaidura.*—ED.

foundations for what is found in *Columbula*.[32] Moreover, a glance into a wholly different family, the Columbidæ, is worth while in a consideration of the status or origin of the *oblique wing-bar* of *C. piqui*.

In a 7-weeks-old common pigeon I find an *oblique light streak*, in which the feathers are gray, without any edging except a trace of darker gray.[33] All the other feathers (coverts) have a tinge of brown in the gray, and are narrowly edged with

[32] In a juvenal ground-dove (*Chamæpelia*) from Santa Martha, United States of Colombia, I find the oblique tract is more strongly marked with spots than other coverts in front of it or behind it. Furthermore, the spots are *darker*, and the light edge is *reduced* in width.

[33] In another common pigeon of 15 days—from a cross of a red barb and a red and white jacobin—of blackish-brown color I find feathers with *dull reddish tips* 1 mm. wide. About 2 or 3 rows of pin-feathers of the oblique tract are beginning to unfold, but are as yet concealed by overlapping lesser coverts, except for 3 or 4 somewhat longer ones near the bend of the wing, which protrude 3 mm. to 5 mm. The interesting point here is that the oblique-tract feathers still show the apical mark, but only about *half width*, and about *half depth of color*.

EXPLANATION OF PLATE 28.

A. Left wing of juvenal female *Chamæpelia passerina*. × 2. Toda del. Completed October 20, 1903, at age of 12 weeks; but wing was outlined four weeks earlier, at age of 8 weeks, just as a few feathers had been molted. All feathers were finished as first feathers.

(1) There are 35 spots visible, some of them weak; (2) posterior areas are much like those in *C. affinis;* (3) all feathers are light-edged.

B. Feathers corresponding to figures of male shown in plate 27. × 2. Toda del., Sept. 1903. Figs. 1 to 4 from juvenal female *Chamæpelia passerina* (left wing, 7 weeks old).

(1) Pigment is weaker than in adult (see pl. 27); (2) the red-vinous of the adult is here pale vinous-gray or gray; (3) in the feathers corresponding to 6 to 13 of plate 27 the dark pigment is found on both sides. These juvenal dark spots are more elongate, as in *Columba;* mid-rib is light fulvous in color (reminds of young *Leptoptila*); (4) all feathers are edged with pale whitish buff; (5) in 14 to 15 the chequers are pointed behind as in *C. livia* (chequered type); evidently homologous in the two forms.

FIG. 1. Thirteenth feather of plate 27; third row of coverts (middle). · Notice two lateral spots or chequers; also median light-buff streak (as in *Leptoptila*).

2. Fourteenth of plate 27; middle second row of coverts. Only one chequer.

3, 4. Fifteenth of plate 27; two upper (inner) long coverts. The median light streak is very narrow. Chequers are pointed and marginal, except for light edge.

C. Selected feathers from a juvenal *Chamæpelia passerina*. × 3. Hayashi del., 1905.

Feathers taken from left wing of mounted skin September 15, 1905, and drawn for transitional phases between central spot and lateral spot or chequer.

On the wing we find about 5 rows of spots:

First row, 3 inner tertials.

Second row, 3 inner long coverts.

Third row, 5 inner posterior median coverts; one or two feathers are double-spotted; spots on inner side are rudiments.

Fourth row, 4 and 5 inner mid-median coverts; several of these feathers double-spotted, but the inner spots still small.

Fifth row, 4 to 6 inner anterior median coverts; all double-spotted, but the inner spots smaller than outer ones.

In front of these four rows of coverts come the lesser coverts on front edge of wing. These do not show spots on surface when the feathers are *in situ*, but several of the posterior row of lesser coverts bear spots.

When the lesser coverts are lifted we find that many of them have the turtle-dove central spot, pointed distally, and some of these present beautiful transitions between the turtle spot and the lateral spots, especially in the posterior row (or two rows) of these coverts.

The coverts have a whitish edge or tip; those bearing spots and some that have no spots have a mesial rufous streak. This streak is the same as those seen in *Zenaida*, *Geotrygon*, European turtle-dove (some young), and in some other species. The streak is sometimes only of the width of the shaft, sometimes it widens a little, extending to different lengths on the barbs.

The feathers of the breast are of the turtle type.

FIG. C 1.—Feather in next to last row of lesser coverts (near outer edge of wing).

C 2.—Feather from last row of lesser coverts (at about middle of row).

C 3, 4.—Feathers from last row of lesser coverts (near outer scapulars).

C 5.—Feather from anterior row of median coverts (first—outermost—at end of row).

C 6.—Feather from mid-median row of coverts (second from outer end of row).

C 7.—Feather from posterior median row or coverts (first—outermost—at end of row).
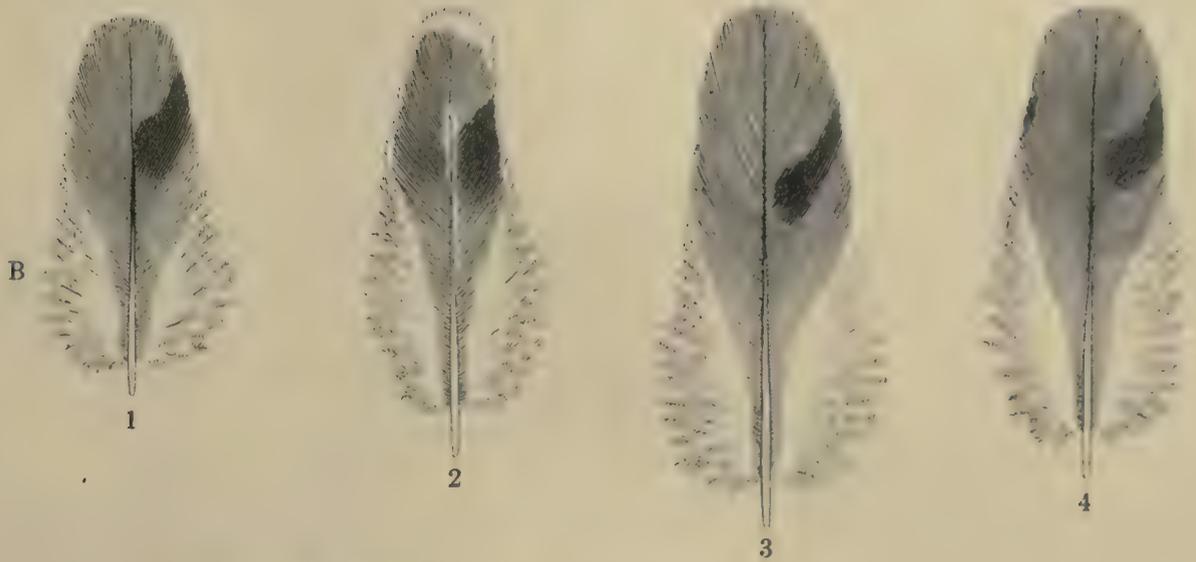
PLATE 28

A. Left wing of juvenal female *Chamæpelia passerina*. × 2. Toda del.
B. Feathers corresponding to figures of the male shown in plate 27. × 2. Toda del., Sept. 1903.
C. Selected feathers from a juvenal *Chamæpelia passerina*. × 3. Hayashi del., 1905.

pale yellowish (text-fig. 15). A pure-gray streak of feathers is also seen along each edge of scapulars, and their feathers are not shaded with dots as are the rest, in which there is a tinge of brown.

The wing-bars in this individual are of special interest, the second being very narrow and the first showing plainly its two different elements—upper and lower.

In front of the oblique streak three or four rows of feathers are tinged with brown, and in front of these the small coverts are again pure gray. These are more sparely dotted in the figure.

Six weeks after this bird was figured with its plumage in the state just noted, it had acquired a large portion of its second plumage, and the coverts were then of the same color as the oblique streak; i.e., the tinge of brown had disappeared and they were pure gray. This gray is a stage that was reached earlier in the oblique streak.

From a young common pigeon of 17 days I have had a further illustration prepared of the feathers of this oblique tract as they emerge in the pin-stage (text-fig. 16). The region of these pins marks out again a region in which the feathers are nearer to the adult color.

The region of the oblique tract in juvenal forms is therefore of great interest in studies of phenomena of recapitulation. The following considerations may therefore be given here:

The biogenetic law certainly holds, and often in the most striking manner, in the sequence of color-patterns in individual development. But these sequences, as a rule, appear to consist of discontinuous stages, between which, in many cases, no connecting phases are normally presented. The appearances, therefore, seem to exactly fulfil the requirements of the mutation theory. But

TEXT-FIGURE 16.

Pin-feathers marking the region of the oblique streak in a common pigeon of 17 days. The region of the pins is the region in which the feathers most nearly approach the adult color.

the possibility of resurrecting missing links, in the manner described below, shows how illusive is the evidence from this source. The phyletic series may have been perfectly continuous, although the ontogenetic series runs off at such speed that relatively few terms appear on the surface. That a real continuity is, nevertheless, maintained is abundantly evident when, by the simple experiment of plucking a feather, and thus making room for development, we can, at will, release the stage or stages that are normally passed before nature opens the door for a new unfolding through a molt.

The same continuity, moreover, is demonstrated in perfectly natural ways, or, as we might say, by nature's own experiments, since some of her regular performances have the value of tests most cleverly executed. In my experiments a feather is removed some time after its appearance in order that a second feather may develop which will show what advance in color or pattern has been made since the issue of the first feather. If the time of the first feather could be delayed for a few days or a week, without checking the general development of the first plumage, we should obviously have a test suited to the same need.

EXPLANATION OF PLATE 29.

A. *Chamœpelia talpacoti.* Natural size. Hayashi del., 1901.

Color paler than *Ch. passerina* (fig. B, this plate). Neck and breast plain, without dark centers. The primaries not perfect when drawn.

(This bird was supposed to have come from Vera Cruz, Mexico. This, however, is considerably beyond the known range of *talpacoti.* There is a possibility of error here. The author notes that he had specimens from both Vera Cruz and Brazil. He uses only the one name—talpacoti—for all.—ED.)

B. Left wing of male *Chamœpelia passerina.* Natural size. Hayashi del., Apr. 1897.

Spots "steel blue, metallic reflections," and high coloration of coverts and primaries; the latter cinnamon-red, edged (outer) and tipped with black.

C. Oblique bar in the "down" stage in male *Geopelia humeralis.* Age 16 days. Natural size. Toda del., Oct. 1906.

To show that the oblique band is still undeveloped and that it consists of about 19 feathers—*i.e.*, of 13 feathers in two rows (8 + 5) and then of 6 single feathers. These feathers are only in the down stage, the feathers not having started as visible pins. The downy feathers are easily recognized in the anterior, otherwise naked, portion of the wing.

I find, on mapping and measuring, two rows of down running along nearly parallel with each other and in line with the radius or anterior bone of the lower arm. These rows are separated by about 1.5 to 2 mm. The posterior row has 8 downs about 2.5 mm. apart. The entire row is 18 mm. long.

The second row has 5 downs, alternating with the downs of posterior row; in front of these rows are the 6 additional downs, only 3 of which are in a row; the remaining 3 are anterior and irregular in position.

In order to see these downs it is only necessary to lift up and press to the front all the small coverts in front of the 4 rows of most regular and conspicuous coverts. The naked space occupied in part by these downs is then seen to be more or less triangular. These downs—particularly the two rows—are destined to appear a little later, and to form "the oblique streak" in which the color-pattern makes a step nearer the adult pattern than does the pattern now seen in the coverts already out.

D. Juvenal *Geopelia humeralis* (GH^1-C^2). First plumage in part. Age 43 days.

Shows two posterior scapulars and three inner tertials. The tertials have streaks of black on the lower edge.

EXPLANATION OF PLATE 30.

A. Wing of adult female *Chamœpelia passerina,* same bird as text-figure 4. Natural size. Hayashi del., Apr. 1903.

Wing outstretched to show the extent of reddish pigment, left white in the figure on primaries and elsewhere. The wing-spots better shown than in the colored wing. Dark centers are seen in a few feathers at bend of wing.

B. Adult *Chamœpelia buckleyi.* Toda del., after Salvadori, figure 2, to show spots of wing.

The following sex comparisons are given by Salvadori:

Male.	Female.
Upper parts *vinous* gray...	Pale brown.
Under parts vinous........................,..............................	Pale buffy brown.
Velvety black spots on some upper wing-coverts, scapulars, secondaries, and tertials.	Spots similar.
Under wing-coverts and axillaries black...................................	The same.

C. Selected feathers from juvenal *Chamœpelia pallescens.* × 2. Hayashi del., June 1907.

Feathers from one of six birds received from Santa Martha, United States of Colombia. This bird was in first feathers for the most part.

FIG. 3. Posterior scapular (adult).
    4. First (innermost) larger covert (juvenal).
    5. Second (innermost) larger covert (juvenal).
    6. Third (innermost) larger covert (juvenal).
    7. Eighth (innermost) larger covert (juvenal).
    (1) The first feathers have the pale edge and the pale median streak.
    (2) The second feathers have no pale edge or median streak.
    (3) A tendency for a dark cross-bar to form close to the pale edge in the larger coverts.
    (4) In the three inner larger coverts the spots are squarish chequers somewhat pointed distally—*i.e.*, they are more like the forms seen in *C. livia* than the same spots in the adult.
    (5) The spots always remain marginal, however much reduced—*e.g.*, the scapular.

PLATE 29
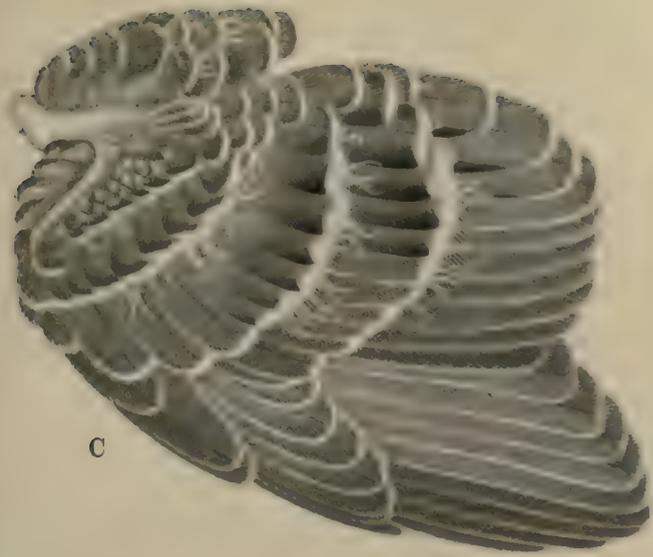
A. *Chamœpelia talpacoti*. Natural size. Hayashi del., 1901.

B. Left wing of male *Chamœpelia passerina*. Natural size. Hayashi del., Apr. 1897.

C. Oblique bar in the ''down'' stage in male *Geopelia humeralis*. Age 16 days. Natural size. Toda del., Oct. 1906.

D. Juvenal *Geopelia humeralis* (GH^1–C^2). First plumage in part. Age 43 days.

PLATE 30
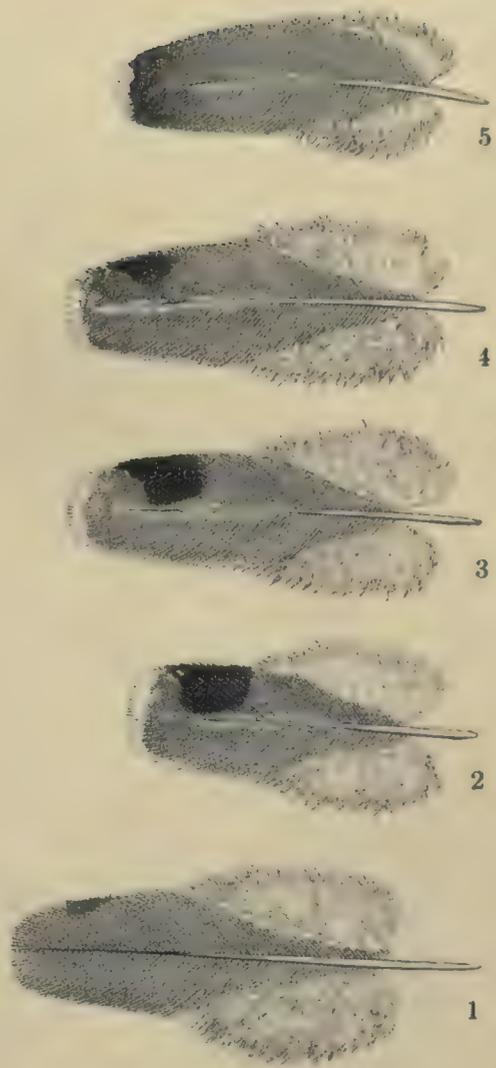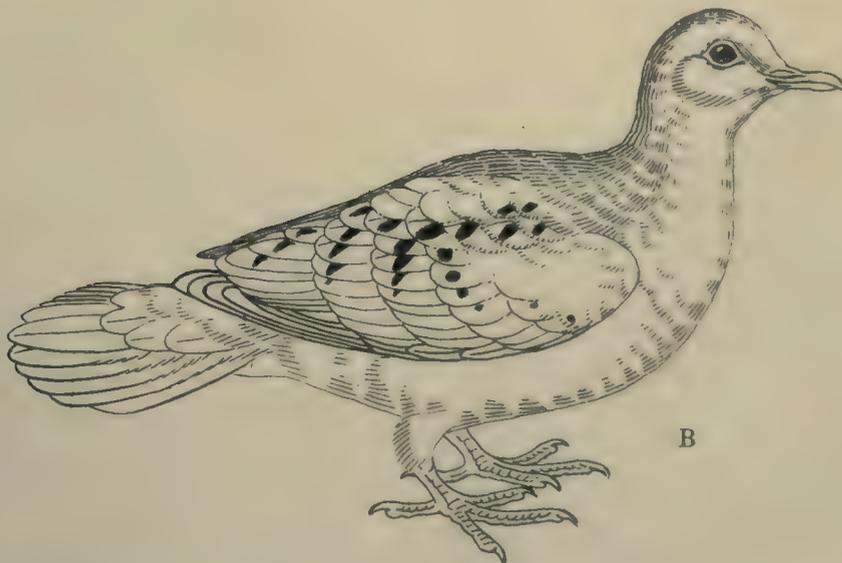
A. Wing of adult female *Chamœpelia passerina*, same bird as text-fig. 4. Natural size. Hayashi del., Apr. 1903.

B. Adult *Chamœpelia buckleyi*. Toda del., after Salvadori, fig. 2, to show spots of wing.

C. Selected feathers from juvenal *Chamœpelia pallescens*. × 2. Hayashi del., June 1907.

Now, nature performs just this experiment on the young of many species of pigeons, both wild and domesticated. By varying slightly the time of delay, and by operating on many different patterns, and in several regions of each pattern, nature offers a profusion of demonstrations, showing that it is not mutation, but the "law of genetic continuity"—one continuous process of development that underlies and connects the phenomena of colors and patterns in successive plumages. The intervals between stages are not periods of rest, but of active progress in transitional elaboration. The visible stages and the invisible flow of transitional latent phases together form a continuum, with some analogy, though only highly fanciful, to the rhizome with its visible nodal growths arranged in serial order, but appearing as isolated generations, because the internodal connections lie hidden beneath the surface of the soil.

One of these natural experiments is realized in this narrow "oblique tract" which, running parallel with the bones of the forearm, crosses the wing obliquely in the region of the anterior or lesser coverts. In this line, for some reason yet to be ascertained, two or three rows of coverts appear a week or two later than the other coverts of the wing, the time varying for different species.

In all cases where there are considerable differences in color or pattern between the first and the second plumage, these belated feathers will appear in more or less conspicuous transitional conditions. When, for example, in the domesticated pigeons, a clear black is to succeed a blackish-red, black will predominate in the streak and thus render it quite distinct. But the black here, as a rule, will not be as strong as it is to be in the second plumage; and as the first molt leaves these feathers intact until after that plumage appears, the streak will still be recognizable, but in this case from deficiency rather than excess of black.

Black pigeons sometimes produce pale or dusky red young, as a pair of black barbs has repeatedly done during the past several years. The streak in these young is a shade or two darker than other parts, and anticipates a still darker red in the second plumage.

In young pigeons of the second or double-barred varieties the colors are commonly paler than in the adult, and the gray ground-color is suffused with brown, which disappears in the second plumage. In such birds the streak shows a stronger black and a clearer gray, approximating more or less closely the adult colors.

It is not in the domestic pigeons, however, that we get the more striking and instructive pictures of progressive transitional change in this region of the wing. For such views we must go to some of the wild species, in which the adult pattern departs more widely from the juvenal pattern. It is in such species, where the gap between patterns seems so wide and so abrupt as to suggest a sudden and wholesale mutation, that we find in this tract of feathers the most complete demonstrations of continuity through intergraded or transitional phases.

For the purpose in view we must of course have young birds accessible for convenient observation from day to day, and such material is obtainable only from species that will breed in captivity. It is for this reason that the phenomena in question have hitherto escaped the attention of naturalists.

The little ground-doves of the genus *Geopelia*, found principally in Australia, answer the requirements named and furnish the best demonstrations I have thus far discovered.[34]

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[34] Recapitulation of the light *apical edge* of *G. tranquilla* and of the bars which precede the white spots or dots of *G. cuneata* are described and figured at the close of Chapter X. For the recapitulation of still other characters in *Geopelia* see the following section.—ED.

THE GEOPELIINÆ.[35]

The genus *Scardafella* is apparently the simplest type, and is perhaps the parent form of the other Geopeliinæ. The color-pattern, size, and shape of *Sc. inca* are in strong resemblance to *Geopelia striata*. The voice, on the other hand, at once reminded me of the Florida ground-dove (*Chamæpelia passerina*). The continuous

[35] See table 3 for genera and arrangement of species.—ED.

EXPLANATION OF PLATE 31.

A. Adult male *Peristera cinerea*. Natural size. Hayashi del., June 1901. Shows closed wing with bars and spots in natural conditions.

The dark centers are here strongest in the anterior lesser coverts, but they are far from being as definite and clear in outline as in *Ch. passerina*. The lack of sharp outline is partly due to the fact that the rest of the feather is gray, while it is vinous in *Chamæpelia*, and so the contrast is greater. But there is no doubt that the marking here is in marked decline.

1 to 9. Feathers from left wing of adult male *Peristera cinerea*. × 2. Toda del., Apr. 1903.

1. Near bend at front edge. The center is strong gray, while the tip is pale gray—without sharp boundaries.
2. Next below 1. The center is a little better defined.
3. Next below 2. The center still better defined.
4. Just behind and below 3. The center about the same as in 3.
5. Near 4. An oblong oval spot on the lower web.
6. Higher up the wing, but a lesser covert. Center is only a shade stronger than tip. Round spot on lower web
7. Third row of coverts. Center very obscure and spot a little larger.
8. Second row of coverts. Center is scarcely perceptible. Spot is more elongate transversely, almost a semilune
9. First row of long coverts, from the upper (inner) part of wing. Spot shaped nearly as in preceding figure.

EXPLANATION OF PLATE 32.

(Illustrating origin of oblique wing-bar in *Columbula piqui*).

A. *Columbula piqui*. × 0.8. Hayashi del., Aug. 1904.

Wing-bar formed by six dark marginal feather edges. Four tertials bear also marginal dark spots on their inner edge.

Dark crescentic edges or tips occur in the *Columbula piqui*, though this is not mentioned by Salvadori or Reichenbach.

Feathers of steel-blue bar are tipped with steel-blue, and these are the same as the crescents in *Scardafella inca*. At first sight I mistook these birds for Inca doves and I found many wing-coverts tipped with dark or black, though not so plainly and regularly as in *Sc. inca*.

In *Chalcopelia afra* (Salvadori, p. 506) from Africa the upper tail-coverts are marked with black crescentic tips

B. *Chamæpelia passerina*, left profile of adult. × 0.5. Toda del., Nov. 1904.

The five anterior chequers are in oblique line, corresponding to the position of the oblique bar in *Columbula piqui*. (See also text-fig. 2.)

C. *Chamæpelia passerina*, right wing. × 1.6. Toda del., Nov. 1904.

EXPLANATION OF PLATE 33.

(Illustrating origin of oblique wing-bar in *Columbula piqui*.)

A. *Chamæpelia passerina*, right wing. Natural size. Toda del., Dec. 1904.
Shows in still another individual an oblique bar of six spots.

B. *Peristera mondétoura*, male. By Toda, after Bonaparte, "Inconographie des Pigeons," 1857, pl. CXXVI; the oblique bar is conspicuously present.

C. From above plate, but does not belong to *mondétoura* species.
The female represented here (fig. C) does not belong to this species. See Salvadori, pp. 495–496, who notes that the female *mondétoura* "has spots on the wing as in the male, but more purple and less blue." And further, the young is "similar to the female · · · . Dark spots on the wings only on the greater coverts." I doubt this latter statement. I should expect to find at least the same spots as in the adults, only weaker.

D. *Peristera geoffroyi*, adult male. By Toda, after Bonaparte, pl. CXXI.
Salvadori (p. 494) describes the bars here as "three oblique bands, one blue on the smaller wing-coverts and the other two of purple-chestnut on the median and greater wing-coverts. · · · The young resembles the female."
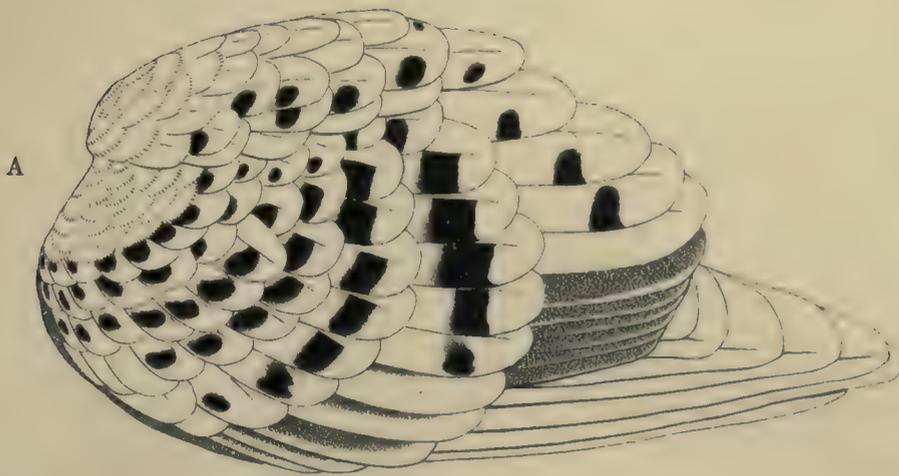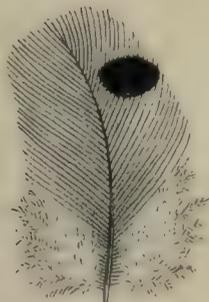
PLATE 31

A. Adult male *Peristera cinerea*. Natural size. Hayashi del., June 1901. Shows closed wing with bars and spots in natural conditions.

1 to 9. Feathers from left wing of adult male *Peristera cinerea*. × 2. Toda del., Apr. 1903.

PLATE 32

Illustrating origin of oblique wing-bar in *Columbula picui*.

A. *Columbula picui*.   × 0.8.   Hayashi del., Aug. 1904.

B. *Chamœpelia passerina*, left profile of adult.   Natural size.   Toda del., Nov. 1904.

C. *Chamœpelia passerina*, right wing.   × 1.6.   Toda del., Nov. 1904.

PLATE 33

Illustrating origin of oblique wing-bar in *Columbula picui*.

A. *Chamœpelia passerina*, right wing. Natural size. Toda del., Dec. 1904.
B. *Peristera mondétoura*, male. By Toda, after Bonaparte.
C. From above plate, but does not belong to *mondétoura* species.
D. *Peristera geoffroyi*, adult male. By Toda, after Bonaparte.

low chucking sound and the quality of the voice, as well as the color of the eyes, the movement of the head, the physiognomy, the manner of huddling together, especially at night, when they frequently sit two tiers deep, and often even three deep—all these things remind of the Florida ground-dove.

They are quite like the chamæpelias also in their quickness of movement and in their shyness. They work hard for the inside berth on the perch. They are

TABLE 3.—*The subfamily Geopelinæ (family Peristeridæ, order Columbæ) according to Salvadori.*

Subfamily and genera.	Species.	Plumage distinctions, Salvadori (in part) and the author (in part).
GEOPELIINÆ. **GEOPELIA.** Burma to Australia. Tail, 14 feathers; first primary attenuated.	*maugei*,[26] Timor group	Feathers of upper parts tipped with *black crescentic bars; neck, breast, flanks, and abdomen* with black and white bars; no vinous underneath. Length, 8.5 in.
	striata, Indo-Malay Archipelago, and Philippines.	Same, *black crescentic tips.* Sides of neck and breast barred with black and white. *Middle of neck* in front, and of breast, *pale vinous.* Abdomen buffy white. Neck-bars are more numerous than in *tranquilla.* Length, 8.5 in.
	tranquilla, Australia.........	Same, *black crescentic tips. Only the neck is* barred all round with black and white. Breast and flanks *pale vinous*, abdomen *white.* Length, 7.5 to 8 in.
	humeralis, Australia and New Guinea.	Same, black crescentic tips. Nape rufous, clearest on sides, tipped with black crescentic tips. Breast and front neck gray—barred in first plumage only. Length, 11 in.
	cuneata, Australia..........	No black crescentic tips; upper parts gray. Subterminal crescentic *dark bars in first feathers.* Head, neck, and breast gray, abdomen *white.* Scapulars and coverts each with two white spots encircled with black. Length, 7.5 to 8 in.
SCARDAFELLA. Southern United States, Mexico and Central America to Brazil. Tail, 12 feathers; first primary not attentuated.	*inca*, Mexico south to Nicaragua.	Same, *black crescentic bars* all over. Juvenal feathers tipped with narrow obscure pale buff—rudimentary. Breast with pale black bars, tinged with vinous. Abdomen and flanks buff, each feather tipped with black. Length, 8 in.
	squamosa, Brazil, Venezuela, and Colombia.	Same, black crescentic bars everywhere except under tail-coverts, which are white. Lower neck and breast pinkish—each feather black-tipped. Abdomen *white.* Upper wing-coverts *white* towards black tips. Length, 8 in.
GYMNOPELIA .... Mountains of western South America. Tail, 12 feathers; first primary slightly scooped. Perioptic area broadly naked.	*erythrothorax*, Peru, Bolivia, Chile.	Upper parts brown with tips of feathers *whitish.* Head, neck, and upper breast vinous. Lower breast and abdomen *whitish* buff. Perioptic space surrounded by line of black feathers. Length, 7.5 in.

[26] Temminck and Knip (p. 115, Vol. I, pl. LII) show this species with bars over the whole under surface. Temminck says it has *twelve* tail feathers.

REMARKS: I have not yet (Jan. 25, 1903) seen *maugei, squamosa*, or *erythrothorax.* The last of these is of much interest. *Squamosa* is close to *inca. Inca* is apparently the simplest type, perhaps the parent form of all the others. All species, so far as I have seen, have the long black spots or streaks in the juvenal feathers. *Scardafella* stands lowest (young have the black streaks), then the others follow in this order: *maugei, striata, tranquilla, humeralis. Cuneata* has made widest departure, losing the crescentic bars. *Humeralis* stands highest of the barred species.

In this table the arrangement of *species* is that of the author; the *genera* stand as arranged by Salvadori. The decisions of the author would place the genera in the following order: *Scardafella, Geopelia, Stictopelia (cuneata), Gymnopelia.*—ED.

EXPLANATION OF PLATE 34.

A. Adult male inca-dove, *Scardafella inca.* × 1.5. Hayashi del., Jan. 1903.

All the feathers, except the pale forehead and throat, are tipped with a crescentic blackish bar. This specimen shows the bars on the breast, but weaker in the middle region, where the feathers show the strongest touch of a delicate vinous tinge. The general brown of the upper parts lightens up decidedly along the lower edge of the wing, becoming light grayish brown, reminding of the light color that marks so many species in this region. The legs and feet are pale flesh-color. The pale vinous of lower parts passes into pale buff on belly, flanks, and lower tail-coverts.

The mate of this bird has a still paler breast, with the apical crescents still fainter in the central part. The crescents are strongest and broadest on the flanks.

B. Feather from middle of left side of neck. × 4.25.

The rows of feathers on the side of the neck in the ring region are very regular, but scarcely any differentiation is to be recognized.

C. Wing of juvenal inca-dove, 3 weeks old. × 1.5. Hayashi del., July 1900.

A few feathers among the scapulars and in the anterior wing-coverts have narrow light tips, but for the most part the black bar is terminal, which represents an advance on the geopelias. The tendency to form pale bars in front of the black bar is well shown. The long black spots are reduced here, compared with the geopelias, and this is another advance. Three scapulars are appearing, showing the adult condition.

D. Scapular from a juvenal *Sc. inca.* Same bird as fig. C. × 7.5. Hayashi del., July 1900.

This feather was taken from just in front of the middle of the scapulars. It shows a pale rudimentary tip. Only a few (4 or 5) anterior scapulars, and a few anterior wing-coverts have light tips; the others are black-tipped. The back feathers are light-tipped.

This species thus seems to be shortening up its development by reducing or skipping the yellow or pale tip. It is remarkable that in first feathers these tips should be so sparely represented as to be overlooked by Mr. Hayashi in drawing the wing (fig. 3). The black bar, which is almost terminal, is followed within by an irregular light area, analogous to what is seen in the young feathers of other geopelias; it is a reminiscence of a barred condition. Compare with this the scapulars and tertials of a young *G. humeralis*, plate 41.

EXPLANATION OF PLATE 35.

A. Wing of adult male inca-dove, *Scardafella inca.* Natural size. Hayashi del., 1900.

(To show pattern in the wing.)

"Upper parts and wing-coverts, grayish brown, each feather tipped with crescentic bar of blackish" (Salvadori, p. 366).

I find the scapulars a shade darker than the coverts. The long coverts are characterized as follows:

Nos. 2 to 6 blackish, narrowly edged below with pale brown.
No. 7 has a streak of blackish on lower web.
No. 8 has a trace of streak of blackish on lower web.
No. 9 has no trace of streak of blackish on lower web.
Nos. 10 and 11 have the streak on both edges. This streak is overlooked by Salvadori.

The same streak is found on the upper three tertials—both sides; also on a few of the upper median coverts. Primaries are cinnamon with blackish-brown tips; all have blackish-brown outer web, but this color retreats towards tip in feathers 1 to 6 and is about the same for Nos. 7 to 10. This seems to be the longitudinal spot or streak. Secondaries Nos. 1 and 2 are blackish-brown on outer web and tips, with cinnamon inner webs reaching slightly over midrib upon lower web. Nos. 3 and 4 have cinnamon inner web less extended. Nos. 3 to 6 are blackish-brown, darker on lower web, the cinnamon of the inner web diminishing. Bastard wing blackish. Primary coverts cinnamon broadly tipped with blackish. Under surface of primary coverts cinnamon; brownish tips extended on secondaries 3 to 6. Inner under wing-coverts are black, outer ones tipped with a narrow edge of black.

B. Adult male *Chalcopelia afra.* Natural size. Hayashi del., Mar. 1904.

This bird is clearly no distant relative of the green-winged pigeon (*Chalcophaps*); both have two blackish bars or stripes across the hinder portion of back, or rump.

The male drawn, and another compared with it (pl. 42, fig. E), supply the following data:

(1) The second row of long coverts: The 4 upper (inner, counting from above) feathers show very dull, shadowy dusky spots (chequers) on both webs, but strongest on the lower (outer) web.

(2) The first row long coverts (posterior): The second, third, and fourth have steel-blue chequers on the outer web (none on inner web); the fifth has a slightly dusky obsolete spot on outer web (partially concealed).

(3) The 3 inner tertials (first, second, and third) have the same chequers on the outer web (largely concealed).

(4) Some upper tail-coverts (longer ones) are edged with black crescents. Two blackish cross-stripes of the lower part of the back are also made up of black tips, homologous with the black crescents.

(5) In the smaller and inner coverts, in front of the long coverts, I find no chequers, but just in front of the spots of the second row of long coverts there seem to be traces of spot-imprints.

(Compare with *Peristera cinerea*, pl. 35.)

PLATE 34
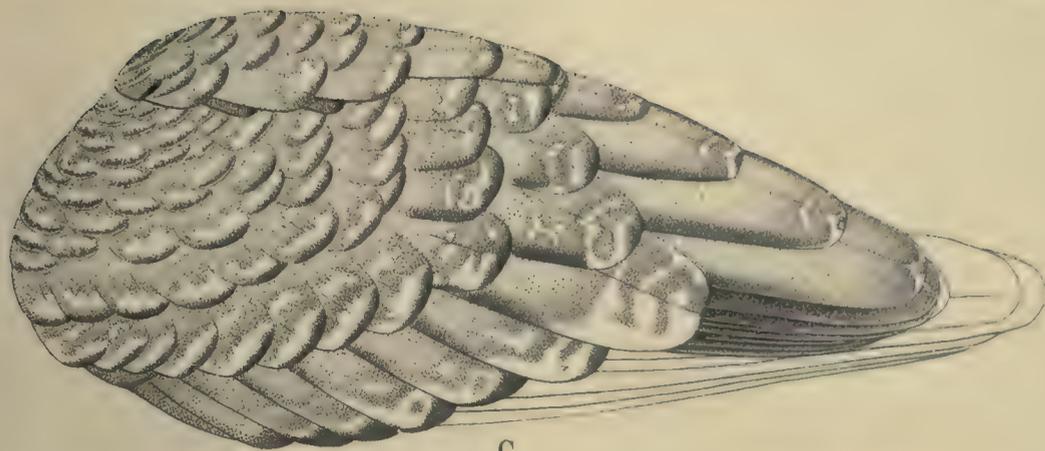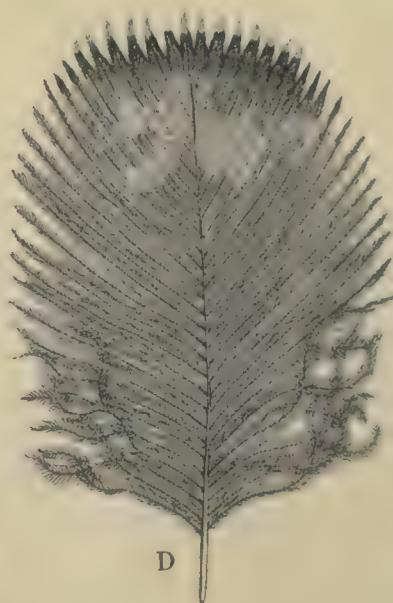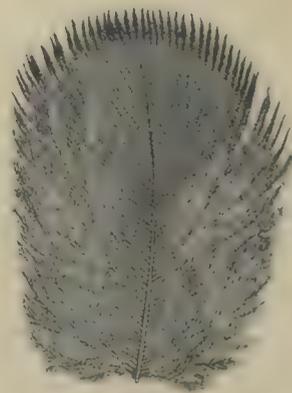
A. Adult male Inca-dove, *Scardafella inca*.   × 1.5.   Hayashi del., Jan. 1903.
B. Feather from middle of left side of neck.   × 3.75.
C. Wing of juvenal Inca-dove, 3 weeks old.   × 1.5.   Hayashi del., July 1900.
D. Scapular from a juvenal *Sc. inca*.   Same bird as figure C.   × 7.5.   Hayashi del., July 1900.

PLATE 35

A

B

A. Wing of adult male Inca-dove, *Scardafella inca*. Natural size. Hayashi del., 1900.
B. Adult male *Chalcopelia afra*. Natural size. Hayashi del., Mar. 1904.

very hearty eaters, fairly stuffing themselves.[37]   Knowing the similarity in behavior of these two forms, one would hardly need other evidence of their close affinity.

In the adult inca-dove all of the feathers, except the pale forehead and throat, are tipped with a crescentic blackish bar (pl. 34, fig. A).   This crescentic bar is weakest in the breast region—the region in which it has disappeared more or less completely in the various species of *Geopelia*.   A detailed consideration of the wing coloration is given in connection with plate 35 (fig. A).   Of particular interest are the blackish streaks found on some of the long coverts and upper tertials.   The female, better than the male, shows a residuum of the turtle-dove pattern and shows also a tendency in this species toward a duplication of transverse bars at the feather's tip (pl. 36, figs. 1 to 9).   The extent of this duplication is greatly increased in some of the (derived) geopelias.   The feathers of the neck region are but little differentiated in these doves (pl. 34, fig. B).

TEXT-FIGURE 17.—Adult Mauge's dove, *Geopelia maugei*. Toda del., after Knip, Temminck and Knip, *Les Pigeons*, pl. III, p. 115, 1808-1813.   × 0.5.

According to original drawing by Madame Knip, the head is not marked by crescentic tips, but the body and wings are so marked.   This species stands below *G. striata* in that the crescents have not begun to disappear on the under side.   Salvadori (p. 461) says: "Neck, breast, and sides with numerous narrow black and white bands; on the hind neck the light bands are grayish; back and upper wing-coverts grayish brown, each feather edged with black at the end.   Abdomen and under tail-coverts white."

The juvenal feathers afford instructive comparisons with the geopelias.   In juvenal geopelias the feathers are edged with a light yellow.   In inca they are edged with black in most cases on the wing (pl. 34, fig. C).   On some of scapulars (pl. 34, fig. D) and on the anterior lesser wing-coverts the edge is pale yellow, but very narrow and obsolescent—*i.e.*, the edge of the feather looks rudimentary; the yellow edge is skipped in most cases, but comes to meager development only in these few parts.

The inca-dove, then, seems to get nearer the adult condition in the first feathers than does *Geopelia*.   There are good reasons for considering *Scardafella inca* the older type, and as such it has shortened up its developmental history.

The scaled dove (*Scardafella squamosa*) is similar in shape and size to *inca*, but the crescents are a little stronger in *squamosa*.   In this species the uniformity of coloration is broken by the appearance of white in the lower half of the feathers

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[37] I have studied individuals from Guaymas, Luna, and Chihuahua, Mexico.

near the tip. This white, however, leaves the dark crescentic tip intact. In the phylogenic series I should place *Sc. inca* as lowest, *Sc. squamosa* (pl. 36, fig. A) coming next above.

The genus *Geopelia* includes 5 Australian species. The 4 species I have studied (*G. maugei*,[38] text-fig. 17, seems from descriptions to stand at least below *G. striata*) may be arranged in the order of their respective stages of development as follows:

(1) *Geopelia tranquilla*, with narrow *white and black bars running entirely across the front of the neck*, with no median interruption.

(2) *Geopelia striata*, with *bars interrupted* in the middle of the neck by a median streak of pale vinous (this species stands lower than *tranquilla* in having barred feathers along the sides of the abdomen. The two are about equal in rank).

(3) *Geopelia humeralis*, with *no bars* on the front of the neck.

(4) *Geopelia cuneata*, with no bars on front of the neck, and bars elsewhere transformed into dots.

Nos. 1, 2, and 3 all agree in the adult in having the feathers of the wings and back edged by a narrow band of black, giving the whole a squamated or scale-like appearance.

No. 4 departs most widely (is really of generic rank), and agrees with the earlier members of the series only partially in the juvenile feathers. In the first feathers the bars run across the neck in *Geopelia tranquilla*, also in *G. striata*, though not so clearly marked. In *G. humeralis* the bars are present but not sharp, and are *interrupted in the median line*, so that the juvenal type corresponds to the adult *G. striata*.

Here is a curious series of stages plainly standing in the relation I have indicated. This group of Australian doves furnishes in some respects the best demonstrations of recapitulation that I have thus far (1903) discovered.

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[38]Temminck says that the black and white bars alternate regularly, and that there is no middle interruption of bars on the neck, breast, or abdomen—all of which puts this bird below *Geopelia striata*. Temminck asserts that *G. maugei* has only 12 tail-feathers; this would correspond to the number in *Scardafella* and *Gymnopelia*. Salvadori (p. 454), however, gives this number as 14, which corresponds with that of other geopelias.

EXPLANATION OF PLATE 36.

A. Adult scaled dove, *Scardafella squamosa*. Toda del., after Knip and Temminck, I, p. 127, pl. LIX, 1808–1813.

This bird should follow *S. inca*, as it is slightly more differentiated on the wings. "Upper wing-coverts light brown, white towards the tips. Under wing-coverts dark brown edged with black." (See Salvadori, p. 464.)

The black crescents here very heavy. In *inca* they are dull. Temminck asserts that this bird has 14 tail-feathers, the 10 central ones of equal length, the 2 lateral ones on each side are strongly "étagées." Salvadori says the tail-feathers are 12 for both species of *Scardafella*, and he is undoubtedly right.

Each feather is edged with a heavy crescentic bar of black, except the under tail-coverts, which are white. The breast and sides have a pinkish (vinous) tinge (similar in *S. inca*). Salvadori's phrase, "Young, feathers faintly mottled," recalls strongly the wing of *S. inca*.

1–9. Selected feathers from an adult *Scardafella inca*. Natural size. Toda del., May 1903.

(Figures 1 to 5 are from right side near wing.)

FIG. 1. From lower breast.
2. From the side, level of wing-bend.
3. From about middle of wing.
4. From close to 3.
5. From the same level, closer to edge of wing. This is the plainest indication of bars, dark and buff alternating.
6 to 9. Successive longer under tail-coverts.

Here again we see the turtle pattern reduced to a thin gray extension of the basal gray. The shaft is dark; then comes a buff area, and finally the dark edge.

The dark edge (terminal or subterminal) occurs generally when the dark center is reduced, replaced in part by light—*e.g.*, in some common pigeons where red replaces black, etc.
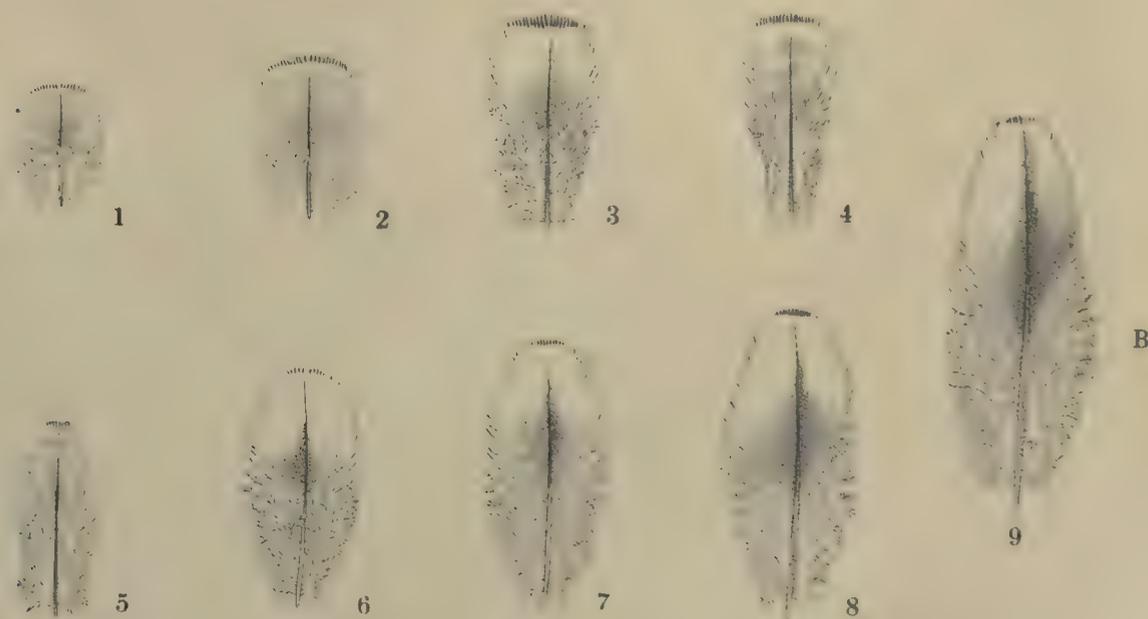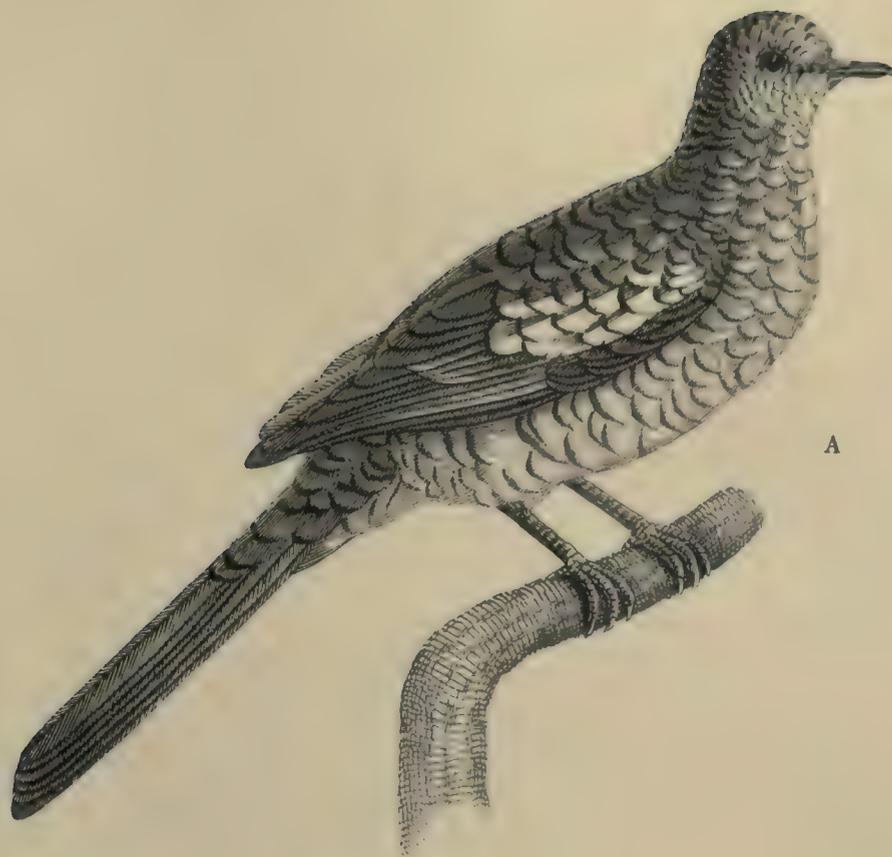
PLATE 35

A. Adult scaled dove, *Scardafella squamosa*. $\times$? Toda del., after Knip and
    Temminck, I, p. 127, pl. LIX. 1808-1813.
B. Figs. 1-9. Selected feathers from an adult *Scardafella inca*. Natural size.
    Toda del., May 1903.

The following detailed description of the several individuals figured will supply some of the evidence for the above conclusions:
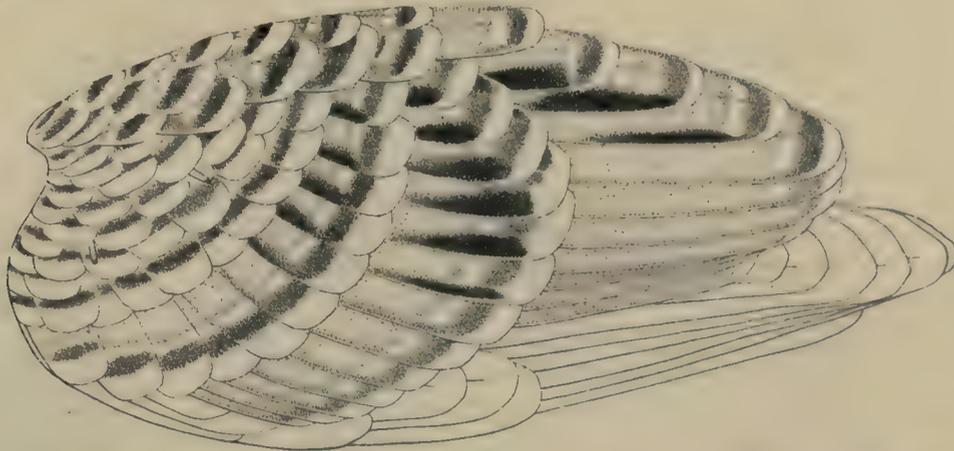
TEXT-FIGURE 18.—Wing of juvenal *Geopelia striata*, 18 days. × 2. Hayashi del., July 1899.

This is stage corresponding with pl. 88 of *Geopelia cuneata;* pl. 41 of *humeralis;* text-fig. 31 of *tranquilla.*

The third and fourth rows of coverts are so close together that they scarcely seem to be set off from the smaller coverts. At this stage I saw two pin-feathers of the oblique streak coming in, in front of the fourth row as nearly as I could tell. They came in along the same line as in *G. cuneata.* In this specimen the terminal yellow edging is repeated as a cross-bar in front of the black bar, and quite distinctly. In the mate of this bird the repeated yellow bar was not so plain. The black streaks are quite pronounced on lower edge of the feather, and some feathers have double streaks, upper as well as lower.

TEXT-FIGURE 19.—Wing of juvenal *Geopelia striata*, 28 days. Same bird as text-fig. 18. × 2.
Hayashi del., July 1899.

Compare with 28-day wings of *Geopelia tranquilla*, text-fig. 32; *G. humeralis*, text-fig. 20; *G. Cuneata*, pl. 88. In 10 days we find the third and fourth bars have been covered by the oblique streak of feathers that had but just begun to appear in the 18-day stage, 10 unfolded feathers and 5 new pin-feathers appearing. The latter and others that will soon come into sight will unfold and lengthen until the second row is covered. We see also about 6 feathers added to the scapulars on the lower side. These are black-edged, the black being deeper than in the earlier feathers. These new feathers still show the yellow cross-bar in front of the black. They do not quite reach the adult condition. They are still only partly grown.

The head, neck, and breast of two adult *Geopelia striata* are shown in the figures. One represents the normal type (pl. 37, fig. A), the other (pl. 38) is atavistic and more like the young (pl. 38, and text-figs. 18, 19).

The marking of the normal male shows that this species stands below *Geopelia humeralis* in having: (1) a smaller size; (2) a lesser area on the breast and neck that is free from bars; (3) the unbarred part pale vinous instead of gray; (4) the vinous area extends downward to about the same level as does the gray in *G. humeralis;* it then fades into the whitish of the abdomen (*G. humeralis* has lower breast only pale vinous); the vinous breast probably stands below the gray breast; (5) there are more barred feathers, and more bars to the feather.

On the wings and back the bars are *apical edge-bars,* as in *G. humeralis,* and are about the same in color and appearance in the two forms. In young *G. humeralis,* as in this species, the *black bar is not terminal, but stands within the apical pale-whitish bar. The black apical bar is therefore secondary, the pale-edge bar primary.* In the adult of this species I find on the neck many feathers which *retain the white apical edge,* while some others show the *apical black bar in all stages of obsolescence. The pale or white edge of the neck-feathers is therefore a still later modification,* the feathers having lost the juvenal pale edge and are now in process of losing the black edge, which is homologous with the black edge of the wing-feathers. *The neck-feathers are, then, higher in development than the wing and back feathers.*

As we pass up from the back to the neck we see the black edge is at first present in full width; on the lower hind-neck we find it looking a little thinner and lower;

EXPLANATION OF PLATE 37.

A. Adult male *Geopelia striata.* × 1.4. Hayashi del., Nov. 1902.

Shows the extent of the unbarred breast region in the normal type of this species. Compare with the more complete barring of juvenal and adult atavistic female (pl. 42). (See text.)

The feathers are all shown with white edges, as they appeared to Mr. Hayashi, but the black apical edge is for the most part present, though inconspicuous.

1 to 7. Separate feathers from normal *G. striata.*

A. Upper part of mid-back of neck. Bars are only 3, the basal one very shadowy. The mid-back neck-feathers are all less differentiated; they have fewer bars and the color of these is intermediate between that of body and wing feathers and of the feathers of the side of the neck, where differentiation is sharpest. The black bars are here only dark brown and the white bars are pale buff.

B. Shows the height of differentiation in mid-back of neck.

C. An ordinary feather from middle of back of body. It has black apical edge-bar, and just inside this an obscure buff bar.

D. Middle height of neck, right side, front edge of barred feathers. Front half of feather is not barred, except that the first black bar runs over the mid-rib a little. This half is vinous. There are four half-bars. The apical black bar is only barely recognizable to the naked eye (on the barred side), and extends just a little over the mid-rib and soon vanishes. The artist at first failed to see and draw the black apical bar.

E and F. Middle right side of neck, where bars are best developed in number and color, the pale bars being almost white and the dark bars black. Figure E has a thin black edge, but figure F has only a trace of it on the left side.

G. Just below middle left side of neck, similar to figure F. To the naked eye there is no apical black, but with a lens I can detect just a touch of blackish on the tips of some of the barbs.

Note that this species has the whole side of the body and under wing-coverts multibarred.

EXPLANATION OF PLATE 38.

A. Juvenal *Geopelia striata.* × 1.5. Hayashi del., Oct. 1902.

This first plumage shows the bars completely circling the front of the neck, but they are not so well marked in the middle region, which is destined to be even unbarred and of vinous color in the second plumage. This condition of bars is permanent in one species, *G. tranquilla.*

B. Adult female *Geopelia striata.* × 1.5. Hayashi del., Nov. 1902.

This represents a variation from the normal shown in plate 37, and approaches the juvenal condition in the bars crossing the front of the neck; but these bars are faint in the middle line.

PLATE 37
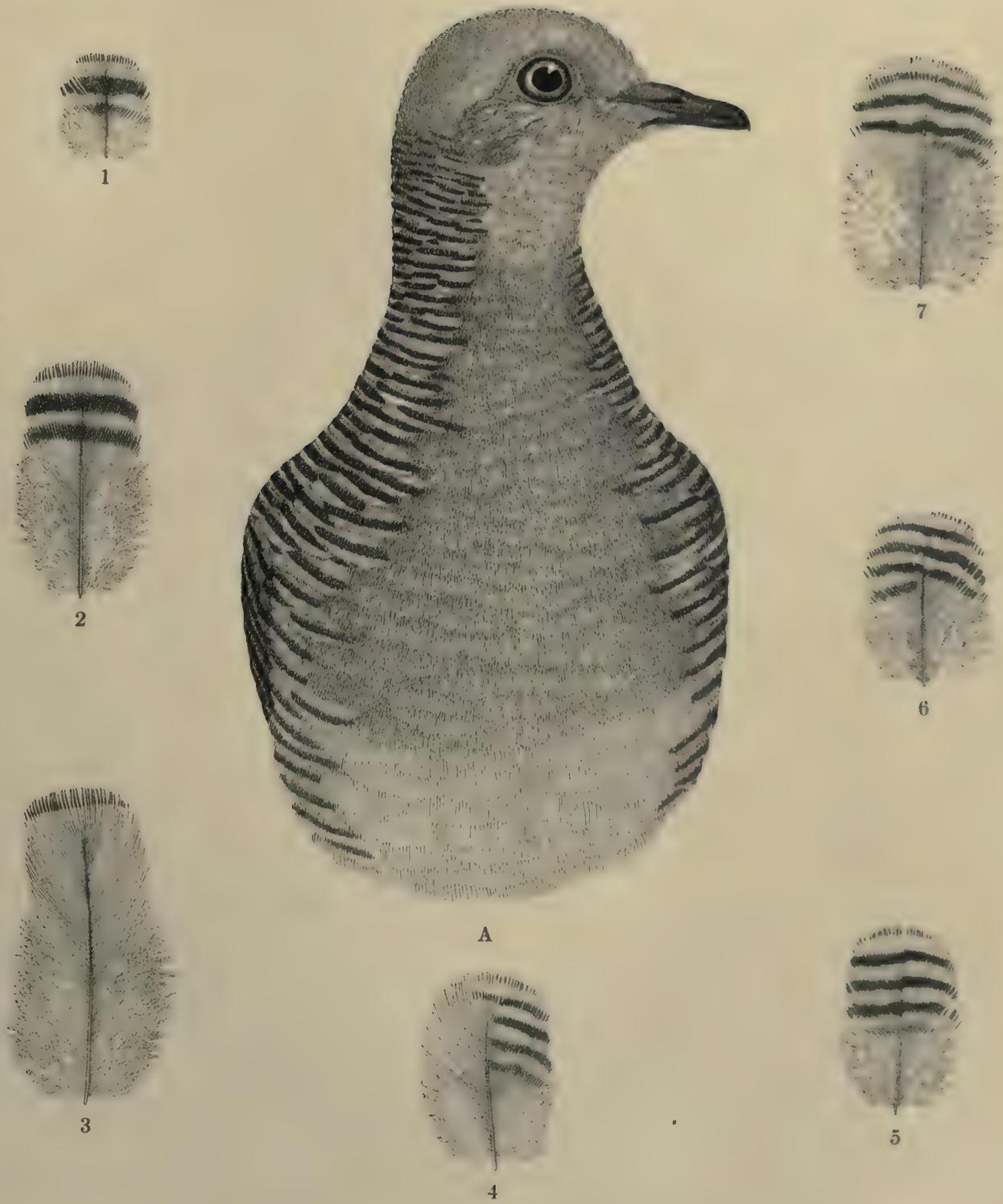
A. Adult male *Geopelia striata*. × 1.4. Hayashi del., Nov. 1902.
Figs. 1 to 7. Separate feathers from normal *G. striata*.

PLATE 38
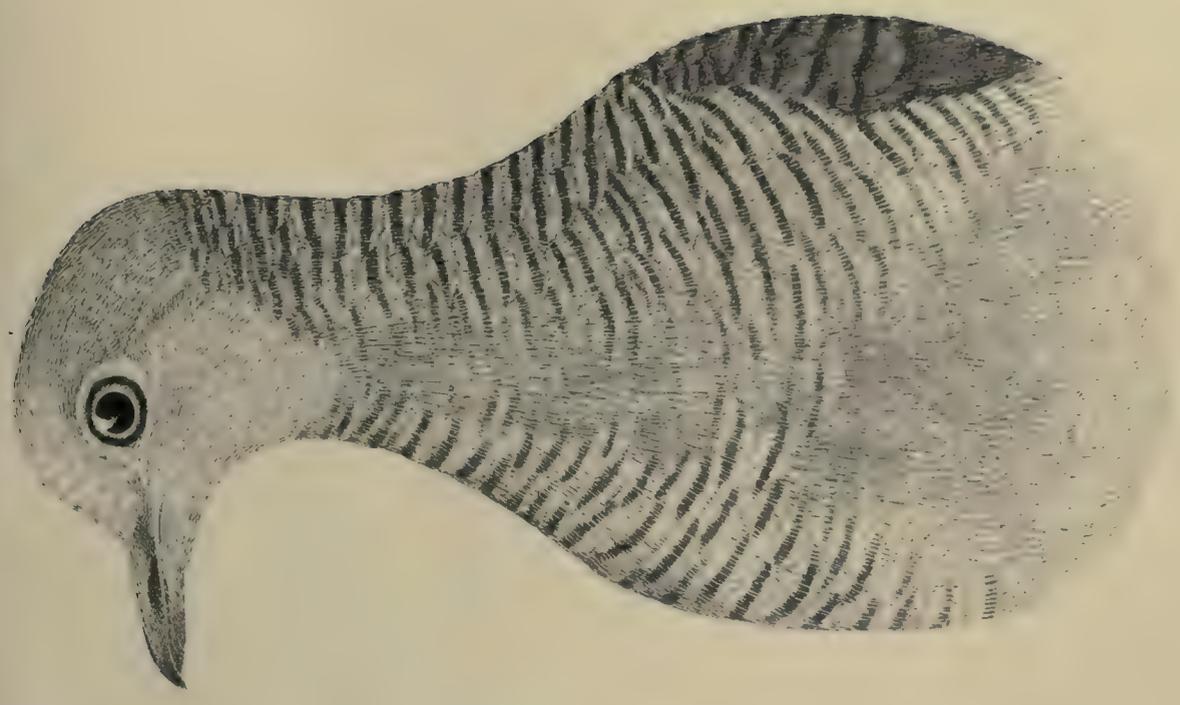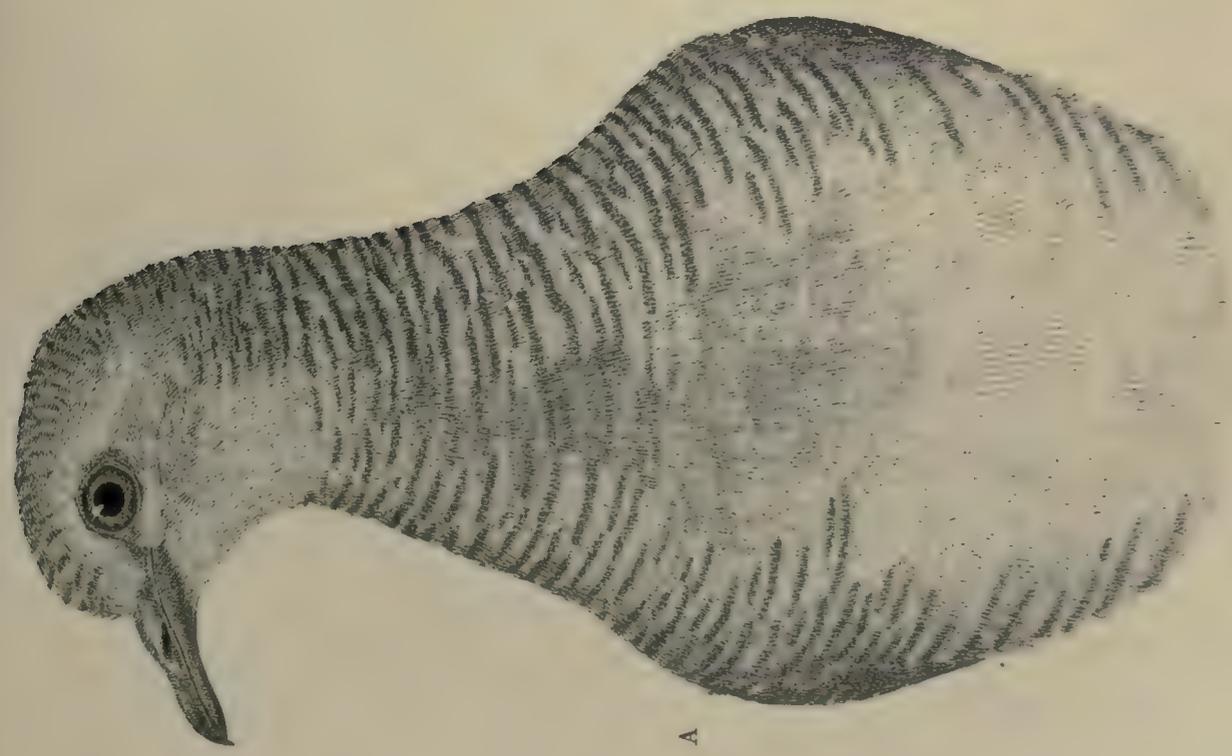
A. Juvenal *Geopelia striata*. × 1.5. Hayashi del., Oct. 1902.
B. Adult female *Geopelia striata*. × 1.5. Hayashi del., Nov. 1902.

still further upward it is shorter, thinner, and more worn; and, finally, just a bare remnant is left.

On the sides of the neck the black edge is wholly absent, or reduced to a mere dotted line that looks as if it were dropping off. The appearance is such as to suggest, at first sight, that the feather is in process of abrasion, but this appearance is probably due to imperfect or arrested development.

On the sides of the neck, in the region of the turtle-dove spots, the feathers show the clearest black and white bars and the nearest approach to pure white apical bars; but this apical white has been gained through the loss of the juvenal pale bar and the first subterminal black bar.

This shortening of the neck-feathers reminds of the fact that the differentiation of *ring*-feathers and *spot*-feathers is invariably accomplished by cutting off terminal parts of feathers. Ring-feathers are shorter than other neck-feathers, and look as if cut off with shears. When a feather is differentiated only on one web, the other web is seen to be much the longer.

In this same normal male (*Geopelia striata*) we find the following facts concerning the number of bars in the individual feathers (pl. 37, figs. 1 to 7):

(1) A feather from the front edge of the barred part of the neck, at about mid-height, shows four black bars (not counting the apical black, which is almost absent; it is barely suggested to the naked eye, but evident with magnifying glass).

(2) A feather from the middle of the left side of the neck shows the apical black bar quite plainly, though it is tapering and very thin. Besides this bar there are two other black bars, wider than those in No. 1 above, and then a third black bar that is very weak (pale gray). Another feather from the same region would show about the same, except that the third black bar is stronger.

(3) The feathers just under the ear have the apical bar very thin, but visible to the naked eye; then follow a white bar, a plain black, a white, and finally a weak but evident dark bar.

(4) Following from the back up along the mid-hind neck,[39] we find, to begin with (on back), feathers which have only the apical black bar; then others with 1 extra black, then 2 extra black, then 3 extra black; still further along, 2, and at the upper limit, only 1 extra black bar.

The front feathers are lighter—clearer white and black—and the back of the neck is darker, the white bar being replaced in the hind-neck with pale brown or fulvous. This is as in *Geopelia tranquilla*. The rudimentary apical black bars of the neck are most reduced at the middle height of the front edge of the neck; these become stronger as we go from here to the mid-back of the neck. This agrees closely with *G. tranquilla*. In *G. striata* I find about one more black bar to the feather than in corresponding feathers of *G. tranquilla*.

In *Geopelia tranquilla* the bars run all around the neck (pl. 39, fig. A). Those on the front half of the neck are of lighter color—clearer white and clearer black—than those on the back half; this of course harmonizes with lighter under parts and darker upper parts of the body as a whole.

Leaving the rudimentary apical black bar out of account—it is so reduced in front and on the sides as to be obsolescent—the rule is that we see two black bars

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[39] The fate of the terminal black bar in this series of feathers was noted above.

alternating with three white bars on feathers of the front neck (pl. 39, figs. 1 to 3). If the apical black be considered, then we have three black and three white bars.

In the lower half of the front neck the rule is three black bars (the inner one being weak) alternating with white ones. In the upper half of the front neck we come to feathers with only two black bars, and below the ear-coverts the little feathers have only one black bar (discarding the apical).

On the back half of the neck, in the middle region (fig. 5) we find two black bars (apical one not counted); and near the upper limit of the bars we find only a single black bar (fig. 4). Besides, in this part of the neck the white bars are replaced more and more with pale fulvous.

The apical black bars are most nearly obliterated in the mid-front of the neck; sometimes they are quite gone, at other times reduced to an extremely thin vestige. These vestiges become stronger as we go from mid-front to mid-back (of neck), and in the lower back part of the neck they finally attain full size (fig. 9), passing into the well-developed black edges of the general surface of the body and wings.

The throat and cheeks are pale gray. The breast below the barred region is delicate vinous, becoming white on the abdomen. There are no bars on the lower breast, abdomen, or sides.

Although the bars run across the whole front of the neck, I notice in the mid-front region just a trace of the vinous tinge, as if this species were in a very low degree anticipating the condition seen in *Geopelia striata*.

The question of the relative rank of *Geopelia striata* or *G. tranquilla* receives a mixed or compounded answer. *G. striata* comes nearer the inca-dove in one respect—

EXPLANATION OF PLATE 39.

A. Adult *Geopelia tranquilla*. × 1.4. Hayashi del., Jan. 1903.
    Shows the bars completely circling the neck.

1 to 9. Neck-feathers of adult *Geopelia tranquilla*. × 3. Hayashi del., Jan. 1903.
    1*a* and 3 from middle front of neck; 4 and 6 from middle side of neck; 7 and 9 from middle back of neck; 1*a*, 4, and 7 taken from corresponding upper height; 2, 5, and 8 taken from corresponding mid-height; 3, 6, and 9 taken from corresponding lower height.
Middle front of neck:
    1*a*. Apical bar quite faint, then a strong bar, then a dark gray bar near middle of feather. There are 3 light or white bars, alternating. Basal portion pale gray.
    2. Apical bar weak, then a strong black bar, then another dark gray, broadly V-shaped. Three light bars, outer one with a slight tinge of fulvous. Basal portion pale gray.
    3. No apical bar. Under a microscope I can detect an intimation of it in a few barbs, but this part is so nearly bleached out that it appears as a part of the white bar. The barbs of the apical-bar region are usually reduced in length to near the point of annihilation.
Middle side of neck:
    4. Just under ear-coverts (at same height as figs. 1 and 7). Apical bar fairly strong; next is the strong bar, and then a faintest touch of another bar. (Mr. Hayashi has separated this rudiment from the strong bar too widely. It should stand as far from the latter as this stands from the apical.)
    5. Apical bar is stronger and wider than in figure 2; first light bar (tinged slightly fulvous) is narrower than in figure 2, but the artist has made it too narrow, relatively; it should be fully two-thirds as wide as in figure 2. The middle black bar is wider than in figure 2, and the inner bar is much weaker than in figure 2; the artist has made it much too strong.
    6. Apical bar about the same as in figure 5. The light bars are pale fulvous. Basal half is pale gray, darker at middle.
Middle back of neck:
    7. Weak apical bar, then a fulvous bar, then a very weak dark bar.
    8. Apical about same as in figure 5, perhaps a little stronger; then a fulvous, then a black or dark-gray bar, then fulvous, then just a faint dark bar, more obscure than in drawing.
    9. Apical bar a little stronger than in figure 6, then a fulvous bar; then even gray to middle of feather; thereafter much paler.

PLATE 39

A. Adult *Geopelia tranquilla.*   × 1.4.   Shows the bars completely circling the neck.
  Hayashi del., Jan. 1903.
B. 1 to 9. Neck-feathers of adult *Geopelia tranquilla.*   × 3.   Hayashi del., Jan. 1903.

in having barred feathers along the sides of the abdomen. But *G. tranquilla* seems to stand lowest (1) in having bars all around the neck; (2) in size; and (3) in having one bar less on the barred feathers.

Geopelia humeralis represents the highest type of the banded or barred geopelias, as is seen in a comparison of the adults of the several species; the same thing is still better shown in the juvenile feathers. Only the diamond-dove (*G. cuneata*) represents a still higher type.

The adult *G. humeralis* shows a considerable regional diversity which in all respects is much more faintly expressed in the juvenal plumage. The back and sides of the neck are bright rufous, each feather being edged with black. This corresponds to the "ring" of the ring-doves and to the neck-spots of the turtle-doves. The feathers are arranged in rows, which are plainer in the young. Those of the
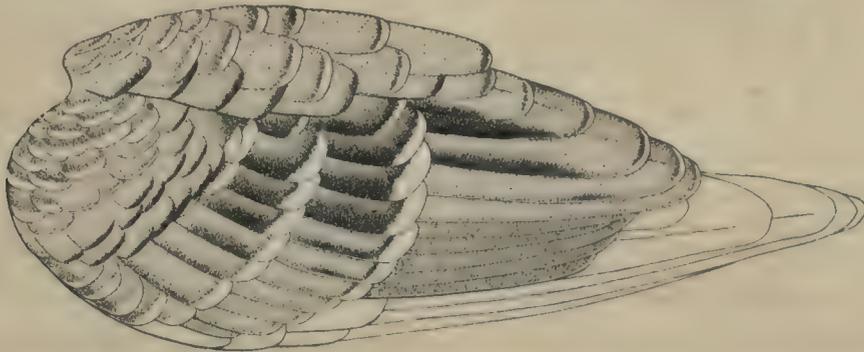
TEXT-FIGURE 20.—Wing of juvenal *Geopelia humeralis*, age 30 days. Natural size.
Hayashi del., July 1899.

The third row is covered except for 4 upper feathers. The oblique streak consists of two rows of black-tipped feathers, in front of which is one row of feathers that have little or no yellow tips. Some new feathers have appeared near lower edge of scapulars.

crown and occiput have a black edge, but the fulvous part is there reduced to a pale fulvous band next to the black edge. The breast and front of the neck are without the barring (pl. 40, fig. A) characteristic of this region in all of the lower species—*maugei, striata, tranquilla*.

The juvenal *Geopelia humeralis* illustrates the biogenetic law in the breast-feathers and in the pale bands at the edge of the feathers (pl. 41, fig. A). The feathers of the head, neck, breast, wing-coverts, and back are all edged with pale whitish; this is slightly tinged with fulvous on the scapulars. These light edge-bands point to the turtle-dove type.[40] In front they are followed by a band of black which becomes terminal in the adult feathers (text-fig. 22), the light edge there failing to develop. Even in the juvenal feathers the light edge is rudimentary in some of the tertials and scapulars, and often so imperfect as to appear to be wearing off (see pl. 41 and text-figs. 20, 21). The pale edges run clear over the forehead, where all becomes gray in the adult.

[40] The under side of an adolescent *Turtur orientalis* is here described for comparison with the coloration of the lower parts of *Geopelia humeralis*: The upper breast and front of neck dusky brown, with a suggestion of grayish tinge. This part is more or less clear gray in *G. humeralis*. The edges of the feathers are slightly paler than the body of the feathers. The lower breast, at the same level at which *G. humeralis* becomes decidedly lighter, becomes lighter here also; the color being dull vinous, clearest along the sides—under or at lower edge of wing—and becoming still lighter along the middle of the abdomen, where we catch a shade reminding of the fulvous color seen in *G. humeralis*. The color fades gradually into whitish in the region of the vent. The under tail-coverts are gray.

These pale edges run entirely across the neck and upper breast, and become pale fulvous tinged with vinous at the sides at the bend of the wing. The black bands within the pale edge-bands become quite pale on the breast, and disappear in the middle line. The juvenal *humeralis* thus stands near the level of the adult *striata*. On the lower breast and abdomen the bands disappear, the feathers becoming pale or whitish. A very faint tinge of vinous can be recognized on the lower breast. In the specimen figured (pl. 40, fig. A) two feathers on the breast have no bands—are pale grayish throughout. Another specimen shows alternating bands at or near the bend of the wing.

EXPLANATION OF PLATE 40.

A. Adult male *Geopelia humeralis*. × 0.7. Hayashi del., Oct. 1902.
This and figure C illustrate the biogenetic law.
Middle of neck in front and upper breast are gray, slightly darker in female. This gray is fairly uniform, but some of the lateral feathers show more or less of a dark edge corresponding to the black edge seen on the upper feathers.
Lower breast pale vinous, stronger on sides, becoming white on abdomen and under tail-coverts. Some of these tail-coverts may have the vinous red.
Lateral feathers of breast that cover the front edge of wing quite bright fulvous; like the fulvous of the neck.

B. From near front edge of neck in "ring" region (left side).

C. Juvenal *Geopelia humeralis*, age 28 days. × 0.7. Hayashi del., Nov. 1902.
This specimen shows light edges on sides of neck. Another specimen about same age shows black edges (appearance as if light edges were worn off?), and the black is followed within by a fulvous band which is more or less irregular in width and outline; this is followed within by a second dark band, and then a second paler and more irregular fulvous band. The increase in number of bands is most noticeable on the sides of neck in region corresponding to the "ring" in the ring-dove.
Lateral feathers of breast at or near bend of wing show also two or more pale bars alternating with dark bars.

D. From side of neck (of above bird) near bend of wing. × 2.
Shows irregular second light band.

E. From middle of breast. × 2.
Shows a paler second light band than does the neck-feather.

EXPLANATION OF PLATE 41.

A. Wing of juvenal *Geopelia humeralis*, age 11 days. × 1.5. Hayashi del., Aug. 1899.
Earlier feathers now present; elbow is still uncovered, and a long pin-feather lies just above it, while a second lies somewhat below it.
On the lower front edge of wing are 4 pin-feathers, the newest in the wing.
Scapulars 24 in number; the posterior is a later feather and has less margin and a darker bar.
Three of the tertials have a long dark streak, the homologue of the chequer; the upper tertial is covered, being yet too short to be seen.
A few of the upper feathers—tertials and longer coverts and scapulars—show an indistinct duplication of the yellow margin (transverse barring).

B. Wing of juvenal *G. humeralis*, age 18 days. Natural size. Hayashi del., Aug. 1899.
Compare this stage in other geopelias.
Three upper feathers of the fourth row are in sight, the lower ones are covered.

C. Four inner tertials of *G. humeralis*. Natural size. Hayashi del., July 1907.
We have here well-marked marginal streaks on the lower edge; also subterminal dark bars followed by faint traces of alternating light and dark cross-bars. Compare with tertials of mourning-doves (figs. D and E).

D. Three inner tertials of *Zenaidura carolinensis* (PP 1). Natural size. Hayashi del., July 1907.
These feathers are double-spotted, the lower margin much the stronger. This young was reared by ring-doves.

E. Three inner tertials of *Z. carolinensis* (PP 2). Natural size. Hayashi del., July 1907.
This bird raised by foster-parents (*Zenaida* hybrids) which fed it badly. Grown under adverse conditions, the tertial spots are mere marginal remnants.
The feathers which grew in the place of these plucked tertials had spots strong and double, like those of its mate (fig. D).

PLATE 40
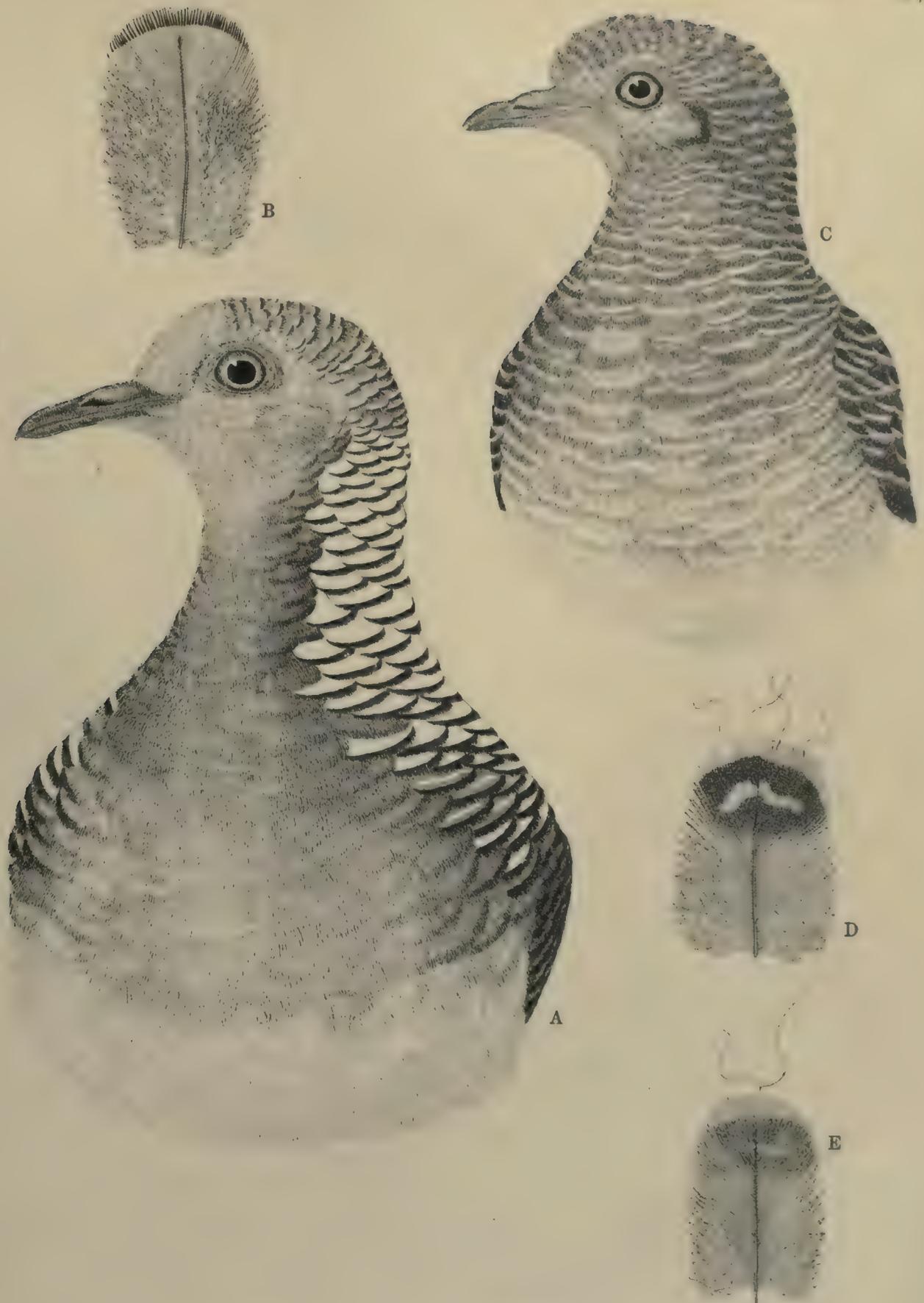
A. Adult male *Geopelia humeralis*. × 1.4. Hayashi del., Oct. 1902.

B. From near front edge of neck in "ring" region (left side).

C. Juvenal *Geopelia humeralis*, age 28 days. × 1.4. Hayashi del., Nov. 1902.

D. From side of neck (of above bird) near bend of wing. × 2.

E. From middle of breast. × 2.

PLATE 41
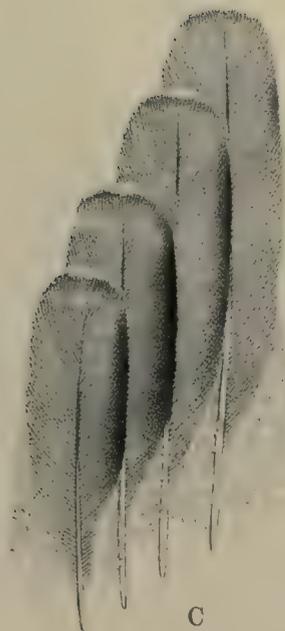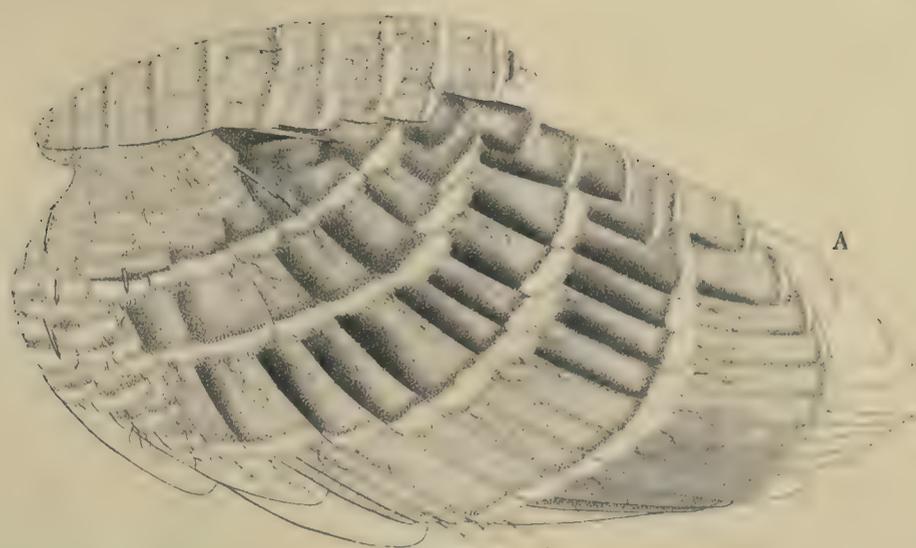
A. Wing of juvenal *Geopelia humeralis*, age 11 days.   × 1.5.   Hayashi del., Aug. 1899.

B. Wing of juvenal *G. humeralis*, age 18 days.   Natural size.   Hayashi del., Aug. 1899.

C. Four inner tertials of *G. humeralis*.   Natural size.   Hayashi del., July 1907.

D. Three inner tertials of *Zenaidura carolinensis* (PP1).   Natural size.   Hayashi del., July 1907.

E. Three inner tertials of *Z. carolinensis* (PP2).   Natural size.   Hayashi del., July 1907.

Spots or marginal streaks are recapitulated in the tertials, scapulars, and coverts of the juvenal wings (pl. 41, A and B, and text-figs. 20, 21). A comparison of these streaks in the tertials of *humeralis* and the mourning-dove (*Zenaidura*) is made possible by figures 3 to 5 of plate 41.

The homology of the wing-chequers of the juvenal geopelias with the chequers in *Columba livia* has been pointed out in the preceding chapter. In all of the geopelias[41] these chequers are completely lost with the first feathers.[42]

In the ontogeny of the geopelias we see the different species all taking departure from a common color-pattern, consisting of longitudinal spots or chequers, dis-
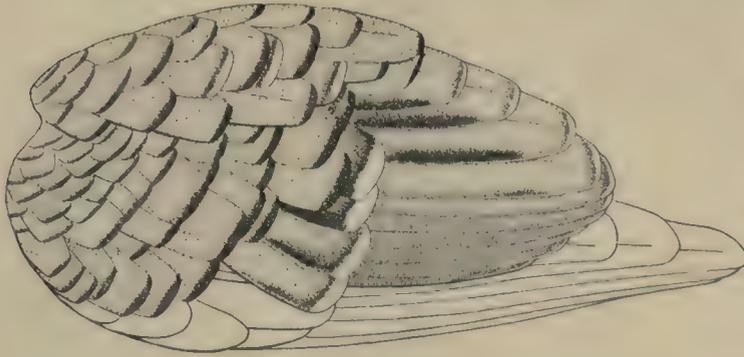
TEXT-FIGURE 21.—Wing of juvenal *Geopelia humeralis*, age 10 weeks. Natural size. Hayashi del., Aug. 1899.

The first row of coverts retains only 4 feathers seen in the previous (30-day) stage, and these are being covered by new black-tipped feathers. Only 3 old feathers remain in the scapulars.

TEXT-FIGURE 22.—Wing of adult *Geopelia humeralis*. Natural size. Hayashi del., June 1899. Drawn for comparison with wings of the young.
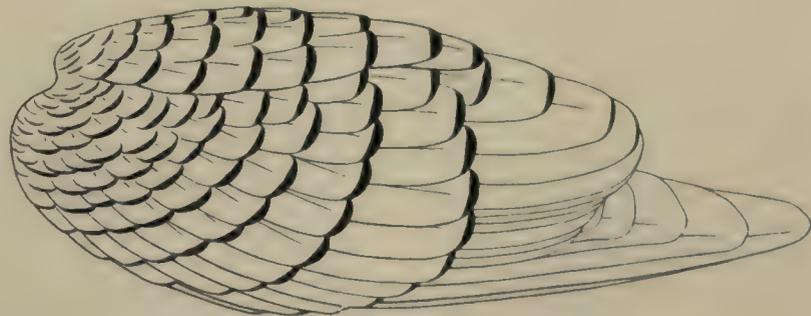
tributed uniformly to all the feathers of the wing. We see this common and earlier pattern retained for only a few weeks, the later pattern developing in two widely diverging directions and leading to two types of generic rank.

THE PHABINÆ.

The relation of the color-pattern of two of the genera of this subfamily has been already described—*Ocyphaps* in Chapters II and III (pls. 8, 14, 15, 16; *Phaps* in Chapter II (pl. 6). (A short treatment of three other genera—*Calopelia, Œna, Tympanistria*—of this group is extracted from a short paper without illustrations published[43] in 1907.—ED.)

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[41] *Geopelia* or *Stictopelia cuneata* is described and figured in Chapter IX.—ED.

[42] It has been observed that the feathers of the oblique streak do not make their appearance at exactly the same age in the several species of *Geopelia*. The order is as follows: (1) *G. tranquilla:* streak out at 17 days and a second row with black tips begins; (2) *G. striata:* streak just begins at 18 days; (3) *G. cuneata:* two rows well started at 19 days; (4) *G. humeralis:* begins about 19 to 21 days; at 28 days one row and three more black-edged feathers (some with very narrow light edge).

[43] Avicultural Magazine, London (Journal of the Avicultural Society), n.s., vol. 5, No. 6, April 1907.—ED.

In a review of my paper, "The Problem of the Origin of Species," Dr. A. G. Butler comments[44] as follows on my conclusion that the bars in pigeons have been evolved from chequers:

This is certainly not the conclusion to which a study of the nestling plumage of some at least of the African doves leads me, inasmuch as the conspicuous spots on the scapulars and inner secondaries appear in the adults with the disappearance of the juvenile bars.

I presume that the maiden-dove (*Calopelia puella*), recently described by Dr. Butler,[45] was one of the "African doves" he had in mind. This species is pictured as having only three "metallic spots on the inner greater wing-coverts and largest scapulars." An immature bird described by Captain Shelley in 1883 (Ibis, p. 322) is referred to as having "black bars on the scapulars, wing-coverts, and secondaries."

These "black bars" of the young are not further described, and I am therefore in doubt as to whether they represent *rows of chequers* or the higher stage of development seen in *apical crescents*, a form characteristic of the inca-dove and the geopelias.

The mature color-pattern in *Calopelia* does not differ widely in essentials from those seen in some American species, *e.g.*, the mourning-dove (*Zenaidura carolinensis*) and the zenaida-dove (*Zenaida amabilis*). In the young of these doves we find many typical chequers, more or less evenly distributed over the whole wing; in the adult we have only a few of these spots left, and left in the same region in which the three spots of the maiden-dove are located. The obliteration of the spots in the American birds has, however, not yet been carried quite so far as in the African dove. In the mature mourning-dove we find not only a larger number of visible spots, but also many concealed vestigial spots. *Zenaida* has carried the reduction of spots somewhat farther, and stands only a little behind the maiden-dove. Our white-winged pigeon (*Melopelia leucoptera*) has practically completed the deletion of spots, only a very few vestigial traces being discoverable in a single specimen obtained from Jamaica. I do not find such vestiges in white-wings from Mexico and Arizona.

In a male cape-dove (*Œna capensis*) that has just come to hand I find indications of a still closer correspondence to the *Zenaida* and *Zenaidura* types. In this dove (pl. 42, fig. A) there are two very short bars, one on the tertials (with one spot on the right wing and two on the left), and another on the inner long coverts (with three spots on the right wing and four on the left). These black ("steel-blue") spots are subterminal squarish blocks on the outer webs. On the inner webs of the tertials bearing the bar-spots I find elongate black spots reduced to *narrow marginal streaks* in most cases. A tertial with such a streak on the inner web extending nearly to its tip and a bar-spot on its outer web at a considerable distance from the tip presents a picture quite characteristic of the zenaidas and the mourning-doves.

So close and peculiar a parallel in the mature patterns of these doves would lead us to expect fully as close a resemblance in the juvenal patterns; but Salvadori's description of the young cape-dove does not seem to confirm this anticipation. "The wing-coverts," as he reports, "are grayish-brown with blackish bands and whitish-buff apical spots."

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[44] Avicultural Magazine, Dec. 1906, p. 74.   [45] *Ibid.*, June 1906, p. 251

According to Dr. Butler (Avic. Mag., n. s., Vol. II, p. 101), the young tambourine-dove (*Tympanistria tympanistria*) is similarly marked: "All the feathers of the wing and tail are of a bright coffee-brown color with broad subterminal irregular transverse black bands." The figure given in a later volume of the same magazine (Vol. IV, page 308) makes it clear that the young tambourine rises to a stage of irregular cross-bars analogous to what is seen in the young inca-doves (*Scardafella inca*) and geopelias, in which we find the feathers edged apically with a pale straw-color (very narrow in inca but conspicuous in geopelias), followed within by a *blackish crescentic* bar, and then one or more quite broken pale dull "bars" (too irregular to be described as bars—mere suggestions of bars). In the mature state the pale apical bar is lost and the blackish crescentic bar becomes terminal.

This form of barring, so far as the black crescent is concerned, is something later in evolution—as I have elsewhere (in the present chapter) made clear—than the lateral chequers of the mourning-dove, passenger-pigeon, etc. In young geopelias (*e.g.*, pls. 38 and 41 and text-figs. 18 to 21) we have transient lateral chequers in the tertials and longer wing-coverts, and in such continuity with the black crescents that the latter must be regarded as derived from the former. Even in domestic pigeons we frequently see chequers reduced to black crescents.

In the young inca-doves (pl. 34, figs. C and D) these same transient chequers are recapitulated on the tertials and the long coverts. Although not so black as in the geopelias, they are yet plain and unmistakable homologues. Only two or three of the inner long coverts have this vanishing chequer as a long lateral streak on *both the inner and outer edge of the feather*. On the remaining feathers of the row the mark appears only on the outer web, and becomes *weaker and narrower* as we descend the row, until on the outer two feathers it is wholly lost. The recapitulation of the marks in the inca and its South American allies, and again in all the geopelias of Australia—even in the diamond-dove, standing at the extreme upper limit of evolution thus far reached in this interesting genus—gives us a very important link in the sequence of phyletic stages.

I venture to predict that the young tambourine, the young cape-dove, and some of their nearer allies will be found to have more or less plain traces of the transient marginal streaks seen in the tertials and long coverts of the inca-dove, and perhaps also dull spots on the outer webs anticipating the spots of the adult.

Without going into the evidence here, I may say that I have fully satisfied myself that the lateral spots or chequers are derived from the turtle-dove spots, such as are still seen in *Turtur orientalis*, and, in a somewhat reduced form, in the European turtle-dove (*T. turtur*). The mode of derivation was by splitting the original central spot into halves. The splitting began at the apex of the feather, a short, wedge-shaped area of lighter color (*i.e.*, reduced in pigment) appearing at this point and extending more and more inward along the shaft, until the divided halves became two separate spots or chequers, more or less pointed at the distal end. The feather thus became double-spotted. Typical "wedge-shaped areas" are not rare in domestic pigeons with the chequered pattern, and they are very characteristic marks in the wing of the guinea-pigeon (*Columba guinea*), where they are described as "triangular white pots." They are seen again as a specific character in the spotted pigeon (*C. maculosa*) of South America. They occur also in the scapulars of *C. albipennis* of Peru and Bolivia.

This simple mode of converting the turtle-dove spot into a pair of lateral chequers is carried out most perfectly in the posterior scapulars and in the inner secondaries and large coverts of the wing of the domestic pigeon. As we pass downward towards the lower (outer) edge of the wing, the chequer on the inner web diminishes in size more or less rapidly and may be continued to or near the outer edge of the wing.

Now, chequers are the elements out of which wing-bars arise. "Rows of chequers," as we see them in the young mourning-dove or in the young passenger-pigeon, or in the chequered rock-pigeon (*Columba affinis*), may of course be called

EXPLANATION OF PLATE 42.

A. Cape-pigeon, female *Oena capensis*. Toda del., after Temminck and Knip, Les Pigeons, I, p. 117, pls. LIII and LIV, 1808–1813. × ?

Temminck and Knip picture both male and female.

A very interesting species for comparison with the crescent-barred geopelias. It is much more highly differentiated than any of the geopelias in that:

(1) The male is differently colored from the female, having its (*a*) forehead, throat, front neck, and breast black; (*b*) the occiput and hind neck are pale brown shading into pearl-gray on the sides of the neck (the female has the whole head and neck and breast pale brown, becoming lighter in front half of head and throat); (*c*) "the inner upper wing-coverts have large steel-blue patches" (Salvadori), which are not seen on the female. These spots remind of the Florida ground-dove.

(2) The dark crescents have all disappeared except in the upper tail-coverts (possibly the few black bands on the lower back are derived from the crescents), where they are still preserved in both sexes.

(3) The great length of the middle tail-feathers.

(4) The 2 (4 in female? Temminck says 3 bands) black bands across the lower back.

According to Salvadori (p. 503), the young has dark crescent-bars on crown and neck, and the wing-coverts are grayish-brown, with blackish crescentic bars and light buff edges.

The pictures (of Madame Knip) of the adult male and female show that the crescents are apical in the male and subapical in the female, the female seeming to keep the pale edge of the young.

B. Right wing of adult female tambourine-dove, *Tympanistria tympanistria*. Natural size. Drawn from U. S. Nat. Mus. No. 116316.

Here we find in the tertials 2 plain spots and 1 very weak spot, ordinarily concealed, and perhaps not always present.

In the long coverts 3 plain spots—one more than in the juvenal male, an indication that female has more spots than male.

In the first row of median coverts we have two concealed spots, seen by lifting the overlying row. These were not found in the juvenal male. (The single juvenal bird examined is elsewhere stated (see figs. C and D) to be a female. I am quite unable to understand this and the earlier reference to a "juvenal male"; unless perhaps a figure or description—by Dr. Butler (?)—of such a bird was at hand.—ED.) Again an indication that spots are more numerous in the female than in the male.

No spots in the scapulars, and no spots or streaks on the inner webs. These spots extend towards the base of the feather, as in the juvenal.

There is probably more pigment in the adult (permanent) spots, but I should expect to find in the young female a little larger number of spots than in the adult.

C. Three inner tertials of juvenal female tambourine-dove. Drawn from U. S. Nat. Mus. No. 117867, July 1907.

Shows rufous apical marks (of 1 to 1.3 mm.) followed by a dark bar, darkest next to the apical mark.

The dark bar is narrow (1 mm.) at the margins and wider (up to 3 mm.) near the feather's shaft. This dark bar is followed by a narrow irregular rufous bar.

Shows also black chequer on the outer web; these are squarish, on the margin and about 10 mm. from tip in first feather, 15 mm. in second feather. Only two chequers in this row; size is about 7 by 6 mm.

D. Two inner long coverts from same bird as above.

In the long coverts I also find only 2 spots, but these extend farther towards the base of the feather and thus show that the chequers are derived from the dark center of the turtle-dove feather.

For a description of general ground-color see Butler, Avic. Mag., Aug. 1906.

E. Wing of adult male *Chalcopelia afra*. Natural size. Hayashi del., Aug. 1904.

This species forms one of the color-types connecting the turtle-doves with *Geopelia*.

Compare with *Peristera cinerea* (pl. 31) and with open wing of another adult male *C. afra* (pl. 35, fig. B), where the legend applies also in part to the present figure.
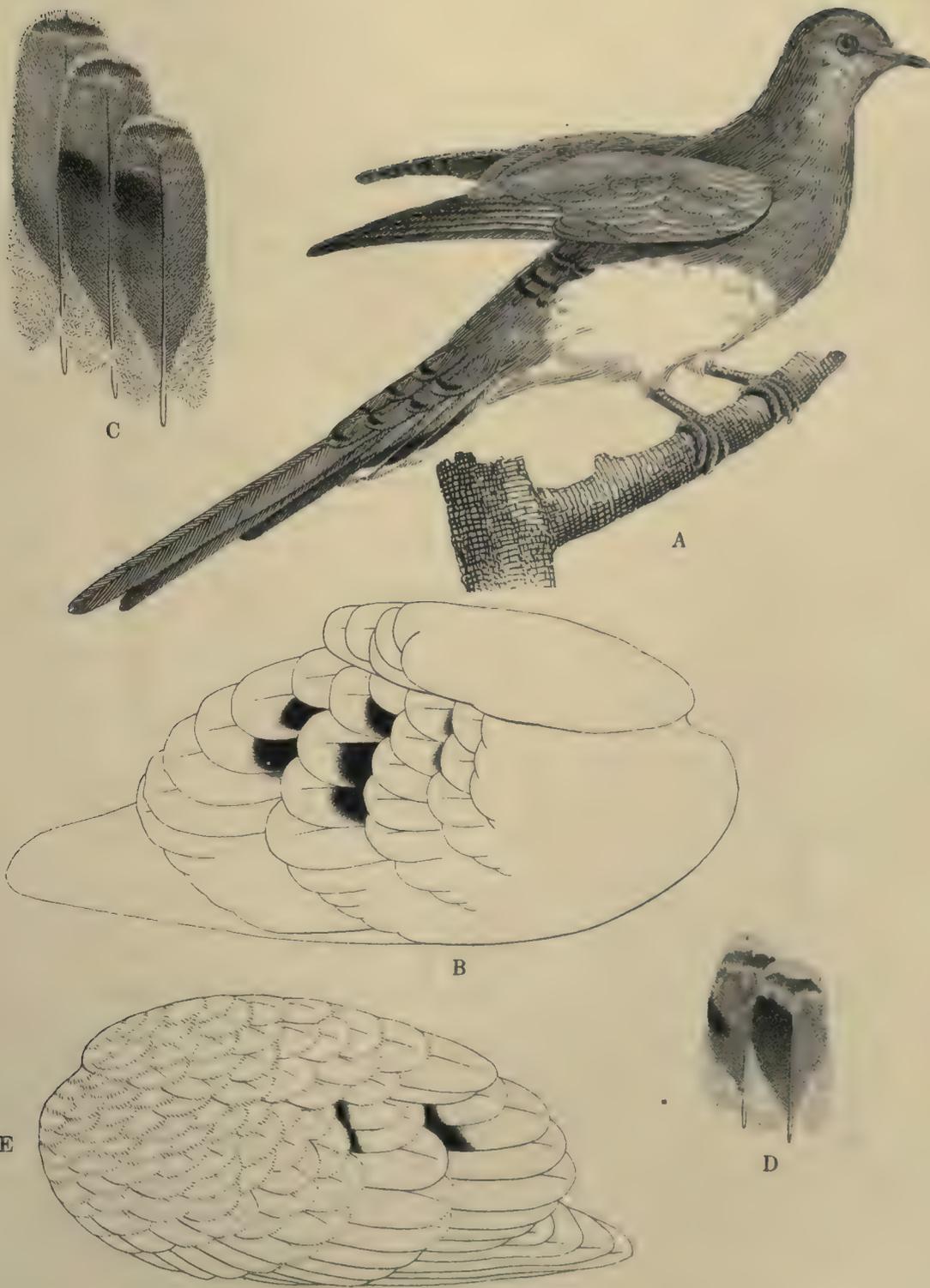
PLATE 42

A. Cape-pigeon, female *Oena capensis*. Toda del., after Temminck and Knip, Les Pigeons, I,
   p. 117, pls. LIII and LIV, 1808-1813.

B. Right wing of adult female tambourine-dove, *Tympanistria tympanistria*. Natural size. Drawn
   from U. S. Nat. Mus. No. 116316.

C. Three inner tertials of juvenal female tambourine-dove. Natural size. Drawn from U. S. Nat.
   Mus. No. 117867, July 1907.

D. Two inner long coverts from same bird as above. Natural size.

E. Wing of adult male *Chalcopelia afra*. Natural size. Hayashi del., Aug. 1904.

"bars"; but in that case we have to remember that they are yet a long way from the finished bars of such birds as *C. livia*, the bleeding-heart (*Phlogœnas*), many Peristeræ, and nearly all pigeons with bars in the adult plumage. So long as the whole wing remains more or less uniformly marked with distinct lateral spots, confusion may be avoided by describing it as spotted or chequered. *C. affinis* has been so described, and *Ectopistes*, which has rows of spots both in young and adult stages, is never described as a barred pigeon. American and European ornithologists have generally, I believe, adhered to this mode of description. Salvadori, for example, in his Catalogue of Pigeons, speaks of *Ectopistes* as having "scapulars, tertials, and median wing-coverts with velvety-black spots," and of *Chamæpelia* as "marked with blotches of a steel-blue with violet reflections." In all typical turtle-doves we have rows of spots, but we never think of describing them as bars. The distinction between spots and bars has become so fixed in the breeder's terminology that I did not realize the danger of any confusion or misunderstanding on this point before reading Dr. Butler's very courteous review. Had it been possible to illustrate my paper with plates my meaning would probably have been clear in regard to the evolution of wing-bars from chequers, at least in so far as concerns the rock-pigeons and their descendants.

The typical wing-bar of the adult bird, as I conceived it, represents a specific regional mark—a continuous band of color on a uniform ground of contrasting color. In such a bar the individualities of the elements are submerged in the individuality of the bar. When, therefore, as in *Columba affinis*, we meet with rows of chequers, and find that the posterior two rows are the homologues of the two black bars of *C. livia*, and, further, that this two-barred condition is reached in domestic birds through the obliteration of the anterior rows of chequers and by cutting down the chequers in the remaining two rows to outlines that in each row flow together in a single band, we are warranted in saying that bars are evolved from chequers.

If we speak of the original rows of chequers as bars, then it becomes necessary to distinguish between juvenal or primary bars and adult or secondary bars. The direction of derivation remains the same. If we find cases in which the deletion of spots has been carried still farther, until only a few of the larger spots in the posterior rows remain, as in *Zenaida* and *Zenaidura*, we may then say that "spots" are the true homologues of typical bar-elements in other species.

I believe that the few spots in the wing of the adult *Calopelia* are such homologues, and that they are preceded in the juvenal plumage by corresponding marks which have been overlooked. I am aware that in the young of this species the scapulars, wing-coverts, and tertials are said to be "barred with black." These juvenal bars are probably of the same nature as those seen in the young tambourine, the relation of which to chequers has already been indicated.

These remarks will make it sufficiently clear that my view does not contradict Dr. Butler's observations on African doves.

In the above remarks[46] I ventured some suggestions as to the phyletic sequence of color-marks in the tambourine-dove and its nearest allies. These remarks on this dove were based on the following description by Dr. A. G. Butler,[47] in which

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[46] The following statements were written several months after the preceding account was published. In the meantime, the author had been able to see and study a few specimens of the tambourine-dove.—Ed.

[47] Avicultural Magazine. Aug. 1906, p. 309.

was included the statement of Mr. Oberholser.   Speaking of the young, 19 days old, Mr. Butler says:

"Colouring of upper parts largely bronze-brown, but the feathers *barred with buff and black;* flights reddish-chestnut; tail feathers vinous brown, the outermost feathers white. Forehead and broad eye-brow streak buff; the feathers at sides of crown standing in curved rows so as to produce a sort of divided crest, buff-brownish; ear-coverts and cheeks leaden gray; the former apparently narrowly barred *white* and *buff,* but this appearance is probably due to the sheaths still remaining on the feathers at this part of the head; sides of neck, throat, and breast buffish brown with narrow *blackish bars;* abdomen white; bill dull black; feet dark leaden gray with a faint sub-tint of flesh color; the eye was too sunken to describe.

"In his account of 'Birds Collected by W. L. Abbot in the Kilmanjaro Region, East Africa' (Proc. U. S. Nat. Mus., Vol. XXVIII, p. 843), Prof. H. C. Oberholser describes the immature tambourine-dove compared with the adult as follows: 'Upper surface of the body more rufescent; forehead grayish, slightly tinged with tawny; crown washed, the *back and rump barred with rusty;* wing-coverts and secondaries duller, as well as rather paler, with mottlings and *some bars of dark brown and tawny,* the *secondaries with a dark subterminal bar,* sides of the head shaded with ashy and brownish; anterior lower parts *more or less barred with dark brown and ochraceous;* lower tail-coverts with *tips, and sometimes bars, of tawny.   This would probably be an intermediate stage between the nestling and adult plumage!'*"

EXPLANATION OF PLATE 43.

Figs. 1, 2, 3. Three wing-feathers of adult female green-winged pigeon, *Calcophaps indica.* × 2 Toda del., Nov. 1903.

These feathers, plucked in May 1903, show transverse bars.

The green portions of the feathers are left white, except for the bars. It looks as if the turtle pattern was the foundation, and as if the light edge had spread inward, becoming green (sometimes bronzy red); or one might think that the exposed part of the black had changed to green. The change, whatever its nature, begins at or near tip and progresses towards base.

The upper feather is an inner long covert (left side).

The middle feather is an inner long covert (the next below).

The lower feather is an upper (inner, left) tertial.

The bars cross both webs, and are on green and dark (blackish-gray) color as well. At the tip they more nearly form a right angle with the shaft; inward they meet at a very obtuse angle. They are visible on the distal two-thirds of the feather.

Figures 1 to 5 all show the "fundamental bars" to which reference in the text has several times been made.—ED.

Fig. 4. A posterior scapular of a male *Phaps chalcoptera.*   Natural size.

The "barring" is very plain, but stands out more conspicuously in the drawing than in the feather.   The bars are pretty regular in their distance apart—about 14 of them on the distal two-thirds of feather.   They are symmetrical and form an obtuse angle at the shaft.   In the long coverts they are also seen, though not so plainly.

The spot or chequer is quite strong in the scapulars of this particular male; in another male the scapulars were without spots.

Fig. 5. From a female nicobar pigeon, *Calœnas nicobarica.*   × 1.4.

One of the long feathers from the back of the neck, showing regularly spaced cross-bars. The feathers of the back were more faintly barred.

Figs. 6, 7, 8. Three wing-feathers of a juvenal (7 weeks) *Leptoptila* sp.?   × 2.   Hayashi del., Oct. 1903.

(The exact location of the feathers drawn is not indicated.—ED.)

The coverts of the wing show rufous apical marks (and in some this is followed by a subterminal bar), and this is soon followed by an intimation of a rufous bar and a midrufous streak.

The subterminal bar was later found to be present on the tertials of another *Leptoptila* (*reichenbachi*), and here the apical mark widens at the middle of the tip; on the innermost tertial this apical white is prolonged to a distance of 4 to 5 mm. as a shaft-streak.

PLATE 43
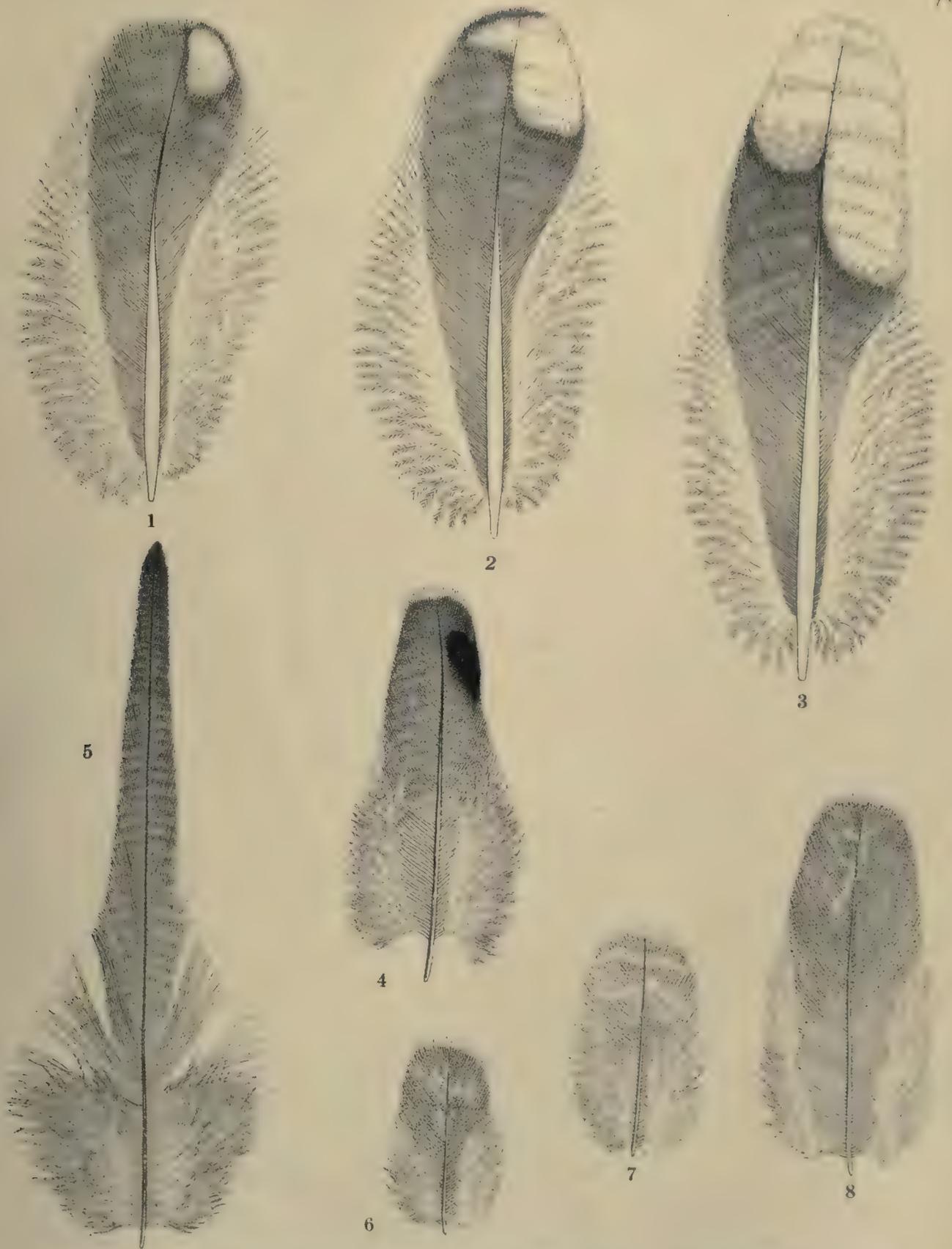
Figs. 1, 2, 3. Three wing-feathers of adult female green-winged pigeon, *Chalcophaps indica.* × 2.
Toda del., Nov. 1903.

Fig. 4. A posterior scapular of a male *Phaps chalcoptera.* Natural size.

Fig. 5. From a female nicobar-pigeon, *Calœnas nicobarica.* × 1.4.

Figs. 6, 7, 8. Three wing feathers of a juvenal (7 weeks) *Leptoptila* sp.? × 2. Hayashi del.,
Oct. 1903.

Although I had not yet seen this species, I felt safe in assuming that the development of its color-pattern would follow the same sequence that I had found to be general among pigeons. Accordingly I ventured to predict that:

"The young tambourine, the young cape-dove, and some of their nearer allies, will be found to have more or less plain traces of the *transient marginal streaks* seen in the tertials and long coverts of the inca-dove, and perhaps also *dull spots on the outer webs anticipating the spots of the adult.*"

Through the kindness of Mr. Rathbun, I have received from the U. S. National Museum three specimens of this dove—a pair of adults and the "immature" specimen described by Mr. Oberholser. The latter, as a moment's examination shows, not only verifies my prediction, but also reveals some other features that still further justify the comparison I made with the zenaidas, incas, and geopelias.

In both the tertials and long coverts (pl. 42, figs. C and D) I find a small number of black chequers on some of the outer webs. These chequers extend very considerably farther toward the base of the feather in the coverts than in the tertials and thus show that the chequers are derived from the dark center of the turtle-dove pattern. The light (rufous) apical edge, the subterminal dark bar, followed by another rufous transverse bar, all reminding of the geopelias, are all found in these juvenal feathers. It is probable, too, that the spots are more numerous in the adult female (pl. 42, fig. B) than in the male.

The wing-bars of *Chalcopelia afra* are figured in plates 35 (fig. B) and 42 (fig. E). Shadowy spots or chequers are found on the tertials and longer coverts. These remnants of spots are mostly on the outer webs. The cross-stripes on the back, or rump, of these birds are formed of black-tipped feathers—the homologues of the black crescents.

The iridescent regions of three wing-feathers of *Chalcophaps indica* are indicated in plate 43 (figs. 1 to 3).

The young of this species seem to have the turtle-dove pattern. Mr. D. Seth-Smith[48] says:

"On leaving the nest the young birds are *dark brown, the feathers of the head, breast, and wing-coverts being broadly margined with chestnut.* Some of the lesser wing-coverts are green, and there is a distinct greenish tinge to some of the secondaries and their coverts."

In *Phaps chalcoptera* (the bronze-wing) we find bars developed over nearly the whole wing;[49] in *Phaps elegans* (the brush bronze-wing) there are only *two posterior bars.*

In *Geophaps smithi* (Smith's ground-dove) we find only a few feathers of the two posterior bars retaining a bronze color (see pl. 48, fig. C).

In *Ocyphaps* (crested pigeon) we have many bars, strongly reduced, and in *Lophophaps* we get a further reduction.

Lophophaps leucogaster (text-fig. 9) stands above *Ocyphaps* also in having no elongated marks or marginal streaks on the long coverts. (Reference to this pattern is made in Chapter II.—ED.)

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[48]Avicultural Magazine, July 1906, p. 277.
[49]A scapular showing a marginal chequer and the "fundamental barring" is shown in pl. 43, fig. 4.

The Geotrygoninæ.

The Geotrygoninæ form a large subfamily of pigeons (see table 2). These are all birds that run on the ground most of the time, and their behavior in fighting, in cooing, and in hiding with tail raised and head down stamps them all, so far as I have seen them, as of common descent. It is in this group that we find the *Leptoptila*, *Osculatia*, *Geotrygon*, and *Starnœnas* of North and South America; the *Phlogœnas* of the Philippines, the *Leucosarcia* of Australia, the *Haplopelia* of the Ethiopian region, the *Eutrygon* and *Otidiphaps* of New Guinea. The group then has a wide distribution, and furnishes another example of birds that have departed from the turtle-dove pattern, mainly by loss of spots.

In a *Geotrygon* (sp. ?) from Brazil I find dark centers reduced to a minimum in the under tail-coverts and on the under surface of the body generally. The long coverts of the wing have dull dark centers and some of them show a light (rufous) edge. In young geotrygons I have seen a dull reddish-brown mid-streak in the upper wing-coverts. This streak is of the same color as that of the same streak found in *Melopelia*.

Leptoptila shows characteristics—in courting behavior and in voice—that seem to match well with those of *Calopelia*. Dr. Butler[50] makes note of the agreement in behavior. The juvenal upper wing-coverts (pl. 43, fig. 6) of *Leptoptila* are of interest in showing the light mesial streak[51] which, as we have already noted, is the means of dividing the dark turtle-dove center into two lateral chequers.

Phlogœnas luzonica—the bleeding-heart pigeon—has three plain wing-bars in the posterior part of the wing. A fourth bar is so covered and irregular as not to appear, but two middle coverts show that the bar-elements are here continued, though reduced in sharpness. The wing-pattern thus strongly reminds of conditions in *Columba livia*.

Leucosarcia picata, the white-faced pigeon, has the turtle-dove pattern in the adult feathers; such feathers are, however, limited to the larger portion of the under surface of the body. A series of 19 feathers, taken from along the right side of the body, from the breast to the under tail-coverts, are shown in plate 44. The pattern exhibited in this series of feathers deserves further consideration.

In the flank feathers (12–14) and under-tail coverts (15) we find the typical turtle pattern. The same pattern, but less perfect, is shown in the under wing-coverts (16–19). Passing forward on the abdomen, we see this pattern so gradually modified, by reduction of the dark center, that we feel sure, when we reach the

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[50] Avicultural Magazine, June 1906.
[51] This median streak is of the same nature as the apical spots of the *Zenaida mutant!* (See Chapter IX.—Ed.)

Explanation of Plate 44.

Selected feathers from white-faced pigeon, *Leucosarcia picata*. × 0.8. Hayashi del., May 1903.

19 feathers along the right side, from breast to under tail-coverts; 16 to 19 are under wing-coverts.

No. 1. From lower breast, right side.

No. 2. From close behind No. 1.

No. 3 to 11. Continue the series and reach about halfway to the leg, or to about the middle of the abdomen.

Nos. 12 to 14. From the flank feathers lying across the leg and reaching to under tail-coverts.

No. 15. An under tail-covert; illustrates all of the turtle pattern.

Nos. 16 to 19. Under wing-coverts. These are in 4 transverse rows.

No. 16. From middle of first (anterior) row.

No. 17. From middle of second row.

No. 18. From middle of third row.

No. 19. From middle of fourth row

The color of 1 to 15 is brown-gray for nearly two-thirds of the feather's length. The distal third is white. Feathers 10 to 14 have a faint tinge of buff in the white.

PLATE 44
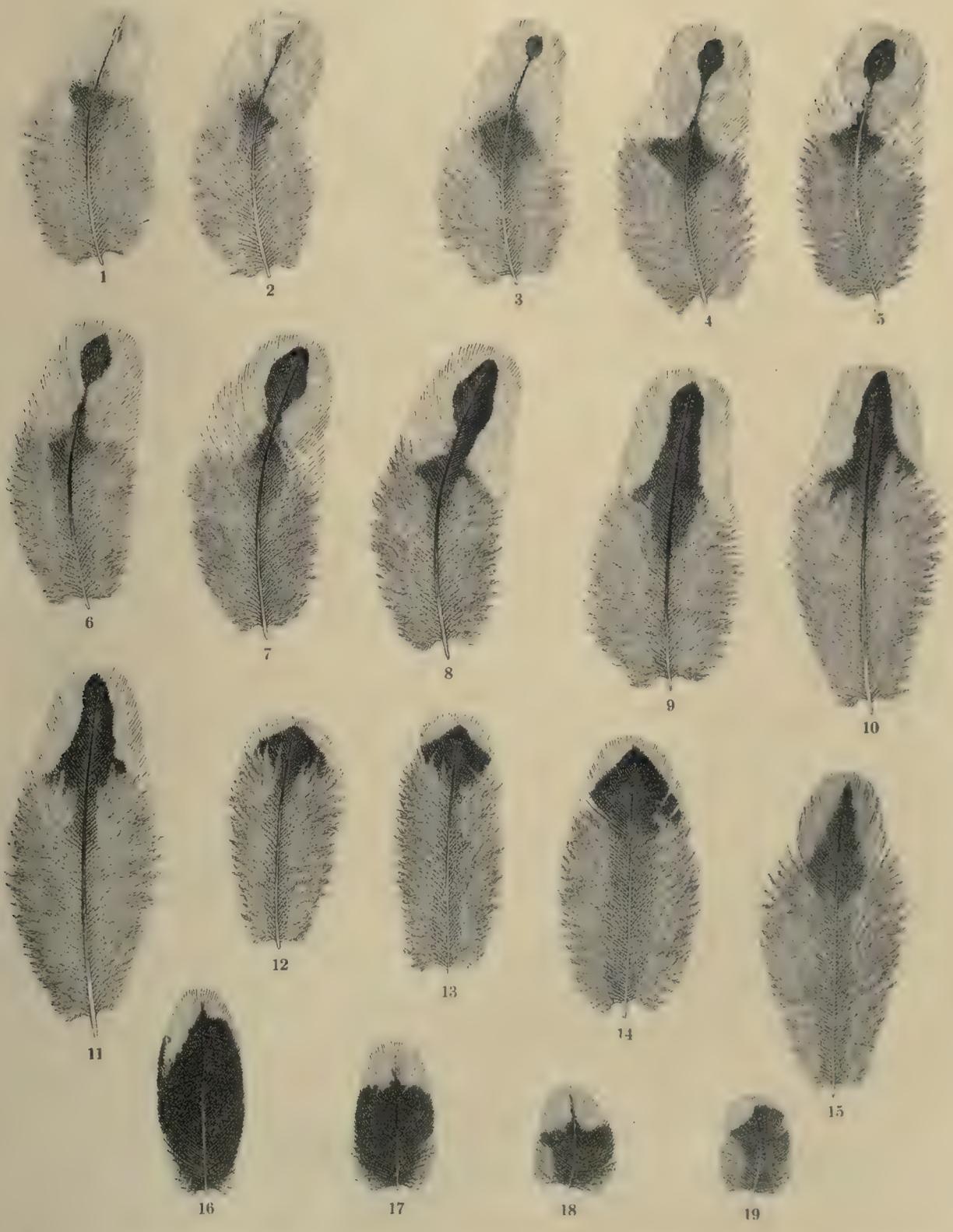
Selected feathers from white-faced pigeon, *Leucosarcia picata*.   × 0.8.   Hayashi del., May 1903.

feathers with roundish dark spots in a white ground, that these spots are remnants of the original dark center.

The most anterior feather (No. 1) shows a mere trace of a spot. But the whole center is not lost—it is only the distal third that suffers reduction. If we begin with 1 and pass backward through the whole series to 15, we could say that the gray of the basal part of the feather is gradually increased, and that the steps in evolution led from a dark feather to one with a dark base and a white end; then to the establishment of a dark spot in the white end-segment, and by increase of dark pigment to a coalescence of the basal pigment with the spot, and finally to the turtle pattern in 15. We should then incline to think that the next step would be to complete the series by extending the dark to the very edge of the feather, and thus reach the highest stage of a uniform color. This mode of reasoning has frequently misled investigators.[52]

According to my view, the original pattern was the turtle-dove pattern. On the upper parts the light edge of the feathers has disappeared; on the lower parts the original pattern is best preserved posteriorly, and more and more modified as we go forward, so that 1 would represent a higher stage than any of the stages that follow. That this is the correct view can be shown by a general comparative survey, by comparing the juvenal with the adult patterns, and by studying the history of transverse bars in such forms as the flicker (*Coloptes auratus*, pl. 59).

Salvadori (page 608) says of the young of this species: "It is similar to the adult, only browner on the wing, and without the dark centers to the feathers of the sides." By "dark centers" Salvadori means such spots as are seen in figures 3 to 8. I find the feathers along the flanks spotted, but the spots are weak and not at all conspicuous. The middle region of the abdomen and lower surface is whitish without spots, showing a faint trace of buff. The feathers of the side, just behind the legs, have a stronger tinge of buff.

The color of the young is closely like that of the old bird, but has a plainly deeper tinge of brownish. The feathers of the forehead are a whitish buff, which becomes lighter from the beak over the eye. The under tail-coverts are nearly buff color, and are without spots.

I find the light apical edge. It is, however, very weak and thin—scarcely noticeable even at close view. It is present in some three or four rows of wing-coverts on the feathers which lie outward (downward) from the middle of each row; above this level (on the inner feathers) it is not visible in these rows, and on the lesser coverts I miss it altogether on all the feathers.

The secondaries and primaries are pale light buff along the outer edge and around the tips; this pale edge grows less in passing upon the inner webs. Three or four outer tertials have a trace of the apical mark from 0.25 mm. to 0.5 mm. in width. In the long coverts, where these marks are somewhat plainer than in the median coverts, the greatest width of the mark is about 0.5 mm.[53]

[52] *E.g.*, Häcker, Keeler, and others. (See Chapter VII.—Ed.)
[53] The general color-pattern of the Caleonadinæ—the last subfamily of the Peristeridæ—has not been described by the author. He has noted however, that "the *white* tail of *Calœnas nicobarica* is a character found only in the adult; in the juvenal stage—called *Cal. gouldiæ* by Gray—the tail is greenish-black (see A. G. Butler: Knowledge Revealing Ignorance, Avic. Mag., Nov. 1910, page 46)." Some will be interested to know that the sentence just quoted seems to be the last statement written by Professor Whitman into his manuscripts. The modified neck-feathers of this species (*Cal. nicobarica*) are figured in plate 33, Vol. II, and a single feather is herewith reproduced in plate 43, fig. 5.
NOTE.—The manuscripts or records used in the preparation of this chapter were found in folders designated as follows: A 4, A 6, A 16, Em 1, Em 4, H 2, K 12, Misc. 6, 04; 005, 7, 9, 11, 16, 17, 18, 20; R 1, 12, 13, 16; Sh 24 3 /1 W 4, 5, 10, 11, 13; WW 6, XW 2; Z 3, 4, 10, 11.—Ed.

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CHAPTER VI.

THE TURTLE-DOVE PATTERN IN THE PHYLOGENY OF PIGEONS (CONTINUED).

THE TURTLE-DOVE PATTERN IN THE TRERONIDÆ

(See table 1, page 66.)

THE TRERONINÆ.

In *Sphenocercus sphenurus*, according to Salvadori (pl. 5) and Bonaparte, the long coverts are green with yellow edges; the secondaries are slate-black, edged with yellow; the tertials are green without bright edges. In many species the primaries are edged with yellow or a bright color. In Siebold's green pigeon (*Sphenocercus sieboldi*) of Japan[1] both male and female have the under tail-coverts dark (olive-green) centered and edged with yellowish white. The dark-centered feathers extend forward to the legs. The long coverts of the wing also have blackish centers and yellowish edges.

THE PTILOPODINÆ.

In *Ptilopus dupetit-thourarsi* the upper parts of the adult bird are mostly green, but the larger scapulars and the tertials have dark (deep blue) triangular centers, which are pointed behind. The shape of these dark areas is that of the dark centers in the European turtle-dove. Five of these spots are shown in a figure by Bonaparte.[2] The secondaries and greater wing-coverts are bright green, edged with yellow. Yellow here takes place of the reddish of the turtle-dove and green the place of dark centers. The scapulars and tertials have centers of deep blue and are edged with golden green. Unmistakably the turtle-dove pattern is preserved here in a case where the colors are most ornamental. Many of the tropical green-winged pigeons of the Treronidæ have the tertials and one or two or three of the rows of longer coverts strongly edged with yellow, the central part of the feather being dark.

Ptilopus xanthogaster, according to Salvadori,[3] has green back, wings, and tail. The gray feathers of the upper breast are bifid—a condition already noted in the neck-feathers of both Peristeridæ (*Spilopelia*) and Columbidæ (*Columba guinea*). The feathers of the thighs and flanks have green centers and yellowish edges. The smaller and median wing-coverts have green centers and golden-green edges; the greater coverts and the secondaries have yellow edges. The scapulars and inner secondaries have deep-blue centers, edged with yellow. These deep-blue centers are not pointed, but fill out the feather as does the black in the Japanese turtle-dove.

Ptilopus chrysogaster[4] has all of the wing-feathers edged with yellow where the turtle-dove has edges of buff color. The feathers of the crop, or upper breast, are bifid.

Ptilopus mariæ is one of the most highly colored and variegated of pigeons. In this species the male differs widely from the female and the young. In the adult male we see nothing that points decidedly to the turtle-dove mark, but Salvadori

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[1] I have a mounted specimen brought from Japan by Mr. Hayashi.

[2] Iconographie des pigeons, pl. xvii.

[3] This is *Thouarsitreron diademata* of Bonaparte (Iconographie, pl. xviii).

[4] The descriptions of *Ptilopus* are based on the statements and figures of Salvadori and of Bonaparte; the latter has figured *P. chrysogaster* in pl. xxix; *P. mariæ* in pl. xvi.

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PLATE 45
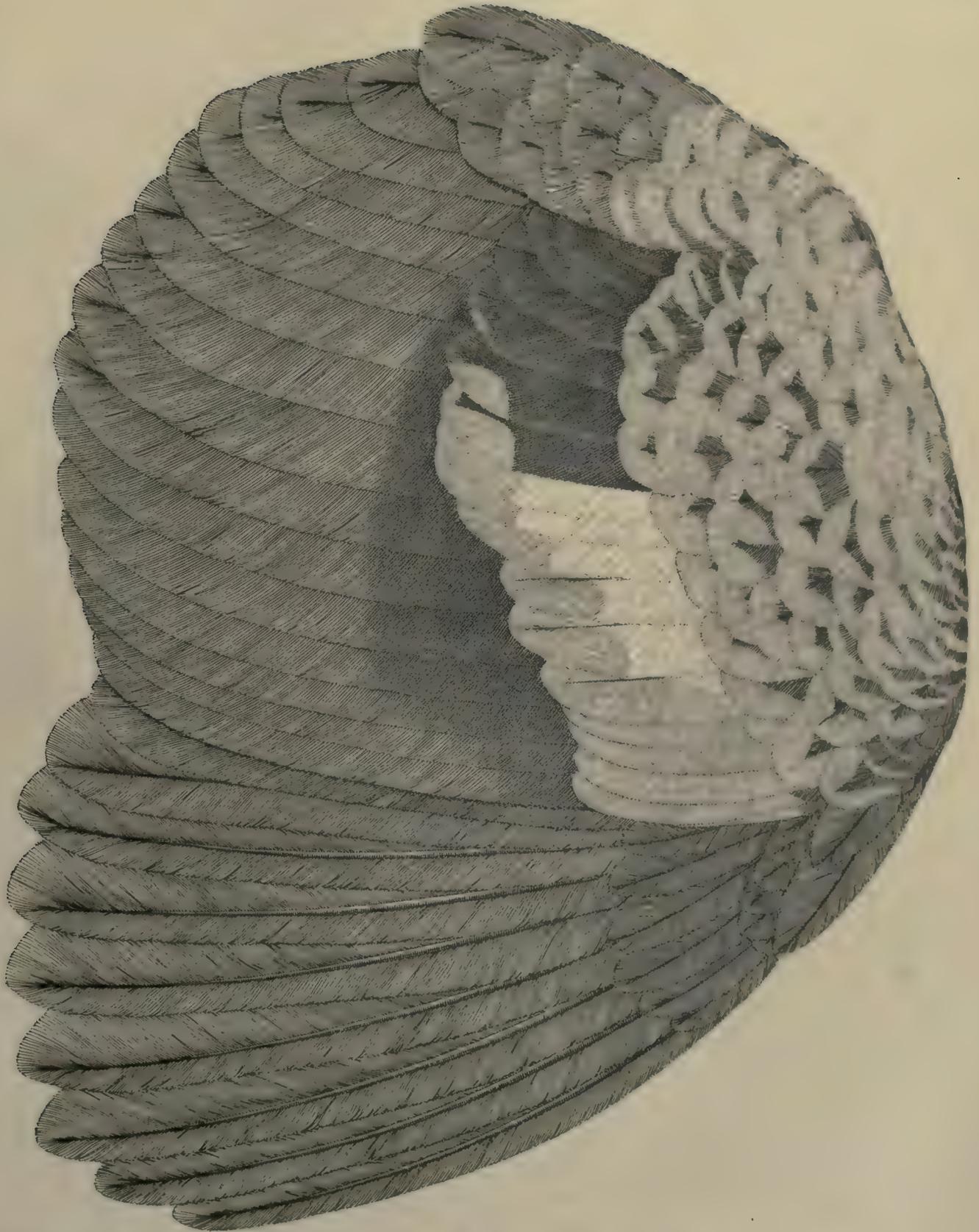
Right wing of adult crowned pigeon, *Goura coronata*. × 0.6. Hayashi del., Feb. 1904. From one of two birds obtained from dealer in autumn, 1900. General color bluish slate-gray, wings darker. Middle and bases of longer wing-coverts (which fall in the center of the plate) are white, very broadly edged with chestnut. The anterior coverts show dark-slate, pointed centers, with broad chestnut-colored tips.

(page 89) notes that "this species passes through many stages before assuming the full dress." The young is so different from the male that some have found it difficult to believe it belongs to the same species. The young, however, does resemble the adult female. The wing is green, but the smaller coverts are edged with a lighter bronze (?), presenting an appearance that closely resembles, in general effect, the wing-pattern in the turtle-dove. The dark (green) centers are more or less pointed, especially on the larger scapulars and inner tertials. The long coverts have green centers and are edged with yellow, and the same is true of the secondaries. The breast-feathers have green centers and light-grayish edges or tips; the upper breast-feathers are bifid and bear whitish tips; the feathers of the lower breast have green centers and wide grayish-yellow edges, just the turtle-dove type of pattern.[5]

THE TURTLE-DOVE PATTERN IN THE GOURIDÆ.
(See table 1, page 66.)

The important differences which separate the Gouridæ from other *families* of pigeons have been stated by Goodchild[6] as follows:

"(1) In the normal pigeons an oil gland is present, but it is absent in *Goura*. (2) In the normal pigeons the tail feathers are 12 in number, while there are 16 in *Goura*. (3) In the normal pigeons the pterylosis is columbine, but it is galline in *Goura* (!). (4) In the normal pigeons cæca are present, but are absent in *Goura*. (5) In the normal pigeons a gall-bladder is present, no gall-bladder in *Goura*. (6) In the normal pigeons incubation lasts 16 days, but extends to 28 days in *Goura*."[7]

I have seen but two individuals of this group—two *Goura coronata*, obtained from a dealer in Antwerp. The white color of several of the greater wing-coverts and the variety of the wing-colors in these birds indicate that their color-pattern is a considerably modified one. In the anterior wing-coverts, however, we find (pl. 45) feathers with centers of dark slate, broadly edged with chestnut. The broad edges and pointed centers clearly suggest the conditions found in the European turtle-dove.[8]

THE TURTLE-DOVE PATTERN IN THE COLUMBIDÆ.
(See table 1, page 66.)
FERAL COLUMBA.[9]

This very large genus, according to Salvadori, includes 58 species. This author says (page 241):

"I feel quite sure that the numerous species of the genus *Columba* ought to be arranged in several subgenera; but as only some of these can be easily defined, while others defy, at least for the present, precise definition, I have thought it best to leave them all, as a whole, in one genus."

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[5] Of the subfamily Carpophaginæ the author seems to have had in his aviary only a single specimen. An Oceanic fruit-pigeon (*Globicera pacifica*) was kept in captivity for a period of 18 months, but it seems not to have been figured or described.—ED.

[6] Proc. Zool. Soc., 1886, page 193.

[7] Huxley (Proc. Zool. Soc., 1868, page 302) noted the aberrant vertebral formula of *Goura coronata*. This bird is about 30 inches in length.

[8] The Didunculidæ—the fifth *family* of pigeons—is now represented by a single species, which has been figured by Bonaparte (Icon. Pig., pl. CXL). Salvadori (page 626) states that the young of this species is entirely brown, but the feathers are edged with "crescentic rufous bands."

[9] Neither of the 7 known species of the other 3 genera of the subfamily Columbinæ was studied, figured, or described.—ED.

My studies of the behavior, voice, and color-pattern of several of these species leave no doubt that some of them have made a much wider departure from ancestral conditions than have others. *Columba unicincta* and *C. palumbus* seem to stand nearest the turtle-doves. Through the courtesy of Dr. Dearborn, of the Field Columbian Museum, Chicago, I have been able to examine the skin and to have a figure (pl. 46, fig. B) prepared of the very rare *C. unicincta*. The wing of this dove has more feathers than the wing of the turtle-dove, but it is clear that the feathers have the turtle-dove pattern—blackish centers with pale-gray edges. The feather-shafts, too, are quite black. The feathers of the rump and upper tail-coverts are edged like those of the wing, though not so strongly or prominently. This seems to me to be a very important connecting link between *Turtur* and *Columba*.

The color of the young of this species has recently become known from a description by Mr. D. Seth-Smith,[10] who says:

"The top of the head has each feather minutely striped with *blackish and tipped with rufous brown or whitish;* the feathers of the nape and mantle have *towards the tip a narrow line of blackish*[11] *fringed with white,* the rump and upper tail-coverts are gray, fringed with white, the lesser wing-coverts becoming black towards the tip [11] and being *broadly tipped with chestnut-brown.*"

Columba palumbus best shows its relationship with the turtle-dove in its neck-mark (text-fig. 6, Vol. II). Like other species of *Columba*, it has a greater number of rows of modified neck-feathers—11 rows in this case—but the light-colored tips are confined to the lower 6 rows, which correspond to the turtle-dove neck-mark (this shown in color, pl. 48, fig. A).

In the young[12] of the wood-pigeon I find the wing-coverts of the first plumage are all edged with light brownish-yellow, while the second feathers show no such edging. The neck-spots have not yet appeared, or at most they are present in only a few feathers.

Columba gymnopthalma of Curaçao and the coast of Venezuela has neck-feathers that suggest (pl. 48, fig. B) the European wood-pigeon (*C. palumbus*), the European turtle-dove (*Turtur turtur*), and the white-crowned dove (*Columba leucocephala*) of the West Indies.

Salvadori (page 278) gives an imperfect or incomplete description of the plumage: "Lower part of the hind neck (side and back) with light grey and dark grey narrow bands above, and with reddish opaline and blackish narrow bands lower down." Comparing this with Temminck's figure,[13] this means that the feathers in the region corresponding to the neck-spot in the wood-pigeon are edged with narrow dark crescents, similar to the white-crowned pigeon (*C. leucocephala*), but these dark crescents are followed within by lighter (whitish) crescents. Temminck says: "Two zones or crescents mark the tips of the feathers."[14]

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[10] Ibis, July 1907, page 464.

[11] This line of *blackish* next to the apical mark reminds of the same subapical or subterminal mark in the tambourine-dove, in *Geopelia*, etc.

[12] Three specimens in their first molt were obtained from Mr. F. Chatwin, of Dover, England, and a comparison of the molted and unmolted feathers of these birds is the basis of these remarks.

[13] Temminck and Knip, Pig., I, 2d fam., p. 48, pl. xviii.

[14] Temminck says there is a black spot beneath the ear-coverts, but, as no such spot appears in his figure, I assume that he is confounding this bird with another species—our white-winged pigeon (*Melopelia leucoptera*).

PLATE 46

A

B

A. Wing of *Columba rufina*. × 0.8. Hayashi del., Aug. 1904. To show persistence of chequers on the *outer* webs of 6 (outer) secondaries. In the outermost feathers the chequer approximates the condition called "marginal streaks." General color of wing chestnut-purple. Specimen from Brazil.

B. Wing of *Columba unicincta*. × 0.8. Toda del., July 1904. Skin prepared for artist by Dr. Dearborn, of the Field Columbian Museum, Chicago. The wing has pattern of turtle-dove, blackish centers with pale-gray edges (reddish in *Turtur*). Feathers in the wing are more numerous than in Japanese or European turtle-doves.

PLATE 47

Adult *Columba squamosa*. ×0.7. Hayashi del., 1907.

A remarkable uniformity in general coloration. All the "cape" feathers with dark (velvety maroon) crescentic tips. The colors of beak and foot are accurately drawn. This bird was one of several obtained from Grenada (West Indies), and kept for some years in captivity.

I find further that the wing is white along the outer edge, exactly as in the white-winged pigeon (*Melopelia leucoptera*), and have had the undescribed color of the eye (reddish orange) and the beak shown in color. Though this bird resembles the white-wing in color, the head, beak, gait, and some of its behavior remind of *Columba flavirostris*.

Columba squamosa is not distantly related to *C. gymnopthalma;* in some characteristics—particularly in the very considerable modification of many rows of feathers of both the side and back of the neck to form a "cape"—it has closer relations with a group of which *C. leucocephala* and *C. speciosa* are members. This "cape," which extends upon the sides of the neck, is of metallic violet, each feather being distinctly bordered with velvety maroon (pl. 47). The occurrence of these crescentic bars in *Columba* is of interest. Occurring as it does also in association with a broad cape of highly modified neck-feathers, it reminds strongly of *Geopelia humeralis*. These two birds are, however, not near relatives. The remainder of the surface plumage of *C. squamosa* is nearly uniform dark plumbeous, and no other feathers show any trace of dark edges.

Columba leucocephala, the white-crowned pigeon, has an iridescent cape, similar to the above. Each feather is here neatly edged with a narrow black crescent. The white crowns of these birds are somewhat different in the two sexes. The crown is a "dirty gray" in the female.[15] It seems probable that a trace of this gray color also persists in some of the side-feathers of the cape. The adult differences are shown in plate 49. The body coloration of an adult male is elsewhere shown (pl. 57, Vol. II).

The affinities of this species, as noted above, are with *squamosa, leucocephala,* and *speciosa*.

Columba speciosa has the "feathers of the neck *regularly margined with dark metallic green* . . . . producing a regular scaly appearance."[16] The whole neck, breast, and under parts are edged with dark—another instance of dark crescentic tips in this group.

On both the sides and back of the neck we have this same type of feather-edge, but the type is here highly modified in an ornamental way. These "feathers of the neck are regularly margined with dark metallic green, more or less with violet or amethystine reflections, producing a regular scaly appearance; on the upper part each feather has a white spot near the margin; on the lower hind-neck the white spots are wanting and the feathers are chestnut in the middle." (Salvadori, page 282.)

The back and wings are maroon (only brown in the female), with no dark crescentic edges. This bird does not, therefore, come very near the geopelias, but the term "scallop-necked," which was applied to this species by Latham (Vol. III, page 26), reminds of *Geopelia humeralis*, which has a broad collar of orange-red (rufous), each feather neatly edged with black.

The young of this species has the neck-feathers *edged with brown-black*, with a pale spot in the middle. The under parts are whitish, the feathers having dusky edges. The wing-coverts have narrow pale edges.

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[15] I find that in the 11-day-old young the crown is neither white nor whitish, and scarcely differentiated from the general plumage. Here, again, the juvenal color (of the crown) more nearly approaches the adult female.

[16] A figure in Temminck and Knip, Vol. I, p. 39, pl. xiv

Columba fasciata seems somewhat separate from the other species I have studied. Its neck-mark involves 11 rows of feathers, with least differentiation at upper and lower borders (text-fig. 5, Vol. II). The white tips of these feathers, unlike those of *C. palumbus*, are carried to both the upper and lower limits of the mark. In the ring-doves the white tips extend to both the upper and lower limits of the mark.

The black bar of the tail is stronger in the female than in the male. In one female that I have kept for three years in captivity I find a few small blotches, or *spots*, of *black* in the *scapulars*.[17] These scattered flecks of blackish were on the outer webs of the feathers, and had the appearance of the last traces of spots. I can only regard them as remnants of former color-marks.[18]

Columba rufina and *C. flavirostris* seem to be related to each other, but I have not satisfied myself of their closest relationships among the other species.[19] It seems clear, however, that *C. rufina* is a few or several steps in advance of *C. livia*, having carried the wing-bars to complete obsoletion or to a few shadowy reminiscences in some of the secondaries. These vestiges of the outer secondaries—the *posterior* part of the wing—are shown in plate 46, figure A. The beak of *C. flavirostris* strongly resembles that of *C. palumbus*.

Columba arquatrix—the olive-dove[20]—is interesting for having the turtle-dove mark—the dark-pointed center—not only on the front neck and breast (to about same extent as in the Florida ground-dove), but also on the sides of the neck, and completely around the neck to the middle of the back.

From the illustrations of Bonaparte's work[21] I learn that the four following species, which I have not seen, show in their color-patterns undoubted relationships with the turtle-doves:

[17] These birds were obtained from a dealer in California, and were stated by him to have come from Mexico. Altogether I have obtained 22 individuals of this species.

[18] Darwin (Animals and Plants, Vol. I, page 240) says: "Certain variations in the plumage are equally common in the wild *C. livia*, in dovecot-pigeons and in all the most highly modified races. Thus, in all, the group varies from white to blue, being more frequently white in Europe, and very generally blue in India. We have seen that the wild *C. livia* in Europe, and dovecots in all parts of the world, often have the upper wing-coverts chequered with black; and all the most distinct races, when blue, are occasionally chequered in precisely the same manner."

[19] I have had about 15 *Columba rufina* from Brazil, but they are difficult to carry through our northern winters. Of *C. flavirostris* I have had a few specimens from southern Mexico.

[20] Illustration in Temminck and Knip, Les Pigeons, I, 1, page 11, pl. v.

[21] Icon. Pig., *C. hodgsoni*, pl. LXI; *C. leucomela*, pl. LXII; *C. laurivora*, pl. LXIX; *G. trocaz*, pl. LXX.

EXPLANATION OF PLATE 48.

A. Colored photograph of head and neck-mark of the wood-pigeon, *C. palumbus*. Natural size. Toda del., Apr. 1910.

10 to 12 rows of neck-feathers are more or less modified. The height or extreme of modification (with white-tipped feathers) is on the lower rows, and the mark is also decidedly lateral, all as in the neck-mark of *Turtur*. A dark or blackish area follows the light tips, and this proximal dark area corresponds to the dark area in neck-feathers of the turtle-doves.

B. Colored photograph of head and neck-mark of *Columba gymnopthalma*. Natural size. Toda del., May 1910.

Feathers of neck-mark with light rufous (above) or darker edgings (below); this resembles *Turtur*. The white tips and increased number of rows remind of *C. palumbus*. The increased number of rows and the extension of these upon back of the neck are as in *C. leucocephala*. The eye is reddish-orange. The bill is whitish beyond the nasals; pale flesh-red proximal of the nasals. The feet are red.

C. Colored photograph of anterior parts of adult male *Geophaps smithi*. Natural size. Toda del., May 1910.

Showing a broad naked region around the eye, as in *C. guinea*, and breast patch of clear gray feathers with sub-apical (not apical, as Salvadori thought) black bars. The extreme tips of these feathers is a clear gray. The feathers of the flanks and the under tail-coverts have dark centers, pointed distally, as in *Melopelia leucoptera*.

PLATE 48

A. Colored photograph of head and neck-mark of the wood-pigeon, *C. palumbus*. Natural size. Toda del., Apr. 1910.
B. Colored photograph of head and neck-mark of *Columba gymnopthalma*. Natural size. Toda del., May 1910.
C. Colored photograph of anterior parts of adult male *Geophaps smithi*. Natural size. Toda del., May 1910.

PLATE 49

Adult male and female crowned pigeon, *Columba leucocephala*. Natural size. Toda del., May 1910.
The "crown" of the female is a very dusky white; that of the male almost if not quite clear. The
irides differ similarly. The modified area of the neck (cape) is notable for its extent, probably
greatest in the male. These feathers are very clear-cut, and margined with velvety black in
central parts and at anterior margins, but gradually merging into rest of plumage above and
below.

PLATE 50

105
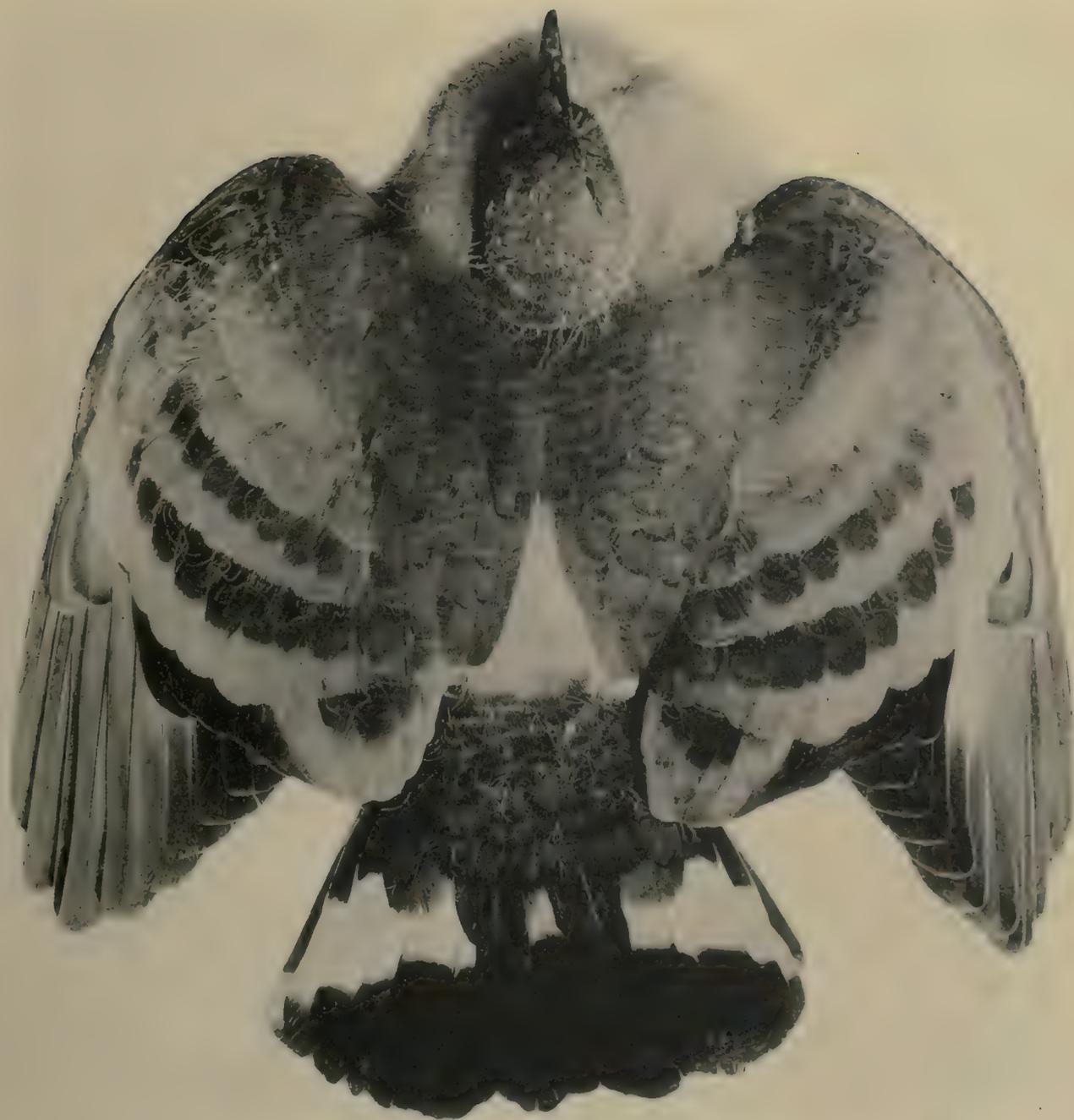
Juvenal *Columba leuconota*, age 4 weeks. × 0.6. Photograph by Dr. R. M. Strong, Aug. 1908. Shows the wing-bars of *C. livia*, also a weaker bar on the medium coverts and traces of a still more anterior bar. Very narrow pale edges as shown in the coverts, scapulars, etc. White tail bar strong in all individuals.

Columba hodgsoni presents two interesting points for comparison with *Turtur*. First, a patch of feathers on the side of the neck have black centers and gray edges; these feathers are acuminate. Second, the feathers of the upper breast and fore-neck are of deep chestnut color, and are broadly edged with pale or gray vinous.

Columba leucomela[22] is black on all of the upper surface of the body, the wings, and the tail; but the interscapulars, scapulars, and feathers of the whole back are edged with purple in some cases, and with greenish purple in others. This seems to be the turtle-dove pattern only a little disguised.

Columba laurivora has feathers of the upper breast and fore-neck with dark centers and with lighter edges, these edges being vinous purple of a metallic cast.

Columba trocaz has the neck-feathers—in the region of the turtle-dove spot— *scale-like*, with dark-pointed centers and with gray tips or edges. The neck is also iridescent. The bird reminds of the wood-pigeon as well as of the turtle-dove.

Three species of *Columba* still preserve the wedge-shaped area, or "guinea-mark," which—as a median extension of the light apical edge—divided the original dark center into two lateral chequers. These are *C. guinea*,[23] *C. maculosa*,[24] and *C. albipinnis*. In the latter species these marks are apparently confined to the scapulars.

Finally, there is a group of 5 species which present stages of wing-coloration rather closely approximating conditions found in *C. livia*. Some have made less, and some more, advance in the transformation than has the rock-pigeon. The species are *C. leuconota* (Tibet), *C. livia* (Europe, India, etc.), *C. rupestris* (Manchuria, China), *C. œnas* (Europe and Turkestan), and *C. eversmanni* (western Siberia to northern India).

Columba leuconota stands below the rock-pigeon in having 3 to 4 wing-bars. The two bars of *C. livia* are represented here as the strongest of the wing, but, in addition, a third and traces of a fourth bar are found just anterior to these, as is shown in plate 50. In the young I find similar bars[25] (pl. 50).

The broad white tail-band of this species[26] is also present in *Columba palumbus*, *C. œnas*, *C. guinea*, *C. eversmanni*, *C. rupestris*, and common pigeons.[27]

Columba rupestris is found in northern China and in Manchuria, and has been described as "intermediate" between *C. leuconota* and *C. livia*. Pallas considered it erroneously as a variety of the stock-dove (*C. œnas*). I have not seen this species, but have had a figure prepared from that of Bonaparte and Pallas (text-fig. 23). It is said to be "much larger" than the rock-pigeon. The posterior wing-bar is wanting in the lower half. The upper half is present, and on the inner (dorsal) side

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[22] Called *Leucomelæna norfolciensis* by Bonaparte.

[23] The relation of the guinea-mark (of *Columba guinea* and *C. maculosa*) to the transformation of the dark centers into two lateral chequers has been stated on page 60. Adult, young (and mutants), of *C. guinea* are shown in color in plates 76 and 77; the neck-mark and its behavior in hybridization are figured and described in Chapter XVII, Vol. II, text-fig. 7. (I find a remark on the relationship of *C. guinea* and *C. palumbus* as shown by their tail-bars. Plates were prepared to illustrate the point, but I find neither legends nor further comment on the matter.—Ed.)

[24] Shown in color, plate 18; single feather enlarged, showing guinea-mark, plate 79, figure C.

[25] The complexion and down of the young are as in common pigeons. One of these young was quite like an albino— very spare down, and this whitish, with only the faintest trace of yellowish. The beak of this young—unlike the others I have examined—had no black, nor even a brown, bar. (Such light-complexioned and barless-beaked young are also sometimes found among common pigeons.—Ed.)

[26] For head, neck, and eye in color, see plate 80, figure F.

[27] This tail-band is apparently not found in *Columba livia*.—Ed.

is connected with the anterior bar, which is narrow and widely separated from the tips of the feathers. The tail has an apical dark-gray band and a subterminal white bar. The whole color shows a reduction of pigment carried beyond the condition seen in *C. livia*. This makes the species of considerable interest from my standpoint of orthogenetic loss of pigment. I should place it as higher than *C. livia*; *C. leuconota* as lower.
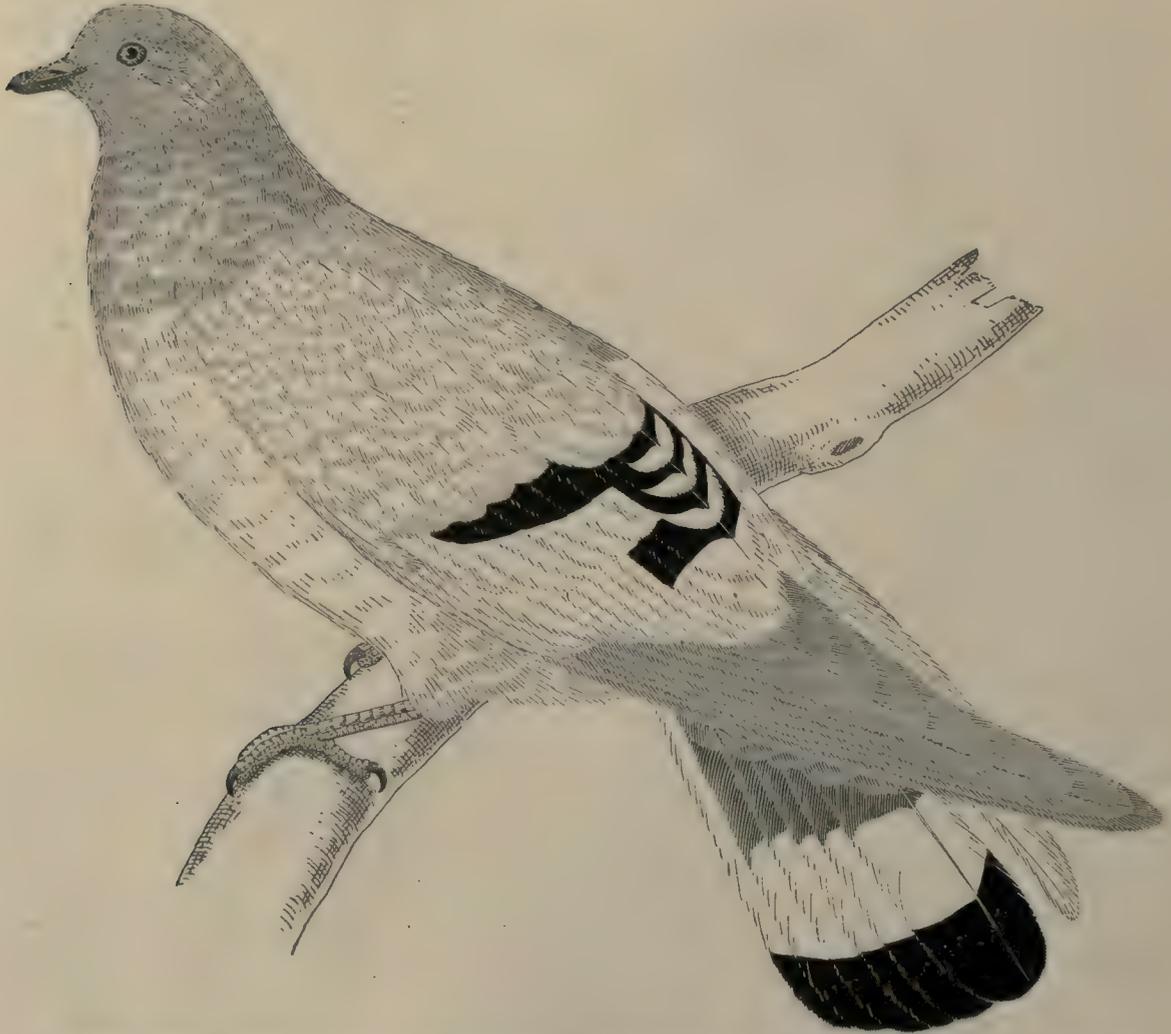
TEXT-FIGURE 23.—*Columba rupestris* (Hayashi del., after Bonaparte, ex Pallas, Icon. d. Pig. 1857, pl. LXXV).

The general coloration of this species shows a greater reduction of pigment than that of the rock-pigeon. The lower half of the posterior wing-bar is not present. The pigment of the bars has retreated farther from the tips of the feathers. A broad white subapical tail-band.

According to Salvadori (page 251), two varieties of this pigeon are now recognized, Rothschild and Hartert having separated the paler form from the Altai from that of eastern Siberia. The same author further states that the wing-coverts and scapulars of the young have "narrow whitish edges."

Columba œnas, the stock-dove, was for long confused with the rock-pigeon. It has, however, advanced beyond the rock-pigeon, the wing-bars being reduced to

PLATE 51   110

A. Adult female common pigeon, No. K2. ×0.35. Nov. 1908. Guinea-mark
   in most wing feathers, quite small and of grayish color. General coloration
   black with blush of reddish and a few white feathers.
B. Adult female common pigeon No. K1. ×0.35. Nov. 1908. Guinea-marks
   present, small grayish. General color black with reddish suffusion.

PLATE 52

A. Adult female common pigeon. No. K3. x 0.4. Nov. 1908. Guinea-mark much larger than in common pigeons (all from dealer) of pl. 51. General color black or blackish.

B. Adult female homer. x 0.4. Nov. 1908. Guinea-mark present, small. Wing color black.

remnants of only 2 to 6 spots.[28] This is not saying that the stock-dove arose from the rock-dove; more probably the two arose from the same ancestor.[29]

Salvadori (page 263) erroneously states that the "black markings" on the wings of the young are "scarcely noticeable." In some young that I have reared the spots are rather more marked than in the adults.

Columba livia may be thus described:[30] The head is dark gray, weakening slightly on the occiput, which is tinged obscurely with brownish. The neck is metallic green, strongest on the sides, *weakening perceptibly in the mid-front and in the mid-back region.* The metallic-green *feathers are widely split at the tips*, especially on the sides, where the barbs look as if broken off at the tips. The green passes into purple on the lower part of the neck, or, better, on the upper breast.

The feathers on the side of the neck are green *only at their tips*, for a length of about 7 mm.; then they are *black*, this color weakening and passing into gray at about the middle of the shaft. The black is strongest in the feathers corresponding to the feathers in the spot of the turtle-dove (*Turtur orientalis*). The split of the feathers extends through the green part of the feather-tips.

The upper back, the scapulars, and the wings are paler gray, with a slight tinge of *brownish;* this brownish being *most decided on the upper webs of the long coverts.*

The rump is white, sharply demarked posteriorly, but blends into gray anteriorly. The upper tail-coverts are dark gray, somewhat lighter than the head. The white of the rump runs forward on each side of the body clear up to wing-bones, so that the upper half of the body, as seen in profile, is white.

The quills and primary coverts are gray, the quills being tipped with blackish. The lower parts are darker gray than is the back; darker on the breast and under tail-coverts. The abdomen is nearly the same. The under wing-coverts are white, becoming gray at the edge of the wing.

The tail is dark gray, with a broad apical black band, and with the outer feathers white on the outer web. The iris is orange-red, becoming slightly lighter in color at the inner edge. The bill is black, with the cere white in its basal half. The legs are red.

I notice in rock-pigeon hybrids obtained by crossing a chequered male (*Columba affinis*, from Innishbofen, Ireland) with a two-barred female (*C. livia*, from Dover, England) that the bars in the young are pale, especially the anterior bar. The same is true of these bars in the young (first feathers) of domestic pigeons. In the young of pure rock-pigeons, however, the bars are both strong black. Besides, the gray is pure in the pure-bred; that is to say, it is about the same as in the adults, while in these impure young rocks there is a decided brownish tinge in the gray. I infer that weak or pale bars in the first feathers are due to degeneration, the degeneration showing itself first in the juvenile feathers. It is certainly interesting that the pure-bred rocks strike so *directly* into the adult color.[31]

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[28] The wing-bars of this species have been fully considered in Chapter II (see pls. 9–13); the neck-mark is figured and described in text-fig. 4, Vol. II.—ED.

[29] *Columba eversmanni* closely resembles *C. œnas*, but is smaller and has a whitish-gray or pure-white rump. (The author had several of these birds in his aviary during 1909–10; but the single illustration prepared—a photograph of four birds, with feathers in disorder from a voyage from India—is without a legend, and I find no further description or reference to the species.—ED.)

[30] I have here enlarged upon Salvadori's description (page 255), so as to give a more adequate account of those characters which seem important in these studies. (The wing-bars of *C. livia* and the chequers of *C. affinis* have been already described in Chapters II and IV. See plates 1 and 2.—ED.) For the birds here described (2-barred rocks) I am indebted to Mr. Cyril Allies, of Innishbofen, county of Galway, Ireland. I have examined also individuals from Dover, England, and from the Caves of Cromarty, North of Scotland.

[31] None of the species of the subfamily Macropygiinæ has been seen, studied, or described by the author. It is noted, however, that Salvadori's description (page 364) of *Macropygia rufa* makes it clear that the dark center and the pale tip are present there. (The single known species (*E. migratorius*) of the subfamily Ectopistinæ has been described in Chapter II, text-figs. 5 to 7; adults and hybrid in color, plates 28 to 30, Vol. II.—ED.)

Domestic Pigeons.[32]

The *guinea-mark* is widely represented in the various breeds of common pigeons. It is here exhibited, moreover, in widely different degrees, even in different individuals of the same breed or race. The tint or color of this typically wedge-shaped area also shows some fluctuation from individual to individual.

I obtained from a dealer two common pigeons which were nearly black, with a suffusion of reddish, in both of which I find quite small guinea-marks (pl. 51). The mark is of grayish color in both of these blackish birds. Another similarly colored common pigeon from the same dealer has much larger marks than the preceding, and larger also than those of a black homer which I have had photographed for comparison (pl. 52).

From two common pigeons—a male of reddish color having strong guinea-marks, and a black female (see pl. 14, Vol. II), also with plain guinea-marks—I obtained from the same nest the two birds shown in plate 53. Both young have relatively strong guinea-marks in the colored feathers of the wing, and both are spotted with white, though the ground-color of one bird is red and the other black.[33]

From a cross of a *Columba guinea* × homer hybrid male (two-barred) with a female dark-chequered homer,[34] I obtained two young which show the guinea-mark in two different degrees, these two grades being intermediate to, but different from, the two strongly contrasting states of the character in the two parents (pl. 54, figs. A to C).

The photographs show that the largest guinea-marks—the most advanced stages of the division of the dark centers into lateral chequers—are associated with a decided reduction of the pigmentation of the feathers of the *anterior* part of the wing. This is shown best in the male parent (fig. A, pl. 54), which is typically two-barred; the guinea-mark, with its lighter apical wings or margins, has here plainly cleared the feather-tips of black—leaving the black of the bar truncate—for a longer distance than is the case in either of the two chequered offspring. Further, the young, with the greater reduction of pigment in the anterior wing (fig. B, pl. 54), has also

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[32] Darwin has considered the origin of domestic pigeons, and the anatomical variations of the several races, in Animals and Plants, Vol. I, Chapter VI.

[33] Other of these young obtained *later in the season* of 1908 had *considerable white*, and at *the last of the season of 1909 were three-fourths white!*

[34] For full pedigree of the three birds see table 69, Vol. II.

Explanation of Plate 54.

A. Adult male *Columba guinea* (¼) × *Columba tabellaria* (¾) hybrid (G 7 CC) Nov. 1908.

This bird —typically two-barred—is an inbred (brother-sister mating) and the father of the two birds of figures A and B. The mother of the latter was a very dark chequered homer, with small "guinea-marks."

Note that the wing-bars are narrowed from behind as compared with the homologues of these bars in the offspring. This narrowing marks the advance of the guinea-mark from its point of beginning, which is the median tip of the feather. The front of the wing is swept free of black centers and of chequers.

Clear traces of the *C. guinea* neck-mark (bifid feathers) are seen, also in both offspring (figs. B and C).

B. Adult male *C. guinea* × homer hybrid. (G 7 CCA, see above) Nov. 1908.

Shows guinea-mark stronger than mother and brother (fig. C), and great reduction of black in anterior wing; less reduction than in father (fig. A) and apical advance (guinea-mark) also less than in father.

The scapulars are well chequered, but the forepart of the wing, in front of the third bar, is nearly bare of chequers.

C. Adult male *C. guinea* × homer hybrid. (G 7 CCB, see above) Nov. 1908.

Guinea mark stronger than mother, less strong than in father and brother (figs. A and B). Little reduction of black in anterior wing. The mark is whitish-gray. In the juvenal stage the two wing-bars of this bird showed considerable traces of reddish brown.

PLATE 53

A. Juvenal (5 weeks) male common pigeon. ×0.4. Nov. 1908. This bird and nest mate (fig. B, pl. 53) from a father of reddish color, with guinea-marks (some white primaries); mother black with good guinea-marks. This young reddish (its mate black) with fairly strong marks and several white spots.
B. Juvenal (5 weeks) common pigeon. ×0.4. Nov. 1908. General color black but like its red nest-mate (see fig. A) has good guinea-marks and white spots.

PLATE 54

A. Adult male *Columba guinea* (¼) × *Columba tabellaria* (¾), hybrid (G7CC).
Nov. 1908.
B. Adult male *C. guinea* × homer hybrid.   (G7CCA, see above), Nov. 1908.
C. Adult male *C. guinea* × homer hybrid.   (G7CCB, see above), Nov. 1908.

larger guinea-marks—*i.e.*, the white of the guinea-mark has made a deeper invasion into the black feathers that still persist.

That stage of the guinea-mark in which the complete separation of the dark center into *two marginal chequers* is effected can be seen in the scapulars and coverts of the juvenal common pigeon. The series of feathers shown in plate 55, figures 1 to 11, shows different stages of the further invasion of the black after the dark center is divided. In the outer (lower) larger coverts the inner chequer is quite gone (figs. 7 and 8), and where the depigmentation is much advanced, as in some of the scapulars and lesser coverts, the vestiges of the chequers become *marginal streaks* (figs. 4 and 11).

One of the long coverts of an adult male satinette-dove has been drawn (pl. 55, fig. 12). It shows the two chequers bleached in their central portions, leaving the marginal portions still pigmented. This bleaching is carried to different extents in different feathers in this species, and the results are interesting for comparison with the marginal and subapical marks in geopelias, the tambourine-dove, and other forms.

The turtle-dove neck-mark is by no means lost in common pigeons. By lifting the feathers one sees that their bases are blacker on the sides of the neck than elsewhere. This is a hint to the turtle-dove neck-mark. In a hybrid common pigeon × *Turtur orientalis* this same mark shows more strongly.[35]

Color and Pattern in Domestic Pigeons According to Prütz.[36]

Mr. Prütz has studied the colors and the color-patterns of many of the domestic varieties of the pigeon with considerable care and has undertaken to give the general laws of coloration for the whole group of domestic pigeons. He has sought to define genetic relationships, to state the correlations and sequences in colors, and to give the behavior of colors in cases of crossing. Some of the conclusions appeal to my interest, and seem to bear upon my own results.

Prütz asserts that "all *white* in pigeons is the same. . . . It is pure white without any admixture of any other color." It is absence of pigment, and must be regarded as albinism[37] (pages 294, 295). On this point I may record a doubt whether any such "pure white" is found in normal pigeons. There is certainly a plain trace of pigment in many so-called "white doves."

Brown, red, and yellow.—These, according to this author (page 295), may properly be regarded as one color. Between brown and red on the one side and yellow on the other there is, to be sure, quite a gap; but birds that bridge this gap are not entirely wanting, although they are rarely met with. "As a peculiarity of the yellow color, it deserves mention that the yellow dove is hatched with very scanty down, almost naked, and is weak in constitution and generally of the female sex."[38] The same is said to hold for the leather or chocolate color, which arises from crossing black and yellow, or black and red.

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[35] For further illustration of neck-mark in common pigeons, see Chap. XVII, and plate 32 and text-fig. 2, Vol. II.

[36] Gustav Prütz, Die Mustertauben Buch. (The quoted matter is from Prütz; the statements not in quotation marks are comments, or original observations, of the author.—Ed.)

[37] It is stated that "white" is always "albinism," but it does not necessarily mean a "weak constitution."

[38] Darwin (Animals and Plants, Vol. I, page 210) earlier noted that "young pigeons of all breeds, which when mature become white, yellow, silver (extremely pale blue), or dun-coloured, are born almost naked; whereas other coloured pigeons are born well-clothed with down." Darwin considered this "an inexplicable case of correlation."

I find that all white doves are born nearly naked, are rather delicate, and inclined to be of the female sex. Some white hybrids show a shade of cream; these have a little more down.

Blue.—This is held to be the "most important" color. While white, brown, red, and yellow are uniform throughout, or should be, this condition is never met in the blue color. "A one-colored blue dove, in the strict sense of the word, does not exist." The blue color, it is noted, conditions certain shades and markings, and never appears without them. Hence the rule: "If shades arise in other colors, these trend towards the conditions characteristic of the blue pattern, and are therefore to be discarded."

Black.—It is stated (page 30) that the black wing-bars often show a tendency to become "reddish fox-color"—and that this is the first step in the transition to "white" bars. The origin of white bars gives the key to variations in the bars.

In juvenile feathers those bars which are destined to be white in the adult, or partially white, "usually appear in the transitional color of red or yellow," and become white or lighter *after the molt.*

It is noted as a "curious fact, that *white* never at first replaces the whole of the black. It always begins near the middle of the black spot, so that the anterior half appears reddish, while the posterior part remains black." This is the law which governs the transformation and differentiation of the black bar. In this way we take the first step and get bars of double-color.

"According to the law that when white once appears in one region, it will extend to others, we may expect that white in the bars will be followed by white in correlated parts; *e.g.*, the tail-bar will begin to be lighter, and will go through the same changes as the wing-bar as illustrated in the Blondinettes and Satinettes" (pages 303, 304).

The "breast, neck, and primaries" tend also, it is said, to become paler. The metallic luster of the neck suffers accordingly. When the bars become white, "a semilunate white spot appears on the breast," the horns of which run up to near the middle of the sides of the neck. The law thus leads to the so-called "Staar-halstaube." The breast-spot becomes whiter with every molt—pure white in very old birds (page 49). The starling, with its white breast-crescent, furnishes the starting-point for still further development (page 304).

As the "black bar" may be repeated in all the coverts of the wing, so the white bars may be extended to the whole wing. The white appears in the black spots of the coverts just as in the bars themselves, beginning near the middle of the spot and spreading over the front half, leaving in the posterior half the transitional red followed behind by a black border, which in turn is followed by the terminal blue or gray. "In this way arises a wonderfully beautiful marking, which, when complete, is not excelled by any other" (page 304). This marking arises in many varieties, as in the Luchstaube (Polish Luchstaube, page 61; a plate precedes), in the modenese (or Modena dove, page 147; a plate precedes), in the pouters, etc. All these varieties arise under the "law of the distribution of white" (page 305).

Prütz states his theory thus: "Alle Zeichnungen entsprechen den bei der blauen Farbe gezeichneten Federtheilen oder Federgruppen." In translation: All color-marks correspond to the colored parts of feathers or groups of feathers which are distinguishable in the typical blue pigeon. The essence of the theory is that "all

color-marks are founded upon the blue color," *i.e.*, upon the color and pattern of the rock-pigeon. The whole series of changes and varieties are regarded as albinism progressing within the limits and in harmony with the areas that preëxist in the original type (309, 310). "We can start with white on the head, or breast, or tail, or wing, and it tends to extend to correlated parts. The law of the distribution of white is based on correlation."[39]

The theory that black bars tend to spread over the whole wing (314 and previous pages) is discussed at length. This theory is that of Darwin, and, as I have shown, is decidedly false.

What I have said above from my own experience I find agrees in many important points with the "laws" laid down (page 300 onward) by Mr. Prütz in the Mustertauben Buch.

BLACK CRESCENTIC TIPS IN TOY PIGEONS.

It is of interest to note that black crescentic tips can be obtained artificially from domestic pigeons which start primarily with two black bars, these arising in the first instance from longitudinal spots or streaks.

These crescentic tips are found in so many different kinds of birds that we can not assume that they have always arisen in precisely the same way. They have been preceded by longitudinal streaks in geopelias and in crested pigeons (*Ocyphaps*). In crested pigeons we have subterminal transverse bars coming in by the direct transformation of the original long spots.

In *Geopelia* the long spot is, at least in some cases, continuous with the lower end of the transverse bar, and the latter in the first feathers is subterminal—*i.e.*, just within a pale edge. But here we do not see that the crescent comes directly by a transformation of the long spot, as we do in the crested pigeon.

These black crescentic tips may arise in the following ways:

(1) They may arise by breaking up the central spot (turtle-dove type of spot) as shown in the francolin (see Chapter VII, page 136).

(2) They may arise by transformation of the ancestral long spots, as in crested pigeons.

(3) They may arise as in geopelias, simply by a new distribution of the black originally deposited in the long spot. This is a rebuilding during development, the long spots ceasing to develop and the crescents succeeding them.

(4) Finally, we may reach this end as in the case of some high-bred fancy or toy pigeons.

How are these transverse bars reached in toy pigeons? They are presented in the ice-pigeon (*Columba farinosa*) as reduced remnants of the two original black bars of the *C. livia* type. A good picture of this bird is given in the Mustertauben

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[39] Among *color peculiarities* I note the following:

(1) The "lace" pattern in common pigeons is a stage towards the end of chequers. Examples are common pigeons and Brünn pouters—a dark border on red-and-white bars.

(2) I have 6 or 7 common red pigeons from a dealer (January 1909) and every one has white tail and primaries. The same is true of red jacobins. The red is thus associated with white, and is probably a weakened stage of black.

(3) The "obsolete spot" sometimes leaves "structural imprints." Besides the case (already noted) of the white-winged pigeon (*Melopelia leucoptera*), I find in red tumblers and red barbs that when the color is thin, the feathers often have spot-areas—of stronger red—in the same place where black spot-areas are found in darker birds.

(4) Black doves have young which, in their first plumage, often show distinctly the two posterior wing-bars, and I have questioned whether the *structural imprints* are not always present and more deeply pigmented even in what seems to be an even black.

Buch of Mr. Gustav Prütz.[40] In the picture we see that the whole bird is one even delicate gray, with the two black bars reduced much in width and each bar of two colors—white followed by a "crescentic black border" (the black is subterminal, not at the ends of the feathers).

How can such results come about? My red-barred pigeons threw gray rock-pigeons with black bars (a third bar present). I mated the male parent with one of these gray birds. The next young were partly one color, partly the other. The young with black bars, after molting a few times, showed the bars subdivided into a wider anterior band of red and a narrow posterior black border. This differentiation came in by degrees and was sometimes weak and sometimes sharp. One of these birds, a female, was then mated with a male of her kind which had considerable white—white primaries and white patches on head and neck. They threw a young male in which the anterior red part of the bar became more or less white—more white towards the lower edge of the wing. This bird I now have (February 1903); he shows white primaries and white patches on the head, neck, and breast, and white mixed into the basal half of the tail-feathers.

I give these facts to show how we can get to a white-and-black bar. The white can be reduced in width and the same marking extended to all the coverts. It is in this way that we get the scaled ice-dove (*Columba badia*).

The same white-and-black bars are shown in *Columba pileata*, the white-headed or priest dove.[41] Here the white part of the feather-tip is wider, and the black is only a narrow border. The monk-dove (*C. albicauda monachus*) shows the same condition.

In the blondinette (*Columba stictæ*) we get every feather actually "tipped with a narrow black crescent," followed anteriorly by a red bar, while the rest of the feather is white. This marking—black, red, white—is carried out uniformly in each feather of the wing, and even in the primaries and tail-feathers.

The black crescentic tip is also well known in the wing of the satinette. This tricolored variegated plumage, in which the colors are arranged in marvelous order and regularity on each feather, is a perfect marvel of beauty. This is the race in which "white spots" with penciled outlines and lacings were first introduced. No spots of this kind were known before the arrival of the satinette, which is of oriental origin, but of unknown history.[42]

The posterior scapulars and long coverts (pl. 55, fig. 12) of this bird illustrate beautifully the fact that these remarkable spots are based on the old black spots or centers. Take the original black spots and whiten the centers until nothing is left but a narrow outline of black; then remove this black outline on the sides or edge of the feather, leaving the spots bounded with black only on their inner and outer ends, and we get feathers edged with black. A specimen at hand has nearly all of the coverts and scapulars of the wing thus edged with these subterminal black bars. The "black edge" is thus reached in the satinette quite differently from the way in which the black edging appears in *Geopelia humeralis*.

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[40] *L. c.;* see one of the plates preceding page 44, where the ice-dove is described.

[41] *L. c.;* see plate following page 51 of that work for a good illustration.

[42] See Fulton's Book of Pigeons, Cassel & Co., London, 1895, and the interesting account given by Mr. H. P. Caridia, who introduced these birds into England (page 380).

Note.—The manuscripts or records used in the preparation of this chapter were found in folders designated as follows: A 6, A 20, C 21, EM 1, H 9, H 11, H 13; 006, 8, 17, 18, 20; P 4, R 16, Sh 9/13, W 8, W 10, WW 2, WW 3 XG 26, XW 1.—Ed.

PLATE 55

Figs. 1–11. Advanced stages of the ''guinea-mark'' in scapulars and coverts of a juvenal (8 weeks)
common pigeon. All from left side. All figures natural size. Hayashi del., 1907.

1, 2, 3. Superficial scapulars.
4. Posterior, deeper-lying scapular.
5. Third larger covert.

6. Fourth larger covert.
7. Eighth larger covert.
8. Thirteenth larger covert.

9, 10. Lesser covert.
11. Lesser covert from *oblique streak*.

Fig. 12. Long covert of adult female satinette dove. This satinette covert shows how the dark
center gives the foundation for the crescentic tips of these birds. Some scapulars show the
more advanced stages of transformation in which the tip is more perfect and the black lateral
margins are lost.

CHAPTER VII.

THE TURTLE-DOVE PATTERN IN OTHER ORDERS OF BIRDS.

HISTORICAL AND INTRODUCTORY.

The question of the original type of color-pattern of birds in general has received attention at the hands of various workers. A brief consideration of the conclusions reached in some of this earlier work may properly precede the presentation of my own excursions into this field.

Newton says:[1]   THEORIES OF COLOR AND PATTERN.

It is a hitherto unsettled question if the longitudinally striated or the cross-barred feathers are the older style of coloration. The general impression of the coloration of a bird is the sum total of the coloration of all the uncovered parts of the feathers. This sounds like a truism, but means that cross-barred feathers can never give the general impression of a striated plumage and *vice versa*.

Kerschner[2] believes that the distribution of coloring matter in transverse lines or bars is the phylogenetically older method, because natural and sexual selection can not well have affected the hidden parts of the feathers. On the other hand, the striated downy or first plumage of the Gallinæ and Ratitæ has been already, by Darwin, taken to be a very old stage. This appearance, however, as in *Struthio*, is not due to striation of the single feathers, but to juxtaposition of colorless and deeply pigmented downs. To judge from the growth of a feather, the production of cross-bars seems to be the older stage, since they will result from the intermittent deposition of pigment, while, on the other hand, the production of shaft-streaks is not yet satisfactorily explained.

At any rate, it must be borne in mind that possibly various groups of birds have gone independently through such stages, and that what is primitive or archaic in one need not be so in all. But a strong proof of the soundness of Darwin's views is that we are able to trace the pattern of the most beautifully adorned feathers of the argus-pheasant or of the peacock step by step backwards to longitudinal stripes, spots, cross-bars, and lastly to insignificant and simple irregular little dots.

Concerning the statements of the immediately preceding paragraph, it is well to recall that when such series are studied only or chiefly by the comparative method, they can usually be read with about equal facility in either direction. We have shown (Chapter IV) that Darwin was thus led to read the chequers and bars of the rock-pigeon wing in the reverse of the true direction of evolution. Again, in attacking the problem of the origin of ocelli, as perfected in the train of the pea-fowl, and in the wing of the argus-pheasant, Darwin's theory gave him a long phy-letic perspective, but it revealed no unity or continuity in variation, except such as was imported adventitiously through long-continued sexual selection. The comparative method, which was the chief reliance, brought no correction to the theory, and, stopping short with *Polyplectron*, issued in the mistaken notion that the ocelli of the peacock were of double origin—each arising by the gradual fusion of two

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[1] Dictionary of Birds, Adam and Charles Black, London, 1893–1896, pp. 99–100.
[2] Zeitschr. wiss. Zool., 1886, p. 681.

distinct ocelli such as are seen in pairs in the tail-feathers of *Polyplectron*. We shall later reconsider the case of the pheasant and *Polyplectron*.

An unusual study of the color-marking of feathers was made by Dr. Valentin Häcker.[3] This author sought to start his investigation from the most original forms, and hence turned to "young" birds in "juvenal plumage," and undertook to find some direct connection between the pigmentation of the down and that of the perfected ornamental feathers.

His first figure (fig. 1, pl. VIII) presents a feather with a "dark crescentic edge" and a "light center."[4] This is regarded as a foundation type for various patterns.[5]

Häcker's first object was to find the "most generally distributed color-mark" in the first plumage, and to see whether like or related markings occur on "corresponding body regions"; and further, to learn whether the marking advances from behind forward according to Eimer's "wave law" (Undulationsgesetz). It is claimed that the results hold for several genera of German birds of the sixth, seventh, and eighth orders (Homeyer, 1885), and (?) for some other species.[6]

In his summary the author states that:

The characteristic thrush pattern takes departure from the stage of edge-pigmentation, which is widely distributed in allied groups. The crescentic, reniform, or cordate thrush-spot is formed from the dark edge, through the forward extension of the unpigmented area, while, at the same time, the secondary pigment begins to advance from the middle of the feather. Gradually the thrush-spot is reduced; and finally, only secondary pigment is left in the feather, with a light edge remaining, as in the ring-ouzel (*Turdus torquatus*), or ending in complete unicolor (as in the adult male ouzel, and the upper surface of most thrush species). . . . The remaining genera of song-birds mentioned in the introduction of this study, soon pass, usually directly, from the stage of edge-pigmentation to that of uni-coloration. Some genera (shrike, wren) have already entered, in the nest plumage, the stage of a secondary cross-barring which is multiplied in the single feathers, and which may be supposed to arise by a symmetrical pushing-forward of rings or bars of secondary or tertiary pigment.

In pigeons we have found that the dark crescentic edge or tip is subterminal in the juvenal plumage, the edge being pale whitish or yellowish or reddish-brown. And further, that the cross-bars are not *pushed outward*, for they appear first on the exposed distal end of the feather; and, when multiplied, the increase advances toward the proximal end of feather, and may extend to the whole covered part of the feather.

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[3] Untersuchungen uber die Zeichnung der Vögelfedern. Spengel's Jahrbücher, Abth. f., Syst. Geog. u. Biol. der Thiere, III, 2, page 309, Jan. 15, 1888.

[4] I note in this figure by Häcker a pointed darker area—just posterior to the light area (called central), to which the author seems to give little attention.

[5] Reference is made to Kerschner (Zur Zeichnung der Vögelfedern. Arbeiten aus dem Zoolog. Institut zu Graz, 1, No. 4, Leipzig, 1886), who, basing his conclusions on a study of the peacock's tail-feathers, takes spots or dots as the point of departure for the development of the various kinds of color-marks. He derived the ornamental feathers from the reddish-yellow feathers of the female (barred with black), and held, contrary to Eimer, that "transverse bars" represent a more primitive form of marking than longitudinal stripes. Häcker says Kerschner's reasoning was unsafe, as he started with "highly differentiated" forms.

[6] A much more extended consideration of Häcker's results was written out; but owing to the absence of suitable reproductions of Häcker's figures, to which the discussion repeatedly refers, it does not seem advisable to attempt to add to what is given here.—ED.

On the question of the primitive color or colors in birds Mr. Keeler's[7] tabulation (page 144) of the frequencies of occurrence of the various colors, in the 209 genera of North American land birds, is of interest. The distribution of the colors is as shown herewith:

Color.	No. of genera in which present.	Color.	No. of genera in which present.
Brown......	172	Yellow......	79
White......	169	Blue........	51
Gray.......	152	Green.......	30
Black	135	Orange......	10
Red........	116	Purple......	3

Brown or gray occurs in almost every genus, either in the young or in the adult stage; these colors are generally present in species in which the markings are not highly developed, and they frequently occur in the young of species highly specialized in the adult. All this, it is noted, indicates that brown and gray are primitive colors.

"The tendency would be to progress from such mixed shades as brown and gray to the pure colors." Taking brown as a primitive color, and the discovery of Krükenberg that brown is chiefly due to two apparently distinct pigments (zoörubin and pseudozoörubin), Keeler formulates a "theory of bird colors."

The "streaked feather" is held to be "the most primitive form," and the more central location of color he considers to be due to secondary pigmentation. Keeler accepts Eimer's view that markings first appeared in the hind-body, and then gradually passed forward. All of this is contradicted by the elucidation of the sequence of pattern in the pigeons.

In a general theory of animal coloration Tylor[8] claimed, and Wallace accepted the view, that the development of marks and patterns depends on "organization," following the chief lines of "structure" and changing at points and regions where function changes.

Tylor held that "spots" constituted the primitive form of ornamentation; that "lines" or "bands" are formed by the confluence of spots; and that by confluence of "bands" arise "patches," or "uniform-color" over larger or smaller surfaces of the body.[9]

Tylor says:

If we take highly decorated species—that is, animals marked by alternate dark or light bands or spots, such as the zebra, some deer, or the carnivora—we find, first, that the region of the spinal column is marked by a dark stripe; secondly, that the regions of the appendages, or limbs, are differently marked; thirdly, that the flanks are striped or spotted along or between the regions of the lines of the ribs; fourthly, that the shoulder and hip

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[7] Chas. A. Keeler, Evolution of the Colors of North American Land Birds, 1893.

[8] Coloration in Animals and Plants, London, 1886.

[9] Examples given are: Young lion and tiger both spotted. Java hog (*Sus vittatus*), very young, have bands, but spots on shoulders and thighs. "The spots run into stripes as animal grows older; then stripes expand, coalesce, and the animal becomes of a uniform dark brown." This agrees with Eimer's law, if the "stripes" are bands or cross-stripes. Pigs and tapirs are banded or spotted when young. A young *Tapirus bairdi* was covered with white spots in "longitudinal rows," here and there forming short stripes. So many of the species of deer are spotted when young that Darwin concluded that the ancestral form must have been spotted. According to Darwin, the horse descended from a striped animal, and is often spotted (dappled). Darwin also pointed out that ocelli may arise from spots or bars.

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regions are marked by curved lines; fifthly, that the pattern changes, and the direction of the lines, or spots, at the head, neck, and every joint of the limbs; and lastly, that the tips of the ears, nose, tail, and feet, and the eye are emphasized in colour. In spotted animals the greatest length of the spot is generally in the direction of the largest development of the skeleton.

"This structural decoration is well seen in many insects," says Wallace.[10] In caterpillars, this authority notes that similar spots and markings are repeated in each segment, except where modified for some form of protection. In butterflies, the spots and bands usually have reference to the form of the wing and the arrangement of the nervures; and there is much evidence to show that the primitive markings are always spots in the cells, or between the nervures, or at the junctions, the extension and the coalescence of these spots forming borders, bands, or blotches, which have become modified in infinitely varied ways for protection, warning, or recognition. Even in birds the distribution of colors and markings follows generally the same law.[11]

Sexual Dimorphism in Color.

The following cases, among the several that might be instanced, indicate not only that sex dimorphism in color depends upon the generative organs, but to me they yield additional evidence that the male and female have *potentially the same characters*. Usually the female lags behind, but sometimes the male lags.[12]

The first two instances are cited from Beddard:[13]

Prof. Max Weber, of Amsterdam,[14] has examined a chaffinch, in which the left side of the body has the coloration of a hen bird, the right that of a cock, which are sharply marked off from each other in the middle line. An examination of the viscera showed that the bird was a hermaphrodite, with a well-developed ovary on that side of the body which was clad with the plumage of the female, and a male gland on the opposite side. The same kind of hermaphroditism has been noticed in other birds. In cases where a female bird has assumed the plumage of the cock, it has been found that the ovary was diseased or atrophied.[15]

The second instance which I shall bring forward is that of a moth—the common oak eggar. Dr. Berthau[16] has figured and described a hermaphrodite specimen of this insect in which the wings of one side of the body showed the coloration, form, and size of those of a male, while the opposite couple of wings had the coloration of the female, and were, as in the female moth, larger than the wings coloured after the male pattern. On a dissection, the insect proved to be not hermaphrodite, like the chaffinch, but a female with degenerate organs, some of the parts typically present being absent. It can not, therefore, be called a hermaphrodite; it should be remarked that the ovary was more degenerate upon the side of the body on which the wings were those of a male than upon the other.

[10] Darwinism, Macmillan, London, 1889, page 289.

[11] Reference to Eimer's theory has several times been made in various chapters of this volume, and convincing evidence for an antero-posterior law of the development of pattern—the opposite of Eimer's contention—has been presented. It seems hardly advisable, therefore, to present here the rather lengthy critique of Eimer's work which was written by the author at apparently disconnected intervals—1899 to 1903.—Ed.

[12] See Darwin's Descent of Man, II, pages 191–199.

[13] Animal Coloration.

[14] Zool. Anzeiger, 1890, page 508.

[15] See Mr. Bland Sutton's An Introduction to Pathology, for further instances. Also, J. H. Gurney (jun.), Ibis, 1888, page 226.

[16] Arch. f. Naturgeschichte, LV, page 75.

Mr. Keeler's[17] observations on sex dimorphism and seasonal color changes of American woodpeckers deserve mention and a word of comment:

The female (at the breeding-season) advances towards the male color, as is shown in the woodpecker, *Sphyrapicus varius*. We have three species—*S. varius* of the East, *S. nuchalis* of the Rocky Mountain district, and *S. ruber* of the Pacific coast. The red color increases from east to west, being least in *S. varius*, more in *S. nuchalis*, and most in *S. ruber*.

Keeler concludes that the variation is a climatic modification. This is an unwarranted assumption. Had the red diminished, the assumption would have been the same; or, if any change whatever of a gradual kind could be found it would be credited to climatic influence.

The young of *Sphyrapicus varius* and *S. nuchalis* are "mottled brown, and with the colored areas of the adult male white." The adult female of *S. varius* in winter still has the white areas, but has black and gray in place of the brown of the young, and only a few dots of red on the forehead. The adult female has the black strengthened in her breeding plumage, and the whole crown of the head is then red. The adult male of *S. varius* has the same red crown and a red throat instead of white. In the adult female of *S. nuchalis* we have a red crown and a little red on the throat, while the adult male has more red than the male of *S. varius*. In the adult male of *S. ruber* nearly the whole head, throat, and front neck are red.

That the female *Sphyrapicus varius* should advance towards the male only "during the breeding season," but still halt behind the male, in that she gets the red crown but not a red throat, suggests that:

(1) The red is not a male attribute, but merely a higher development, which the female accomplishes only imperfectly at the time of her highest energy, in winter sinking back still lower, or nearer the juvenal condition.

(2) Both sexes have the same germ foundation, the distinctions of the male being, as it were, the distinctions of the female carried higher.

(3) In this one species (the lowest of the three) we have four stages: (*a*) juvenal—brown and white areas; (*b*) female winter plumage—black and white areas; (*c*) female summer plumage—red, black, and white areas; and (*d*) adult male plumage—black, white, and two red areas. The red throat is a male distinction in this species, but in another species (*Sphyrapicus nuchalis*) the female rises to the same distinction, but in weaker development, and the male also goes a little higher than in *S. varius*, enlarging somewhat both the red crown and the red throat. Finally, in *S. ruber* the two red surfaces are further increased in the male until they fuse on the sides of the head. Thus we have in the three species at least seven stages, in six of which red is present in as many different degrees.

THE TURTLE-DOVE PATTERN AND ITS MODIFICATION IN VARIOUS FORMS.

Paying special heed to the color-patterns of immature birds, and to sequence of patterns presented in the young and the adults of both sexes, I soon found convincing evidence, in great abundance, that the pigeon unit of pattern was at the same time the avian unit.

Pattern in the juvenal robin—In view of Häcker's investigations on the evolution of pattern in birds, and especially the thrushes and their allies, the markings

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[17] *L. c.*, pages 244, 245, pl. xv.

in the first feathers of young robins are of some interest. I made an examination of the feathers of some young robins shortly after reviewing Häcker's paper,[18] and find that their markings verify results obtained on the pigeons. I have taken feathers from the same points in three individuals for reproduction (pls. 56 and 57).

Häcker's figures 1 and 14 represent, as he believes, two of the "most primitive types of marking"; the latter, being slightly lower in the scale of development, has "as a rule, no light edge." I find both types represented on the young robin, and the "light edge" is generally quite plain, although it is often narrow, and sometimes so weak that it would escape attention if not kept in mind and carefully looked for. I find this "edge" best represented in the median wing-coverts (next in front of the long coverts) and scapulars.

Häcker was aware that these two forms are essentially one, as they often replace each other in corresponding areas. My figures demonstrate this conclusively (pl. 56, fig. 1, in each I, II, and III, from middle upper breast).

In the second series (III b of pl. 57) the clear edge is 0.5 mm. wide, and the black bar is about 1 mm. in width. The clear edge is widest where the clear center is widest; narrowest where the clear center becomes a mere line, as in plate 56, figure 1 b.

In the mid-back, between the scapulars, the clear edge is obsolescent in I a and II a (pl. 57) requiring a lens to discover it, and is only just visible to the naked eye in III a. Notice here (III a) that by extension of basal gray pigment the light middle area becomes simply a wide transverse bar. We have the order thus: first, a rudimentary apical light bar; second, a black bar; third, a light pale-yellowish bar.

In the second series c.c.c. and d.d.d.—the figures are of median and long wing-coverts—the "median streak" is continuous with the light-buff tips. There is here no subterminal black bar. It looks as if the black had vanished, thus bringing the median streak and the apical light edge together. In d.d.d. the median streak is absent in I, largest in III.

The clear or light edge can not be made out on the first series (pl. 56) on I 1 and II 1, but it is faintly present on the tips of about four of their barbs; in 2, from mid-

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[18] Before the Zoological Seminar, May 13, 1903.

EXPLANATION OF PLATE 56.

Selected feathers from the juvenal robin, *Merula migratoria*, age 3 weeks. × 1.6. Toda del., May 1903.

First series.—Three rows of feathers from three robins (I, II, III):
Under side of body:
   In the three birds I have the shaft-streak scarcely wider than the shaft itself; in II the streak is widened, and in III it is widest—about 1.5 mm. at widest part. The narrower this streak the darker the bird as a whole. So my three birds represent three degrees that probably show the average in II.
   Figure I 1. From mid-upper breast.
   Figure I 2. From mid-lower breast.
   Figure I 3. From abdomen; a small apical dark spot or edge, or no dark edge (III 2).
   Figure I 4. From bunch of flank feathers just above the upper half of leg, mostly covered by wing (right side).
   Figures II 1, 2, 3, 4. From corresponding points in a second individual.
   Figures III 1, 2, 3, 4. From corresponding points in a third individual.
   Third series.—Single row of outer scapulars from before backwards (IV):
   Figure IV 1. Anterior scapular.
   Figure IV 2. Front of middle scapular.
   Figure IV 3. Behind middle scapular.
   Figure IV 4. Posterior feather.
   See text for further explanation.

PLATE 56

IV   III   II   I
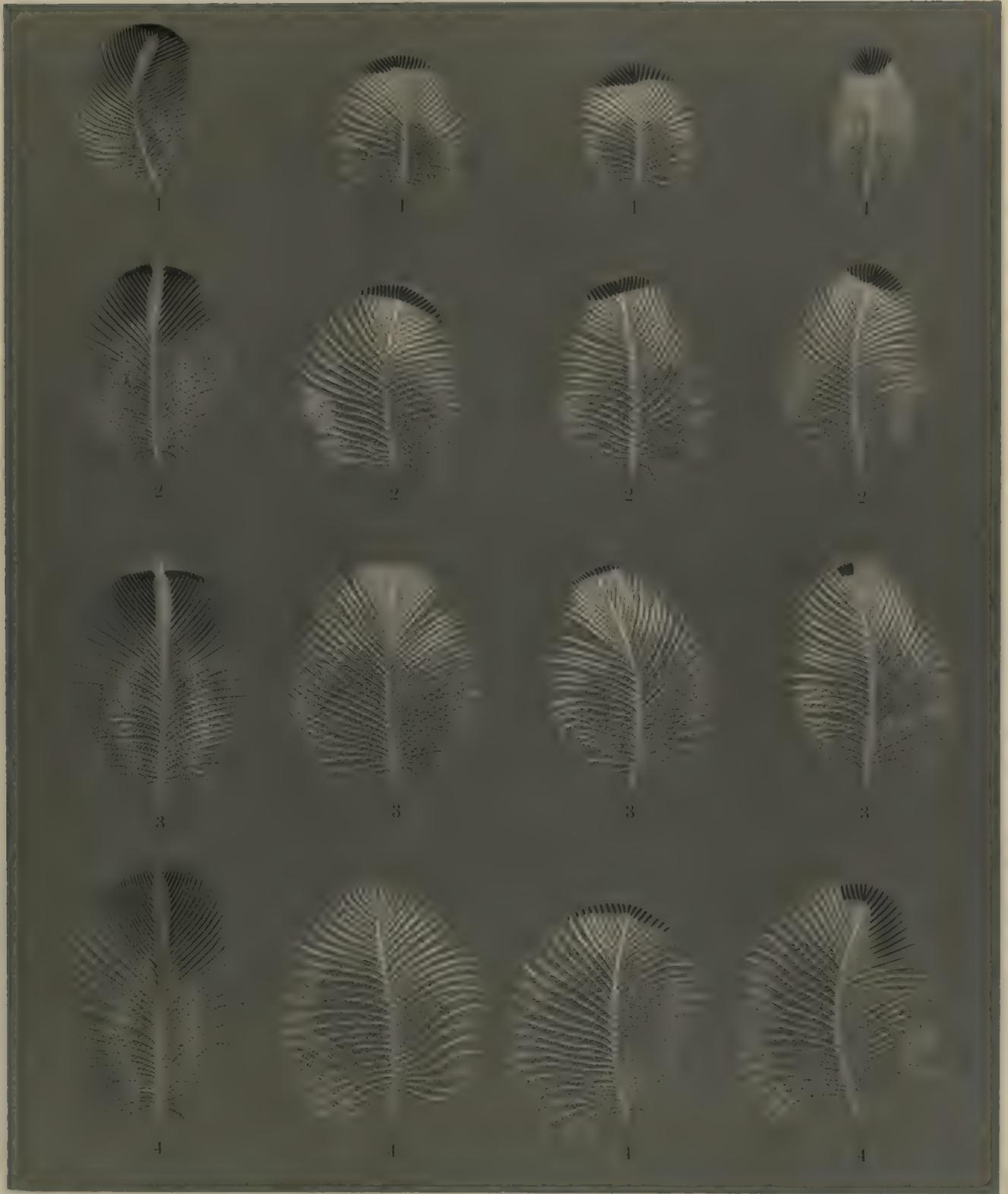
Selected feathers from juvenal robin, *Merula migratoria*, age 3 weeks.   × 1.6.   Toda del. May 1903.
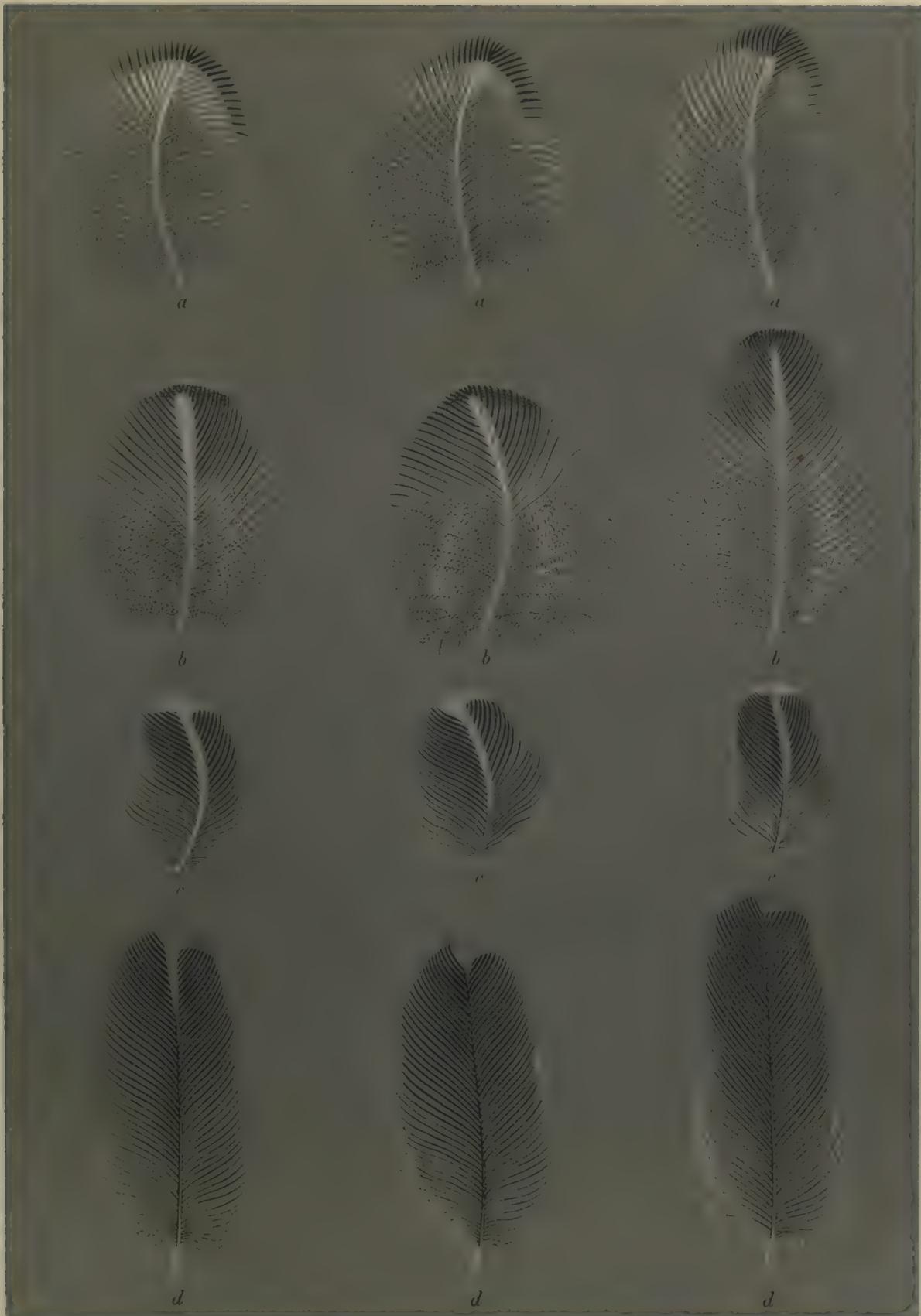
From juvenal robin.   × 2.   See explanation pl. 56.

Second series.   From upper side of same birds and in same order as pl. 56.

    I*a*.   From mid-back, between scapulars.

    I*b*.   A middle scapular.

    I*c*.   An anterior median covert (left wing).

    I*d*.   An inner long covert (left wing).

    II*a* to *d*.   Corresponding feathers from a second individual.

    III*a* to *d*.   Corresponding feathers from a third individual.

lower breast, it is present in all three, but is very minute in I 2 and plainest in III 2. The edge is clearly present in 3, of I, II, and of III (the black crescent absent in III 3). It is present also in 4 of I and II and in III (the black crescent is absent in in III 4).

In all of these feathers from the under side of the body we see Häcker's three-segmented feather. It is essentially a simple type of barring, in which we have not three but four segments.

It is difficult to decide in the second series, c.c.c., whether the "primitive" yellow edge is present. It may be wholly a secondary yellow edge. The lesser coverts are all marked like c. To settle this question, I have examined another young (IV of pl. 56), corresponding to III (May 1903), and have selected four scapulars from the outer edge (right side) of scapulars, beginning anteriorly (IV 1) and running back to the posterior scapular (IV 4). The anterior one (IV 1) has the "apical light edge" plain, and about 0.5 mm. wide; the dark crescent is about 1.5 mm. wide; the shaft-streak cuts its way into about one-third of the dark crescent. In IV 2 the white streak just cuts through the black crescent, which is reduced in width, while the light (buff) edge is increased in width. In IV 3 the black crescent is still narrower and the light edge still wider. In IV 4 the black crescent is still narrower and the light edge still wider.

In this last series (from right side) we see that the apical light edge is increased, not at the expense of the median streak, but at the expense of the black crescent. Now we may say with certainty that in the coverts shown in plate 57 (c.c.c. and d.d.d.) the apical light tip *does* include the original light edge *plus* the bleached black crescent. In all of these feathers the color of the apical edge is buff, the streak is white, just tinged with buff. In IV of plate 56 the contrast is diminished, but it is not lost, and all parts are still present.

On examining the lesser coverts of this specimen I find that they confirm this result, as they stand between the more advanced "scapular type" and the type shown in c.c.c. (pl. 57). The type advances in the coverts from anterior to posterior, the latter being most advanced (d.d.d.). It is therefore abundantly clear that the feather is primarily four-segmented, two light bars and two dark bars, light and dark alternating.

The color-pattern of the robin is not an isolate pattern. Analogous conditions are readily found in the common pigeons, in hybrids of the guinea-pigeon and common pigeon (pl. 58), and in the American quail (*Colinus virginianus*), as is shown in plate 60.

Pattern in the flicker.—In *Colaptes auratus* we find a relatively highly modified pattern, but one which has plainly departed from the turtle-dove type. The resemblance of the simpler conditions found in a series of feathers selected from an adult male flicker (pl. 59), with the conditions still found in the white-winged pigeon (*Leucosarcia picata*, pl. 44), is quite marked. The same series of feathers show that in this form, too, the original pattern, in contradiction to Eimer's view, is best preserved posteriorly and most modified anteriorly.

From the juvenal flicker further evidence for the same conclusion is easily obtained. The primaries, secondaries, tertials, and long coverts[19] are most instructive.

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[19] A group of these feathers was arranged for the photographer, and several feathers accurately described. If a photograph was prepared, it is not available to the editor. Excerpts from the explanation of this plate, describing a male bird whose age is given as "one week after leaving the nest," are given above.—ED.

They show that we must read, not from bars to whole color, but from a dark center to bars.[20]

The first (subterminal) bar grows gradually wider as we follow down the series of long coverts, until, on the ninth feather, it fuses plainly with the dark center,

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[20] I find a narrow apical edge on all of the long coverts, and also on the upper tertials.

EXPLANATION OF PLATE 58.

Analogies of the robin pattern in common pigeons.

No. I *a*. An upper (inner) long wing-covert (right side, May 1903) from my white-red barred dove. When gray is replaced by white and black by red, a black crescent is formed at the tip, or at distal end of the colored area. When the central (middle) area is lightened up, the black crescent boundary tends to appear. It may be at or near the edge, according to position of the normal black area.

No. I *b*. A mid-scapular from the above bird. Shows the black concentrated in a median subterminal spot. The flecking outside this spot indicates that the black chequers are here obsolescent, and that only scattered remnants are present.

No. II *c*. An upper long wing-covert (right side, May 1903) from a black chequered male homer, to show the area occupied by black, for comparison with area of red in No. I *a*.

No. II *b*. A mid-scapular to correspond with No. I *b* from same chequered homer. Here we have a median streak of gray dividing the black into two spots; the streak enlarges distally into a triangular area that may expand into a light-gray margin, such as Häcker finds and as I find in the robin.

No. II *b*. A mid-scapular from young of the same (chequered) homers, at age of 3 weeks. Notice median streak. This will close up, leaving only a small apical spot in second feathers, much as in II *b*.

The five figures, III¹ to III⁵ are from a chequered juvenal common pigeon about 6 weeks old (May 1903).

No. III *b*¹. A mid-scapular (right side) showing the light edge or margin; the median streak shows just a trace only.

No. III *c*¹. An upper long wing-covert (right side). The apical gray spot is destined to be more or less filled up with black in adult. The black is more intense next to the gray spot. Notice a few prolonged barbs at tip; these are remnants of the pale edge.

No. III *c*². Upper covert from the second row (next in front of III *c*¹). The median streak wider, there being less pigment on the inner web (upper web). Notice in all these young feathers the narrow pale-brown or yellowish-brown edge, and that some barbs are prolonged beyond the rest into a fine hair-like part.

No. III *c*³. Upper covert from the third row. The median streak reaches into the light margin, which is very plain and about 1.5 mm. at center to 1 mm. at lateral parts of tip.

No. III *c*⁴. Covert from the fourth row. The median streak does not reach the light edge.

No. III *c*⁵. Covert from the fifth row. The median streak still a little farther from tip and also a little narrower.

In these five coverts (III *c*¹ to III *c*⁵):

(1) The black becomes more and more intense as we go backward, and more intense in the outer web than the inner. The young of the cowbird, *Molothrus ater*, have "feathers bordered with pale buffy" (see Bendire, p. 590).

(2) The light margin is plain in *c*³ to *c*⁵; less so in *c*², and still less in *c*¹, where we see some hair-like prolongations of the barbs, remnants of the light edge, or rather perhaps imperfect reminiscences of a once wider light margin.

(3) The light median or shaft-streak is something quite distinct from the light apical margin.

(4) The triangular gray area at the tip may be reduced by increasing the size of the two chequers until no apical gray is left, or it may be increased by reducing the two black chequers from their distal ends, as is done in all pigeons with gray wings and two bars, the distal ends of the chequers being cut off more and more.

(5) The median light streak is not a primitive mark. It is wholly secondary, if we remember that the turtle-dove pattern is the starting-point.

(6) These shaft-streaks in the young robin, and in the birds described by Häcker, are secondary, as is probably the clear middle area of Häcker's feathers.

Analogies of the robin pattern in a hybrid pigeon, C. guinea × domestic pigeon (black chequered), juvenal, age 13 days. May, 1903. Nos. IV b to IV⁴.

The coverts and scapulars are developed enough to show the color of the first plumage. The coverts and scapulars are all edged with a rich red only a little paler than the red of adult Guinea pigeon. The edging contrasts with the dark brown of the rest of feather. All wing-coverts, except a very few at the anterior inner limit of the wing, have the pale-gray median streak, beginning as a narrow and obscure line in the lesser coverts, just a little widened at the tip, and growing stronger and wider at the tip towards the long coverts. The median light streak runs up to the red edge, but does not cut through this edge. Thus we see here, more plainly than in the robin, that the streak is not one and the same with the light margin. Only the posterior third of the scapulars has this median gray streak, the rest being of the turtle-dove type.

No. IV *b*. A mid-scapular (of above hybrid).

No. IV *c*¹. A long wing-covert at about middle height.

No. IV *c*². A covert from the second row, at about the same height.

No. IV *c*³. A covert from the third row, at about the same height.

No. IV *c*⁴. A covert from the fourth row, at about the same height.

No. V *c*². From the wing of juvenal *St. humilis* (10 days).

PLATE 58

Ia Ib IIc IIb IIb¹

IIIb¹ IIIc¹ IIIc² IIIc³ IIIc⁴ IIIc⁵
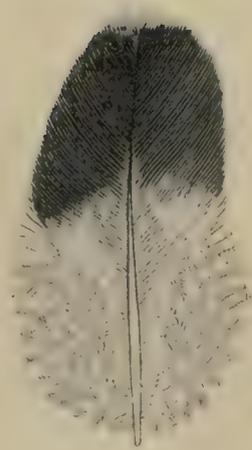
Vc² IVc⁴ IVc³ IVc² IVc¹ IVb

Analogies of the robin pattern in common pigeons.

the center being undivided on the upper (inner) and covered web. On the lower (outer) web, the bars of the basal half fuse more or less completely in the lower four or five feathers.

Examining the tertials and secondaries, we find the bars completely separate on the uppermost feather, but from here onward we see the division of bars gradually reduced, the bars coalescing, first at the shaft, and then gradually, as we descend the series, the bars are lost more and more in an increasing dark center. Since the upper part is most modified, we must read the series from below upward—from dark center to bars.

Only one of the primaries—the uppermost—has a completed bar. The light area diminishes downward, and the lower (outer) primaries are whole color with a small light tip.

In a juvenal female flicker, examined a few days before flying, the spotted feathers run clear up to the black crescent and on the side up to the middle of the crescent. The spots are broader and more pointed distally (less rounded) than in the adult male. According to Mr. Burns,[21] "the pattern of coloration of the fully fledged young is very nearly the same as the adults, but the spots and bars are usually much broader, giving a coarser and darker effect." I may add that not only are the bars broader, but they are less deeply outlined; i.e., they frequently fuse with one another in the middle portion, the light interval being less deeply extended.

"The white-edged black feather" is regarded by Mr. Burns as "its present highest stage of color-pattern development."[22] (page 72).

In this same juvenal female I note that the "malar stripe" is dark gray in color, and plainly narrower than in three males where the stripe is black. Dr. Allen,[23] who has carefully described the color variation of these birds, thinks that the malar stripe is a character of little service as an index to ancestral relationship. I think, however, that this is a character of deep significance, and one that should be studied on hybrids[24] of known origin—i.e., from birds bred in confinement.

One may grant that this stripe, as it is described by Allen in two species of *Colaptes*, presents a situation of much seeming confusion:

(1) In *C. auratus* the stripe is present in both sexes in the first plumage (weaker in the female), but is absent in the adult female.

(2) In *C. cafer-mexicanoides* the stripe is absent in the female in the first plumage, but present in the adults of both sexes.

With the facts obtained from the neck-marks of ring-doves (*Streptopelia*) as a guide (Chapter V), let us assume that No. 2 is the earlier form, and that stripe is absent in the ancestral form. In the present form, then, stripe has been acquired and has already begun to appear in the first plumage of the male, but not in the female, which remains nearer the ancestor.

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[21] F. L. Burns, A Monograph of the Flicker (*Colaptes auratus*). The Wilson Bulletin, No. 31, 1900.

[22] This author illustrates the supposed progressive series of variations in color. The more primitive pattern is "a black feather with a minute white spot at the tip." The white spot cuts deeper, and by repetition leads to cross-bars. The bars are enlarged to even black—"the white-edged black feather."

Mr. F. M. Chapman (Bull. Am. Nat. Hist. Vol. III, No. 2, page 311), holds the barred feather to be the first in a series that terminates in a "white-edged black feather."

[23] J. A. Allen. The North American species of the genus *Colaptes*, considered, etc. Bull. Am. Mus. Nat. Hist., Vol. IV, No. 1, page 21.

[24] *Colaptes hybridus* is described by Allen, page 24.

In No. 1 the character has made greater progress, appearing in both sexes in the first plumage, but weaker in the female than in the male. The adult female loses the stripe—a reversion to a simpler type—but in the stronger (more advanced) stage of its development in the male it is still preserved.

EXPLANATION OF PLATE 59.

Selected feathers from an adult male *Colaptes auratus* flicker. × 0.8. Hayashi del., Apr. 1903. A series of 24 feathers from the pectoral crescent back to the tail, along the left side just below the wing.

Nos. 1 to 3. From just below the crescent.
No. 4. From just behind 3.
No. 5. From nearly midway.
No. 6. From side of body behind 5.
Nos. 7 and 8. From close to 6 (long side-feathers).
Nos. 9 and 10. From close to 7 and 8 (posterior of the side-feathers reaching back a little beyond the middle of the wing).
No. 11. One of first (anterior) feathers, starting on the leg.
No. 12. From close to 11.
No. 13. From the same level.

No. 14. From the same level (more dorsal).
No. 15. From just behind 13.
No. 16. From same level.
No. 17. An anterior under-tail covert.
No. 18. From close to 17.
No. 19. From near hind limit of tail-coverts.
No. 20. Next to posterior longest tail-coverts.
No. 21. From level of 20.
No. 22. The last feather of white rump.
No. 23. The last upper-tail covert.
No. 24. The mid-tail feather (left side).

It is very instructive to compare this plate with that showing feathers of white-faced pigeon (pl. 44). The flicker stands plainly above the pigeon, but as evidently has the same starting-point, the turtle-dove pattern. To start from the barred feather as primary, we should fail of getting the direction of evolution. These feathers speak for themselves and show that the original pattern is most nearly preserved behind and most departed from anteriorly, the contrary of Eimer's view.

EXPLANATION OF PLATE 60.

A. The sharp-tailed sandpiper, *Tringa acuminata*. Copy by Toda, from Buffon (Ois., vol. VII, p. 553, pl. enl. 852 = Le Cincle).

The turtle-dove pattern prevails throughout. The feathers have dark or blackish centers. The edges of the scapulars and coverts of the upper parts are reddish; lighter or whitish on lower parts.

Selected feathers from an adult quail (bob-white), *Colinus virginianus*. Natural size. Toda del., June 1903.

The chin is white, turning to buff on the throat. Figures 1 to 9 are of feathers from the throat; figures 10 and 11 are from the upper side-breast.
FIG. 1. Narrow black tip, a short gray base, and a large middle buff part.
FIG. 2. Gray base a little longer, black tip more concentrated, leading to the triangular spot of figures 3 to 9.
The three-segmented condition (Häcker) is shown in figures 1 to 5. That this condition is a foundation for barring is seen as we pass downward on the throat (figs. 5 to 9). In figure 9 the distal spot is partly ruddy brown. Figures 1 to 5 represent the conditions already noted in the robin.

EXPLANATION OF PLATE 61.

Figs. 1–11. Selected feathers from an adult female ring-necked pheasant of China, *Phasianus torquatus*. Natural size. Toda del., June 1903.

FIGS. 1 and 2. Middle interscapular feathers. The turtle type modified; note the dark tip in both feathers. Also, a shaft-streak and extensions of the light color along the lateral margins. Color blackish-brown, with a buff edge.
3 and 4. Two anterior scapulars, left side; pattern of figures 1 and 2 varied toward barring.
5. From upper neck, just left of median front line.
6. Just below figure 5; figures 5 and 6 show simple form of bars.
7 and 8. Below figure 6 on breast; figure 7 from near mid-front line and figure 8 a little to left of figure 7. Figure 7 is of the turtle type reduced to a V-shaped spot, and figure 8 is the same with a constriction, pointing toward the condition seen in figures 10 and 11.
9. From still lower on breast than figure 7; figures 10 and 11 are from the same level, but more to the side.
The V-shaped figure seen in figures 9 to 11 and in so many birds comes, then, directly from the dark center. It is not a bar "tilted," as Keeler expresses it.

A. Wing of juvenal pheasant, 20 days. × 2. Toda del., June 1904.

Shows dark centers, light edges, and very simple feather-bars, all grades from a few flecks to a fully formed bar. The long coverts show only one light bar (tips excepted). The primary coverts show the same light bar less developed.

PLATE 59 , 2 6'
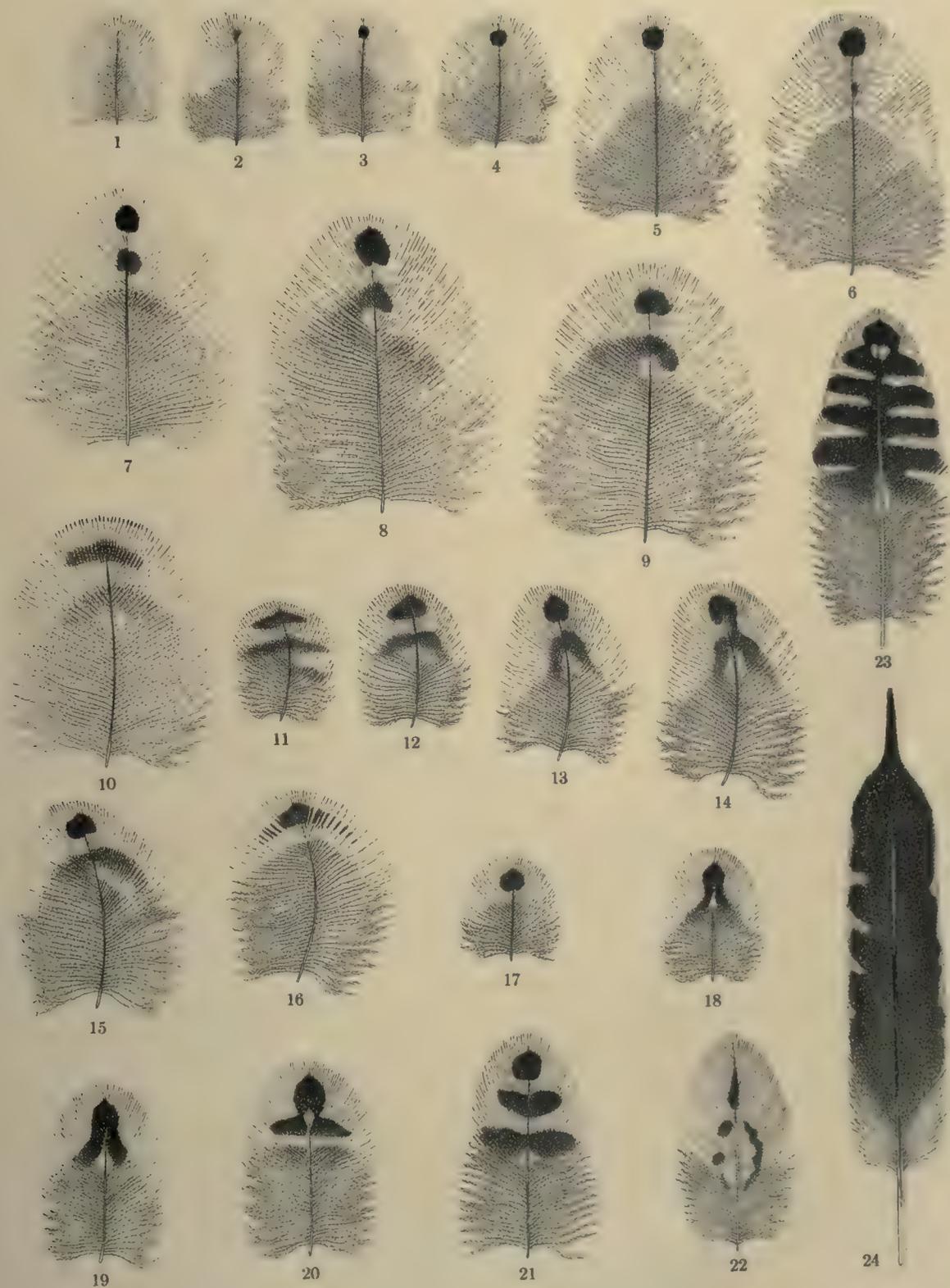
Selected feathers from an adult male flicker, *Colaptes auratus.*   × 0.8.   Hayashi del., Apr. 1903.
Series of 24 feathers from pectoral crescent back to tail, along the left side just below the wing.
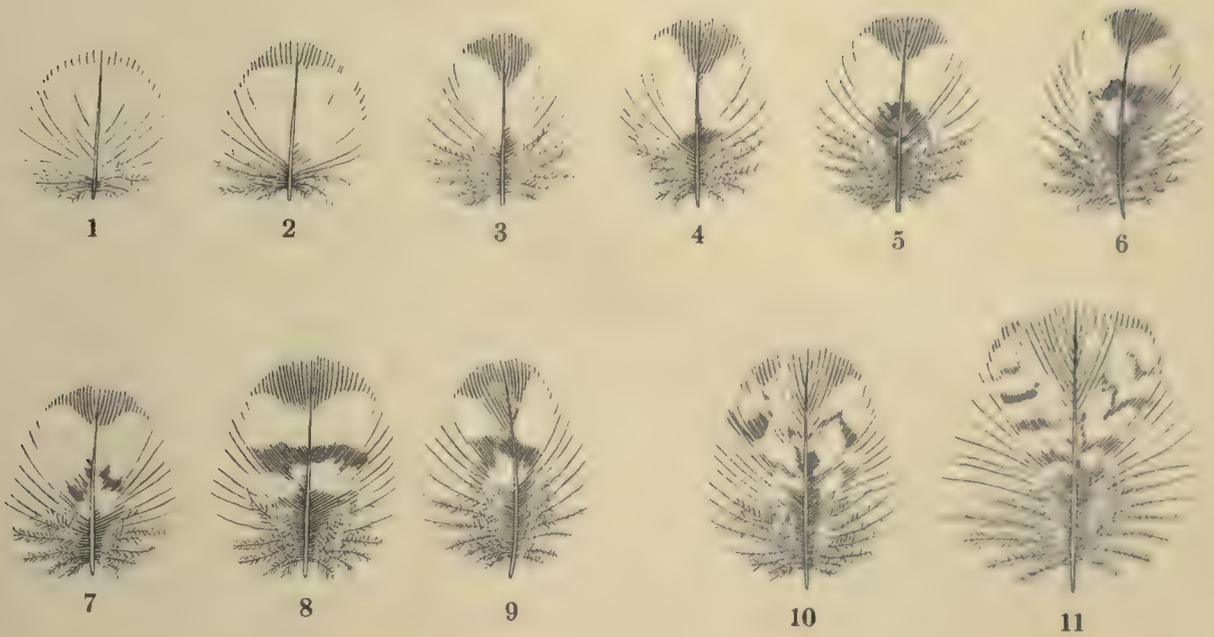
PLATE 60

A. The sharp-tailed sandpiper, *Tringa acuminata*. Copy by Toda, from Buffon (Ois., vol. VII,
    p. 553, pl. enl. 852 = Le Cincle.)

Figs. 1–11. Selected feathers from an adult quail (bob-white), *Colinus virginianus*. Natural
    size. Toda del., June 1903.

PLATE 61
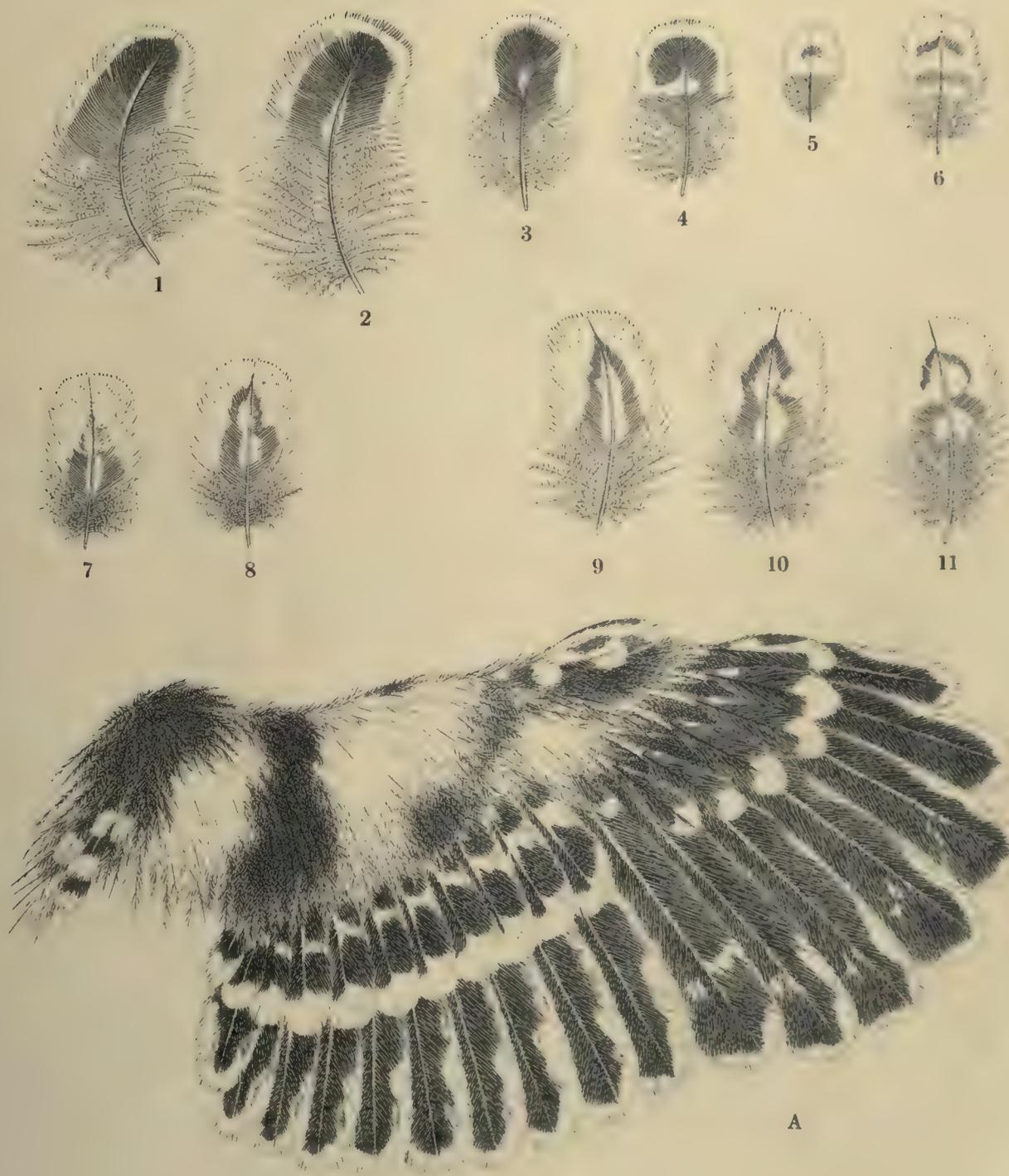
Figs. 1–11. Selected feathers from an adult female ring-necked pheasant of China, *Phasianus tor-
quatus*. Natural size. Toda del., June 1903.

A. Wing of juvenal pheasant, 20 days. ×2. Toda del., June 1904.

The sharp-tailed sandpiper.—In *Tringa acuminata*, according to the figures and description of Brisson[25] and of Buffon,[26] the turtle-dove pattern prevails throughout. The feathers have dark or blackish centers. The edges of the scapulars and coverts of the upper parts are reddish, while lighter or whitish prevail on the lower parts (pl. 60, fig. A).

The splendid parrakeet.—According to Gould's[27] figures and descriptions, *Platycercus splendidus* has dark centers in both the juvenal and adult plumage, but these extend farther up the back of the neck in the juvenile feathers. Further, the head in the young has much less red than in the adult (pl. 62, fig. A).

The black-backed hemipode.—From the same sources I learn that *Hemipodius melanotus* has feathers with pale edges—brown on the head and buff-yellow on the wings. The black center seems to be variously modified in the several regions of the wing; sometimes it is a reduced black spot, other times it simulates a transverse bar (pl. 63, fig. A).

The collared plain-wanderer.—According to Gould,[28] *Pedionomus torquatus* has black centers in the feathers of the neck region, where all of the feathers are broadly tipped with white; the "flanks with large irregular spots of black," and with transverse barring much more complete than in *Hemipodius* just described. The bars are not only more complete in *Pedionomus*, but also much more numerous on the individual feathers (pl. 63, fig. B).

The curlew.—From the works of Brisson[29] and of Buffon,[30] data of interest are to be obtained on 4 of the 5 species to which we next refer. In *Numenius arquata* the turtle-pattern prevails on the head, neck, breast, and on the whole wing and back. The feathers have brown or brown-black centers and light edges. The beginning of bars on the secondaries and tertials is carried out on the tail and the tail-coverts (pl. 62, fig. B). These beginnings of bars are of much interest when compared with their more extended distribution in the rail and the wood-sandpiper, where "white dots" have also made their appearance.

The Philippine rail.—In *Rallus pectoralis* the feathers are strongly barred transversely below. On the upper parts the turtle-dove pattern prevails, but with the additional feature of a roundish white spot on each web of the feather near the margin (text-fig. 24, A). These spots, both in position and in general appearance, appear to be like the white spots on the wing of *Geopelia cuneata;* and in the latter bird the spots are known to be of later origin than transverse bars, and are also there known to represent the lateral portions of such bars.

The Virginia rail.—In *Rallus virginianus* we find again roundish white dots or spots which are derived from bars, in the same manner as in *Geopelia cuneata*. This is seen in the feathers of the back (interscapular region), in the scapulars, the tertials, in the inner upper wing-coverts, and on the sides of the breast. Dark centers are present in most of these feathers marked with spots[31] (or white streaks).

[25] Brisson Ornith., V, p. 216, pl. XIX, fig. 2.

[26] Buffon, Ois, vol. VII, p. 553, pl. enl., 852.

[27] Proc. Zool. Soc., pl. XIII, p. 105, and Birds of Australia, Vol. V, 1848.

[28] Birds of Australia, Vol. V, 1848 and Proc. Zool. Soc., 1840.

[29] Brisson, Ornith., Vols. V and VI.

[30] Buffon, Ois, Vols. VII, VIII, and IX. The descriptions of *Rallus virginianus* are my own, from individuals kept in captivity.

[31] I have (1909) a pair of Carolina rails in which I find that the female has the turtle dark center on the wings, while the male has advanced beyond—is lighter in most parts than is the female and has more variegation with white on the back.

The white streaks, which are sometimes found instead of white spots, are not even, but constricted more or less at regular intervals; in other words, they represent spots that are confluent in longitudinal lines. In some feathers we see two parallel lines of white on the outer web. In the shorter anterior feathers the lines shorten up, leaving only one or two pairs of spots near the tip. On the sides of the breast these spots are seen to be only the outer portions of transverse bars, the bars being various in their extent.

In an axillar feather I find a most interesting condition, 1 to 6 or more conspicuous white bars, with an equal number of shadowy light bars midway between the

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EXPLANATION OF PLATE 62.

A. The splendid parrakeet, *Platycercus splendidus* Gould. Copy by Toda, after Gould (Birds of Australia, vol. v, 1848). × 0.7.

From a figure (pl. 28, upper figure) by Gould, described as the "plumage of youth," I see that the dark centers are about the same as in the adult, but they extend farther up the back of neck. The head has much less red in the juvenile than in the adult. The description is given as follows:

"Head, sides of the neck and center of the breast scarlet; cheeks white, faintly tinged with blue; feathers of the back and scapularies black, broadly margined with gamboge-yellow; lower part of the back and upper tail-coverts pale green; on the shoulder a patch of black; wing-coverts pale blue, primaries black with the exception of the basal portion of the external web, which is rich deep blue; two central tail-feathers dark green at the base, passing into deep blue on the apical half of the external web and tipped with black; the next on each side is black on the internal web, green at the base of the external web, blue for the remainder of its length, and slightly tipped with white; the remainder of the tail-feathers are deep blue at the base of the external, and black at the base of the internal web, the remaining portion of both webs being pale delicate blue, passing into white at the tip; sides of the breast and abdomen bright gamboge-yellow; vent pale green in some, in others pale bluish-green; under tail-coverts scarlet; irides dark brown; bill horn-colour; feet mealy brown."

B. The curlew, *Numenius arquata* Latham (Le Courlis). Copy by Toda, after Buffon (Ois, vol. VIII, p. 19, pl. enl. 818.) × 0.9.

The turtle pattern prevails on head, neck, breast, and the whole wing and back. The beginning of bars on the secondaries and tertials is carried out on tail and tail-coverts. The feathers have brown or brown-black centers and light edges.

EXPLANATION OF PLATE 63.

A. The black-backed *Hemipodius melanotus* Gould. Copy by Toda, after Gould (Birds of Australia, vol. v, Proc. Zool. Soc., pl. v, p. 8, 1848).

The female is said to be larger than the male; otherwise alike. Described as follows:

"Crown of head black, each feather fringed with brown at the tip; space between the bill and the eye, stripe over the eye and cheeks, light yellowish-brown, the feathers of the latter slightly tipped with black; back of the neck rich chestnut-red; scapularies deep chestnut-red, with a large transverse black mark in the centre of each feather, and a longitudinal stripe of fawn-yellow on their outer edges; rump and upper tail-coverts black, each feather freckled with fine markings of brown, with indistinct spots of buff on the external edges of the upper tail-coverts; greater and lesser wing-coverts buff-yellow, each feather having a spot of black in the centre; primaries brown; throat whitish; front of the neck and chest deep buff; sides of the neck and flanks light buff, with an oblong spot of black transversely disposed in the centre of each feather; centre of the abdomen and under tail-coverts buffy-white; bill and feet brown."

B. The collared plain-wanderer, *Pelionomus torquatus* Gould. × 0.75. Toda del., after John Gould (Birds of Australia, vol. v, 1868, pl. 80).

The following is Gould's description:

"Crown of the head reddish-brown, speckled with black; sides of the head and the neck light buff, speckled with black; neck surrounded by a broad band of white, thickly spotted with black; all the upper surface reddish brown, each feather having several transverse crescent-shaped marks in the centre, and margined with buff; tail buff, crossed by numerous narrow brown bars; centre of the breast rufous, the remainder of the under surface buff; the feathers on the breast marked in a similar manner to those on the upper surface, and the flanks with large irregular spots of black; irides straw-yellow; bill yellow, passing into black at the point; feet greenish-yellow."

C. Adult female European widgeon, *Anas penelope*. × 0.75. Toda del., after Buffon (Ois., vol. IX, p. 216, pl. enl. 803, Le Millouin).

Head and neck rufous brown (or reddish); breast vinaceous. Sides and back finely marked with transverse, wavy, or zigzag lines or bars, dark brown alternating with whitish-gray. This picture illustrates the fineness to which bars are developed.

PLATE 62

A. The splendid parrakeet, *Platycercus splendidus* Gould. Copy by Toda, after Gould (Birds of
    Australia, vol. v, 1848). ×0.7.

B. The curlew, *Numenius arquata* Latham (Le Courlis). Copy by Toda, after Buffon (Ois., vol.
    VIII, p. 19, pl. enl. 818). ×0.9.

PLATE 63
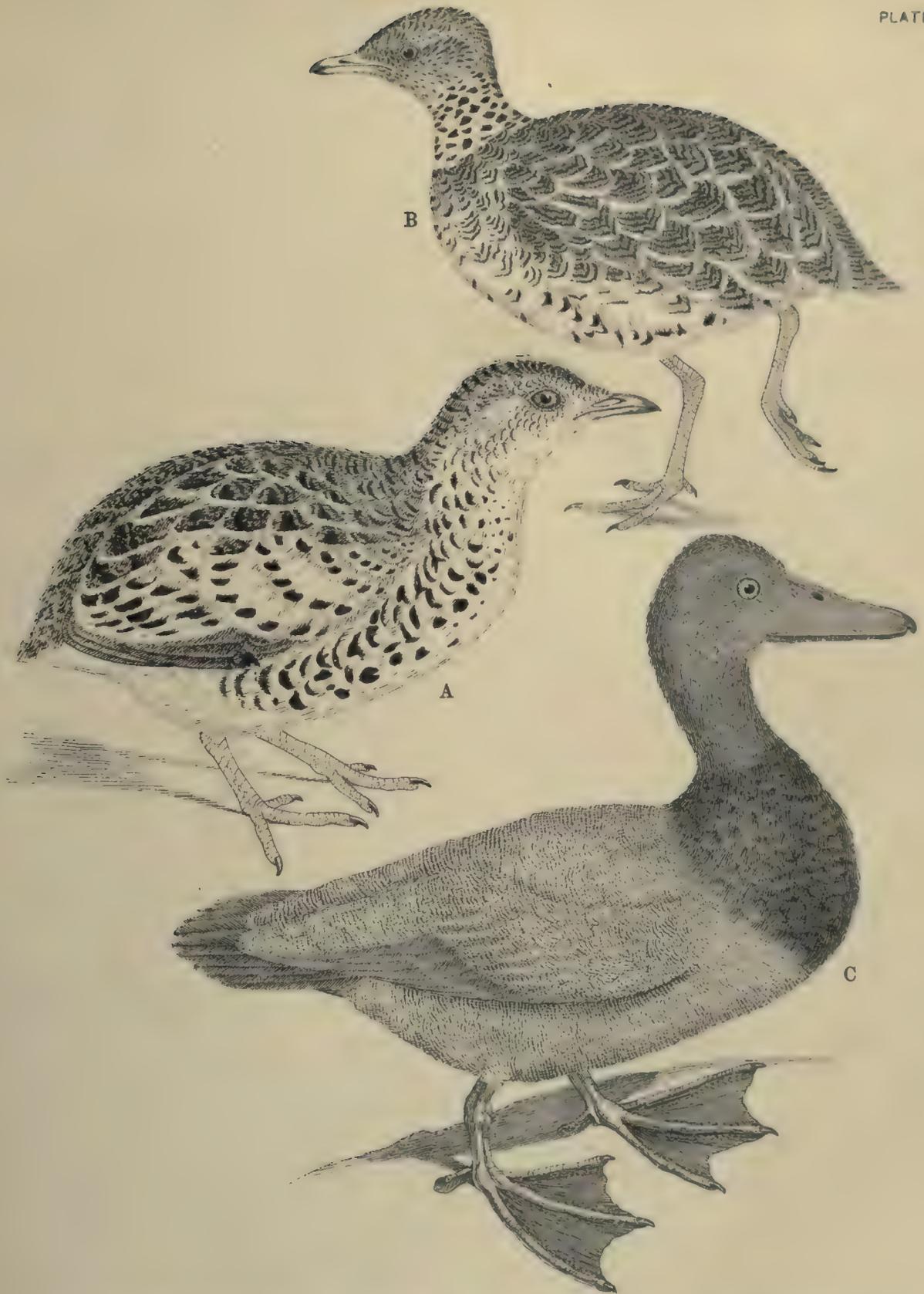
A. The black-backed *Hemipodius melanotus* Gould.   Copy by Toda, after Gould (Birds of Australia,
   vol. v, Proc. Zool. Soc., pl. v, p. 8, 1848).
B. The collared plain-wanderer, *Pedionomus torquatus* Gould.   ×0.75.   Toda del., after John
   Gould (Birds of Australia, vol. v, 1868, pl. 80).
C. Adult male European widgeon, *Anas penelope*.   ×0.75.   Toda del., after Buffon (Ois., vol.
   ix, p. 216, pl. enl. = 803.   Le Millouin).

conspicuous white ones; dark bars alternate with both the conspicuous and the shadowy white ones. Thus there are three bars, rather obscure, intervening between
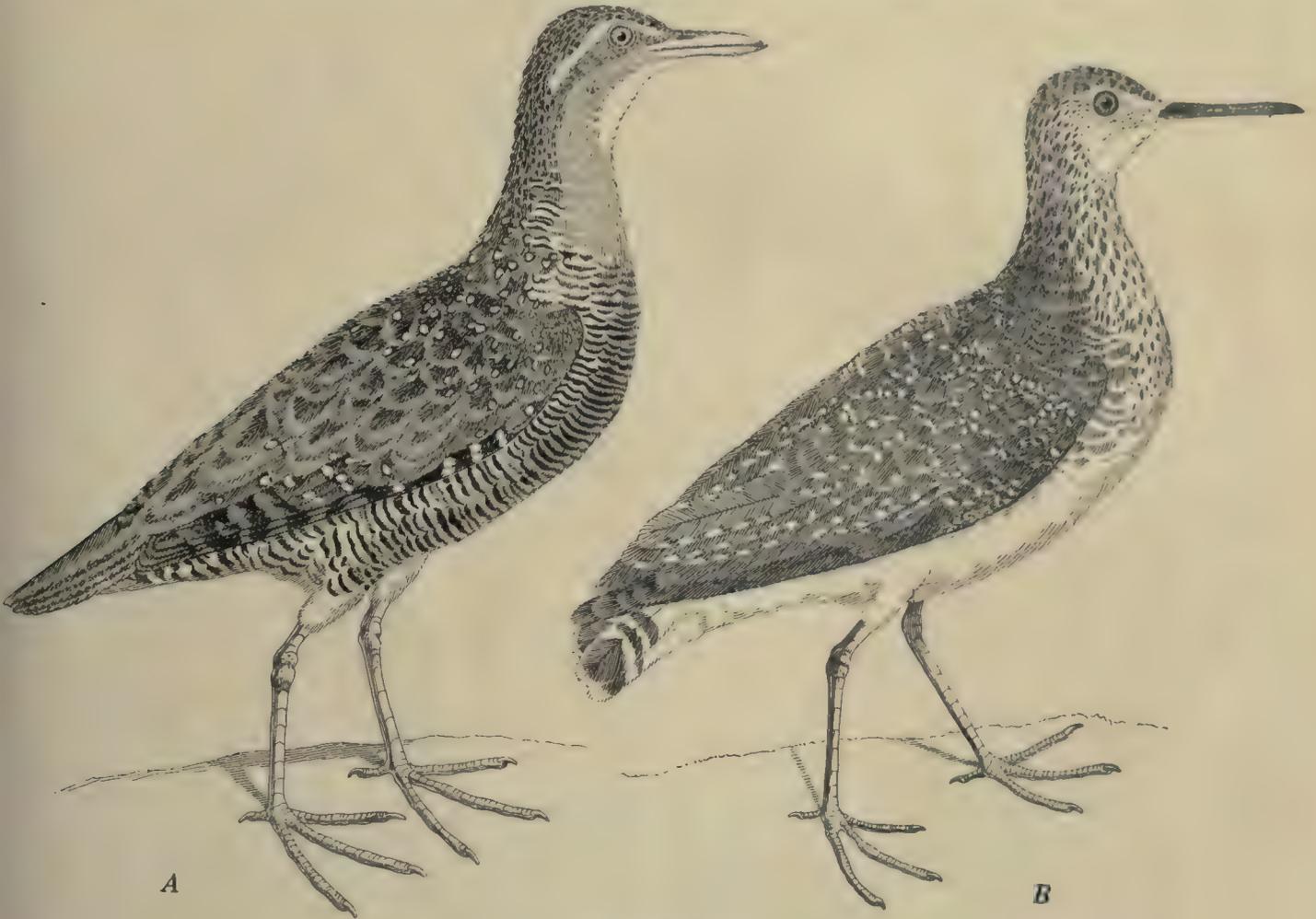
TEXT-FIGURE 24.

A. The Philippine rail, *Rallus pectoralis* (=*Rallus striatus* Linn.). Copy, same size, by Toda, after Buffon (Ois., VIII, p. 160, pl. enl. 774. Le Tiklin). This rail is strongly barred transversely below. The turtle-dove pattern prevails above, but with the additional feature of a roundish white spot on each web of the feather near the margin. These spots, both in position and in general appearance, appear to be like the white spots on the wing of *Geopelia cuneata*; these spots, in the latter bird, are known to be of later origin than transverse bars, and to represent lateral portions of such bars.

B. The wood sandpiper, *Totanus glareola* Temminck. Copy, same size, by Toda, after Buffon (Ois., vol. VII, p. 534, pl. enl. 843. Le Beccasseau). This bird has the turtle-pattern of feather on the neck and side of the breast (ashy-brown centers with white edges). The feathers of the back and the wing-coverts are clear-brown with small whitish spots on the edge of each web. The long coverts and the tertials have these spots repeated at regular intervals along the outer margin of the feather, showing plainly their relation to bars. This is a very fine illustration in connection with *Geopelia cuneata* (Brisson gives a good description, pp. 180–182). In the tail-feathers the bars are fully developed.

every two successive conspicuous white bars. In this case we have proof that the feather has many bars, but only every other white bar comes to strong development.[32]

[32] According to W. E. Teschemaker (Avic. Mag., n. s., Vol. IV., Oct. 1906) round spots are derived from cross-bars in the red-headed finch (*Amadina erythrocephala*). This author gives some figures (page 357) to illustrate the point. It is also stated that: "Corresponding feathers of an adult and immature specimen of the same sex are of a quite different pattern—the former being spangled, the latter barred."

The wood sandpiper.—*Totánus glareola* has the turtle-pattern of feather on the neck and on the side of the breast, the centers being ashy-brown with white edges. The feathers of the back and the wing-coverts are of clear-brown color, with small whitish spots on the edge of each web. The long coverts and the tertials have these spots repeated at regular intervals along the outer margin of the feather, showing plainly their relation to bars (text-fig. 24, B).

This is another very fine illustration of the method of origin of white dots. Everything indicates that the dots arise as in *Geopelia cuneata*, where I have shown that they arise from the lateral portions of transverse bars. The bars are fully developed in the tail-feathers of this species.

The widgeon.—The remarkable extent to which transverse barring, with very narrow bars, may be developed is well shown in *Anas penelope* (pl. 63, fig. C). We shall later see that plain remnants of the turtle-pattern, dark crescentic tips, and very fine barring, are all frequently found in this genus.

The crowned guinea-fowl.—The adult wing of *Numida coronata* shows numerous white dots, and a relation between these and white bars is plainly indicated in the proximal exposed parts of the primaries (pl. 64, fig. B). In the juvenal stage the feathers of the wing have dark centers and light edges (pl. 64, fig. A).

The ring-necked pheasant of China.—The male *Phasianus torquatus* has departed notably more from ancestral conditions than has the female. The latter still plainly preserves the dark center and the pale tip, though both are somewhat modified (pl. 65).

EXPLANATION OF PLATE 64.

The crowned guinea-fowl, *Numida coronata*. Copy by Toda, after Elliot (Monograph of the Phasianidæ, vol. ii).

A. Juvenal; shows dark centers and light edges in feathers of wing.
B. Adult; description according to Elliot:

"Upper parts, neck and breast brownish-black, thickly covered with white spots; between the spots a fine network of white lines. Rump and tail black, with the same coloured spots and pattern as the back. Flanks and under tail-coverts pure black, spotted with white; without any tracing. Primaries and secondaries dark brown, covered with white spots, with the edges of the outer webs having short lines of white cutting into the black. Head and neck-bars, bluish in colour. A high bony casque on the top of the head, in some specimens curving backwards. Wattles elongated, longer in some individuals than in others, and not of specific importance. Bill, legs, and feet black."

EXPLANATION OF PLATE 65.

The ring-necked pheasant of China, *Phasianus torquatus*. Toda del., 1904, after Elliot (Monograph of Phasianidæ, vol ii).

A. "*Male.*—Upper part of head light green; ear-tufts and neck dark green, with bluish reflections. Collar around the neck white, divided in front by the green. Upper part of back red, the feathers tipped and margined with black. Wing-coverts buff in the centres, followed by a line of black, and tipped with purplish-red. Rump red, with green reflections, the buff centres of some of the feathers usually showing amid the red. Shoulders of the wings light brown, with a greenish lustre. Secondaries light brown, with deep chestnut margins. Primaries brown, barred irregularly with yellowish white. Upper tail-coverts red. Breast rich metallic purplish red, the feathers margined with bluish black. Flanks golden chestnut, centre of each feather tipped with dark blue. Abdomen black, with greenish reflections. Upper tail-coverts red. Tail very long, yellowish brown, irregularly barred with black, and margined with red. Bare skin of face scarlet. Bill horn colour. Feet and legs dark grey.

B. "*Female.*—Upper part of head black, tipped with light brown. Throat yellowish-white. Rest of neck reddish brown, tipped with black. Upper part of back has the feathers chestnut in the centre, followed by a bar of black, and tipped with very light rufous brown. Feathers of back black in the centre, margined with light brown dotted with black. Feathers of the rump black, margined with yellowish-brown. Secondaries blackish brown, mottled and barred with rufous brown and buff. Primaries dark brown, barred with yellowish-white. Upper part of breast rufous, dotted with black. Under parts yellowish brown. Tail shorter than that of the male, dark chestnut in the centre, crossed with black bars broken in the middle by an irregular buff line, and the outer margins of both webs light yellowish-brown, mottled with black; tips black. Bill horn colour. Feet and legs dark grey."

PLATE 64
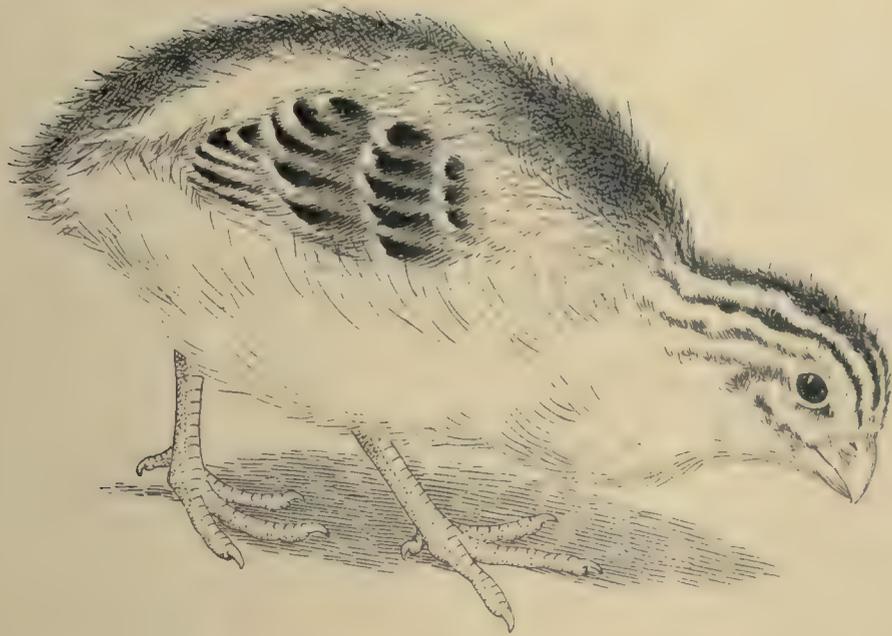
A
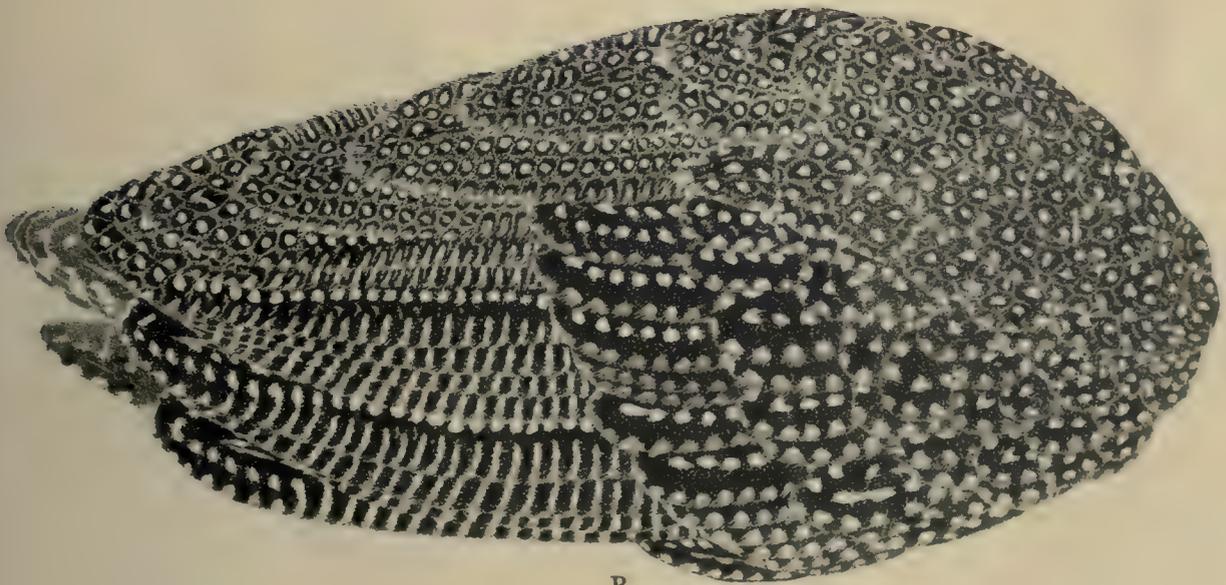
B

The crowned guinea-fowl, *Numida coronata*. Copy by Toda, after Elliot (Monograph of the Phasianidæ, vol. II).

PLATE 65

The ring-necked pheasant of China, *Phasianus torquatus*. Toda del., 1904, after Elliot (Monograph of Phasianidæ, vol. II).

The middle interscapular feathers show the slightly modified turtle-dove pattern. The dark center and the pale tip are both present, the latter having extended upon the lateral margins of the feather. Coincident with the earlier extensions of these lateral margins, a slender shaft-streak makes its appearance. Other feathers show that further increase of the lateral margin is accompanied by enlargement of the median shaft-streak.

In the feathers of this bird it is clear that the V-shaped figure arises from the turtle-dove pattern. It is not a "tilted" bar, as Keeler believed (pl. 61, figs. 1 to 11).

The wings of the juvenal pheasant show dark centers, light edges, and a very simple type of barring. This barring is present in all grades, from a few flecks to fully formed bars. This light-colored bar is more complete on the long coverts than on the primary coverts (pl. 61, fig. 12). The wings of still younger birds (pl. 79, fig. A) show that the color of the pale edge is practically identical with that of the down.

Phasianus wallachii.—In this species the pattern is, in the main, similar to that just described for *P. torquatus*, but the turtle type is here still further modified. Here, too, the males stand above the females in the extent to which the ancestral pattern has been transformed (pl. 66).

ON THE EVOLUTION OF THE OCELLUS OF THE ARGUS PHEASANT AND THE PEACOCK.[33]

Several instances of the origin of white spots from preëxisting white transverse bars have already been noted (the immediately preceding pages, and *Geopelia cuneata*, Chapter X). Because of its relation to the present subject it is interesting to find indications that this rule of origin holds for one of the Phasianidæ—*Numida coronata* (pl. 64). It is of even greater interest to be able, in the Simla horned pheasant—a form showing large, distinct, white ocelli—to show that the smaller white spots of some of its feathers are actually parts of white transverse bars (pl. 67, fig. 1).

Other feathers of this same species (*Tragopan melanocephalus*) offer evidence that the large, single, subterminal white spot, which is borne near the tip, represents a fusion of several bars. And in these same feathers it is quite clear that the dark center is primary, and bars and spots secondary in origin (pl. 67, figs. 2 to 4).

As is well known, the argus-pheasants (*Polyplectron*) and the peacock (*Pavo cristatus*) show in many of their feathers eye-spots, or ocelli, of fine finish and of brilliant color. The bronze-winged pigeon (*Phaps chalcoptera*) seems to present the beginnings of such marks when a brilliant iridescence is superposed upon the black of its considerably reduced chequers (pl. 6, fig. A).

In *Polyplectron bicalcaratum* the female retains unmistakable elements of the dark-centered feather; the male has made a greater departure from earlier conditions, having more ocelli, and also ocelli of higher finish (pl. 68). A highly finished black border surrounds each ocellus in this species. In the bronze-wing a similar black border is present on the "terminal end" of the spot, half converting it into an ocellate form.

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[33] The author grouped together certain materials on this topic, and indicated "a paper to be worked out on this subject." This paper was not completed. A few original observations, together with the illustrations, and the more extensive review of Kerschner's work on the subject, will at least make clear the author's opinion, namely, that this finely finished and most remarkable color-mark takes its departure from a feather with a dark center; that it does not arise from the coalescence of two lateral spots.—ED.

In view of these facts the question of the origin of ocelli should be revised from the standpoint of the dark central spot as a primitive avian character. In considering this subject, Darwin took "gradual evolution" as his principle, and did not go far into the development of the various components of the ocellus, beyond comparing all of the conditions found in adult species. He was thus led to the view that the peacock's ocellus arose by the coalescence of two ocelli. Kerschner[34] has made a much more detailed study of the development of the ocellus. He finds a coalescence of black bars, and records a number of observations concerning regions and directions of color-transformation ¦which have a bearing upon the principles which I have found to apply to many ¦characters, and in several different families of birds. Kerschner starts with bars of black and yellow, which are supposed to arise from a "yellowish-brown, dark-gray, speckled condition." I am confident that this earlier condition is a feather with a dark center.

[34] Zeit. f. wiss. Zool., vol. 44. 1886.

EXPLANATION OF PLATE 66.

Phasianus wallachii. Toda del., 1904, after Elliot (Monograph of the Phasianidæ, vol. II).
    The descriptions are those of Elliot:
    A. "*Male.*—Top of head and lengthened crest dark brown. Neck, back, and wings yellowish brown, crossed with black. Rump rufous, with occasional black bars. Primaries dark brown, with broad buff bars on the outer webs. Secondaries buff, barred with brown, and mottled with black. Throat light brown. Breast ashy, barred with black. Flanks rufous, barred with black; abdomen dusky. Tail long; middle feathers brownish white crossed with broad irregular black bars; lateral feathers crossed with yellow, black and chestnut. Bill horn colour; legs and feet brown.
    B. "*Female.*—Top of head and crest brown, with a black central streak in the feathers. Feathers of the neck and breast dark brown, with white margins. Throat white. Upper part of back rufous, barred with dark brown, and margined with white. Rump reddish brown, mottled with black. Primaries dark brown, barred with buff. Secondaries chestnut, barred with black and buff, and mottled with black. Flanks and lower part of breast reddish buff. Tail reddish brown, barred with black and buff, and mottled with black. Bill horn colour."
    For selected feathers of female and wing of juvenal see plate 67.

EXPLANATION OF PLATE 67.

Selected feathers from a male Simla horned pheasant, *Tragopan melanocephalus.* × 1.6. Toda del.,
        Aug. 1904, from a mounted specimen in the Field Museum, Chicago.

A. A rump-feather; shows that small white spots are parts of discontinuous bars. Passing towards the base of feather spots are actually parts of continuous bars. The neat network forming circular or hexagonal figures, inclosing each a spot, are derived from narrow bars that alternate with wider bars, as the feather shows plainly towards base.
B. From back of neck, lateral, just in front of scapulars. A white spot only a little wider than long, in center of a blackish area; elsewhere bars that are wavy or zigzag in form, due to tendency to form narrow bars alternating with wider ones.
C. From the flank at level of leg. The dark center and white center are larger.
D. An under tail-covert. Dark center scarcely marked by more than a few touches of white bars; white center extends nearly across feather, showing more of the bar nature. It may be regarded as a fusion of several bars. These feathers show that dark center is primary, bars and spots secondary, in origin.

EXPLANATION OF PLATE 68.

Polyplectron bicalcaratum. Toda del., 1904, after Elliot (Monograph of the Phasianidæ).
    The descriptions are those of Elliot:
    A. "*Male.* —Head covered with a lengthened crest, grey and black alternating at the base, and tipped with bluish. Throat covered with brownish-white feathers. Neck and upper part of back brownish white, crossed by narrow lines of blackish brown. Back, wings and tail yellowish brown, spotted with blackish brown, with a luminous spot of brilliant green, surrounded with black near the end of each feather. These spots are very large on the tail feathers, and confined *on the lateral ones to the outer web.* Rump yellowish brown, minutely dotted with blackish brown. Primaries and inner webs of secondaries dark brown, the outer webs of the latter yellowish brown, mottled with dark brown. Entire underparts yellowish brown, minutely mottled with dark brown; the shaft white. Bill, upper mandible blackish brown; under mandible horn colour. Feet and tarsi black. Naked space around the eye red.
    B. "*Female.*—Similar to the male; but the brilliant spots upon the back are black without lustre, and those on the tail, though metallic, are much smaller than those of the male."

PLATE 66

Phasianus wallachii. Toda del., 1904, after Elliot (Monograph of the Phasianidæ, vol. ii).

PLATE 67
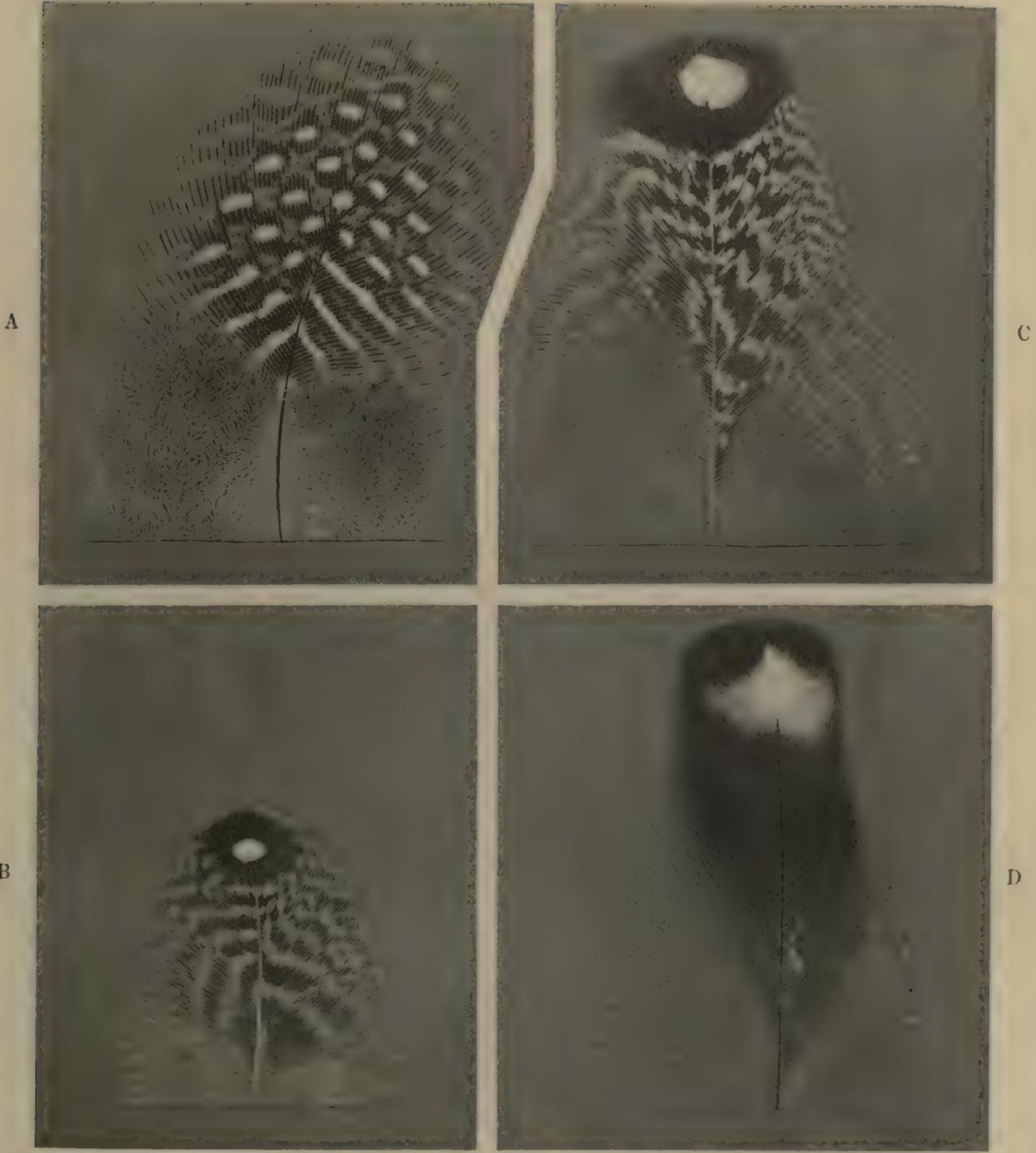
Selected feathers from a male *Simla* horned pheasant, *Tragopan melanocephalus*. × 1.6. Toda del.,
Aug. 1904, from a mounted specimen in the Field Museum, Chicago.

PLATE 68

Polyplectron bicalcaratum. Toda del., 1904, after Elliot (Monograph of the Phasianidæ).

Kerschner shows that the earliest stage of this eye-spot (ocellus) is found in feathers "barred with black and reddish yellow." According to his description the most distal black bar first shows a weak "metallic green"; this green becomes brighter, only the outer border-line remaining plain black. The bar becomes wider and shows, proximally, a narrow but gradually "growing zone of bronze." [35] We thus have two zones: a "distal green and a proximal bronze" within the border-line of black. The bar grows wider, encroaching upon and at length occupying the space of the light bar proximal to it. The bar and the two zones of metallic green and bronze continue to expand in growth inward (proximally). The feather becomes more pointed, the bronze zone expands more rapidly in the middle—to either side of the shaft—than at the sides. The metallic color spreads over the next black bar, i.e., it begins on one bar and gradually spreads inward over two black bars; the intervening light bar and the last light bar following the second black bar being replaced by the pigment of the growing spot.

The original bronze-colored cross-bar (zone) contracts in its cross-length and expands along the shaft, becoming pointed distally and thus triangular as a whole. This bronze triangular spot has its basal angles first rounded, and then the distal angle is rounded, so that we have an ovate bronze disk sharply defined against the proximal green ground. By widening at its distal end, the disk becomes at first "elliptical," then obovate, and then triangular, with its point directed proximally. Next, the angles on the distal base are rounded, and the bronze disk expands to a nearly "circular form," with a small triangular tip proximally.

Close upon the shaft, below the center of the bronze spot, "where green persists in all earlier stages," there appears a narrow green stripe, which gradually lengthens to some extent, but its expansion is mainly in width, and especially in its middle portion; and so by degrees it grows into a rectangle, with somewhat rounded angles, inclined at an angle of about 45° to the long axis of the feather. Near the upper angle of this area there appears a dull, "dark-blue point," which gradually expands to a "small circle," centered on the shaft.

The peripheral black border has meanwhile become wider. That part of the external green zone that comes in contact with the black border shows a purplish gleam, while next to the bronze disk the black border becomes blue-green. The rest of the black border remains yellowish green. Meanwhile, the lower barbs have been lengthening and closing in distally around the ocellus, which is now essentially complete. The "yellowish green" portion of the black border becomes olive-green, and that part of the outer zone, described as purplish, is now a coppery-brown zone, like the "bronze disk."

The bronze disk elongates a little during these last changes; the green disk (inclosing the central dark-blue spot) grows a little in width, and the central dark-blue spot, which at first expanded evenly in all directions, later ceased to expand at its lower pole, and so left here the "indentation" filled by the rich green zone. At the apex of feathers now before me, for comparison with Kerschner's descriptions, the barbs become very slender for a distance, and in this part have no barbules. Thus there is formed the "transparent zone."

"The highly elaborate tail-feather of the peacock may thus be traced back through quite gradual transitions to a feather relatively simple in its color-marking. The same may be said of every other ornamental feather of this bird; each and every one of them leads us back, directly or indirectly, to a feather barred with black and reddish yellow. This course of development repeats itself in a generalized way in the young peacock, but does not advance so far, as the barring persists a long time in relatively low stages." [36] (pp. 683, 684).

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[35] This is as in the bronze-wing (*Phaps chalcoptera*).
[36] Kerschner takes the side of gradual evolution against mutation.

Studying the marking in the various feather-tracts, Kerschner found that color differentiations went hand in hand with an "increase in the number of elements of the tracts," as Wallace maintained was the case in respect to the size and form of the ornamental feathers.

Kerschner admits that he finds among the "tail-coverts of the peacock some feathers with paired ocelli." If Darwin had seen these he would have considered them strong evidence in favor of his view. Kerschner still holds, however, that these cases are not "phyletic stages," but rather "stages of degeneration." The complete developmental series is said not to show these double stages.

The results of this investigation contradict Eimer's law that longitudinal striping precedes cross-barring. "Eimer's law of postero-anterior development," if applicable to feathers, should become the "law of antero-posterior development" (page 690). But even in this form the law would not hold according to Kerschner, neither in respect to the entire plumage nor to the single feathers. He thinks the differentiations occur in many directions, and even in opposite directions. "For the single feather I could not find any rule, although generally new characters arise near the apex, while the apex itself retains the older characters, and the covered portions of the feather usually show the more original marking." But he finds many exceptions even to this. Against Eimer's wave-law Kerschner asserts: "The development of the new characters of a series, viewed as motion, is always in a straight line."

FURTHER EXAMPLES OF THE TURTLE-DOVE PATTERN AND ITS DERIVATIVES IN BIRDS.
DARK CENTERS.

In the genus *Anas* are included species which retain the dark centers, and others with barring carried out to a very high degree. These species often show, also, a higher modification of the ancestral pattern in the males than in the females.

(1) In the blue-winged teal[37] (*Anas discors* Linnæus) the male has the lower part of the front-neck, the breast, and the feathers of the whole under surface with dusky centers and pale rufous edges. The mantle is dark brown, with feather-edges of pale rufous or gray. There are also one or two semicircles parallel to the edge of the feather of the same color with the feather's edge.

In the female the back is deeper brown, the feathers margined with yellowish buff; the breast and sides are similar but paler. The belly and vent are pale yellowish brown, but with dark centers. Over all the neck and head small dark centers are present, giving a spotted appearance. The male has extra crescents in the mantle feathers; the female has only the crescentic margin.

(2) In the pintail[38] (*Dafila acuta*) the male is extensively and finely barred on the back and wings; the female has dark centers in these same regions.

DARK CENTERS AND TRANSVERSE BARS.

The central dark spots, similar to those of the turtle-dove, may break up into transverse bars. I find such spots in hawks and other species.

(1) In *Falco tinnunculus japonicus*[39] the female has triangular spots on the lower parts, and these are reduced on the neck and upper breast to elongated central streaks. The wing-coverts have broad "triangular dark spots" near the ends of the feathers, then a light transverse bar, and then a dark bar. The row of long coverts shows this best. These three dark bars, alternating with three light ones,

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[37] Buffon, Ois, Vol. IX, p. 279; ♂ pl. enl. No. 966; ♀ pl. enl. No. 403.
[38] See Nuttall's Ornithology, Vol. II, page 309.
[39] See pl. 1, Temminck and Schlegel, Fauna Japonica, 1850.

are seen before we come to the end of the feather, where we find the central dark spot. The whole feather is edged—on the sides as well as the tip—with pale brown. The conditions are here such as plainly to show that the central spot may break up directly into transverse bars.

(2) This same process is shown in a less advanced stage in *Charadrius pluvialis orientalis*.[40] In the longer tertials of this bird the lateral margins of both sides have invaded the dark centers, at several and corresponding levels, to a depth that cuts away about one-half of the center. I have seen such beginnings of bars in still other birds.

(3) The European woodcock[41] (*Scolopax rusticola* Linnæus) is generally marked with transverse bars. The breast, under parts, wings, and back have narrow bars; the primaries have wider transverse bars.

(4) In the great northern diver[42] (*Colymbus glacialis* Linnæus) the back and wing-coverts have dark (grayish-black) centers like those of the turtle-dove, and the feathers are edged with a light-ashy color. Latham (Vol. X, p. 89) says this bird is the *young* of the black-throated loon (*Colymbus arcticus* or *Urinator arcticus*). The young is said to have the same dark centers with light edging.

(5) In the whimbrel or lesser curlew[43] (*Scolopax phaeopos* Linnæus) the scapulars and wing-coverts have dark-brown centers and light grayish edges. Some of the feathers of the side of the body have transverse bars; the upper tail-coverts are also barred. The tail has 7 to 8 transverse bars. The longer primaries are dusky black, marked on the inner web with incipient transverse bars; the next shorter ones are marked on the inner web with semicircular transverse spots; the 4 or 5 shorter quills, next to the body, have no bars or spots. Here we have both dark centers and incipient bars.

TRANSVERSE BARS.

In several species having transverse bars the two sexes have been noted by various observers[44] to show unequal stages of barring.

(1) Around the whole lower half of the neck in the female of the Coromandel teal transverse bars are present, while in the male only a few obscure remnants of such bars remain in this region. Everywhere we find the male in advance of the female and the young. If the female has bars, the male has finer bars, or bars obsolescent.

Latham says of the male: "Lower part of the neck striated across with fine lines of the same (dusky black). . . . The female differs in having the lines on the lower part of the neck broader, and less distinct." The plates cited, however, do not agree with this.

(2) In the gadwal duck (*Anas strepera*) the breast and all of the lower neck are richly "festooned" or "scaled" in the male. The back and flanks are finely transversely barred ("vermiculate"). In the female the lower parts are not barred, and the feathers of the upper side are brown and edged with pale reddish—*i.e.*, these feathers are marked like those of the Japanese turtle-dove.

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[40] *Ibid.*, pl. LXII.
[41] Buffon, Vol. VII, page 462, pl. enl. No. 885.
[42] Buffon, Vol. VIII, page 251, pl. enl. No. 914.
[43] Buffon, Vol. VIII, page 27, pl. III.
[44] Buffon, Hist. Ois., Vols. VI, VII, and IX; Brisson, Ornithologie, Vol. VI; and Latham, Vol. X, are cited as authorities.—ED.

(3) The male francolin presents a good type of transverse bars in its tail; the female is of a more uniform color. In the tertials and in a few wing-coverts the male shows how a dark center, pointed as in the European turtle-dove, can be changed into transverse bars. In these more elongated feathers the lateral light margins invade the dark center at more or less irregular intervals, cutting it nearly to the shaft. The invasions from the opposite sides may, or may not, be directly opposite each other, but in either case a barred effect is produced.[45] Some hawks have the same kind of irregular or intermittently invaded dark center.

The following are examples of the most finely barred feathers:

(4) The long-tailed gray currucu (*Trogon currucui*) has the whole wing (primaries excepted) marked by fine transverse bars, dark alternating with light.

(5) In the red-tailed currucu the wings are very finely barred, dark and light bars alternating. The lateral tail-feathers are also barred, but more coarsely.

(6) In the wild duck (*Anas boschas* Linnæus) the whole under surface of the male, the scapulars, and a portion of the neck are very finely barred—more so than in the currucu. That the bars of the male are not the first color-pattern of the species is shown in the female, where no bars are seen; the feathers of the whole of the under surface and the scapulars of the female have dark centers.

(7) The male Chinese teal or mandarin duck (*Anas galericulata*) has its flanks finely and closely barred (dark and light). The female has no bars; is mostly brown variegated with some white. According to Wood,[46] the male, during May, June, July, and August, loses his crest, his wing-fans, and all his brilliant colors, and assumes a color resembling that of his mate.

Black Crescentic Tips and Transverse Bars.

The quails and pheasants[47] exhibit bars and crescentic tips more or less generally.

(1) *Perdix græca* is a case in which the bars are limited to the flanks and to a few on the abdomen. I think the bars here are plainly a remnant of an earlier more general type.

(2) In the *valley partridge* the tawny feathers of the lower breast are all edged with black crescents. The chestnut feathers of the abdomen (just behind the tawny feathers), are also edged with these black crescents, and here we find "two black bars" in addition to the black edge.

Transverse bars are also common in hawks, owls, woodpeckers, jays, etc., and the simplest form of these bars is the black or dark crescentic tip.

(3) The *rails* are quite generally marked with transverse bars below, and some with crescentic dark tips (see Latham, Vol. IX, pl. clviii, p. 373).

(4) The *undulated parrot* (see Latham, Vol. II, page 179, pl. xxvi) shows fine transverse bars of brown on the head and neck. Crescentic dark tips are present on the body and wings.

(5) The *variegated tinamon* (see Latham's Hist. of Birds, page 219, pl. cxxvii) shows each feather over the back, wings, sides, and thighs tipped with crescentic dark edges. The *elegant tinamon* of Chile is also extensively barred (see Wood's Nat. Hist. of Birds, page 643).

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[45] Sketches illustrating this condition in the francolin were made, but they are not suitable for reproduction. Reference is made to "Bonhote's pamphlet showing a similar mode of origin of the cross-bars."—Ed.

[46] Wood's Nat. Hist., page 728.

[47] See Brisson's figure of Faisan Panaché, Ornith., Vol. VI, pl. xxv.

(6) The *hutum eared-owl* (see Latham, Vol. I, page 307, pl. XIII) has the wing-coverts, scapulars, and back-feathers all broadly "dark on the edges and streaked with the same down the shafts." The feathers on the front-neck, breast, and flanks are transversely barred, each feather showing 3 to 4 bars. Even the primaries and the tail are transversely barred.

(7) In the *little pin-tailed grouse* (Brisson, Ornith., Vol. I, pl. XIX, page 195 of text) the female has bars in the whole back, wings, back and sides of neck, and the upper parts of the head; many of the wing-coverts have the dark crescentic tip. Some of the coverts are crossed by several dark bars which alternate with light ones.

In the male we find an advance which is marked by a total disappearance of bars from a large portion of the feathers. There are no bars on the head, only a few scattered feathers of the back are barred, and many wing-coverts are unmarked by bars. Evidently we must take the female as standing nearer the original type and the male as a departure. All this reminds of the tendency in pigeons to lose the spots and bars.

Many grouse are more or less evenly or uniformly barred, *e.g.*, *Bonasa scotica*. The several species exhibit variations comparable with those found in *Geopelia*.

(8) The *channel-bill* (Latham, Vol. II, page 300, pl. XXXII) has the back and wings of bluish-ash color, each feather tipped with a strong crescentic black edge. All except two middle tail-feathers are transversely barred with white and black bars. The thighs and vent are similarly barred. The black crescentic edges here remind strongly of *Geopelia humeralis*.

(9) In the *Japanese sparrow-hawk*[48] (*Astur gularis*) the female has transverse bars on all of the under parts, while the male has a reddish breast and abdomen, with only a few dark bars on the sides of the body posteriorly, between the legs and tail. The male seems to be most differentiated, having lost nearly all of the bars, a plain reddish tint having been substituted. This reminds of the advance made in *Geopelia striata* over *G. tranquilla*, the central part of the breast having there also lost its bars and become plain vinous.

(10) In the *cuckoo of Malabar* (*Cuculus honoratus* Linnæus) transverse bars and crescentic edges coexist in the same species.[49] The head, neck, and back are covered with feathers edged with dark ashy crescents. "Each feather with two light spots next to the crescent—one on each web." The scapulars and coverts of the wing are marked in the same way. The two light spots are, in some areas, united as one light center at the feather's tip, the feather still being edged with the dark crescent. Brisson does not refer to the dark edge, but both his figure and that of Buffon represent it plainly, and it reminds strongly of the same mark in geopelias.

In the tail-feathers, the tertials, and the long feathers of the wing, the "two subapical light spots" are repeated for the whole length of the feather as "regular transverse bars." This shows that the white spots behave like the light centers in *Geopelia*, the centers either breaking up or repeating themselves, not as spots, but as transverse bars. The whole under side of this bird is transversely barred.

(11) The *emu* (*Dromæus novæ-hollandiæ*) is now considered one of the highest order of birds. Mr. Le Souef,[50] of the Zoological Gardens at Melbourne, reports

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[48] See Temminck and Schlegel, in Siebold's Fauna Japonica, 1850, pl. II.
[49] Brisson, Orn., IV, page 136, pl. XI A, fig. 2.
[50] Emu, Vol. I, Oct. 1901, page 6.

that the "immature plumage" is generally more or less barred, and that in adults (3 or more years old) the bars are lost. This is another case of the disappearance of color-marks. In geopelias we have, similarly, bars in all of the young, but these, after one molt, are lost in different degrees in the different species.

In the emu it seems that the barring varies greatly. Some young may have "no bars," and others may have nearly every feather barred. At the end of the first year, when the barred feathers are shed, they are, as a rule, replaced with feathers "without bars." Occasionally, barred feathers again appear after the first molt, and sometimes they appear again in the third year, "especially on the upper part of the back and the base of the neck." The male seems to lose his bars sooner than the female. Of two young from the same nest, the male lost his bars at the end of the first year, but the female had many barred feathers the second year, and in the third year she had "a few only faintly barred." All of her bars disappeared in the fourth year.[51]

Concentric Crescentic Bars.

These are found in some birds, but they are perhaps plainest in certain species of *Anas*. In some of these species it is clear that the crescentic bar is closely akin to the transverse bar.

(1) Buffon[52] calls attention to the feathers of the neck, breast, and whole under surface of *Anas javana* which are "richly adorned with festoons of black and white." The dark and light crescents alternate and are parallel to the edge of the feather. Near the vent they become less curved and are more like the usual transverse lineation. These concentric semicircles are seen in a less-marked condition in other ducks and in other birds.

(2) In the common sarcelle (*Anas clypeata* Linnæus) the female has dark centers in the feathers of nearly the whole surface, while the male has them only in the mantle. His breast has each feather marked along its tip and lateral edges with a single crescent of black; this is followed by a fairly broad light crescent, and this by a (black?) spot which is variously shaped, but which is plainly in its place as the rudiment of a dark center. From the legs backward to the tail we find narrow transverse bars. In the smaller teal, or common teal of Europe, the transverse barring of the male is carried out on the back and under sides, while the front breast and the lower neck have dark centers in all or most of the feathers.

Transverse Bars in Common Fowls.

Tegetmeier[53] remarks (page 278) as follows on these bars:

The singular character of plumage known as the cuckoo feather, consisting of transverse pencillings of bluish-gray on a lighter ground, is found in many varieties. In England we have Cuckoo Dorkings, Cuckoo Cochins, Cuckoo Polish, Cuckoo Bantams, etc.; in France there are several races with "Plumage Coucou," although the characters are not very distinct; and in America a breed of Cuckoo or, as they are called, Dominique Game, are frequently exhibited. In addition to these breeds there are others which are constantly characterized by the cuckoo plumage, such as the Scotch Grays of North Britain and the Dominiques of America.

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[51] The color of the adult is nearly black, or it may be light grayish brown, or any variation between. One albino is reported, besides several individuals with a few stray white feathers.

[52] Ois., vol. IX, page 275, pl. enl. No. 930.

[53] The Poultry Book, 1873.

The Penciled Hamburghs have the same transverse bars. "In adult cocks there is a general absence of these bars" (page 178). "The markings of the hens is very seldom so correct as in pullets. The pencil-marks are fewer in number in each feather, and in general fade more or less at each molt, especially in the tails and tail coverts" (page 281). "The young cocks, before molting, are penciled much the same as the pullets."

All this would seem to indicate that such transverse bars are not solely due to crossing black varieties with white, but that they are rather a type of feather-marking widely distributed among fowls.

With reference to the origin of the dark and light transverse bars of the American Dominique, Mr. McGrew[54] says (page 8):

"The Dominique color is a combination of black and white. It comes as one of the results of crossing black and white fowls. The mottling of the Java and Houdan and the Ancona are other results of the same methods of mating pure black and pure white fowls together."

In the Barred Plymouth Rock the dark bars are more or less "crescentic" in form, and each feather usually ends with the "dark" bar (page 18). The curve points towards the tip, not towards the base. But in some tail-feathers (of his figures, pl. I) these point backward toward the base of the feather. The broad V-shaped bars are considered "defects" (page 17). The V-shape of bars, with the V pointed toward the base of the feather, is well shown in the male Dorking (Nütz and Ziergeflügel-Rassen, pls. II and XXIII); the hen shows a broad V pointed towards the tip.

Concerning a law of the multiplication of bars, it may be observed that the bars in *Geopelia* extend to near the middle of the feather, being strongest near the tip and weakest towards the inner limit. In the Plymouth Rock the breeder demands distinct bars for the whole length of the feather.

The bars, then, may be supposed to have begun at the end or near the end of the feather, and to have multiplied towards the inner end of the feather's base. The highest development is with the oldest bar, but it may shift forward so that the second or third bar may be the strongest.

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[54] T. F. McGrew. American Breeds of Fowls, I, The Plymouth Rock. Bull. 29, Bureau of Animal Industry, U. S. Dept. of Agriculture, 1901.

Note.—The manuscripts used in the preparation of this chapter were found in folders designated as follows: A 14, Em 1, O 4, 0010, 0014, 0018, W 4, W 11, W 13, WW 2, WW 9, Z 7, Z 11.—Ed.

CHAPTER VIII.

FRILLS AND FUNDAMENTAL BARS AS PLUMAGE CHARACTERS.[1]

In pigeons *domestication* leads to inactivity, and to less strong development of the bones and muscles and to greater variation in form and length of feathers. Witness the elongated and fluted primaries, the frills of the wing and breast, and the ruffles and hoods and similar structures so often found in common pigeons. The tails of fantails, the pouting of pouters, and the excessive cooing of males are further examples of characters favored in their development by domestication and inactivity.

As instances of domestication leading to lengthening of feathers we may cite the following cases: I now have a rock-pigeon, obtained from Dover, England, some four years ago. She is of typical slate-color with two black bars. She became lame while being bred with an owl pigeon, both being kept confined in a pen. Lameness first came on just before eggs were due. She has never recovered, although she is now able to fly. The remarkable thing about her is that her wings seem to have lengthened quite to the end of the tail. This lengthening is here associated with weakness. The Tosa fowl of Japan would seem to be another example of domestication leading to an elongation and multiplication of feathers. Here the feathers are said to "grow throughout life," and they certainly continue to grow beyond the usual growth period.[2] Again, in common fowls the hackles show some tendency to multiply and elongate.

FLUTED AND FRILLED WING-FEATHERS.

I find among the wild species and domestic varieties of pigeons occasional individuals which show wave-like foldings, or fluting, near the tips of some of their primaries. The appearance of these flutes is shown in plate 69. Figures A and B are from a dark primary of the wild *Columba guinea*, and afford a comparison with the corresponding primary, of white color, of a guinea-marked common pigeon (mondain, figs. C, D). These flutes are more emphasized in the domestic. Such undulations when present on the primaries have a restricted distribution. They are best developed on the *longest* feathers,[3] on the *broader* web, and on the *oldest* part of the feather, the tip.

In the more anterior feathers of the wing, particularly in the coverts, one occasionally (as in the case of flutes, just described) finds a variation from the normal

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[1] Frilled feathers were under observation for a period of 12 years, and the fundamental bars for a period of 7 years, but the author did not summarize the results of his studies on either of these characteristics. He has stated some of his conclusions, however, and these, together with his carefully prepared illustrations, are of interest and value, even though incomplete. It should be noted at once that the term "frill" is sometimes used by the author to describe either of three somewhat different conditions, or, better, to describe what he considers the same condition—weakness—exhibited in three different ways, or on three different body regions. All of these concern a twisting or curling of feathers. The modification of the elongated primaries he sometimes calls "fluting"; that of the wing-coverts, etc., is the true "frill"; the "crease" of the throat, or of the throat and breast, sometimes has recurved (frilled) feathers in it and sometimes not. I have taken the liberty, in some places, to restrict the terms "flute," "frill," and "crease" to the regions just indicated.—Ed.

[2] Davenport (Inheritance in Poultry, Carn. Inst. Wash. Pub. No. 52, 1906) finds that when Tosa is crossed with White Cochin Bantams (short tails) that "the males of the first generation have the tails abnormally long"; and that "the long-tailed characteristics of the male have been inherited, but in a reduced form."

[3] For a detailed description of one such series of primaries see explanation of plate 70, figure A.—Ed.

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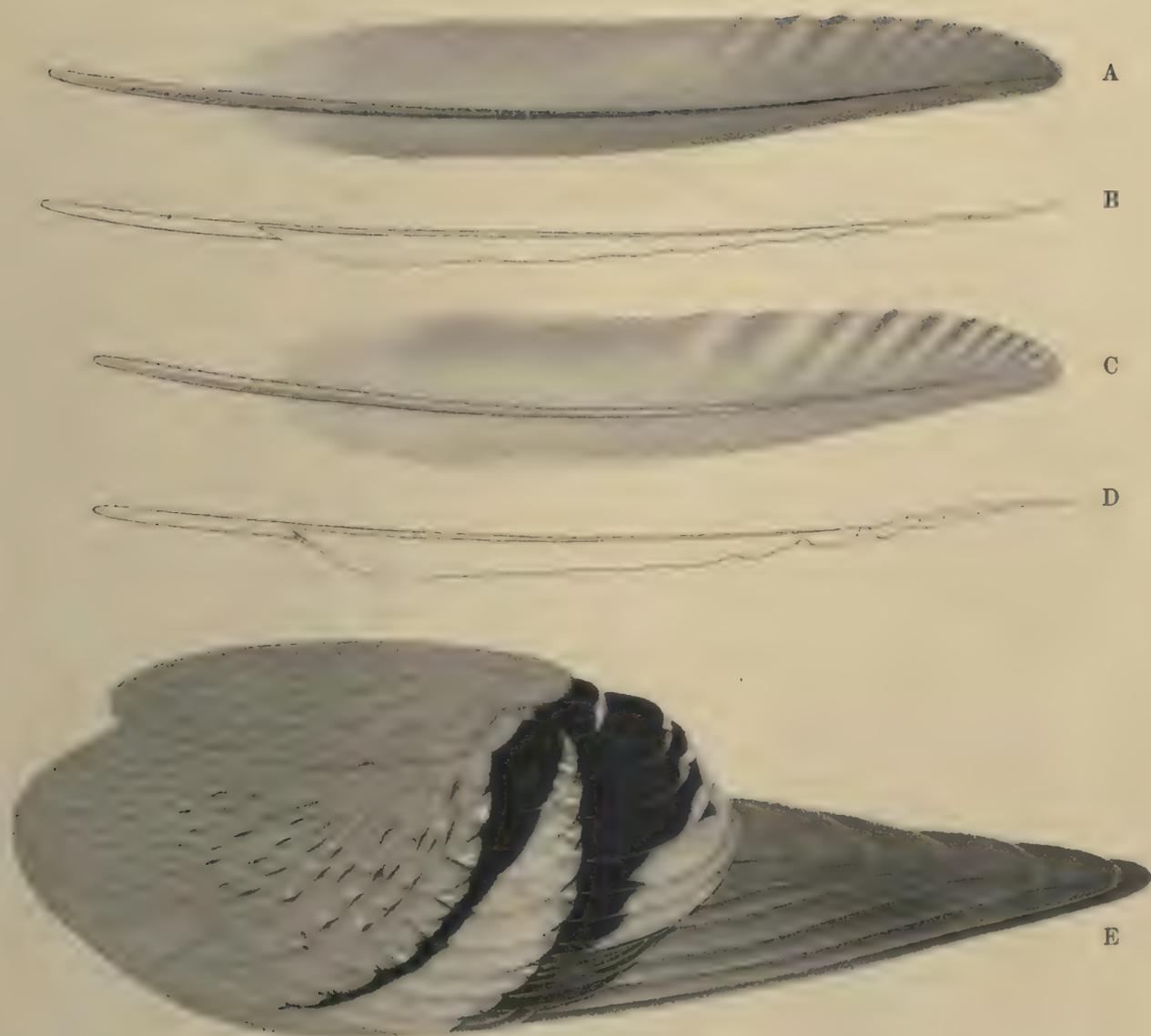
A, B. Third left primary (dark) of *Columba guinea* (of pl. 70, fig. B). The fourth primary of the
  left side was about the same, but was not taken, as it was imperfect. Undulations (flutes)
  restricted to region of tip and to wider (upper) web; about 8, not deep.
C, D. Fourth left primary (white) of common pigeon (mondain) of pl. 70, fig. A. Undulations
  (flutes) similarly restricted, about 10, deeper. Toda del., June 1905
E. Frilled wing-coverts in an adult female owl-rock hybrid. Toda del., June 1905. Shows plain
  rudiments of frills. Color of bird rather pale; the wing-bars somewhat reduced. This bird
  lame, the right wing touching the ground.

feather structure in that the tips are raised, or slightly recurved. An early stage of such "frilled" feathers is shown in plate 69, figure E, the bird there shown being an owl-rock hybrid of rather pale coloration and with wing-bars somewhat reduced. This bird illustrates the fact that the frills *may* appear in the coverts while the primaries remain free of flutes,

Common Pigeon (Mondain) and Guinea-Pigeon (Columba Guinea).

A male common pigeon obtained from a dealer was found to have fluted feathers. This bird was of medium size and with nearly all the primaries of *white* color. The ground-color of the coverts was nearly black, with gray triangular spots at tips of feathers (pl. 70, fig. A); these were remarkably similar to those seen in a *C. guinea* with fluted primaries, with which the common pigeon is compared. A large white patch was present on the upper part of the breast; the rump was white, and the tail was of the usual dark color.

This bird shows us an early stage in the development of frills or curls in three of the upper long coverts. The secondaries in the folded wing show plainly a wavy undulating appearance in the lower web, there being from 3 to 5 of these folds or flutes in the apical inch of each feather. The tertials show only 1 or 2 such folds, and these are not so deep. The fourteenth, fifteenth, and sixteenth long coverts show the same feature at the tip of the feather, where the fold in 14 is about 2 mm. high and 2 mm. wide, showing a rather regular dome-shaped outline when seen from behind. In 15 the fold is nearly twice as high, with the sides pinched up close and a slight twist at the summit, thus presenting a quite different figure or structure. In 16 we have a much broader elevation and a trifle less height than in 15, which thus presents still a different figure. In 17 there is no elevation.

In the primaries, where the lower web is narrower and stiffer than in the upper, we see only faint traces of undulations in the lower web, but quite strongly marked ones in the upper webs, in the *terminal portions*. The details of the modification on the several primaries, as these are recorded in the legend of the figure (pl. 70, fig. A), show that the longer feathers have the stronger fluting.

In the Guinea-pigeon the upper (inner) webs of the primaries seem to be longer than the lower, and are folded alternately in and out, or fluted—sinuous, so to speak (pl. 70, fig. B). Seen from above, the upper edge takes the form of an undulating line (pl. 69, figs. A and B). The fluting extends over the distal third or less. In the illustration this is shown to be less emphasized than in the common pigeon; in the latter the flutes are a little deeper and more extended on the feather. This fluting occurs just where the feather is most strongly bent in flight, and evidently permits of considerable upward and downward movement without causing any break in the web between the veins.[4]

Flutes Pass into Frills.

The common pigeon described above exhibited a tendency to the peculiar twisted and recurved condition seen in the race of frill-back pigeons, in the upper second-aries, tertiaries, and in a few of the posterior scapulars; in addition to these, about three of the upper long coverts were also affected. This twisting occurred near or

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[4] I notice a similar folding in the primaries of a *Calænas nicobarica*; in one of several *Turtur chinensis* the fluting is quite marked; while in the others it is scarcely to be recognized, or is quite absent; in a green-winged pigeon, in hybrids between domestic pigeons and Japanese turtles, and between *Zenaidura* and the blond ring-dove; in fact, it has been quite generally observed in certain individuals of both wild and domestic pigeons.

at the tips of all these feathers, and it seems to be of the same nature as the flutes of the primaries—*i.e.*, due to unequal development of the web. It is the lower web and the tip of the feather—in all except the primaries, in which it is the upper web—that is modified. These feathers show plainly that the fluted condition passes by degrees into the frilled condition.

The Association of Frills with Other Evidences of Weakness.[5]

Photographic illustrations have been prepared to assist an understanding of the conditions presented by the following cases:

(1) An adult female homer (E) which was hatched "late in the season" (November 15, 1908) has a number of small frills on the wing-coverts (pl. 71, figs. B, C) and has fluted primaries. This bird came from a mating in which the wing-bars were

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[5] The author seems to have made but little special study of the inheritance of the small or relatively rudimentary "frills" which are discussed in this chapter, though the references to the homers which are referred to at this point have a bearing on the subject. The reason for his scant attention to the behavior of the character in heredity is easily found in his point of view, which, in short, was that the basis for production of frills exists in most or all pigeons—perhaps in most birds—and that "weakness," perhaps particularly the weakness associated with domestication and inactivity, seems to magnify the exhibition of the character. It therefore seemed necessary to examine the *points of weakness* in the frilled individual in order satisfactorily to account for its presence. The question of the heredity of these early stages of the character—a thing probably not easily proved in view of the important rôle of *strength* and *weakness*—possibly seemed of less importance, because higher grades of "frill" have been attained in pigeons, fowls, canaries, etc., and are there well known to be transmitted from parent to offspring. Inbreeding is one such cause of weakness, and white color is one evidence of it. The several conditions which make for weakness in the offspring of pigeons are fully treated in Volume II.—Ed.

Explanation of Plate 70.

A. Adult male common pigeon (mondain) from dealer. × 0.8. Hayashi del., Jan. 1900.

Flutes or folds in several primaries (see below) in lower webs of tertials and secondaries; these are terminal in three long coverts giving rise to rudimentary frills. Flutes thus pass into frills.

Color almost black, with pale-gray chequers like those of the guinea-pigeon. Fluting strongest on the longer (left side) primaries, as follows:

First shows only faint trace of them in distal 25 mm.
Second shows decided folds for terminal 37 mm.
Third shows about same number, but slightly stronger.
Fourth shows about 7 folds in 31 mm., about equally strong.
Fifth shows about 6 folds in 25 mm., still more shallow.
Sixth shows about 5 folds in 25 mm., still more shallow.
Seventh shows about 5 folds in 25 mm., but folds a little less marked and smoothed out before reaching the mid-rib.
Eighth shows about 4 open shallow folds near tip.
Ninth shows only faint traces.
Tenth shows only faint traces.
Primaries 9 and 10, dark; all others white.

B. Adult male guinea-pigeon, *Columba guinea.* × 0.8. Hayashi del., Jan. 1900.

The color shown is hardly that of the bird, but the triangular spots are practically the same. Coverts less in number than in the domestic pigeon. The long coverts have the shape and arrangement characteristic of wild pigeons. Flutes or folds seen in primaries. In a second specimen I could scarcely see any trace of these folds. They are here less developed than in the guinea-marked common pigeon shown above. The flutes are present in the primaries, without any sign of modification of any of the anterior feathers of the wing.

Explanation of Plate 71.

A. Adult male common pigeon, red with white primaries and smaller guinea-marks. From a dealer in 1906; in 1909 noted frills on the wings; primaries fluted.

B. Adult female homer (E) hatched Nov. 15, 1908; photographed Sept. 1909.

From a mating in which bars were being narrowed in the young. She had a half-sister (nearly white) and a half-brother with wing frills, and still another half-brother (H 1) with a breast frill.

C. Adult female homer (E) same as above. Four small but plain frills seen from behind wing (held in hand).

PLATE 70
142ª
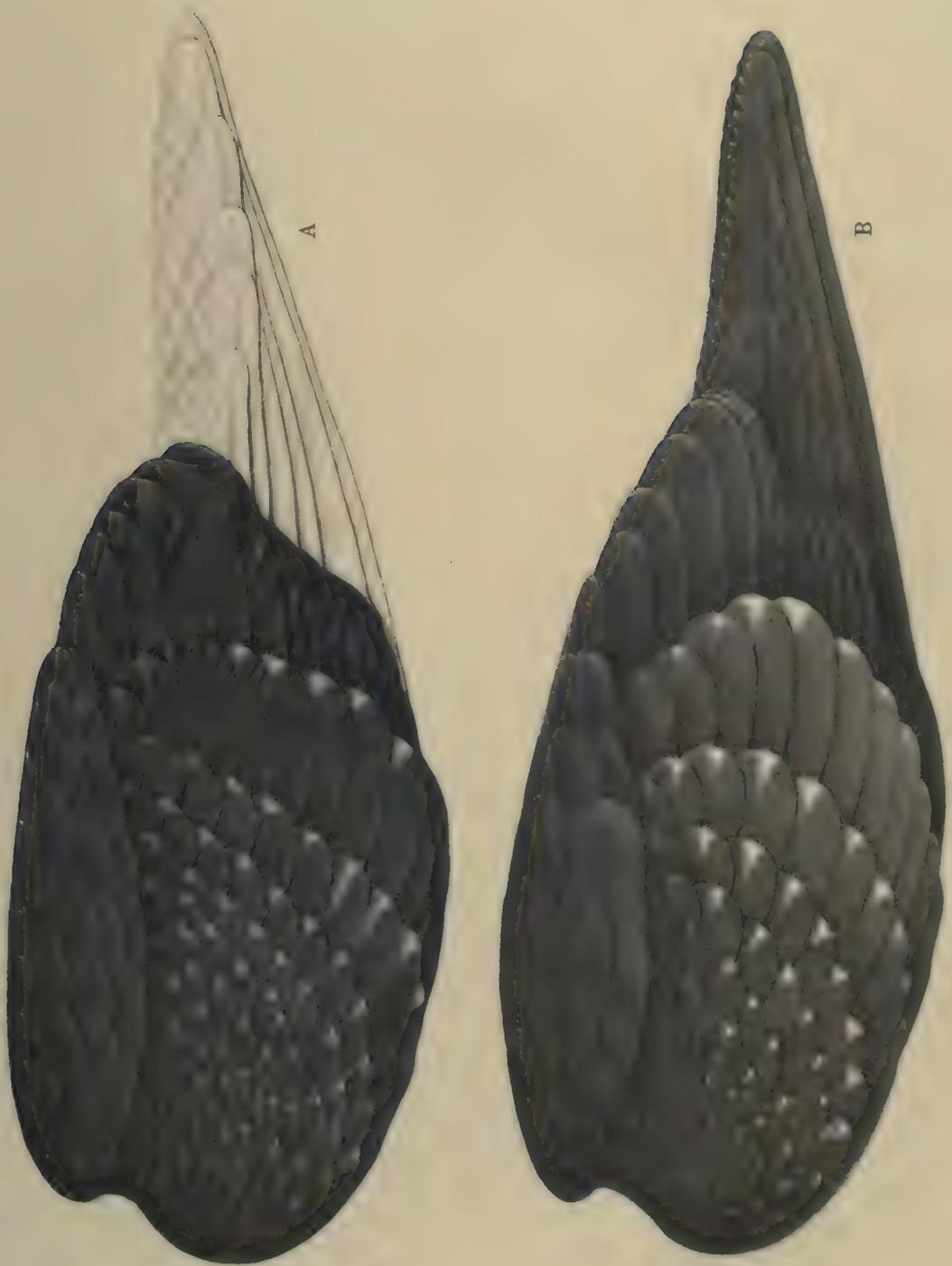
A. Adult male common pigeon (muondain) from dealer. × 0.8. Hayashi del., Jan. 1900.
B. Adult male guinea-pigeon. *Columba guinea.* × 0.8. Hayashi del., Jan. 1900.

PLATE 71

A. Adult male common pigeon, red with white primaries and small guinea-marks. From a dealer in 1906; in 1909 noted frills on the wings; primaries fluted.

B. Adult female homer (E) hatched Nov. 15, 1908; photographed Sept. 1909.

C. Adult female homer (E) same as above. Four small but plain frills seen from behind wing (held in hand).

being narrowed in the young; her nest mate was a *sister*, and *two females from a clutch* show weakness in parents, and weakness in parents leads us to expect it in the young. She had a half-sister which was nearly white; a half-brother with wing-frills, and still another half-brother with a breast-frill (see table 75, Vol. II). When paired with a weak (immature) male this homer produced two young, one of which was much whitened[6] (see pl. 14, Vol. II).

(2) An adult male common pigeon (red with white primaries and with small guinea-marks) was obtained from a dealer in 1906. In 1909 I notice this bird has small frills on the wings; they are quite small, but visible over the whole wings. The primaries are strongly fluted (pl. 71, fig. A). (A son of this frilled male, by a black and guinea-marked homer, was the immature mate of the above-described homer (E); the pair produced two young, one of which was much whitened.—Ed.)

(3) Another case of frills was found in *inbred* pouters (table 80, Vol. II), where the colors of several of the offspring were much lightened (see pl. 17, Vol. II).

THE BREAST-CREASE AND FRILL.

In the median line of the throat and breast a notable variation from the normal plumage condition is sometimes found. This variation is seen in both old and young, and concerns the inadequate growth or placement of the feathers which should fill out this area. Some of the feathers in, or bordering upon, this tract are often re-curved or frilled.

The Breast-Crease in Hybrids from the Common Pigeon (¾) and the Japanese Turtle (¼).

Of two young hatched from the same nest in February 1900, one (1) shows a breast-crease, while the other (2) is perhaps nearly normal. At the age of 18 days, the color of (1) is black, and (2) is more nearly the color of the male parent, but its dark spots are more definite, approaching the chequered pattern of *Columba livia*.[7]

The variant (which will be spoken of as *one*, in contrast with *two*, the normal) has a remarkably wide median tract, without any visible feathers or pin-feathers within the region marked by the dotted lines on text-fig. 25. The feathers of the breast were well unfolded and covered over much of the unfeathered tract, closing up for about an inch of the middle breast, but leaving a naked area above and still another below. The line of junction of the feathers formed a deep crease or groove. This bird had very scanty down at the time of hatching. *Two* had more down, and the unfeathered tract is not more than one-fourth of the width seen in *one*. It seems to me that *two* represents the condition generally seen in domestic pigeons, while *one* is certainly a wide variation. In *two* the feathers come more smoothly together; though they are behind *one* in unfolding. I find that the unfeathered tract in *one* agrees in width with the condition seen in the young "African owl" shown in text-fig. 28.

When nearly 4 weeks old, *one* was able to fly. The unfeathered tract is then represented (between the dotted lines in the illustration, text-fig. 25, figs. C, D) as of the same width as before; but beneath the feathers of part of this area I find pin-feathers coming in, advancing from the sides toward the middle, some of the outer ones just beginning to unfold. The middle and wider portion of the tract still has only a few pin-feathers close to the older feathers, the central part for about an inch in length being still quite bare. Above and below this naked area pin-feathers

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[6] Another homer (4) and his daughter (8) both have frills on the inner long coverts.
[7] The general shade of the spots very strongly reminds of the same spots in the young of the passenger-pigeon.

have appeared (few in number over the whole surface), but less advanced in the middle than at the sides. At this age *two* has a smooth breast and a short crease above of about 1 inch in length, and shallow as compared with *one*. *Two* is larger
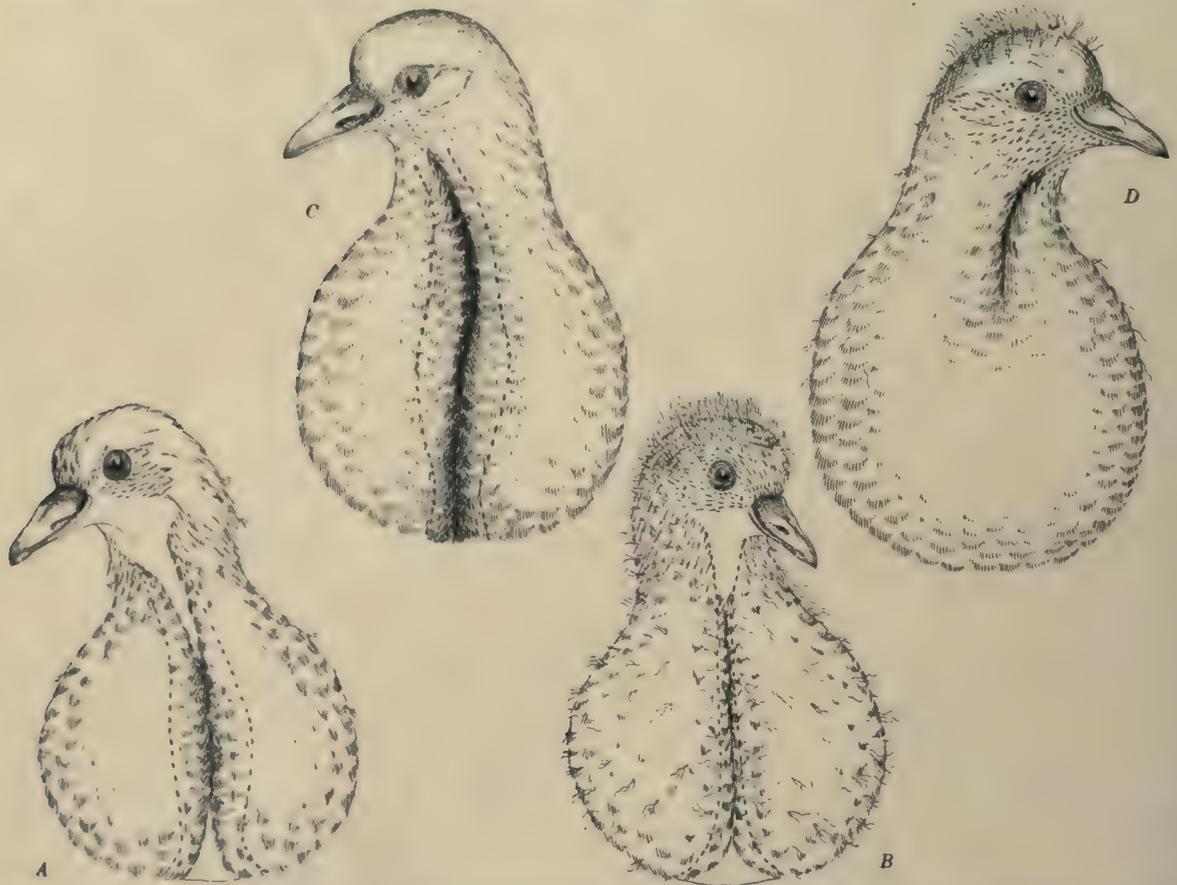
TEXT-FIGURE 25.—The breast-frill in juvenile hybrids, hatched February 16, 1900. 18 days old. Same size. Wilson del., March 6, 1900. Sire, a hybrid from common pigeon × *Turtur orientalis*. Dam, a common pigeon.

A. Hybrid (No. I 1) is black in color. A remarkably wide median tract, without any feathers or pin-feathers in sight, within area marked by dotted lines. The feathers of the breast were well unfolded and covered over much of the unfeathered tract, closing up for about an inch of the middle breast, but leaving a naked area above and another below. The line of junction of feathers formed a deep crease or groove. Very scanty down at time of hatching.

B. Hybrid (No. I 2) was less black. It had more down that its nest mate, and the unfeathered tract is not more than one-fourth the width seen in No. I 1. No. I 2 seems to me to represent the condition generally seen in domestic pigeons, while No. I 1 is certainly a wide variation. In No. I 2 the feathers come more smoothly together; they are behind No. I 1 in unfolding.

C. Same as A above, age 26 days. × 1. Wilson del., March 14, 1900. Hybrid No. I 1 is now nearly 4 weeks old and can fly. The unfeathered tract (between dotted lines) is represented as same width as before, but within this pin-feathers are coming in, advancing from the sides toward the middle—some of the outer ones just beginning to unfold. The middle and wider portion of the tract still has only a few pin-feathers close to the older feathers—the central part for about an inch in length being still bare. Above and below this bare area the pin-feathers have appeared (over the whole surface, though few in number), less advanced in middle than at sides.

D. Hybrid No. I 2 has a smooth breast and a short crease above, about an inch in length, and shallow as compared with No. I 1. No. I 2 is the larger bird, and though strong and robust is behind its mate in feathering; it can not yet fly.

than *one*, and is a little behind its mate in feathering, though strong and robust; it can not yet fly.

Two other hybrids of this same fraternity show the breast-crease. One of these was of white color (text-fig. 26, fig. C), and the other (text-fig. 27, fig. A) was black.

I find that the maternal grandmother (*Turtur orientalis*) of these birds shows the same crease to nearly the same extent.

THE BREAST-CREASE AND FRILL IN OTHER HYBRIDS AND IN FERAL SPECIES.

A hybrid (B 2), from a male mourning-dove and a female *risoria* × *alba* hybrid, shows most of time, but not continuously, a short crease or dimple below the chin
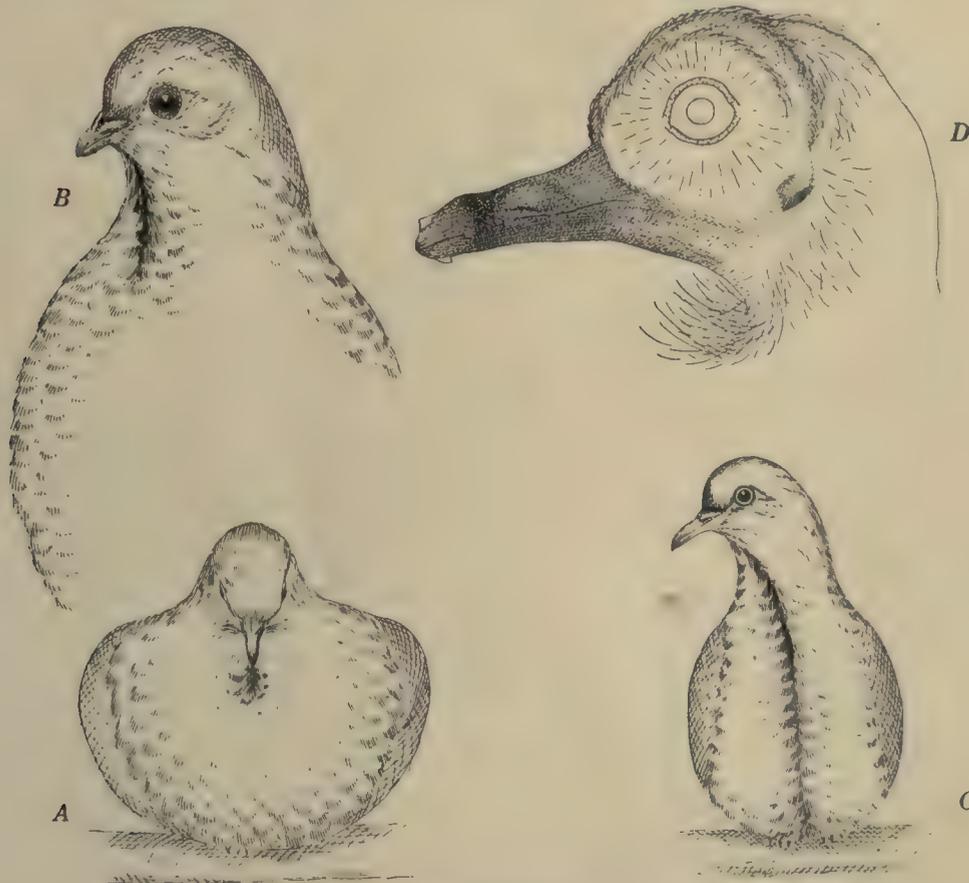
TEXT-FIGURE 26.

A. Hybrid; mourning-dove × ring-dove (B2); hatched Aug. 1, 1898. × 1. Wilson del., March 17, 1900. Sire, *Zenaidura carolinensis*; dam, hyb. *St. alba-risoria* × *risoria-alba*.
  Most of the time, but not continuously, shows a short crease or dimple below the chin. The dimple tends to persist, but the projection of one or two feathers is a purely transient phenomenon. It is not due to feathers being ruffed by external means, but to the position which they assume automatically and occasionally, showing that the condition is such that a very slight variation—such as arises spontaneously and disappears as readily—expresses itself now in projecting feathers, now in feathers lying more smoothly.
B. Adult *Geopelia striata*. × 1. Wilson del., March 1900. Showing a full breast crease. This is transient and is sometimes visible only in one or another part.
C. Same fraternity with three-fourths hybrid of text-fig. 25; white (B2), hatched Aug. 24, 1899. Wilson del., March 1900. This bird shows quite uniformly a crease of about the length indicated. I find that its paternal grandmother (*Turtur orientalis*) shows the same crease to a similar extent.
D. Juvenal *Geopelia humeralis*, just hatched. × 4. Hayashi del., Aug. 1904. The down feathers of the upper throat curve upward. If the later feathers should be similarly oriented they would form frills.

(text-fig. 26, fig. A). To-day a single feather on each side is tipped edgewise so as to project like frill-feathers, although not strongly. These feathers were noticeable for most of the day, but later were smoothed out, leaving only the dimple. The dimple

is fairly persistent, but the projection of one or two feathers is a purely transient phenomenon. It is not due to feathers being ruffed by external means, but to the position which they assume automatically and occasionally, showing that the condition is such that a very slight variation—such as arises spontaneously and dis-
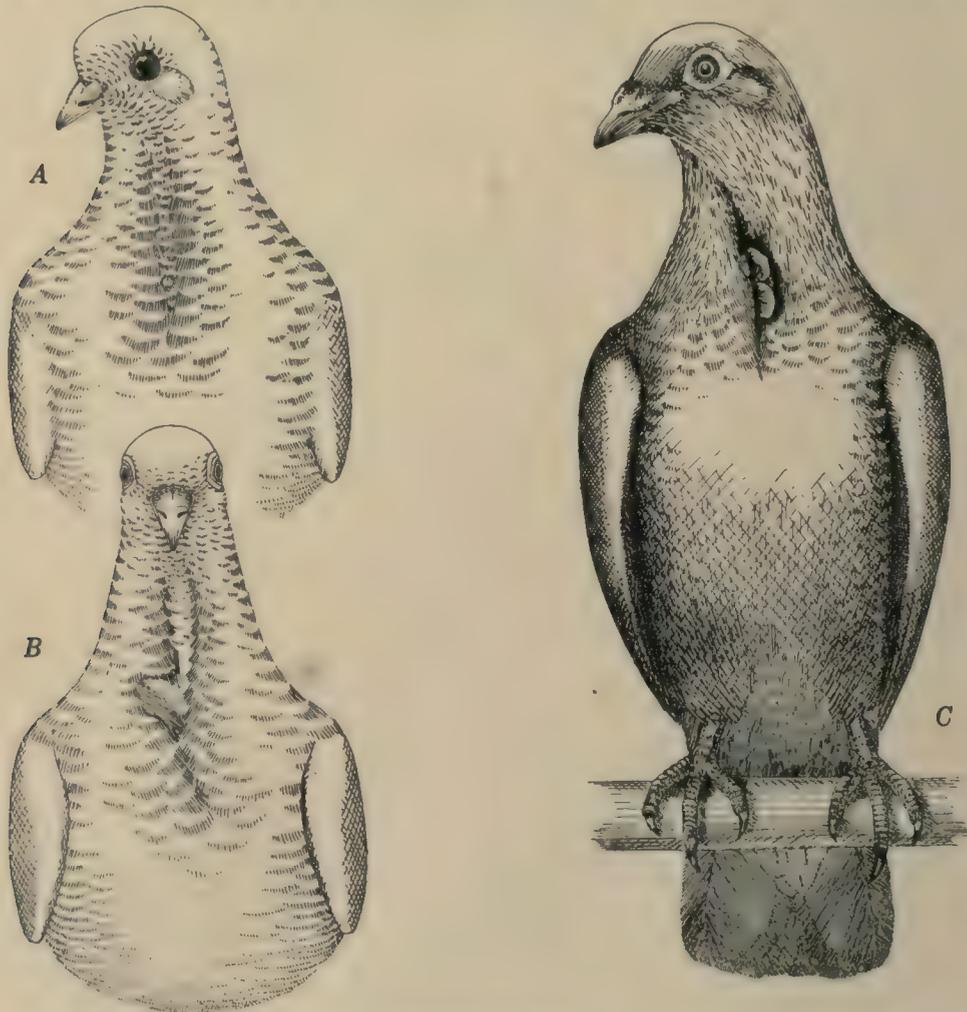
TEXT-FIGURE 27.

A. Juvenile, three-fourths hybrid, same fraternity with text-fig. 25; age 80 days; black (I 1), hatched Feb. 16, 1900. × 0.5. Wilson del., May 7, 1900.

This bird was beginning first molt. When the breast-feathers are held in open and loose order a median streak of feathers is seen as shown in the drawing. When the feathers are held in close order these feathers are covered up, but still there is usually a distinct median line formed by the meeting of the feathers from the two sides. The medium streak of feathers covers the part previously naked, these feathers coming in considerably later than the other breast-feathers. The median feathers are somewhat smaller and more thinly set, hence lie deeper than the other breast-feathers. Towards the beak the median line of feathers widens somewhat, and the feathers are evidently lighter in color. At times one or more of the breast-feathers may be tilted outwards, somewhat as a result of crowding against the middle feathers.

B. Juvenile homer (C 2), age 66 days; in first plumage. × 0.5. May 11, 1900.

The condition of breast is similar to that seen in figure A above, but one of the mid-tract feathers turns up and out, frill-like, and a pin-feather just above it turns upward. The space just above the unfolded feather is almost naked and the tract is thinly covered with small feathers. This homer has gray wings and black bars, but no chequers.

C. Adult male homer (B1), chequered. × 0.5. Wilson del., March 1900.

This bird is the father of the young unchequered homer of figure B. He shows two or three frilled feathers. Sometimes these are smoothed out so that the breast is without any frill, but it then remains creased. Usually, however, a few feathers are turned outward and more or less upward.

appears as readily—expresses itself now in projecting feathers, now in feathers lying more smoothly.

Another similar hybrid shows similar conditions, except that the median crease extends down the whole throat and breast (text-fig. 29, B, C), and more feathers may sometimes be curled or tilted out of position.
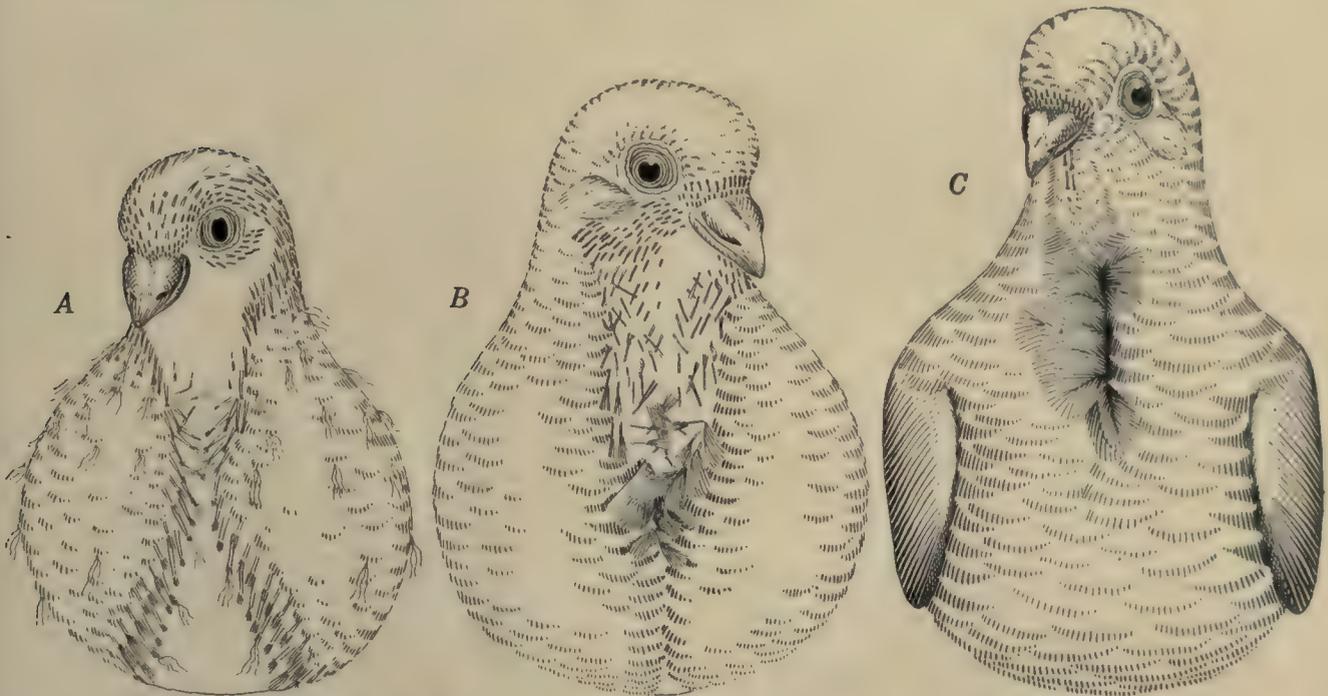
TEXT-FIGURE 28.—Three stages of frill and feathering in a juvenal African owl-pigeon (C 2) hatched May 4, 1900. × 1. Wilson del., 1900.

A. Age 17 days, shows the wide median tract, which was unfeathered at first and in width and appearance much like that seen in the common × *orientalis* hybrid of text-fig. 25.   Pin-feathers are appearing, and a few are turned mediad and a little upward; about 5 pins point upward.

B. The same, May 30, 1900; age 26 days.   The mid-tract still bare above; under base of beak this tract is 12.5 mm. wide; but the sides of this area are covered with pin-feathers. A few pins on each side are turned upward; some turn up and inward.   In the very center of this mid-area may be seen two pins parallel, but turned in opposite. Lower down the side-feathers meet in middle line; and just above place of meeting are about 9 feathers of the mid-area turning in different directions. The upper side-feathers are pushed apart in the figure, to show the area covered with pin-feathers. *In situ*, the feathers are 15 mm. apart near the middle height, *i.e.*, midway between the beak and the place where the feathers first meet in middle line.

C. The same, June 9, 1900; age 36 days. The bare under-chin area of the 26-day stage is now covered, some feathers still showing there as pins.   Lower on throat and upper breast the oppositely directed pins of the earlier stage have expanded and (still in opposition) form a frill.

In an adult *Geopelia striata* I have seen a full breast-crease showing something of the same transient nature (text-fig. 26, fig. B).   In a just-hatched *G. humeralis* I found the down feathers of the throat curved upward—the contrary of the normal slant of the later feathers of this region—and presenting a bristling appearance.

THE BREAST-CREASE AND FRILL IN COMMON PIGEONS.

An adult male homer (B 1) shows a breast-crease and a small breast-frill. This breast-frill is somewhat of a puzzle, as neither parent shows any trace of such a thing.[8] It may be, however, that all pigeons are "liable" to this. It corresponds

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[8] A young of this homer—the next bird to be described—has the breast-frill.—ED.

to the dividing-line that is often seen in young pigeons; but in adults this fold is usually smoothed out, either by the feathers of the two sides coming together or
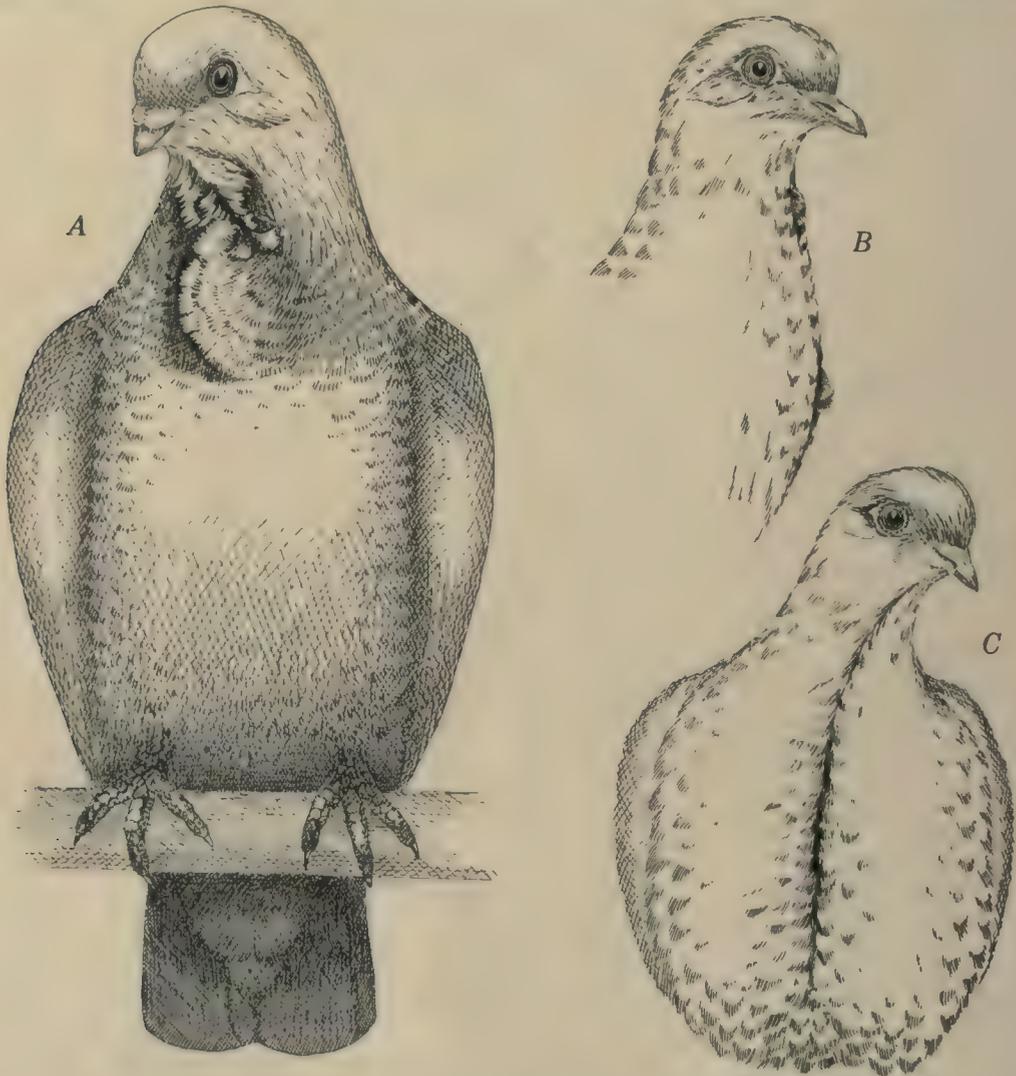
TEXT-FIGURE 29.

A. Adult male, African owl. × 1. Wilson del., March 1900. In this owl-pigeon the frill is more highly developed than in the homers shown in text-fig. 27. Some feathers of the left side of the upper breast turn strongly towards the right side. Just above this misdirected mass of feathers are two imperfect rows of feathers which curve outward—to right and left—away from the median line. These variant feathers arise from the median tract and develop later than the lateral feathers.

B. Adult hybrid, *Zenaidura* × *Streptopelia risoria*. × 1. Wilson del., March 1900. Usually there is a well-marked crease running through whole breast. At times one or more feathers at different points are tilted up edgewise.

C. The same. The profile view shows the condition seen at one time.

by new feathers coming in, so as to make the tracts coalesce and form one even surface. This pigeon has sometimes only 2 or 3 feathers twisted or turned out at the middle height of the breast; above this point the median seam or fold extends well up the neck, much as it does in young birds in first plumage. Sometimes more feathers—3 to 5—are turned out into the frill. Apparently there is some slight con-

dition here that favors this position of the feathers. They are certainly the same feathers that are normally present, but here for some reason they are turned or curled out of position (text-fig. 27, fig. C). I did not notice this frill in the bird until it was about 4 weeks old, and I think I should have done so if it had been present; the bird was often looked at in the nest, and I sometimes took it in my hands. This fact makes the recurving or twisting of the breast-feathers seem, in some way, a result of the later development. I find that the wing-bars are obsolete in this bird, and that the black or dark colors are everywhere reduced below that of either parent.

One of the offspring (C 2) of the above-described homer at the age of 9½ weeks showed a similar condition of the breast. Here a feather in the pin-stage, lying just below a frilled or upturned definitive feather, was found turned upward (text-fig. 27, fig. B). This homer has gray wings and black bars, but no chequers.

A juvenile African owl-pigeon which showed a very wide median unfeathered tract was figured at three different juvenile stages (text-fig. 28). This bird hatched, from the second egg of the clutch, on May 21. At the age of 2½ weeks the wide median tract, which was unfeathered at first, has several pin-feathers appearing, and a few of these are turned mediad and a little upward; about 5 pins point upward.

At the age of 3 weeks and 5 days (fig. 2) the mid-tract is still bare in the upper part of the earlier-unfeathered area; this quite bare region is nearly 13 mm. broad at a point just below the base of the beak; the sides of the former naked area are now covered with pin-feathers. A few pins on each side are turned upward; some turn up and inward. Directly in the middle of this mid-area may be seen 2 pins parallel, but turned in opposite directions. Lower down, in what was formerly unfeathered area, the side-feathers now meet in the middle line; and just above the place of meeting are about 9 feathers of the mid-area turned in different directions.

When 5 weeks old (fig. C) the last pin-feathers necessary to cover the naked space under the chin are in place. On the lower throat and upper breast, however, a part of the crease persists; and some of the upturned and variously turned feathers, which should smooth and fill the crease, are expanded into a frill.

In an adult male owl-pigeon of light silver color the frill is more highly developed than in the homers described above. The feathers of the left side of the upper breast here turn strongly towards the right side. Above this shell-shaped mass of feathers are two imperfect rows of feathers which curve outward, or away from the median line (text-fig. 29, A). These curving feathers are evidently feathers of the median tract, and it has already been noted that the feathers of this area develop later than the lateral feathers.

ON FRILLED OR FRIZZLED RACES OF BIRDS.
The Pigeon.

The frill-back race or variety (*Columba hispida*) of domestic pigeon is described as follows by Fulton and Lumley:[9]

This pigeon belongs to the German toy class, but on account of the conspicuous reverse growth of the feathers, it frequently has a separated class allotted to it in exhibitions. . . . The legs are rather short and closely grouse-muffed. The flights are quite long, and fluted on both webs, but more strongly above than below.

Book of Pigeons, Cassell & Co., London, 1895, page 481.

The more usual colors are "grizzled blues and sandy reds or mealies." The feathers appear as if they had been curled evenly with curling-tongs; they are longer and more pliable than in other pigeons. "The longer these feathers are, and the more evenly curled or frilled, the greater is the value of the specimen."

According to Mr. Prütz,[10] the feathers of this race are not smooth and rounded at the end, but terminate in a point which is rolled up into a frill or curl that looks forward. This author recognizes the identity of the "frills" with the "undulations" ("sanfte Wellen") or flutes of the primaries, but he does not attempt to show that such undulations are very common, and that they represent the initial step to this interesting feather variation.

Two varieties of this race are distinguished: (a) the Hungarian or Australian frill-back (smooth head, muffed, and with frills longer than in b); (b) the Dutch or French frill-back (frills not so high as in a, eyes are pale yellow, head has shell-crest or hood, and the legs are naked or muffed).

De Roo[11] points out the differences between pigeons with "frilled" plumage and "silky" plumage. Of the "silky" variety (Pigeons frisés, ou de soie) he asserts (pages 140–143) that the feathers are "similar to those of the negro hen of Mozambique" ("poule de soie"). This race does not have the power of flying, the barbs of the feathers being separated, hair-like, and curled, resembling hair rather than feathers. It is further stated that the peculiar structure of the feathers—barbs long and not adherent—is found in "all races of domestic pigeons, and can not therefore be a race character."[12]

The true frill-backs (Pigeons frisés milanais) are not to be confounded with the preceding. The frill-backs have only the feathers of the wing and back frilled, while the Pigeons frisés, ou de soie, have a very fine silky or hairy plumage, the barbs of the feathers being separated, hair-like, and falling like fringes of silk. The frill-back has the head crested or smooth, the legs feathered or naked, and its feathers recurved or curled in a spiral. This race can fly well, and can find a part of its own food if compelled to do so.

<div align="center">FOWLS.</div>

Tegetmeier[13] (page 268) says:

Frizzled fowls, or those with feathers more or less completely recurved, are not uncommon in many parts of the East. In a large collection of the domesticated birds of nearly every country in the world, formed by Mr. C. Darwin, and placed at our service, many specimens occur with recurved feathers, some with short frizzled hackles only, and others with the peculiar plumage passing over the entire body.

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[10] Mustertauben Buch, plate pages 64, 65; description pages 67, 68.

[11] Monographie des pigeons domestiques, Paris, 1883.

[12] "Par leur conformation, ces oiseaux se rattachent à toutes les races de pigeons connues, car, à ma connaissance, il existe des pigeons trembleurs paon de soie, Columba laticauda setacea; des pigeons pattus frisés, Columba pedibus crispa, en allemand, wollechte Tauben; des pigeons bagadais bataves de soie, Columba tuberculosa setacea batava, etc., etc. La qualité d'avoir les barbes des plumes dècomposées, longues et non adhérentes entre elles, ne saurait donc être considérée comme une caractéristique de race, puisqu'on rencontre dans toutes les races de pigeons domestiques des individus ou des variétés revêtus de ce plumage." De Roo says that Aldrovandi regarded this pigeon as a true species, and named it Columba crispis pennis. I find that Boitard and Corbie (page 165) give all the names, but do not distinguish the frill-back from the silk pigeon, as does de Roo. Temminck (page 454) and Buffon (page 518) both refer to the frill-back.

[13] This is Gallus crispus of Brisson, Gallus pennis revolutis of Linnæus, Gallina frislandica of Willoughby, and, Tegetmeier thinks, the "monstrous hens" of Aldrovandus.

Temminck calls this race[13] the "Coq à plumes frisées," and states that the prevailing color of the race is "white." He quotes Mr. Hewitt, who says "all body-feathers, without exception, appear twisted similarly to the curled feathers in the tail of a drake." These birds are spoken of as a rather "weak" race liable to disease, poor layers, and generally thin.

Tegetmeier made an interesting cross of the silky and frizzled breeds. He obtained as hybrids, "white frizzled negro fowls conjoining the dark leaden skin of the silky with the white recurved feather of the frizzled variety" (page 272).

Davenport[14] has recently repeated this cross with like results. Frizzling, according to this author, seems to be a Mendelian "dominant," and "the frizzled characteristics a typical sport" (page 56). The further statement that "curving of shaft, barb-length, and barb-form are all correlated in the first generation" is of interest.

Geese.

In the Sebastopol geese the feathers are very long and curled and twisted. According to Tegetmeier (page 366), "the shafts of these long feathers split down their entire length, and then become twisted, so as to give rise to the peculiar curled appearance."

Bullfinch.[15]

Buffon[16] figured and described a peculiar bird under the name "Bouvreuil à plumes frisées du Brésil." It is said that "the lower part of the body is white, the feathers of the abdomen and under coverts of the tail are 'curled' in some[17] individuals."

FRILLED FEATHERS AS A CHARACTER OF GRADUAL DEVELOPMENT RATHER THAN SALTATIVE.

If a character represents a *unit whole* from the first—*i.e.*, if it is not reached or reachable through continuous variation advancing cumulatively from generation to generation, if it be as fixed as a chemical molecule, then if it disappears it should go as suddenly and abruptly as it came. Yet it is well known that characters often disappear by degrees, not all at once. In crossing species we rarely find the hybrid with *pure* characters. A character may be halved, quartered, etc., to any fractional part of the original.[18]

Minute frills may occur in one or two feathers only, and they may occur in any number, or in all of the feathers. They may be so minute as to escape attention, and every stage in size and number may occur. It is not, then, comparable to a chemical body of a "precise" and "constant" make-up.

The full character is reached, not by a jump, but through a process of modification, carried farther and farther, from the initial starting-point. This starting-point presupposes the normal feather with all its elements intact as the foundation on which the variation can begin, and from which it can gradually be molded into its ultimate shape.

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[14] Inheritance in Poultry, Carn. Inst. Wash. Pub. No. 52, 1906.

[15] Frizzled canaries are said to have been exhibited.

[16] See Buffon, Ois, text, Vol. XIX, page 389.

[17] The word "some" is here used because Buffon regards this bird as identical with Brisson's *Pyrrhula africana nigra minor* (which has no sign of frilled feathers). Buffon is doubtful about the habitat, which was reported to be Brazil.

[18] See Vol. II, Chap. XVII.

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The first stages of the variation are usually too minute to attract attention. They are preparatory stages that lead sooner or later to visible phases. The visible phase, if cultivated by artificial or natural selection, can be developed to almost any extent compatible with the existence of the organism. The higher stages may differ more and more in some structural element, so that the form presented changes progressively, the final form being very different from the initial form.

FUNDAMENTAL BARS.

A still older character than the dark center of the turtle-dove feather is seen in the cross-bars, or *fundamental bars*, that appear to mark all feathers of all species in birds. These bars were first noticed in pigeons in the summer of 1903, and were soon found to be common to all species of pigeons and birds in general. From these fundamental feather-bars, or their secondary derivatives, a multitude of specific characters have been evolved by gradual modification. The continuity in the evolution of some of these characters can be experimentally demonstrated. The little diamond-dove (*Geopelia cuneata*) of Australia owes its small white spots (two to each feather) to these bars. The transitional stages connecting the spots with the bars are not wholly given in passing from the juvenal to the adult plumage. But if we pluck a few of the juvenal feathers at suitable intervals, their places will be filled by new feathers of different ages, and in this way we may get the stages intermediate between the bars of the young and the spots of the adult. Thus we see that the adult pattern, which normally appears to come in as a striking mutation, by a single jump, is only an end-stage in a continuous process of differentiation. So it is everywhere. Suppression of stages in ontogeny looks like saltations; but whenever we can get at the history of the character, we find the continuity comes to light.

The characteristic secondary cross-bars of many races of the common fowl, pheasants, guinea-fowl, ducks, woodpeckers, etc., have been molded more or less directly out of or upon these fundamental cross-bars, which everywhere underlie other color-marks, even the universal avian character already described, and its latest derivatives.

The discovery of the universality of this character—fundamental bars—and its far-reaching significance as an initial foundation for numerous specific characters, suggested the need of a thorough investigation to determine its nature and mode of development. This task has been undertaken and brought to a conclusion by Mr. Oscar Riddle, who has not only reached a physiological explanation of the character, but has fully confirmed and established the following anticipation I ventured to make in 1903:

Allowing that the feathers of the common pigeon get their full length in 4 weeks, and that the terminal half of the feather (on which the bars are distinct enough to be counted) is formed in 14 days, it is found that the number of bars corresponds nearly to the number of days of growth. If this be so, then the bars would be zones of daily growth (light = day; dark = night, or *vice versa*).[19]

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[19] The preceding paragraphs form part of the abstract of a lecture delivered before the Wisconsin Natural History Society on December 20, 1906, and published in the proceedings of that society in 1907. For the introduction, and the remainder of the published abstract of that lecture, see the beginning of the following chapter.—ED.

At this point it seems necessary for the editor to supplement the above paragraphs with a statement of what has been learned of the physiological basis of the fundamental bars, and later to add a further word to the author's meager discussion of this subject. The first of these objects will perhaps be best accomplished by the following quotation (pages 356, 357) from our own publication:[20]

It has been shown that there exists in certain elements of the rapidly growing feather-germ a rhythm of growth which is dependent upon the nutrition. Those parts of the feather which are grown under the poorest nutritive conditions show defective structure—"fault-bars"—of all grades of imperfection. Those regions of the feather—normally the larger part—which are produced while growth and cell-division are more nearly in full swing, form the "fundamental bars."

In pigmented feathers, the development of pigment is modified *at night* along with the other elements and there results a structurally weakened and less-pigmented area. This region we have thus far spoken of as a fault-bar; since, however, this same area has been found in some cases to lose considerable pigment without having lost any barbules, we speak of it also as a "light fundamental bar." On the other hand, pigment develops uninterruptedly during those hours of the *day* when growth is most rapid, and the well-pigmented portion of the feather then laid down forms the "dark fundamental bar."

Fault-bars and fundamental bars are universal in feathers (in white feathers there is, of course, no rhythm of pigmentation), and are direct expressions of the rhythmic nutritive[21] conditions. The poorest food conditions obtain at night. A reduced blood-pressure, probably much emphasized in the later hours of the night, is to be regarded as a factor (by affecting the nutrition) in the production of all fault-bars and of the light fundamental bars, while the better normal nutrition of the day and of the first part of the night is associated with the production of the dark fundamental bars.

The large light and dark transverse bars with which we have all long been familiar in Plymouth Rock fowls, in hawks, in jays, etc., are of course not the light and dark fundamental bars with which this work deals, and are not each the growth of a day or night; it is perfectly evident that in them a single broad black or white bar may include the growth of 2, 3, or more days. But even these broad bands of white and black may later be found to bear secondary or derivable relations to the fundamental bars.

The alternating light and dark fundamental bars are only rarely seen in their fullest development, *i.e.*, as well-defined alternating bands of lighter and darker color. Experience would indicate that they are found to best advantage in pale feathers rather than in those with a superabundance of pigment. . . . It is, then, through such a mechanism as has been described in the foregoing pages that the melanin pigment of feathers comes to be laid down in alternating light and dark transverse bars.

Several aspects of the occurrence, nature, and variation of this type of barring are made clear by the following records and illustrations, all of which were prepared by the author:[22]

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[20] Riddle, Biol. Bull., vol. 14, pages 328–370.

[21] The words "food" and "nutrition" are used in a general sense and include oxygen. It is not improbable that the slower growth and cell-division, and the diminution of the production of melanin pigment under fault-bar-producing conditions, are in part at least due to a reduced oxygen-supply. In all my experiments, and in every lowering of the blood-pressure, the oxygen-supply of the tissues is diminished. The probability here stated grows in importance when it is remembered that free oxygen plays an important rôle in the germination of seeds, the segmentation of ova (mitotic activities), and probably also in the oxidation (Samuely) of tyrosin (Gessard, v. Furth, and Schneider) to form melanin.

[22] Much of the record on this subject was made before the cause of the barring was determined, and made, therefore, with a view to obtaining light on this point. It seems necessary to present but little of this part of the record.—Ed.

In a 6-weeks-old homer I find the tertials and a few secondaries are transversely barred. And, as a second surprise, the second (anterior) wing-bar is reduced on the lower web of the long coverts to a "marginal remnant," looking like a long edge-streak that we find on these feathers in the young of *Geopelia humeralis*.[23]

This bird is the first pigeon in which I have noted these peculiar barred feathers.[24] For the first 10 days or more this bird fell far behind its mate in size and weight, but kept healthy. I then began giving the old birds extra food and they fed it better; it then grew rapidly, and is now an average-sized bird—very pale gray— and with the weakest second wing-bar that I have yet seen. The long coverts show at their tips parallel fine lines—dark and light alternating—due probably to defective nourishment during the first two weeks of life. This suggests that the bars (marginal remnants) on the tertials may be due to the same cause.

[23] The author made no further note on this matter, but to the editor it seems most interesting that a reduction of pigment in the ontogeny (of this homer) should so closely parallel the state and appearance of the character in a form (*G. humeralis*) which has made the reduction in its phylogeny.

[24] In October 1903 I find the same in a bronze-winged pigeon; a little later in two old *pale-gray* owl-pigeons, and still later in a green-winged pigeon, where the bars are plainest in the *gray* part of the feather.

EXPLANATION OF PLATE 72.

Transverse barring in an adult male owl-pigeon. Toda del., Feb. 1905.

This bird was 4 to 5 years old when these feathers were plucked (July 23, 1903). The feathers are somewhat worn and faded, the bird having already begun to molt the primaries. The color of the bird is a pale silver, with brown-black bars.

Notice in the lower two-thirds of the row of long coverts (smaller feathers of the figure) that the transverse bars can be clearly seen all the way from the dark chequers to the tip of the feather. The same can be seen in the lower web of the secondaries and the tertials. These bars are strongest in the tertials and inner (upper) long coverts.

Measurements of feathers and width of their bars:

In upper tertial (57 mm. long), 10 bars, 19 mm.   In fifth tertial (61 mm. long), 10 bars, 31 mm.
In second tertial (67 mm. long), 10 bars, 21.5 mm.   In lower secondary (108 mm. long), 10 bars, 32 mm.
In third tertial (75 mm. long), 10 bars, 23 mm.   In third long covert (50 mm. long), 10 bars, 20 mm
In fourth tertial (84.5 mm. long), 10 bars, 28 mm.   In eleventh long covert (64 mm. long), 10 bars, 25 mm.

The bars (light and dark) are wider in the longer feathers. Allowing that the feathers get their whole length in 4 weeks, and that the terminal half is formed in 14 days, it is found that the number of bars corresponds nearly to the number of days of growth. If this be so, then the bars would be zones of daily growth (light = day, dark = night, or *vice versa*).

EXPLANATION OF PLATE 73.

Fundamental bars and extended wing-bars in adult male owl-pigeon, same as pl. 72. × 0.8. Toda del., Mar. 1905.

These feathers plucked from above bird when nearly 2 years older than when feathers were taken for plate 72.

The two rows of feathers bearing the two wing-bars of the right wing. The chequers are much darker than in plate 84, and the barring would not be noticed at first sight. On closer examination I can make out very obscure cross-bars (to compare with pl. 72).

The artist has strengthened the bars considerably. The chequers are much darker and larger than in plate 72; so much so that one would hardly suspect that one bird had furnished both sets of feathers. The cross-bars are correspondingly obscured, but they can be detected in favorable light.

Notice that the feathers (especially the long coverts) are decidedly larger than in plate 72.

The important point to be here noted is that the first wing-bar extends clear down through the primaries, only the two outer primaries being without any mark.

In the first (inner) primary, the spot is 25 mm. long, on the lower edge of the feather, extending in width to about midway to shaft. It is more or less flecky. It is 37 mm. from the tip of the feather.

The remaining 7 chequers are more and more thin-flecked, the eighth being only a trace. The chequers form a bar on the primaries, which does not run vertically, but downward and backward at about 45° inclination.

A similar flecky series of chequers is found on six of the inner primary coverts; this series has same slanted direction, and lies just in front of the series on the primaries.

I have seen such extensions of the wing-bars in some other domestic pigeons.
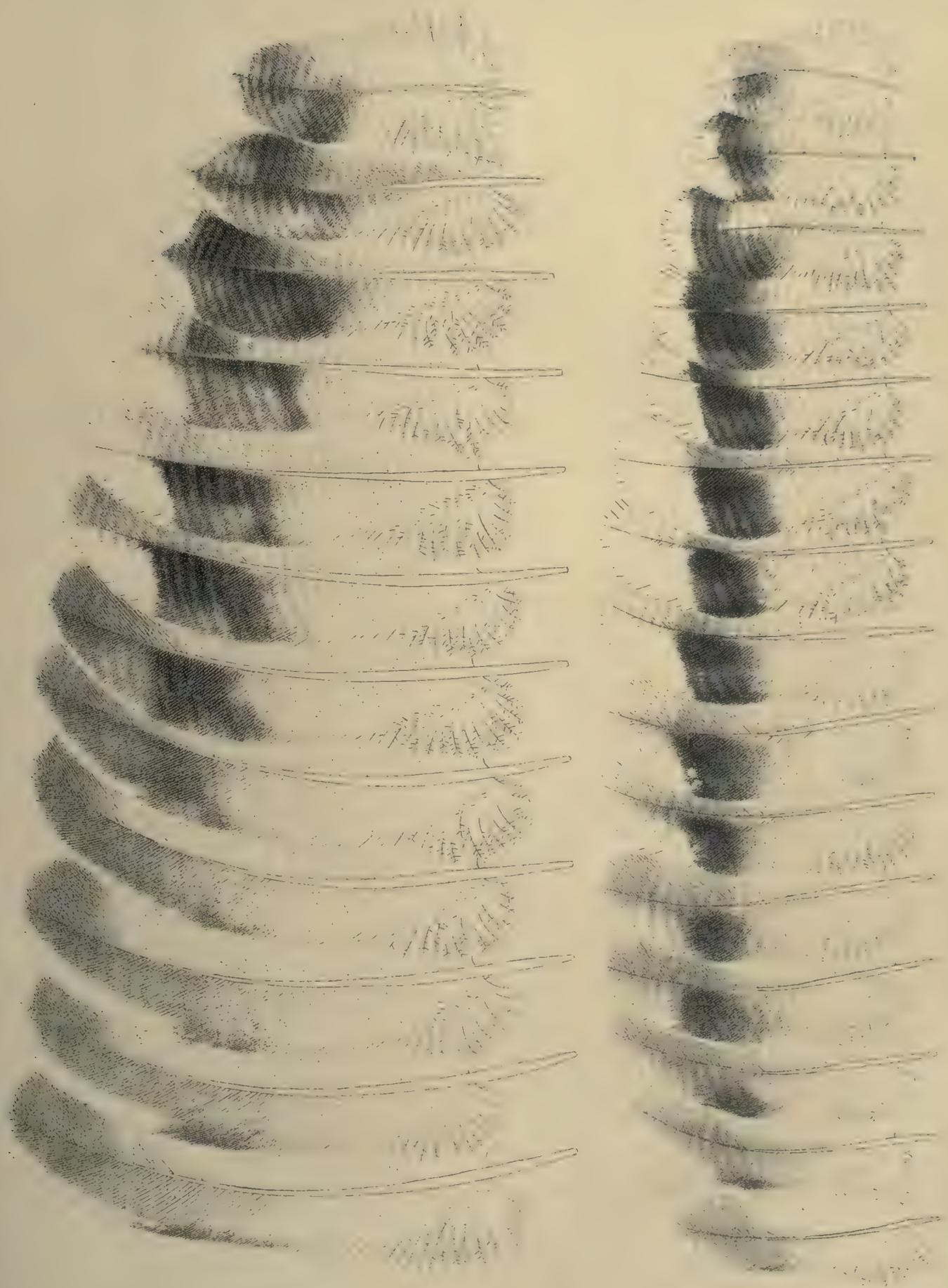
PLATE 72

Transverse barring in an adult male owl-pigeon. Toda del., Feb. 1905.

PLATE 73
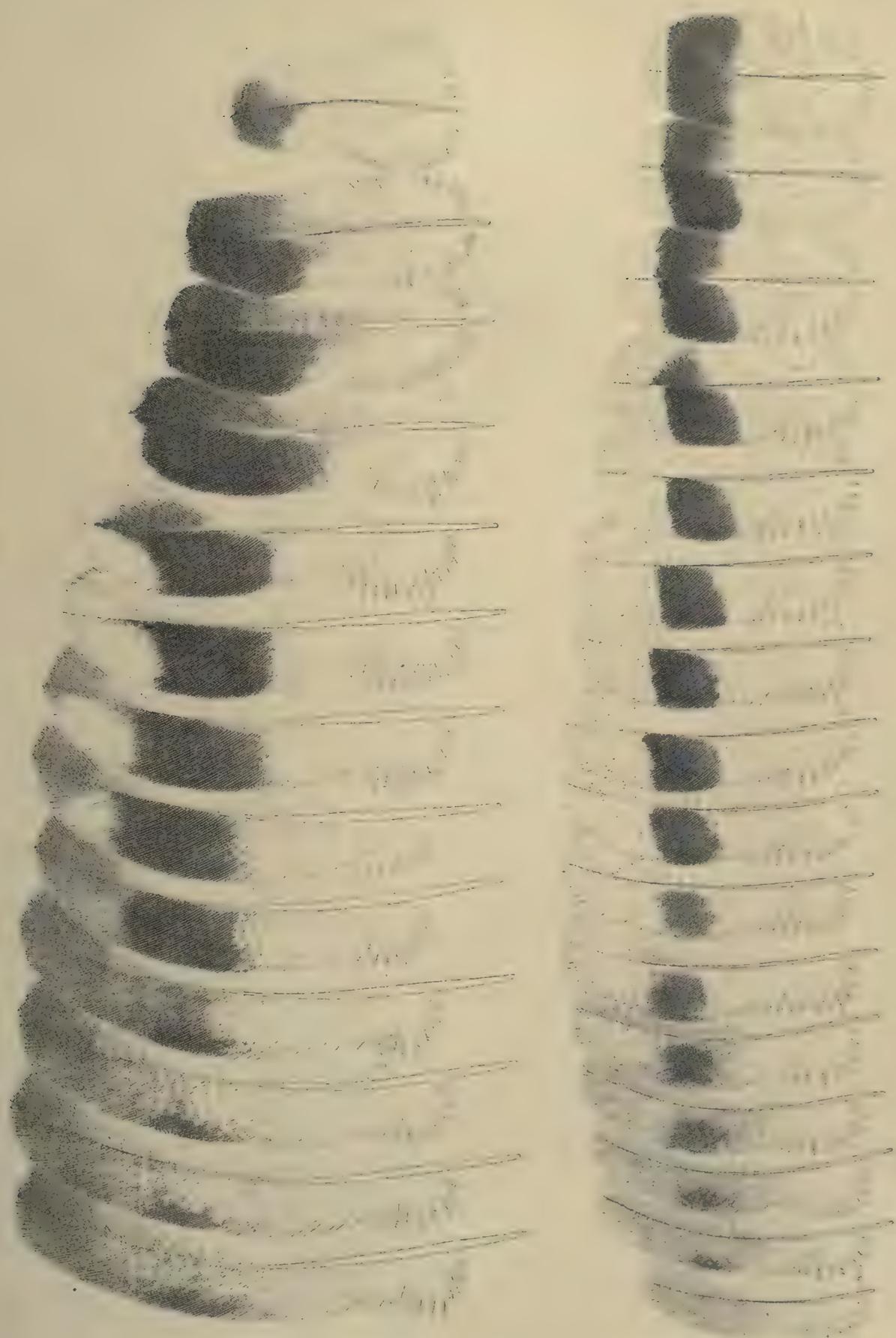
Fundamental bars and extended wing-bars in adult male owl-pigeon, same as pl. 72.
Toda del., Mar. 1905.

Thinking it of interest to see the second feathers, I plucked and mounted these juvenal feathers and awaited the growth of others. The bird died when 10 weeks old, but the plucked feathers were already replaced, and here both of the wing-bars are well-developed and complete.

The peculiar transverse bars which were seen in the first feathers have been lost by the deposition of more pigment, which is also more evenly distributed; only faint traces of the bars are visible in 3 or 4 of the secondaries; traces are seen also in a few of the long coverts. The increase in pigment is very marked, especially in the long coverts.

In an old owl-pigeon of pale-silver color I find similar, very distinct, transverse bars. From measurements of the bars in the distal ends of the feathers, where the bars are plainest, I learn that the light and dark bars are *wider* in the *longer* feathers, and that the bars are of nearly equal width in an individual feather, though they vary a little (pl. 72).

The feathers of this same bird were re-examined 2 years (1905) and 4 years 1907) later. In the feathers of 1905 (pl. 73) the transverse barring is present, but quite obscure. Comparing this set of feathers with the earlier strongly barred ones brings out the interesting fact that the chequers of the wing-bars are larger and darker, and extend upon more feathers in the 1905 series; and, further, that the feathers themselves of this latter series are decidedly larger.[25]

In 1907 some feathers of this bird showed rather plainly the fundamental barring. These bars were more obscure on the lower than on the upper webs. The "defect bars"[26] are also present in these feathers as narrow lines—one on the proximal edge of each dark fundamental bar.

Very pronounced transverse barring was found in two juvenile Jacobins, from red-and-white parents. The wing of one of these, while in molt, showed the first feathers strongly barred, while the new set of feathers were without barring and decidedly *black* (pl. 74); the other was at first similarly barred (pl. 75), but showed none of the barring in its adult feathers.

The editor would here venture a concluding statement: If the author is correct in his conclusions, stated in the first two paragraphs of this section, we are in a position to obtain a close view, in the case of this character, of the basis upon which an hereditary character rests. For, if "from these fundamental bars, or their secondary derivatives, a multitude of specific characters have been evolved by gradual modification," it follows that these specific characters have arisen from a much simplified situation, which can now be described with considerable completeness in terms of physiology. My own studies showed conclusively that a daily rhythm of growth accompanies the development of the feathers of birds; that the period of slowest growth, in the several species examined, is during the later hours of the night (1 to 5 a.m.); that the reduced pigmentation characteristic of the "light" fundamental bar coincides with this period of slowest growth; and that the periods of slowest growth and reduced pigmentation further coincide with the

[25] The size differences will doubtless not be apparent after the plates have been reduced in size for reproduction. The editor has therefore measured the two series of long coverts (all drawn to natural size) of plates 72 and 73. The two series were to each other as 61 : 67.

[26] See Riddle, Biol. Bull., vol. 12, Feb. 1907.

period of lowest vascular pressure, and therefore with the period of least favorable nutrition. These, then, are at the basis of the production of the fundamental bars. The growth-rhythms occur equally in feathers with and without pigment; the light and dark fundamental bars are of course obtained only in (melanin) pigmented feathers, and there, conspicuously or usually, only when a temporarily or permanently unfavorable nutrition or metabolism in the organism is superposed upon the nutritive fluctuations of the daily rhythm.[27]

[27] Since it is the division or separation of a pigmented area that gives rise to fundamental bars (from which, according to Whitman, "specific characters have been evolved") the question of the origin of the melanin pigment concerned is here not the point of primary importance; I have, however, elsewhere (Biol. Bull., vol. 16, 1909) discussed this topic, and have pointed out that the formation of melanin lies close to *generalized* protoplasmic functions, rather than to intricately *specialized* and segregable ones.—ED.

NOTE.—The manuscripts and records used in the preparation of this chapter were found in folders designated as follows: BB 10, G 10, G 12, G 13, G 23, 0011, 0013, R 16, W 2, W 12, WW 1, WW 6, XG 24, XG 26, XW 2.—ED.).

EXPLANATION OF PLATE 74.

Fundamental bars in wing of juvenal Jacobin. Toda del., Aug. 1904. Natural size.

This bird is black with red bars crossing the tertials and long and median coverts.

The parents are red, with white head, tail, and primaries. The young has white parts, the same as the parents, whose red is replaced by black in this young. This black is pure black, without the transverse barring, in the adult feathers, a few of which (small coverts) are already present and shown in the drawing. The feathers of the later development, therefore, are free from transverse bars and are blacker than the first feathers.

The parents have produced such young twice this season (1904). I have black barbs (Jacobins) that produce usually black young, but occasionally red, and in one case a gray.

EXPLANATION OF PLATE 75.

Barred secondaries and long coverts of a juvenal Jacobin, age 8 weeks. Toda del., Feb. 1905. × 0.8.

This is a second young (pl. 86 being the first).

Feathers plucked August 25, 1904. The parents were both red and white, as described under plate 86.

These bars are narrower above than below, and stronger in the exposed part of the feather—*i.e.*, they weaken gradually as we pass towards the inner end. The inner or basal half of the feathers shows only very obscure bars, and these are hard to see.

In the secondaries, reckoning 6 feathers, the barring is very obscure—hardly noticeable. The artist has exaggerated somewhat. In the tertials—inner (upper) eight feathers—the bars are strong only in the terminal third.

In the second feathers the black prevails to such an extent that I should describe it as a black Jacobin (white head, tail, and primaries). No bars are visible in adult feathers.

PLATE 74

Fundamental bars in wing of juvenal Jacobin.   Toda del., Aug. 1904.   × 0.8.

PLATE 75
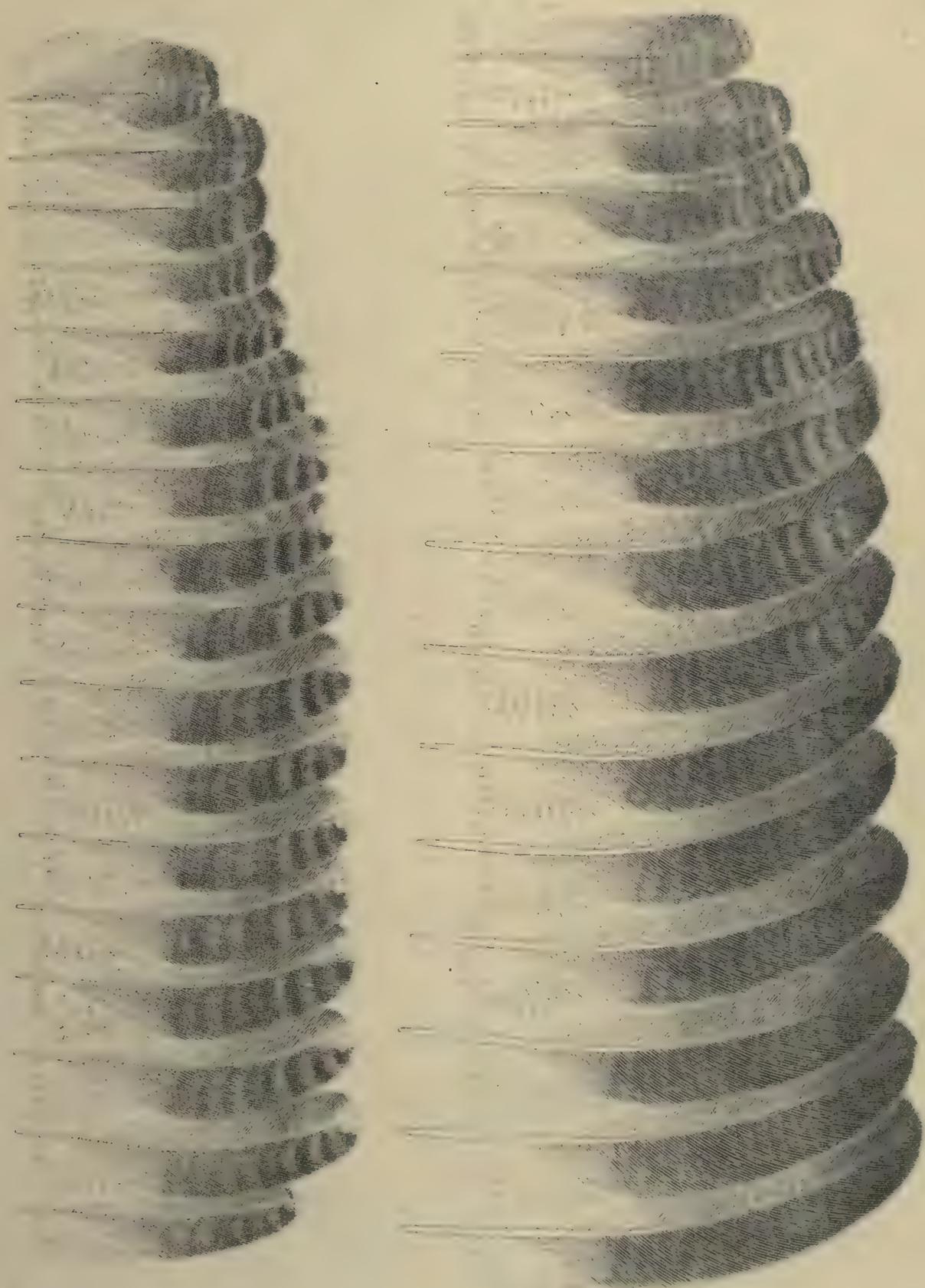
Barred secondaries and long coverts of a juvenal Jacobin, age 8 weeks. ×0.8. Toda del., Feb. 1905.

CHAPTER IX.

THE MUTATION THEORY AND MUTATIONS.

INTRODUCTORY.[1]

Much has been said and written on the subject of the origin of species, and yet the solution of the problem is far from complete. The latest advances in investigation reveal matters of deeper and wider interest, but in no direction do they bring us to final limits in the field. The foremost workers take their turns in revising the theories of their predecessors and in proposing new ones; and so, as we glance backward, the most revered investigators appear as peerless pioneers of their time, and their longest reaches of vision seem to be but *primæ vistæ*, and their greatest achievements but stepping-stones.

In fact, it seems as if Darwin and Wallace, Nägeli, Haeckel, Dohrn, Weismann, de Vries, and a host of other investigators had grappled with an all-embracing problem—a problem that must engage the best energies of all the sciences for centuries yet to come.

The era now dawning presents us with three leading rival theories. From Darwin and Wallace we have received the theory of natural selection, which has been powerfully supported by Spencer, Huxley, Haeckel, Weismann, Dohrn, and many others. This history and its triumphs are familiar history.

In 1901 de Vries brought forward his famous mutation-theory, based upon "Experiments and Observations on the Origin of Species in the Plant Kingdom." This work of de Vries is truly a great achievement, rising above any other that has appeared since Darwin's "Origin of Species." It is not only comprehensive in scope, consistent in its logic, and charming in style, but it is also epoch-making in its method of research. In this latter respect it sets an example which is having a world-wide influence—emphasizing as it does the supreme importance of studying living organisms, and of keeping observations and experiments running continuously through a long sequence of generations. This is the method of the new era in biology—steady, unbroken continuity in experiment under controlled culture. Here the example of Mendel, de Vries, and a few others will be potent for centuries to come.

As to the real merit of the theory of mutation, only extended research can bring a final decision. In dealing with such a theory, we must grasp clearly its fundamental conceptions. The whole superstructure stands or falls with them.

The central foundation-idea of this mutation-theory is that of "unit-characters." The species represents always a definite number of distinct unit-characters, each as sharply defined and independent as are the elements of a chemical compound. Consequently all upward progress in the organic world depends upon adding new

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[1] This section of this chapter is the introduction and abstract (partly omitted) of a lecture delivered before the Wisconsin Natural History Society by Professor Whitman at the meeting of December 20, 1906 (published in the proceedings of that society, Vol. V, January 1907). A few slight changes in this manuscript seem to have been made by the author after its publication; these changes are utilized here. The mutations described and figured in the final part of the chapter have been arranged, and their description amplified from the records, by the editor. The best cases of "mutation" observed and studied by Whitman belong to the period following the date of the above address. These later studies on mutation reinforce and confirm the conclusions formed from the earlier studies.—Ed.

unit-characters to those first organized. Furthermore, these unit-characters are held to be essentially unchangeable, and hence the species compounded of them are viewed also as essentially immutable. A unit-character, it is true, may undergo transmutation—*i.e.*, it may become a wholly new unit-character. Such transmutation, however, is always *sudden*, never by slow, *intermediate* degrees. Any slow and gradual transition, such as Darwin and Wallace maintained, never, under any circumstances, according to de Vries, could lead to the formation of a new species. The utmost that could be attained by such variation would be only an improved race—*i.e.*, merely a better variety of the same species, a variety that remains better only so long as cultivated under favorable conditions, reverting to the common level as soon as left to itself under normal conditions.[2]

The fundamentals in the mutation-theory, then, are:

(1) Every species consists of a fixed number of unit-characters.

(2) The species and the component units are alike sudden in origin and unchanging in type.

(3) Old characters may be suddenly transmuted into new ones, but between the two there is always a gulf of absolute discontinuity, with no possible bridge of gradual modification.

(4) Continuous intergradations may connect a species with an improved race, but never one species with another species.

(5) Species-formation is kaleidoscopic—*i.e.*, chance-wise in direction—never resulting from a tendency to vary in any one determinate direction.

(6) Natural selection can not give origin to new species; it can only weed out from those already in existence such as are incapable of sustaining themselves.

Of these fundamentals, that of "unit-characters" is the pivot on which all the others revolve. This conception implies that every character of the adult organism preëxists in some rudimentary form in the germ-cell from which the organism develops. These assumed unit-characters must be as fixed in number and constitution in the fertilized egg as in the adult. Moreover, unless we assume that these units may mutate at any stage of development, we must suppose that all mutations destined to appear in adult stages must originate in the very first stage of existence of the primordial units. Thus mutation would be carried back to the "premutation" not easily reached by investigation. Such conceptions help us in no wise to understand the *origin of species*. To claim that we can actually see mutation performed is the climax of absurdity.

De Vries has seen offspring differing more or less constantly from the mother plants. These visible differences are referred to invisible differences in one or more of the invisible unit-characters conjectured to exist in the seed before germination. The initial differences, in which, *ex hypothesi*, the whole mutation is given, de Vries has never seen and probably never expects to see. If there be any such thing as mutation, as conceived by de Vries, it is safely beyond human ken, and it remains to be seen if it be approachable through experimental investigation.

This theory of mutation coincides well with Bateson's doctrine of "discontinuity." Discontinuity in evolution has all the elusiveness of mutation. The discovery of such a negative is tantamount to a failure to discover anything just where the *instantia crucis* is most manifest. A new form appears; it differs in one or more

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[2] Several quotations from de Vries at this and other points are omitted.—ED.

respects from its parents. The difference is labeled a "discontinuity"; *i.e.*, the offspring is assumed to have obeyed the law of heredity in so far as it resembles the parental stock, and to have jumped hereditary bonds in so far as it departs from such resemblance. The "jump" signifies a sudden, unmediated translation from one sphere of existence into another. To put it in another way, the organism, in its germ state, makes a shift from the ancestral track to a new track, without a connecting switch. As immutability of species is held to be incompatible with gradual convergence or divergence, the mutant is conceived as set off at one stroke and at full distance, and so it must henceforth run its course exactly parallel to that of the parent species.

This conception is obviously the negation of a *branching* genealogical tree. Instead of a tree with a single trunk and many divergent branches, we have only naked, branchless stems, shooting up from different levels and to different heights, around the original central type.

The terms "discontinuity" and "mutation," as used by de Vries and Bateson, have their significance fixed in one and the same idea—that of unit-characters. However small the variations to which they apply, these never become synonymous with slow, cumulative variations. The whole theory of mutation would fall if in a single case the assumed discontinuity could be covered by *transitional* gradations. Although de Vries suggests that mutations may be provisionally compared with chemical substitutions, he nowhere confounds the mutation with ordinary chemical changes that underlie development, differentiation, and all so-called vital processes. To do so would of course annul all distinction between variation and mutation, between qualitative and quantitative changes, or between continuity and discontinuity.

In order to realize how indispensable to the whole mutation fabric is this unit-character concept, let us glance at its history for its source and its alleged justifications in facts.

As to its source, we have only to turn to an earlier work of de Vries, his "Intra-cellular Pangenesis" (1889), to learn that the concept comes directly from Darwin's discarded "Hypothesis of Pangenesis." De Vries recognized two distinct parts in the hypothesis, one of which is designed to account for the transmission of acquired characters, the other for the transmission of hereditary characters through the germ-cells.

With Weismann, de Vries denies the transmissibility of acquired characters; but he accepts the other part of the hypothesis, together with the idea that adult characters are represented in the germ-cell by distinct unit-elements.

Darwin's assumption that every cell in the body from the inception of germ-life to the end of development, and on to the end of mature life, is continually throwing out inconceivably small "gemmules" or unit-characters, that in some mysterious way are distributed not only to the reproductive cells, but to all other cells of the body, stretches the idea of transmission to the brink of absurdity. To eliminate the whole soma from the field of such emission and distribution, and thus limit transmission to the reproductive cells, was surely a long step; but the myth of transmission was not eliminated; it was only reduced in its field. The pangenesis of the *whole body* became the "intra-cellular pangenesis" of the germ-cell. Transmission thus became more direct, but its mysteries remained as unfathomable as

before. The unit-characters are assumed to preëxist in the chromosomes and to stand in need of transportation from the nucleus to the body of the cell in order to develop. Minute particles are known to pass out of the nucleus into the cytoplasm, and hence such migrations of "pangens," if they exist, would not startle us.

But the whole difficulty still remains. If an innumerable host of specifically distinct unit-characters are let loose in the cell-plasma, how are they to reach precisely predetermined points in the organism, and at just the time when needed? It is right here that the theory breaks down, for the difficulty is not one that further investigation may hope to solve, but one that lands us in hopeless speculation. So long as the primary assumption is that of ready-made unit-characters, specifically distinct and independently variable, whether located in the nucleus or in the cytoplasm, or in both, the problem of development will remain inscrutable.

De Vries does not overlook the difficulty, but he consoles himself with the fact that we have still much to learn in regard to the "extremely complex processes of nuclear division," in which, accepting the current view, he believes the purpose to be "manifestly a determinate distribution of hereditary characters to the two daughter cells." "The fact," continues de Vries, "that we do not know how the hypothetic pangens are held together (in a determinate order), is therefore no objection to this assumption, that they are so held in order."[3]

The refuge here becomes precarious when we reflect that heredity can be just as perfect by amitotic as by mitotic division, and that regeneration in Protozoa may take place in pieces containing a whole or even a fragment of a nucleus, without the aid of a distributing mitotic process. Moreover, when we consider the recent experimental demonstrations showing that hereditary processes may run on to a stage as late as the trochosphere in the egg of the annelid *Chætopterus*, without a single division of the nucleus, either mitotic or amitotic, it becomes abundantly clear that differentiation and its accurate localization do not depend upon any mitotic distribution of hereditary units.

I believe that these experiments settle once for all the untenability of all theories of heredity based upon the hypothesis that the nucleus furnishes the regulating machinery for the delivery at definite times and places of appropriate specific hereditary units.

As we review the grounds on which such theories have been erected, we can hardly fail to see that they all find their exigencies in a few gratuitous assumptions, chief of which is that heredity means transmission or transportation of qualities from parent to offspring, or from nucleus to cytoplasm during development. Since Darwin's herculean effort to meet this imaginary exigency through the hypothesis of pangenesis, we have seen the doctrine of "acquired characters" practically disposed of, and the "transportation hypothesis" consequently reduced to the "intracellular" field. Here the assumption still lingers, in spite of the universally accepted fact that the likeness of sister germ-cells does not depend upon transmission in the strict sense of the word, but upon the fact that each represents a moiety of the mother-cell, in which all essential parts were duplicated before and during its division as a whole. The mother-cell exists no longer as one cell, but as two cells—each an exact copy of the original, with a full and equal equipment. All this marvelous likeness was generated *within* the mother-cell, by assimilation, growth, and division.

[3] Intracellular Pangenesis, page 67.

Division neither added nor transferred anything, but left each moiety with all its parts intact.

Assimilation is the biochemical mill by which like material with like constitution and like organization is generated. The power of assimilation is never "transferred," for it always retains its seat while extending it. As in the growth of a crystal likeness is the necessary result of the apposition of like particles under like conditions, so in the intussusceptive growth of a cell likeness is not received or imparted, but is the necessary product of self-regulating metabolism.

This is all commonplace, but not entirely out of place whenever confronted with the assumption that heritable qualities are stored in special reservoirs, from which they have to be transported each at its appointed time and to its appointed place, through the help of a complex distributing apparatus.

The hypothesis of transportation with predetermined distribution is not made any less objectionable by reducing the number of the conjectured pangens. It is no less difficult to guide one pangen and its progeny to precisely the right destinations in each generation than to guide two, three, or many. It would be the same inscrutable miracle every time repeated. Hence, de Vries gains no real advantage for his theory when he contends that "a relatively small number of such hypothetical pangens suffices to explain all specific characters, if we allow for the various possible combinations."[4]

These "combinations" of the units have to be maintained in transportation, from stage to stage of development. Says de Vries:

The pangens must stand in such correlation in the larger or smaller groups [5] that the units of a group, as a rule, will enter into activity at the same time.

Thus the theory involves not only the difficulty of guiding single pangens, but whole constellations of them.

Darwin closed his chapter on pangenesis with these words:

Each living creature must be looked at as a microcosm—a little universe, formed of a host of self-propagating organisms, inconceivably minute and as numerous as the stars of heaven.

De Vries finds in this an appropriate epigraph for the title-page of his Intracellular Pangenesis. A more fitting selection could not have been made with which to announce the parentage of the newborn faith in pangenesis. With the substitution of the single-word "germ-cell" for "creature," the manifold miracle of Darwin's pangenesis is transmuted into that of the cellular pangen-firmament of de Vries.

In either form of the theory, the visible characters of the species, the origin, relation, variability, heredity, behavior, and control of which constitute the problem of science, are referred to antecedents that vanish in an infinitude of hypothetical entities. These ultimate living units are sometimes singly disposed, sometimes clustered into definite constellations, but in all cases they are held to be separable units, each capable of independent growth, variation, transmission, and precise distribution through the aid of a dividing apparatus evolved for this all-important function.

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[4] Intracellular Pangenesis, page 67.   [5] Synonymous with Darwin's "compound gemmules."

If a visible character varies it is not accounted directly responsible, for the change is referred to a "premutation" accomplished in the corresponding primordial pangen. Thus the visible appearance and the initial, responsible change are at least as far apart as the origin of the germ and that stage in its development when the variation first manifests itself; and in the case of a latent pangen they may be many generations, or even ages, apart. Through all these generations and ages, the pangen must be steered onward and finally delivered at the exact time and place of destination, not by autonomous migration, but by the aid of a distributing apparatus that must arise *de novo* at every transfer-station. The old pre-formation theory of Bonnet settled all at a single miraculous creation; but here we have self-propagating miracles *ad infinitum*.

NOTE.—With these introductory remarks, the lecturer turned to the consideration of a few specific characters which are found in various species of pigeons.

The wing-bars found in domestic races and in the wild rock-pigeons were taken as an example to illustrate orthogenetic evolution by *gradual progressive modification*. It was shown first of all that the two-barred condition seen in the typical *Columba livia* is derived from the chequered condition seen in the wild *C. affinis*. It was then shown that this mode of derivation is widespread among wild species of pigeons, the bars always resulting from a reduction of the chequers, proceeding from before backward, the direction being the same as that of embryonic development.

Experiments with domestic pigeons demonstrate that it is easy to reduce the chequered. type to 4 bars, then to 3, 2, 1, and finally to a uniform gray color without a single bar. Another set of experiments, to test the possibility of reversing the process, by advancing from the two-barred condition to the uniformly chequered type, showed that the direction could not be reversed.

It was next shown that among wild species of pigeons we have the same law of orthogenesis illustrated over and over again, in almost endless variety of conditions. The wild passenger-pigeon, the mourning-dove, the zenaida, the ground-dove of Florida, and a number of Old World species were shown in colored drawings and on charts.

After tracing wing-bars of the most diverse kinds to chequers, the origin of the latter from a still earlier and universal avian character was explained. This earlier color-mark still persists in many pigeons and other avian types, and is well preserved in the oriental turtle-dove of Japan and China. It consists of a single dark spot occupying the center of the exposed part of each feather. In the course of evolution this spot has been divided into two lateral spots by the disappearance of pigment along the shaft, beginning at the apex of the feather and advancing gradually inward. The old turtle-dove character thus passes by a continuous process of division into the rock-pigeon pattern, consisting of two chequers on each feather, more or less completely separated. The evidences showing such a gradual transmutation are still to be seen, and in such profusion as to wholly exclude doubt. Hundreds of species have been formed in this simple way, leaving no room for the claims of sudden, non-transitional mutations.

The transitional stages between the turtle-dove pattern and the chequered pattern of the rock-pigeons are exhibited not only as we pass from one species to another, but often as we advance from the juvenal to the adult plumage; and frequently they may be seen in different parts of one and the same individual plumage.

This passage from the juvenal to the adult plumage often presents us with two or more quite strongly contrasted color-patterns. The mutationist might see in this a striking illustration of discontinuity in the evolution of species. In the normal course of events the gap is often very wide between two successive patterns, but closer study and experi-

PLATE 76

Mate (♀-normal) of *guinea* mutant (No. 20), at age of 5 months. Colored photograph. Toda pinx, Feb. 1910. × 0.8. Much chestnut-red in plumage. Apical marks small, white. The naked periobital space is large.

PLATE 77
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Columbia guinea No. 20, "mutant" (nest mate of bird of the preceding plate) at age of 5 months. Colored photograph. Toda pinx., Feb. 1910 × 0.8   Faint traces of chestnut or reddish. Apical marks large, gray, their extensions clearly forming lateral blackish chequers and presenting a plumage like a chequered rock-pigeon. The naked periorbital space quite small.

PLATE 77

ment teach us that, while the visible stages may seem entirely disconnected, they are in reality genetically bound together by a continuous differentiating process, or system of processes. In most cases, perhaps in all, the apparent discontinuity in phenomena means nothing more than a discontinuity in our knowledge.

Several other specific characters, usually regarded as "sports" or "mutations," were considered, and the continuity of their development from minute incipient stages was clearly established.

THE GUINEA-PIGEON MUTATION.

The evolutionist has to deal with specific characters, for with them are given the origin of species, the laws of variation, and heredity. The prime question is how to deal with such characters. We know what are called specific characters; but what do we mean by specific? If some characters are specific, others not, how are we to distinguish the one from the other? Shall we be able by any process of Mendelian segregation to circumscribe this evasive something called specific character? Shall we reach it by first trying to eliminate "fluctuating variations," and then calling all the rest "mutations"? These methods presuppose the unit-character as a pre-formed element already present in the primordial germ-cell and already endowed with a specificity that will enable it to find a definite location in the adult organism and there unfold into the definitive form of the character, which, if a color-mark, can be seen, photographed, measured, and described with considerable detail. This is the pangenesis theory of Darwin, with the Lamarckian part left out.

For reasons already stated, I believe we can profitably concentrate attention on the history and development of individual specific characters and their behavior under both natural and experimental conditions. In short, we must run down the specific character by any and all possible methods that may lead to the capture of its secret or secrets.

I take as a first example, a small color-mark that is sharply and specifically defined in a wild African pigeon, known as *Columba guinea*. The guinea-pigeon is of the size of the common domestic rock-pigeon, but there is not a shadow of doubt of its specific distinctness, for it has a well-defined color-pattern, with voice, behavior, and other peculiarities that are constant. The ground-color is vinous or ruddy chestnut, and the feathers of the wing (wing-coverts) are each marked at the tip with a white triangular spot (pl. 76). This apical mark is the specific character I propose here to consider first.[6]

This small white triangular spot, which I sometimes call the "guinea-mark," is itself but a mesial extension of the light apical edge, and this latter mark seems to be universal among birds. The "guinea-mark" itself is known to exist as a specific character also in *Columba maculosa* (pls. 18 and 79), as well as in *C. albi-pinnis*—where apparently it has made less advance from the stage of the light apical edge than it has made in *C. guinea* and *C. maculosa*. It has also been shown to exist in the darker (chequered) forms of common pigeons (pls. 51 to 55), in juvenal quails (pl. 60), robins (pls. 56, 57), black-crowned herons, and in still other species.

In the rock-pigeons, the advance of the guinea-mark towards the base of the feather divides the dark center into two lateral chequers, as noted elsewhere (Chapters I and IV); but the point of interest here is that this advance to the gray or

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[6] The description of this mutation was not reduced to writing in the above address; from this point the editor is compelled to consult the author's records and notes, and to seriate the materials as well as their nature permits. Much of this was written many months after the preceding introductory paragraphs.

white mesial guinea-mark is the means by which the gray (blue) color of the wing is extended. In the rock-pigeons and their closest allies the ruddy or chestnut suffusion of the plumage is absent, and the naked periorbital region is quite small. Now, in a guinea-pigeon mutation which occurred during 1909, all of these characters are affected, and the variation is toward the rock-pigeon type in them all.[7] This mutant demonstrates perfectly the community of patterns in the guinea-pigeons and the rock-pigeons.

The extent of these variations[8] from the normal *C. guinea* type is shown in the illustrations. The second plumage of the mutant and its nest-mate are shown in colored photographs in plates 76 and 77; the first plumage of the same two birds is shown in an untouched photograph in plate 78. The guinea-mark and the naked periorbital region of normal and mutant *C. guinea* are compared with the same characters in other *Columba* in plates 79 and 80. The mutant's modification of the light tail-band into a weaker band, placed in the middle of the black band of the normal, is shown in plate 81.

The editor has prepared tables 4 and 5, which give the available necessary data for the origin and the breeding record of the guinea mutant.[9] That the mutational characters were transmitted by the mutant is indicated by the data of table 5. One (MN 1) of the two offspring (pl. 82) which lived long enough to permit a definite decision on the point proved to be essentially like its mutant father; and the other young, its clutch-mate, which died at the age of 14 days, was also believed to show the mutational characters of the father. Indeed the descriptions of the two birds when 2 weeks old (see below) would indicate that the short-lived bird (whose muta-

TABLE 4.—*The parentage and co-fraternity of the Guinea "mutant" No. 20.*

♂ C. guinea from dealer April 1908; typical.
♀ C. guinea from dealer April 1908; typical.

A1. Sept. 28, 1908, broken.	J1. June 24⌠21, ♂; typical; dead Dec. 20, 1909.
A2. Sept. 30, 1908, broken.	J2. June 26⌡22, other; typical; alive Feb. 7, 1911.
B1. Oct. 17⌠[10] 10, one = ♀, typical, nearly.[11]	K1. Sept. 24....23, ♀; typical; dead Dec. 12, 1909.
B2. Oct. 19⌡11, other typical; dead Mar. 24, 1909.	K2. Sept. 26....24, ♀; typical; dead Nov. 24, 1909.
C1. Nov. 21⌠12, typical.	L1. Jan. 30, 1910....weak shell; broken.
C2. Nov. 23⌡other not hatched.	L2. Feb. 1, 1910....weak shell; broken.
D1. Jan. 3, 1909⌠13, ♂, typical.	M1. Feb. 24⌠25, ♂; typical; dead Jan. 19, 1913.
D2. Jan. 5, 1909⌡other not hatched.	M2. Feb. 26⌡other not hatched (care?).
E1. Jan. 21....14, dead Feb. 16, 1909.	N1. Apr. 12....0; dead at 12 days.
E2. Jan. 23....15, dead Feb. 16, 1909.	N2. Apr. 14....0; killed day of hatching.
F1. Feb. 16....not incubated.	O1. May 11....26; ♀; typical; dead July 9, 1912.
F2. Feb. 18....not incubated.	O2. May 13....no development.
G1. Feb. 27....16, ♀; typical.	P1. June 30....0; dead (killed?) at few days.
G2. Feb. 29....broken.	P2. July 2....0; dead at 10 days.
H1. Apr. 3....17, ♂; typical; dead June 26, 1909.	Q1. Aug. 24....27; typical; dead Jan. 6, 1916.
H2. Apr. 5....18, typical; dead (care?) Apr. 24, 1909.	Q2. Aug. 26....28; typical; alive Nov. 20, 1910.
I1. May 5....19, ♀; typical; alive July 28, 1910.	Certainly no other eggs before Dec. 1, 1910; later records
I2. May 7....20, ♂; MUTANT; dead Nov. 17, 1914.[12]	not kept.—ED.

[7] No reference is made to the changed character of the "bristling" bifid neck-feathers of the mutant, but the illustrations here reproduced and all of the photographs made of this bird show much less of the "bristling" effect in the mutant. In this character also, therefore, the mutant approaches the rock-pigeon type.—ED.

[8] An additional variation—in the "dark spot" of the iris—in the guinea mutant is figured in plate 80, and described in the accompanying legend. In this character, too, the mutation approaches the conditions now present in *Columba livia*.—ED.

[9] Though the parents were obtained from a dealer, probably no one who has worked with this species would doubt that the author, who had long had this species under observation, would have quickly detected any impurity or hybridism in the birds which were thus obtained and used as parents. This possibility is still further minimized by the difficulty of getting hybrids of this species. (Chapter VIII; see Vol. II.)

[10] Brackets indicate that the first and second eggs of the clutch were not properly identified.

[11] The third (right) primary has two white spots near the tip—one on each side; this is a case of abnormal albinism.

[12] Note that the following clutch is succeeded by a period of "rest."—ED.

PLATE 78

Mutant *Columba guinea* (20) and nest-mate, normal *C. guinea* (19), at age of 26 days. Photo. June 18, 1908.
First plumage, see plates 77 and 78. x 0.5.

PLATE 79
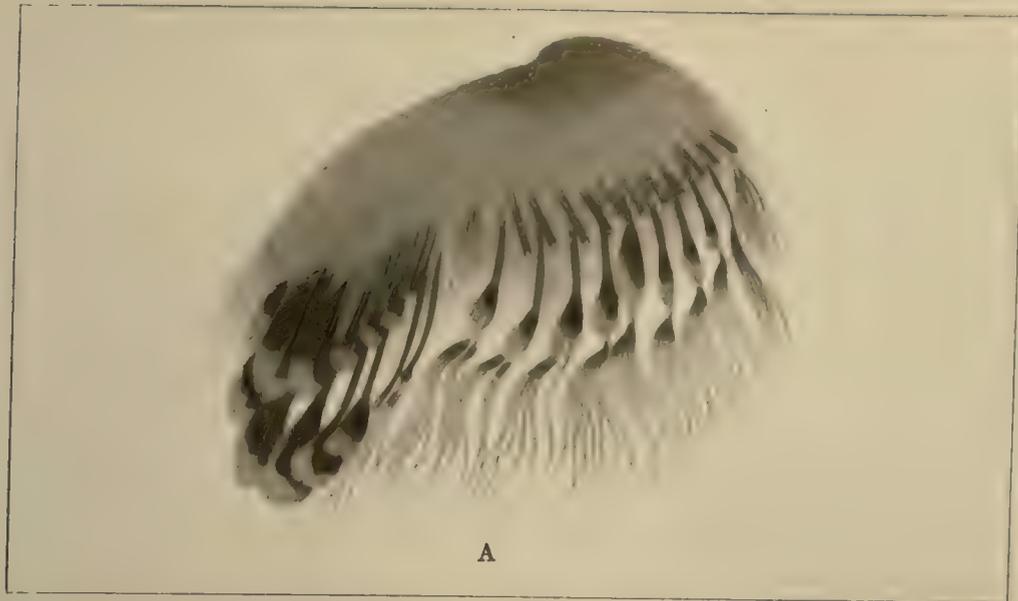
A

B   C   D   E   F

A. Left wing of a juvenal pheasant, 6 days. × 2. Hayashi del., Aug. 1905. Shows broad pale-buff irregular tips of primaries, secondaries, and primary coverts. This edge of the same color with down shown still attached to the secondaries.

B–F. The inner greater coverts, left wing, of *Columba guinea* and other species of *Columba*. Colored photograph. Natural size. Toda pinx., July 1910.

B. *C. livia domestica*, adult. Guinea-mark very strong, gray, with evident apical lateral extensions. The body of feathers with amounts of gray and red not markedly different from *C. guinea* mutant (fig. D).

C. *C. maculosa*, adult. Guinea-mark strong, whitish and grayish. Body of feathers with less red and more gray than in normal *C. guinea*.

D. *C. guinea*, mutant (20) adult; age 14 months. Guinea-mark extended more plainly on lateral apical edge, grayish. Body of feather with less red and more gray than in normal adult.

E. *C. guinea*, normal (19) adult; age 14 months. Guinea-mark of moderate size, whitish; no lateral extensions at tip. Uncovered part of feather, largely chestnut-red.

F. *C. guinea*, normal juvenal; age 4 weeks. The light apical edge is here a prominent part of the guinea-mark. Feather has more dark and less red than adult (fig. E).

tional nature is left somewhat in doubt) was more clearly like the mutant father than its mutant nest-mate; the latter lived much longer and was unquestionably like its father in respect of the mutational characters. The description of these birds when 14 days old, follows:

The color of *MN 1* is nearly the usual guinea-red, but the characteristic white apical spots are more grayish and hence not so conspicuous as in the typical *Columba guinea*. In some feathers there is a bare trace of such marks, but not enough to amount to anything in determining the pattern.

The second young (MN 2)—dead at 14 days—is closely like a young rock-pigeon of the same age, but there are *no bars*. The white spots (guinea-marks) are present but rather light grayish in color. The feathers are not far enough along to make sure whether these white spots are to extend over the whole wing. The coverts at the fore end of the wing are not red, but grayish brown—nearly the color seen in the spotted pigeon [13] (*C. maculosa*). The posterior coverts are paler gray—nearly the shade of young rocks of the same age, but lighter.

The feathers of the breast are dark brown, of nearly the same shade as that in *C. affinis*. The feet and legs are a little more blackish than in young rocks of the same age. The beak is darker than in the rock. I think this bird would have been nearly an intermediate between the guinea-pigeon and the rock-pigeon, except for a lack of wing-bars. I can not be sure on this point, for bars at this age are not to be seen in the common pigeon.

At 6 weeks the other young (MN 1) was again described as follows: "This bird is now 6 weeks old lacking 1 day. The photograph (101) was taken November 7, 1910, at the age of 4 weeks, and is now being colored by Mr. Toda. The bird was taken into the house, to be brought up by hand, when between 3 and 4 weeks old. It has been 'remarkably tame' from the first. I have kept it in a small cage with a young rock-pigeon and a Japanese turtle of the same age. The young rock and turtle-dove learned very quickly—within a day or two—to eat seed without help, but the young guinea insisted on my feeding it by opening its beak and crowding in seed. He is so tame that he sits half-asleep on the artist's finger while his picture is being colored.

"On November 21, at the age of 6 weeks, I again photographed this young guinea alongside a juvenile normal guinea (of 10 weeks) to show that the white spots are much sharper and whiter in the normal than in *MN 1*.[14] I note these further differences: (1) the reddish tips of the feathers of the basal half of the neck are very weak in *MN 1* and conspicuous in the normal. In the normal these reddish tips run up to and over the top of the head. (2) The 'vinous-chestnut' of the chequers of the wings is darker in *MN 1* than in the normal, as we should expect.[15] (3) The head is smaller and darker gray in *MN 1* than in the normal. (4) I think the skin around the eye is smaller in *MN 1* than in the normal. The color of this skin is darker gray—about that of the feathers of the head in shade."

The following word concerning this bird (MN 1) can be added by the editor: During 1911 the rock-pigeon and the Japanese turtle, referred to above, were left with this "remarkably tame" *C. guinea*, until late summer, when the rock was

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[13] This species has much "gray" and little "red" in its plumage; *i.e.*, has much of the gray ground-color of *Columba livia*; see plate 18.—ED.

[14] Apparently no prints from these negatives were ever made; the author's last illness began 9 days later. When the need of this illustration became evident the negatives were no longer available to the editor.

[15] That is, the color approaches that of the chequers of the rock-pigeons.—ED.

removed on account of his insistence upon sole possession of the ledge of their ample breeding-pen. None of these birds had really shown any inclination to mate, and the sex of none of the three was known. Beginning in the winter of 1911–12, a more determined attempt was made to mate *MN 1*. Three or four *Columba guinea*—which I later found included both sexes and included also the mutant father—were offered, one after the other, without the slightest success. The "tameness" of this bird remained undiminished, until it died of tuberculosis at just 2 years of age; it was then found to be a female. This record would seem to indicate that the bird was a *weak* individual. The later plumages, when 1 and 2 years old, were certainly as strikingly different from the normal as when 4 weeks old. It was often noted that it had less of the lighter gray of its mutant father, but was much farther removed—in the direction of its sire—from the normal guinea type, the red being greatly diminished and the guinea-mark dark grayish, with much less distinct boundaries, the effect always suggesting the black-chequered wing of the chequered rock-pigeon. The bird always bore its feathers somewhat loosely, as if it had just shaken them and then failed to pull them into place.

The breeding of the original mutant (20) was wholly neglected during 1911. Much of the season of 1912 was lost in the attempt to effect a mating with his mutant

TABLE 5.—*Breeding record of mutant Columba guinea, No. 20.*

♂ C. guinea (20), May 7, 1909 to Nov. 7, 1914; mutant; brother.
♀ C. guinea (10), Oct. 18, 1908; normal (or nearly [16]); sister.

A1. May 5, 1910; no development.	C1. May 9; no development (care?).
A2. May 7, 1910; no development.	C2. May 11; broken.
B1. May 28; no development.	D1. June 16; broken.
B2. May 30; no development.	D2. June 18; no development.
C1. Sept. 23; MN1; ♀ MUTANT, like sire; dead Oct. 8, 1912	E1. Aug. 7; hatched; dead at 3 days; ♂ (?).
C2. Sept. 25; MN2; MUTANT (?); dead at 14 days.	E2. Aug. 9; hatched with help; upper beak too short; died
♀ C. guinea [17] (had lost tag); normal; probably a sister	at once; ♂ (?).
to mate (No. 20).	F1, G1, H1, I1, J1 \ used in other studies (analyses of yolk).
A1. Apr. 6, 1914; broken.	F2, G2, H2, I2, J2 /
A2. Apr. 8, 1914; broken.	K1. Nov. 5; no development.
B. Apr. 20; broken; no second.	K2. Nov. 7; live 7-day embryo.[18]

The sire (♂ No. 20) died of fright (?) and hemorrhage from liver, Nov. 17, 1914.

[16] The third right primary has two spots near the tip—one on each side; this is a case of abnormal albinism.
[17] This female was mated to the "mutant" (No. 20) in 1914; the record is that obtained by the editor.
[18] Yolk-sac so little advanced that egg was opened by mistake; possibly would have hatched.

EXPLANATION OF PLATE 80.

Head, eyes, and naked periorbital areas of *Columba guinea* (mutant and normal) and of other *Columba*. Colored photographs, Mar. and Apr. 1910. Natural size. Toda del., June 1910.

A. *C. guinea* normal (19), adult. Greatest length of naked periorbital area, 27 mm.; greatest width, 15 mm. Color nearly blood-red. The pupil is here bordered by two dark spots; there is a smaller one above in addition to the larger one below. (Pupil as seen in shade.)

B. *C. guinea*, same as above. (Pupil as seen in sun.)

C. *C. guinea* mutant (20), adult. Greatest length of naked periorbital area, 17 mm.; greatest width, 10 mm. The red color less intense—a plainer trace of gray. Only a trace of an upper dark spot bordering pupil.

D. Colored photograph of head and neck of *C. eversmanni* (× 1/1, Toda pinx, June 1910).
Shows naked space about eye, moderate, greatest length, 20 mm., greatest width, 12 mm.; size intermediate of *C. guinea* normal and mutant; color, dusky lemon-yellow. Outer iris, dusky red; inner, yellowish-red. Neck-mark lateral, distinct, of few rows; feather-tips with coppery iridescence.

E. *C. domestica*. Naked area about eye quite small; nearly slate or horn color. Iris with much red and little (modified) yellow.

F. *C. leuconota*. Naked periorbital area none, except a little at anterior and posterior angles of eye. The iris is yellow with a slight shade of greenish below the pupil, and somewhat in front of the pupil it has a large spot a full 3 mm. long.

Thus we have in: *C. guinea*, a plane spot above and below; *C. guinea* mutant, a very small spot above and a large one below; *C. leuconota*, none above, but a very large one below.

PLATE 80
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Head, eyes, and naked periobital areas of *Columba guinea* (mutant and normal) and of other
 Columba. Natural size. Colored photographs, Mar. and Apr. 1910. Toda del., June 1910.
A. *C. guinea*, normal (19), adult.
B. *C. guinea*, same as above. Pupil as seen in sun.
C. *C. guinea*, mutant (20) adult.
D. Colored photograph of head and neck of *C. eversmanni*. Natural size. Toda del., June 1910.
E. *C. domestica*.
F. *C. leuconota*.

PLATE 81   166²

A. Tail of *Columba guinea* (19, nest-mate of mutant 20), age 79 days; shows normal whitish tail-band in dark feathers.
B. Tail of *C. guinea*, mutant (20), age 78 days; shows a weakened whitish tail-band, misplaced, in center of normal black-band.
C. Tail of *C. guinea* (10, sister to mutant), age 125 days.

PLATE 82

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A. Young (MN1) of *Columba guinea* mutant, age 4 weeks. Colored photograph, Toda del., Nov. 1910. ×0.85. See text.

offspring (MN 1). In 1913 reduced available breeding-space prevented attempts to mate this bird. The results for 1914 are included in table 5. The results then obtained indicate much *weakness* on the part of one or of both of these parents.

It remains to consider the question whether the mutational character of the original guinea mutant (20) can be attributed to "weakness" of the germ from which it arose. The author has recorded no statement whatever on this point.[19] But all of the color mutations recorded by the author depart from the normal in the direction of *lighter* (or white) color; and he has elsewhere pointed out that "the direction of evolution" in the pigeon world is also toward *light* (or white) color. In the case of each of the three color mutations which he did more fully describe, he has pointed to *weakness*—in the parents, or sometimes more specifically to the weakness of particular germs from which the mutant arose—as the basis of the mutation. These several facts make it seem quite probable that the author would have discussed this mutation from a similar standpoint.

The several conditions which tend toward the production of weakened offspring or of weakened germs need receive but little attention here, since they are fully treated elsewhere.[20] It may be said at once, however, that the breeding-record given (for this purpose) in table 4 apparently does not wholly accord with the view that mutant No. 20 arose from a "weak" germ. For example, the mutant *lived longer*, perhaps, than did any of its brothers or sisters.[21] Again, it is not evident that the other eggs of the same period—laid immediately before and after the mutant-producing egg—were producing females predominantly.[22] On the other hand, the following can be said: The data of the table are not very complete; the mutant arose from one of a series that was being produced with abnormal rapidity, and was the eighteenth of such a series; only one later clutch was laid before the parents began their season of rest—freedom from egg-production—and the length of life of the fraternity probably indicates weakness throughout the fraternity. A further and unquestionable expression of weakness in this fraternity is given in the breeding-record of two or (probably) three of its members. The result, as seen in table 5, shows extraordinary developmental weakness, and the two offspring which here lived long enough to develop plumage characters both shared the mutational characters of their sire.

THE ZENAIDA MUTATION.[23]

In the preceding section the "guinea-mark" was the point of departure for a mutation. That mutation took the *direction* which the author had concluded from other studies[24] was the direction of evolution in the Columbæ. The mark itself represents an *extension* of the pale apical edge—considered universal in pigeons either as a permanent (*e.g.*, *Turtur orientalis*) or as a recapitulated (*e.g.*, *Zenaida*, *Geopelia*) character; and the further extension of this particular mark is the means

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[19] There are, however, the best of reasons for this omission. First, offspring from this mutation were obtained only a few weeks before the author's final illness; and, second, other unfortunate affairs quite precluded this sort of work during the 5 or 6 months which preceded his brief and fatal illness.—ED.

[20] Vol. II of these works; also see under "the *Zenaida* Mutation," the next topic in this chapter.—ED.

[21] It is conceivable, but rather doubtful, that because of its value it received much better care than other members of the fraternity.—ED.

[22] The author considered this an evidence of weak germs; my own experience fully confirms this view.—ED.

[23] Three mutations—all similar—in the Japanese turtle-dove (*Turtur orientalis*) are fully described in Volume II, Chapter V.

[24] See the preceding chapters of this volume.

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of breaking up the dark center into lateral, gradually disappearing chequers. The present section is concerned with another aspect of this same "guinea-mark" which in 1906 came under observation, as a mutation, in a single individual of the species *Zenaida vinaceo-rufa* Ridgway. This genus and the other genera of Zenaidinæ[25] have passed beyond the phylogenetic stage which is represented by the "guinea-mark," *Nesopelia* not far beyond it; but in *Zenaida* and *Zenaidura* even most of the chequers which arose from the later extensions of the mark have been obliterated, while in *Melopelia* only a few structural imprints of obsolete chequers remain.

It is only with the aid of this phylogenetic perspective that the total behavior of the *Zenaida* mutation can be understood. But, because this perspective is available, and because some of the special conditions which attended the origin of the individual bearing the mutational character are known, this mutation contributes perhaps more to our knowledge of the phenomenon of mutation than does any mutant, or group of mutants, hitherto recorded.

The further important facts concerning this mutation, as they may be stated in a preliminary or introductory fashion, are as follows: (1) The mutational character is not a really *new* thing; a very weak stage (a smaller area affected, and usually of buff color, not white) is often seen in *some* restricted regions of the body in *young* zenaidas and in many other forms; (2) the mutational character is exhibited only in the juvenal plumage; representing, as it does, *delayed* or *halted* development, it attains in *later* plumages the normal state of the species; (3) the author's knowledge of the place of this character in pigeon phylogeny enabled him to predict its disappearance in these later plumages; (4) the original mutant arose from a germ which, from other and previous studies, could be identified as a "weakened germ"; (5) the mutation has now been perpetuated—undiminished—into the fifth generation, in a generic cross.

The author did not prepare these data for publication. Fortunately, however, he made fairly complete notes concerning the essential aspects of the mutation, and recorded his views and conclusions with sufficient fullness to permit a fairly adequate presentation of the subject. The editor chooses the following topical arrangement of materials, because more of the author's statements may thus be utilized with least change or transposition. The breeding of the later generations of this mutation has been continued (early 1911 to 1916) by the editor. The author's data on the breeding of the mutant, and of her offspring, have been tabulated and presented in full in Chapter X, Volume II. The mutant was not bred to one of her own kind, but with a mourning-dove (*Zenaidura*); this makes necessary the author's description of the normal young of both of these species.

On the Color of the Young of Zenaida and Zenaidura.

In making a comparison of the juvenile color of *Zenaida vinaceo-rufa* and *Zenaidura carolinensis* I have before me one of each kind about 2 weeks old (June 7, 1905). The *Zenaida* (No. 12 = mother of the original mutant, No. 21.—Ed.) has more of the *red* color of the turtle-dove. Both species have two light streaks on the side of the head, one running over the eye (superciliary), the other below it, and running through the ear-coverts (auricular). The feathers in these streaks have the 'light edge' (which is characteristic of the entire body-surface—head, neck,

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[25] See Chapter V of this volume.

and body) in a more or less extended or intensified condition. The extension is less in *Zenaida*, where the type-marking is preserved; the typical light edge is here merely emphasized. In *Zenaidura* this typical light edge is still apparent in the superciliary streak, but in the auricular streak it is extended until it represents the dominant color. The color-marks are not carried quite so far—*i.e.*, are not so highly developed in *Zenaida* as in *Zenaidura*.

The feathers of the breast in *Zenaidura* are ashy-brown, with a pale, almost whitish edge; in *Zenaida* the color is stronger and richer. The pale edges are more conspicuous, and the feather *is neatly divided by a median streak, which widens at the tip,* just where the tuft of down is attached, and which is a strong shade lighter than the rest of the distal edge (pl. 83, fig. B). This median streak I frequently find in young Japanese turtle-doves, and occasionally in the European turtle-dove. I have seen it also in the young of Florida ground-doves and of *Leptoptila*.

The general color of *Zenaidura* is more grayish; *Zenaida* has a little more reddish-brown. This indicates a higher development in *Zenaidura*. Thus, in head, neck, and breast, *Zenaida* comes nearer the turtle-dove pattern in general color and in the color of the feather's edge.[26]

Most of the scapulars bear two dark spots in both of these birds. The spots on the tertials, long coverts, and the second row of coverts are larger and more numerous in *Zenaidura* than in *Zenaida*. In this respect *Zenaidura* seems nearest to the original turtle-dove condition.[27]

Other young *Zenaida*[28] compare as follows with the zenaida (12) just described: In zenaida *10* the breast is duller in color in every way than in *12*, and the median

TABLE 6.—*Reconstructed* [29] *breeding-record of Zenaida, 1905–06.*

Pair 1. ♂ Zenaida vinaceo-rufa (2) (imported, probably from Venezuela, 1904).
♀ Zenaida vinaceo-rufa (2) (imported, probably from Venezuela, 1904).

?1. May 26, 1905*; 11; normal; dead Mar. 1907.
?2. May 27, 1905*; 12; ♀; normal; shade darker than 13 (see pl. 83).
?1. June 24*; 13; normal; shade lighter than 12.
?2. June 25*; 14; normal? or weak mutant?; shade lighter than 13.

Pair 2. ♂ Zenaida vinaceo-rufa (0), imported from Venezuela 1905.
♀ Zenaida vinaceo-rufa (12), May 27, 1912 (see above, and pl. 83).

?
? } Aug. 18, 1906*; 20; normal; alive June 10, 1907 (see pl. 84).
?1. Sept. 12 (?); not hatched.
?2. Sept. 28, 1906*; 21; ♀ MUTANT; dead Sept. 21, 1908 (see pl. 84).

* Indicates date of hatching.

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[26] The beak of *Zenaida* is "fleshy white," just beginning to show a tinge of duskiness, or horn-color. In *Zenaidura* the beak is dark horn, except the *operculum* (nasal scale), which is still very light horn-color. The feet and legs are only a shade lighter in *Zenaida* than in *Zenaidura*. The color is "reddish flesh-color."

[27] A pair of young mourning-doves, about 10 days old, were found and kindly brought to me by Dr. R. M. Strong in June 1905. In these birds every scapular seems to be double-spotted; the spots are, however, not as dark as in the adult. Elsewhere also the spots are fairly numerous. As the bird sits at rest, there are to be seen about 5 spots on the tertials; 3 on the long coverts; 5 on the next row of coverts; 3 to 4 on the third row of coverts; and 3 to 4 on the fourth row of coverts. In the coverts anterior to these rows, the spots are seen in most of the feathers in the upper half of the wing, but they are dull and not at all conspicuous. At the fore end of the wing the coverts are each marked with 2 dull spots. In these birds also it is the *operculum* that has a whitish horn-color—not quite so light a flesh-color as in *Zenaida*.

[28] No. *11* is a nest-mate of *12; 13* and *14* are sisters of *12* (see table 6); the relationship and age of *10* can not be learned from the available data.—ED.

[29] Complete records were of course made by the author, and I find specific references to them; but unfortunately they are not available to the editor. The tabulation represents that part of the record which is *repeated*, either in summary comment on breeding records (where these offspring were used as parents), or in legends for illustrations, etc. The interrogation points in the first column indicate that the "number of eggs," which had been laid during the season prior to the egg described, is unknown.

streak (homologue of the guinea-mark.—E𝐃.) of the feather is less conspicuous, and often fails to *reach fully to the tip of the feather*.[30] It thus ends somewhat more nearly as in the young of *Leptoptila*.

In the breast feathers of both *10* and *11* the *Leptoptila* condition is feebly indicated. In *10* the lower black mark on the side of the head has each black feather narrowly edged with whitish. This is less plain in the upper streak. Both of the black head-streaks are present in the young *Zenaida*.

Two other young (*13* and *14*) of about 5 weeks, are of a lighter shade than *12*; *14* is of lighter color than *13*. No. *13* is in turn a shade lighter than *12*. In *14* the mid light line dividing the feathers is white or nearly so, and very strongly marked, especially on the breast. Note should be made of the fact that there is a narrow streak of feathers running longitudinally through the middle of the breast where this mid-line (part of guinea-mark) of the feather is not seen; *i. e.*, these feathers are the later ones to appear,[31] and they have a stronger tinge of brown than the more lateral (ashy-brown) feathers. In some of the feathers of this breast-streak, especially in its lateral boundaries, the dividing-line of the feather is present as a triangular mark, but it is weaker and more nearly like the general color of the feather, so that it ceases to be conspicuous. This median streak in the breast and neck feathers is a *pale brown*—perhaps to be regarded as a grade towards the adult color (this color is a little stronger brown on *13*).

The mid light line (part of guinea-mark) is seen not only on the breast, neck, and head (it vanishes in the lower half of the posterior neck-feathers and the interscapular region), but is also well-marked in the lesser wing-coverts, and is present in all of the coverts, but becomes less sharp in outline in the two longer rows of coverts; it is obsolete in the tertials.

The primaries are not very dark brown, and they lighten up at the edges and tips; the shaft-line is pale reddish. The flanks above the legs are gray. The spots (chequers) are weak. On the tertials 2 are visible, on the long coverts 3, and on the second coverts there are 3. On the scapulars the spots are very feeble. The under tail-coverts are pale rufous-vinous, and are nicely marked at the tip with

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[30] The mutational mark that appeared in the mutant—No. 21—was thus observed to be slightly *accentuated* in the mother of the mutant.—E𝐃.

[31] This fact was noted in the preceding chapter to hold for "young" birds in general, and the "breast-crease" of these birds was thus explained.—E𝐃.

EXPLANATION OF PLATE 83.

M. Adult male *Zenaida vinaceo-rufa*. × 0.9. Toda del., Jan. 1907.
Imported direct from Venezuela, May 1906; died of tuberculosis March 1907. This bird was slightly larger than other birds obtained from the same region. The number of spots (chequers) is notably small. The tail is short, as in other zenaidas, and has 14 feathers. No trace of modified edges or median (normal buff) streaks of the juvenile. Also, none of secondaries or coverts with any white as in *Z. amabilis* (pl. 87). The color is strong with red.

B. Juvenal female *Z. vinaceo-rufa* (12), age 7 weeks and 5 days. Natural size. Hayashi del., July 1905.
(For origin, see table 6.—E𝐃.)
This is a rather dark specimen, some being a few shades lighter (first plumage). The feathers of the lower neck, in front and on the sides, have very narrow mesial streaks (pale-rufous) widening a little at the apex, where they become continuous with the pale apical margin. This same streak appears in some of the upper tail-coverts. This dam, then, exhibits in a very weak way the marks presented in the daughter (No. 21). Ordinarily such marks are not to be seen in this species.

PLATE 83

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A. Adult male *Zenaida vinaceo-rufa*. × 0.9. Toda del., Jan. 1907.

B. Juvenal female *Z. vinaceo-rufa* (12), age 7 weeks and 5 days. Natural size. Hayashi del., July 1905.

PLATE 84
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A. Juvenal normal (20) *Zenaida vinaceo-rufa*, age about 8 weeks. First plumage from photograph; and bird at somewhat older stage, for size, etc. × 0.8. Toda del., Dec. 1906. For description see text; pedigree, table 6.

B. Juvenal, mutant (21) *Z. vinaceo-rufa*, age 6 weeks (from photograph of Nov. 9, 1906, and bird at somewhat older stage for size, etc. × 0.8. Hayashi del., Mar. 1907. For description, see text; breeding data, tables 6 and 7.

the white triangular mark. The tail-feathers below are also similarly marked, though less strongly.[32]

The eye-streaks are not conspicuous in these birds. The ear-coverts forming a part of the lower streak are buff or pale brown, passing into whitish under the eye. Over the eye no streak is visible, but the portion of this streak lying in front of the eye is present and is whitish. The forehead at the base of the beak is pale-brown or buff. In the back-feathers of *13* some feathers of the second plumage—not fully unfolded—are intermingled with the first feathers. I found in some of these new feathers some persistent traces of the turtle-dove pattern, in the form of two lateral dark spots on the basal half of the feather. I then examined the juvenal feathers in the same place (near the rump), and also found faint outlines of the spot-areas there.[33] This seems of some interest, as spots have disappeared in this as in other species.[34]

ON THE JUVENAL PLUMAGE COLORS OF A "MUTANT" AND NORMAL ZENAIDA.

A juvenile *Zenaida vinaceo-rufa* (21) presents an interesting "mutation." This bird was hatched September 28, 1906. The front and sides of the head, neck, breast, and abdomen; the wings, scapulars, and under tail-coverts; and even the tail-feathers (below), are all marked with this mid-terminal, triangular white spot, which is the characteristic mark in the wing of the guinea-pigeon (pl. 84, fig. B).

This bird is just a little larger than *20* (which is of normal color, hatched August 18, 1906, from the same parents), but only a little younger. Both birds are now (November 9, 1906) in juvenal plumage and can be compared and photographed side by side. No one would take them for the same species, and yet they are from the same pure-bred parents.

I expect that these marks will disappear in the adult plumage.[35] If they do, then we have what might be called a "juvenal-stage mutation"; in other words, a character with all the appearance of a mutation, but transient. (See adult normal *Zenaida vinaceo-rufa*, pl. 83, fig. A, and adult *Z. amabilis*, pl. 87.)

It is important to know if this character is *entirely* new, or is it a great enlargement of a minute feature of the normal juvenal feathers. On this point the photograph of *20* supplies evidence (see pl. 84, fig. A); it shows just a beginning of this character on the neck—just a mere line.[36] This terminal dividing-mark is not *white* in the normal form, but pale buff or pale brown.[37] I have seen the same mark nearly,

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[32] Several of these feathers were plucked and preserved. From their appearance, and the above description, one would strongly suspect, after the test with mutant *21*, that the lesser degree of the guinea-mark exhibited by this bird (14) would also have perpetuated itself in its offspring. It is almost certain that the bird was not bred, and it probably died young. On the basis of the above description, I have ventured to question (table 6) the "normality" of this individual.—ED.

[33] These feathers were removed and mounted, but were never figured. After 11 years the outlines of these spots can still be seen.—ED.

[34] The feathers in the median back region of the European turtle-dove have "dark centers," especially on the rump.

[35] This prediction proved entirely true.—ED.

[36] Further evidence of the beginnings of the mark in *Zenaida* young has already been given in the preceding pages.—ED.

[37] From a *Zenaida* × *Zenaidura* hybrid (ZZC), which was hatched one day later than the mutant *Zenaida* (21), feathers were taken (from the same regions which were strongly modified in the mutant) for comparison with the latter. The following conditions were found: "The median buff or fawn streaks sometimes found in these feathers are not at all conspicuous, but they are evidently homologues of the mark seen in the *Zenaida* mutant. In a feather taken high up on the (right) side of the neck the mid-area is indistinct, but about 2 mm. wide at the tip; here, however, "gray" is so intermixed (with buff) that there is really no clear figure. A feather from just below the preceding shows the same mixed condition. Four other feathers from still lower on the neck show no apical figure, though there is a glimmer of buff in the form of a figure widening apically. In an upper tail-covert there is no sign of a figure." Of another similar hybrid (ZZ 2, sister to the above, see table 91, Vol. II) the author had earlier written (May 1905): "On the breast-feathers there is a reddish mid-streak (as in *Leptoptila*), which is wider at the tip, gradually narrowing inward to a point. The reddish is seen at the middle of the tips of the primaries, though there it is not regular in form, as on the breast. It is found also in the primary coverts. The nest-mate of this bird is quite similarly marked. *It looks as if this was the way the black center became divided into two lateral spots.* If so, it is essentially as in the common pigeon and in *Columba livia.*"

and of similar pale-brown color, in some Japanese and European turtle-doves, in the young of *Leptoptila*, and in the young of Florida ground-doves.[38]

This character (white guinea-mark) is a permanent character in the guinea-pigeon of Africa. In this species we should have no doubt about calling it a character. The mutationist would hold that it was an "immutable unit." Yet we see that it certainly is only an enlargement of the very minute dividing-line. Even in this specimen it is reduced to mere lines on the crown of the head and on the throat. What appears then to be a mutation turns out to be *not a really new thing*, but an extension and intensification of the normal mark.

Is there any explanation for this? I can account for it only by referring it to the hard time the bird passed during the first 2 or 3 days of its life. The old birds seemed to me to be a little unsteady about the time the egg was due to hatch. I decided therefore to place the egg under a pair of white rings which had a young nearly 2 days old. The egg hatched and the young was strong and tried hard to get food from the foster-parents; but they did not feed it. I held it up and gave it every chance, but they still refused to feed it, although they kept on feeding their own young, which was larger and stronger. I left it for a whole day to them and then placed it under another pair. The latter had an egg due to hatch, and the male fed the zenaida a little. After a few hours I again returned it to the white rings, taking away from them their own young, thinking that by the next morning they would feed. They sat on the nest, but refused to feed. When the zenaida was fully 2 days old I tried it under another pair that had eggs due to hatch. These birds fortunately fed the zenaida, and it grew rapidly, as these foster-parents were comparatively large birds. The zenaida flourished henceforth with plenty of food. It may be that the *lack of food* for the first two days was the cause of this enlarged mark—a sort of albinism.[39]

The editor should at this point call attention to the fact that the preceding account was written, as noted above, when this bird was but 6 weeks old and before a breeding-test of the mutation had been made. At the time this was written the author well knew that lack of food, tuberculosis, etc., were able to produce feathers with a reduced pigmentation, or even to suppress it altogether (albinism).[39]

In a note written two years later (in 1908) the author wrote: "This mutant (21) hatched *September* 28, 1906, from the *second* egg of the clutch"; underscoring the words "September" and "second." In view of the other data then at hand on the relation which both *season* and the *order* of the eggs of the clutch bear to the weakness of germs, it seems certain that these points were then in his mind as the chief explanatory features of the appearance of this mutation.

It has already been noted that the breeding data for the offspring of the mutant (21) are fully given in Volume II. The results in the first generation are, however, also given here in table 7. This table should prove of assistance in an examination of the illustrations of the subject, these illustrations being confined to this volume.

The offspring of several generations—to 1916—are shown in plates 85 and 86. The figures of these plates and the tabulated breeding data show, among other facts,

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[38] The young of *Zenaida auriculata*, according to Salvadori (Catalogue of Birds, Brit. Mus., Vol. XXI, p. 386), "have feathers of the upper parts and breast with white mesial streaks and edges; the primaries and primary-coverts edged with rufous."

[39] See Volume II, particularly Chapter XIV. It will (later) be seen that the author later recognized—after a breeding-test—that the cause of the variation or mutation was *germinal*, not environmental.—Ed.

A   B   C

D   E   F

Offspring of mutant *Zenaida vinaceo-rufa* (21). To show the transmission of the "mutational" character in a cross with a male *Zenaidura carolinensis*.

A. *Zenaida* mutant (21), age 6 weeks.

B, C. First generation hybrid, Z-ZN5 (see table 7); the mutational character fully present. on head, neck, breast, and wings, about the equal of its dam.

D, E. Two views of first generation hybrid, Z.ZN1 (see table 7); the mutational mark is represented on head. neck, and breast; on the wing coverts the apical mark is whitish, but it does not form a mid-streak (see text). Photo. Sept. 7, 1907.

F. Two third-generation "mutant" hybrids, 3Z-6ZN3 and 4. In No. 3 (right) the mark is stronger; it is present in all the tail feathers. No. 4 (left) a slightly weaker but good mutant, has the mark in two tail feathers.

the following: (1) The mutation behaves[40] more as a "dominant" than as a "recessive" character; (2) the character often appears in a reduced or fractionated form,[41] the white triangular spot of the wings assuming the form of a white crescentic tip;[42] (3) only two of the first-generation hybrids (Z-ZN 1 and 6) seem to have been bred (most of this progeny died early); one of these (Z-ZN 1) was mutational (pl. 85, figs. D, E) and the other "normal or nearly"; it seems probable that all of the mutants that have appeared (in other than the first generation) are derived[43] from Z-ZN 1— the first mutant young (from a first egg in life) of the original mutant; (4) the inheritance of the mutation, in neither the first nor later generations, is limited by sex.

TABLE 7.

♂ Zenaidura carolinensis (11) May 27, 1906.

♀ Zenaida vinaceo-rufa MUTANT (21), hatched Sept. 28, 1906; August 21, 1908; 24 months.

♀ A1. July 15, 1907. Z-ZN1—"mutant" on breast, lower neck, sides of head; Oct. 11, 1911; 52 months.
  A2. July 17, 1907. Z-ZN2—normal; Dec. 5, 1907; 4½ months.
  B1. Mar. 21, 1908. failed to hatch (exposure).
  B2. Mar. 23, 1908. failed to hatch (exposure).
♀ C1. Mar. 28. Z-ZN3—"mutant"; strong, except at bend of wings and back; May 17, 1908; 1 month.
  C2. May 30. Z-ZN4—relieved, died before feathering; ⅔ month.
♂ D1. Apr. 10. Z-ZN5—"mutant"; strong on head, breast and wings; Jan. 25, 1910; 21½ months.
♀ D2. Apr. 12. Z-ZN5—normal or nearly; Mar. 19, 1910; 23 months.
♂ E1. Apr. 24. Z-ZN7—normal, like D2; Oct. 1, 1910; 29 months.
  E2. Apr. 26. Z-ZN8—normal, like D2; June 9, 1908; 1½ months.
  F1. May 14. developed near to hatching, but parents deserted.
  F2. May 16. developed near to hatching, but parents deserted.
  G1. June 19. "development not completed" ⌈"I now notice (July 9, 1908) that the dam (21) is not quite well.
  G2. June 21. "development not completed"⌊ —legs weak;[44] this continued till death, Sept. 21, 1908."
♀ H1. July 11. Z-ZN9—normal; Jan. 20, 1908; 6 months.
  H2. July 13. fully developed embryo, thrown from nest and broken.
  I1. July 31. "failed to develop."
  I2. Aug. 2. "failed to develop."   (K, CCOO)

One or two of the above topics are touched upon in the author's description of the first mutant offspring (Z-ZN 1); this statement is therefore given herewith in full:

"This hybrid (Z-ZN 1) hatched July 30, 1907.[45] The mother of this hybrid is a pure-bred *Zenaida vinaceo-rufa* and the father a pure-bred *Zenaidura.*

"The mother has her juvenal feathers marked by a *conspicuous white triangular or wedge-shaped spot*, dividing the tip of the feather, as do similar marks in the guinea-pigeon; hence I called her a 'mutant,' as she was quite strikingly different from her mate or any other young zenaida I had raised. She had these spots on the head, neck and breast, and wing-coverts and scapulars; but this, her hybrid offspring, has *smaller* white spots, and only on the front neck and breast and on the sides of the head (none on the wings); in short, it inherits the *juvenal* mark of its mother—but in a degree that stands midway between the two parents—the mourning-dove sire having had no such mark.

"This hybrid has of course the apical edge marks on the wing-coverts, and these are quite whitish, but they do not dip in at the middle to form a dividing-mark.

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[40] See note to table 7.
[41] See Vol. II, Chapter XVII. This character was thrown into a cross generally considered of *generic* value, and the author has insisted (Vol. II) that when the wider crosses are made there is less of segregation, and clearer "fractionation," of the characters involved.
[42] The editor finds that the feathers of other regions than the wing may sometimes show only an enlarged, crescentic white tip; such birds are clearly intermediates of the normal and the strong or usual "mutant" offspring. To distinguish them I have called them "crescentics"; but on either side of these the lines are not sharp.
[43] As stated elsewhere, some of the *Zenaida* records were only very temporarily in the hands of the editor and were never later available to him. In the absence of the complete record we can not be more definite on the above point.
[44] "The weakening probably began some time before noticed. This female (21) began strongly transmitting her juvenile pattern, but as she weakened the male gained control and produced the normal type."
[45] Photographed, kindness of Professor Reighard, September 7, 1907.

"It is remarkable that a character of one parent that was entirely lost with the juvenal feathers should reappear in one of her hybrid offspring, but not in the other. Z–ZN 2, the mate, has no such marks. The inheritance in one offspring, however, shows that the mother still carries these spots potentially in some of her germs.

"This white mark is, however, only an 'enlarged copy' of the obscure mid-streak—*pale reddish or buff in color*—which generally can be seen on close examination in the breast-feathers of the more typical young zenaidas."

GENERAL CONSIDERATIONS.

The mutation hypothesis offers an easy escape from the difficulties presented in getting from one color-pattern to another. Like the creation hypothesis, mutation just covers each problem with an infallible and inscrutable saltation.

As Darwin[46] has well said, this view forces one "to admit that these great and sudden transformations have left no trace of their action on the embryo. To admit all this is, as it seems to me, to enter the realms of miracle, and to leave those of science."

If refuge from this truth-telling criticism be sought in minute invisible premutations, assumed to occur in the primordial germ-cells, then the "transformations" would shrink to the dimensions of ordinary heritable germ-variations and be quite indistinguishable. Mutations would thus merge in minute variations and leave only an empty name for an explanation.

Mutation stands for gaps and no bridges—jumping the very problem to be solved. Its discontinuities are unpredictable breaks in the lines of derivation, precluding both foresight and hindsight.

Specific characters are not separate units, but qualities belonging to the *whole organism*. When albinism occurs we see that it tends always to be wholesale; that is, the whole color is bleached. If it comes into greater prominence in one region than elsewhere, we do not find a sharp boundary-line, but rather a gradual reduction or increase in this or that direction. The *Zenaida* mutation shows this beautifully.

In the same way, if we find a particular color-mark in one feather—say the light edge, or the dark center, the transverse bars, the white dots (*Geopelia cuneata*)—we find this mark tending to appear in all feathers; or we find it in derivative forms, or possibly in faded or weak forms. The loss of spots in pigeons, the turning to gray, etc., are all phenomena of the bird as a whole. We accept neither the *monotone* germ-plasm nor the *polymikt* germ-plasm of Weismann.

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[46] Origin of Species, Chapter VII, p. 241.

EXPLANATION OF PLATE 86.

A, B, C. Later offspring (1910) of the original *Zenaida* mutant (21).

A and B. Front and rear views of two good mutants (at ends) and one weak or "crescent" mutant (center) in juvenal plumage. (Of complex derivation, hatched 1911, reaching to No. 21 through Z–ZN 1.—Ed.)

C. Two second-generation (1910) mutants, 2Z–3ZN 7 and 8, age 6 weeks. The breast has guinea-marks well-defined, but rather smaller than in the best mutant offspring. The head had very small or narrow spots. The wing-coverts were white-edged, but without the triangular spots, except very weak marks at the bend.

D, E. *Zenaida* mutant offspring of 1915 and 1916.

D. Fourth-generation normal (nearly) and mutant offspring (B227 and B229, hatched July 30, 1915). Dam, 3Z–6ZN 1 (see chap. 10, vol. II); sire, 876, hatched 1912 (from complex *Zenaida* × *Zenaidura* parents). (Photographed Aug. 1915 by C. W. Palmer.—Ed.)

E. Fifth generation of mutant offspring, Nos. 82 and 83 (smaller pair); hatched June 30 and July 1, 1916. Dam, 916 (1915 sister of birds of fig. 4, above); sire, 876 (1912, from complex *Zenaida* × *Zenaidura* hybrids of incomplete pedigree). The two larger birds (at ends) are 1916 offspring, of the fourth generation, hatched May 23, 1916, from same parents as 1915 young shown in figure 4. These birds had probably molted some feathers. Both are fairly strong mutants. (Photographed July 11, 1916, by C. W. Palmer.—Ed.)

A, B, C. Later offspring (1910) of the original *Zenaida* mutant (21).

D, E. *Zenaida* mutant offspring of 1915 and 1916.

PLATE 87

Adult female *Zenaida amabilis*, slightly larger than natural size. Hayashi del., Mar. 1906. Imported (said to have come from Cuba) Nov. 1905. Color and chequers much as in *Z. cinareoenia*, except that the secondaries are tipped with white. According to the (rather unsatisfactory) descriptions of the zenaidas by Salvadori, two other species (*Z. aurita* and *Z. yucutanensis*) share with this species the white-tipped secondaries. There are here 12 tail feathers. The adult is wholly free of triangular spots or guinea-marks.

De Vries holds that mutation is directionless. How does it happen that the same set of mutations continually recur year after year in a succession of generations from a single stock, and likewise from different stocks or families?

This is conclusive that the character of the mutation is nothing *accidental;* the mutations are not one thing in one plant, another thing in another plant, one thing this year, another next. They are the same kinds repeated, some with more, some with less, frequency in each sowing.

The doctrine of multifarious mutation has to be saved by an assumption that has no foundation in observation, namely, that mutation started originally in a haphazard direction; but it was then passed on as a "latent" thing by heredity. It is, then, founded on a pre-existing, definite basis every time, except the time when it first made its appearance as an internal character. This is a premutation—actual mutations are all preceded by latent ones appearing in a premutation period.

If white dots, formed in the same way, in *Geopelia cuneata* and in a rail are a mutation, then mutation follows in one way rather than many ways. The same mutation occurs in different species. Spots appear in homologous places and according to the same law. These facts tell against an "orderless" mutation.

De Vries holds that species are separated by absolute gaps that can not be closed up. They arise by jumps or as sports. Were this the case we ought to see sudden gaps in fertility. I find that fertility is a thing of degrees—*i.e.*, it is at an optimum within the species, but it diminishes gradually, not by steps, as we pass from the crosses between species closely related to crosses of species wide apart.[47]

Again, fertilization within the species is of every degree, and results therefore in simple penetration of sperm which fails to make more than an early beginning of development or nothing at all, or it may give stages of change, etc., up to blood formation, and from this point it may go on and stop after forming an embryo, or at any point up to hatching; and when hatched, the fate is not yet settled; the bird may be deformed and still live; it may be too weak to develop further or go on and die at 3, 4, 5, 6, or more days.[48] All along the line we see that development requires energy and stops or goes wrong for failure in this.[49]

We have to remember that all permanent modifications in species have to be represented in the germs. Further, that "continuity of germ-plasm" is the fundamental fact in heredity. There is really no transmission of characters anywhere in the organic world. There is growth by assimilation and self-division, but no transference of characters from parent to offspring. Parent and offspring are each independent developments, alike or different according as the germs from which they develop are alike or different, and according as the conditions of development and life are alike or different.

All organic likeness depends on assimilation—the physical process of intussusceptional growth—akin to crystallization. In the crystal we have stable equi-

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[47] Examples of such a series are the following: White and blond ring; Japanese ring and blond ring; blond ring and Chinese ring; blond ring and European turtle, blond ring and tiger turtle; blond ring and homer. And similar to the last named, blond ring and *Ectopistes;* white or blond ring and mourning-dove; blond ring and white-wing; common pigeon and Japanese turtle. (These five last-named crosses are all of *family* or of *subfamily* rank. —ED.)

[48] Young birds often make failures. Doves reach the highest point at 3 to 4 years.

[49] The energy of development and degree of fertility appear to be correlated. May the same developmental process *run to different lengths,* according to the greater or less strength or energy? I think the male in many species of birds passes directly through and beyond the female stage. In many cases even the females may now and then pass beyond the normal female and advance towards the male condition. *Ontogenies seem to lengthen,* if the biogenetic law is true, and perhaps all evolution depends as much on *lengthening* as on *modification.*

librium; in the organism we have a fluctuating equilibrium kept up between loss and replacement.

A form that is constant in nature is a form in which the characters have reached a condition of balance—of stable equilibrium. If we select a variation in one direction—deal with a single character—we find the variation can be maintained only by the continued aid of selection. Without this aid regression carries the form towards the type.

The variation is transmissible, but liable to regress, because the other characters have not moved with it. For stability, the organism must change as a whole. The center of gravity for the whole organism must shift; all of the parts must be readjusted.

Artificial selection is one-sided, and works with forms that are the expression of weakness, abnormal strength, and with features that are in reality deformities due to internal derangement or abnormal external influences.

In ontogeny we have invisible changes going on for a longer or a shorter time, and then the outward change appears as the summation of the internal steps. This is illustrated in color-patterns that come on at the end of periods of apparent rest.

Ontogeny teaches us, then, that there are no disconnected jumps in its processes. The visible surface-changes are often separated by intervals of apparent rest; but these periods of seeming inactivity are filled with subtle internal processes that bind all the external form-changes into one unbroken sequence. The invisible work going on beneath the surface follows steadily in a definite direction, culminating at the appropriate times and places in all of the outer and inner form and structure characters peculiar to the species. Every organ and tissue has its history running continuously back through serial form-changes and differentiations that become more and more simple, until finally even the rudiments sink out of sight and are lost in primordials indistinguishable with the most powerful microscopes.

When we reflect that the periods of development required to individualize the rudiments of organs must correspond in many cases to ages of phylogenetic history, we begin to realize that the *time* of specific characters does not date from the moment of becoming visible, but from the very first inception of the primordial.

If we shrink from the idea of a primordial carried along in the germs of successive generations for long periods without revealing itself in a visible character, it may help us if we recall the fact that primordials that have already come to full development as visible characters may remain latent and invisible for many generations, and then reappear in perfect forms.

The guinea-mark thus comes as a "mutation" in a young *Zenaida*, but it has a premarked adumbration in the breast-feathers of many *Zenaida* young, in the young turtle-dove, and other species. Moreover, it lasts here only in the first feathers, being lost in the second plumage. But these marks in the juvenal feathers, although they disappear in the adult, are yet hereditary, for they appear in the juvenal feathers of the second generation.[50] They are therefore referable to the germ-cells rather than to any special conditions of environment.

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[50] If these first feathers had been pulled out at short intervals, in an early period, I believe the marks could have been *made to disappear gradually*, and show its continual gradual elimination, just as continuity can be shown in the diamond-dove and other forms. (See Chapter X).

NOTE.—The manuscripts and records used in the preparation of this chapter were found in folders designated as follows: C 21, CC 2, CC 3, C 000, CC 0, CC 000, H, H 12, I, K, L 10, Misc., W 2, W 6, WW 1, WW 6, XS 1, XS 3. XW 2, Z 3, Z 8, Z 9.—ED.)

CHAPTER X.

THE PROBLEM OF ORGANIC DEVELOPMENT—FACTS AND THEORIES.[1]

"Die allegemeinen Probleme gehören doch zum Wesentlichen jeder Wissenschaft, und die allegemeinen Erkenntnisse sind die Krone unseres Wissens."—PAUL JENSEN, Organische Zweckmässigkeit, page vii.

If all branches of biological research may be said to have a common goal, and if the present trend of theories, methods, and interests in morphology and physiology has real prospective significance, then we have not far to look for a proximate definition of that goal. Variously aimed as are our many strivings, they appear to me to have a common focal point in a comprehensive understanding of the nature, laws, and limits of organic development.

Development is the one word that seems to me to best circumscribe the more general problems of biology. It is also the one word that best emphasizes the essential unity of ontogeny and phylogeny. These two terms have been used as if they stood for two distinct series of phenomena, when in reality they apply to one and the same series. The misconception is far-reaching and fruitful in mystification, as the never-ending controversies over the biogenetic law well illustrate. These controversies have turned on the question of the causal relation affirmed to exist between ontogeny and phylogeny, the latter being supposed to furnish a causal explanation of the former.

As a clear apprehension of this law is of crucial importance in the interpretation of such phenomena as I have to present, and as an examination of its contents will, I think, bring us somewhat nearer to the fundamental problem of organic development, let us see if we can get at its essential truth.

As all know, it is to Professor Haeckel that we are indebted for the name and the current formula of this law. Professor Haeckel's formula, now nearly half a century old, runs thus: *"Ontogenesis is a brief and rapid recapitulation of phylogenesis."*

Phylogeny is viewed as the primary fact upon which ontogeny is causally founded, being conditioned by heredity and adaptation. Now, we must admire the genius that can take the problem of development as Haëckel found it and so concisely and luminously state the great riddle in its fundamental facts and cause. Of course we do not forget that before the appearance of Haëckel's "General Morphology" the greater minds in biology for more than half a century had been moving toward such a formula. The whole grand procession, led by such men as Kielmeyer, Geoffroy Saint Hilaire, Lamarck, Meckel, Von Baer, Johannes Müller, Louis Agassiz, Vogt, and last, but not least, Darwin and Fritz Müller, must be said to have a voice in Haeckel's delivery.

The progress of bilogy since 1866 has raised an increasing number of critics of the biogenetic law, but they have not seriously weakened the general conviction of its validity.

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[1] An address before the Seventh International Zoological Congress, Boston Meeting, 1907. No part of this address (SS 13) has hitherto been published. A few pages of a manuscript (Z 10, on the *Geopelia cuneata* experiment) written in the same year on a wholly similar subject has also been included.—ED.

The formula, as I have said, makes phylogeny the primary fact and ontogeny merely its hereditary repetition, condensed and modified in adaptation to conditions. Phylogeny is thus viewed as the necessary antecedent, and hence as the causal foundation of ontogeny. Phylogeny is viewed as the outcome or product of environmental causes, while ontogeny appears as the hereditary re-rendering of this product in the order of its cumulative acquisition.

We have then, according to this view, two quite distinct series of events, with causal relations equally distinct. In one case the causes are predominantly internal and limited to specific ends, and their work proceeds with clock-like regularity, ending punctually and within a brief time in the production of the individual.

In the other case, the causes are predominantly external, multifarious, and directionless, and their work is aimless and tentative ending in this, that, or other unpredictable result. Chance and utility are supreme in this field.

So far I have but sketched the prevailing view, and have barely alluded to what seems to me to be a source of misconception and confusion to the advocates of the law, and at the same time a fair provocation for criticism. We may now look for the essential truth of the biogenetic formula. When we take two aspects of one and the same thing and dwell on their contrasts, the point of departure, where truth lies, may be lost sight of.

In the case of ontogeny and phylogeny we push the error to the point of self-contradiction, by putting phylogeny before ontogeny. The moment we return to basal facts we discover that apart from ontogeny there is no phylogeny. All that we call phylogeny is to-day, and ever has been, ontogeny itself. Ontogeny is, then, the primary, the secondary, the universal fact. It is ontogeny from which we depart and ontogeny to which we return. Phylogeny is but a name for the lineal sequences of ontogeny, viewed from the historical standpoint. It gives us the lines of continuity in descent and enables us to read illuminating sequences in the origin of species, characters, structures, etc. When we can arrange ontogenetic events in the order of genetic dependence, we are in a position of great advantage in the search for causal relations. But these relations have no physical basis outside of ontogeny, and no outside existence except as mental constructions.

From this point of view the biogenetic law stands for an indisputable, fundamental, and universal fact—indeed, the central fact of all organic development. Stated in conformity to facts now known, the formula may be revised as follows:

Ontogeny is reproductive recapitulation, and germinal variation is the source of all phyletic deviation in ontogeny.

Thus stated, we remove the source of contention, namely, the assumption that phylogeny shapes itself through the transmission of characters acquired in the Lamarckian sense, and that ontogeny comes in secondarily to retrace the path determined by somatic modifications. The old formula obscures the fundamental fact that recapitulation is simply reproductive repetition, and at the same time misrepresents causal relations. To say that modifications functionally acquired in the soma are reflected back upon the germs of the coming generation in such a precise way as to repeat themselves in ontogeny, independently of original causes, is to turn the original sequence upside down. The form-sequence in ontogeny always runs forward or upward, and the causal sequence must of necessity run in the same direction. The contrary view is a wholesale perversion of the problem

of development, which leaves heredity to recapitulate in the absence of the original causes.

When we put upon heredity the task of recapitulating, in the sense of echo-like reverberations of ancestral experiences, or by the aid of an omnipotent entelechy, or through swarming pangen-deities, the door of mystification is wide opened. The unity of ontogeny and phylogeny is lost sight of, and recapitulation looks like a stupendous myth invented in order to bring together two independent miracles.

On the other hand, when we recall that ontogeny, or development, circumscribes the whole field, that recapitulation is the law throughout this field—a law referable everywhere and always to primordial processes physico-chemically determined, such as assimilation, growth, and self-division—then it becomes a most impressive fact, with no shadow of myth about it.

When the crystal recapitulates the form and symmetry of other crystals formed of the same material under like conditions, we are content to view the matter from a physical standpoint, and we postulate no ancestral echoes, no entelechies, no mysteriously circulating pangens. Recapitulation in the organic world is in principle the same. It calls for no architect, no agencies of any description except the physico-chemical elements combined in a system of metabolic relations, to which we give the name germ-cell. This germ-cell develops true to its species and type; another germ-cell from the same parents does the same; hundreds and thousands of these cells repeat the same steps, at the same times or at different times. They do not imitate, they do not catch the art from one another; they do precisely what they are physically bound to do, each for itself, and each the same just because each is the unit-system of energies. *All reproduction is recapitulation in the same sense.* Recapitulations are alike because the germ-cells in which they occur are alike, and germ-cells are alike because they arise by equal self-division of mother cells. Likeness is not an infection; it is not transmission at all; it is wholly and only *original* wherever it appears in development.

But if this be true, what becomes of transmission, pangen theories, and circulating unit-characters? We have long been taught that heredity means transmission, and upon this idea theories have been built.

Every theory founded on the postulate of unit-characters or specific determinants stored in the nucleus is necessarily committed to some form of centrifugal distribution during the course of development. Herein every such theory breaks down, for it is utterly inconceivable that preformed specific elements could ever be transported each in its time to a particular point in such a complex mosaic field as the organism represents. It is, I believe, a waste of time to try to conceive development as thus prepunctuated in all its space and time relations. It is to indulge in ultra-scientific teleology.

When we take from these pangen deities all that speculation has injected into them or wrapped around them, nothing remains but physical elements in self-sustaining organic relations. In brief, we have a primordial germ-cell of the same specific constitution as the mother-cell that preceded it. The mother-cell transmits nothing. When it divides into two daughter-cells it merely divides itself, and each moiety has the constitution it had before division. If, then, the daughter-cell is an exact copy of the mother-cell, there is no wonder, since it really is the mother-cell in substance, constitution, behavior, and potentialities. It is all this, and yet

no transfer of qualities has taken place, and it is plain that transference or transmission is absolutely impossible in the nature of the case.

It is well to remember that we have in every ontogeny a flowing sequence of specific forms, for every stage is as specific as the end stage. In this progressive change of form we see an interesting difference between the development of the organism and the development of the crystal; nevertheless the form is as certainly a "physical determination" in the one case as in the other. The crystal has its specific form, and sometimes several specific forms. In every case it owes the form to the nature of its material elements and the conditions under which it arises. We would not think of ascribing its form and symmetry to hereditary transmission; neither would we think of intercalating any directing or formative agent, distinct from the material elements composing it.

Fundamentally considered, the organism and the crystal are equally *self-determining* at every step, equally the products of intrinsic physical properties and conditions.

The crystal is said to grow by "accretion," the organism by "intussusception." But this is merely a superficial difference that does not affect the general standpoint. From a physical standpoint the essential thing is not where the elemental particles attach themselves, whether interstitially or superficially, but that they attach themselves in a self-regulating determinate way, so that the typical form at every step is autogenic rather than allogenic (Jensen).

Now, while developmental recapitulation is so wonderfully exact that we never cease to be amazed at the accuracy of its reproductions, we do not forget that germ-cells are subject to slow variation. Absolute perfection of reproduction could, of course, not be expected, even if outside influences should remain uniform. It is this germ-variation—which we may regard as the error of recapitulation—that becomes so all-important for phyletic departures, for it is the only variation that can be hereditarily recapitulated and thus perpetuated. When the germ-cell begins with a slight initial deviation, the whole series of developmental stages is affected, as we must infer, even though we may be unable to discover the digression until near or at the end of development. Succeeding generations begin recapitulation at the same level, or at the new point in the same level. Through germ-variation, then, recapitulation makes all its permanent advances.

But how comes it to pass that these advances are, on the whole, adaptive, and progressively so? Recapitulation can only conserve what is given. If it moves onward in a progressive way, there must be some way of limiting germinal variations to lines of cumulative improvement. Here we find ourselves confronted with the difficulty which has long led investigation and theory, and the solution is yet a long way ahead.

The creation hypothesis may be said to have passed out of science with Louis Agassiz, and to have received its death-blow at the hands of Darwin. The old teleology has lost all standing in science; and vitalism, entelechy doctrines, and the like are no less incompatible with science. Lamarckianism has been effectually silenced by Weismann. The mnemogenesis dreams of Hyatt, Cope, Hering, and Haeckel have not saved the doctrine of the transmission of acquired characters. The "centro-epigenesis" theory of Rignano, suggestive and instructive as is the attempt to approach the explanation of vital phenomena, fails to revive the lost

faith in the old transmission theory. Richard Semon's recent work, "The Memory as the Conservative Principle in Evolution," appeals to admiration as a splendid contribution in behalf of the same defunct theory.

The principal theories now in the field are three: selection (Darwin and Wallace); mutation (de Vries); orthogenesis (Nägeli and others).

The only tests for theories are, of course, facts; and by facts I mean not such facts as we may compile by the hundreds, when we are merely counting variations the relations and origins of which we only know by report, or by hurry-scurry observation, but facts that can be examined in their natural connections, facts that have an approachable history and are open for consecutive study and experimental handling. The worst of all faults in research is to snatch at facts and ignore their genetic relations.

In order to show how selection, mutation, and orthogenesis differ in attitude toward facts I now bring before you a single brief study in the transmutation of a color-pattern. It is a study in specific characters that admit of being traced step by step in the living bird and that are amenable not only to comparative and genetic study but also to simple experimental test. It is a study which will also illustrate the biogenetic law—continuity in the processes of specific development, actual flowing transitions between characters which, at first sight, appear to be separated by mutational discontinuities. The importance of such transitions is at once apparent when we recall that the mutation theory is based on the assumption of discontinuous unit-characters, between which there can be no real transitions.

Possibly some who are not familiar with color-marks as specific characters may feel, as we have elsewhere remarked, that they have not the same genuine tangible specificity as is exhibited in bones, tissues, and organs. Colors may fade and pass through shadowy phases that to the casual observer give them an air of insubstantiality. Then, too, there is such profusion and intermingling of colors, especially in domesticated animals and plants, that they are apt to impress us as emblematic of inconstancy.

When, however, we turn to wild species, we get a very different impression. Here color-characters are as constant as other characters, and as they are displayed at the surface, they have the great advantage of accessibility for study and experiment.

One other point may be briefly touched here. Prevailing methods of collecting data, especially in the field of evolution, have tended to overmagnify the importance of mass and large numbers and to underestimate the value of the all-round study of the individual case. The pressing need of the hour, as I see it, is the persistent exhaustive study of the single favorable cases. Crucial evidence is always individual in the last analysis. Many half-truths can not make a whole truth, and the omnivorous rambling collector should learn from Darwin, Mendel, and de Vries how much more effective attention becomes when it dwells intensively on some advantageous focal point.

Let this be my apology, if one be needed, for inviting attention to a single color-pattern, as one among many available cases in which to point out a test for theories.

Our three theories again briefly characterized are as follows:

(1) *Mutation* stands for gaps and no bridges—jumping the very problem to be solved. Its discontinuities are unpredictable breaks in the lines of derivation, precluding both foresight and hindsight.

(2) *Selection* follows chance advantages, and is impotent to *guide* incipient stages or to explain the presence of non-useful or neutral characters. It enthrones multifarious variation and refers continuity in progress to external fortuitous control rather than to internal self-regulating processes. *Germinal selection* (Weismann) recognizes the necessity of "internal regulation," but finds only chance-loaded dice, and selection still supreme.

(3) *Orthogenesis*, as here conceived, enables us to predict, to some extent, stages yet to come in the evolution of color-patterns; to trace histories of past sequences; to put order and meaning into fragmentary taxonomic descriptions; and to anticipate the discovery of elements that have been overlooked. It enables us to understand parallel evolution in allied species, even when living under quite unlike conditions. It saves us from the stultification of holding selection sufficient to account for those long and definite lines of evolution revealed by paleontology. It helps us to see that *biogenetic recapitulation* rests in a physical basis and must therefore be taken as an indispensable guide to phyletic sequences, especially in the stages of immaturity, in which allied species frequently differ, not so much in *divergence* of development as in the *extent* to which development is carried in one and the same line. That is, two species may differ from each other in the same way that the two sexes in the same species differ, when the male passes on beyond the stage in which the female halts.

Recapitulation is no myth. Everyone knows that ontogeny repeats its sequence of stages with an accuracy that approaches physical exactness; and that such repetition is attributable to germs of like constitution, developing under like conditions. It is impossible to conceive of such sequences resulting from kaleidoscopic mutations, or from chance-deliveries of any description. The best proof that the organic world is the product of evolution, the first term or terms of which were the units we call cells, is the fact that ontogeny in every species keeps on ever repeating this stage, not as a chance conglomerate, but as a primordium of very definite constitution, capable of developing with clock-like regularity to a specific goal. Consider, too, the remarkable uniformity that prevails in the stages leading up to fully formed germ-cells; the processes of fertilization and maturation; the essential likeness in cleavage-processes, however much obscured by the presence of inert food-yolk; the irreversible sequence of the ascending form-phases, etc.

In view of all this, what are we to expect in the later stages of closely allied species descended from a single parent form in relatively recent times? Whether we have one-sided branching, equal divarication, or unequal prolongation of the parent line of evolution, the presumption is all in favor of the recapitulation of the ancestral end-phases in more or less typical form in the first or juvenal plumage.

The immature geopelias offer some convincing illustrations of recapitulation. As an example, we may consider the apical marks of the feathers of *Geopelia tranquilla*.

THE APICAL MARK AS AN EXAMPLE OF RECAPITULATION.

This apical mark, which is seen on the feather tips only for the few weeks during which the juvenal feathers are retained, and then completely vanishes at the first molt, is a character common to all pigeons, if we except a few species that have

undoubtedly lost it.[2] It differs in different species in width, in color and shade. Only a few pigeons preserve the mark in the adult feathers; the greater number lose it with the first molt and exhibit it as a mark in almost every stage of decline in the juvenal feathers. I may add also that the pigeons share this character with a very large number of birds, probably with the avian phylum as a whole. In other birds the character is also sometimes permanent, but generally transitory, and frequently reduced to vestiges that are scarcely more than just visible in the first feathers. This interesting vanishing stage is seen, for example, in the young robin.

These apical marks are very obscure or nearly wanting in the young of the more highly bred fancy races, especially in those of a pale-gray color. They are best defined in dark-chequered or blackish birds of the *Columba affinis* type. The mark is crescentic in form, 0.5 mm. to 1.5 mm. wide at the shaft-line in the larger coverts. As these crescents edge the tips of the feathers arranged in transverse rows across the wing they produce a more or less obscure "lacing" effect, but as they stand alone on each feather they do not suggest cross-bars. It is only very rarely that we find in juvenal pigeons anything that would pass as cross-barring,[3] as this term is commonly understood, and it is only in such exceptional cases that the apical crescents could be confounded with bars.

I was for some time puzzled to find any meaning for this transient character. I soon noticed, however, that it was invariably narrower in the two-barred than in the chequered type of rock-pigeons, and further, that its vanishing-limit was reached in races that had made the widest departures from the ancestral rock-pigeons. As I carried the search for this character among the wild species of pigeons, I found that the same rule generally held true, the mark tending to a vanishing-limit in the higher species, although with some exceptions.

As I had already discovered a tendency prevailing among both wild and tame pigeons to lose spots and chequers, I began to realize that the apical crescent was a thing of history and destiny; and that, in the case of the entire group of rock-pigeons and their domestic descendants, it was a character slowly verging to complete disappearance.

But in a few of the "exceptions" just alluded to I found this character in what seemed to be a primitive and typical condition. The oriental turtle-dove (*Turtur orientalis*) of Japan and China and its two nearer allies, *T. ferrago* of India and *T. turtur* of Europe, are good examples. In these doves the apical mark appears at full width in the juvenal plumage and persists practically unchanged in the adult bird. Herein these turtle-doves betray a phyletic secret of no doubtful significance when supplemented by another presently to be mentioned.

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[2] Even such a transient color detail as the apical mark, which at first sight seems too trivial to deserve more than mere mention, may have a wholly unsuspected significance when its genetic and phyletic relations are discovered. If these marks have any significance beyond that of giving the plumage a "barred" appearance, we can only hope to find it by tracing their history in the species, and by a comparative study of other species having a similar character. The study of single characters from this point of view becomes a study in the evolution of species, and should give us *test-cases* for theories far more conclusive than any furnished by sport-hunters and compilers of reported discontinuities, and far beyond the depth of pretentious statistical curves, in which a linear series of multifariously collected units is expected to reveal the secrets of an *assumed* multifarious variation. The *artifice* reveals the assumption necessarily. No disrespect for the curve, for the curve tells the truth even when it gives us back the lie we put into it. It is *genetic history* that gives us the sequence of variation—the true linear series. Such history can not be read in the "large-number" curve. Comparative research and experimental culture are what the problem demands.

[3] "Fundamental bars," as I have called them, are always present; but these are so obscure that they have been universally overlooked, and hence may be left out of consideration here. These have been studied recently by Mr. Riddle (Biological Bulletin, xii, 3, page 165, Feb. 1907). (These are figured and described in Chapter VIII.—Ed.)

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Eventually, after a comparative study of the various neck-patterns in different species and finding that they all pointed to the turtle-dove as a progenitor, and after learning to read phyletic relationships in the voices, in the courtship behavior, and in the general color-patterns, I came to see in the "dark center" and the "light apical edge" of the turtle-dove feather a simple unit of coloration reduced to paleness at the distal edge, and thus converted into the simplest element possible for an archetypal plumage-pattern. From this source have arisen, as I have elsewhere pointed out, all the varied color-patterns of the pigeon world.[4]

This conclusion naturally turned my attention to the color-patterns of birds in general. Paying special heed to the patterns of immature birds, and to the *sequence of patterns* presented in the young and the adults of both sexes, I soon found convincing evidence in great abundance that the pigeon unit of pattern was at the same time the avian unit. If any one doubts this let him glance at almost any available material, such as the jungle-fowl, the pheasants, ducks, gulls, terns, etc.

Later, a discovery of cross-bars in the feathers of a pigeon led me to another series of problems, the study of which has opened new vistas in the feathered world, confirming the conclusion just stated, and at the same time revealing a secondary relation of the apical mark. The juvenal patterns of the geopelias and of several American species (*inca, Zenaida*, etc.) were most instructive, enabling me to see in this mark a *forerunner*, so to speak, of cross-bars appearing first near the distal end of the dark center of the feather and increasing in number gradually in a basipetal direction.

If any one doubts that we have here continuous transitions, and demands demonstration by experimental breeding and establishment of new species, my reply is that this has all been done over and over again in the case of domestic pigeons, and the results are open to inspection in not less than 150 species, all obtained by breeding and selecting from the parent stock—the rock-pigeons. The breeder has neglected to keep written records, but his methods for thousands and thousands of years have undoubtedly been essentially the same as to-day. Nowhere in the plant or animal kingdom can we find achievements more remarkable or more simple and instructive for study.

Fancy has dominated the breeder's operations, but in the main he has only augmented and intensified natural productions. The apical mark had probably vanished from the mature plumage when man first began to cultivate the pigeon, and it was therefore past his control and too inconspicuous and transient even to appeal to his interest. The trend of evolution in this character has certainly continued the same as in the majority of the wild species, and the fancier has at most only hastened its evanescence.

Moreover, nature has performed similar experiments in hundreds of wild species, and has left the results of her work in stages that keep on repeating in invariable sequence. No single experimenter could ever approach the perfection of nature's experiments, or ever hope to pile up such confirmations as ages of domestication have turned out.

But the field of experiments remains ever open, and out of nature's hand we may take one that is direct, unequivocal, and at the same time simple in execution. The natural experiment occurs regularly and automatically in the first plumage of

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[4] See Chapters II, III, V, and VI.—Ed.

many pigeons; and if we wish to take a part in it, all we have to do is to provoke its repetition at proper intervals.

First, let us see what nature does, and then what we can add to the demonstration. In the common pigeons, as I have said, the apical mark is a vanishing character which comes to an end with the juvenal period of development. In the second plumage no trace of it appears. There seems to be a sudden jump from one stage to the next, with no intermediate transitional phases. To a mutationist it might seem that ontogeny was recapitulating a final phyletic sault—"*a sudden strange transfigurement.*"

If such be the nature of the passage from the juvenal to the adult plumage, what should we expect in case a number of the first feathers should begin development later than the rest? Would the belated feathers appear in the juvenal or the adult pattern? Certainly it should be either one stage or the other, for the mutation theory does not admit of midway transitions.

We have just this test of the theory given regularly in a small tract of the lesser coverts of the wing. Two or three rows of these coverts, forming an oblique tract crossing the fore-end of the wing, from wrist to elbow, in line with the bones of the forearm, appear 10 to 14 days later than the rest.

In our common two-barred pigeons this tract of feathers always makes a nearer approach to the adult color than do the other juvenal feathers. Its gray is freer from the brownish tinge characteristic of the first plumage, and the apical marks are lost, or reduced to vestiges difficult to recognize (text-fig. 15). In chequered varieties more distinct traces of these marks are generally visible, but it is only now and then that our domestic birds give us the test in a fairly satisfactory form. A single example happens to be available at this time; it is a young blackish-brown hybrid, about 15 days old, from a male red barb (offspring of a pair of black barbs) and a female red and white jacobin. The feathers of this hybrid have dull *reddish tips* 1 mm. wide. The oblique tract, lying between the lesser and median coverts, has 2 to 3 rows of pin-feathers, which are nearly all concealed by the overlying lesser coverts. Some of these pins are just beginning to unfold, and 3 to 4, near the bend of the wing, are long enough to protrude 3 to 5 mm. beyond the lesser coverts. In this specimen (text-fig. 16) the feathers of the oblique tract, so far as unfolded, show the apical mark, but weaker in color and reduced to about half width. We see here progress halted about midway between juvenal and adult conditions.

In this connection I may refer to another hybrid, now a year old and in adult plumage. This hybrid was obtained from a male homer (black-chequered) and a female oriental turtle-dove. The homer has no apical marks; the turtle-dove has the mark as a permanent character. What should we expect in the hybrid? In the juvenal feathers the mark was much stronger than in common pigeons, but weaker than in the turtle-dove. In the adult feathers I find that the mark has been preserved, and at a width of about 1 mm., or nearly the maximal width seen in the *juvenal* feathers of common pigeons.

These two hybrids exhibit the mark in intermediate conditions, the one in the juvenal feathers, the other in both juvenal and adult feathers. Such evidence can be easily multiplied to various degrees of transition, but the test would be more demonstrative if the degrees were presented in natural sequence in a single individual.

Nature meets our need much better in some wild species, in which the apical mark has been well-preserved in the immature feathers. The ground-doves of the genus *Geopelia* amplify the test to multiple demonstrations, in one and the same plumage.

Let us examine three successive stages in the wing of the young peaceful ground-dove (*Geopelia tranquilla*). At the age of 17 days (text-fig. 31) the earlier feathers (shown in text-fig. 30) are already well-developed and the oblique tract is only partially feathered. Excluding for the moment the scapulars, primaries, secondaries, and tertials, we see three conspicuous rows of coverts (I to III); then a fourth row
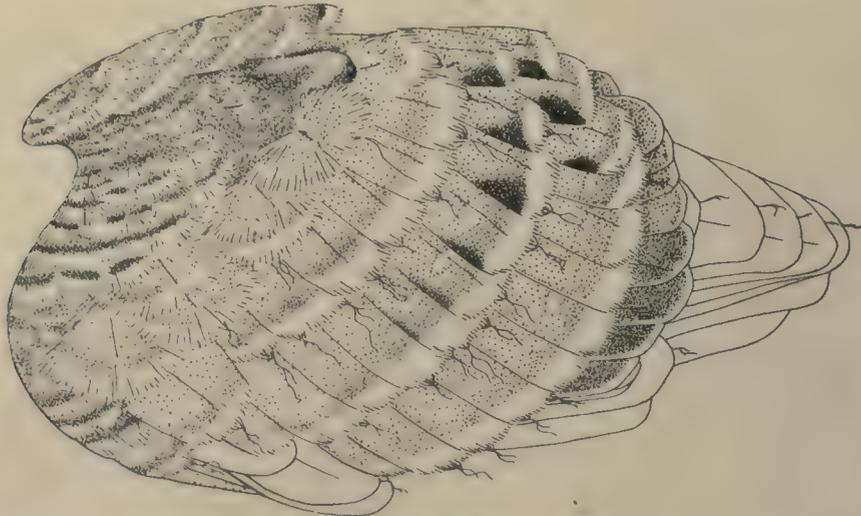
TEXT-FIGURE 30.

Juvenal *Geopelia tranquilla* (Gt 1-B 1), age 10 days. Hatched July 14, 1899. Hayashi del., July 24, 1899. × 2.

The scapulars number 14 or 15 in about two rows. The fourth row of coverts are conspicuously downy in appearance, but form a distinct row with whitish-yellow tips. The barbs are loose, spreading wide apart. These are represented roughly in lines across the light tips. The feathers in the third row are also somewhat of the same character, but yet more compact and regular, as are the posterior rows. In front of the fourth row there are shorter feathers, more thickly set, with light tips, but dark elsewhere. There are 6 or 7 rows of these feathers. The elbow is bare. The fourth row runs along the forearm bone, but between it and the anterior feathers will soon appear one or two rows of feathers that have a tip of less than one-half the width of the earlier feathers, and these will grow over and completely cover the fourth row before these latter feathers fall out. Indeed, some feathers with black tips will appear behind these later feathers before the fourth row is lost.

(IV) covered to near the tips by the feathers of the oblique tract; and in front of this tract, 15 lesser coverts. The apical mark is 1.5 mm. wide in the lesser coverts, and from 1.5 mm. to 2 mm. in the three posterior rows.

In the oblique tract we see 13 feathers arranged rather obscurely, in from 2 to 3 unevenly developed rows (1, 2, 3). Five of these feathers, of which 2 are only pins, have no pale apical marks, but instead, narrow black tips, differing from the black crescents of the adult only in their lesser width and depth of color. These are the most belated feathers of the tract that are visible at this age. Between the innermost half-expanded, black-tipped feather and the black-tipped pin below are seen 6 feathers, in which the pale apical mark is present, but reduced to about one-third its width in the lesser coverts. In line with these 6 feathers, near the bend of the wing, is a single feather (1 *b*) with the apical mark reduced to about one-half width; while just in front of the lower two of these feathers, and second in front of

the upper pin, comes a feather (1 a) with the apical mark reduced to two-thirds width. At the bend of the wing, overlying the outer pin, are 2 lesser coverts having the mark at full width.

Comparing the feathers in front of the four rows of coverts (I to IV) as to width of the pale tip, and taking them in the order of their development, the relation may be expressed as shown in the accompanying table:

	Width of pale tip.		Reduction of pale tip.
	mm.	p. ct.	p. ct.
Lesser coverts, 15.....	1.5	= 100	0
1a.............	1.0	= 66.66	33.33
Oblique tract, 13 1b...	0.75	= 50	50
6.............	0.5	= 33.33	66.66
5.............	0.0	= 0	100
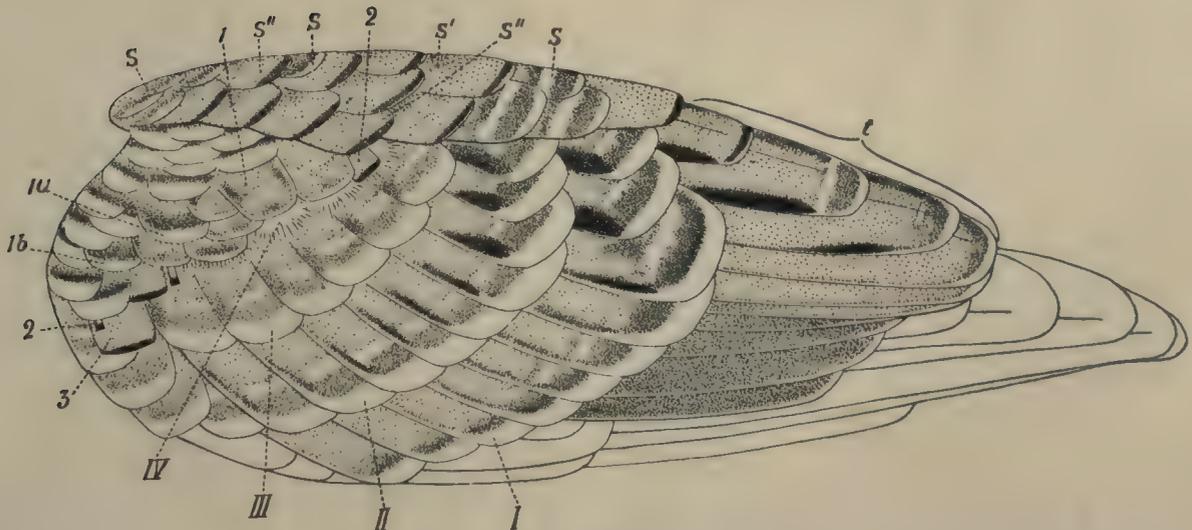
TEXT-FIGURE 31.

Same as text-figure 30, age 17 days; drawn by Hayashi, July 31, 1899. × 2.

The fourth row is here covered up by later narrow-tipped feathers, and 5 new black-tipped feathers are coming in. Some later feathers are among the scapulars. Arrangement: *I–III* are first to third rows of coverts. *IV* shows fourth row of coverts—covered to near tip by the feathers of the oblique tract. 1–3 are two or three unevenly developed rows of the oblique tract. 1a–1b, see text. *s* is early juvenal; *s'*, later juvenal; *s''*, post juvenal feathers; tertials are indicated *t*.

This stage brings out the interesting fact that the width of the pale apical mark varies according to the age of the feathers. The lesser coverts in front of and the four rows of coverts behind the oblique tract were the first to appear, and they all have the apical mark at full width. The 13 feathers of the oblique tract are belated to four different degrees, the 5 black-tipped feathers being the youngest, the rest older in proportion to the width of the pale tips. We have, then, in this narrow tract, the pale tips at three ages. The mark has gradually sunk from a width of 1.5 mm. to zero, and then the black-tip has appeared.

Is the black a sudden apparition? It might seem so, and yet its gradual rise is as certain as the gradual loss of the pale tip. We only have to look a little more closely in order to see that the black does not first appear *after* the pale tip has

vanished, for it is already present from the first. In all the earlier feathers we see a broad, thin band or bar of dark pigment, next to the pale tip. Now, a closer inspection of this and the following stages shows that this dark bar becomes gradually narrower and denser, and approaches the distal edge of the feather as rapidly as the pale tip narrows; and when the latter vanishes, the former is left as a black tip, slightly crescentic in form, and 0.5 to 0.6 mm. in width.

At this stage we no longer have a single color-pattern before us. The first molt has begun in the scapular tract, and there we see early juvenal (s), later juvenal (s′), and post-juvenal feathers (s″), the latter approximating the adult condition. The molt has not yet begun in the wing-coverts, but the oblique tract has belated feathers that tell of progress in several degrees towards the adult pattern. We have, then, intermixture and intergrading of patterns; ascending and receding characters;
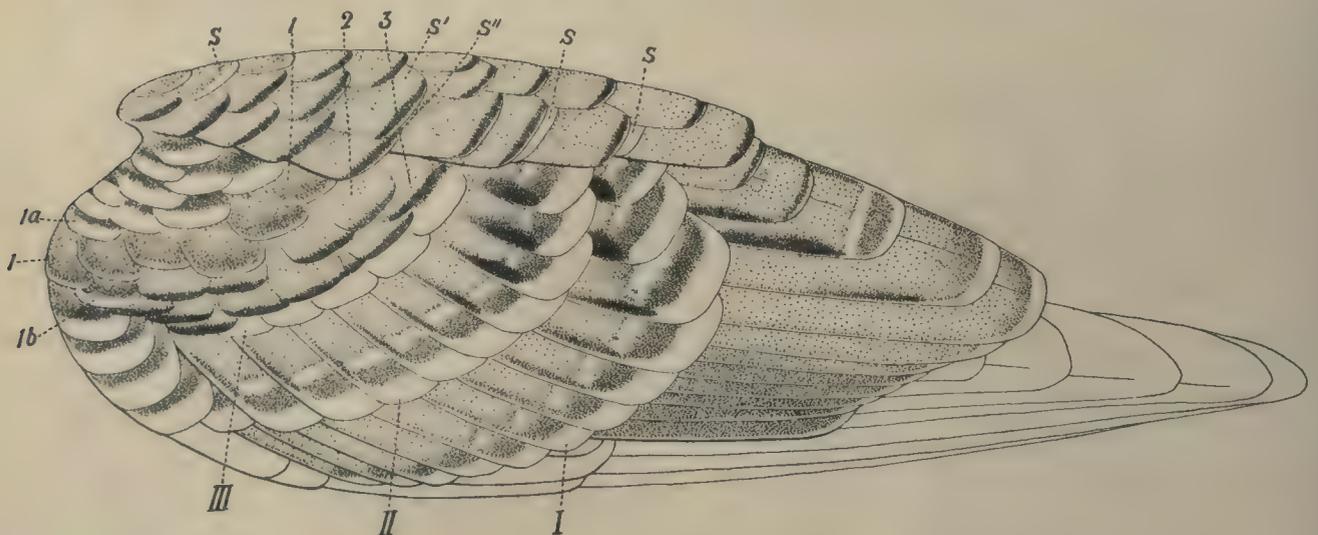
TEXT-FIGURE 32.

Juvenal *Geopelia tranquilla* (Gt 1-B 1 continued), age 28 days; drawn by Hayashi, Aug. 11, 1899. × 2.

About two rows of black-tipped feathers have come in and are fast covering up the third row of original coverts. The fourth row (IV) has been molted. More black-tipped feathers are now present in scapular region. Designations are the same as in the preceding figure (see text).

reduction graduating to complete erasure; advance in concentration and definition; in short, progressive transmutation, recession, and substitution all combined.

The differentiating processes are at work behind the scenes. Each new feather is a faithful record of just what and how much had been accomplished at the place and time of its elaboration. Unfolding in age-sequence, the feathers give us something more than a panoramic succession of disconnected stages. Although the successive pictures presented do not exhibit perfect continuity, they follow a time order close enough to remind one of a "motion picture," and leave little room to doubt that the process of development runs on in flowing continuity.

Passing on to the next stage (text-fig. 32), at the age of 28 days, we find that the molt has left but few of the earlier feathers (s) in the scapular tract, and only 9 of the 15 lesser coverts seen in the stage of 17 days. The oblique tract is now completed, and consists of 20 feathers in 3 distinct rows (1, 2, 3). The anterior and earlier row (1) remains the same as in the previous stage, its 6 feathers forming a

single line, supplemented by *1a* and *1b* at the bend of the wing. The next row (2) consists of the 5 black-tipped feathers, which we saw emerging at 17 days; and the third row of 7 feathers has been added in the interval.

It is about this time, or a few days earlier, that the fourth row of coverts (IV) after having been overgrown by the feathers of the oblique tract, is molted. From this time onward, the remaining rows of coverts fall one after the other, the molt in each row proceeding from the inner end outward.

In this stage, then, the scapular tract excepted, we have only original feathers in sight, the whole oblique tract consisting of first feathers. The four rows of coverts
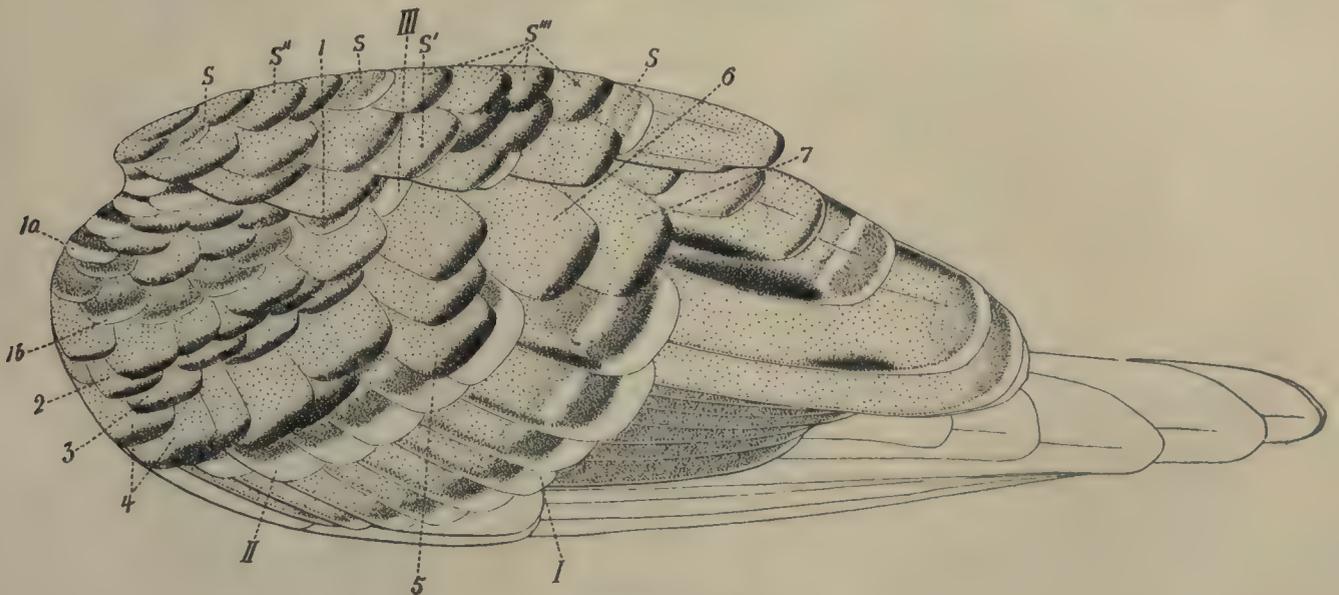
TEXT-FIGURE 33.

Same as text-figure 32, age 38 days; drawn by Hayashi, Aug. 1899. ×2.

Another row of dark-tipped feathers, with wider tips than the earlier oblique streak, are growing over the second row, and above we see three feathers that have advanced farther. A few (four) feathers in scapulars are wide-tipped with black. Arrangement: 1 shows the first row of later feathers with narrow light tips. 2 and 3, the second and third rows of narrow black tips. 4, the fourth row of wider black tips (about complete in number). 5, feather of fifth row; overgrowing the second (*II*)—light edge—row. 6, a feather of the sixth row, next to scapulars, reaching a little over the second (*II*) light row. 7, a feather of the seventh row, in line with first row (*I*) of light-edged feathers. *s'''*, later scapulars with very wide black tips. Other designations as in figures of 17-day stage. Behind the first two rows of black-tipped feathers we are to have 4 rows of black tips—that is, *twice the number* of light-tipped rows. Beginning with the first row (narrow light tips = *I*) we have 7 rows which take the place of the 4 original rows.

(I to IV) are each to be replaced by black-tipped feathers. Thus the field behind the lesser coverts is to be occupied by *seven* rows of feathers, of which three are original and four are replacements, following the molt.

Ten days later (text-fig. 33), we find four of these rows completed (1 to 4), and three (5 to 7) represented each by a single feather. Most of the lesser coverts have been cast, and 6 black-tipped feathers are here in sight. The later feathers have everywhere the wider and blacker tips. In the scapular region 5 of the later feathers (*s'''*) are readily recognized by the greater width of their black tips. The original tertials are still in place, and they give us another series of grades running from the earlier pale-tipped to the later black-tipped condition.

The three figures we have examined show that the wide passage between the juvenal and the adult pattern is no saltation void, but rather a plenum of development, with transition-phases leading straight from one to the other. We see a juvenal pattern of quite uniform type for all feathers unfolding at the same age. In the oblique tract there is, for some reason, a belated coming of the feathers; but there is no halt in the tide of development, for we see the color-characters are more and more advanced in proportion as the delay is greater, the successive steps marking a definite age-sequence. We infer, therefore, that the intervals between steps may be reduced indefinitely, and the whole series be thus made to approximate a perfect continuum. In that case, we should have to conclude that the developmental processes underlying these steps are moving onward continuously during the intervals between steps.

But do we really require more evidence of this than the normal course of development reveals? We have seen a very wide gap between two color-patterns largely bridged by steps running in a close progressive sequence. To one who watches the operation from day to day in the several species of the same genus, and in different individuals of each species, and sees that, when all are considered together, the intervals between steps are practically all covered, the evidence of complete genetic continuity seems all-sufficient. To those who see only what can be diagrammatically represented on paper, the short intervals between steps may still seem to be suggestive of diminutive jumps. If we exclude the opportunity for such an assumption, through an experimental test, the evidence for continuity will be as complete as we can at present hope to make it.

The steps between the juvenal (text-figs. 30 to 33) and mature (pl. 39) patterns are obviously transitional. The intervals are conditioned by discontinuities in the issue of the feathers. If the feathers could follow one another in an unbroken sequence, the intervals would disappear and the steps fall into a flowing line.

We have two sets of feathers to experiment with. We have seen that increasing *delay* in the time of bringing forth the first feathers results in more and more advanced stages of the color-pattern. We can not readily force such delays in the first plumage; but we can *hasten* the appearance of the second feathers by removing the first feathers before they are ready to fall by molt. The second feather that appears in the place of a first feather plucked before its time to fall should present a phase in the development of the color-pattern grading towards completion in proportion as its time approaches that of the mature pattern. That it will do so can be experimentally demonstrated.

The transition phases form a true linear series, *ortho* in direction and *genetic* in composition, since there is a common generative bond that makes each step a necessary link in the chain. With the end-term—the dark tip at its full—the generative power rises to its highest level, and henceforth manifests itself only in a regenerative way at each molt. Exhaustion attends every renewal of activity, and in the intervals between molts there is recuperation, but no measurable advance in specific elevation. If renewal of activity be artificially provoked much in excess of the normal requirement, the power may be weakened, so that it will fail of full quantitative achievement. But, however much weakened, there is never a reversal or retreat, in a qualitative sense, from the specific type.

The intervals between steps may, then, be reduced indefinitely, and the whole series be thus made to approximate a perfect continuum. The developmental

processes underlying these steps must therefore be moving onward during the intervals as well as during the steps.

In such a series of stages the direction of progress is certainly as definite as the bird is true to its type. The steps are seriated in a causal, genetic order—an order that admits of no transpositions, no reversals, no mutation-skips, no unpredictable chance intrusions. The series may conceivably be lengthened or shortened, strengthened or weakened; indeed, we may multiply the number of steps at will;

FIG. 34.—*Geopelia cuneata*, age 68 days. Bird in the second plumage, which is like that of adult.

that is, we may provoke one or more steps to arise between any two normal steps; but in that case the new steps will be measured true to the time and place of introduction, and their direction will invariably coincide with that of the series as a whole, so that if the time and place of origin are noted, the nature and extent of the strides may be approximately predicted.

Specific characters often appear to come in suddenly and to be immutable. This seems often to be so in passing from the juvenal to the mature plumage, with one or several molts. The earlier color-pattern is often succeeded by one so different that we are puzzled to see any possible way of continuous differentiation from one to the

other. Here, if anywhere, we should expect to see the mutationist triumphant. His biometric curves would surely declare gaps in abundance beyond the span of any conceivable bridges. Just as surely is he a too willing believer in miracles. The supposed breaks in continuity between stages are, at least in many cases, only discontinuities in observation.

It is the history of specific characters that turns apparent discontinuities into continuities; the lack of it that multiplies mutations into premutations, and premutations into hypothetic pangens. Complete histories are indeed rarely attainable, but so much the more significant are they, if just so far as they can be established, they remove all necessity for resort to mutation hypotheses.

In further illustration, I will refer to the case of the little diamond-dove (*Geopelia cuneata*) of Australia. In passing from the juvenal color-pattern to that of the adult, we seem to pass to a pattern that is wholly new, and without transitional phases. It looks like an unmediated jump, such as we should expect in biogenetic recapitulation, if mutation were the law of the origin of species. In the adult bird (text-figs. 34 and 36) we have a gray ground with the coverts of the wing very regularly marked each with two white dots, one on each side of the feather, equidistant from the apex. In the young bird we have no white dots, but some irregular cross-

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EXPLANATION OF PLATE 88.

A. Juvenal *Geopelia cuneata* (Gcl-A 2), age 15 days. Hatched June 15, 1899. × 2. Hayashi del., June 30, 1899.

This bird (A 2) differs from its mate (A 1) in having the brownish-yellow edge repeated as a more or less perfect cross-bar in front of the black or blackish bar. The conditions on two rows of coverts show that the anterior yellowish bar is the one out of which the spots arise. The spot (of some brownish yellow with edge) is connected frequently with the "edge," but seems to be either a part of the yellowish edge which is continued forward on the lower edge of many feathers or a part of the anterior yellow bar. It seems to arise about where the edge yellow joins the anterior bar. This pattern marks the tertials, coverts, and scapulars.

The blackish bar runs into a black streak seen in lower edge of 3 or 4 upper tertials, and in both the upper and lower edges of some of the three rows of coverts. The streak is the equivalent of the ancestral element of the bar.

The black bar is the same as seen in *G. humeralis* and in the crested pigeon. Both streak and bar disappear in the adult.

Three rows of coverts with three yellowish-brown bars are here typical as in other species of *Geopelia;* and a fourth is quite regular, but it consists of short feathers and is part of the feathers at anterior end of wing. Three rows cover the greater surface of wing.

B. Juvenal *G. cuneata* (Gcl-Cl), age 19 days. Hatched July 3, 1899. × 2. Hayashi del., July 22, 1899.

Notice that this is not the same individual as the one shown above. It is a slightly older stage in which about two rows of the oblique streak, which comes in just in front of the fourth row of coverts, are seen. These have already covered the fourth row, one feather of which is seen above next to scapulars and one more at the lower edge of the wing. The feathers of this streak have come in within about four days and they differ from other feathers as follows:

(1) They are more gray, less of brownish tinge.
(2) The edge is about half the width of that of the earlier feathers.
(3) The edge runs forward into imperfect cross-bars in which we see very irregular and imperfect spots. These spots were whitish yellow in Gcl-A 2, but here they are brownish yellow, just like the color of the terminal edge. These feathers came in much later in Gcl-A 1 than in (nest-mate) A 2.

The yellowish edge in this individual is only faintly repeated as a cross-bar in some of the posterior scapulars. Elsewhere it is not repeated, except in faint indications in upper tertials.

C. Juvenal *G. cuneata* (Gcl-Cl), same individual as figure B, age 32 days. × 2. Hayashi del., Aug. 4, 1899.

The oblique streak is a little longer, but has apparently no more feathers. A new row of feathers at the lower side of the scapulars has come in. They are grayer than other feathers and have very narrow edges, and these edges are not so light in color as those of first feathers, but are light yellowish-gray.

In Gcl-A 2 these feathers came in somewhat earlier and had brownish-yellow edges two-thirds as wide as the other scapulars. In the first and second rows of coverts notice also three feathers that have come in later; these have narrow, light edges and irregular spots of yellowish-white.
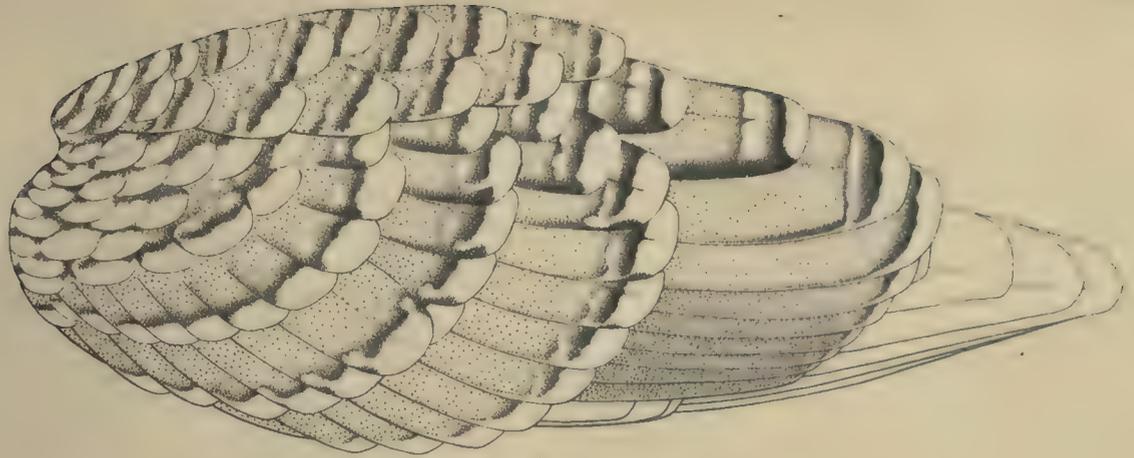
PLATE 88

19.
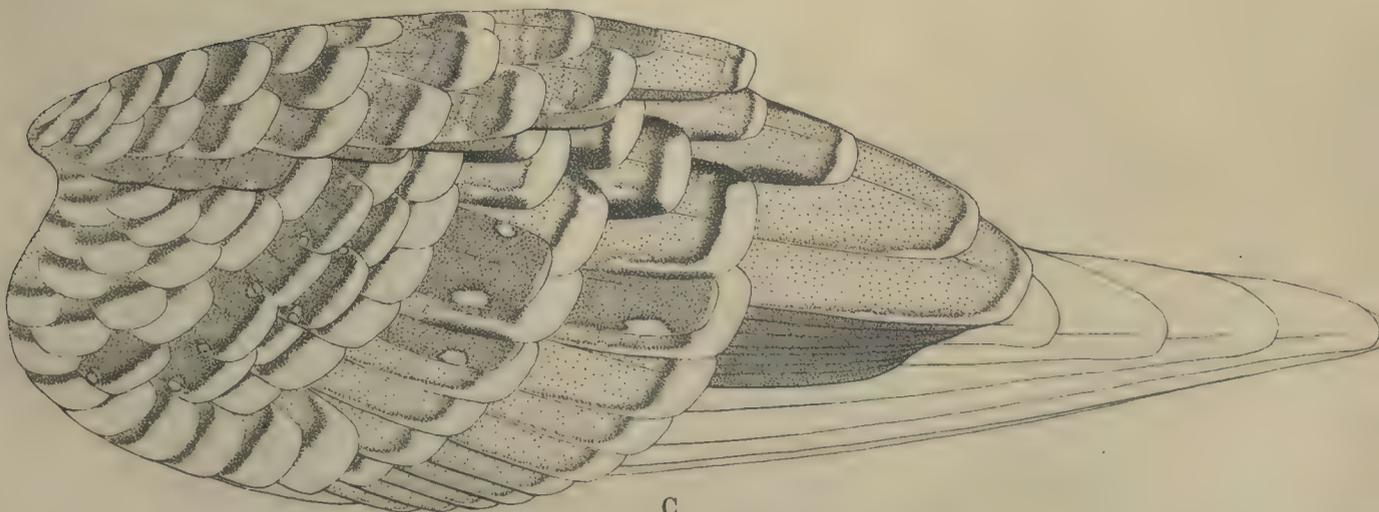
A. Juvenal *Geopelia cuneata* (Gcl-A2), age 15 days. Hatched June 15, 1899. × 2. Hayashi del., June 1899.
B. Juvenal *G. cuneata* (Gcl-Cl), age 19 days. Hatched July 3, 1899. × 2. Hayashi del., July 1899.
C. Juvenal *G. cuneata* (Gcl-Cl), same individual as figure B, age 32 days. × 2. Hayashi del., Aug. 1899.

lines ("bars") of a light color. How can we pass without a jump from one pattern to the other?

A very simple experiment will show us how this may be done. All we have to do is to pull out a few of the juvenal feathers at suitable intervals of time. Their places will soon be filled by new feathers of *different ages* (pl. 88 and text-figs. 35, 36),
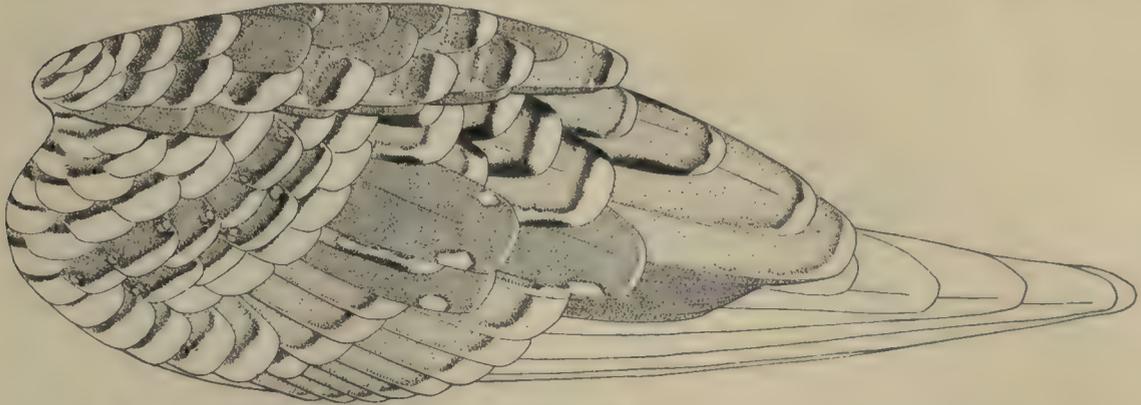
TEXT-FIGURE 35.

Juvenal *Geopelia cuneata*, same as B and C of pl. 88, age 44 days; drawn by Hayashi, Aug. 1899. × 2.

Some new feathers have developed in the scapulars. The three feathers in the first two rows of coverts are now much longer than the feathers they cover. The oblique feathers are only a little longer.
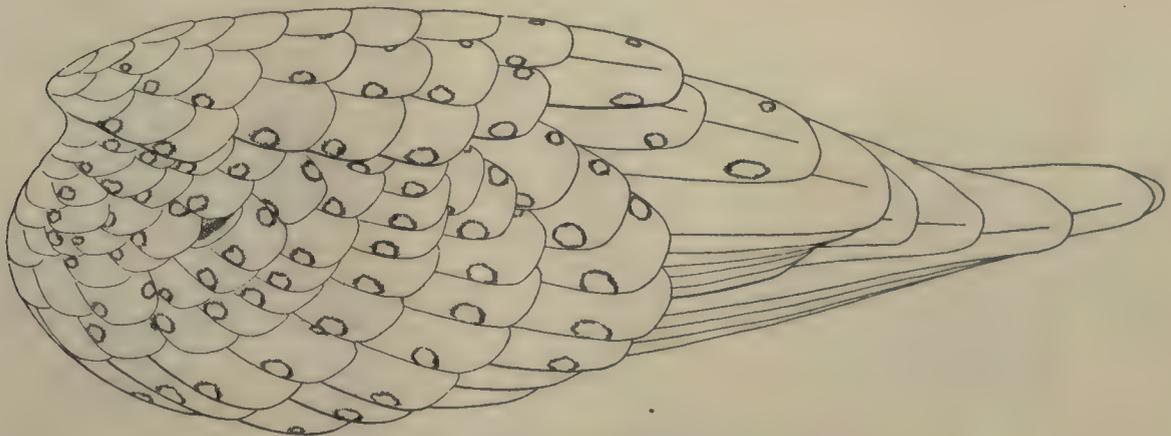
TEXT-FIGURE 36.

Geopelia cuneata (Gc 1-A 1), age 68 days. Hatched June 14, 1899; drawn by Hayashi, Aug. 21. × 2.

In this second plumage only one feather of the first plumage is still visible among the small coverts; elsewhere the second plumage and this is like the adult. The spots are on the edges of feathers on both sides; they are irregular and narrowly bordered with black. This bird and its mate have acquired the feathers of the second plumage much more rapidly than Gc 1-C 1. (See photograph of this bird at this same age in text-fig. 34.)

and these will give intermediate stages in the transformation of the cross-lines of the young into the white dots of the adult.[5] The adult pattern is thus revealed as an end-stage of a continuous process of differentiation. The same experiment may be made in other species with similar results.

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[5] The results of this experiment are apparently nowhere fully described, and illustrations of the *experimental* results were apparently not made. The formation of the spots from the cross-lines in the feather of *different ages* are, however, beautifully illustrated in the plate and figures above cited; the descriptions which accompany these figures supply additional and valuable data.—ED.

The pigeons, wild and domestic, present a considerable number of specific characters, the histories of which can be traced with exceptional fullness, sometimes in great detail. In the wing-bars for example, where we have, not one such character merely, but many, it is possible to read the several histories with much greater fullness and certainty than would be the case if they occurred only in a single species.

In the genesis of these bars it is possible to see that natural selection has not been the primary factor, and that mutation, as defined by de Vries, has not been required either as primary or secondary factor. It is only on Darwin's hypothesis, that bars came first and chequers afterwards, that mutation would find a *locus standi*. But origin *de novo* is an entirely inadmissible hypothesis when we can trace the history of the bars back step by step to remote ancestral foundations.

The steps are *orthogenetic* rather than *amphigenetic; ecbatic* rather than *telic*. A definite goal is reached, but as a direct sequel of that step in the series which immediately preceded it; not, I believe, as the result of activating an entirely new pangen or set of pangens hitherto held in reserve, and liberated just in time and place to unfold as independent units.

The doctrine of germs laden with independent unit-characters, or pangens, each predestined, so to speak, to flower in its own place and time, strikes me as teleological mythology, fine-spun to the verge of absurdity. We have not yet fathomed primordial organization, but it is safe to assume that the germ sets out with a biophysical constitution of a given specific type, within which metabolic, generative, and differentiating processes, under normal conditions, run on in a *self-regulating way*. Developmental and regenerative regulation, as it becomes ever clearer, can not, in my opinion, be reconciled with any scheme of pangen-regency. No determinants preside over the building of a crystal, and yet there we have specific form and symmetry in perfection. If we are to draw the line sharply between science and all transcendental and telestic mysticism, we must regard the germ-organism as wholly mundane in origin and nature. If the germ is a thing of evolution from purely physical foundations—and any contrary assumption is a denial of the evolution principle—then we may say that it is a *self-builder* within the limits of physical conditions, and just as truly autonomic in its forms and behavior as is the crystal. In the formation of a crystal self-determination is ever present, and so it must be in the case of the organism.