

PTERYLOSIS OF THE MALLARD DUCK

By PHILIP S. HUMPHREY and GEORGE A. CLARK, JR.

Although several studies of the distribution of feathers on the wing and other parts of various species of the Anatidae have been made, there is no general account of the pterylosis of any one species.

The present study is a preliminary attempt to describe the general pterylosis of the Mallard (*Anas platyrhynchos*). Much yet remains to be done. It would be most desirable to delimit more precisely the extent of variation in number and distribution of feathers in various tracts. Attempts should be made to comprehend the geometry underlying the distribution of the minute feathers of the head, neck, and other regions of the body. The great abundance of feathers on the Mallard (Knappen, 1932, counted 11,903 contour feathers on a female) accounts for an unevenness in our treatment: the larger, more prominent and less numerous feathers have inevitably received more attention than the very abundant small feathers.

ACKNOWLEDGMENTS

We are grateful to the State of Connecticut Board of Fisheries and Game for obtaining for us the majority of specimens examined in the course of this study. We wish especially to thank Mr. Arroll L. Lamson, Chief, Game Division; Mr. Theodore Bampton, Biologist; Mr. Leslie Williamson, Biologist; and Miss Ruth Billard, Biologist, of that organization for their generous cooperation, and Mr. Ralph Morrill, who initiated this arrangement and gave us additional specimens as well. We gratefully acknowledge the assistance we have received from the following people and organizations: the White Memorial Foundation, the Michigan Conservation Department, Drs. S. Dillon Ripley and Russell Mumford, and Mr. David Parsons for assistance in obtaining specimens; the Bingham Oceanographic Laboratories for use of darkroom facilities; Drs. Peter Stettenheim and Dorothea Rudnick for helpful discussions and advice; Dr. A. M. Lucas for allowing us to study his unpublished manuscript on the pterylosis of the domestic chicken; Mrs. Shirley Hartman for preparing illustrations; the Yale University Department of Zoology for use of facilities; and Dr. J. Jacobs and Mr. F. M. Williams for help with translation.

This research was supported in part by the National Science Foundation as a project collateral to a study of the trachea of ducks and the classification of that group.

METHODS AND MATERIALS

A total of about 30 specimens was examined. This number included males and females, adults and first-year birds, and birds in molt. Most of the specimens were received alive and examined soon after they were anaesthetized. These were subsequently preserved in formalin and re-examined.

In describing each feather tract we made detailed examinations of two or three specimens and attempted to clarify any apparent inconsistencies by the examination of several additional specimens.

We have used several methods of examining specimens. Freshly killed, unpreserved specimens were first examined to determine direction of overlap of feathers in the alar tract. We attempted to count feather rows and feathers in each row in the intact specimens. Once the feathers had been disturbed it was difficult to determine their manner of overlap. Detailed examination of unclipped feathers was made in an attempt to relate feather orientation, shape, size, color, and pattern to the arrangement of intersecting feather rows.

Following examination of unclipped specimens, various tracts of feathers were clipped and the initial interpretation checked against the now more easily apparent pattern of feather rows.

Examination of the spinal and other tracts was undertaken in part using soft-ray X-rays. Drawings were traced from X-ray positive prints and then compared with clipped specimens.

The relationship of some of the wing feathers to the underlying skeleton was determined by dissection.

ALAR TRACT

Several authors have studied the alar tract of various species of ducks; there is, however, no comprehensive discussion of this tract for any species of duck. Nitzsch (1867), Sundevall (1886; translation of 1843 paper), and Goodchild (1886; 1891) discussed some aspects of the pterylosis of the wing of *Anas*. Wray (1887) and Pycraft (1890) presented the most complete discussions of the pterylosis of the wing of *Anas*. Other papers which have an important bearing on the pterylosis of the wing of ducks are those of Gerbe (1877), Degen (1894), Reichling (1915), Steiner (1918; 1956), Bates (1918), and Verheyen (1958).

The most conspicuous feathers on the wing of the Mallard and most other birds are the REMIGES, or flight feathers. These extend from the trailing edge of the wing and are divided into two major groups, PRIMARIES and SECONDARIES. The most distal set of remiges, the primaries, are attached to the skeleton of the hand. The secondaries are attached to the forearm and distal part of the upper arm.

Large areas of the upper and lower surface of the wing bear coverts which are arranged in rows extending the length of the wing. The rows of coverts lie more or less parallel to one another and to the row of remiges. Coverts on the dorsal surface of the wing are called UPPER WING COVERTS; those on the ventral surface are termed UNDER WING COVERTS. The leading edge of the wing is considered to be anterior, and the trailing edge posterior. The most anterior of the wing feathers are the MARGINAL COVERTS; these are largely confined to the leading edge of the wing. In general, the most anterior rows of wing coverts contain the smallest feathers; posteriorly the feathers become progressively larger. The most posterior feathers, the remiges, are for the most part the largest feathers of the wing. Exceptions to this general rule are certain large marginal coverts along the anterior margin of the ventral surface of the propatagium (cf. Fürbringer, 1902:pl. 20) and ALULA QUILLS and their coverts.

In addition to the remiges, coverts, and alula quills, the wing bears two other sets of feathers: the POSTHUMERALS, attached to the dorsal surface of the upper arm, and the AXILLARIES, attached to the ventral surface of the upper arm.

The feathers of the wing are for the most part arranged in a grid comprising rows extending proximo-distally and, roughly at right angles to these, rows running approximately antero-posteriorly. The remiges, comprising the most prominent row of wing feathers, form the basis for the nomenclature of most of the feathers of the forearm and hand. However, the remiges have been interpreted as being a composite row which comprises parts of what may have been two distinct rows earlier in the phylogeny of the wing. One or more additional rows of wing feathers are also thought to be of composite origin (see discussion of diastataxy). If this is true, as Steiner (1918; 1956) and others believe, then discussion of the possible homologies of feathers or groups of feathers is potentially confusing from the nomenclatorial standpoint. One could discuss the possible homologies and names of parts of feather rows in terms of their presumed ancestral or developmentally precursor positions although the current shortage of information makes

this inadvisable. We have chosen not to attempt this. Instead we have named feathers—sometimes perhaps arbitrarily—in terms of our understanding of the geometry of the adult wing. In short, we have been content to try to follow the established nomenclature, which attempts to relate feathers and rows of feathers to the pattern as seen in the adult wing.

We have used several sources of evidence in deciding what names to apply to feather rows or parts of feather rows:

1. Relation to geometry of feather row grid
 - a. Relation to antero-posterior row
 - b. Relation to proximo-distal row
2. Relation to morphology of wing
3. Feather morphology
 - a. Feather shape
 - b. Feather size
 - c. Feather pattern and color
4. Feather orientation
 - a. Direction of feather shaft
 - b. Overlap
 - c. Reversal
5. Relative stage of growth of developing feather

Primaries.—The Mallard has eleven primaries, numbered from 1 to 11, proximal to distal. The most distal primary (the REMICLE) is very much reduced and markedly different in shape from the ten, more proximal primaries. This eleventh primary is a stiff, lanceolate feather with narrow vanes. It is not superficially visible on either the dorsal or the ventral surface of the wing, being covered dorsally by the tenth greater upper primary covert and ventrally by the tenth and eleventh greater under primary coverts.

The ventral surface of each of primaries 1 through 9 overlaps the dorsal surface of the next distal primary; the tenth primary does not overlap the eleventh.

We have used the more conservative system for numbering the digits of the manus (digit I=pollex; digit II=main digit, bearing the majority of the primaries; digit III=a reduced digit bearing primary No. 7). Montagna (1945) has concluded that digits II, III, and IV are retained in the avian wing, but the evidence for this view is not sufficiently convincing.

Primaries 1 through 6 are attached to the dorsal surface of the carpometacarpus and have been called METACARPAL PRIMARIES (see figs. 1, 2). The calami of the five most proximal metacarpal primaries pass over the intermetacarpal space from the dorsal surface of metacarpal II. The calamus of the sixth primary passes over the proximal border of the distal METACARPAL SYMPHYSIS from the distal end of metacarpal II. The seventh primary is attached to the single phalanx of digit III and has been termed the AD-DIGITAL PRIMARY. Primaries 8 and 9 are attached to the proximal phalanx of digit II and have been named the MID-DIGITAL PRIMARIES. The tenth and eleventh primaries are attached respectively to the second and distal phalanges of digit II and have been called collectively the PRE-DIGITAL PRIMARIES. The distalmost pre-digital primary (the eleventh) is the remicle.

Greater upper primary coverts.—The Mallard has eleven greater upper primary coverts, numbered 1 to 11, proximal to distal. Each of these feathers lies distal to the primary with which it is associated; neither the calamus nor the rhachis of any given greater upper primary covert crosses the calamus or rhachis of its associated primary remex. The greater upper primary coverts overlap one another in the same manner as do

the primaries ("conforming overlap," cf. Bates, 1918:532-533; "contrary overlap" of coverts is overlap opposite to that of the remiges).

The tenth greater upper primary covert is somewhat reduced (about three-fifths the length of the ninth) and lanceolate in shape. The eleventh greater upper primary covert is even more reduced than the tenth (about a third the length of the ninth) and is not lanceolate. Petrides (1943:264) noted that in *Anas* the outermost greater upper primary covert was small but of easily visible size (type 2 of Petrides). Measurements of these feathers were made from the point at which the calamus leaves the skin to the tip of the feather.

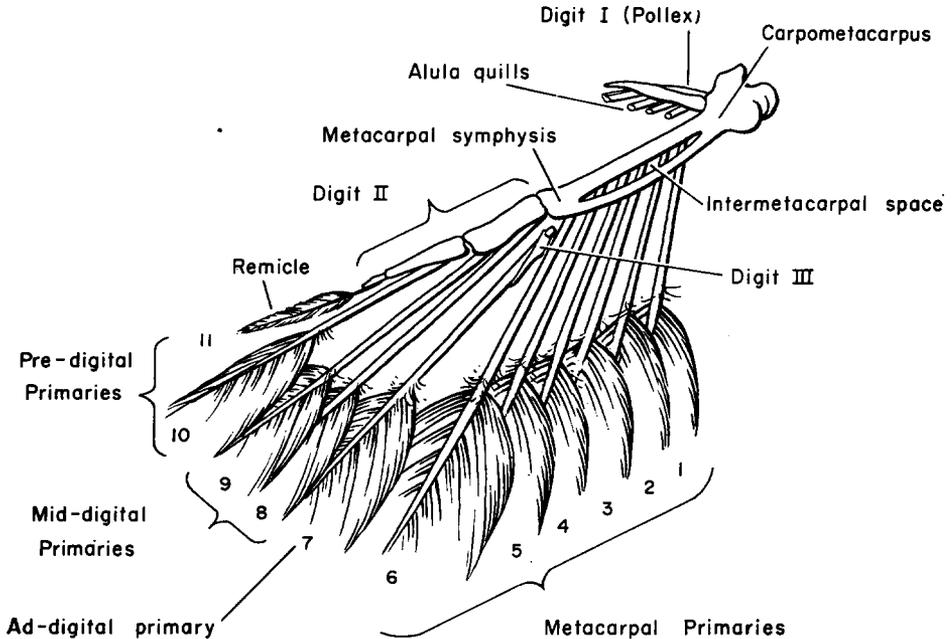


Fig. 1. The relations of wing bones and primaries in the Mallard (*Anas platyrhynchos*). Ventral view. (After Wray, 1887.)

Middle upper primary coverts.—Our first counts of middle upper primary coverts seemed to show that the Mallard has eleven feathers in this series. However, examination of a young specimen with partly grown wing feathers leads us to conclude that the Mallard has only ten middle upper primary coverts. These are numbered 1 to 10 from proximal to distal along the manus to correspond with the numbering of the primaries and their greater upper coverts (fig. 2).

Because of crowding at the distal end of the wing, it is difficult in some cases to determine to which proximo-distal row a particular feather belongs. In the young specimen the middle upper primary coverts protrude 14 or 15 millimeters from their sheaths. The questionable eleventh middle upper primary covert protrudes only 3 millimeters from its sheath. In this respect, as well as in coloration, it resembles the more proximal feathers in the marginal series along the leading edge of digit II. The position of this distalmost marginal feather is appropriate for an eleventh middle upper covert; however, this feather is sufficiently different from the middle upper primary coverts in color and stage of growth that we consider it to be a marginal covert.

The calamus of each middle upper primary covert lies distal to that of its corresponding greater upper primary covert. The middle upper primary coverts have conforming overlap.

The first middle upper primary covert is considerably reduced compared to the more distal members of the series; it is approximately three quarters the length of the second. The tenth middle upper primary covert is approximately the length of the ninth but has somewhat narrower vanes.

PRIMARIES	No.	METACARPAL PRIMARIES					AD-DIGITAL PRIMARY		MID-DIGITAL PRIMARIES		PRE-DIGITAL PRIMARIES	
	11	1	2	3	4	5	6	7	8	9	10	11
	11	carpometacarpus					digit III	prox. phal. digit II	2nd phal. II	distal phal. II	REMICLE	
Greater UPPER PRIMARY COVERTS	11	+	+	+	+	+	+	+	+	+	+	+
Middle UPPER PRIMARY COVERTS	10	+	+	+	+	+	+	+	+	+	+	-
Lesser UPPER PRIMARY COVERTS	7-9	+/-	+/-	distal to bases of greater upper primary coverts 3,4,5,6,7,8					+/-	-	-	-

Fig. 2. Occurrence and distribution of feathers on the dorsal surface of the manus in the Mallard; + indicates presence of feather, - indicates absence of feather.

Lesser upper primary coverts.—There is apparently individual variation in the number of lesser upper primary coverts in the Mallard. We have examined wings with seven, eight, and nine lesser upper primary coverts (fig. 2). In the case of nine lesser primary coverts these correspond to primaries 1 through 9 and are numbered accordingly. When less than nine lesser upper primary coverts were found, the feathers were missing at either or both ends of the row. We do not know whether these variations from the maximum count are due to accidental or natural (molt) loss of a feather or feathers.

Each lesser upper primary covert originates slightly distal to its corresponding middle upper primary covert. The lesser upper primary coverts have conforming overlap.

Carpal remex and its coverts.—The carpal remex in the Mallard is a somewhat degenerate, down-like feather with a very fine, almost hair-like rachis. It is approximately 3 centimeters in length, measured from its apex to the point at which the calamus enters the skin. A gap, or DIASTEMA, at the wrist joint separates the row of primary remiges on the manus from the row of secondary remiges on the forearm. The insertion of the carpal remex is located 2 or 3 millimeters proximal to the skin-covered calamus of the first primary. Extending from the first secondary to the insertion of the carpal remex is a fold of skin known as the PLICA SEMILUNARIS, which bridges the diastema of the wrist joint (Lowe, 1931:509).

The GREATER UPPER CARPAL REMEX COVERT originates 2 or 3 millimeters anterior and slightly distal to the point at which the calamus of the carpal remex inserts in the skin. The greater upper carpal remex covert is a well-developed feather similar in size and shape to one of the distal middle upper secondary coverts; it is approximately 4.5 centimeters in length from its apex to the point of insertion in the skin.

About 4 to 6 millimeters anterior to and slightly distal to the point where the calamus of the greater upper carpal remex covert disappears into the skin, there arises a MIDDLE UPPER CARPAL REMEX COVERT. This feather has the same relation to the carpal remex and its greater upper covert as do the middle upper primary coverts to their respective primaries and their greater upper coverts. The middle upper carpal remex covert is about 3.5 centimeters in length and comparable in shape and development to the underlying greater upper covert.

Prior to Degen's paper (1894) on the carpal remex and its covert, Wray (1887), Gadow (1891), and others did not distinguish these feathers from the series of greater and middle upper primary coverts. The carpal remex and its covert were considered to be the most proximal of the upper primary coverts; that is, they were thought to be coverts for the first primary. All the greater and middle upper primary coverts were thought to lie proximal to their respective primaries. According to this early system of counting greater and middle upper primary coverts (see fig. 3A), the second middle upper primary covert is missing in the Mallard (Gadow, 1891:558).

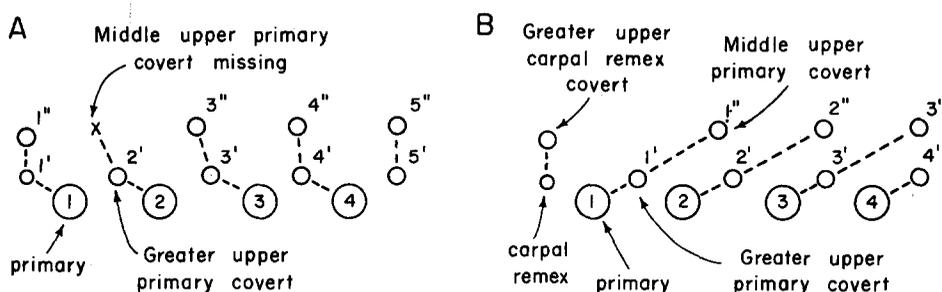


Fig. 3. A, nomenclature of the proximal primaries, their coverts, and the carpal remex, according to Wray (1887). B, current nomenclature of the proximal primaries, their coverts, and the carpal remex.

Degen demonstrated that what had been considered the greater and middle upper coverts of the first primary were really a highly modified remex and its greater upper covert. Furthermore, he presented evidence that the carpal remex and its covert are more closely allied to the secondary remiges and their coverts than to the primaries. Under Degen's system the upper primary coverts are located distal to their respective remiges. According to this revised system, the second primary does not lack a middle upper covert (see fig. 3B).

With regard to ducks, Degen (1894:xiv-xv, fig. 4) stated: "In the *Anatidae* the disputed 'covert' [= carpal remex] is placed midway between the metacarpals [= primaries] and the cubitals [= secondaries] . . . The space between these two series of feathers is greater in the Ducks than in any other birds with which I am acquainted, and is far in excess of the interspace between any two of the cubital [= secondary] remiges. In the wing of *Dendrocygna* . . . the position of the 'covert' is seen to perfection . . . Here we find the 'covert' resting on the metacarpus, leaving the carpus proper free from contact with any flight-feather. Its position is seen in the figure just referred to [Degen's figure 4], and its independence from the 1st metacarpal [= primary No. 1] is established."

Figure 4 of Degen's paper (1894) shows the relationship of the carpal remex to other nearby feathers on the dorsal surface of the wing of a Mallard.

Boulton (1927:392, 397) reported an under carpal remex covert in the House Wren (*Troglodytes aëdon*), but Van Tyne and Berger (1959:81) have commented that "the homology seems uncertain at best."

Diastataxy.—Gerbe (1877) was apparently the first to note the absence of the fifth secondary in various birds including the Palmipedes (which presumably contained the Anatidae); the coverts for this missing secondary were found to be present. Goodchild (1886) reported the occurrence of an accessory row of upper secondary coverts on the dorsal surface of the wing in ducks; the presence of this accessory row may be interpreted as supporting Steiner's (1918) explanation of the absence of the fifth secondary. Wray (1887:345) noted the absence of the fifth secondary in the duck and termed this the "aquintocubital" condition. Wray (1887:350) found the fifth secondary absent in young ducklings as well as in adult birds. Pycraft (1890:127) noted in the Mallard an interruption of the row of middle upper secondary coverts above the region of the missing secondary. Degen (1894:xix) expressed the view that there was a possibility of finding a vestigial form of the fifth secondary. He presented an elaborate hypothesis to explain the absence of the fifth secondary. Degen postulated that during the phylogenetic history of diastataxic birds there was a relocation of feathers from the third and fourth digits to the ulna. He suggested that in the course of this transfer of feathers to the ulna, the fifth secondary was lost.

Mitchell (1899) proposed the terms "diastataxic" to replace "aquintocubital" (absence of the fifth secondary) and "eutaxic" to replace "quintocubital" (presence of the fifth secondary). These terms were suggested in connection with his opinion that the diastataxic gap did not represent a phylogenetic or ontogenetic loss of a secondary. Mitchell described the wings of certain pigeons which were essentially eutaxic except for the presence of two (instead of the usual one) greater upper secondary coverts over the closed diastataxic interspace. He believed that the eutaxic condition was secondarily evolved from the diastataxic arrangement. Mitchell postulated that diastataxy originated from shifts of rows of scales or feathers in a hypothetical pentadactyl wing. According to Mitchell, the eutaxic condition was formed from the diastataxic condition by a closing of the gap.

Pycraft (1899), on the basis of a study of the anatomy of the wings of embryos, including those of the Mallard, argued that diastataxy did not involve the loss of a fifth secondary but merely the embryonic downward rotation of the four most distal feathers of the forearm resulting in the apparent absence of a fifth secondary. The downward rotation of the distal secondaries and their associated coverts was thought to result possibly from a slight lengthening of the forearm. According to Pycraft, the eutaxic condition was phylogenetically and ontogenetically primitive. The diastataxic condition came later in the evolutionary and developmental sense and did not involve the loss of a secondary. Certain eutaxic forms such as some kingfishers, swifts, and pigeons were thought by Pycraft (1899:254) to be secondarily derived from diastataxic ancestors. Pycraft (*op. cit.*:246) mentioned briefly an otherwise unpublished hypothesis of E. S. Goodrich to account for diastataxy. Goodrich thought that the diastataxic condition could have arisen through the bifurcation of a row of feather papillae, probably those of the greater upper secondary coverts 1 through 5.

Steiner (1918, 1956) presented additional hypotheses to account for the diastataxic and eutaxic conditions. He (1918:254) showed that the diastataxic condition is already present with the first appearance of feather papillae in the embryonic duck. Steiner believed that the diastataxic condition arose phylogenetically through the upward rotation of the five distalmost feathers of each of several feather rows on the posterior margin of the distal end of the forearm (see fig. 4). He presented data indicating that in phylogeny the eutaxic condition is secondarily derived from the diastataxic condition.

Representations of Steiner's hypotheses on the origin of diastataxy by Miller (1941:

114) and others (cf. Van Tyne and Berger, 1959:81-82) do not correspond with Steiner's (1956:4-6) views on the subject. Steiner did not state that diastataxy arises through the shifts of parts of embryonic feather rows during the ontogeny of an individual bird. Steiner (1918:446-447) made the following statements (translated from German):

"If we do not make the completely improbable assumption that diastataxy was formed several times independently and always by coincidence in the fifth or rather sixth [including the carpal remex and coverts] transversal row, then there is no choice but to assume that it was acquired by one ancestor common to all birds . . . Most probably the transformation of the reptilian forelimb into the bird's wing caused the formation of diastataxy."

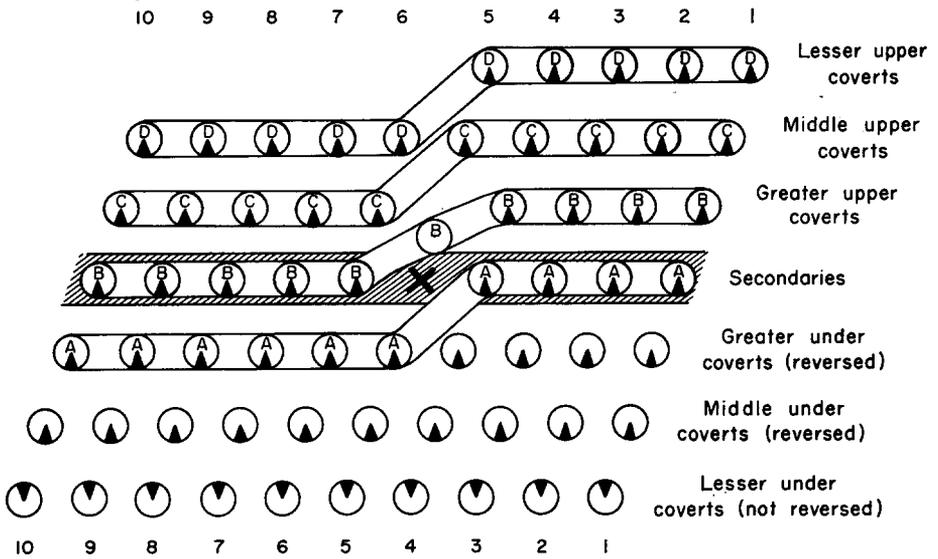


Fig. 4. Graphic representation of Steiner's hypothesis on the phylogenetic origin of diastataxy. Letters indicate ancestral rows.

Verheyen (1958) has developed the most recent hypothesis to explain the diastataxic condition. According to him, in diastataxic birds the fifth greater under secondary covert is homologous with members of the secondary series. All rows but the fifth transversal (antero-posterior) row have moved from ventral to dorsal in diastataxic wings. The fifth transversal row does not move because the fifth lesser under secondary covert is attached to the radius by a ligament, thus effectively immobilizing the entire row. Eutaxy is thought to result from the weak development or absence of this ligament.

Steiner's hypotheses raise problems concerning the homology and nomenclature of secondaries and their coverts. The secondaries are a functional row which is derived, according to Steiner, from two phylogenetically precursor rows. This is illustrated diagrammatically in figure 4. According to Steiner, neither diastataxic nor eutaxic birds have ever had a fifth secondary. The apparently "missing" fifth secondary is represented by the fifth greater upper covert. The numbering system used by Steiner for the secondaries and their coverts is a practical one. In diastataxic birds the diastataxic gap is counted as a fifth position in the row of secondaries. Some authors (for example, Van Tyne and Berger, 1959:82) assign the number "5" to the secondary proximal to

the diastataxic interspace; such a numbering system has the unfortunate disadvantage that the secondaries do not have the same numbers as their associated coverts.

In the eutaxic bird, according to Steiner's scheme, secondaries homologous to 4 and 6 of the diastataxic wing come together (during phylogeny) closing the diastataxic gap.

The relationship of the practical numbering system of feather rows (as seen in the adult wing) to the original rows as hypothesized by Steiner is shown in figure 4.

Secondaries.—As found by Wray (1887:pl. 29), there are 18 secondaries in the Mallard (some individuals have 17 secondaries). An apterium is present on the proximal end of the secondary series and continues proximally into the axilla. The secondaries are numbered from 1 to 19 from distal to proximal. There is a conspicuous gap between secondaries 4 and 6; this diastataxic condition has long been known for the Anatidae (Gadow, 1891:567).

Secondaries number 1 through 12 (exclusive of the nonexistent number 5) are ordinary secondaries; they are approximately equal in length and bear the "speculum." Numbers 10, 11 and 12 are longer than any of the more distal secondaries. Number 12 is longer than number 11 which is longer than 10. Secondaries 13 through 16 are all longer than any in the secondary series 1 through 12. Numbers 13 through 16 are elongate, rather pointed feathers. Secondaries 14 and 15 are the longest of the secondaries. Proceeding proximad from secondary number 16, the secondaries become progressively and rapidly much shorter. Secondary number 13 is somewhat pointed; number 14 is more pointed. Numbers 15, 16, and 17 are very pointed. Number 18 is slightly rounded at the tip. Number 19 (when present) is more rounded at the tip than is 18.

Greater upper secondary coverts.—The number of greater upper secondary coverts in the Mallard seems to vary between 19 and 20. We are not certain how variable this count may be since these feathers are difficult to identify accurately in the region of the elbow. These coverts are numbered to correspond with their appropriate secondaries except in the case of the fifth covert for which there is no corresponding secondary. In those individuals in which secondary number 18 is the proximalmost of the series, greater upper secondary covert 19 is present; those in which secondary number 19 is present have a greater upper secondary covert number 20. The rachis of each of the greater upper secondary coverts for which there is a secondary lies distal to the rachis of its respective secondary. Greater upper secondary coverts 1 through 13 have conforming overlap. Greater upper secondary covert number 14 overlaps both 13 and 15 and marks the beginning of contrary overlap which persists to the proximalmost of the greater upper secondary coverts. In the fully spread wing, greater upper secondary coverts 1 through 5 appear to be two or three millimeters longer than the rest of the series.

Middle upper secondary coverts.—Each of the 19 middle upper secondary coverts originates distal to its respective greater upper secondary covert. The fourth middle upper secondary covert is the longest. With some irregularity, there is a tendency for middle upper secondary coverts to be progressively shorter on either side of the fourth middle upper secondary covert. The middle upper secondary coverts have contrary overlap distally; proximally, in the region of the elbow, overlap is conforming (Wray, 1887:345).

The five distal middle upper secondary coverts form a row which is not directly continuous with any other row of feathers. See figure 5, which diagrammatically shows the arrangement of the upper secondary coverts. This row of five distal middle upper secondary coverts is an extra row such as might be expected according to Steiner's (1918) hypothesis on the origin of diastataxy.

Lesser upper secondary coverts.—As is indicated in figure 5, there are four rows of lesser upper secondary coverts. These rows extend varying distances along the forearm. Proximally they are in contact with the rows of marginal coverts covering the dorsal surface of the patagium. The three most posterior rows of lesser upper secondary coverts are at their proximal ends separated from the marginal coverts of the patagium by an apterium lying over the elbow joint. Distally the upper surface of the forearm becomes narrower, and the rows of lesser upper secondary coverts merge with the marginal coverts of the leading edge of the wing.

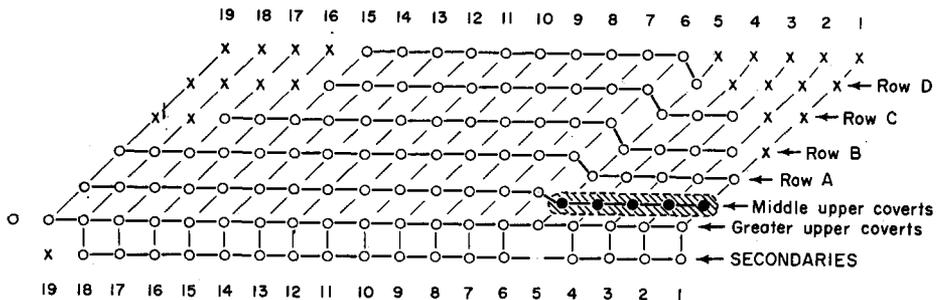


Fig. 5. Diagrammatic representation of the distribution of feathers on the dorsal surface of the forearm in the Mallard, showing the secondaries, their upper coverts, and the so-called accessory row (shaded).

Lesser upper secondary coverts lie distal to their respective middle upper secondary coverts. Distally on the forearm, the overlap of the lesser upper secondary coverts is contrary.

In one specimen there were 19 feathers in row A of the lesser upper secondary coverts. In row B, coverts number 1, 18, and 19 were absent; in row C, coverts 1, 2, and 16 through 19 were absent; in row D, coverts 1 through 4 and 16 through 19 were absent (see fig. 5).

Under wing coverts.—Sundevall (1886:418–419) noted the so-called reversed under coverts of birds. The reversed coverts lie on the ventral surface of the wing but have an orientation like that of the feathers on the dorsal side of the wing. Sundevall distinguished the reversed feathers by means of the orientation of the grooved shaft and other points of feather structure. He hypothesized that the reversed feathers were merely strongly developed aftershafts of typical feathers in which the usual development of the normal feather had been suppressed.

Wray (1887:345) noted that the greater and middle under secondary coverts of the duck's wing were reversed. He criticized Sundevall's hypothesis on the origin of the reversed under coverts and presented evidence (*op. cit.*:353–354; figs. 1 to 5 of pl. 32) that during ontogeny the two rows of reversed under coverts first appear on the dorsal surface of the wing and are later carried to the ventral surface.

Bates (1918:534–536) described the reversed under coverts of *Pteronetta hartlaubi* (Anatidae) and many other birds.

The two rows of reversed under coverts in the Mallard show no indication of having been affected by the development of the diastataxic condition; that is, there is no displaced row of five distal under secondary coverts. If Steiner's (1918) hypothesis is correct, the reversed under wing coverts presumably appeared later in anatid phylogeny than did the diastataxic condition.

Greater under primary coverts.—The 11 greater under primary coverts are numbered from 1 to 11, proximal to distal. Each lies proximal to its respective primary. The tenth and eleventh greater under primary coverts are moderately reduced. The eleventh greater under primary covert is about 30 mm. in length (measured from point of insertion in the skin to the tip of the rachis) and is about three quarters the length of the tenth.

All of the greater under primary coverts are reversed; in each the superior umbilicus is on the exposed surface of the feather shaft. The calami of greater under primary coverts 1 through 5 lie each on the ventral surface of the calamus of its respective primary. The calami of greater under primary coverts 6 through 11 lie each on the proximal side of the calamus of its respective primary. The greater under primary coverts exhibit conforming overlap.

Middle under primary coverts.—According to W. deW. Miller (1919:563), "in the Anseres the standard number of middle primary coverts on the under side of the wing is six." In the Mallard, middle under primary coverts 1 through 6 are present; each lies slightly proximal to its corresponding greater under primary covert. The six coverts are reversed and exhibit contrary overlap.

Lesser under primary coverts.—There are two rows of lesser under primary coverts. We have assigned the letter "A" to the posterior row (the row closest to the trailing edge of the wing) and the letter "B" to the more anterior row. Row A has 11 feathers; row B has 10. Row B might be included among the marginals since it lies close to them, but we have arbitrarily included it with the lesser under primary coverts. The calami of row A originate proximal to those of their respective middle under primary coverts.

Neither row A nor B has reversed feathers; both rows have contrary overlap.

Greater under secondary coverts.—In two specimens we counted 17 greater under secondary coverts; in another specimen we counted 18 with a possible nineteenth. Pycraft (1890:128) reported that there were no greater under secondary coverts for the eighteenth and nineteenth secondaries.

The greater under secondary coverts are numbered, starting with number one, distal to proximal. Each greater under secondary covert (except the fifth) originates proximal and ventral to its corresponding secondary. The greater under secondary coverts have conforming overlap and are reversed.

Middle under secondary coverts.—In one specimen 17 middle under secondary coverts were found; each inserts proximal to its respective secondary and its associated greater under covert. The middle under secondary coverts are reversed and exhibit contrary overlap. Sundevall (1886:419) noted the difference in mode of overlap between the greater and middle under secondary coverts.

Lesser under secondary coverts.—There are five rows of lesser under secondary coverts distributed along the ventral surface of the wing from the elbow to the wrist. Pycraft (1890:129) reported four rows of lesser under secondary coverts. Wray (1887:347) and Pycraft (1890) noted the relatively great separation between the second and third rows as counted posterior to anterior.

From posterior to anterior the rows of lesser under secondary coverts have been assigned the letters A through E. None of these coverts is reversed. Lesser under secondary covert rows A, B, C, and D exhibit conforming overlaps. Overlap could not be determined for row E because the feathers in this row are rather widely separated.

The following feather counts for the five rows of lesser under secondary coverts are based on examination of two clipped wings: row A, 17; row B, 16; row C, 14; row D, 14 or 15 (uncertain); row E, 10 or 11 (uncertain). Some arbitrary allocation of feathers to particular rows was necessary for rows D and E.

Posthumeral.—The feather rows along the caudal margin of the skin covering the humerus are termed the posthumeral region of the alar tract. The distalmost feather of this series lies proximal to the proximalmost secondary. The series terminates proximally at the caudal end of the scapulohumeral tract. The feathers which we term posthumeral (nomenclature of A. M. Lucas, MS) are termed tertiaries by Compton (1938:201–202), humerals by Wray (1887:347) and Pycraft (1890:126–127). The term "tertiaries" has also been used for the proximalmost secondaries (Dwight, 1900:89–90). The term "humeral tract" was used by Compton (1938:199) and Humphrey and Butsch (1958:13) to refer to what we call the scapulohumeral tract (see following).

We have used the term posthumeral to avoid the ambiguity of the terms "tertiaries" and "humeral."

Wray (1887:346-347) was of the opinion that the posthumerals are continuous with the lesser upper secondary coverts; this view perhaps stemmed from the apparent correspondence of the posthumerals to the axillaries, a group of feathers on the ventral surface of the wing. (The axillaries were believed to be continuous with the lesser under secondary coverts.) Pycraft (1890:127, 138-139) thought that the posthumerals were continuous with the greater upper secondary coverts. Compton (1938:202) stated that in Falconiformes, the posthumerals are continuous with the lesser upper secondary coverts.

The posthumeral region of the alar tract and the scapulohumeral tract come together at the posterior distal margin of the scapulohumeral tract. The feathers of the two groups blend in this region so that the distinction between scapulohumeral tract and posthumeral quills is arbitrary. We were able to count 11 posthumeral quills; only six of these are prominent feathers. Counting proximal to distal, numbers 4 through 9 are the prominent posthumeral quills.

The six prominent posthumeral feathers are overlain by greater upper posthumeral coverts. Each of these coverts originates slightly distad and 7 or 8 mm. anterior to the point at which the rachis of the respective posthumeral quill passes from the skin. In addition to these 6 greater upper posthumeral coverts, there is possibly a seventh, distal to the others. This seventh feather is very small and quite down-like. Distal to this seventh feather is a series of little down-like feathers. These form the caudal margin of a small apterium on the dorsal surface of the elbow joint. The first three feathers distal to the possible seventh greater upper posthumeral covert are downy. The feathers of this series distal to the first three are larger and slightly more pennaceous. This last described series is possibly a continuation of the greater upper posthumeral coverts.

Ventral to the posthumerals are the under posthumeral coverts; these are separated by an apterium from the more anteriorly lying axillaries.

Axillaries.—Six or seven large axillaries originate on the ventral surface of the upper arm beneath the humerus. Wray (1887:347) and Pycraft (1890:138-139) noted that the axillary row was continuous with a row of lesser under secondary coverts. As Pycraft noted, the axillaries are not reversed in their orientation, unlike the greater and middle under secondary coverts.

There are two complete rows of under axillary coverts and, most anteriorly, a third partial row. Row A is the first row anterior to the axillary row. Row B is the next row anterior. Row B is apparently continuous with a row of the lesser under secondary coverts. The calamus of each of the feathers in row A originates proximal to its respective axillary. The partial row C of under axillary coverts is found anterior to the four most proximal of the axillaries.

An apterium lies anterior to row C of the under axillary coverts and to the distal end of row B of the under axillary coverts. Anterior to this apterium lie the marginal coverts of the ventral side of the upper arm. Posteriorly the axillaries are separated from the under posthumeral coverts by an apterium which is located on the postero-ventral surface of the upper arm.

Alula.—In the Mallard there are five alula quills, each with its own greater covert. Wray (1887:347) reported that there were four alula quills, each with a covert; he apparently did not count what we consider the most proximal of the alula quills.

The five alula quills are numbered 1 to 5 proximal to distal along the pollex. The alula quills become progressively longer going proximal to distal. The most proximal

or first alula quill stands in the proper relation to the middle upper carpal remex covert to be considered as possibly a lesser upper carpal remex covert.

Degen (1894:xxix) recognized greater, middle, and lesser upper coverts on the alula. He also reported two reversed greater under coverts on the alula; we found one such reversed covert. Degen believed the alula quills were true remiges; Wray (1887:347) thought the feathers of the pollex were derived from the marginals and the lesser upper coverts of the primaries.

Marginal coverts.—The marginal coverts are arranged in several rows along the leading edge of the wing. Due to the small size of these feathers and their dense arrangement, we have not attempted to study this region on a feather by feather basis. The following is a general account of the distribution of the marginal coverts.

On the dorsal surface of the manus these feathers extend proximally from the base of the eleventh primary to an apterium lying under the alula quills. The distal margin of this apterium is marked by the anterior end of the calamus of the fourth primary. The thickly clustered marginal coverts continue proximally from the alula along the leading edge of the fore and upper arm to merge with the anterior end of the scapulo-humeral tract. On the dorsal surface of the wing the marginal region is expanded to cover the propatagium.

On the ventral surface of the wing the marginal coverts extend the length of the leading edge distal to the base of the eleventh primary. The marginal coverts on the ventral surface do not take origin from the entire propatagium but are confined to the leading edge. These marginal coverts in front of the propatagium are longer than typical marginal coverts so that they serve to conceal the apterium of the ventral propatagium (Wray, 1887:347).

SCAPULOHUMERAL TRACT

This tract lies dorsal to the proximal end of the humerus. Antero-laterally the scapulo-humeral tract is continuous with the sternal region of the ventral tract. Anteriorly and antero-laterally it fuses with the marginal coverts of the alar tract. The humeral apterium lies lateral to the scapulohumeral tract ("humeral tract" of Humphrey and Butsch) which is not bounded laterally by the lateral thoracic apterium contrary to Humphrey and Butsch (1958). The lateral thoracic apterium lies adjacent to the scapulohumeral tract only on the postero-medial edge of the latter. The humeral apterium separates the scapulohumeral tract from the marginal coverts of the patagium. The interscapular apterium lies medial to the scapulohumeral tract. Postero-laterally the scapulohumeral tract is continuous with the posthumeral region of the alar tract.

The scapulohumeral tract is a little over one centimeter in width and contains posteriorly six rows of feathers aligned antero-posteriorly. The feathers toward the posterior end of the scapulohumeral tract are much larger than those located more anteriorly.

SPINAL TRACT

Our study of the pterylosis of the spinal tract of the Mallard was undertaken by attempting to compare a clipped specimen with a detailed drawing made by tracing positive prints of X-rays of a flattened skin. Our attempt was not entirely successful for several reasons: (1) the tremendous number of feathers involved made the comparison laborious and subject to error; (2) distortion of the dried skin and the fact that it had many incompletely grown feathers made the X-rays difficult to interpret; and (3) we have no way of knowing whether certain irregularities or discrepancies can be ascribed to individual variation, to our own errors of misinterpretation, or to artifacts.

Nitzsch (1867:146-148) presented a comparative account of the spinal tract of

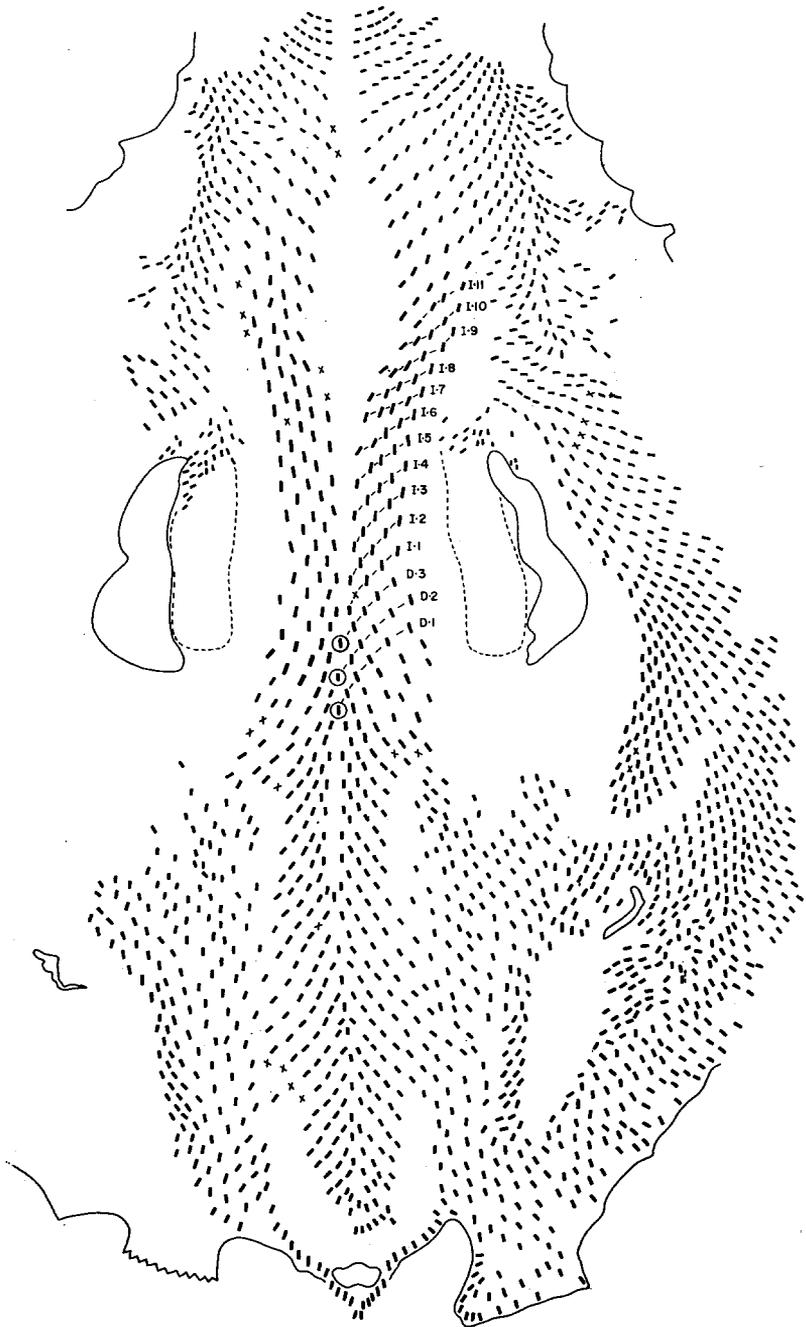


Fig. 6. Pterylosis of the trunk of the Mallard. For nomenclature see figure 7 and the text.

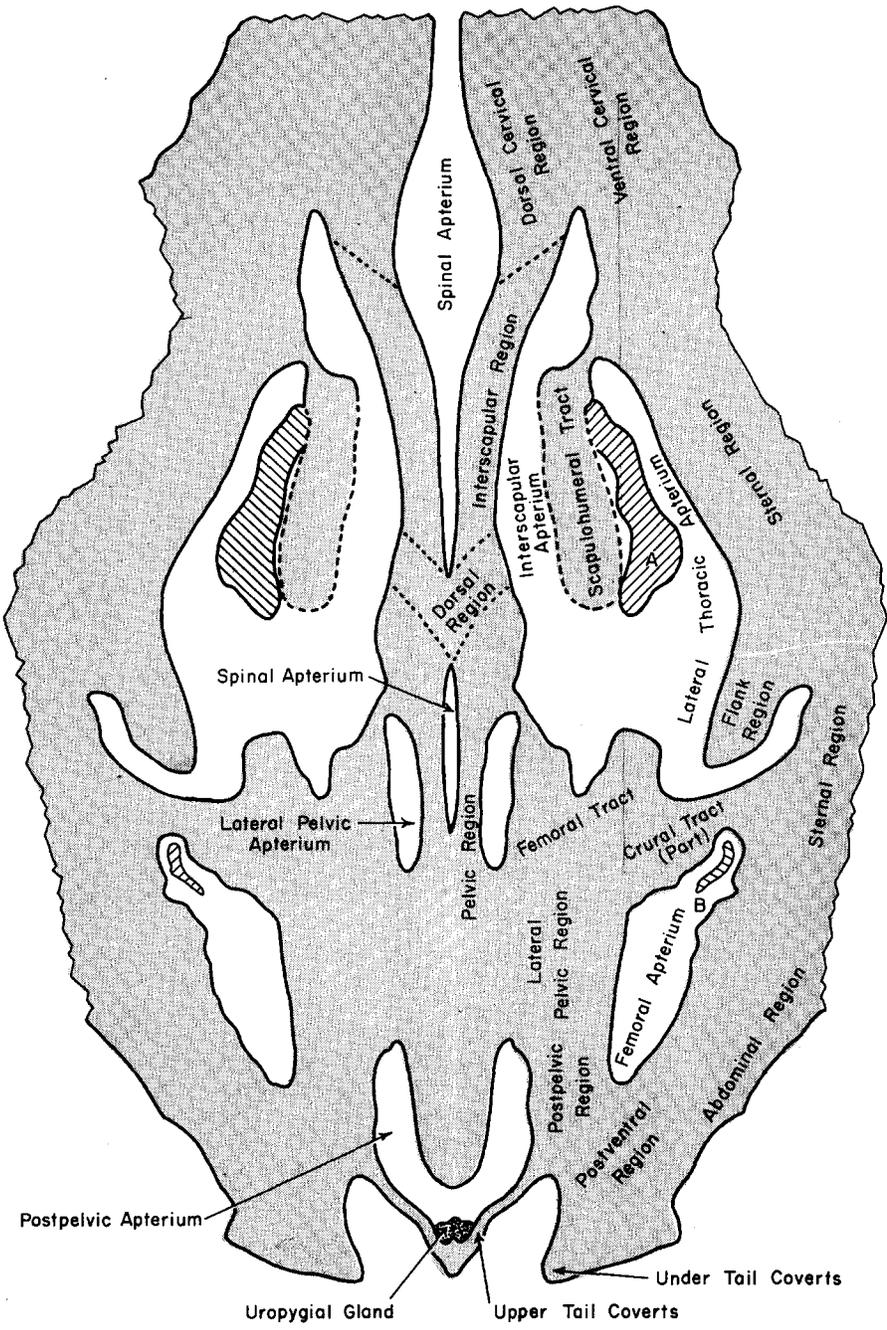


Fig. 7. Nomenclature of the feather tracts (and their regions) of the trunk of the Mallard. Feathered areas are shaded; hatched regions are holes where wings (A) and legs (B) were removed.

waterfowl (including *Anas platyrhynchos*) and noted that this tract is uniform throughout the family. He found that two characteristics of the spinal tract show interspecific variation: (1) the antero-posterior extent of the spinal apterium, and (2) the anterior extent of the so-called "lateral neck space" or lateral cervical apterium. What Nitzsch called "true ducks" correspond to the tribes Anatini, Cairinini, and Tadornini. Nitzsch characterized these as having—in common with the Aythyini, Mergini (except *Mergus*), Oxyurini, and Somateriini—(1) a longer and stronger terminal branch of the ventral tract than in swans and geese, and (2) a shorter lateral cervical apterium than in swans and geese. He stated that the lateral cervical apterium is lacking in *Mergus*. According to Nitzsch, the "true ducks" (Anatini, Cairinini, Tadornini) have a spinal apterium which extends from the base of the neck to the "caudal pit"; in other ducks it never extends much beyond the interscapular region.

Humphrey and Butsch (1958) used the X-ray method to study the spinal tract of the Labrador Duck (*Camptorhynchus labradorius*). They were unable to determine the anterior extent of the spinal apterium in this species; they made no mention of the lateral cervical apterium.

Compton (1938:183) divided the spinal tract of the Falconiformes into six regions as follows: (1) dorsal cervical, (2) interscapular, (3) lateral scapular, (4) dorsal, (5) pelvic, and (6) lateral pelvic. We include a seventh region, the postpelvic. Compton considers the postpelvic region to be a part of the caudal tract. Compton stated that the spinal tract "extends from the base of the head to the uropygial gland." We can see no clear boundaries to the spinal tract in the Mallard except (1) the lateral margins of the interscapular region, and (2) the caudal margin of the pelvic region. Otherwise, the spinal tract merges (1) anteriorly with the capital tract, (2) anteriorly and laterally with the ventral cervical region of the ventral tract, (3) posteriorly and laterally with the femoral tract, and (4) far posteriorly and laterally with the post-ventral and/or the abdominal regions of the ventral tract.

Dorsal cervical region.—Only the posterior part of the dorsal cervical region is shown in figures 6 and 7. The right and left parts of the dorsal cervical region become more widely separated posteriorly as the spinal apterium becomes broader. According to Compton (*loc. cit.*) the dorsal cervical region terminates at the trunk. In the Mallard this point corresponds to the anterior limit of the lateral cervical apterium.

Interscapular region.—The interscapular region commences anteriorly as two relatively widely separated branches which are continuations of the right and left parts of the dorsal cervical region. The anterior part of each branch of the interscapular region is bounded laterally by a narrow lateral cervical apterium. More posteriorly the lateral cervical apterium continues as the interscapular apterium, bounded laterally by the scapulohumeral tract and medially by the corresponding branch of the interscapular region. The spinal apterium becomes narrower posteriorly and terminates at an unpaired median dorsal feather. Between this point and the anterior limit of the lateral cervical apterium each branch of the interscapular region comprises eleven rows of feathers (rows I-1 through I-11, fig. 6). We interpret each feather row as being oriented from postero-medial to antero-lateral. The first feather row anterior to the posterior termination of the spinal apterium consists of five feathers. Rows 2 through 8 also comprise five feathers each. Row 9 has six feathers; row 10, five; and row 11, four feathers. These counts may not be accurate in the anterior part of each branch of the interscapular region since we did not obtain the same feather row count on each side in this area.

Dorsal region.—We judge that the dorsal region of the spinal tract begins at the posterior termination of the interscapular part of the spinal apterium. In the Mallard the dorsal region comprises three rows of 11 feathers (D-1, D-2, D-3, fig. 6), each row comprising a row of five on either side of the midline and a median unpaired feather (encircled in fig. 6). The dorsal region is bounded laterally on each side by the posterior part of the interscapular apterium.

Lateral scapular region.—We were unable to distinguish a lateral scapular region.

Pelvic region.—The pelvic region begins anteriorly at the posterior termination of the dorsal region. The first or anteriormost six rows of the pelvic region are divided medially by a narrow apterium, a posterior extension of the spinal apterium. The seventh row has a medial unpaired feather; in the eighth row the medial feather is lacking. Rows 9 through 17 each have a medial unpaired feather. We are uncertain about the pattern of distribution of feathers in rows 18 through 21 of the pelvic region; some of the rows appear to have medial unpaired feathers.

		PRIMARY						SECONDARY							
		UPPER COVERTS			UNDER COVERTS			UPPER COVERTS			UNDER COVERTS				
		NUMBER	NUMBER	CONFORMING OVERLAP	CONTRARY OVERLAP	NUMBER	CONFORMING OVERLAP	CONTRARY OVERLAP	NUMBER	NUMBER	CONFORMING OVERLAP	CONTRARY OVERLAP	NUMBER	CONFORMING OVERLAP	CONTRARY OVERLAP
REMIGES		11							17-18						
GREATER			11	✓		11 *	✓			19-20	1-13	15-19	17-18 * (19?)	✓	
MIDDLE			10	✓		6 *	✓			19	prox- imal	distal	17 *		✓
LESSER	row A		7-9	✓		11	✓			19	"	"	17	✓	
	B					10	✓			16	"	"	16	✓	
	C									13	"	"	14	✓	
	D									11	"	"	14 ^{or} 15?	✓	
	E												10 ^{or} 11?	?	

* = REVERSED

Fig. 8. Number of remiges and coverts in the Mallard.

Counting from anterior to posterior, the seventh through tenth or eleventh rows of the pelvic region are bordered laterally on each side by a narrow lateral pelvic apterium. The posteriormost five rows of the pelvic region are bordered laterally by the postpelvic apterium. The pelvic region terminates caudally at the postpelvic apterium.

Lateral pelvic region.—The lateral pelvic region of each side is bordered (1) anteriorly by part of the posterior margin of the lateral thoracic apterium, (2) medially by the lateral border of the lateral pelvic apterium and, more posteriorly, by the pelvic region, (3) posteriorly by the anterior limit of the postpelvic apterium and by the anterior limit of the postpelvic region, (4) laterally by the dorso-medial border of the femoral apterium and, more anteriorly, by the dorso-medial limit of the femoral tract. Except where bounded by the margins of apteria, the lateral pelvic region cannot be clearly delimited.

Postpelvic region.—We include the postpelvic region in the spinal tract rather than in the caudal tract (cf. Compton, 1938:197). Anteriorly the postpelvic region merges with the posterior part of the lateral pelvic region. The postpelvic region is bounded (1) medially by the lateral margin of the postpelvic apterium, (2) laterally by the femoral apterium, and (3) postero-laterally by the post-ventral and/or abdominal regions of the ventral tract.

CAPITAL TRACT

It does not seem profitable to attempt to distinguish in the Mallard subregions of the capital tract as did Compton (1938:177-178) for the Falconiformes. There are no true apteria in the capital tract of the Mallard. Along the posterior margin of the auditory meatus there is a narrow bare region. There is no middorsal apterium and none about the eye. Body downs are present over the entire head, although their presence may be far from obvious to the unaided eye in examination of a pickled specimen.

VENTRAL TRACT

Compton (1938:189-191) lists the following regions as comprising the ventral tract: (1) ventral cervical, (2) sternal, (3) axillar, (4) subaxillar, and (5) abdominal. We have considered the axillar region in the section on the alar tract; we were unable to distinguish a subaxillar region. We have limited the caudal tract to the rectrices, their coverts, and the uropygial gland; the postventral region is considered as a part of the ventral tract. We have given the name "flank region" to that part of the ventral tract which contains the flank feathers. This region was considered by Compton to be a part of the sternal region.

The ventral tract of the Mallard extends from the head to the under tail coverts. It is divided for most of its length by a narrow midventral apterium. The anterior limit of this apterium lies about 6 cm. anterior to the cranial crest of the keel of the sternum or approximately 3 cm. anterior to the termination of the lateral cervical apterium. The midventral apterium is approximately 1 cm. in width; anterior to the sternum the midventral apterium becomes slightly narrower then tapers to its anterior termination. Toward the posterior end of the sternal region the midventral apterium becomes slightly narrower and is somewhat less than a centimeter in width throughout the abdominal region.

The ventral tract has definite limits at (1) the lateral cervical apterium where the posterior part of the ventral cervical region and/or the anterior part of the sternal region terminates dorso-laterally; (2) the lateral thoracic apterium which provides the dorso-lateral margin for most of the sternal region and the dorso-lateral, posterior, and ventro-lateral margins for the flank region; and (3) the femoral apterium which provides the dorso-lateral margin for much of the abdominal region. Otherwise, the ventral tract has no definite boundaries. It merges with the following tracts and regions: (1) anteriorly with the capital tract; (2) dorso-laterally with the dorsal cervical region of the spinal tract; (3) more posteriorly and dorso-laterally with the antero-lateral termination of the interscapular region of the spinal tract; (4) at the level of the hindlimb it merges dorso-laterally with the femoral tract; (5) toward the tail it merges dorso-laterally with the postpelvic region of the spinal tract; (6) most posteriorly it merges caudally with the caudal tract.

Ventral cervical region.—Anteriorly the ventral cervical region merges with the capital tract; it merges laterally with the dorsal cervical region. In neither case is there a definite boundary. Posteriorly the ventral cervical region merges with the sternal region; here again the boundary is indefinite. The posterior three or four centimeters of the ventral cervical region is divided by the narrow anterior part of the midventral apterium.

Sternal region.—The sternal region merges anteriorly with the ventral cervical region. This junction is at about the level of the anterior limit of the lateral cervical apterium. The sternal region of each side is limited medially by the midventral apterium. Near its anterior end the sternal region gives off a narrow branch which extends dorsally and medially and merges with the anterior end of the scapulohumeral tract. Anterior to this branch the sternal region is limited dorsally by the ventro-lateral margin of the lateral cervical apterium. Posterior to the branch leading to the scapulohumeral

tract the sternal region is limited dorsally by the ventro-lateral margin of the lateral thoracic apterium. Toward the posterior end of the lateral thoracic apterium the sternal region gives off a large branch, the flank region. At the postero-ventral point of junction of the flank region with the sternal region the lateral thoracic apterium borders the dorsal limit of the sternal region. Finally, the sternal region toward its posterior limit merges dorsally with the femoral tract. The sternal tract merges caudally with the abdominal region. The posterior limit of the sternal region corresponds to the posterior margin of the underlying sternum.

Flank region.—The flank region diverges posteriorly and slightly dorsally from the dorsal margin of the sternal region. It overlies the knee and a small part of the tibiotarsus immediately distad of the knee. The flank region is bounded dorsally, posteriorly, and ventro-laterally by the lateral thoracic apterium. The lateral thoracic apterium has a narrow, hook-shaped extension which borders the flank region posteriorly and ventro-laterally. Nitzsch (1867) stated that the flank region is relatively inconspicuous in Anseres and that it is more pronounced in Procellariiformes.

Abdominal region.—The abdominal region merges anteriorly with the sternal region; posteriorly it merges with the postventral region. Medially the abdominal region of each side is bounded by the lateral margins of the narrow midventral apterium. Laterally and dorsally the abdominal region of each side is bordered by the ventro-lateral margin of the femoral apterium.

Postventral region.—The postventral region merges anteriorly with the abdominal region; dorso-laterally it merges with the postpelvic region. The right and left sides of the postventral region merge medially posterior to the anus and anterior to the under tail coverts. We consider the anal circling a part of the postventral region. Anterior to the anus the right and left sides of the postventral region are separated by the midventral apterium.

FEMORAL TRACT

This tract lies on the upper part of the leg. It is bounded medially by the lateral pelvic apterium. Posteriorly the femoral tract merges with the lateral pelvic region; laterally it merges with the crural tract. The femoral tract is bounded anteriorly by the lateral thoracic apterium.

The acetabulum lies deep to the postero-lateral margin of the lateral pelvic apterium, and the femur extends antero-laterally from this point to the knee joint which lies deep to that part of the lateral thoracic apterium immediately medial to the posterior end of the flank region of the ventral tract.

The knee area and tibiotarsus immediately distad to the knee area are covered by the region of scutellation superficial to the distal end of the tibiotarsus.

CRURAL TRACT

This tract overlies the main muscle masses of the shank. The crural tract merges medially and ventrally with the posterior part of the sternal region. Anteriorly the tract is limited by the posterior margin of the lateral thoracic apterium. Dorsally and medially the crural tract merges with the femoral tract.

The knee area and tibiotarsus immediately distad to the knee area are covered by the flank region. The crural region extends over the remainder of the tibiotarsus to the region of scutellation superficial to the distal end of the tibiotarsus.

CAUDAL TRACT

Witherby *et al.* (1939) reported for the Mallard, "Tail rounded, 18 to 20 feathers, two central pairs (in some only one pair) curled, in eclipse straight." Phillips (1923) noted for the Mallard, "Four central tail feathers sharply upcurled and glossy black; rest of tail ashy colored with the margins of the feathers white." H. L. Clark (1918) reported on the number of rectrices and upper tail coverts in a number of genera of waterfowl. In *Anas* he found 16 rectrices and 18 upper coverts; however, we have been unable to confirm his results. In three specimens (two adults and one juvenile) of the Mallard we found 20 rectrices. Any recognition of a precise number of upper tail coverts must be made rather arbitrarily; there are at least as many upper tail coverts as rectrices.

Included in the caudal tract are the feathers of the uropygial gland and those located

laterally and posteriorly to that gland. The feathers anteriorly bordering the uropygial gland are included in the pelvic region. Humphrey and Butsch (1958) figured the distribution of the feather tufts around the two orifices of the uropygial gland in *Camptorhynchus labradorius*. In the Mallard there is a similar distribution in the form of a figure eight about the two orifices. Marked individual variations were found in the number of tufts surrounding these orifices in the Mallard; the respective numbers of such tufts in three specimens were 34, 30, and 27.

SUMMARY

The pterylosis of the Mallard (*Anas platyrhynchos*) is described, based on the examinations of fresh and preserved, clipped and unclipped specimens, and on soft-ray X-rays of the feather tracts of the trunk.

The carpal remex, diastataxy, and the reversed under wing coverts are discussed. It is noted that Steiner's hypothesis regarding diastataxy has been misinterpreted in the American literature.

The term POSTHUMERALS is used for the feather rows along the caudal margin of the skin covering the humerus. The group of feathers called by various authors the "scapular tract" or the "humeral tract" is here called the SCAPULOHUMERAL TRACT. The term FLANK REGION is given to that part of the ventral tract containing the flank feathers.

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