Article III.—ALLEGED CHANGES OF COLOR IN THE FEATHERS OF BIRDS WITHOUT MOLTING.

By J. A. ALLEN.

As is well known, as soon as a feather has completed its growth it merely rests on the follicle which produced it; the sheath which enclosed it while growing has fallen off; the pulp which nourished it has wholly disappeared from the base of the calamus, which is now filled with a chain of dry 'caps'; the blood vessels which supplied the growing feather with nourishment have become obliterated. The perfected feather, though worn for from a few weeks to a year, according to the species and the character of the feather, is in one sense practically a dead organ, inasmuch as it is insusceptible of further growth or repair. If its edges become abraded, or the shafts or barbs become broken, they remain so till the feather falls out and is replaced by a new one. It is to this extent comparable to a perfected leaf of a tree,[1] which, while retaining vitality for months, has not the power of self-repair; if it becomes wormeaten or otherwise mutilated, so it remains till its appointed time to ripen and fall. It may, in many cases, cling to the tree during the following winter, but when spring comes and the sap again ascends, the leaf, instead of receiving the sap and again proceeding to turn green, and to replace any parts of its structure it may have lost during the former season, is loosened from its attachment and falls to the ground, giving place to such new growth as may be destined to succeed it.

The simile of the leaf and feather is thus apposite and true. Yet if we can credit the allegations of some ornithologists the simile is far from representing what actually occurs in the case of feathers, which, it has often been claimed, as will be shown in the following pages, take on new life after a long period of rest, becoming permeated by secretions, which not only transmit new coloring matter, transforming pure white feathers into jet black

[1] Since writing this I find Dr. Bachmann made the same comparison in 1839, using much the same phraseology. See his 'Observations on the Changes of Colour in Birds and Mammals,' cited later. I find the same simile was also employed by Brehm in 1853, as also noted below.

ones, but solid material for restoring the ragged edges of the abraded feathers to their original size and form—in other words, transforming, just before the breeding season, the worn, faded plumage of the winter dress to the fresh, brightly, and often wholly very differently colored dress of the nesting season.

A brief account of this delusion, for such it may be justly termed, forms a most instructive chapter in the general history of the origin and persistency of error.

The assumption that birds change the color of their plumage without undergoing a molt, to the extent even of replacing one coloration by another radically different, crops out here and there at a quite early period in the history of ornithological literature, and probably dates back as a popular belief for centuries. As first expressed by the earlier writers it was little more than a belief or an opinion, advanced with little or no attempt at proof, and obviously originated in superficial or faulty observation ; while later the strong bias of an hypothesis has often blinded the observer to the real facts and conditions of the case.

The Rev. John Fleming appears to have been the first to propose and advocate the theory that "the colours of the hair of quadrupeds, and the feathers of birds, change with the season, independent of the ordinary process of *casting and moulting*," in his article on 'Hibernation' in Brewster's 'Edinburgh Encyclopædia,'[1] published in 1817. This he further elaborated and republished in 1820,[2] to which a note is appended by Professor Jameson. In the meantime the Rev. William Whitear had published a paper on the same subject,[3] in which he announced it as also his conviction that in "some birds the full-grown feathers themselves change colour, without being replaced by new ones." This opinion, he says, was based on some recent observations he had made on several different kinds of birds; a few of these 'observations' are worth quoting to show the nature of this alleged evidence. For example: (1) He says a Mr. Youell, of Yarmouth, had sixteen young wild Mallards, confined in a small pond by netting, which "put on a great deal of the beautiful plumage of the old bird, and yet that no feathers were found

[1] "Vol. XI, 1817, —" Am. Ed., 1832, X, p. 732.
[2] On the Changes of Colour in the Feathers of Birds, independent of Moulting. Edinburgh Phil. Journ., II, 1820, pp. 271–276.
[3] Remarks on the Changes of the Plumage of Birds. Trans. Linn. Soc. London, XII, pt. 2, 1819, pp. 524–526.

floating on the water or scattered on the banks of the pond." (2) He received, he says, a young wild Mallard which had nearly assumed the plumage of the adult bird; "many of the feathers were particolored, the same individual feathers retaining in some parts the color of the bird during the first months and in the other parts exposing those of the perfect bird." (3) "A male Chaffinch killed in February had the feathers of the crown of the head bluish ash-color, except at their extremities, which were rufous-brown, apparently still retaining the colour of the young bird." (4) A Reed Bunting was examined, which, in these particulars, resembled the Chaffinch; (5) the Swiss Sandpiper, the Dunlin and the Black-headed Gull are mentioned as changing color in March. Of course, the Chaffinch and Reed Bunting were changing color without molt, simply by the wearing off of the edges of the feathers, while in the Gull and Sandpipers the birds were in reality undergoing a spring molt; in the case of the Mallards, the change was also of course due to a molt, although no loose feathers were observed.

But Professor Jameson, in his note above cited, claims priority for the discovery for Captain Cartwright,[1] who, in 1792, had something to say about the changes of plumage in Ptarmigan as observed by him in Labrador, namely, that they get in fall a large addition of white feathers, "and that the coloured feathers at the same time change to white."

Dr. Fleming propounded three "laws" on the subject of the changes of the color in the plumage of birds, namely: (1) That the change in spring is from "a light to a dark colour, and that in autumn this arrangement is reversed;" (2) that the change is "regulated by the temperature of the atmosphere;" and (3) "that these changes assist in regulating the temperature of the animals in the different seasons of the year." He says he was at first inclined to believe that many species of birds must be subject to "five or six different moultings in the course of the year," but failing to find satisfactory evidence of this he adopted the view that the seasonal change of color was a true change of color in the feather—a view, as thus practically admitted, based on belief or opinion rather than on evidence.

[1] "Journal, I, p. 278."

In 1830 George Ord[1] published "some observations" on the molting of birds, in which he says: "The object of this inquiry is to ascertain whether the opinion of Temminck, that some birds change their plumage *twice* a year, is founded in fact" (l. c., p. 293). He argues that because birds suffer in health when molting, and in spring show no evidence of ill health, but are tuneful and happy, it is evident that they do not molt. He further accepts Whitear's observations and conjectures (as noticed above) as proof of change of color without molting, and further states it as a well-known fact that in male Bobolinks, kept in aviaries, "there is no change of feathers: their colours being altogether the result of organical secretions."[2] He thereupon, by a simple process of reasoning, reaches the conclusion that no birds molt more than once a year, as expressed in the following: "Is there any physical necessity, then, for *two* moultings in the course of a year?—or even *three*, as some pretend? I know of none" (l. c., p. 297).

In 1835 William Yarrell, the celebrated English ornithologist, published a paper on the same subject,[3] which, through its somewhat more scientific aspect, carried great weight and has been often quoted as offering conclusive evidence of change of color in feathers without molting. According to this author there are three ways in which changes in color are effected, only one of which, however, calls for consideration in the present connection, namely, "by the feather itself becoming altered." The most surprising part of this 'classic' proves to be the character of the evidence upon which the alleged change of color rests. Yarrell himself admits that "it is certainly difficult to understand how this is so constantly effected in the web of the feather, where no vascularity can be shown to exist even when the part is growing: but the fact is certain;....and of this fact further proof will be adduced in the course of this paper."

His evidence may be divided into two kinds: (1) His own observations; and (2) those of other persons; the latter, so far as his paper shows, being his main reliance. First, as to the evi-

[1] Some Observations on the Moulting of Birds. Trans. Amer. Phil. Soc., III, 1830, pp. 292–299.

[2] On the spring molt of the Bobolink, see p. 44.

[3] Observations on the Laws which appear to influence the Assumption and Changes of Plumage in Birds. Trans. Zoöl. Soc. London, I, 1835, pp. 13–19. An earlier abstract appears in P. Z. S., 1833, p. 9.

dence given on his own authority. He says: "Several birds examined in April were changing the colour of some parts of their plumage from that which is peculiar to winter to that of the breeding season. Many of the old feathers obtained at the preceding autumn moult still retained the colours they had borne through the winter; others were changing; and some had entirely assumed the colours peculiar to the breeding season, bearing precisely the same tints and markings as some new spring feathers, the webs of which were but partly exposed." He cites as among the birds in which this change was noticed the "Black and Barred-tailed Godwits," and "several Golden Plovers." Of the latter he says: "On the breasts of several Golden Plovers some of the feathers were entirely white, the colour peculiar to all the feathers of that part of the bird in winter; some were entirely black, being the colour assumed at the breeding season; while others bore almost every possible proportion of well-defined black and white on the same feathers; *from which it appears that the same cause of particular colour in new feathers can also partially or entirely change the colour of old ones.*" Of the *facts* as stated above there is no question, for in the perfect breeding plumage of the Golden Plover the feathers on the sides of the breast are partly black and partly white, the amount of either black or white varying with the position of the feather in the pterylæ—a fact of which apparently Mr. Yarrell was ignorant. Yet these particolored feathers are the basis of his *inference* (italicised in the above quotation) that the white feathers of the winter plumage on the breast of the Golden Plover turn black to form the breeding dress! The 'proof' in this case is of course pure inference, based on lack of knowledge of the condition of the plumage on the Plover's breast in normal breeding condition. No other evidence is here offered, his reference to the Barred-tailed Godwits being general, and probably based on that given later in the same paper at second hand.

His next and only other personal evidence is that based on the Herring Gull. In this case "Several tertial feathers were found to have their basal halves blue-grey, the other parts mottled with brown." Two of these feathers were marked at Christmas by cutting notches in them with scissors, and "re-examined in April," after an interval of nearly four months. "The tertial feathers,

which, when marked, were of two colours, were now entirely blue-grey; one was tipped with white." In the meantime this Gull, if it did as other Gulls commonly do, underwent a complete molt of all the feathers except the quills, including what are here called "tertial feathers." Now Mr. Yarrell was either mistaken in his identification of his supposed marked feathers, or he was not. The probabilities seem to favor the first alternative.

So much then for Mr. Yarrell's personal evidence, half of which is *nil*, and the other half seriously open to question. Now as to the evidence given at second hand. First are the observations of "the Rev. Mr. Whitear and Mr. Youell," previously published (Linn. Trans., XII, p. 524), which are merely referred to in general terms as "confirming" the fact of change of color in feathers. The worthlessness of these observations having already been shown, no further comment here is required.

The second-hand evidence consists further of "the notes of James Hunt,[1] one of the Keepers, made at the Gardens of the Zoölogical Society in the Regent's Park, during the seasons of 1831, 1832 and 1833, but principally in 1832." These relate to seven species, but in reference to only four do the observations bear on the points here at issue. First is the "Black-tailed Godwit, *Limosa melanura* Liesl." In this species the change was noticed as in progress on the breast as early as the 24th of February, and on the 29th of April had extended to the "scapulars, wing-coverts and tertials," completing the change. The observations were made on a live bird, which was examined "day by day," but how closely—whether it was handled and the plumage thus examined, or only at a distance—is not stated. The importance, or rather the absolute necessity, of closely examining the plumage by raising the surface of the feathers to see what is beneath, can scarcely be appreciated unless one has made a special study of the subject of molt. It is affirmed, however, that the change "is absolutely an alteration of colour, and not produced by moulting." But excellent authorities place this species in the list of those which undergo a full spring molt, by which they acquire the colors of the breeding dress.

The next species is the Ruff, the notes on which state that the head and neck acquire a new spring plumage *by molting*, "while

[1] Published also earlier, in abstract, in P. Z. S., 1833, p. 9.

the feathers on the body were not thrown off." Nevertheless, the Ruff is thoroughly well known to molt its body plumage in spring.

The next species in point is the Herring Gull, in which "the moulting.... does not appear to expedite the change of colour. The new feathers have much the same hue as those that have been shed." Yet reference is made to "a constant change of colour going on in the feathers." A spring molt, it is to be noticed, is admitted.

The fourth and only other species bearing on the question is the "Laughing Gull, *Larus ridibundus* Linn." "The feathers on the head of this Gull began to change colour from white to black on the 11th of March. It was a change of colour, and not an act of moulting; no feather was shed, and the change was completed in four or five days." As it is now well known that Gulls and Terns are among the birds that undergo a general spring molt (the flight feathers excepted), and with specimens before me of this and various other species of Black-headed Gulls, taken in spring, and showing that not only is the black head acquired by the growth of new black feathers and the shedding of the old white ones, but that the whole clothing plumage is also at the same time renewed,[1] it is evident that not much credence is to be given to these notes of Mr. Hunt on the subject of change of color in birds without molting. The birds were probably not taken in hand by Mr. Hunt and systematically examined, he simply giving his impressions of what he thought was going on as he made his daily rounds as one of the keepers of the Zoölogical Gardens.

As already intimated, Yarrell's paper has by common consent taken the position of a classic on the subject of change of color in feathers, if we may judge by its frequent citation as an authoritative utterance from which there is no appeal. Yet it is somewhat surprising to find that as late as 1884 Mr. Howard Saunders, in his 'Yarrell's British Birds,' repeats Yarrell on the Golden Plover (Vol. III, p. 272) and Black-headed Gull (*ibid.*, p. 603) without any hint that his statements are erroneous. The following sentence about the Golden Plover, from the first edition

[1] There are specimens in the collection of the Museum, showing a general spring molt, of the following species: *Larus ridibundus*, *L. atricilla*, *L. franklini* and *L. philadelphia*; also of several species of *Sterna*.

of Yarrell's 'British Birds' (Vol. II, 1839–41, p. 386), is worth quoting on account of its reappearance in the fourth edition without change, the part here italicised being of special interest in the present connection: "Some new feathers, which are obtained in the spring, are black, whilst the old white feathers of winter may be seen in change to black, some of them bearing almost every possible proportion of well-defined black and white on the same feathers, *the colouring secretions having equal influence over the old as well as the new feathers.*"

In 1837, Edward Blyth, an English naturalist of standing, made the first really important contribution to the general subject, his papers[1] giving evidence of much familiarity with the questions at issue. Yet, while aware of the fact that many birds undergo a spring molt, whereby they acquire their breeding dress, he was seriously and strangely misled into the belief that old feathers also were susceptible of change of color; apparently through not sufficiently recognizing the fact that many young birds after their first spring molt still show more or less well-marked traces of immaturity. Still some of his statements are difficult of explanation on even the hypothesis of unfamiliarity with the progressive stages of change with age, as witness the following quotations from his paper: "I had previously noticed the highly interesting fact, which had long puzzled me, that, in the same specimen, it was not unusual to perceive new feathers shooting forth in abundance, simultaneously with the most complete and surprising changes of colour in those loose, and about to be shed; and, as I knew, from observation, that many species underwent their seasonal changes exclusively in the one way or in the other, it became difficult sometimes to assign to which class such specimens should be referred. A Golden Plover, for instance, that is now before me, is every where in deep moult, renewing both its upper and under plumage; while, coincidently, most of the loose old feathers of the lower parts have changed, more or less completely, from white to black, the hue of the new feathers which are growing" (l. c., p. 261).[2] Again: "But, to return

[1] On the Reconciliation of certain apparent Discrepancies observable in the Mode in which the seasonal and progressive Changes of Colour are effected in the Fur of Mammalians and Feathers of Birds; with various Observations on Moulting. Charlesworth's Mag. Nat. Hist., I, 1837, pp. 259–263, 300–311. Also, Some Remarks on the Plumage of Birds. *Ibid.*, pp. 477–481.

[2] On the Golden Plover, see *antea*, p. 17.

from this digression to the Ducks, it will be observed that, in the latter, a varying amount of change of colour in the old feathers is a most ordinary concomitant of the assumption of the mature plumage by moult; and the formerly disputed fact, therefore, is thus demonstrably established, that, as the secretions which colour the growing feathers also tinge those which are about to be renewed, a circulation (evidently nutrimental; for where a bird is ailing or ill-fed, the consequences soon appear in their diminished lustre) must, consequently, obtain in feathers, even to the extreme period of their remaining attached, so that the hypothesis is unsupported by evidence which ascribes the moulting of a bird to the same cause which has been erroneously supposed to bring about the fall of a leaf; namely, that the pores through which the fluids circulate become gradually obstructed, and that it consequently dies, and falls off" (l. c., p. 262).

Thus Blyth, in predicating that old feathers about to fall, in birds undergoing a spring molt, share the secretions, and become changed in color by them, of the growing feathers by which they are surrounded, goes far beyond the later German and French writers (presently to be noticed), who claimed that old feathers in spring become freshened and recolored to form the breeding plumage.

In 1839 the well-known American naturalist, Dr. John Bachman, contributed a notable paper on the subject of molt and change of color in birds,[1] written, largely in reply to Yarrell, Fleming, Ord, and other earlier writers on the subject.[2] While not absolutely denying the possibility of change of color in feathers, he says: "If the feathers in birds, then, which have been long stationary in their growth, are capable of receiving a new set of secretions, and of assuming opposite colours, we must seek for some new law of nature not hitherto discovered" (l. c., p. 210). His memoir abounds with valuable observations on cage birds and on fresh specimens taken in South Carolina in the spring for the express purpose of determining what species do and what do not acquire the breeding dress by a spring molt; from which it appears that most of our Sparrows, Wrens and Warblers, so far

[1] Observations on the Changes of Colour in Birds and Mammals. Trans. Am. Phil. Soc., VI, 1839, pp. 197–239.

[2] Bachman's paper was apparently written before he had seen the article by Blyth, noticed above.

as observed, and some of the Thrushes, and various species of Gulls, Ducks, Plovers and Sandpipers, undergo a spring molt.[1] It also appears that Orioles (*Icterus galbula* and *I. spurius*), Painted Buntings, and some other species, acquire changes of color when kept as cage birds only at the season of molt.

Yet change of color in feathers without molting has been independently affirmed, and even advocated with great earnestness, by many writers during the last half century, the writings of only a few of which can be noticed in the present historical review of the subject. Dr. C. W. L. Gloger makes the claim that Audubon was the first to confess belief in a change of color without molt,[2] basing the claim on the following passage in Volume IV, p. 213, of the 'Ornithological Biography:' "Since I began to study the habits of Gulls," says Audubon, "and observe their changes of plumage, whether at the approach of the love season, or in autumn, I have thought that the dark tint of their hoods was in the first instance caused by the extremities of the feathers then gradually changing from white to black or brown, without the actual renewal of the feathers themselves, as happens in some species of land birds." Several long quotations are also made from Audubon's account of the Black-headed Gull (l. c., pp. 120–123), leading to the inference that Audubon believed the breeding dress was acquired by change of color without molt; but Audubon does not so state, much less does he offer any proof that such is the case. Yet Gloger makes these quotations the basis of a long disquisition on 'Umfärbung ohne Mauser.' Although Audubon's work was not published, says Gloger, until 1838, his studies of Gulls date much earlier, and therefore some forty years before the revival of the doctrine by Schlegel and others, in 1852, as presently to be noticed. In passing, however, it may be observed that these statements of Audubon's—a mere opinion or belief—furnish a fair sample of the 'evidence' offered by Gloger and others for a change of color without molt.

The papers of Yarrell and Blyth seem not to have been known to the German and other continental writers, who, from 1852 to

[1] Dates are given as to when the specimens were taken, and also notes as to the progress of the molt in the same species at different dates.

[2] Audubon als der erste Bekenner der Ansicht von 'Umfärbung ohne Mauser.' Journ. für Orn., II, 1854, pp. 328–334.

1856, published so much on the subject in 'Naumannia' and the 'Journal für Ornithologie.' The theory started afresh with Hermann Schlegel's address before the Altenburg Congress of Naturalists, held July 6, 1852.[1] In this paper Schlegel formulates various rules or laws respecting the season, manner, degrees and methods of molt, and the changes of color without molt, which are followed by a somewhat detailed account of the observations on which they purport to be based. Some of his 'laws' prove to have been well founded, while others were based on faulty observations, as was soon made known by various commentators on Schlegel's paper. He was not, however, the first, as he supposed himself to be,[2] to formally announce that in many species the distinctive coloration of the breeding plumage may be acquired by the shedding of the edges of the feathers of the winter plumage. Among other things, he affirmed that after feathers had reached their full maturity, they may, after a longer or shorter period of rest, by a fresh influx of secretion ('Saft') be made new, even to the restoration of their ragged edges by the formation of new barbs and new barbules. The color, he distinctly states, passes into the feathers, as well as into the bill, the feet, and the naked parts of the skin, and that it is by this process only, and not by molting, that the breeding dress in most birds is acquired.[3] The process of color change, he asserts, proceeds in many cases from the root of the feather outward, as when white, yellow or brown feathers change to black, etc.

We naturally turn to the observations on which such startling announcements rest. And what do we find? The results of microscopical examinations and systematic study of living birds? Nothing of the sort; merely off-hand assertions based mainly on the inspection of museum specimens. He takes up in systematic order the leading groups of birds, beginning with the Vultures and ending with the Ducks and other water-birds, and states how they acquire their breeding plumage. For example, to give

[1] Sendschreiben an die am 6. Julius 1852 zu Altenburg versammelten Naturforscher. Naumannia, II, Heft 2, 1852, pp. 19–40.

[2] See E. von Homeyer, Rhea, II, 1846, p. 159; Naumannia, 1853, pp. 64–78; Journ. für Orn., III, 1855, p. 113; IV, 1856, p. 129.

[3] "Zu dieser Zeit tritt auch eine grössere Menge Pigment in die Federn (wie dies auch in dem Schnabel, den Füssen und den nächsten Theilen der Haut stattfindet). Durch diesen Prozess nun, und nicht durch die Mauser entsteht das vollkommene oder Prachtkleid der meisten Vögel."—Naumannia, II, Heft 2, p. 22.

a free translation: "*Catharistes papa.* The young bird, as is known, is grayish brown-black. In this species the beautiful gray-yellow and the other colors of the old bird arise through change of color without molting. At this time appear the bright colors of the naked parts" (l. c., p. 24).

Again he says: "The origin of the breeding dress through color change (Verfärbung) I have observed in many species of the genus *Icterus.* In the following was this appearance especially striking. *Ict. icterocephalus* is yellow-gray when young with a yellow throat, black with a yellow neck and head when adult. In specimens in transition this color change is clearly seen. The black head and back of *Ict. baltimore* is wholly obtained through the change of color in the feathers without molting. *Ict. spurius* is yellowish below and green above when young, but changes to black, with reddish brown lower back, shoulders and lower belly. This color change is entirely due to change of color in the feathers without molting, the black appearing first at the base of the throat feathers, and later, like the reddish brown, spreads over the other parts" (l. c., p. 25).

Again: "In the species of *Cœreba* the change in color without molting from the greenish dress of the young to the full blue and black dress of the adult is easily seen."[1]

This is a sample of the proof offered in support of his statement that the breeding dress in most birds is acquired by a change of color in the plumage without molting! There is running comment of a similar character respecting several hundred species. The above is doubtless enough to show its utter worthlessness. He has simply looked at birds in transition stages of plumage and mistaken the intermediate phases as proof of an actual change of color without molt; whereas by means of large series of specimens, as in the cases above cited, as well as in countless others, the change from one phase to another can be traced through specimens that were actually molting when taken.

A few months later Dr. E. F. von Homeyer replied at length[2] to Schlegel's remarkable paper, premising that it contained much

[1] In the collection of this Museum are many specimens of various species of this group, taken while in molt, and showing feathers of the adult plumage in all stages of growth appearing in the immature greenish dress.

[2] Ueber den Federwechsel der Vögel; mit Rücksicht auf H. Schlegels Sendschreiben an die Ornithologen-Versammlung zu Altenburg. Naumannia, Jahrgang 1853, pp. 64–78.

that was true and much that was new, but that he had important reasons for believing that not all that was new was true, and that not all that was true was new.[1] Dr. Homeyer takes up Schlegel's ten laws or propositions seriatim, commenting on each, approving some, qualifying some and rejecting others. This is followed by critical comment on individual species, chiefly European, in rebuttal of statements by Schlegel. In the present connection we are interested mainly in Homeyer's position on the subject of change of color in feathers without molting. Such changes as Herr Schlegel claims, as from white to black, etc., he says he has never observed in any bird, and until it has been proved to take place in some particular species he shall maintain that it does not occur. He recognizes only such changes as are due to the wearing off of the edges of the feathers, and the slight changes due to exposure to light and atmospheric influences. He then proceeds to remark upon many of the commoner birds of northern Germany, which he has carefully studied in life, with special reference to the molt, correcting many of Schlegel's false statements in regard to particular species, and instancing numerous birds which acquire their breeding dress by a spring molt.

Homeyer concludes his paper by formulating his own conclusion on the general subject of molting and color change in feathers. Respecting the rejuvenation or 'Nachwachsen' of the feathers, he says that no growth takes place that is not uninterruptedly continuous from the molt. A later occurring period of growth after the maturation of the feather is beyond imagination and contrary to the whole course of nature.[2]

Dr. C. W. L. Gloger continues to believe in the change of color and in the regeneration of feathers in spring without molt. In one[3] of his several papers on the subject he says that many birds fail to acquire in the fall the full colors of their perfect plumage, the deficiency being supplied in the spring by a new influx of nourishing secretion and pigment![4] Not only this, but the abraded

[1] "Dieselbe enthält allerdings viel Richtiges und viel Neues; indessen habe ich gewichtige Gründe, weder alles Neue für richtig, noch alles Richtige für neu zu halten" (l. c., p. 65).

[2] "Ein Stillstand oder ein Absterben des Gefieders und ein später eintretendes Nachwachsen ist undenkbar, und mit dem ganzen Wesen der Natur—wo es überall keinen Stillstand gibt—im grellsten Widerspruche" (p. 77).

[3] Zur Erklärung der Verfärbung des Gefieders. Journ. für Orn., I, 1853, pp. 268–276.

[4] "Das hieran Fehlende wird im Frühjahre durch neu eintretendes Zuströmen ernahrender Säfte und färbender Stoffe nachgeholt" (p. 270).

edges of the feathers are restored by a renewal of the lost portions![1] These ideas are elaborated at length, but wholly on hypothetical grounds.

Pastor Chr. L. Brehm follows with a paper[2] in the same journal which forcibly supplements that by Homeyer already noticed, and in which he vigorously attacks Schlegel's 'Verfärbungstheorie,' and incidentally exposes the erroneous observations of Herr Leopold Martin on the change of color in the Scoter.[3] Brehm calls attention to the fact that the spring plumage is acquired in many birds through a spring molt. He considers Schlegel's belief that an old feather can increase its size and build out its broken edges as a strange assertion; a feather being like a leaf of a tree in that when once grown it cannot alter its size or form by the addition of new substance. Also, he says, no bird can pass from the plumage of the young into that of the adult through a simple change of color without molting. Such a change he declares to be simply a physical impossibility; in support of which he offers, not speculation and theorizing, but facts derived from direct observation in the field of what birds actually do.

Later Herr Brehm returns to the subject in a paper on the relationships of the Blue-throated Warblers (genus *Cyanecula*) and their molts.[4] These species molt in northeast Africa in February and March, by which process they acquire their breeding dress, and in no way by a change of color in the feathers themselves ("keineswegs aber durch Verfärbung"). When the new feathers first appear they are dull in color, lacking the brilliancy of tint they acquire later. This is due to a gray border which soon wears off—a color change long known to him—giving place to the lustre and brilliancy of the perfect breeding dress.

Brehm later writes of the changes of plumage in the Terns,[5] based on a large series of specimens collected by his son Alfred

[1] "Auch findet hierbei, oft sehr sichtlich, eine mehr oder weniger bedeutende Erweiterung der Federränder, mithin eine theilweise Erneuerung derselben durch Fortwachsen Statt. Ins Besondere können auf diese Weise die jüngeren Vögel ihr so genanntes erstes Herbstkleid zum nächsten Frühlinge in das vollkommene ('ausgefärbte') der älteren verwandeln" (p. 270).

[2] Gegen Schlegels Meinung über die Verfärbung des Gefieders. Journ. für Orn., I, 1853, pp. 347–351.

[3] Zur Verfärbung des Gefieders, namentlich bei *Anas nigra* [*Oidemia nigra*]. Journ. für Orn., I, 1853, p. 208.

[4] Zur Sippe der Blaukehlchen (*Cyanecula*) und deren Mauser. Journ. für Orn., II, 1854, pp. 33–36.

[5] Verfärbung und Federwechsel der europäischen Seeschwalben. Journ. für Orn., II, 1854, pp. 317–321.

in Africa. He traces the changes from the first or nestling plumage to the adult, showing how and when the various stages are acquired, and that each stage or change of plumage is due to molting and never to color change in the feathers themselves. After a review of the facts in the case, as shown by his specimens, he states that there is no room for doubt that Schlegel's 'Verfärbungstheorie' is entirely groundless.

Another contemporaneous contributor to this lively discussion is A. Hessler, who writes on the changes of color in various tropical and other Finches,[1] as observed by him for many years in confinement, in opposition to Dr. Schlegel's theory that the full breeding dress of the males is due partly to a change in the form—through a later aftergrowth (Nachwachsen)—and partly to a change of color in the feather itself without molting. While in these birds the color may be heightened by the well-known process of the wearing off of the edges of the feathers, the long tail feathers of certain of the species can be produced only by molting.

Herr Böck writes of the changes of plumage in the Ducks and Loons, with particular reference to the Scoter,[2] in correction of Herr Martin, and against Schlegel's theory. He had had before him large numbers of specimens taken in spring in which the fresh new feathers were coming in *en masse* without meeting with a single example showing color change in progress without molt.

Of special interest in this connection is a paper by Herr H. Gätke,[3] in which he claims to substantiate Schlegel's theory by numberless direct observations from nature, and in which he here sets forth all the wonderful things one finds in his chapter on 'Farbenwechsel der Vögel durch Umfärbung ohne Mauser' in his 'Die Vogelwarte Helgoland,'[4] published in 1892. Although he speaks in praise of Schlegel's paper in general, he differs from many of his conclusions, considering it as incomprehensible that Schlegel should attribute the change of color of the Snowbunting and some other species in spring to 'Verfärben,' instead of to the wearing away of the edges of the feathers. This method of change,

[1] Federwechsel und Farbenänderung bei tropischen und subtropischen Finken-Arten. *Ibid.*, pp. 185–187.
[2] Die Mauser von *Platypus niger* [*Oidemia nigra*]. *Ibid.*, pp. 309–311.
[3] Einige Beobachtungen über Farbenwechsel durch Umfärbung ohne Mauser. *Ibid.*, pp. 321–327.
[4] See English translation, pp. 149–164.

however, in Herr Gätke's opinion, is exceptional. In the case of *Motacilla lugubris*, of which he had had in hand hundreds of specimens in all stages of change from the winter to the breeding dress, he had never been able to find a new or half-grown incoming feather, the change being entirely due to color change without molting. Indeed, not only is there change of color in the old feathers, but a change of texture and form as well! Many of the back feathers become softer, weaker and more silky looking, and, what is more surprising, he says, the feathers become again whole-edged—that is, the barbs which had become more or less broken at the tip are again restored, so that the feather presents a regular unbroken border similar to that of a newly-grown feather in the fall.[1] This restoration extends also to the posterior wing feathers and wing-coverts. He says he was very much surprised to see this, but would not, with Schlegel, call it an aftergrowth ('Nachwaschen'). He also believes the barbs undergo a sort of scaling off process by which some parts become weaker and thinner or more silky, while, through the removal of the outer surface ('Haut oder Schale'), the color of the summer dress, which has been thus concealed during the winter, becomes perfectly exposed.[2]

He states further that he has found that changes in the external appearance of birds occur in many different ways, not only in different genera or species, but on different parts of the body of the same individual bird. He cites in illustration different examples of *Motacilla lugubris* and *Anthus littoralis*.

But in the case of *Charadrius auratus*, he says, Herr Schlegel is again wholly in error, for, instead of changing color without molting, they get their black breasts and yellow-spotted backs through change of feathers. But while he had found in spring these birds having on the breast and back the old bleached feathers of the winter plumage mixed with the more or less grown

[1] "Und, was wohl nicht weniger überraschend ist: diese Federn werden auch wieder *ganzrandig;* d. h. die Federstrahlen, von welchen die Spitzen mehr oder weniger abgenutzt (verstossen, abgebrochen) sind, werden wieder ausgeglichen: so, dass die Spitzen aller Strahlen wieder eine regelmässige, ununterbrochene Rundung der Federspitze bilden, ähnlich, wie die im Herbste neu gewachsene Feder sie zeigte" (p. 323).

[2] "Vielmehr glaube ich, dass dieselbe auf gerade entgegengesetztem Wege bewirkt wird; nämlich dadurch, dass in solchen Fällen, wo ausser der Farbe auch die Textur verändert wird, die einzelnen Federstrahlen ('Baarten') einer Art von Schälung unterliegen, durch welche sie eines Theiles schwächer oder dünner werden und das mehr seidenartige Ansehen erhalten: während anderen Theiles durch Entfernen der äusseren, die Färbung des Winterkleides gebenden Haut oder Schale die, schon seit Vollendung der Herbstmauser fertig darunter verhüllt gelegene Färbung des Sommerkleides sichtbar wird" (pp. 323, 324).

new feathers of the incoming summer dress, with no feathers showing change of color, he still believes that the feathers of the throat and sides of the head acquire their black color through an actual change of color without molting! In regard to *Podiceps minor*, and as he believes, in regard to many other genera, he finds Schlegel likewise in error, as he had had fresh spring specimens which were thickly clothed with still growing feathers. But in the case of *Larus minutus*, on the other hand, he had found the change from the winter to the summer dress due entirely to color change without molting. At first he could not believe it possible that the pure white feathers of the head could through simple change of color become deep black, but later he had the good fortune to receive specimens that completely disclosed the secret: in one the head was already black; the others showed the change just beginning. His account of how the change occurs deserves to be here given in his own words as one of the curiosities of ornithological literature.[1] To summarize, he says, in effect, that the winter white and gray head of *Larus minutus* changes to the black head of the summer dress wholly by a change of color in the feathers themselves without molting. The change begins in January, when there are already gray feathers on the hind head. These darken, simultaneously and little by little, becoming first dark gray, darkest along the shaft, and later clear black. At the same time the darkening extends forward on to the front of the head. Scattered feathers are at first blackish only along the apical half of the shaft, from which the color extends till the whole front half of the feather is gray; which then, little by little, turns to black, the edges of the feather changing last. But the change from the clear white feathers of the lower side of the head and throat proceeds differently, becoming black at once without passing through gray;

[1] "Der imWinter weiss und hellgrau gefärbte Kopf von *Larus minutus* verwandelt sich durch *Umfärben, ohne Mauser*, in den reinschwarzen des Sommerkleides. Die Umfärbung beginnt schon in Januar, und zwar an den, bereits grau gefärbten Federn des Hinterkopfes zuerst. Dieselben verdunkeln sich, gleichzeitig fortschreitend, nach und nach alle; sie werden zuerst schwarzgrau, an den Schäften am dunkelsten. und späterhin rein schwarz. Von dem grauen Scheitel erstreckt sich das Dunkelwerden zu gleicher Zeit auf den weissen Vorderkopf. Zerstreute Federn desselben werden Anfangs nur an der Spitzenhälfte des Schaftes schwärzlich. Von hier ausgehend, färbt sich die vordere Federhälfte erst grau; dieses Colorit verdunkelt sich nach und nach, und wird sodann völlig schwarz: am spätesten an den Seitenrändern der Federn.—Ganz anders geht aber die Umfärbung der rein weissen Federn an der Unterseite des Kopfes und der Kehle vor sich. An diesen Theilen tritt nämlich *sogleich, ohne* einem *Uebergang durch Grau*, die rein schwarze Farbe auf: und zwar an den *Spitzen* der Federn zuerst, als ganz feiner Saum. Dieser geht bald in ein halbmondförmiges Endfleckchen über, welches, sich wurzelwärts vergrössernd, nach und nach die ganze Feder mit Schwarz bedeckt" (pp. 326, 327).

the black begins at the tip of the feather first, as a lunate terminal spot, which extends gradually towards the root of the feather, until the whole feather becomes black. The change begins at the lower border of the hood and extends upward toward the bill till the change is completed, the chin feathers being the last to turn black.

With our present knowledge that the change of color is produced by a spring molt, and that not only the feathers of the hood are molted in spring, but also the whole clothing plumage, such a description as the above seems simply incomprehensible. It certainly indicates the untrustworthy character of Herr Gätke's investigations where even merely a simple matter of observation, or alleged observation, from specimens is concerned, to say nothing of more abstruse matters, where much is necessarily open to uncertainty, as for example, the varied phenomena of bird migration.

Gätke's remarkable paper did not pass unnoticed by other investigators, sharing with Schlegel's much unfavorable criticism at the hands of several subsequent contributors to the discussion. Dr. Eugen von Homeyer returns to the subject[1] in the January, 1855, issue of the 'Journal für Ornithologie.' The same volume also contains a very important paper by W. Meves[2] on color changes in birds through and without molting, in which he gives the results of his investigations on the changes of color in Swedish birds, with special reference to Schlegel's theories upon the subject. He considers first the general question of molt, and then that of color change without molt, and finally, in a supplemental note, expresses his dissent to some of Gätke's remarkable statements.

Meves recognizes: 1. A single complete molt—the fall molt, common to all birds towards autumn, whereby all of the wing and tail feathers, as well as all of the clothing feathers, are renewed. Under this heading he gives a list of the genera and species which have only this single complete annual molt. This table includes nearly all of the Fringillidæ, the Alaudidæ, Corvidæ, Kinglets, Wrens, Titmice, Nuthatches, Swallows, Shrikes, Woodpeckers, Cuckoos,

[1] Ein ferneres Wort über das Ausfärben. Journ. für Orn., III, 1855, pp. 113–117. See also, Noch ein Wort über die Verfärbung. *Ibid.*, IV, 1856, pp. 129–132.

[2] Ueber die Farbenveränderung der Vögel durch und ohne Mauser. *Ibid.*, III, 1855, pp. 230–238, pll. ii, iii. Translated, with additions, from the Oeversigt of K. Vetenskaps. Akad. Förhandl., 1854, No. 8.

Swifts, Birds of Prey, Pigeons, Herons, Rails and Gallinules, some Grouse, some Ducks, and some Grallæ. Among the song birds not already named are many species of the genera *Sylvia*, *Saxicola* and *Muscicapa*, while some of their congeners[1] fall into the next category, namely:

2. A 'double,' second, or spring molt. This is distinguished as: (*A*) complete, including all or nearly all of the clothing feathers, and sometimes the last four wing feathers and the two middle tail feathers; and (*B*) partial; that is, only some of the feathers of the head and neck.

As this table has special bearing on what has been quoted above from Schlegel, Martin and Gætke, I transcribe in full the list, given under 2, *A*, of the birds that he has found to molt in spring.

Anthi.	Coracias garrulus.	Lestrides.
Motacillæ.	Merops apiaster.	Procellariæ.
Saxicola rubetra.	Tringæ.	Colymbus rufogularis.
Sylvia nisoria.	Phalaropodes.	Totani.
Sylvia cinerea.	Hæmatopus.	Limosæ.
Sylvia curruca.	Charadrii.	Strepsilas.
Sylvia hortensis.	Anas glacialis.	Uriæ.
Muscicapa collaris.	Sternæ.	Mormon.
Muscicapa atricapilla.	Lari.	Alcæ.

Under 2, *B*, or in the division having only a partial spring molt, he places *Sylvia suecica*, *Emberiza nivalis*, *E lapponica* and *Vanellus cristatus*, and also a large number of young males, especially Linne's Passeres, in the first spring following their birth year.

3. The summer molt, after the pairing season. This again is divided into *A*, complete, and *B*, partial. The *A* section is restricted almost entirely to the Anatidæ, which molt the body feathers and sometimes part of the wing and tail feathers, by means of which the males and females assume a more or less similar dress. The *B* section includes various species of Grouse which molt the feathers of the head and neck.

[1] It appears to frequently happen that closely allied species differ in respect to whether or not they undergo a spring molt. Thus in the Charadriidæ, judging by the abundant material in the American Museum, while apparently all the species of *Charadrius* proper, and of such allied genera as *Arenarius*, *Squatarola*, etc., acquire their breeding dress by a spring molt, the more uniformly colored species of *Ægialitis* show no indications of a spring molt. Again, while the Phalaropes, the Curlews, and many of the Sandpipers molt in spring, in the Pectoral and Bartramian Sandpipers, and in some other species, large series of spring specimens give no evidence of molt.

4. A threefold ('dreidoppelte') molt, or a union of the spring, summer and fall molts. This is also divided into *A* complete, as in *Lagopus alpina* and *L. subalpina*, and *B* partial, as in the Grebes and Cormorants.

In addition to the changes of plumage produced by molt and the growth of new feathers, Meves distinguishes changes of color due to the wearing away of the edges of the feathers. This he has found, by microscopical examination, is produced in two ways—(1) through a simple falling off of the tips of the barbs; (2) through a falling off of not only the tips of the barbs, but of the barbules as well. In the first case the coloring matter in the clothing feathers of the winter plumage which have white, dark, or colorless edges, is found in the barbules and barbs; in the second case only in the barbs. These fugaceous tips begin to fall gradually soon after the fall molt, but only in spring or later do they wholly disappear and reveal the previously concealed color in its full beauty.

In order to show the very different structure of feathers of the winter and summer plumage in some birds which have a double molt, he gives numerous figures, which he hopes will have some influence against the views of Schlegel and others who believe that one plumage can be transformed into another without molt.

In 1856 Dr. D. F. Weinland published two short papers on the subject of change of color in feathers without molting.[1] They are of interest mainly from the historic point of view, since they contain an original suggestion that later met with some favor. He accepts as a fact, to begin with, the change of color in feathers claimed by Schlegel and his followers, and considers the question, "how can a feather change its color, when its blood-vessels and nerves are dried and dead, as is the case with every feather soon after it has reached its full growth" (Proc. Boston Soc. Nat. Hist., VI, p. 35). He refers to the bleaching of specimens in museums, and to the fact that some birds, as the Merganser (*Mergus merganser*), soon lose after death the rosy tinge which in life pervades the plumage of the breast. He states that on examining a feather thus colored, taken from a freshly-killed bird, under a high

[1] Zur Verfärbung der Vogelfeder ohne Mauserung. Journ. für Orn., IV, 1856, pp. 125-129. The Cause of the change of Color in the feathers of Birds, and in the hairs of Mammalia, and the manner in which this change is effected. Proc. Bostor Soc. Nat. Hist., VI, 1856–59, pp. 34–37.

power of the microscope, he "found all the pinnulæ filled in spots with *lacunes* of a reddish fluid, which.... seemed to be of an oily character." Some weeks afterwards the same feathers, having been exposed to light, had become nearly white, and "instead of the reddish *lacunes*, only air-bubbles, which it is known produce a white color," were found. The evaporation of this reddish fluid, and its replacement with air-bubbles, he concluded produced the change of color. After rejecting as "unphysiological" the well-known fact that change of color is often produced by the wearing away of the edges of the feathers, he proceeds to formulate the following hypothesis, to account not only for the change of color in birds in acquiring the breeding dress, but also the changing to white in winter of many northern mammals and birds, and the sudden change to gray or white of the hair in man and the mammalia, or the feathers in birds: "If this fluid is an oily matter, as there is reason to suppose, it will be readily admitted, physiologically, that it may be furnished by the organism, by imbibition through the tissues, in consequence of a certain disposition of the nerves leading to the skin, (even if the vessels and the nerve in the feather itself should be dried,) for fat goes through all tissues without resistance, and also through horn. Thus the fat coloring matter may flow into the feathers during the time of reproduction, which is the richest season in every living organism; and then again, from want of food, cold temperature, weakness, decrepitude, or from strong emotions of the central nervous system, from sudden terror or grief,—the same coloring fat may be called back to furnish the suffering organism" (l. c., p. 36). The same hypothesis is stated, but in less detail, in his paper in the 'Journal für Ornithologie' (l. c.), which, however, in other respects is a quite different paper, dealing somewhat at length with the probable or supposed influence of climate upon seasonal change of color in mammals and birds.

As will be seen later, the idea underlying Weinland's hypothesis was subsequently elaborated in great detail as an original theory by Victor Fatio.

In 1863 N. Severtzof published a paper which, from its title,[1]

[1] Mikroskopische Untersuchungen über die Verfärbung der Federn zum Hochzeitskleide bei einigen Vögeln, nebst Betrachtungen über das Verhältniss derselben zur Mauser. Bull. de l'Acad. Imp. des Sci. de St. Pétersbourg, VII, 1863, pp. 330–346.

one would naturally expect to contain most important information. It proves, however, quite otherwise, consisting of hypothetical explanations of well-known phenomena. He makes few direct references to the literature of the subject, beyond an allusion in general terms to Schlegel, whom he calls the first discoverer of 'Verfärbung.' He states, however, that so far as he had read, no one had previously made use of the microscope in such investigations[1]—an omission he proposes to supply. He bases his investigations primarily on a series of spring specimens of *Vanellus gregarius* (=*Chettusia gregaria*) taken on the Ural River. This series consisted of birds in various stages of transition from the winter to the breeding plumage, which seemed to him to 'point to' color change in the old feathers. Examination under the microscope of a much variegated specimen, taken in April, and showing every stage of color change, convinced him that 'Verfärbung' was indeed an actual fact, although in the feather itself no vital process was taking place, the phenomenon being purely physical, and such as may occur even in a dead feather so long as it is attached to the skin, or indeed in a stuffed cabinet specimen.[2] This physical process is simply endosmosis.[3]

The *modus operandi* of the process is thus explained. He conceives first the existence of a coloring fluid, which enters the feather from the body. From the general context it would seem that he supposes the fluid to be part of the natural juices of the body, but near the close of the paper (as will be noticed later) he states that the pigment is set free from the blood, but in what way it becomes separated he fails to clearly state. At all events, under his hypothesis there is a supply of this colored secretion somewhere in the tissues of the body at the base of the feather, and this colored fluid, at the time when the dry dead feathers ('die schon trockene und abgestorbene Feder') of the autumn plumage are to be transformed into the fresh brightly colored breeding dress, it enters by endosmosis through the base of the feather and ascends, by the laws of capillarity, between the walls

[1] He must have overlooked Meves's important paper, published, as noted above, in 1854.

[2] "Ich untersuchte dieselben unter dem Mikroskop: es ergab sich, das die Verfärbung wirklich stattfindet, dass aber in der Feder selbst kein Lebens-, sondern ein rein physikalischer Process vor sich geht, der also auch an der abgestorbenen Feder möglich ist, so lange sie an der Haut haftet (was jedoch nicht unbedingt nöthig ist)" (l. c., pp. 331, 332).

[3] "Meine Beobachtungen umfassen drei Arten von Verfärbung, denen derselbe physische Process, die Endosmose, zu Grunde leigt: (1) normale Frühlingsverfärbung der lebenden Vögel; (2) anomale Sommerverfärbung derselben; (3) Verfärbung der todten Bälge. Diese drei Arten der Verfärbung erklären sich gegenseitig" (l. c., p. 332).

of the quill and the 'medulla,' reaching the vanes and passing on from cell to cell through the barbs and barbules to their extremities,[1] and even sometimes exuding from their broken tips. In this way the old feather is rejuvenated, taking on all the freshness of a newly-grown feather.[2] As this fluid dries the new pigment is deposited in successive layers on the cell walls within the feather. In the feathers of the lower body the drying is less complete than in those of the head; in the former this coloring fluid is merely concentrated by evaporation to about the consistency of a saturated solution of gum. The drying is gradual, and is not completed till the process of color change is fully ended.[3] He admits that it is not quite clear to him how in mottled and particolored feathers the pigments are able to arrange themselves so as to form the different patterns of color-marking, but he believes it is due to bleaching and abrasion, and is conditional upon the structural differences that characterize different parts of the feather.

In regard to the origin of this color-bearing fluid, his explanation is brief and unsatisfactory. He reiterates near the close of his paper the statement that the color change in a feather is a purely physical and not a vital process. But in the skin, which is not dead, the process is vital, and is similar in character, and only differs in degree, from the formation of new feathers. The pigments set loose in the 'blood plasma' are in some way separated and enter the feathers in the manner already described.[4]

[1] "Die Färbende Flüssigkeit dringt endosmotisch durch die Federbasis und steigt, nach den Gesetzen der Capillarität, zwischen den Wänden der Federröhre und der Medulla auf" (l. c., p. 333).

[2] "Unter den Mikroskop ist noch etwas zu sehen, was die Richtigkeit meiner Erklärung beweist: Pigmentausschwitzungen an den Spitzen der abgeriebenen Barbillen und verstossenen Federbärte. Eben diese Ausschwitzungen verursachen die Erscheinung, dass die verfärbte Feder dem blossen Auge wieder eben so frisch erscheint, wie eine neugewachsene" (l. c., pp. 334, 335).

[3] "Diese Flüssigkeit trocknet im Gefieder des Leibes nach und nach schichtweise auf der inneren Seite der Zellenwände; aber es sind viele Schichten nöthig, um jede Zelle, also auch die ganze Feder, vollständig zu färben.... Auch ist das schichtweise Trocknen der färbenden Flüssigkeit in den Zellen der Unterleibsfedern nicht als vollständiges Trocknen zu verstehen, sondern als Concentration durch Verdampfen etwa bis zur Consistenz einer gesättigten Gummilösung. Vollständig trocknet die Feder im Frühjahr erst nach geschlossenem Verfärbungsprocesse" (l. c., pp. 334, 335).

[4] "Kehren wir nun zur Verfärbung durch Saftzufluss zurück. Diese Verfärbung der Feder ist, wie gesagt, eine rein physikalische, keine Lebenserscheinung. Aber in der Haut, die nicht abstirbt, ist dieser Saftzufluss eine Lebenserscheinung, dieselbe Erscheinung, welche, nur in stärkerem Grade, auch bei der eigentlichen Mauser vorkommt. Bei einem schwächeren Saftzuflusse findet Abscheidung von Pigment statt, welches wohl im Blutplasma aufgelöst war und in der beschriebenen Weise in die shon vorhandenen Federn dringt. Bei einem stärkeren Saftzuflusse ist Neubildung von Federn bedingt, welche die alten verdrängen (normal), oder zwischen ihnen wachsen (Halskrausen des Kampfhahns und des Kragentrappen). Den Uebergang beider Processe in einander habe ich, wie gesagt, bei *Limosa melanura* beobachtet, so dass irhe wesentliche Einheit nicht bloss eine theoretische und abstracte, sondern eine concrete, thatsächlische ist" (l. c., p. 345).

That he is here grossly in error from a physiological standpoint need not be urged. His statement of the similarity of origin of his supposed coloring fluid, which enters the feather by a "purely physical process," with the formation of a new feather, is too obviously absurd for serious consideration.

It is unnecessary to follow his elaborate descriptions of the various alleged steps in the process of color change in the feathers ; suffice it to say that they are as detailed and similar in character to those given by Gätke for the Sanderling and other species, and doubtless have scarcely more basis in fact. As already said, his investigations are based primarily on *Vanellus gregarius*, but include also *Limosa rufa*, *L. melanura*, *Tringa subarquata*, *T. variabilis*, *Numenius arquata*, and *Fuligula rufina*— all species that are known to acquire their breeding dress by a spring molt. In the genus *Limosa*, however, the spring molt is often only partial, many of the feathers of the winter dress being retained, while others are replaced by new ones.

In 1866 Victor Fatio published an extended memoir[1] on the structure and coloration of feathers, reviewing briefly the work of previous writers in the light of his own investigations. He treats the subject under five headings, as follows: I. De la structure des plumes (pp. 251–261); II. Des mues réelles ou par renouvellement (pp. 261–265); III. Coloration et mue ruptile (pp. 265–282); IV. Développments parallèles des plumes et des couleurs (pp. 282–298); V. De la décoloration (pp. 298–305). His paper calls for notice here mainly on account of his peculiar views on the manner in which changes of color occur in feathers without molt. He very truly says at the outset that when the feather has completed its growth it has received all the coloring matter it can ever obtain from the body. The blood vessels then become obliterated, the creative lymph gradually disappears, the inferior umbilicus is closed by an operculum, the now useless sheath falls away in little flakes, and the pulp which constituted the life of the feather dries up from the summit to the base. The feather having completed its development falls into a state of apparent death, receiving nothing more directly from the

[1] Des diverses modifications dans les Forms et la Coloration des Plumes. Mém. de la Soc. de Phys. et d'Hist. Nat. de Genéve, XVIII, Pt. 2°, 1866, pp. 249–308, pl. i–iii.

body.[1] Through exposure for a greater or less length of time to external influences, it progressively deteriorates, and later falls, pushed out by the new feather which comes to replace it. A feather once dry receives no longer any blood or pigment from the body.[2]

Yet Fatio admits an almost constant change in the color of the mature feathers, and it is of interest to examine what he says of how it is brought about, and his evidence of the existence of such change. The changes, he says, may be effected gradually with the advance of autumn, or, with the approach of spring, declare themselves much more rapidly. The first, he says, is illustrated in the Starling and in some Finches; the second, frequently so sudden, is seen in the new coloration of some parts of the plumage of certain birds, as in the hood of *Larus ridibundus!* And here comes to light again the old case published by Yarrell—already noticed at length in this paper—which seems to have instigated Fatio's whole assumption of a radical and rapid change of color in feathers.[3] As already shown, he disagrees radically with Schlegel, who, he says, "n'émettait qu'une pure hypothèse" when he explained the change of color at the approach of the breeding season by a renewal of life in the feather, with the transmission into it of blood and pigment. But Fatio appears to have emitted an equally pure hypothesis to account for supposed changes of color in feathers, for many of the phenomena he attempts to explain are purely imaginary, as especially those in Chapter V, 'De la décoloration.' Believing strongly in a change of color in feathers, and also that they are practically dead organs capable of receiving nothing from the body after they have matured, he conceived the idea that fat, derived from the bird's body, penetrates the structure of the feather and acts as a solvent for the pigment con-

[1] "Plus tard les vaisseaux sanguins se sont oblitérés, la lymphe créatrice qui a subsisté encore quelques temps a disparu petit à petit, l'ombilic inférieur s'est couvert d'un opercule, la gaine inutile est tombée par feuillets jusqu'au niveau de la peau, et nous voyons alors que la pulpe constituant l'âme de la plume s'est peu à peu desséchée, du sommet à la base, mais d'une manière plus ou moins complète suivant les différentes plumes. La plume qui a fini son développment est tombée dans un état de mort apparente, et, quoique bien souvent elle ne reçoive plus rien directement du corps, nous verrons qu'elle n'en est pourtant pas complétement indépendante" (l. c., p. 260, 261).

[2] "La plume une fois desséchée ne reçoit plus ni sang ni pigment du corps, pas plus qu'elle ne croît encore par sa base" (p. 266).

[3] "....et nous voyons un exemple du second dans l'apparition, souvent si prompte, d'une nouvelle coloration pour quelques parties du plumage de certains oiseaux, comme dans la calotte du *Larus ridibundus*. Tandis que beaucoup de plumes sout renouvelées au printemps à la tête de ce Larus, plusieurs passent, en effet, très-vites du blanc au brun, en peu de jours même, comme Yarell [sic] affirme l'avoir observé" (l. c., p. 267).

tained therein, he being led to this by sundry primitive experiments of his of soaking feathers in oil. Through the supposed action of fat, moisture, light, heat and cold, either separately or variously combined, he attempts to account for a wide range of color changes, either real or imaginary, but mainly the latter. Yet he discards Weinland's hypothesis of the passage from the body into the feather of a colored fat capable of tinting the feather, and also Severtzof's supposition of an extraneous foreign principle, 'l'ozon,' which penetrates the feather and dissolves in it the pigment, and which then, through a process of endosmosis, colors all its different parts. Without taking space here to refer in detail to his experiments, explanations and arguments, we may give the gist of his conclusions in the following extract: "Ainsi donc, sous l'influence, d'abord d'une humidité tour à tour absorbée et évaporée, comme agent développant préparateur, puis de la graisse du corps comme dissolvant, puis enfin de la température et de la lumière comme agents facilitant les actions chimiques, la plume se colore, change ou augmente sa coloration" (l. c., p. 279).

The action of humidity, in his hypothesis, plays a minor but important part in expanding the cortical substance of the feathers, the chief rôle being that of the fats from the body, which by some means, either external or internal, gain access to the pigment granules and dissolve them, so that the coloring matter is, at least hypothetically, held for the most part in solution, subject to extravasation, to transportation, and even to decoloration. As, however, his treatment of the subject is for the most part in generalities, and from a purely hypothetical basis, and as his illustrations are often obviously malapropos—changes of coloration well known to be brought about by molt being cited as illustration of changes of color without molt—his conclusions seem scarcely entitled to serious consideration. Nor do they appear to have made a very profound impression upon the literature of the subject.[1]

Since 1866 little has appeared on the subject of change of color in feathers. Although the erroneous character of the theories and opinions of Schlegel, Gloger, and Gätke was soon made thor-

[1] We do not refer here to his earlier chapters, which, although tainted with his hypothesis of the solution and transformation of the coloring matter of feathers, are, for the time, important contributions to our knowledge of the growth and structure of feathers.

oughly evident, similar beliefs have still a firm lodgement in the minds of many writers of the present day. Not only has Herr Gätke republished his early absurd views within the last few years, but similar notions appear to have arisen independently among those who have perhaps never read either Schlegel's or Gätke's papers, or the later memoirs of Severtzof and Fatio.

And now comes the exceedingly unpleasant duty of instancing a few modern cases of belief in the addition of pigment, and its free movement, in old feathers. A conspicuous instance is of course Mr. Charles A. Keeler,[1] who believes that pigment "travels through the various branches of the feather, advancing farthest and most rapidly along the lines of least resistance and accumulating in masses where the resistance is greatest," etc. (l. c., p. 159). In other words, the inference is fairly deducible that the feather first grows and is then decorated, and may also change color by "an addition of pigment without moult."

Mr. F. W. Headley[2] evidently accepts a somewhat similar view, as he says: "A far more remarkable cause of change of colour [than the shedding of the tips of the feathers] is the entrance of fresh colouring matter into the feather, which cannot therefore be an entirely dead thing. This is what takes place when the Blackheaded Gull puts on his spring head-dress, the colour, according to Gätke [!], appearing first at the edges of the feathers and gradually extending till the whole is dyed. In winter the breast of the Dunlin is almost white, in spring it becomes black, the pigment working its way to every part of the feathers through channels as yet undiscovered. By a similar process the head of the Little Gull changes in spring from white with a dash of ashen-gray to black," etc. (l. c., p. 160).[3] To show how little Mr. Headley really knows of the subject of which he is here writing, it is sufficient to say that these and all the other species he mentions in this connection, as the Knot, Wood-sandpiper and Herring

[1] Evolution of the Colors of North American Land Birds. 8vo, San Francisco, 1893.

[2] The Structure and Life of Birds. Sm. 8vo, London, 1895.

[3] Mr. Headley is evidently not the only one who has been dazed or misled through lack of familiarity with the subject, by Gätke's strange statements. Thus a writer in 'The Auk' (XII, 1895, p. 346) alludes to Gätke's researches in the field of 'aptosochromatism' as an "extremely valuable" contribution to the subject, and proceeds to approvingly enumerate its leading points. Also a reviewer of Gätke's work in 'The Ibis' (Jan., 1896, p. 142) refers to the chapter "relating to colour changes without a moult" as "perhaps the most valuable chapter in the book"! In this relation attention is called to Mr. Chapman's paper (*antea*, pp. 1–8) on 'The Changes in the Plumage in the Dunlin and Sandpiper,' written apropos of this particular chapter in Mr. Gätke's book.

Gull, are birds that have long been known to acquire their breeding dress by a spring molt.[1]

It is even more surprising to find men of the scientific standing of Dr. R. Bowdler Sharpe asserting that the striped plumage of the young Sparrow Hawk (*Accipiter nisus*) becomes changed to the barred plumage of the adult through "a gradual change in the markings of the feather, and not by an actual moult,"[2] or that *young* Wagtails (*Motacilla lugubris*) gain their first full spring plumage by a molt, while the old birds of the same species do *not* molt in spring, but acquire gradually the black on the back and throat "without loss of a feather;"[3] the same being also affirmed of other species of the genus *Motacilla;* although Meves and various other writers ascribe to these birds a spring molt, through which they obtain their breeding dress.

Also that Mr. W. R. Ogilvie-Grant should assert that the female Red Grouse (*Lagopus scoticus*) acquires its summer dress mainly by molt, but partly by a change in the spring in the pattern of the markings in some of the "same feathers which in autumn and winter" were differently marked;[4] or, as he more fully states it: "The summer flank feathers are produced in two ways, either by the gradual rearrangement and change in the pigment of the autumn feathers or by moult. In some birds the whole of the alteration in the plumage of the flanks is produced by change of pattern in the old autumn feathers, in others the change is entirely produced by moult, while sometimes both methods are employed by the same individual. In the former case the first indication of the coming change may be observed in the beginning of the month of November, or even earlier, when many of the flank feathers show traces of an irregular buff stripe or spot next the terminal half of the shaft. As the bird only changes about half the flank feathers, these buff marks are only to be observed on such as are destined to undergo alteration of pattern, which, roughly speaking, means every second or third feather. The buff gradually spreads along the shaft, then becomes con-

[1] See, for example, Macgillivray's 'British Water Birds,' under these species, to say nothing of authorities already cited in other parts of this paper.

[2] P. Z. S., 1873, p. 418.

[3] Cat. Birds Brit. Mus., X, 1885, p. 461.

[4] Cat. Birds Brit. Mus., XXII, 1893, p. 37, footnote.

stricted and broken up into patches, which gradually spread laterally towards the margins of the webs, forming wide irregular buff bands. Meanwhile the interspaces become black, and the rufous of autumn dies out.... It may very naturally be asked why some females should change their flank feathers by moult, while others are enabled to go through the much less exhaustive process of redecorating their old autumn feathers and making them serve the purpose of new summer plumage. This is a difficult question to answer, but it seems natural to suppose that the more vigorous birds gain their summer flank feathers by moult, while nature has enabled the weaker individuals to obtain the necessary protective nesting plumage by a more gradual and less exhaustive process."[1]

In view of what is known of the growth and structure of feathers, and of the character and nature of pigment, such suggestions as the above are simply incomprehensible. To speak, as above, of the "redecoration" of feathers, through the "rearrangement and change in the pigment," involving both change of color and "change of pattern" in the markings, is to imply histological conditions such as no microscopist in studying feather structure has yet discovered; and not only this, but such a reorganization of the internal structure of a practically lifeless organism as is entirely opposed to the known conditions of the case.[2] On the other hand a more reasonable explanation is available. Every ornithologist of experience knows that in birds which are several years in acquiring their adult plumage, or which have a very varied and irregular pattern of markings, it is possible to find, by means of a good series of specimens, almost every imaginable stage and combination of markings, and such a connected series of gradations, as to seem to prove a continuous change in both color and markings from the younger stages to the adult by simply change of color without a molt. In other words, a given molt by no means affects all individuals alike, but carries some to a considerably more advanced stage in the series of changes than others; also, that in the case of irregular and varied patterns of color markings,

[1] On the Changes of Plumage in the Red Grouse (*Lagopus scoticus*). Annals of Scottish Nat. Hist., No. 11, July, 1894, pp. 129–140, pll. v and vi. The above extract is from pp. 135–137.

[2] The consideration of the microscopical structure of feathers, and the nature of pigment as affecting coloration, is quite beyond the scope of the present paper, respecting which the reader is referred to Dr. Gadow's well-known memoir 'On the Colour of Feathers as affected by their Structure' (P. Z. S., 1882, pp. 409–421, pll. xvii, xviii), and the papers he there cites.

it is not uncommon to find in one and the same individual, feathers, so far as their markings are concerned, which represent phases peculiar to several distinct molts. Indeed, it was just such intermediate stages, combined with hasty observation and faulty reasoning, that led Schlegel, half a century ago, to announce that nearly all birds obtain their breeding dress simply by change of color in the feathers without molting, and later misled Severtzof, and Fatio to the construction of elaborate theories to account for imaginary facts.

If one will take a good series of specimens in molt (unfortunately such specimens are rare in collections[1]), in the case of species which are alleged to, and which have the appearance of, changing color without molting, it will be found that the parti-colored and apparently changing feathers have this appearance when they first break from the sheath in which they are formed, and that these deceptive feathers have not necessarily acquired their peculiar appearance by a subsequent and quite inconceivable change in the amount, arrangement and character of the coloring matter.

As already shown, and as most ornithologists know, many birds do undergo great change of color without molting; but it is equally well known that this striking change in color, as from the winter to the breeding dress, is due not to any addition of pigment, or to any marked change of color in the feathers, but simply to a gradual wearing off of the light colored edges of the feathers of the winter dress, leaving, as the breeding season approaches, the already existent colors of the breeding dress exposed. Combined with this is more or less blanching of the color of certain parts. Striking illustrations of such changes are afforded by the Snow Bunting (*Plectrophenax nivalis*),[2] the Bobolink (*Dolichonyx oryzivorus*), and numerous other species that might be mentioned. In a less striking degree the change is common to nearly all single-molting birds, and also to many that undergo a second or spring molt, in which the feathers of the new dress are at first more or less dis-

[1] It is to be regretted that birds in molt are generally looked upon by collectors, and too often by ornithologists, as undesirable because not in 'good plumage,' whereas such specimens often prove to be the most valuable and instructive that can be obtained.

[2] On this species see *antea* (pp. 9–12), Mr. Chapman's paper, entitled 'On the Changes of Plumage in the Snowflake (*Plectrophenax nivalis*).' Also the same author's papers 'On the Changes of Plumage in the Bobolink (*Dolichonyx oryzivorus*),' Auk, VII, 1890, pp. 120–124, and *ibid.*, X, 1893, pp. 309–341, pl. vii.

tinctly skirted with a fringe or superficial wash of ash, buff or olive, which more or less quickly disappears, often by the double process of abrasion and fading. Exposure to the elements and friction also produce more or less marked change in color where there is no conspicuous loss of tissue from the border of the feather. Generally this is simply an obvious loss of color by fading, but in some instances the color becomes somewhat heightened, as in the case of some browns which change from a grayish brown to a more reddish tint; this may be due in part to abrasion, but probably somewhat also to chemical action consequent on exposure. In such changes, however, there is no transposition of pigment, nor any radical modification of pattern—no "redecoration," and no transformation of white feathers into black—but merely a slight change in tone.

It is noteworthy that while many writers have believed in and have advocated change of color in feathers, of even the most radical kind, the theories as to the causes and methods of the change are as diverse and as numerous as their ingenious inventors. In several instances the fat of the body has been presumed to be the vehicle of the colored secretion that is supposed to flow, by imbibition, or capillarity, or by some unknown process, from the body into the feather; in one case (Fatio) it is not a vehicle for the transportation of pigment, but merely a solvent for the pigment granules already in the feather; in another case a 'secretion' (not a fat) flows from the body into the feather and spreads by endosmose to its remotest cells, depositing in layers the pigment it carries till the feather is duly colored (Severtzof). How the supposed secretion, which mechanically (not physiologically) acts as the coloring agent becomes charged with its burden of pigment no one really attempts to explain; yet some of these theory builders do confess themselves puzzled to understand how under this mechanical or 'purely physical' (Severtzof) process the pigments can so accurately assort and arrange themselves as to produce the color patterns of variegated feathers.

While there may be a slight basis in fact for some of these speculations, if there really is such a thing as an increase in the quantity, and any radical change in the position, of the pigment in a dead feather, it is still, as stated by Bachman in 1839, by

virtue of "some new law of nature not hitherto discovered." Finally, as has already been stated in substance, the inventors of these diverse theories have assumed, and attempted to explain, conditions that in nine cases out of ten had no existence; namely, a color change, demonstrably due—normally at least—to molt, which they have supposed must happen in some other way.

Supplemental Note on the Spring Molt of the Bobolink.—Since the foregoing was made up for the press I have had opportunity, through the kindness of Mr. Thomas Proctor of Brooklyn, of examining *twenty-five* live Bobolinks (*Dolichonyx oryzivorus*) in the bird stores of that city, and two others in Mr. Proctor's own extensive aviary. The examination was made on the 14th of March, and the molt was in all stages, from birds showing only here and there the tip of a black feather on the breast, to those that were in nearly full breeding dress. A large number were in the highest stage of the molt, pin-feathers being distinctly visible, especially among the wing-coverts and scapulars and interscapulars, even when the birds were several feet distant. Generally the black appeared in patches scattered irregularly through the autumn plumage; on the lower parts, where the change was most striking, sometimes the black prevailed and sometimes the olive buff tints of the fall dress. In short, the birds presented the same conspicuously pied appearance seen during the molt at the end of the breeding season, except that the incoming colors were reversed, the black now replacing the autumn dress instead of the reverse.

Of course, since the publication of Mr. Chapman's papers 'On the Changes of Plumage in the Bobolink' (cited *antea*, p. 42, footnote 2), there has been little reason to doubt that the Bobolink acquired its breeding dress by a spring molt; yet as his conclusions were based on the examination of scanty material, and as there has been a tendency in some quarters to question their correctness, and as the contrary has often been asserted (see the case of Ord, *antea*, p. 16), it seems worth while to record in this connection the overwhelming proof of the fact I am now fortunately able to adduce.