PTILOSIS OF THE HOUSE WREN (*TROGLODYTES AEDON AEDON*).[1]

BY RUDYERD BOULTON.

THE arrangement and distribution of feathers in oscine birds is remarkably uniform;—so much so, in fact, that one may almost search in vain for constant differences between major taxonomic groups. Many variations and adaptive modifications occur, but those differences and similarities which may be regarded as phylogenetic are few and far between. As far as known, all song birds (Oscines) are eutaxic,[2] with a few exceptions the aftershaft is present (Miller, 1924b), and the oil-gland is always nude.[3] These three characters are important in the classification of non-passerine birds. On the other hand, natal down is absent in such unrelated oscines as Migrant Shrike (*Lanius*), Oropendula (*Gymnostinops*),[4] Blue Jay (*Cyanocitta*),[4] Magpie Jay (*Calocitta*),[4] Java Sparrow (*Munia*),[4] Cedar Waxwing (*Bombycilla*),[4] and House Sparrow (*Passer*). Variations in the distribution of natal down in the young of passerine birds are endless, and while this field of study has not been thoroughly worked, it may eventually prove valuable in the determination of the relationships and dividing lines between genera and families.

The observations which form the basis of this paper were made while I was an assistant of Mr. S. Prentiss Baldwin at his unique Bird Research Laboratory, Gates Mills, Ohio. Mr. Baldwin's co-operation has made this paper possible and I am deeply indebted to him for permission to publish it. My thanks are also due Mr. Waldron DeWitt Miller of the American Museum of Natural History, New York City, for criticism freely and generously given.

Observations were made on living birds and later checked by an examination of specimens,—skins and alcoholics. Notes on

[1] Contribution No. 11 from the Baldwin Bird Research Laboratory.

[2] Miller, W. DeW. Notes on Ptilosis with Special Reference to the Feathering of the Wing. Bull. Am. Mus. Nat. Hist., XXXIV, pp. 129–140, 1915.

[3] Beddard, F. E. The Structure and Classification of Birds, 1898.

[4] Miller, W. DeW. Further Notes on Ptilosis, Bull. Am. Mus. Nat. Hist., L, pp. 305–331, 1924.

the growth and distribution of feathers were taken on 23 nestling wrens, as well as 42 nestlings of twelve other species. Two broods of wrens were studied intensively.

METHODS OF MAKING THE OBSERVATIONS.

In the first brood of six young Wrens that was studied from day to day (June 11–21, 1926), notes were made on the number and arrangement of downs (neossoptiles), the order of appearance of feather papillae and the areas in which they first developed, the progress of the feather after breaking through the skin, the rupturing and disintegration of the sheath, and the feather tracts (pterylae and apteria) were plotted. As soon as the birds were hatched, they were marked by tying a colored thread on the tarsus, loose enough so that it would not retard growth or inhibit the circulation. Silk thread was used at first, but because of the tendency of even a square knot to become untied, it was found that cotton thread was better. Various other methods of marking were tried, such as painting diagnostic marks on the body with india and indelible inks, but the continual rubbing and jostling of the birds and the abrasion of the nest material, caused the marks to become faint if not absent in twenty-four hours, Marking by means of threads was therefore adopted as being far superior to other methods.

Observations were made daily at the same hour with a hand lens of low power. Each bird was handled on an average of half an hour a day and in this time was rolled about (gently however) as no other young bird probably ever had been. When eight days old the birds were banded with their permanent Biological Survey bands. It is interesting and gratifying that all left the nest at the proper time, in no wise harmed by their novel experience, and it indicates that the popular idea, "to touch a young bird will kill it," is without any foundation. When the birds were eleven days old, three days before leaving the nest, this type of observation became unproductive of results, for the nestling downs had practically disappeared and the feather tracts had become established in their adult relationships.

Observations on the second brood of seven Wrens (August 9–18, 1926) consisted in making daily measurements of the growth of 36 feathers and their sheaths from the various tracts in different

parts of the body. The methods used were much the same as in the first brood. The birds were marked as soon as hatched and measurements commenced when the first feather had broken through the skin. These were continued daily at the same hour until all the birds had left the nest. Measurements were made with an ordinary pair of dividers, sometimes aided with a hand lens. They were read in millimeters, interpolated to tenths, and while it is not easy to hold a lively young Wren and measure various feathers, the growth curves of individual series, even when plotted on a large scale, are reasonably smooth and uniform, indicating accuracy of measurement to a marked degree.

The identification of the feathers that were measured from day to day was a problem which necessitated a little experimentation. The primaries, secondaries and tail feathers, being of definite number, could be located easily by counting, and the feathers in the various series of coverts were readily found by their relation to the larger quills which they overlie. The small feathers in the other six tracts presented greater difficulties. Marking the feather by staining its tip was tried, but here again wear and fading made it difficult, twenty-four hours later, to be sure that the same feather was being measured. Accordingly the tips of all feathers surrounding the one to be measured were clipped off, and no difficulty was experienced later in identifying the one desired. It may be argued that the clipping of feathers affected the growth of the remaining ones in that area, but as only those parts of the feathers that were dry and thoroughly cornified were removed and their growth continued to be normal, I believe that absolutely no distortion of growth occurred.

CLASSIFICATION OF FEATHER TRACTS.

Before entering upon a minute description of distribution and growth of feathers it is deemed advisable to define the terms which I propose to use. The following arrangement of tracts and their sub-regions is in large measure adapted from Nitzsch, Dwight and Witherby, and I believe that it is applicable in detail to all oscine birds.

Capital Tract: Frontal region, Coronal region, Occipital region, Superciliary region, Loral region, Rictal region, Ocular region, Malar region, Auricular region, Post-auricular region.

Spinal Tract: Cervical region, Interscapular region, Dorsal region, Pelvic region.

Caudal Tract: Upper tail-coverts, Rectrices, Under tail-coverts, Anal circlet.

Ventral Tract: Inter-ramal region, Sub-malar region, Cervical region, Sternal region, Axillar region, Abdominal region.

Humeral Tract.

Alar Tract: Primaries, Greater Primary coverts, Middle Primary coverts, Secondaries, Greater Secondary coverts, Middle Secondary coverts, Carpal Remex covert, Lesser Secondary coverts, Marginal coverts, Alula, Alula coverts, Carpo-metacarpal coverts, Under Greater Primary coverts, Under Lesser Primary coverts, Under Middle Secondary coverts, Under Lesser Secondary coverts.

Femoral Tract.

Crural Tract: External region, Internal region.

The Caudal and Alar tracts require special comment. In this paper I will regard the first primary as the innermost, the tenth (or eleventh) as the outermost. The first secondary lies next to the first primary, the rest are numbered progressively inwards toward the ulnar-humeral joint. The various coverts are numbered to correspond with the quills which they overlie. In the Caudal Tract I regard the middle pair of rectrices as the first, and number the others progressively outwards. As in the wing, the upper and under tail-coverts are numbered to correspond with the numbers of their respective rectrices.

PTILOSIS OF THE ADULT.

Although the arrangement of feathers in the adult is an end result of feather growth in the nestling, the discussion of the development of tracts and the rate of growth in the latter will be more easily understood if a clear idea of the final arrangement in the adult is first established. I will therefore reverse the chronological order and describe and figure the adult first. Measurements of the mature feathers are included with those of the nestlings in Table III for the sake of comparison.

Capital Tract.

The frontal and coronal regions are composed of three rows of feathers on each side of the median line which extend from the

posterior margin of the nares to a point at the top of the head, some distance behind the eyes. There is no definite line of demarcation between the two regions. The frontal is limited to that area which lies over the base of the maxilla while the coronal begins at the point where the skull proper ascends backwardly. At the top of the head the six lines of feathers, which point directly backward, lose their individual distinctness and spread in a fan-shaped area over the back of the head, forming the occipital region. This extends approximately to the junction of the head and the neck where it forms the anterior half of a diamond-shaped whorl of feathers, caused by the meeting of this and the cervical region of the Spinal Tract. Here, the rows of feathers are again more or less distinct and point ventrally around the sides of the neck to form the post-auricular region. The superciliary region consists of four or five indistinct rows of small feathers extending from in front of the orbit along the side of the coronal region to merge with the occipital region. The loral region is the anterior end of this area and lies on either side of the frontal region at the sides of the maxilla and in front of the eyes. The feathers of the superciliary region point outward, their bases lying proximally, their tips distally, with reference to the median line, and this character clearly distinguishes them from the feathers of the coronal region. The rictal region is absent in the House Wren for there are no rictal bristles. The ocular region is composed of two series of very minute feathers, one on each eyelid. The remainder of the lower lid is very sparsely covered with small down-like feathers. The malar region extends from the fork between the ramus and tomium of the mandible backward to a point just below the opening of the external ear where it fuses with the upper edge of the submalar region of the Ventral Tract. The auricular region occupies the area below the eye and surrounds the opening of the ear. At its upper posterior edge it meets with the occipital region, but the feathers point at right angles to the axis of the feathers of that region. The lower anterior margin of the ear opening bears the most important feathers, and these form the major part of the ear covert. The longest feathers are most anterior and point backward over the opening. They grade imperceptibly along the lower margin into the smallest which are

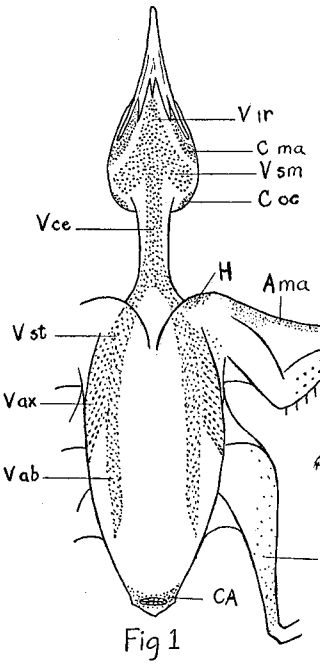

Fig 1

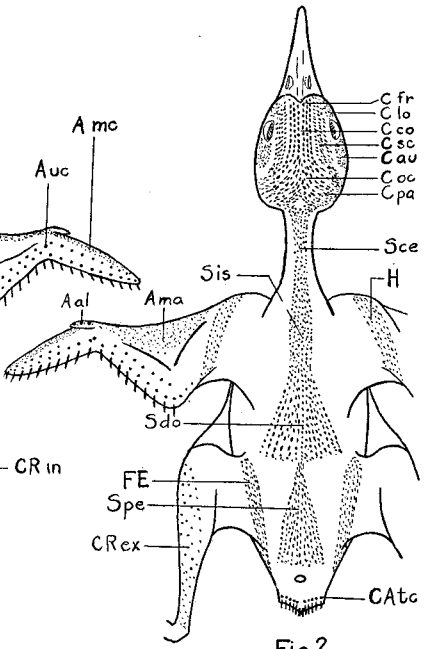

Fig 2

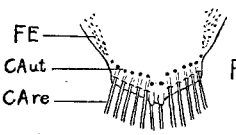

Fig. 3

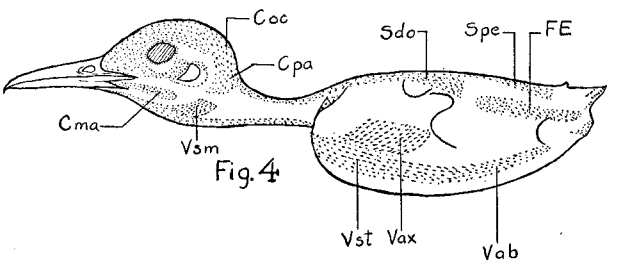

Fig. 4

Key to lettering on figures 1–4.

Aal = alula and alula coverts. Ama = marginal coverts. Amc = carpometacarpal coverts. Auc = carpel remex covert. Cau = auricular region. Cco = coronal region. Cfr = frontal region. Clo = loral region. Cma = malar region. Coc = occipital region. Cpa = post-auricular region. Csc = superciliary region. CA = Caudal Tract. CAre = rectrices. CAtc = upper tail-coverts. CAut = under tail-coverts. CRex = Crural Tract, external region. CRin = Crural Tract, internal region. FE = Femoral Tract. H = Humeral Tract. Sce = Spinal Tract, cervical region. Sdo = dorsal region. Sis = interscapular region. Spe = pelvic region. Vab = abdominal region. Vax = axillar region. Vce = Ventral Tract, cervical region. Vir = interramal region. Vsm = sub-malar region. Vst = sternal region.

Figure 1. Natural Size. Ventral view of adult House Wren showing pterylae and apteriae.

Figure 2. Natural size. Dorsal view of adult House Wren.

Figure 3. Enlarged, × 2. Ventral view of Caudal Tract showing arrangement of rectrices, under tail-coverts and Femoral Tract.

Figure 4. Natural Size. Lateral view of adult House Wren.

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most posterior and point backward also but away from the opening. The post-auricular region cannot be clearly differentiated from the occipital region. It is characterized by smaller feathers, all of which point ventrally.

Spinal Tract

The cervical region, where it meets the occipital region of the Capital Tract, forms the posterior border of the diamond shaped whorl described above. It divides medially and the feathers orient themselves to point ventrally around the sides of the neck to conform with the direction of the feathers of the post-auricular region. In the anterior part of the cervical region the feathers point forward, at about the mid point of the neck they are rotated on their bases vertically (a few at the sides of the region rotate laterally) and in the interscapular region they all point backward. This last region is very dense and sharply delimited from its adjacent apteria. At a point opposite the proximal origin of the posterior patagium of the humerus the Spinal Tract spreads laterally to form the saddle-shaped dorsal region. The posterior margin is almost truncate or slightly rounded and is slightly anterior to the line between the posterior femoral

patagia. The feathers of the sides and posterior part of the dorsal region are exceptionally long and suffice to clothe completely the back and sides of the body. These are the feathers which bear the peculiar silvery mirrors at their extremities. Immediately behind this lies the pelvic region, a triangular area with its apex touching the dorsal region and its base just anterior to the oil gland, which is of course unfeathered.

Caudal Tract

The middle tail feathers are the longest rectrices and their quills are of slightly greater diameter than are the others. They are inserted in a pair of prominent papillae which project beyond the pygostyle. The other rectrices apparently are not furnished with these papillae. The tail is strongly rounded as may be seen from the following measurements: I,44.3 mm; II,44.0 mm; III,43.7 mm; IV,43.4 mm; V,42.0 mm; VI,36.0 mm. The rounding is much more apparent than the measurements show, due to the fact that the bases of the feathers lie on a diagonal, not on a line at right angles to their axes. There are five pairs of upper tail-coverts, the first being absent. There are at least six pairs of under tail-coverts. The first pair lies above and posterior to the second. A pair of feathers, exactly intermediate in position, length, strength of shaft and character of web, lies between the sixth pair of coverts and the most posterior feathers of the Femoral Tract and it is questionable whether they constitute a seventh pair or not. The anal circlet consists of two concentric series of small feathers surrounding the anus. At the lateral ventral margins there are a few small scattered feathers without any definite arrangement.

Ventral Tract

The inter-ramal region is a triangular area extending from the junction of the rami of the mandible to a point immediately under the orbits. Here, on either side, the submalar regions branch off and extend in slightly widening bands until they almost meet the post-auricular regions of the Capital Tract. The cervical region runs down the ventral median line of the neck, slightly widening posteriorly until at approximately the mid-point it branches to form the two sternal regions. The feathers of these two regions

point backward and inward and serve to cover the breast and belly. On each side of the body, where the humerus articulates with the shoulder girdle, the axillar region branches off from the sternal region. It extends almost to the knee joint when the leg is folded up against the body. The feathers of this region are long and fluffy and cover the sides of the body and the flanks. They point backward and outward and thus are clearly separable from the feathers of the sternal region. From the point where the inner edge of the axillar region leaves the sternal region, the abdominal region extends, slightly decreasing in width, almost to the anus, but well on the side of the body. The feathers of this region point inward and cover the large ventral apteria.

Humeral Tract

The Humeral Tract, from which arise the scapulars or humerals, is a very dense and compact series of about four rows of feathers extending backward from the junction of the axillar region and the sternal region. It crosses over the top of the humerus from the outside to the inside, following a spiral path, and ends on the distal margin of the posterior humeral patagium. The most distal feathers of this tract can scarcely be distinguished from the most proximal secondaries.

Alar Tract

There are ten well developed primaries with what appears to be a vestigial eleventh lying on the base and slightly on the upper surface of the tenth. I cannot be sure that this feather is homologous with an eleventh primary. Its shaft is slightly stiffer and it is more lanceolate in form than the adjacent carpo-metacarpal coverts. The tenth greater covert, with which it might be confused, is almost twice as long, measuring 2.6 mm. The wing formula is 8, 7, 6, 5, 4, 3–9, 2, 1, 10, 11 (?), and the wing is very strongly rounded as may be seen from the accompanying measurements: (1), 38.0 mm; (2), 38.4 mm; (3), 38.7 mm; (4), 39.0 mm; (5), 39.4 mm; (6), 40.3 mm; (7) 40.2 mm; (8), 39.5 mm; (9), 34.0 mm; (10), 21.0 mm; (11), 1.5 mm. The apparent discrepancy between the wing formula and the measurements is due to the fact that the bases of the primaries are on a diagonal in the folded wing.

Thus the eighth primary appears to be longer than the seventh although it is actually shorter. The greater primary coverts are ten in number, the tenth being very much smaller than the rest. I can find no trace of an eleventh greater covert. There are seven middle primary coverts, the first three and the eleventh being absent. The tenth is proportionally much smaller than the others. The series of lesser primary coverts is not present in the House Wren. There are nine secondaries, each of which is provided with a greater covert. Lying beside the ninth greater covert is a feather which obviously is a tenth covert although its secondary has been lost. There are two other feathers in the same series, lying between this tenth covert and the distal feathers of the Humeral Tract, which may very well be the eleventh and twelfth coverts, but they are much smaller and their relationships are not so clear. It is very interesting that while the eighth and ninth secondaries are much reduced and the tenth is absent, the corresponding coverts are but slightly reduced, much less in proportion than their corresponding secondaries. The complete series of measurements (in millimeters) of these feathers is given in Table I.

TABLE I.

Position of feather	1	2	3	4	5	6	7	8	9	10
Secondary	38.0	38.0	37.3	35.5	34.0	32.0	31.0	27.0	22.0	....
Covert	16.6	16.8	17.5	17.9	17.8	17.5	16.6	16.0	14.9	14.0

There is no carpal remex but its covert is present in the same row as the greater secondary coverts and lies on the base of the first primary, more proximal than the greater covert of that feather. Its shaft is more slender than the shaft of the first greater secondary covert and it measures 8.9 mm. in length while the first covert is 15.5 mm. long. The middle secondary coverts number seven, there being no covert of this series over the first and ninth secondary. The lesser coverts lie directly over the ulna and it is difficult to distinguish them from the marginal coverts which are adjacent to them on the humeral-ulnar patagium. There is, however, a row of six feathers which, because of their different orientation and definite alignment, I regard as lesser coverts. The marginal coverts are short and densely inserted on the upper

surface of the patagium, rather longer on the extreme edge, and very sparsely distributed on the under surface. The most proximal feathers on the under side of the wing are long, plumulose and sickle-shaped. There are three alula quills which measure 14.1 mm; 12.0 mm; and 7.0 mm. in length. Their coverts which can be easily seen on the nestling's wing are difficult to distinguish in the adult. The carpometacarpal coverts extend from the pollex along the outer edge of the manus to its extreme tip. At the proximal end of this area they are continuous with the marginal coverts. The feathers are small, slightly plumulose and are sharply demarked from the adjacent apteria on both under and upper sides of the wing. All the coverts on the under side of the wing are smaller and more plumulose than the corresponding feathers of the upper side. There are ten under greater primary coverts and ten under lesser primary coverts. It will be noticed that this last series is not present on the upper surface and the middle coverts, well developed on the upper surface, are totally absent underneath. The under carpal remex covert is but 5.0 mm. long and a very different appearing feather from the corresponding feather on the upper surface of the wing, being much more downy and weaker. The under secondary coverts are difficult to homologise in the material at hand. There are two series of soft downy feathers which are presumably the middle and lesser under coverts. In the former there appear to be eight, in the second, seven feathers.

Femoral Tract

This tract extends from the anterior end of the knee, when the leg is drawn up against the body, along the sides parallel to the Spinal Tract and almost to the anus. The posterior part of this tract merges with the under tail-coverts.

Crural Tract

The external and internal surfaces of this tract are found on the tibia extending from the scutellation of the tarsus slightly more than half way to the tibia-femur joint. They are irregularly arranged and the internal surface is less densely clothed than the external surface. The most distal feathers are shortest, the proximal feathers longest.

Aftershaft

The aftershaft is not well developed in the House Wren. A feather from the dorsal region measuring 26.0 mm. in length had an aftershaft of 11.5 mm., while in one from the abdominal region measuring 10.0 mm. the aftershaft was only 2.0 mm. long. The remiges have only a single row of barbs extending across the ventral surface of the shaft at the base of the web.

Filoplumes

These degenerate feathers are well developed and traces at least are found in all of the major tracts. In no case, however, are they long enough to extend beyond the contour feathers, as they do in some of the *Timaleidae* and *Turdidae*. One from the dorsal region measured 7.5 mm., and in the axillar region one was found measuring 8.5 mm. in length. There is at least one filoplume at the base of each of the remiges and rectrices.

Downs (Plumulae)

Apparently the down feathers of the adult are found only on the apteria and along the edges of the pterylae. I do not find any downs growing among the contour feathers. The abdomen or ventral apterion of the adult male is fairly well covered with short, silky downs of a bluish gray color. In the adult breeding female, however, these are not present. I have not determined whether their absence is due to wear or whether a moult of these feathers takes place at the beginning of the period of incubation. Whichever is the case, the result is the same, namely, that the bare skin of the abdomen in its increased vascular condition and consequent higher temperature can be applied directly to the eggs. In the femoral-spinal apteria and in the axillar apteria the downs in both sexes are present.

GROWTH OF FEATHERS IN THE NESTLING

While a newly-hatched Wren is helpless, blind and practically naked, its feathers are well started in their development. The sheaths have not, however, pushed through the skin, although in some cases they may be faintly seen as dark bluish gray spots or streaks. I have not made an histological examination of these

embryonic feathers, but it is my opinion that their visibility depends on the amount of pigment deposited in them, a condition which does not appear to be correlated with the actual time of hatching. In the majority of young birds no sign of feathers is visible but in one, less than an hour old, the rectrices showed faintly, and in another about two hours old, the secondaries and the proximal five or six primaries were barely discernible.

Downs (Neossoptiles)

The first feathers of a young Wren, the neossoptiles, are present when it is hatched. They appear to have attained their full size before the bird emerges from the egg. As they are attached to the tips of the forthcoming contour feathers (Jones 1907), it is obvious that they may lengthen only as much as the distance from the tip of the feather to the surface of the skin. In order to substantiate this further, I attempted to mark a definite point on a down with ink and measure the feather from day to day. Although these results were inconclusive due to wear and fading of the ink spot, it was evident that no appreciable growth took place. The history of the neossoptiles is one of continual disintegration. From the moment the young bird is hatched, wear, abrasion of the nest, and jostling by other nestlings and the parent combine to break the tips, strip off the barbules and even remove the downs entirely. By the time the birds have left the nest only a few filaments remain attached to the juvenal feathers (teleoptiles).

The neossoptiles are arranged in a fairly definite pattern. An examination of over one hundred young Wrens revealed that they were confined to the coronal, occipital and dorsal regions. There is a certain amount of variation in the number of downs in each region as will be seen from the accompanying table. Typically there are five neossoptiles on each side of the coronal region. These are attached to the tips of the outermost row of feathers and extend from a point slightly anterior to the eye to a point slightly posterior. In the occipital region there are four downs in a double row on each side of the median line slightly anterior to the diamond shaped whorl. In the dorsal region there are three downs on each side with one at the posterior end on the median line.

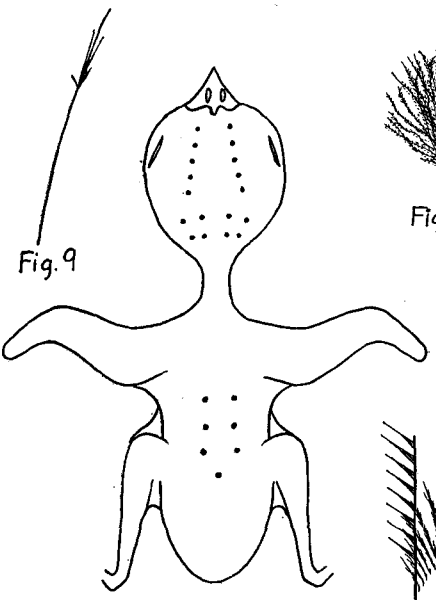
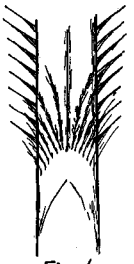


Fig. 5

Fig. 9

Fig. 8



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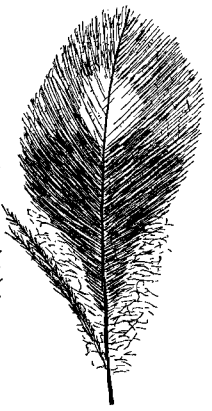


Fig. 7

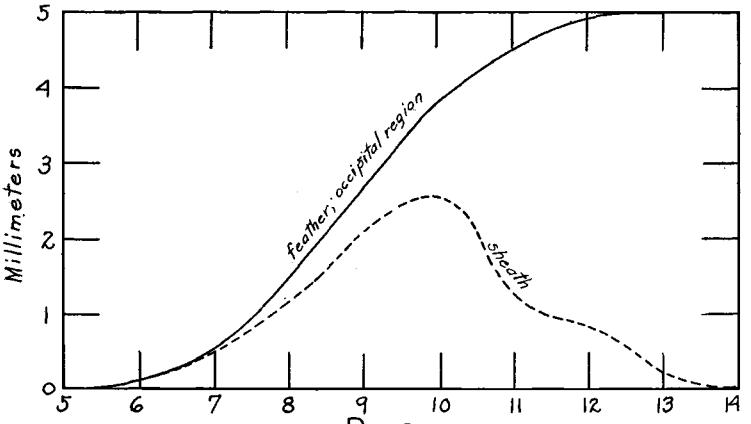


Fig. 10

Figure 5. Enlarged, × 2. Dorsal view of nestling House Wren showing arrangement of neossoptiles.

Figure 6. Enlarged, × 10. Ventral view of shaft of fourth secondary of adult showing rudimentary aftershaft.

Figure 7. Enlarged, × 2. Feather from dorsal region of adult showing aftershaft.

Figure 8. Enlarged, × 4. Down (plumule) from axillar apteria of adult.

Figure 9. Enlarged, × 10. Tip of filoplume measuring 8 mm. in length, from dorsal region of adult.

Figure 10. Graph showing the disintegration of the feather sheath in the occipital region. This is typical of all contour feathers. After the twelfth day the feather grows slowly. Until the tenth day the feather grows more rapidly than the sheath breaks, but after the tenth day disintegration takes place at a rapid but irregular rate and by the fourteenth day the sheath has entirely disappeared.

TABLE II

VARIATION IN THE NUMBER OF NEOSSOPTILES IN 15 NESTLING WRENS.

	Min.	Avg.	Max.
Coronal right	3	5.5	8
Coronal left	4	5.3	7
Occipital right	3	4.0	5
Occipital left	4	4.0	5
Dorsal right	2	3.3	5
Dorsal left	2	3.5	5
Dorsal median	0	.6	1

When the young bird is first hatched, there appear to be filaments of down at the tips of both the rectrices and remiges. Each filament is less than half a millimeter long and consists of a single shaft without any barbs or barbules. It may be that this structure is merely the attenuated tip of the forthcoming feather sheath. I am inclined, however, to regard it as a neossoptile, probably degenerate, although possibly primitive, but I have not made an histological examination of it.

Capital Tract

First Day. There is no sign of developing feathers.

Second Day. The first sign of feathers (or rather feather sheaths which can be seen through the semi-transparent skin) is at the center of the frontal region. Development proceeds backward

along the two middle rows of coronal feathers. At the same time it spreads laterally to include the rest of the frontal and loral regions and the lateral rows of the coronal regions.

Third Day. Most of the sheaths in the frontal and coronal regions and those in the center of the occipital region show clearly, but none have pushed through the skin. At the lower anterior margin of the external ear opening (auricular region) a few sheaths show faintly.

Fourth Day. All the sheaths of the frontal, coronal and occipital regions show through the skin. Development of the feathers in the auricular region proceeds backwards from the most anterior point, being most rapid on the lower margin of the ear opening and much slower on the upper margin. In the anterior half of the malar region two and possibly three rows of sheaths show.

Fifth Day. Development of the auricular region has proceeded so far that the circlet of sheaths around the ear opening is almost complete, those at the anterior margin being largest. Development of sheaths has extended from the occipital region down into the post-auricular region. Almost all the sheaths show in the malar region.

Sixth Day. Feather sheaths have just broken through the skin in the frontal and coronal regions and in the center of the occipital region. Those in the frontal region appear first and are followed by the sheaths in the coronal and occipital regions. The loral and post-auricular regions still completely underlie the skin. The innermost sheaths of the superciliary region are beginning to show.

Seventh Day. Sheaths at the anterior margin of the ear opening have just emerged from the skin, as have also those of the most dorsal part of the post-auricular region. Most of the frontal, coronal and occipital sheaths are outside the skin. Sheaths of the superciliary region show distinctly under the skin.

Eighth Day. The tips of the sheaths in the centers of the frontal and coronal regions are broken, exposing the feathers. In the auricular region all the sheaths have emerged except on the posterior upper margin. Sheaths of the inner row of the malar region, nearest the median line are longest, those of the center row are just emerging outside the skin, while the sheaths of the outer

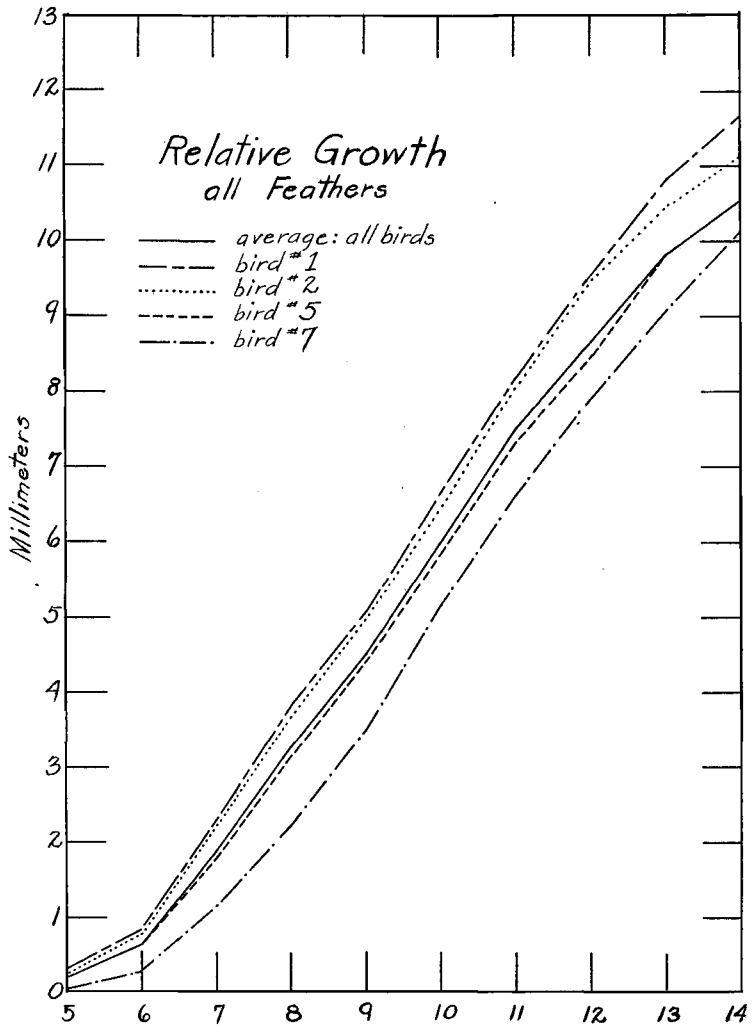
row, which is slightly irregular, still underlie the skin. In the superciliary region the sheaths are beginning to push through the skin, and those of the ocular region on the upper and under eyelid are just beginning to show under the skin.

Ninth to Fifteenth Days. All of the sheaths having emerged, this period is merely one of active growth and disintegration of the feather sheaths. In general, the sheaths of feathers most subject to wear and abrasion are the first to break and expose the feathers within. It is generally true, however, that the sheaths which have emerged first are the ones most likely to disintegrate first. In support of the latter case, the sheaths at the anterior margin of the ear opening break before the others of this region, all being subjected to about the same amount of wear. On the other hand, the sheaths at the anterior end of the malar region are protected by the projecting edges of the tomium and ramus, and by the "wattle" at the gape. Therefore, although they are the first to emerge from the skin, they are the last to expose their enclosed feathers. On the twelfth day the tips of all sheaths except those of the loral and ocular regions, are broken, exposing the feathers. In one nestling at this stage only two neossoptiles remained on the coronal region and two on each side of the occipital region.

Spinal Tract

First Day. When the young bird is about 20–24 hours old, traces of sheaths can be detected under the skin. Apparently those in the cervical region are the first to appear, closely followed in order by those of the interscapular, dorsal and the base of the pelvic regions.

Second to Fifth Days. The center of development seems to be the mid-point of the cervical region, and sheaths appear from there progressively forward along the median line to the occipital region of the Capital Tract and progressively backwards to the posterior margin of the dorsal region. The pelvic region in its development is quite distinct from the rest of the Spinal Tract, for here the first sheaths to appear are at the posterior margin, followed by others more anterior. This causes the apex of the pelvic region to lag behind the rest of the tract, not only in first appearance of the sheaths but in all the other phases of development. It is con-


Relative Growth
all Feathers
average: all birds
bird # 1
bird # 2
bird # 5
bird # 7
Millimeters
Days
0
1
2
3
4
5
6
7
8
9
10
11
12
13
5
6
7
8
9
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13
14

Fig. 11

Figure 11. Graph showing the relative feather growth in nestling House Wrens. The data for this was obtained by taking the mean of the daily measurements of thirty-six feathers of each bird. It is therefore an index of feather growth as a whole. It will be noticed that the curve for the seventh bird runs considerably behind the average for all birds and the curve for the first bird is somewhat in advance of the average. This is taken to indicate that the birds which are hatched first are more vigorous and grow relatively faster than those which are hatched later.

venient, therefore, to refer to it as the "pelvic constriction." At about the fifth day this area is filled by a single line of sheaths showing underneath the skin, and there is no longer any hiatus between the dorsal and pelvic regions.

Sixth Day. Although the cervical region was the first to develop by a very slight margin, the dorsal region has by this time outstripped it, and on the sixth day some of its sheaths begin to push through the skin. Curiously enough, they first come through at the lateral and posterior margins, and it is at this place only that development begins at the periphery of a region and proceeds inward toward the center. Coincident with the first appearance of sheaths outside the skin in the dorsal region is the further development of the posterior margin of the pelvic region. Here the sheaths push through first and the more anterior ones follow them, gradually closing the pelvic constriction.

Seventh to Ninth Days. By this time all the sheaths have emerged from the skin and the tips of those in the dorsal and pelvic regions have broken, exposing the feathers. The lateral margins of the dorsal region and the posterior margin of the pelvic region show the greatest disintegration of the sheath.

Tenth to Fifteenth days. On the tenth day the sheaths of the cervical and interscapular regions burst their tips and expose the enclosed feathers. During these last five days growth, with an accompanying reduction of sheaths, is rapid, and by the time the young birds leave the nest, their backs appear to be uniformly and continuously feathered.

Caudal Tract

First Day. The rectrices do not show underneath the skin when the bird is first hatched, but at the age of about four hours the

first pair shows faintly, followed by the others. The sixth pair of tail feathers can be seen before the bird is twenty-four hours old.

Second to Fifth Days. On the second day the upper coverts can be detected under the skin. Apparently they all appear at about the same time. The under coverts are first seen on the third day. The sixth pair develops first, followed by the others in order. The first pair appears by the end of the fourth day. On the fifth day a few small sheaths show at the lateral lower margins of the anal circlet. In this region development proceeds from these two points as centers in both directions around the anus to meet in the median line at the anterior and posterior margins.

Sixth Day. The upper-tail coverts push through the skin. The second pair shows first closely followed by the others in order, the sixth appearing last. The anal circlet is not entirely complete, there being slight gaps at the median line on the anterior and posterior margins.

Seventh Day. The rectrices begin to emerge, the sixth pair being the first to show, the first pair the last. For all practical purposes, however, they all push through the skin at the same time as there is almost no difference in length after they are long enough to measure. The outermost (sixth) under tail-coverts also show outside the skin.

Eighth to Fifteenth Days. By the end of the eighth day all sheaths have emerged except those of the outer anal circlet. By the tenth day these also have pushed through the skin. Between the eighth and eleventh days the tips of all sheaths burst and expose their feathers. After this, rapid growth and disintegration of feather sheath are the only events worthy of note. The last sheaths to appear are those which lie between the anal circlet, the under tail-covert region and the Femoral Tract.

Ventral Tract

First Day. There is no sign of developing feathers.

Second and Third Days. At the end of the second day sheaths begin to show in the axillar region. Development proceeds anteriorly and by the end of the third day sheaths can be seen throughout the sternal regions and on the cervical region to a

point slightly in advance of the junction of the two former areas. The most lateral rows of sheaths in these regions are the first to develop. In the abdominal regions the two lateral rows of sheaths can be seen to the extreme posterior end of the tract. Simultaneously with the expansion of this center of development, the sheaths of the anterior and lateral margins of the inter-ramal region begin to show. From this center, development spreads backward, eventually meeting the expansion of the axillar developmental center at about the mid point of the cervical region.

Fourth to Sixth Days. On the fourth day all the sheaths of the inter-ramal region appear and those on the dorsal margin of the sub-malar region show under the skin as far back as the anterior margin of the eye. By the end of the fifth day the two centers of development have coalesced in the mid-point of the cervical region and all the sheaths of the sub-malar region can be seen under the skin. On the sixth day the sheaths at the posterior lateral margin of the axillar region begin to emerge, together with those of the inner margin of the sternal region.

Seventh and Eighth Days. During this period all the sheaths emerge. The last to push through the skin are those which lie in the cervical region at the point where the two centers of development joined. Many of the sheaths are broken at the tip and expose their enclosed feathers. The greatest wear and abrasion undoubtedly occurs on the abdominal regions, and all of these feathers are exposed, although they were not the first to be developed and are much shorter than many others in this tract.

Ninth to Fifteenth Days. During this period no further modifications or developments take place. The last feathers to be exposed are those of the inter-ramal region where a minimum of abrasion occurs.

Humeral, Femoral and Crural Tracts

First Day. There is no sign of feather sheaths.

Second Day. In the Humeral Tract, a few sheaths in the most distal row begin to show faintly under the skin. The dorsal row of sheaths of the Femoral Tract can be seen.

Third to Fifth Day. During this period, development of sheaths in the Humeral Tract proceeds from the posterior distal margin

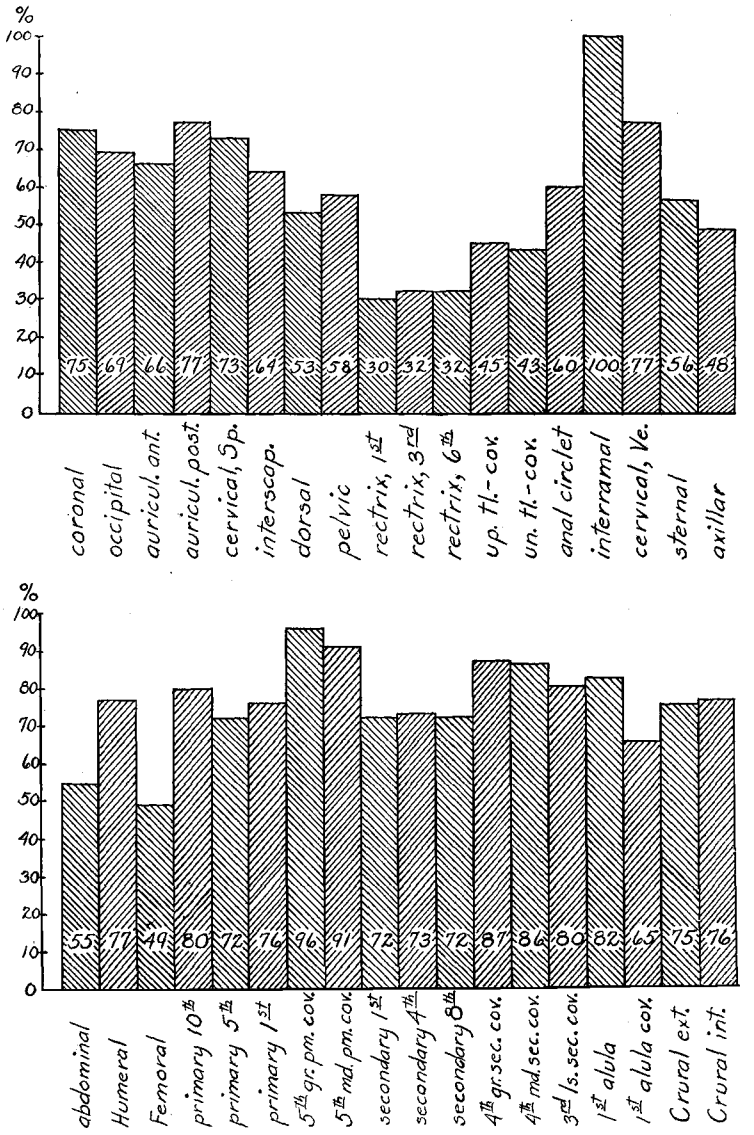
%
100
90
80
70
60
50
40
30
20
10
0
75 69 66 77 73 64 53 58 30 32 32 45 43 60 100 77 56 48
coronal
occipital
auricul. ant.
auricul. post.
cervical, Sp.
interscap.
dorsal
pelvic
rectrix, 1st
rectrix, 3rd
rectrix, 6th
up. tl.-cov.
un. tl.-cov.
anal circlet
interramal
cervical, Ve.
sternal
axillar
%
100
90
80
70
60
50
40
30
20
10
0
55 77 49 80 72 76 96 91 72 73 72 87 86 80 82 65 75 76
abdominal
Humeral
Femoral
primary 10th
primary 5th
primary 1st
5th gr. pm. cov.
5th md. pm. cov.
secondary 1st
secondary 4th
secondary 8th
4th gr. sec. cov.
4th md. sec. cov.
3rd ls. sec. cov.
1st alula
1st alula cov.
Crural ext.
Crural int.

Fig. 12

Figure 12. Graph showing the percentage of ultimate growth which thirty-six characteristic feathers have attained by the time the young birds leave the nest. This is calculated on the basis of one hundred for the same feathers in the adult. It is interesting that the anterior end of the body (Capital Tract and anterior end of the Ventral Tract) is well advanced, varying from 66% to 100%, while the posterior end of the body is relatively little advanced, varying from 30% to 60%. The important feathers of the wing and tail show remarkably constant percentages; rectrices, 30–32%, primaries, 72–80%, secondaries, 72–73%. Less important feathers, as regards size, position and function show greater extremes, although they are obviously of close relationships; auricular anterior, 66%, auricular posterior, 77%; first alula feather, 82%, first alula covert, 65%.

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forward. At the proximal end, the tract is almost continuous with the sternal region, and at the distal end, with the alar tract. In the Femoral Tract development proceeds from the dorsal anterior margin backward and by the end of the fifth day all of the ultimate feathers are indicated by their sheaths. On the third day sheaths first appear in the Crural Tract at the lower posterior margin of the external region. Soon after others appear at the anterior edge and then development extends upward, all the sheaths in the region showing by the end of the fifth day. On this day a few sheaths can be seen underlying the skin at the lower end of the internal region.

Sixth and Seventh Days. In the Humeral Tract sheaths begin to push through the skin at the posterior distal margin. In the anterior end of the Femoral Tract the cornified feather follicles first appear outside the skin, development proceeding backward. The most distal sheaths of the Crural Tract also emerge.

Eighth to Fifteenth Days. During the first few days of this period the sheath tips of all three tracts burst or are worn away and expose their feathers. The latter part of nestling life is characterized by rapid growth of the feathers and disintegration of the feather sheath, designed to provide the young bird with nearly uniform and continuous feathering by the time it leaves the nest.

Alar Tract

First Day. No sheaths can be detected underneath the skin when the bird is first hatched, but very soon thereafter, perhaps

two or three hours, the primaries and secondaries begin to appear. The most distal secondaries, that is, the first, second, third and so forth, are apparently the first to appear, closely followed by the others. The seventh, eighth and ninth do not appear until the second day. The fourth, fifth and sixth primaries seem to be the first to show, followed soon after by the others, both inner and outer. The sequence of appearance is so rapid that it is difficult to say which one is actually the first to be developed, but the middle of this series definitely appears before either the innermost or outermost.

Second Day. By the end of the second day the major regions of the wing, except those of the under surface, have been delimited. All of the primaries and secondaries can be seen. The greater primary coverts, development apparently proceeding from the middle of the series outward, three alula quills, the first (most distal) appearing first, and the alula coverts, have made their appearance. All of the greater, middle and lesser secondary coverts are well defined, as well as the innermost row of marginal coverts. In the last four series, development apparently begins at the distal end of the region and proceeds towards the proximal end.

Third Day. The carpo-metacarpal coverts appear at the distal end of the manus. Some of the primaries and secondaries and their major coverts are just beginning to show outside the skin.

Fourth and Fifth Days. The carpo-metacarpal coverts increase in size and prominence. The series of lesser secondary coverts grade imperceptibly into the marginal coverts which are best developed at the distal end of the region. A few more of the larger feathers emerge from the skin but on the fourth day at least, this is fortuitous and the general period of emergence has not yet begun. On the under surface of the wing, a few sheaths can be detected showing through the skin, but they are poorly developed and their relationships obscure.

Sixth Day. Practically all the feathers of the wing begin to emerge on this day. Primaries, greater primary coverts, secondaries, greater, middle and lesser secondary coverts, marginal coverts, alula and alula coverts have all pushed their way through the skin. The carpal remex covert and the carpo-metacarpal coverts are still covered by skin.

Seventh and Eighth Days. Curiously enough the tips of the greater coverts, primary, secondary and alula, are the first to break and expose the enclosed feathers. The tips of the carpo-metacarpal coverts also burst, probably due to excessive wear, although the feathers themselves are very short, less than 2 mm. in length. The coverts of the under wing emerge from beneath the skin.

Ninth to Fifteenth Days. During this period the wing feathers lengthen greatly, their sheaths break and disintegrate so that by the end of the nestling period, practically the entire feathers are exposed. The diameter of the carpal remex covert, as long as its sheath is present, appears to be about one-half that of the adjacent greater primary and secondary coverts. The feathers in the series of under wing-coverts lag behind all other feathers in the wing. This is paralleled by the internal surface of the Crural Tract and is perhaps occasioned by the fact that, in both cases, the feathers in question are closely applied to the body, light and free circulation of air being excluded. At first sight, however, this interpretation seems to be rather bizarre, as undoubtedly the rate of growth is determined by internal metabolic factors before the feathers emerge and is not influenced by external stimuli. Perhaps the explanation is due to the fact that these feathers have largely lost their function and are in a sense vestigial, as is evident from their structure.

In Table III are given the measurements of the growth of thirty six feathers in the various tracts. Each measurement for each day is an average of the measurements of seven birds belonging to one brood and is a fairly typical index of the growth of the feathers concerned.

SUMMARY

While, in general, young Wrens at the time of hatching show no external trace of their future feathering, a few are hatched in a more advanced stage in this respect.

The distribution of neossoptiles is constant but the number of individual downs is subject to a certain amount of variation.

The neossoptiles do not grow after hatching but are pushed out of the skin on the tips of the forth-coming contour feathers.

The first appearance of feathers and the sequence of their de-

TABLE III.

(MEASUREMENTS IN MILLIMETERS.)

Age in Days	5	6	7	8	9	10	11	12	13	14	adult
Coronal	0.0	.3	1.0	2.2	3.1	3.7	4.2	4.9	5.1	5.2	7.0
Occipital	0.0	.2	1.4	1.9	2.8	3.7	4.3	5.0	5.1	5.2	7.6
Auricular (anterior)	0.0	0.0	.3	1.0	1.6	2.2	2.8	3.1	3.7	4.0	6.0
Auricular (posterior)	0.0	0.0	.2	.5	.7	1.6	1.9	2.6	2.7	3.0	3.9
Cervical (Spinal)	0.0	.1	.8	2.4	3.6	5.0	7.2	8.3	9.9	11.0	15.0
Interscapular	0.0	.3	1.5	2.8	4.1	6.0	8.1	9.1	10.5	11.6	18.0
Dorsal	.1	.4	1.7	3.3	4.6	6.1	8.0	10.3	11.4	12.8	24.0
Pelvic	0.0	.4	1.2	2.5	3.2	4.5	6.0	6.5	8.3	9.8	17.0
Rectrices (first pair)	0.0	.1	1.0	1.8	2.9	4.6	6.8	8.3	10.9	13.1	44.0
Rectrices (third pair)	0.0	.2	1.2	2.1	3.3	5.5	7.2	9.5	11.7	14.1	43.7
Rectrices (sixth pair)	0.0	.2	1.2	2.1	3.2	4.7	6.4	7.9	9.7	11.5	36.0
Upper tail-coverts	0.0	.1	1.2	2.2	3.3	4.7	6.4	7.2	8.7	9.9	20.0
Under tail-coverts	0.0	0.0	.6	1.7	2.6	3.7	5.2	6.0	7.4	9.4	21.0
Anal circlet	0.0	0.0	.1	.1	.9	1.3	1.7	2.1	2.8	3.2	5.5
Interramal	0.0	0.0	.2	.8	1.1	1.9	2.3	2.5	3.5	3.8	3.8
Cervical (ventral)	0.0	0.0	.5	1.2	1.9	2.6	3.6	4.2	4.5	5.4	7.0
Sternal	0.0	.4	1.5	2.6	3.8	5.1	6.6	8.4	8.8	10.1	18.0
Axillar	.1	.5	1.7	3.1	4.7	6.4	8.4	9.8	11.5	12.4	26.0

TABLE III (*Continued*)

Age in Days	5	6	7	8	9	10	11	12	13	14	adult
Abdominal	0.0	.2	.8	1.9	2.7	3.9	5.6	6.3	6.9	8.2	15.0
Humeral	.1	.8	2.2	3.5	5.0	6.9	8.5	9.8	11.6	12.3	16.0
Femoral	0.0	.6	1.9	3.3	4.1	5.6	6.3	6.8	8.2	9.3	19.0
Primary (tenth)	.7	2.0	4.0	5.9	7.6	9.5	11.3	13.1	14.6	16.2	21.0
Primary (fifth)	1.0	3.0	6.5	9.8	13.1	16.7	20.4	23.0	25.4	28.2	39.4
Primary (first)	.9	2.5	6.0	9.3	11.9	15.7	18.9	21.7	25.1	28.6	38.0
Fifth greater primary covert	0.0	1.3	3.4	5.5	6.9	8.9	10.2	11.3	11.4	12.0	12.5
Fifth middle primary covert	0.0	0.0	.9	1.9	2.2	2.7	3.1	3.1	3.1	3.2	3.5
Secondary (first)	.9	2.5	5.9	8.6	11.7	15.2	18.8	21.9	24.2	27.2	38.0
Secondary (fourth)	.8	2.2	5.4	8.1	11.1	14.3	17.8	20.6	23.3	25.8	35.5
Secondary (eighth)	.6	1.4	3.6	5.9	7.9	10.4	13.0	15.3	17.7	19.5	27.0
Fourth greater secondary covert	.7	1.6	4.1	6.0	7.8	9.9	12.3	14.0	15.1	15.5	17.9
Fourth middle secondary covert	0.0	1.0	2.0	3.1	4.1	5.3	6.4	7.1	7.5	7.8	9.0
Third lesser secondary covert	0.0	.1	1.0	2.0	2.8	3.9	5.0	5.5	6.2	6.8	8.5
Alula (first)	.5	1.4	3.0	4.3	6.0	7.8	9.7	10.7	11.4	12.6	14.1
Alula covert (first)	0.0	.7	1.0	1.7	2.2	2.7	3.4	3.5	3.6	3.9	6.0
Crural (external)	0.0	.1	.7	1.6	2.2	2.7	3.6	3.8	4.3	4.5	6.0
Crural (internal)	0.0	0.0	.3	1.1	1.5	1.7	2.6	2.9	3.0	3.8	5.0

velopment in the various regions follow in definite pre-determined order, constant for any one region but varying among different regions.

Development usually begins at one side or end of a region and spreads progressively over it until growth is completed.

In at least one case (primaries), development begins in the middle of the region and proceeds simultaneously toward each end.

In another case (Ventral Tract), there are two centers of development. One appears in the middle of the tract and spreads both posteriorly and anteriorly. The other starts in the inter-ramal region and spreads backward until it meets the anterior portion of the other developmental center. In the Spinal Tract is found a somewhat parallel case.

The feather sheath, after emerging from the skin, has no function and its rate of disintegration is primarily correlated with the amount of abrasion to which it is exposed.

The growth of feathers appears to be retarded until the second week of nestling life, but, to a large extent, this is actually due to the fact that development is going on beneath the skin during the first week and is often over-looked, while the rupture of the feather sheath and consequent exposure of the feather during the second week makes growth appear more noticeably.

BIBLIOGRAPHY.

1840, NITZSCH, C. L., Pterylography (English translation edited by P. L. Sclater in 1867 for the Ray Society) pp. 1–178.

1898, BEDDARD, F. E., "The Structure and Classification of Birds."

1900, DWIGHT, JONATHAN, 'Moults and Plumages of the Passerine Birds of New York,' Ann. N. Y. Acad. Sci., XIII, pp. 73–360.

1907, JONES, LYNDS, 'The Development of Nestling Feathers,' Laboratory Bull. No. 13, Oberlin College, pp. 1–18, 8 plates.

1915, MILLER, W. DEWITT, 'Notes on Ptilosis with Special Reference to the Feathering of the Wing,' Bull. Am. Mus. Nat. Hist., XXXIV, pp. 129–140.

1920, WITHERBY, H. F., "A Practical Handbook of British Birds," Vol. I.

1924a, MILLER, W. DEWITT, 'Further Notes on Ptilosis,' Bull. Am. Mus. Nat. Hist., L, pp. 305–331.

1924b, MILLER, W. DEWITT, 'Variations in the Structure of the Aftershaft,' Am. Mus. Novitates, No. 140, pp. 1–7.

Amer. Mus. Nat. History,
77th St. and Central Park, W., New York.