VARIABILITY IN BODY PTERYLOSIS, WITH SPECIAL REFERENCE TO THE GENUS *PASSER*

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Pterylography, the study of avian feather tracts, is an old field of ornithology, rich in history but comparatively neglected in recent years. The first recorded observation that feathers are distributed over a bird's body in specific patterns predates Linnaeus (Scherren, 1903), but not until the early 19th century studies by C. L. Nitzsch was pterylography established as a branch of avian anatomy. Nitzsch made the fundamental descriptive studies in the field and gave it much of the terminology still used today. He described the pterylosis of many hundreds of species, and built a system of classification upon those studies. His "System der Pterylographie," compiled and published posthumously in 1840, has never been surpassed in scope and remains the basic reference in the field. In the decades following 1840, and especially after 1867 when Nitzsch's monograph was translated into English, other anatomists contributed pterylosis descriptions to the literature, most of them isolated studies of the general anatomy, including pterylosis, of new or difficult genera. Pterylosis was then considered of basic importance as a taxonomic character, and was used to help define orders and particularly to place passerine families in many of the classifications proposed in the latter half of the 19th century (e.g. Sharpe, 1891).

At about the beginning of the 20th century pterylosis began to be neglected; it was used less often as a taxonomic character, and was gradually omitted from most general anatomical studies. This rejection was probably due to several factors. The entire field of anatomy declined as other aspects of ornithology became more popular. When the few remaining anatomists had occasion to reexamine some of the species studied by Nitzsch, they occasionally found errors in his descriptions. These inaccuracies were attributed to Nitzsch's use of dried study skins when fresh or alcoholic specimens were not available. Unfortunately the "Pterylographie" does not indicate which type of material was used for any given species description, leaving open the question of relative degree of accuracy. It also became apparent that although a large number of species had been described by Nitzsch and others, no study of the variability of pterylosis, vital to its evaluation as a taxonomic character, had yet been made. Several authors, from Lucas (1895) to Berger (1957), have called for a thorough study of the variation in some group of birds, particularly of a passerine family, in order to be better able to evaluate the accuracy of the existing descriptions and the potential taxonomic contribution of pterylosis. It is hoped that the present analysis of *Passer* and its allies will contribute at least a partial solution to this problem.

MATERIALS

For examination of variation within a representative passerine, 190 specimens of *Passer,* the nominate genus of the order, were assembled. Collected over a 12-month period were 176 *Passer d. domesticus,* including both male and female nestlings, partly- and fully-grown juveniles, and adults in first and second (or later) basic plumage. As it was necessary to have fresh undamaged skins, most of the birds were either trapped, drugged with chloral hydrate, or netted at night from breeding or roosting colonies. To avoid possible bias of results from a group of closely interbred birds, several widely spaced colonies in New Haven, Connecticut were sampled extensively. This main series was later compared with much smaller series from West Hartford and Litchfield, Connecticut, and also with a few from Pennsylvania, Illinois, and Texas, and two specimens from England. The series of *P. d. domesticus* was then compared with the following related forms (all specimens preserved in alcohol unless otherwise noted): two *P. d. indicus,* two *P. d. niloticus* × *rufidorsalis,* three fresh *P. hispaniolensis,* two *P. melanurus,* one *P. griseus,* one *P. iagoensis* (= *motitensis*), two *P. montanus,* one fresh *P. luteus,* one *Pseudonigrita cabanisi,* one *Plocepasser rufoscapulatus,* and one *Sporopipes frontalis.* The last three specimens were studied as additional genera in the subfamily Passerinae. The system of classification followed here is that of Moreau and Greenway (1962).

TECHNIQUES

Several different techniques have been employed to study the feather tracts of birds. Nitzsch and most subsequent workers used three: plucking or clipping whole adult specimens, relaxing study skins and examining the calami from the underside of the skin, and studying the emerging feathers of embryos or nestlings. These techniques were tested in the present study and found to have several drawbacks.

Plucking or clipping fresh or preserved whole specimens produces good results if carefully done, but both are very time-consuming procedures. Naik (1965) developed a refinement of the plucking technique in which the follicles are stained with hematoxylin before study; this enhances pterylosis visibility but also increases the time involved for preparing each specimen.

Otto M. Epping (pers. comm.), Carnegie Museum taxidermist, experimented with another variation of the plucking technique. Using a Starling

(*Sturnus vulgaris*) as well as several nonpasserines, he skinned the birds, soaked the skins in a lime solution until the feathers slipped out, and then chrome-tanned the defeathered skins. This resulted in specimens that were not only remarkable for their pterylosis visibility, but were also exceedingly durable. No other technique I know of allows such convenience of study, as one is handling a dry but supple and tough skin. It is ideal for examining large nonpasserines with numerous down follicles. Tanning's one drawback is the long and rather complicated preparation process.

Studying the inside of museum study skins is unsatisfactory because the feather tracts are dried and contracted, and often obscured by the remains of dermal musculature, connective tissue, and whatever absorbent (such as cornmeal) was used in the original preparation. It is usually impossible to relax and clean old study skins satisfactorily.

The third traditional method has been employed in several recent studies. It is based on the plumage stage of very young passerines in which the feathers have emerged far enough to be discernible, but are still short or in sheath and do not obscure one another. The use of young birds to describe the pterylosis *of a species*, however, can be misleading. Cases are known (e.g. Sutton, 1937; Naik and Andrews, 1966) in which additional rows of feathers appear long after the nestling period of "pterylosis visibility" has passed. Further remarks on this are made below.

A new technique, that of using soft ray radiographs, was first experimented with by Humphrey (Humphrey and Butsch, 1958) following the techniques suggested by Miller (1957). This method was developed further in the present study and used on most specimens after comparison with the other techniques proved it to be the most accurate and convenient way to record the pterylosis of a large number of specimens. In preparing the material, I skinned fresh or preserved birds by a lateral incision extending from the corner of the mouth, down the side of the body, to the tail. The incision can be confined to apteria (bare skin) except for part of the head, the legs, and the midsection of the scapulohumeral tract on the shoulder. The main body tracts are thus completely undisturbed, and only the sparse crural (leg) tracts are damaged on both sides. The skin is freed from the body at the bill margin, the elbow (distal to the scapulohumeral tract), the tarsal margin of the legs, and at the base of the tail. No skeletal elements are retained, nor is any absorbent material (e.g. cornmeal) used in the skinning; neither is necessary and both obscure the pterylae. The undersurface of the skin is then superficially cleaned of muscle and connective tissue. Next, additional incisions are made to permit the skin to lie perfectly flat and open; usually a single cut from the posterior margin through the lateral apterium to the

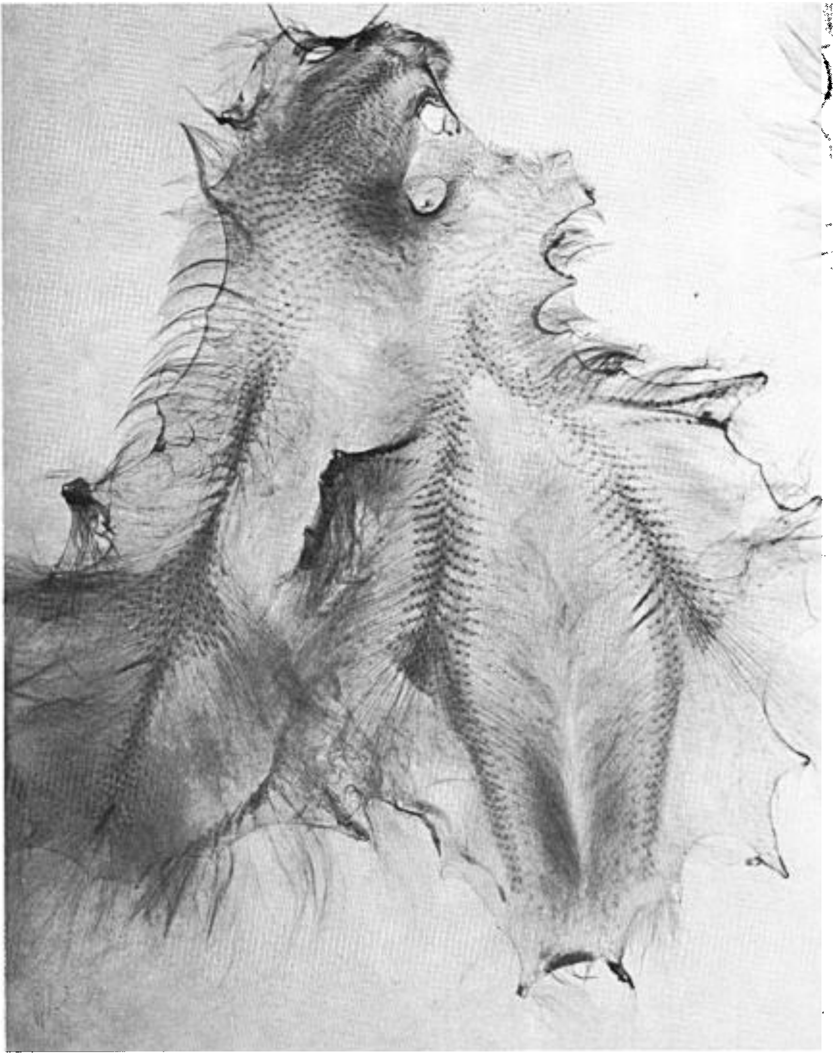

Figure 1. Radiograph of a female *Passer d. domesticus* in first basic plumage, collected by H. Holzberg in New Haven, Connecticut, 7 December 1960. Dorsal tract on left, two horns of ventral tract on right; compare with Figure 2. Note large dark growing feathers: one on lower margin of saddle element; one in posterior element; and two in flank element.

leg is sufficient. The feathers are then smoothed by hand to their normal positions and the specimen is pinned out, feather side down, on a drying board. After the skin has dried, it is unpinned and stored flat in a press until it is X-rayed and studied.

Pinning out a flat skin holds it open as it dries, prevents the dermal musculature and connective tissue from contracting and bunching parts of the tracts, and leaves the pterylae in their natural contours. Although bird skin is elastic and the apteria are easily stretched, the feather muscles in the tracts hold the follicles firmly and do not allow them to be pulled out of their normal positions. Thus a "stretched" flat skin preserves the pterylae in their natural configuration, neither contracted nor distorted, and leaves the follicles naturally arranged with respect to one another.

The X-ray equipment employed in this study was a modified dental machine fitted wth a beryllium window to emit long wavelength rays at low voltages: "soft" X-rays. Dry flat skins of *Passer* were placed on a thin black envelope containing a sheet of film, positioned 24 inches beneath the X-ray element, and exposed to 20 kilovolts for approximately 7 minutes. The voltage (up to 25 KV) and time (from 5–25 minutes) were varied for other specimens of different skin and plumage thickness in an extension of the present study. A soft X-ray, having relatively low energy, also has low penetrability, but high contrast. The densest structures in a bird skin, the calami and the proximal ends of the feather shafts, will absorb all the rays that strike them, while the lighter distal ends and the skin proper will absorb few. In a radiograph (positive print) the calami appear as small dark rectangles with thin black lines, the shafts, emerging from them. The skin and feather vanes are visible only as a faint haze (Figure 1). The pterylosis therefore can be determined directly from a radiograph by examination of the pattern of the calami.

Soft X-rays allow the use of single emulsion photographic film and standard darkroom techniques. This is simpler than working with double emulsion X-ray film and produces much sharper, higher contrast prints. The prints may be enlarged and finished with a glossy surface, so that the pterylosis pattern can be directly worked out on the radiograph with a grease pencil. Having a large, permanent, easily visible, and erasable surface on which to experiment with various row patterns is an invaluable aid when first working out a species pterylosis.

The X-ray technique, like the others, has several disadvantages and advantages. The disadvantages lie primarily in the skinning procedures, but most of these may be overcome by minor technique adjustments: changing the incision locations to allow for maximum visibility of the particular tracts under study, or comparing a flat skin with a second, whole specimen to record the positions of the pterylae relative to other parts of the anatomy. Each specimen requires approximately 3 hours to skin, X-ray, and examine, but this is faster and at least as accurate for the body pterylae as plucking or clipping. After becoming familiar with the pterylosis of a group, one can often omit the X-ray step, thereby saving an hour or two, and work directly from the flat skin. Examination of the skin under a dissecting microscope yields high accuracy when the investigator is familiar with pterylosis patterning. In this study I analyzed all but the last few specimens by both radiographs and microscopic examination of the skin; the two procedures acted as reciprocal checks. Toward the end of the study of *Passer,* its pterylosis was so familiar I could omit the X-ray step.

The other disadvantages, inherent in the other techniques as well as in the X-ray method, are concerned with the types of specimens available. Preserving birds in formalin causes certain changes that may interfere with radiography and the microscopic study of the skin's inner surface. In many preserved birds the dermal muscles, connective tissue, and fat deposits are so hardened and X-ray dense that the pterylae cannot be cleaned and flattened satisfactorily for X-raying. In such cases the flat skins may be examined directly for whatever detail is visible; depending on the condition of the skin, one can usually see all the feathers in the main body tracts. Molting specimens also present difficulties. A growing feather appears in both the skin and radiograph (Figure 1) as a dense black structure, much larger and darker than a mature feather. Empty follicles are usually visible, but in heavily molting birds the new feathers are so large and numerous that they cover up the empty follicles nearby. The ideal material for pterylography is a fresh, fully-plumaged bird, and such birds were used in this study to determine the species pterylosis of *P. domesticus.* Later, with the experience gained from this good material, it was possible to work out the patterns of related taxa available only as preserved and/or molting specimens. It is an unhappy fact of life for anatomists that so many specimens in alcoholic collections were preserved that way because they were too badly shot, too rotten, or in too heavy molt to make into satisfactory study skins. Such specimens are not much better for most anatomical studies, but they must be used because they are all that are available for particular, often rare or extinct taxa.

TERMINOLOGY

In pterylography, as in other branches of avian anatomy, a plethora of terms and concepts has been used for the same structures, or in this case, for the various groupings of feathers. Nitzsch (1840) used "flur"/"pteryla" to denote a large feathered area; this was translated by Dallas (Nitzsch, 1867) as "tract." Nitzsch considered that a bird's body has nine tracts: the spinal, humeral, femoral, ventral, lateral neck, capital or head, alar or wing, crural, and caudal. Since Nitzsch's time the term "tract" has been used for several different concepts, ranging from its original designation as a major division all the way down to its use for any discernible group of feathers, however small. Probably the major difficulty with pterylosis terminology is that no satisfactory term has ever been coined for the various subdivisions of tracts. Nitzsch (as translated by Dallas) used such words as "portion" or "branch"; others have used "region," "area," etc., and some (e.g. the illustration labels in Lucas and Stettenheim, 1965) have called each a "tract." In the present study I have followed Nitzsch in his concept of only nine tracts on a bird's body, and have generally used his tract delineations and terminology with the following major exceptions:

I have used "dorsal tract" for "spinal tract." These two terms, plus "dorsal spinal tract" have been used interchangeably by pterylographers with about equal frequency (although most of the recent American workers have preferred "spinal tract"). "Dorsal tract" is the natural opposite of "ventral tract" and it is also more generally descriptive of the tract's form and situation. In many birds, particularly nonpasserines, the dorsal tract does not overlie the spinal column completely, but is a divided band of feathers, often widely displaced to either side of the midline. *Passer* does not have a paired dorsal tract, but I selected the term for general utility in describing both passerines and nonpasserines.

In using "scapulohumeral tract" I have followed Humphrey and Clark (1961), as this term is more descriptive of the tract's position than Nitzsch's "humeral tract"; in some birds it lies over the scapula, in others it is over the middle of the humerus, and in still others it lies somewhere in between.

The third departure from Nitzsch's terminology concerns the margin between the capital and ventral tracts. I consider the anterior margin of the ventral tract to be on the upper breast rather than on the upper neck. This is discussed in detail below.

To denote the various subdivisions of the tracts, I have used the term "element" in order to stress the concept of a few large tracts which in turn are composed of smaller parts. The elements studied in *Passer* are described and discussed below.

The feathers in tract elements are organized into rows. I use the term "row" to indicate either a simple straight line of feathers, or one that is angled into some sort of chevron shape. In the chevrons, the apical feather is the anteriormost, and the "row arms" extend out from it posterolaterally. Rows are counted and numbered from the anteriormost to the posteriormost.

PRINCIPAL TRACTS AND THEIR ORGANIZATION

Reading through the literature of pterylography, one is struck by the lack of descriptions of certain parts of the body. Usually the alar and caudal tracts are described in good detail, giving the numbers of feathers present and their row patterning. In contrast the body pterylosis is most often given by general tract shape and position only. I felt it would be useful to do as detailed an analysis of the body feathering as possible, on a feather-by-feather, row-by-row basis wherever feasible. If the wings and tail were organized into rows, there was no obvious reason why the body tracts should not be also. Consequently I studied the flat skins and radiographs of the *Passer d. domesticus* series in an effort to find some pattern or geometry in the body feathering.

The capital tract has good organization at the anterior end (the feathering about the eyes, the frontal and occipital regions, and the chin), but not posteriorly. The patterns established on the head cannot be extended to connect with the dorsal and ventral tracts, as they lose organization and become sparse and irregularly arranged posteriorly (the same is true of other ploceids; see Morlion, 1968). The crural tract apparently has no pattern at all, being a thin scattering of feathers over the legs. The scapulohumeral and femoral tracts are simple, basically rectangular pterylae in even rows, with little or no obvious variability within the order Passeriformes. The present report is limited, therefore, to the dorsal and ventral tracts. These two were selected because they have a high degree of internal organization, and traditionally have been of the greatest interest to taxonomists because of their different shapes in passerines. The dorsal and ventral pterylae are also clearly visible in both radiographs and flat skins, and can be studied with precision.

In the dorsal tract the only consistent pattern is one of chevron- or V-shaped rows, with the apex of the chevron pointing anteriorly. Other patterns, such as simple straight rows at right angles to the long axis of the body, may be apparent in some areas, but they cannot be followed the full length of the tract. A similar chevron pattern is present in the ventral tract, with modification into a simple oblique row posteriorly. Additional clues come from feather size in the ventral tract; the central (apical) row calami in the flank area are considerably larger than those in the row arms. It is also pertinent to report that, in a continuation of this study covering the Passeriformes as a whole, the basic row patterning worked out for *Passer* fits all other studied species in the order. It is also possible to see the same type of pattern in literature descriptions of nonpasserines where the pterylosis is figured with precision (e.g. *Melopsittacus* in Golliez, 1967; *Anas* in Humphrey and Clark, 1961).

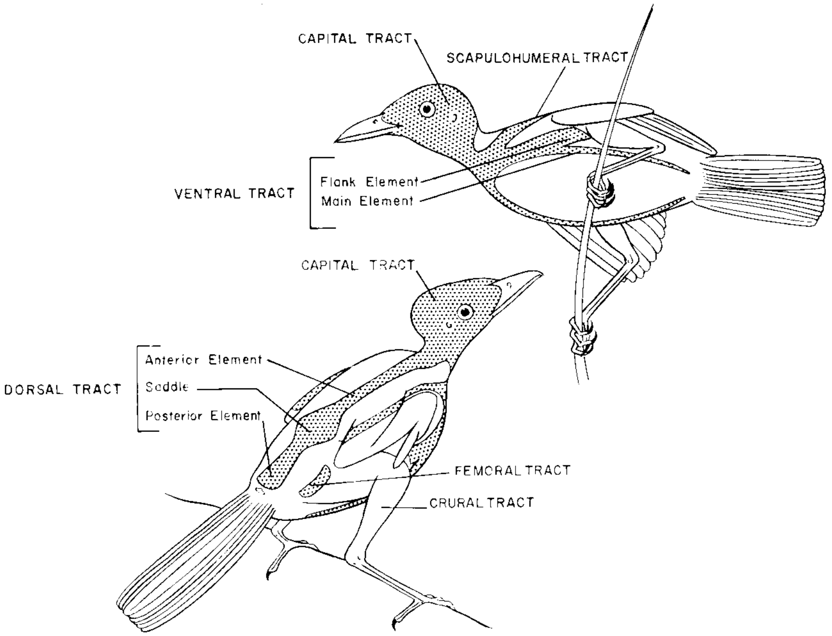

Figure 2. Positions of body tracts, shown on a generalized passerine. Redrawn from Ames (Ames et al., 1968). The crural tract, very sparse feathering on the legs, lacks well-defined margins and thus is not delineated here.

Holmes (1935), Burckhardt (1954), and others have demonstrated that the first feathers formed in early embryos are in a single line per body tract, extending anteroposteriorly along the main body axis. Later in development the initial line lengthens to the full extent of the tract and additional feathers appear on either side of it to form the complete pteryla. These observations on embryos support the pattern of rows worked out from adult material in the current study. Holmes also states that in *Gallus* the line of origin is usually, but not necessarily, in the center of the completed tract. She found bilaterally symmetrical dorsal and internally asymmetrical ventral tracts in the chick, based on the location of the initial line of feathers. I found precisely the same condition in *Passer* based on the geometry of the adult pterylosis.

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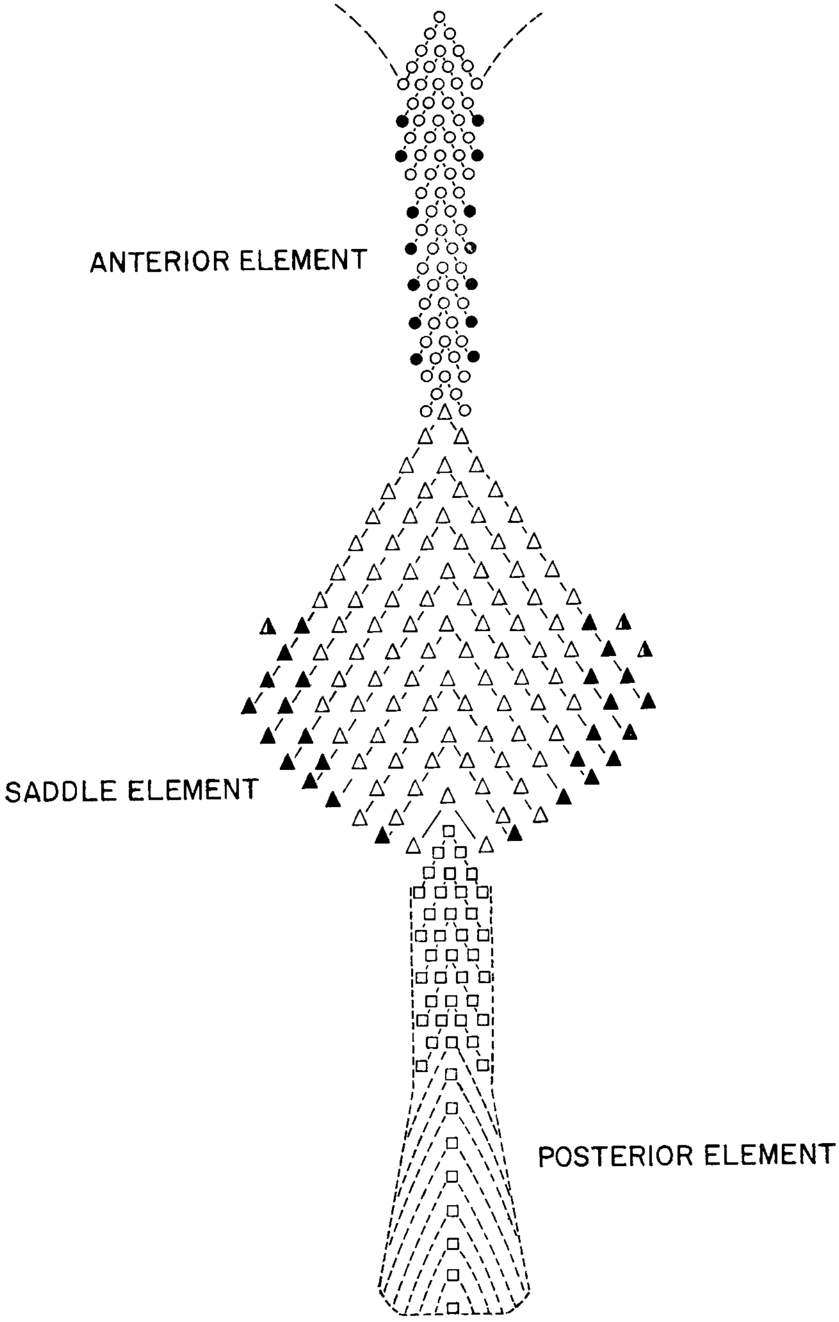
Figure 3. Dorsal tract of *Passer d. domesticus* (schematic). Open circles: feathers of the anterior element. Open triangles: saddle element. Open squares: posterior element. Solid circles and triangles: basic plumage feathers not present in a 7-day-old nestling. Partly solid triangles: example of the extra lateral row present in some specimens. Dashed lines in posterior element: irregular rows; see text.


ANTERIOR ELEMENT
SADDLE ELEMENT
POSTERIOR ELEMENT

When the entire series of 176 radiographs and flat skins of *Passer d. domesticus* was examined to determine the fundamental pattern of the species, the pterylosis was found to have little variability, with the exception of the nestlings. Then a representative sample of 59 fully feathered specimens was selected for detailed study and counting; those that were missing large numbers of feathers or that were in molt were excluded. The selected sample contained males and females of all age classes and, with few exceptions, those in basic plumage were taken soon after the molt (late October through January). Some of the comparative material (from Texas and England) was collected in March and April, but was also well feathered. Most of the main series taken in breeding condition (February through early August) and those undergoing the annual molt had lost too many feathers to record their pterylosis accurately. They were examined, however, for general pterylosis and possible seasonal effects.

BODY PTERYLOSIS OF *Passer domesticus*

DORSAL TRACT (Figures 2 and 3)

The dorsal tract of *Passer d. domesticus* is a continuous band of feathers extending down the midline from the neck to the rump. It is composed of three sections, here named the anterior, saddle, and posterior elements.

Anterior element.—A narrow band of feathers extending from the posterior limit of the capital tract on the nape of the neck, to the anterior limit of the saddle in the interscapular region. The rows of the capital tract have only a partial organization, with many displaced feathers and row segments; the capital rows are also longer and more widely spaced than those of the dorsal tract in the area where the two abut. In contrast, the anterior element of the dorsal tract has almost perfect organization and symmetry, and the rows are relatively short and densely feathered. Gross examination may not show these differences, as the capital and anterior dorsal tract feathers are generally the same size and their rows merge without an obvious interruption. Their junction, however, can be distinguished by close examination for row regularity and feather spacing.

After this junction was found by row geometry in *Passer*, its location was verified by the discovery of either a small apterium (gap) or a marked difference in feather size between the two pterylae in many suboscine families.

From the nape, the anterior element extends posteriorly down the neck as a gradually narrowing band. In *P. d. domesticus* this element averages 11 chevron-shaped rows in length; the 3 anteriormost rows have 9 feathers, the next 6 have 7, and the last 2 have 5. The amount of variation in this element is summarized in Table 1.

TABLE 1
THE DORSAL TRACT OF *PASSER D. DOMESTICUS* IN BASIC PLUMAGE

	Males						Females						
	1st basic	2nd and ff. basic	Basic, age unknown	Total males			1st basic	2nd and ff. basic	Basic, age unknown	Total females			Total basic adults
				x̄	v	s				x̄	v	s	
No. specimens	13	3	5				15	1	5				42
ANTERIOR ELEMENT													
Total length, no. rows	10.9[1]	10.3[1]	10.2[1]	10.6[1]	4.6	0.49	10.9[1]	–[1,2]	10.4[1]	10.8[1]	0.4	0.04	10.7[1]
Total no. feathers	76.7	73.7	70.2	74.7	8.1	6.08	77.3	–	74.0	76.5	4.8	3.68	75.6
No. rows, 11 feathers	0.2	0	0	0.1			0	–	0	0			0.1
No. rows, 9 feathers	2.4	2.7	1.8	2.4			2.7	–	2.6	2.7			2.6
No. rows, 7 feathers	6.1	5.7	6.0	6.0			6.1	–	5.8	6.0			6.0
No. rows, 5 feathers	2.2	2.0	2.4	2.2			2.1	2	2.0	2.1			2.2
No. rows, 3 feathers	0.1	0	0	0.1			0.1	0	0	0.1			0.1
SADDLE ELEMENT													
Total length, no. rows	8	8	8	8	0	0.00	8	8	8	8	0	0.00	8
Total no. feathers[3]	116.3	112.0	115.2	115.4	5.2	5.96	113.7	116	116.4	114.5	3.8	4.32	115.0
Total no. feathers[4]	118.9	112.0	115.4	117.1			114.9	116	117.0	115.5			116.3
No. feathers, row 1[5]	12.1	11.3	12.0	12.0	6.0	0.72	11.7	12	12.0	11.8	0.5	0.06	11.9
No. feathers, row 2	11.1	10.6	10.8	11.0	5.3	0.58	11.0	11	11.0	11.0	0.3	0.03	11.0
No. feathers, row 3	10.0	9.7	9.8	9.9	5.3	0.53	9.9	10	10.0	10.0	0.2	0.02	10.0
No. feathers, row 4	8.7	8.7	8.2	8.6	7.8	0.66	8.5	9	8.8	8.6	5.8	0.50	8.6
No. feathers, row 5	7.4	7.4	7.4	7.4	7.8	0.58	7.2	7	7.4	7.2	7.4	0.53	7.3
No. feathers, row 6	6.3	6.0	6.2	6.2	8.5	0.53	6.1	6	6.2	6.1	10.5	0.64	6.2
No. feathers, row 7	4.6	4.0	4.8	4.6	14.3	0.66	4.4	5	4.8	4.5	14.7	0.66	4.6
No. feathers, row 8	2.0	2.0	2.4	2.1	13.8	0.29	2.0	2	2.0	2.0	0	0.00	2.0
POSTERIOR ELEMENT													
Total length, no. rows	13.6	14.7	14.0	13.8	7.3	1.01	14.0	–	14.2	14.0	7.1	1.00	13.9

[1] Values given in these columns are means.
[2] A dash (–) indicates that the specimen was not in good enough condition to count feathers accurately.
[3] Excluding extra lateral row.
[4] Including extra lateral row.
[5] Saddle counts by number of feathers per row arm, plus midline feather.

Saddle element.—A wide, expanded band covering the central area of the back, from approximately the posterior interscapular region to the acetabular region. It has an almost perfect bilateral symmetry that is an uninterrupted extension of the chevron-shaped row organization established in the anterior element. The posterior margin of the anterior element is easily distinguished from the saddle by row lengths: the first row of the saddle is always much longer than the last row of the anterior element. This junction was also later confirmed by the discovery of a small gap or apterium between the two elements in certain genera of the Sylviidae. The central feathers of the entire dorsal tract can be distinguished easily, and are quite evenly spaced, except in the posterior saddle. In this latter region they are slightly wider apart, a condition also found in many other passerines.

The first saddle row has an average of 23 feathers (or 11 on a side, plus the midline feather), and is followed by seven gradually shorter rows with counts of 21, 19, 17, 13, 11, 9, and 3. This pattern forms a rhombic or diamond-shaped configuration. The number of rows in the saddle, eight, is absolutely constant; the individual rows vary little in length anteriorly (Table 1), but posteriorly they are more variable. The total number of feathers in the saddle, however, is regular.

Of the 42 specimens of *Passer d. domesticus* in basic plumage that were examined feather-by-feather, 15 had a minor variant in the saddle: an additional partial row on the anterior lateral edge. This extra "lateral row" was extremely irregular in length, position, and feather size. It was present in none of the nine nestlings or individuals in juvenal plumage examined, and in only 36 per cent of the birds in basic plumage. It showed no correlation with season, being as common in November as in June. Its total length varied from 1 to 7 feathers on a side, most commonly a single feather (9 of the 15 specimens). The position of the extra lateral row usually was opposite the posteriormost feathers of the first saddle row (Figure 3) and was seldom bilaterally symmetrical. The relative size of the feathers also varied, but generally they were smaller than the feathers of the first true saddle row. The significance of this extra lateral row is not clear; it might be interpreted as a vestigial or incipient ninth row, or simply as a somatic irregularity. Its erratic occurrence and particularly its lack of bilateral symmetry (otherwise so consistent in feather tracts) leads me to place little significance on its presence in a specimen.

Posterior element.—A band of feathers that extends from the saddle to just anterior to the uropygial gland, and covers the lower back and rump. It is formed by a continuation of the chevron-shaped rows of the anterior and saddle elements, but without as much organization in the lateral arms.

The first row of the posterior element can be differentiated from the last row of the saddle by its greater length; the latter ends in an average chevron of 3 feathers, and the posterior element begins with a row of 7. The junction between these two elements, as between the capital tract/ anterior element and the anterior element/saddle, was confirmed by the later discovery of an apterium in this region in a number of other passerine genera.

From its first row the posterior element extends toward the rump as a regular, narrow, parallel-sided band for approximately five or six rows. At about the midpoint of the element the rows lengthen, but not in a regular manner; the outermost feathers are unevenly arranged, and curve posterolaterally to surround the terminal half of the element in an asymmetrical conformation. It is therefore difficult or impossible to count them with accuracy, although the central and first few row arm feathers are regular and easily discernible, and are shown in Figure 3. The general configuration of the element is an attenuated triangle, with its base just anterior to the uropygial gland. The last three or four rows are much shorter than those immediately anterior to them, and the last row contains but a single midline feather, giving the element a truncated base in configuration. The average length is 14 rows.

VENTRAL TRACT (Figures 2 and 4)

In overall aspect the ventral surface of *Passer domesticus* appears to be feathered by two tracts: the capital covering the chin and upper throat, and the "ventral" which emerges from the capital at the base of the throat, extends down the neck as a single midline band, bifurcates on the breast, and continues as a paired tract to cover the two sides of the lower breast and abdomen. Though most previous workers have thus considered it, close examination reveals that the wishbone-shaped "ventral tract" extending from the throat to the cloaca is composed of not one but two distinguishable tracts, each with a different row pattern. The band of feathers covering the neck and upper breast is made up of chevron-shaped rows, and its midline is coincident with the ventral midline of the body. The bifurcation on the upper breast is accomplished by a simple splitting of the chevrons at the midline, and the paired tract continues down over the anterior breast as single-armed, oblique rows. The internal organization of this tract is strong enough to be discernible, but is not regular enough to afford detailed analysis: many of the central feathers are not present, especially at the anterior end; the rows are not perfectly bilaterally symmetrical in length; and the paired, single-armed rows demonstrate very little internal organization. Posterior to the bifurcation it is difficult to follow the row pattern, especially where the scapulohumeral tract intermingles with it.

One or two rows posterior to the intersection with the scapulohumerals, the ventral tract again has organization, but with a different pattern and a high degree of regular internal structure. In the present study of passerines I have confined the term "ventral tract" to this well-organized, paired pteryla that extends from the region of its "intersection" with the marginal coverts of the alar tract, posteriorly over the two sides of the body to the cloacal area (Figure 4). The ventral tract therefore has two horns, not directly connected to each other. The geometry of the feathering on the neck and upper breast seems to have more relation to that of the dorsal head and chin, and so I consider it part of the capital tract.

This redefinition of the ventral tract beginning on the breast rather than the neck is strengthened by the presence of a gap or narrow apterium in that region in *Seleucidis melanoleucus*, the Twelve-wired Bird of Paradise.

The marginal coverts do not actually reach and intermingle with the main breast feathering as do the scapulohumerals; rather they extend only to a point just lateral to the lateralmost feather of the first row of the ventral tract, and may be used by a pterylographer as indicators or "pointers" for that row. From the anterior limit each horn of the ventral tract extends down over the lateral pectoral region as a broad band, and approximately midway down the trunk separates into two independent elements: a wide lateral flank element, and a narrow, more medial main element.

Flank element.—Originates at the anterior limit of the ventral tract and is composed of chevron-shaped rows (Figure 4). The first row contains an average of seven feathers. As the element extends posteriorly it gradually widens by the addition of feathers onto the medial arm; the lateral arm remains four feathers long (including the apical). By about the fifth row (this varies considerably; see Table 2), the average maximum row length of 10 feathers is reached, and the tract continues with a constant width until the 14th row, when the first of two additional lateral feathers appears, to begin the flank expansion. At row 17 the flank separates from the main element and extends for three rows before ending

→

Figure 4. Ventral tract of *Passer d. domesticus* (schematic). Open squares: feathers of the flank element. Open circles: main element. Solid squares: example of extra lateral feathers. Solid circles: medial extension of the last row of the main element, present in some specimens.

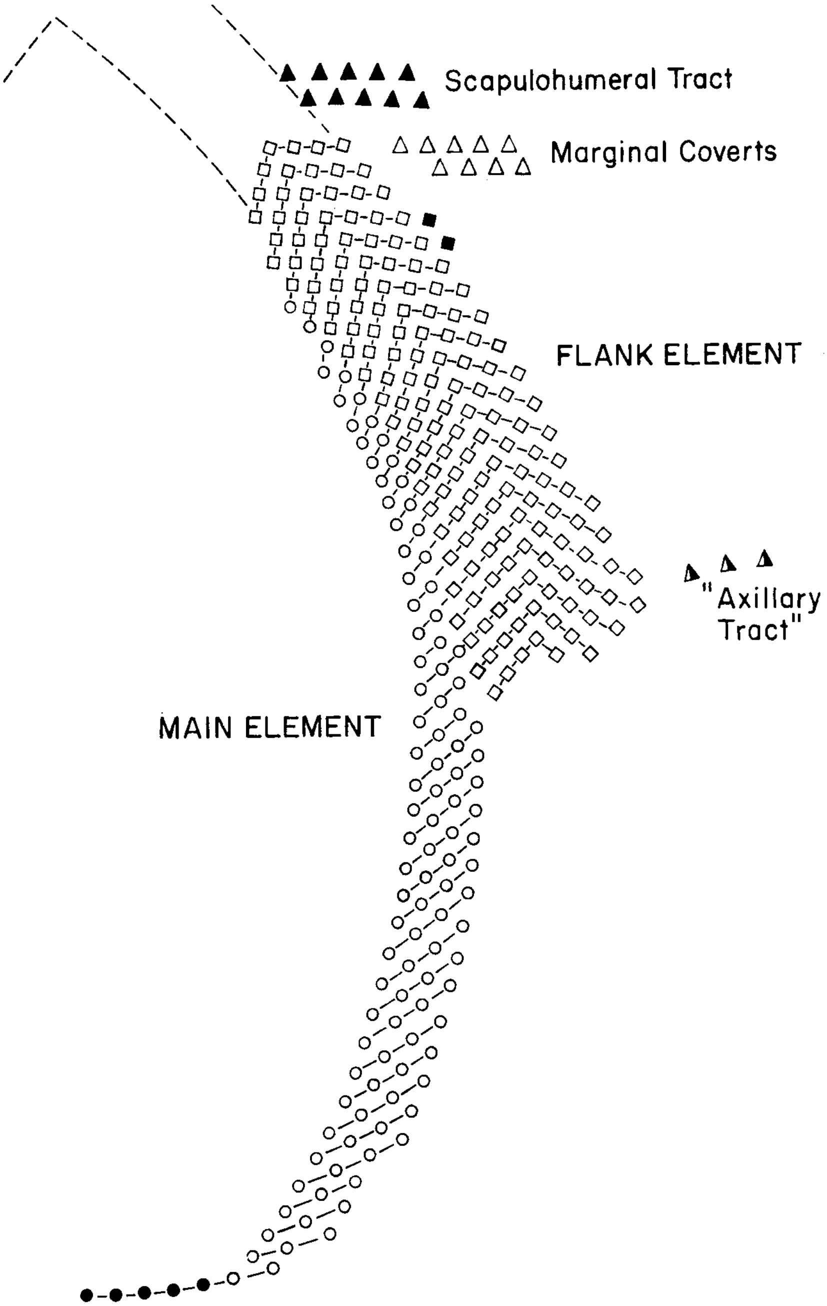

Scapulohumeral Tract
Marginal Coverts
FLANK ELEMENT
"Axillary Tract"
MAIN ELEMENT

TABLE 2
THE VENTRAL TRACT OF *PASSER D. DOMESTICUS* IN BASIC PLUMAGE

	Males						Females						
	1st basic	2nd and ff. basic	Basic, age unknown	Total males			1st basic	2nd and ff. basic	Basic, age unknown	Total females			Total basic adults
				$\bar{x}$	v	s				$\bar{x}$	v	s	
No. specimens	12	3	5				15	1	5				41
No. rows betw. scapulohumerals and marg. coverts	1.5[1]	1.0[1]	1.4[1]	1.4[1]	3.6	0.05	1.1[1]	1	1.2[1]	1.1[1]	5.4	0.06	1.2[1]
No. feathers in 1st row	6.9	6.7	7.2	7.0	0.9	0.06	7.1	6	7.2	7.1	0.6	0.04	7.1
No. rows to complete maximum width	5.0	4.3	4.2	4.8	30.2	1.45	5.0	6	4.6	5.0	21.8	1.09	4.9
Maximum width anterior to flank separation[2]	9.8	9.7	9.6	9.8	0.4	0.04	10.0	10	9.8	10.0	0.2	0.02	9.9
Row no. beginning flank separation	14.3	14.3	14.8	14.4	0.5	0.08	14.4	15	13.8	14.3	0.5	0.07	14.3
Maximum width at flank separation[2]	12.4	12.3	12.0	12.3	0.4	0.05	12.5	12	12.4	12.4	0.4	0.05	12.4
Row no. of flank separation	16.8	16.7	16.8	16.8	0.4	0.07	16.5	17	16.2	16.5	0.4	0.06	16.7
No. rows in separated flank	3.3	3.3	3.4	3.3	1.5	0.05	3.5	3	3.4	3.4	1.5	0.05	3.4
Row no. of flank end	20.2	20.0	20.0	20.1	0.2	0.04	20.0	20	19.6	19.9	0.2	0.05	20.0
Row no. of main element, 1st row with 4 feathers	21.1	20.7	21.4	21.1	0.4	0.08	20.9	21	21.0	20.9	0.2	0.04	21.0
No. main element rows with 4 feathers	14.4	14.0	14.4	14.4	7.1	1.02	14.4	14	14.4	14.4	7.8	1.13	14.4
No. main el. rows with 3 or 2 feathers	4.5	5.3	4.4	4.6	23.3	1.07	4.4	4	4.2	4.3	1.6	0.07	4.4
Tot. no. rows on left side of body	39.0	39.0	39.2	39.1	2.7	1.05	38.7	38	38.6	38.6	2.7	1.05	38.9
Tot. no. rows on right	39.0	39.0	39.8	39.2			38.5	38	37.8	38.3			38.7
Tot. no. feathers from ant. margin to flank end	199.9	194.0	195.6	198.0	3.4	6.78	199.5	194	193.4	197.8	4.0	7.89	197.9
Tot. no. feathers from flank end to post. limit	69.6	67.3	70.6	69.5	4.0	2.80	69.2	67	70.8	69.5	6.0	4.16	69.5
Tot. no. feathers in ventral tract (one side)	269.5	261.3	266.2	267.5	2.7	7.17	268.7	261	264.2	267.3	3.0	8.16	267.4

[1] Values given in these columns are means.

[2] Values given in numbers of feathers.

in an oblique margin. In the region of the division some variability may be seen in both the flank and the main elements. The separation itself may be marked by a gap in the medial arm that detaches the medialmost three feathers from the rest of the row arm, or they may be continuously and evenly spaced but with an additional feather inserted between the fourth and fifth feathers of the arm row. Any disruption of the regular pattern in this area is considered the beginning of the flank separation. The addition of feathers on the lateral side of the flank is not constant in either number or position; the average condition is illustrated in Figure 4, and some of the variation recorded in Table 2. The three rows of the free (separated) flank are also variable in length, the averages being 9, 8, and 5 feathers across. Less variation is present in the last (20th) row, with the medial arm containing two more feathers than the lateral arm; this asymmetry in arm lengths forms an oblique posterior margin to the flank. The condition of the final row, and its consequent effect on the marginal configuration of the flank, have since been found to be a potentially important taxonomic character in passerines.

A minor variant in the flank element appears to be similar to the extra lateral row of the saddle. An additional (fifth) feather was present on the lateral ends of the first few rows in 6 of the 45 individuals examined. Such feathers were found in male and female juvenal plumages, and in birds in both first and later basic plumages. They appeared to be completely random in their occurrence, number, and position. Two of the six specimens had only a single feather on one side of the body; in the other four birds the extra lateral feathering was bilaterally symmetrical, the position ranging from the first to the fifth row, and the anteroposterior length varying from one to five feathers. This feather might be interpreted as a vestigial or incipient fifth feather on the lateral arm of the flank element, as other passerine families were found to have different numbers of feathers in these row arms.

Several pterylographers have described a tract in passerines that extends dorsally from the lateral posterior margin of the flank element to the region between the wing insertion on the body and the saddle. Miller (1931) termed this narrow band of feathers an extension of the axillar region (= flank) of the ventral tract. In *Passer* I found these feathers in some, but not all, specimens. They formed a single or double row of small feathers that extended from near the lateral posterior margin of the flank toward the wing insertion. They were not connected to the ventral tract, nor did they extend posterodorsally toward the saddle, thus differing from the condition Miller described for *Lanius ludovicianus*. Because of its apparently random occurrence, the generally small size of the feathers, variability in row length, and lack of connection to the ventral tract, I did not study (count) this "axillary tract" in detail. As a practical matter, it would be a difficult structure to study with precision, as the feathers are so small and weak they are easily lost in preparation. In a continuation of the present study this "tract" was found to be at least vestigially present in most passerines, but well-developed in only a few genera. A specimen of *Lanius schach* had a line of small feathers extending from the posterolateral corner of the flank toward the wing insertion, but it did not seem to be any sort of extension of the ventral tract pattern.

Main element.—Composed of single-armed rows that originate as extensions of the medial arms of the anteriormost flank rows. It is not spatially distinguishable from the flank between its anterior origin and the region of separation; at row 17 certain irregularities of pattern appear that suggest the medianmost two or three feathers may be arranged independently of the flank element. The first three separated rows (numbers 18 through 20) contain an average of 3 feathers. An additional lateral feather is acquired at row 21, and the element continues down over the side of the abdomen as a band of oblique, simple rows 4 feathers long. At the posterior end of the tract the rows curve medially toward the cloaca and gradually diminish in length and feather size. Considerable, but bilaterally symmetrical, variation is present in the last few rows of the tract; on the average, row 35 is the posteriormost row with 4 feathers, 36 through 38 have 3, and 39 ends the tract with 2 very small feathers.

In a few individuals (of many other passerines as well as *Passer*) the final row extends medially across the lower abdomen to meet its similarly extended opposite member just anterior to the cloaca. This apparent joining of the two horns of the ventral tract varies from specimen to specimen, and seems to occur at random. In some individuals the extended rows contain large, regular, obvious feathers, but in most the pattern is barely discernible either from feather loss or because the feathers are very small and irregularly placed. I noticed that only the freshest birds tended to retain these small feathers. Specimens that were not skinned immediately after collection, but which had not obviously begun to "slip" over the abdomen, often lost them. Because the regular tract feathers were retained, the loss would not be noticeable unless careful microscopic examination were made for empty follicles. Birds collected several months after the annual molt also usually lacked these feathers.

In all cases it was clear that the ventral tract itself did not curve medially to join opposite horns; it was simply the final row extending across the abdomen from both sides. This distinction is important because of the many apparently contradictory illustrations or descriptions in the literature of the ventral tract meeting above the cloaca. Most passerines are figured with the two horns of the tract well-separated; some (e.g. *Bradypterus cinnamomeus* in Pycraft, 1910) are shown with them connected by a narrow line of feathers, and others (e.g. the grossly erroneous figure of *Bombycilla cedrorum* in Shufeldt, 1890) are illustrated as a broad band enclosing the cloaca. These apparent differences are almost certainly artifacts, depending upon the freshness of the specimen or its plumage.

The occasional extension of the last ventral row is also an example of the almost perfect bilateral symmetry observed throughout the study. Virtually any minor variant recorded on the left side of a tract was also present on the right; the pteryloses on each side of the body midline were mirror images of each other.

APTERIA

The apteria, or "bare" spaces between pterylae, do not entirely lack feathers. The skin on either side of the dorsal tract has a very sparse covering of plumulaceous, modified contour feathers, arranged in an apparently random manner. However the apterium contained within the two horns of the ventral tract has some degree of organization in its feathering; the feathers are small and sparsely distributed, but their distribution reflects the row pattern of the ventral tract. The general appearance is a weak and widely-spaced extension of some of the medial arms of the ventral rows, with the feathers gradually becoming smaller and more widely spread as they approach the body midline. Some specimens, especially those with a maximum tract width of 9 rather than 10 above the flank separation, have strong first apterial feathers on the medial side of the horn. These may be interpreted as incipient, vestigial, or simply misplaced 10th ventral feathers.

VARIATION

After the pterylosis of the main series of *P. d. domesticus* was recorded, the data were summarized and statistical tests applied where possible. Tables 1 and 2 present the condensed data arranged in age, sex, and plumage classes. Standard deviations (s) and coefficients of variation (v) were computed for some of the series and Chi-square (χ^2) tests were run both for row patterns and numbers of feathers. In the χ^2 tests males in basic plumage (all age classes; see below) were used as the standard for comparison.

Individual variation.—Only relatively minor individual variations, such as the row lengths discussed above, were found in the series. *No* specimen demonstrated a significant departure from the species pattern. The gen-

TABLE 3
THE DORSAL TRACT OF *PASSER DOMESTICUS* SUBSPP. AND OTHER PASSERINAE

	Passer d. domesticus						*P. d.* subspp.		*Passer* spp.			Passerinae spp.	
	Northern U. S. adults	Northern U. S. fledged juvs.	Northern U. S. nestlings, 4–7 days old	Texas adults	England adult	England fledged juv.	*P. d. indicus*	*P. d. niloticus* × *rufidorsalis*	*P. montanus* fledged juv.	*P. hispanio-lensis*	*P. melanurus*	*Plocepasser rufoscapulatus*	*Sporopipes frontalis*
No. specimens	42	5	5	5	1	1	2	2	1	3	2	1	1
ANTERIOR ELEMENT													
Total length, no. rows	10.7[1]	10.8[1]	11.0[1]	–[1,2]	–[2]	–[2]	–[1,2]	–[1,2]	–[2]	10.7[1]	–[1,2]	–[2]	–[2]
Total no. feathers	75.6	69.6	62.6	–	–	–	–	–	–	78.0	–	–	–
No. rows, 11 feathers	0.1	0	0	–	–	–	–	–	–	0	–	–	–
No. rows, 9 feathers	2.6	1.0	0.8	–	–	–	–	–	–	3.7	–	–	–
No. rows, 7 feathers	6.0	6.4	2.6	–	–	–	–	–	–	5.0	–	–	–
No. rows, 5 feathers	2.2	2.8	7.2	–	–	3	–	–	–	2.0	–	–	–
No. rows, 3 feathers	0.1	0.6	0.4	0	0	0	–	–	0	0	–	–	–
SADDLE ELEMENT													
Total length, no. rows	8.0	8.0	8.0	8.0	8	8	8.0	8.0	8	8.0	8.0	8	6
Total no. feathers[3]	115.0	94.8	94.0	115.0	106	100	101.0	109.0	96	109.3	110.0	117	56
Total no. feathers[4]	116.3	94.8	94.0	117.5	106	101	101.0	109.0	96	109.3	119.0	118	56
No. feathers, row 1[5]	11.9	8.6	8.0	11.8	11	8	10.0	10.5	8	11.0	11.0	12	5
No. feathers, row 2	11.0	8.6	8.5	11.3	10	10	10.0	10.5	9	10.7	11.0	11	8
No. feathers, row 3	10.0	8.4	8.3	9.8	9	9	9.0	9.5	9	9.7	9.5	10	7
No. feathers, row 4	8.6	7.6	7.5	8.8	8	8	7.5	8.0	7	8.3	8.0	9	5
No. feathers, row 5	7.3	6.8	6.5	7.5	7	7	6.5	7.0	7	7.0	6.5	7	4
No. feathers, row 6	6.2	5.8	6.0	6.0	6	6	5.5	6.0	6	5.7	6.0	6	2
No. feathers, row 7	4.6	3.8	4.3	4.3	4	4	4.0	4.5	4	4.3	4.5	5	0
No. feathers, row 8	2.0	2.0	2.0	2.3	2	2	2.0	2.5	2	2.0	2.5	2	0
POSTERIOR ELEMENT													
Total length, no. rows	13.9	13.2	13.0	13.3	14	–	13.5	14.5	14	13.3	13.5	–	13

[1] Values given in these columns are means.
[2] A dash (–) indicates that the specimen was not in good enough condition to count feathers accurately.
[3] Excluding extra lateral row.
[4] Including extra lateral row.
[5] Saddle counts by number of feathers per row arm, plus midline feather.

erally high stability of the pterylosis of *Passer* is reflected in the small standard deviations and coefficients of variation in Tables 1 and 2. This stability was later confirmed by examination of two or more specimens each of more than 40 other passerine species (see discussion below). I conclude, therefore, that pterylosis is a constant anatomical feature, and is not subject to significant random individual fluctuation.

Sexual variation.—Comparison of the sexes within various age classes and the total specimens in basic plumage in Tables 1 and 2 indicates that, except in the degree of variability, males and females are similar in all respects. In this sample females showed a generally smaller amount of individual variation, but the x^2 tests on these data gave confidence levels (p) greater than 0.99. This lack of significant sexual influence was also confirmed on many other passerine species. Of particular interest is the study by Stonor (1938) reporting identical patterns in male and female birds of paradise, even in genera with strikingly specialized male plumage.

Age and plumage variation.—The first and second (or later) basic plumages were found to be identical in both male and female *P. d. domesticus* ($p = 0.98$ or greater). Comparison of 5 individuals in fully-grown juvenal plumage with 42 in basic plumage (Tables 3 and 4) showed them to be the same in the ventral tract ($p > 0.99$) and in the length of the dorsal elements ($p > 0.98$). Some of the dorsal rows were not fully feathered in the juvenal plumage ($p > 0.70$); the majority of the anterior element and saddle rows were two to four feathers shorter than those in the basic plumage, resulting in some (insignificant) statistical differences ($p = 0.50$–0.70 in the anterior element and 0.80–0.90 in the saddle). The absence of feathers in the row ends caused the tract to appear narrower, and the rhombic saddle to look more rounded in the young bird than in the adult. In certain juvenal specimens one or two empty follicles were clearly visible at both ends of the rows (Figure 3). This indicated that although all the follicles of the basic plumage have formed in a young bird, they are not filled with the complete complement of feathers until just before or as part of the first prebasic molt. This observation lends support to the terminology of molts and plumages proposed by Humphrey and Parkes (1959) that is used here. "Prebasic" molt stresses the plumage gained whereas "postjuvenal" places the emphasis on the plumage lost; in *Passer* the former term is more truly descriptive, as the basic plumage is the total species complement and contains more feathers than the juvenal. It is also erroneous to refer to the "molting," implying loss, of feathers that have not yet existed.

In view of the many pterylosis descriptions in the literature based only on nestling material, I made careful comparisons between 42 adults and

TABLE 4
THE VENTRAL TRACT OF *PASSER DOMESTICUS* SUBSPP. AND OTHER PASSERINAE

	Passer d. domesticus						*P. d.* subspp.			*Passer* spp.		Passerinae spp.	
	Northern U. S. adults	Northern U. S. fledged juvs.	Northern U. S. nestlings, 4–7 days old	Texas adults	England adult	England fledged juv.	*P. d. indicus*	*P. d. niloticus* × *rufidorsalis*	*P. montanus* fledged juv.	*P. hispaniolensis*	*P. melanurus*	*Plocepasser rufoscapulatus*	*Sporopipes frontalis*
No. specimens	41	5	4	5	1	1	2	2	1	3	2	1	1
No. rows betw. scapulohumerals and marg. coverts	1.2[1]	1.6[1]	–[1,2]	1.0[1]	1	1[2]	1.5[1]	1.0[1]	1[2]	–[1,2]	1.0[1]	2[2]	1
No. feathers in 1st row	7.1	7.0	–	7.0	7	7	7.0	6.5	7	6.7	7.0	9	7
No. rows to complete maximum width	4.9	5.8	–	3.3	5	5	4.0	3.5	4	–	3.0	2	3
Maximum width[3] anterior to flank separation	9.9	10.0	10.0	10.0	10	10	10.0	9.0	10	9.7	9.0	10	9
Row no. beg. flank sep.	14.3	13.8	–	14.0	15	16	14.5	15.0	15	–	15.0	13	12
Maximum width[3] at flank expansion	12.4	12.0	–	12.0	12	12	11.5	11.0	12	–	12.0	–	12
Row no. of flank separ.	16.7	15.6	–	16.0	16	16	16.0	15.5	17	16.7	15.5	15	14
No. rows in sep'ed flank	3.4	4.0	–	3.5	4	4	3.0	4.0	3	3.0	4.0	4	3
Row no. of flank end	20.0	19.6	20.0	19.5	20	20	19.0	19.5	20	19.7	19.5	19	17
Row no. of main element, first row with 4 feathers	21.0	21.0	–	20.5	21	19	20.5	21.0	21	–	20.0	–	16
No. main el. rows with 4 feathers	14.4	13.0	–	13.5	15	14	12.0	13.5	14	–	12.5	–	14
No. main el. rows with 3 or 2 feathers	4.4	5.0	–	4.5	3	3	4.5	5.0	4	–	5.5	–	3
Tot. no. rows on left side of body	38.9	37.8	37.7	38.3	38	36	36.0	38.5	38	38.0	37.0	–	33
Tot. no. rows on right	38.7	38.3	–	39.5	38	–	36.0	38.5	36	–	37.0	–	33
Tot. no. feathers from ant. margin to flank end	197.9	192.8	–	195.5	200	197	183.0	175.5	–	–	179.5	–	157
Tot. no. feathers from flank end to post. limit	69.5	66.0	–	67.0	68	62	62.0	68.0	67	–	63.5	–	60
Tot. no. feathers in ventral tract (one side)	267.4	258.8	–	262.5	268	259	245.0	243.5	–	–	243.0	–	217

[1] Values given in these columns are means.

[2] A dash (–) indicates that the specimen was not in good enough condition to count feathers accurately.

[3] Values given in numbers of feathers.

5 nestlings in partially-grown juvenal plumage (Tables 3 and 4). The ventral tract of a 4-day-old *Passer domesticus* is essentially fully developed and indistinguishable from the adult condition. Similarly the posterior element of the dorsal tract is fully feathered, but in the saddle and anterior elements, marked differences exist both in feather counts and general configuration of the tract. Only the central feathers and innermost arms of the rows have developed, causing the tract to appear very narrow and the saddle rounded. In the past pterylographers have believed that the shape of the saddle has great significance. If *Passer* had been described from a nestling it would have been reported to have a narrow, lanceolate saddle; if from an adult, it would have had a wide, acutely-angled rhombic saddle. These two shapes are illustrated in Figure 3. Statistical tests also confirm the difference; the relative widths of the anterior element ($p < 0.01$) and saddle ($p = 0.30–0.50$) differ between adults and nestlings, and the total numbers of feathers in the two elements ($p = 0.01–0.02$) are significantly different.

The problem of pterylosis differences between young and adult birds needs a great deal more study. Some of the other passerine species I have examined suggest a variety of age influences (pattern as well as feather number) which may have evolutionary significance. The nonpasserine literature indicates that embryonic or juvenal pterylosis patterns may be more primitive than those of the adult. For example, Nassonow (1895) reported that Ostrich (*Struthio camelus*) embryos clearly have pterylae and apteria, in contrast to the much more uniformly feathered adults. In certain passerine family groups also, important clues to the evolution of their feather tracts may be found by comparing series of adults with juveniles.

Seasonal variation.—The seasonal variation examined in this study indicates that no changes in the pterylosis *pattern* occur at any time of year, but striking differences are apparent in the *number* of feathers present in a given season. House Sparrows in breeding condition do not replace feathers that are lost from the body; thus an individual in June that has gone through several months of accidental feather loss by fighting, preening, and general abrasion, will be missing a great many feathers from its body tracts. As an illustration, two males collected in June each had lost 29, or approximately one-fourth of the feathers in their saddles. Adults in midsummer, just before the prebasic molt, have so few feathers that it is almost impossible to trace the pterylosis: a female on 16 July had lost 55, or almost one-half of her saddle feathers. After the molt is completed no additional regular feather growth occurs in either the tracts or the apteria. Plumage that is lost accidentally will be replaced until the onset of breeding, but I find no indication in *Passer domesticus* of the birds taking on any additional "winter" coat as suggested for certain other species by Wetmore (1936: 164) and discussed by Staebler (1941). On the other hand, the gradual loss of feathers during the breeding season is probably an adaptation for thinning the insulation coat in warm weather (see also Markus, 1963a; Brooks, 1968; and discussion beyond).

In summary, the data from *Passer d. domesticus* indicate that a single adult specimen, regardless of sex, plumage stage, or season (provided it is reasonably well-feathered) will offer an accurate picture of the species' pterylosis. Nestlings may not be used safely as substitutes for adult material, and juveniles may be used only when the specimens are in good enough condition to allow the recording of empty follicles. However, young individuals may offer interesting evidence on the evolution of certain taxa, when compared with adult material.

Intrapopulational variation.—In addition to the main series from New Haven, Connecticut, I obtained small samples from nearby Litchfield and West Hartford (each approximately 30 airmiles away). These proved to have pteryloses identical with those of the New Haven populations. The Connecticut series was then compared with a few birds of various ages from Pennsylvania, Illinois, and Texas. These too were identical with the main series. The χ^2 tests run on five Texas specimens, collected approximately 1,700 airmiles west-southwest of New Haven, and from a very different climate, produced confidence levels greater than 0.90 for the number of dorsal rows, and > 0.99 for the number of dorsal and ventral feathers and ventral rows (see also Tables 3 and 4). Two specimens (one adult, one juvenile) from the British Isles also had pteryloses identical with the corresponding plumages in American populations ($p = 0.95$ or greater).

Subspecific variation.—Concluding that the pterylosis of *Passer d. domesticus* is the same in any adult specimen, regardless of the population or climate it comes from, I then compared the nominate race with two others (see Tables 3 and 4). A pair from the introduced population of *P. d. indicus* in Pretoria, South Africa, proved the same as *domesticus* in the dorsal tract ($p > 0.90$ in row numbers and > 0.95 in numbers of saddle feathers) and in ventral row numbers ($p > 0.99$). The numbers of feathers in the ventral tract were slightly fewer, but similar ($p > 0.50$).

A male and a female from the hybrid population near Wadi Halfa on the Nile River (Gebel Adda, Egypt) were also studied. These were particularly interesting because they were not only from the zone where *P. d. niloticus* (of the "*domesticus* group" of Vaurie, 1956) meets *P. d. rufidorsalis* (of Vaurie's "*indicus* group"), but they were also collected in an extremely hot climate. They proved to be virtually identical with nominate *domesticus*: $p > 0.80$ in dorsal rows, > 0.99 in dorsal feather numbers, > 0.99 in ventral rows, and < 0.50 in ventral feather numbers. Both *indicus* and *niloticus* × *rufidorsalis* had slightly fewer feathers in their ventral tracts than nominate *domesticus,* but the differences were not statistically significant.

Intrageneric and subfamilial variation.—The series of *P. d. domesticus* was then compared to representatives of six other species of *Passer* and of three other genera in the Passerinae. These were all the alcoholic specimens I could locate in existing museum collections and not all of them were in good enough condition to permit detailed feather and row counts. χ^2 tests run on *P. montanus, hispaniolensis,* and *melanurus* (each against *domesticus*) indicated that the four species were virtually identical in their pteryloses; the p values ranged from 0.90 to greater (usually > 0.99) with only two exceptions: > 0.80 for the number of dorsal rows in *montanus* and < 0.50 for the number of ventral feathers in *melanurus.* It is interesting to note that a juvenal specimen of *montanus* had the same pattern of dorsal featherless follicles as juvenal *domesticus*; also when all its follicles were counted and compared to adult *domesticus,* the pteryloses were identical ($p = 0.95$ or greater). Rather poor specimens of *P. iagoensis* (= *motitensis*), *griseus,* and *luteus* were also examined, but could not be studied in detail; their tract configuration and all possible counts were the same as *domesticus.*

A specimen of *Pseudonigrita cabanisi* also appeared to be very similar to *Passer,* but it was in very heavy molt when collected, and few details were visible. The saddle contained eight rows, and the ventral tract was nine feathers wide anterior to the flank and four wide in the main element, substantially like *Passer.* A specimen of *Plocepasser rufoscapulatus* was in better condition and permitted some counts (Tables 3 and 4). The number and general pattern of the saddle feathers were the same as those of *Passer* ($p > 0.99$) but the ventral tract indicated some differences: $p = 0.50–0.70$ in the ventral rows, and 0.30–0.50 in the number of ventral feathers, neither value being significant. Another departure from the *Passer* pattern was noticed in the saddle: the posteriormost row was damaged, but appeared to be lacking the central feather, thus producing a very small apterium. Similar small saddle apteria were seen in other ploceid genera (e.g. *Ploceus*), but a better specimen of *Plocepasser* will have to be examined before any conclusions can be drawn.

Sporopipes has long held an anomalous position within the family Ploceidae. Sushkin (1927) found it to be a problem genus, anatomically intermediate between *Plocepasser, Bubalornis,* and the primitive Estrildinae; he therefore placed it in a subfamily of its own. Mayr and Amadon (1951) thought it "unnecessary" (no explanation) to retain subfamilial status for *Sporopipes* and so included it in the Ploceinae. White and Moreau (1958: 141) discussing their Ploceidae manuscript for the Peters Check-List, remarked (in connection with Mayr and Amadon's action): "Of these. . .proceedings, that which unites the Sporopipinae with the Ploceinae is the less readily acceptable, since the birds strike us in the field as so unlike; but on the other hand the reasons given by Sushkin for erecting the two *Sporopipes* spp. into a subfamily are, as Mayr remarks (*in litt.*) not particularly cogent. Provisionally, then, and pending further studies of *Sporopipes,* especially in the field, we include it in the Ploceinae." I can only assume that this last word is an error for Passerinae, because Moreau and Greenway (1962) placed *Sporopipes* as the last genus in the Passerinae, and White (1963) followed suit. Pocock (1966) studied certain skull foramina and Ziswiler (1968) examined the breeding biology as well as the structure of the horny palate, the alimentary tract, and the "seed-opening mechanism" in *Sporopipes* and other oscines; both concluded that *Sporopipes* differed sufficiently from its nearest relatives to be raised to full subfamily status.

The pterylosis of *Sporopipes* supports the separation of this genus from *Passer* and its allies. Dorsally, *Sporopipes* differs by having a shorter, more sparsely feathered saddle (56 feathers in 6 rows compared to an average of 115 in 8 in *Passer d. domesticus*). Ventrally the feathering is also (but less) sparse: a total of 217 compared to 267 in *Passer*. χ^2 tests on the numbers of dorsal and ventral feathers indicate the differences are highly significant ($p < 0.01$) but the numbers of rows and row patterning are less so (dorsally, $p = 0.30$–0.50; ventrally, $p > 0.80$). Visual examination of the pterylosis yields no striking pattern differences; the tracts of both genera have the same configuration. Further discussion of these differences, including the effect of body size on feather number, is given below.

PTERYLOSIS VARIATIONS IN PASSERINES

The purpose of this study was to sample and assay the range of variation in the dorsal and ventral tracts of *Passer,* in order to provide a yardstick for the future use of body pterylosis as a taxonomic character in passerines. After I found that in *Passer* the pterylosis of these tracts did not vary significantly, and that a single adult specimen, regardless of age, sex, or plumage stage, would offer an accurate picture of the species' pterylosis, I extended the study to sample other Passeriformes. This continuation of the original study is still in progress, and now includes some 450 additional specimens representing almost 300 genera and all the generally recognized families of the order. The parts of this expanded investigation that are pertinent to the *Passer* study are mentioned here. Detailed reports on the pterylosis of various other passerine groups will be presented in future papers.

The lack of individual random variation was confirmed by examination of 2, 3, or 4 specimens each of more than 40 additional passerine species, including comparisons among different sexes, ages, and plumages. Although several types of minor deviations were recorded, they were generally of the same sort as seen in *Passer* and none were of any great magnitude. The only exceptions were possible age variations in certain corvids and vireos. The most common variants throughout passerines were the lengths of certain rows and elements. In most species the element lengths were constant, and if they differed it was to a very slight degree. The saddle varied occasionally by one row, but this was usually due to a very gapped first row, or to a single midline feather as a last row, and not to any basic change. The anterior element sometimes varied by one or two rows, but some of the counts may have been in error because of difficulty in determining the anteriormost row in skins taken from alcoholic specimens. The anterior element in many alcoholic skins is often partially obscured by connective tissue and fat deposits that are difficult to clean off satisfactorily. The posterior element had a wider range of variation, up to four rows in *Passer* and one or two rows in other species; this reflects the general lack of organization and stability of that element. The flank of the ventral tract was relatively constant, rarely differing by one row, even less often by two or three. The length of the main element, as indicated by the overall length of the tract, commonly varied by one or two rows; a maximum of four was observed in *Passer*.

The lengths of individual rows also varied to a small degree. In the dorsal tract, and especially in the saddle, the rows tended to differ slightly from specimen to specimen. This was not significant in the overall count of the elements, but could affect the general configuration slightly. In contrast the ventral tract had great stability in row length, and in the few cases where differences were seen, they were never of more than one feather.

Certain aspects of the conclusions of this study have been confirmed, in varying degrees of detail, by the recent work of others. Morlion (1964) conducted a fine and very detailed study of the wings of certain Ploceidae (*Ploceus* and *Vidua*) and Estrildidae (*Estrilda*). She found these pteryloses to be perfectly bilaterally symmetrical (the right wing identical to the left in any given individual), and subject to virtually no random or sexual variation. She also reported almost no variation within these genera, but some minor differences among them, as might be expected in representatives of three separate families or subfamilies. In an extension of her wing study, Morlion (1966) examined the entire pterylosis of 40 species from these three groups, and confirmed the above principles on the body as well as the alar and caudal tracts.

Naik and Andrews (1966), in a study of the Jungle Babbler (*Turdoides striatus*), found the same sorts of differences between nestling and adult pterylosis that I saw in *Passer,* but to an even greater degree. This babbler has a remarkably protracted and complex sequence of molts and plumages, including a slow development of the juvenal plumage. Whereas a fledgling *Passer* has anterior element and saddle rows that are only two to four feathers shorter than an adult's, *T. striatus* of a comparable age still has not grown most of its posterior element and saddle, as well as parts of other body and wing tracts. The contrast between fledgling and adult pterylosis is striking. After the babbler fledges, it continues to grow in most of the remainder of its juvenal plumage. Some follicles, however, remain dormant until the onset of the "postjuvenal molt" or later. These are unspecified, except that many are on tract margins. This latter condition appears to be similar to that in *Passer,* but direct comparisons are prevented by complications arising from the difficulty in distinguishing between juvenal and "first-year" feathers in *Turdoides,* and the indication that some late-hatched individuals may not molt until they are well over 6 months old (in the next breeding season).

Very recently Gwinner (1969) found what he interprets as a "second set of feathers," a delayed completion of the juvenal plumage, in four species of *Phylloscopus.* It is clear from his discussion and figures that many of the body feathers on the edges of the pterylae do not develop until after the birds have left the nest. His results cannot be compared directly to the *Passer* data without an illustration showing precisely where and how this delayed growth takes place in *Phylloscopus.* Certain inconsistencies between text and figures also cast doubt on some of his conclusions. For instance, he states (p. 20): "During the juvenile moult, the Bonelli's Warbler, the Wood Warbler and the Willow Warbler replace only the body feathers developed in the nest. Only the Chiffchaff replaces in addition, all the feathers of the second set, the 3 to 5 innermost secondaries and some of the inner wing coverts." It is difficult to understand how the Chiffchaff can replace all the second set of feathers when many of these are shown in Gwinner's Figure 4 as growing in, presumably for the first time, *during* the molt. Also, Gwinner's Figure 2 does not support his concept of the postfledging feather growth as a "second set," as feather growth appears to be continuous somewhere on the birds before, at, and after fledging. On the other hand, Gwinner's data do indicate that, in *Phylloscopus* as in

Turdoides, initiation of juvenal feather growth in some follicles takes place after fledging; this is not true of *Passer,* in which nestling and flying juveniles are virtually identical in pterylosis. Further studies of the timing of juvenal feather initiation are obviously desirable.

Another recent paper that should be mentioned is a study by Foster (1967) on the Orange-crowned Warbler (*Vermivora celata*). Working with a sample of six, she reported (p. 3): "no differences in pattern among the sexes or [two] races were noted. Also, there appears to be little or no difference in pterylography among immatures [birds in first basic plumage], first-years [first alternate plumage], and adults [second basic ff.], all of which differ only slightly from juveniles [natal and juvenal plumages combined]. These differences include narrower interscapular and pelvic regions in the spinal tract of the juveniles. . . ." Foster included some rough drawings of her work, with a pterylosis description characterized as "an approximation intended to represent the shape and extent of feathered areas. No attempt has been made to record each body feather." She, like so many others who have studied general tract shapes rather than doing a more careful analysis, missed several important features and drew some unwarranted conclusions. She found no flank separation in the ventral tract, and apparently mistook some apterial feathers posterior to the saddle as a connection with the femoral tract. I have studied 23 specimens of Parulidae (17 species of 11 genera, including 2 *Vermivora pinus*) and did not find either of these features. It seems highly improbable that *V. celata* would differ so extremely from the rest of the family, even more than such long-recognized "problem" genera as *Icteria, Coereba,* and *Peucedramus.* Foster's uncritical acceptance of Stewart's (1952) very poor sketches of the pterylosis of (a probable juvenal) *Geothlypis trichas,* makes her comparisons between the two species of little value. And her remark that "juveniles appear to be more densely feathered in all areas" than are birds that have reached at least the first basic plumage, cannot be accepted until substantiated by actual feather counts of the two age groups.

It has been suggested (e.g. Wetmore, 1936) that pterylosis may be influenced by body size. If this were true, morphologists might expect larger birds to have either proportionately more feathers, in longer tracts, elements, and rows, or the same number of larger feathers, to cover the greater expanse of body surface. Unfortunately, simple counts of all the feathers on a bird give no indication of how they are distributed, and hence how much of the body is effectively covered. If one can generalize from the pterylae counts of Markus (1963a, 1963b) then roughly one-third of a land bird's feathers are on the head, one-third on the body, and one-third on the wings, legs, and tail. Therefore, for example, a major change on the head resulting in a larger number of smaller feathers might not affect the extent of the covered area at all. But a simple feather count of this change would make it appear that the bird had increased its effective feathering by a significant amount. It is important to know not only how many feathers are on a bird's body, but also their size and location, and thus whether an increase in body size will truly result in an increase in effective feather coverage.

Physiologists might expect that smaller birds would have proportionately more feathers, for heat retention in a relatively larger body surface (Hutt and Ball, 1938). Recently (e.g. Turček, 1966) physiologists have approached the problem by dealing with plumage weight rather than absolute numbers of feathers. They have found that when expressed as a percentage of total body weight, smaller birds do have a greater amount of plumage. The differences are not striking; Turček (op. cit., p. 627) calculated that "an increase of 100% in body weight results in an increase of about 95% in plumage weight." Nor are the differences consistent, either in relation to body size, or by taxonomic groups. Turček found the average plumage/body weight percentage to be 6.3, with two-thirds of all observations falling within the limits of 4.85 to 8.08 per cent. In his sample of 249 passerines and nonpasserines, the two species with the heaviest recorded plumage percentage were also among the smallest in body size; *Parus major* and *P. caeruleus* had values of 12 per cent of the body weight, yet *Parus palustris* had an anomalous "too low percentage" for its family (no value given). Similar variation was found in the Sylviidae with all species of *Sylvia* and *Acrocephalus* cited as "too low" and *Phylloscopus* as "too high" for the family.

I recorded a similar lack of consistency in counting body pterylosis. In the ventral tract I found no direct correlation between body size and tract width, although some was apparent in tract length; larger birds tended to have longer pterylae, both anterior and posterior to the flank separation. No correlation at all was seen in the dorsal tract. One of the largest oscines examined, the Hill Myna (*Gracula religiosa*), had almost the shortest and least feathered saddle: a total of 57 feathers in 6 rows, interesting compared with the tiny specimen of *Sporopipes* that had 56 in 6. Another very large oscine, the Twelve-wired Bird of Paradise (*Seleucidis melanoleucus*) had just 95 feathers in 7 saddle rows, compared to the much smaller *Passer* that averaged 115 in 8. The most heavily feathered oscine saddle counted was the large Satin Bowerbird (*Ptilonorhynchus violaceus*), which had 273 in 15 rows. The striking pterylographic differences between bowerbirds and birds of paradise, exemplified here by the numbers of feathers, have led anatomists such as Stonor (1937) to doubt the supposed close relationship between these two families.

Several very small oscines also were comparatively densely feathered for their body size; a Ruby-crowned Kinglet (*Regulus calendula*) had 143 feathers in 9 saddle rows, and a Black-capped Chickadee (*Parus atricapillus*) had 161, also in 9 rows. Thus in the Passeriformes as a whole, body size alone does not necessarily influence the size and density of pterylae. Within a family, however, the larger members of a closely related group tended to have slightly longer or more heavily feathered tracts: e.g. eight specimens of the five species of North American thrushes of the genera *Catharus* and *Hylocichla* had ventral tracts ranging from 35 to 40 rows long; two considerably larger Robins (*Turdus migratorius*) were 44 and 47 rows long.

POSSIBLE FUNCTIONAL SIGNIFICANCE OF VARIATIONS IN PTERYLOSIS

I noticed that species resident in cold northerly regions tended to have more heavily feathered pterylae than those that migrate south for the winter. This trend seemed also to be generally true of most passerines that breed in temperate Connecticut: e.g. six migratory species of Parulidae averaged 114 feathers in 9 saddle rows, compared to two specimens of the similar-sized but usually resident *Parus atricapillus* which had an average of 151 in the same number of rows. In contrast a specimen of the congeneric but more south-ranging Tufted Titmouse (*Parus bicolor*) had 143 saddle feathers in 9 rows (not significantly different from *P. atricapillus*), although it is a much larger bird (live body weights of *bicolor* average twice those of *atricapillus*).

I could not see any simple overall trend in the Passeriformes that might be interpreted as a single type of climatic reaction. Certain families, particularly the Fringillidae, have groups of genera with very heavy dorsal feathering (see below) that is fairly clearly an adaptation to very cold climates. Other families, like the tropical or semitropical Rhinocryptidae, Ptilonorhynchidae, and Campephagidae, have equally heavy dorsal feathering. This latter might be interpreted as increased protection from heavy rains or some other aspect of tropical climates. In some groups it might also be a type of adaptation to ground living. Both the Rufous-sided Towhee (*Pipilo erythrophthalmus*) and the Oven-bird (*Seiurus aurocapillus*) are particularly terrestrial members of their respective families, and both have heavier saddles than their more arboreal relatives. On the other side of the coin are the very lightly feathered families. My sample indicates that all of these live in temperate to (mostly) tropical climates. The sylviid genus *Cisticola* and the Estrildinae have noticeably sparse dorsal tracts that could be interpreted as a reduction of insulation in warm, relatively dry climates, analagous perhaps to the feather loss by *Passer domesticus* and temperate climate species during the breeding season. Other lightly feathered species, however, are found in hot wet climates, e.g. a Cock-of-the-rock (*Rupicola rupicola*) that had only 88 saddle feathers in 11 rows. This last species is particularly anomalous for it has a large body, terrestrial habits, and lives in jungle habitats, yet it is strikingly lightly feathered.

Clearly, therefore, pterylosis does not react in any single or simple way to selective pressures. Climate, particularly temperature, obviously has an effect in certain species, but the type of reaction may vary in different families. Rainfall and terrestrial vs. arboreal habit may also have an effect, but these are also unpredictable.

Within the large body of literature on feather function, and especially that dealing with body temperature regulation, I have been unable to discover any study concerned with the function of feather tracts and apteria *per se*. Most physiological studies have considered just the effect of the entire feather coat on temperature regulation. A few (e.g. Brush, 1965) have dealt with the normally unfeathered regions such as the legs and feet, or with experimentally totally defeathered individuals. It is a common observation that overheated birds will hold their wings out, thereby exposing the apteria on the sides of their bodies. Less common are records of other apteria exposed when birds are forced to endure extreme heat. Two recent papers (Bartholomew, 1966; Maclean, 1967) on species incubating exposed nests in full sunlight report the raising of dorsal feathers (especially the scapulars) in addition to other heat-dissipating activities such as gular fluttering and exposing, but shading, the legs and feet.

It seems probable that a system of pterylae and apteria offers a good means of body temperature control. Bare skin is an excellent thermal conductive surface, and it offers cooling without substantial water loss, which is not true of panting or gular flutter (Brush, 1965). If apterial exposure to the environment can be controlled by the raising and lowering of the feathers that normally overlie the bare areas, a bird can more efficiently respond to temperature changes. The control system exists in the feather muscles in the pterylae (e.g. Stettenheim et al., 1963); in addition the complexity of these muscles indicates that considerable latitude and precision is possible in feather movement. This finely controlled movement is well-known, of course, in courtship and other displays. Given, therefore, this system of areas of bare skin which can be covered or uncovered by elevating the adjacent feathers, and the musculature to do this, it is reasonable to suppose that birds can and do employ the system to control heat exchange. Laboratory and field observations of birds under temperature stress are needed to confirm or disprove this hypothesis. I wonder also if some birds, lacking natural air movement in a hot environment, might periodically raise and lower their feathers, producing a bellows effect that would exchange air over the apteria and produce additional cooling.

In studying environmental adaptations of redpolls, Brooks (1968) found the head and body plumage of *Acanthis hornemanni* to weigh slightly more than that of *A. flammea*; the latter was generally less able to withstand extreme cold. Brooks and others have also reported that far northern passerines have numerous downy feathers in their apteria in winter that function to increase body insulation. Apparently this observation has never been quantified, and I question whether it is an increased number of apterial feathers or the size and fluffy structure of these feathers that is important in winter heat retention. A flat skin of *Acanthis flammea*, collected in Connecticut on 6 March, was not noticeably more heavily feathered in the apteria than are *Passer* skins; possibly this date was too late in the winter for the reported heavy feathering still to be present. The *Acanthis* flat skin was, however, very densely feathered in the pterylae, particularly for so small a body size: 160 in 10 saddle rows. Irving (1960) rated the Pine Grosbeak (*Pinicola enucleator*) as the highest of 12 fringillids in the "apparent usefulness for insulation"; he was primarily referring to the quality of the feathers for entrapping air. Two flat skins of this species, both males in first basic plumage collected in Connecticut in November, had exceptionally heavy pterylosis (268 and 254 feathers respectively in 12 saddle rows) but they did not appear to have an unusual number of feathers in their apteria. Yet the apterial feathers were large and very fluffy. For comparison with *Acanthis* and *Pinicola*, I counted several other cardueline saddles: an Evening Grosbeak (*Hesperiphona vespertina*, of similar body size to *Pinicola*) had 215 in 11 rows; a House Finch (*Carpodacus mexicanus*, intermediate in size and from a warm climate) had 158 in 10; and three American Goldfinches (*Spinus tristis*, small in size, also from a warm climate) had an average of 133 in 10. Thus, considering body size, *Pinicola* and *Acanthis* do have exceptionally heavily feathered tracts for cardueline.

Brooks (1968) also conducted high temperature experiments that produced several reactions from the redpolls. They consumed less food and reduced their activity to lessen their production of body heat, and they drank large quantities of water for evaporative cooling. They also sleeked down their feathers (p. 274) "to decrease the thickness of insulation and expel trapped warm air." But most remarkably, when these captive birds were subjected to high temperatures in winter plumage, they plucked out both "body contour" feathers (presumably in the pterylae) and "down" feathers in the apteria. Brooks further states (p. 275): "birds in summer plumage (24-hour photoperiod) had already reduced their plumage in the normal spring feather loss, and started their postnuptial molt during the experiment. Nevertheless, self-plucking was observed here, also." This phenomenon of birds actively plucking themselves when subjected to heat stress is of great interest, and it will be important to confirm this behavior in other species, if possible in individuals not in captivity. Birds are well known to pull out an occasional feather while preening, but actively plucking (presumably tightly rooted) feathers is a new and important observation.

Much is still to be learned about the role of feathers in temperature regulation. It is hoped that consideration of feather distribution on birds' bodies, such as feather counting by pterylae and physiological studies on the insulation values of the different pterylae and apteria, will increase our understanding of the function of feather coats.

PTERYLOSIS AS A TAXONOMIC CHARACTER

Apparently pterylosis is just as uniquely avian as feathers themselves. No other land vertebrate has its units of epidermal covering arranged in quite the manner a bird does; that is, in some type of ordered grouping, with "bare" spaces in between. And contrary to the statements in much of the literature, *all* birds have this ordering. In most species the pterylae form in the embryo and remain as obvious and distinct tracts of contour feathers throughout adult life. The apteria may be completely bare, or they may contain varying amounts of downy feathers. In a few species the embryonic tracts merge so that the adult feathering may be virtually (but never completely) without apteria, and may even seem to lose all of the original organization.

General ornithological works usually state that those birds without pterylae are ostriches (Struthionidae) and other ratites, screamers (Anhimidae), penguins (Spheniscidae), and sometimes mousebirds (Coliidae). Yet in each of these families examination of the embryos or even the adult skins will reveal a pterylosis. As long ago as 1900, in a detailed review and description of the feathering of ratites, Pycraft (p. 168) stated: "The existence of apteria has long been known—at least in *Struthio* and *Apteryx*; though these facts had [sic] not yet found their way into the text-books, which still repeat the old error that the feathers of the Palaeognathae were evenly distributed over the body." DeMay (1940), following the much earlier work of Nitzsch and Garrod, studied an adult

Chauna chavaria (Anhimidae) and stated (p. 117): "Pterylae may be distinguished in certain regions by differences in the size of the feathers." Screamers also reveal a pterylosis in the axillary region and the dorsal side of the tail that lack contour feathers. I have briefly inspected two nestling *Colius striatus*, and even a superficial examination reveals a clear pterylosis: large lateral neck apteria, a long narrow apterium extending down the midline of much of the dorsal tract, and wider apteria on either side of the posterior elements. These two specimens do, however, appear to lack apteria on the ventral surface of the body (see also Pycraft, 1907). The pterylosis of penguins is more difficult to document, as it apparently is visible only in rather early embryos and has never been studied thoroughly. Parsons (1932: 151) reported that in embryos: "Feather papillae first show themselves in the skin of the tail. . . . According to Anthony and Gain (1915, p. 22) the later papillae arise in isolated feather tracks [sic] which spread and fuse with one another as development proceeds. It is a remarkable fact that the last feather rudiments to appear are those which occur on the wings. In actual distribution the feathers of penguins are unique. They occur uniformly all over the body in the adult and only one apterium persists (Pycraft, 1907, p. 2)." My own preliminary study of an adult male *Eudyptes crestatus* in nonbreeding condition shows that this narrow apterium lies on the posterior midventral line.

Thus it is apparent that all birds demonstrate organization of their feathers into pterylae and apteria. As a basic avian phenomenon, therefore, pterylosis (and differences therein) should offer an important anatomical complex for use in taxonomic studies. That modifications in pterylosis (as for example the almost complete loss of apteria in adult penguins) may be adaptive is no barrier to use as a taxonomic character; the concept of "nonadaptive" characters is now virtually obsolete among taxonomists.

From a practical viewpoint, pterylosis has several useful qualities for taxonomic work. Individual variation in patterns is not significant, and patterns may be studied confidently from a limited number of specimens per species. The overall patterns also seem to be remarkably consistent and evolutionarily conservative within the class Aves as a whole; the pterylographic differences between taxa are thus believed to be highly significant indications of relationships, especially at higher taxonomic levels.

The *Passer* study, and more particularly the general passerine survey, have shown that two types of variations may be important for taxonomic use:

1. *Patterns.*—By far the most significant differences are in the pterylosis patterns: the shapes and locations of rows (which may or may not be reflected in the general configuration of the elements), and the presence or absence of parts of rows, entire rows, or even entire elements. Of particular interest are the apteria, how they are formed, their relative sizes, and their locations.
2. *Numbers of feathers.*—Also of considerable importance are major differences in row lengths and the numbers of rows per element, hence tract widths and lengths. The general quantity of feathering is also important, but body size must be taken into consideration. Most or all of the characters based on feather numbers can be analyzed statistically for significance.

Within the passerines as a whole, differences observed in pterylosis pattern and feather numbers may not have the same degrees of taxonomic importance, depending on their locations in the tracts. Those that occur in the dorsal saddle and ventral flank elements seem to have the greatest significance; the many patterns thus far studied are absolutely consistent within genera (and usually within subfamilies or even higher categories) and the relationships thus indicated are in close agreement with the accepted taxonomy. The anterior element of the dorsal tract does not show the kinds of striking pattern differences seen in the saddle or the flank, but at least in one case (the apterium separating the anterior element and the capital tract in suboscines) it offers an important character. Otherwise the anterior element is consistent among passerines, differing from group to group only by a few feathers in width and a few rows in length. In my passerine survey the main element of the ventral tract has thus far been found to differ significantly in pattern only in lyrebirds (*Menura*); otherwise it is like the anterior element, varying only slightly from group to group, and then just in feather numbers. The posterior element of the dorsal tract commonly varies individually, so the differences in pattern and feather number seen here must be treated with caution. Within some families the posterior element has two or more strikingly different configurations (supported by row patterns), and in others this element is entirely absent; differences of this magnitude clearly have taxonomic significance.

In general pterylosis differences occur on two levels. Closely related forms (subspecies, species, and genera) can show minor variations, especially in feather counts, that may be useful for taxonomic decisions within a family. Gross differences, particularly in pattern, are seen on higher taxonomic levels. In a few groups such as the Formicariidae that are well known to be anatomically diverse, strikingly different pterylosis patterns are found among subfamilies. Most often pterylosis varies significantly on the family level, or higher. The great majority of passerines have a complete pattern homogeneity within any given family, and several groups of families known to be similar in other anatomical systems have virtually identical pteryloses as well.

Throughout the passerine survey the implications of the pterylosis differences observed were in general agreement with the accepted taxonomy of the group. In several instances where "unexpected" pterylosis was found, and other aspects of the anatomy could be investigated (e.g. the family Conopophagidae, Ames et al., 1968), the pterylosis agreed completely with the taxonomic indications of the more traditionally acceptable anatomical characters. It seems clear, therefore, that within the bounds of variability discussed above, pterylosis can be a highly useful taxonomic character. In particular it offers an important potential contribution toward a better understanding of the relationships of birds, and especially the higher categories of passerines.

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SUMMARY

This study was conducted to sample the variability of body pterylosis in passerines, and thus to evaluate the potential contribution of pterylography to passerine taxonomy.

Study material included 176 specimens of *Passer d. domesticus* (House Sparrows): male and female nestlings; partly- and fully-grown juveniles; and adults in first and second (or later) basic plumage. Birds were collected from several different populations and climates. This series was studied in detail and then compared to additional related forms: two races

of *domesticus*; six species of *Passer*; three genera of the Passerinae; and a broad sample from the order Passeriformes.

The traditional techniques of pterylography are discussed and a new method introduced. In the latter, flat skins from fresh or alcoholic specimens are studied both by "soft" X-ray radiographs and by microscopic examination of the underside of the skin.

The study is limited to the two main body tracts, largely because of their high degree of internal organization, interesting variation within passerines, and traditional importance to taxonomists. The dorsal and ventral tracts of *Passer* are described in detail: the numbers and distribution of feathers in rows, the rows in tract elements, and the elements in tracts. The dorsal tract is considered to have three elements (anterior, saddle, and posterior) and the ventral to have two (main and flank).

Variability is analyzed in detail. No marked individual variation is present in *P. d. domesticus*. The generally high degree of pterylosis stability is supported both by the absolutely consistent pattern in all specimens and by small standard deviations and coefficients of variation in the feather counts. Statistical tests also show no significant differences in pterylosis by sex, plumage stage, climate, season, or population, once an individual has reached the first basic plumage. Nestlings and juveniles may differ significantly from adults in some tracts. Comparison of the main series with other races of *domesticus* and other species of *Passer* indicates that minor differences exist, but none is statistically significant. *Pseudonigrita* and *Plocepasser* are similar to *Passer*, but no conclusions may be drawn until better specimens of the former two genera become available. *Passer* differs significantly from *Sporopipes*, supporting the many previous suggestions that the latter should not be included in the Passerinae.

A continuation of the study into the Passeriformes as a whole, still in progress, confirms the variability principles established by the *Passer* analysis: no significant variation between individuals of the same species, and no effect on a specimen by its sex, plumage stage, etc. The same kinds of differences between juveniles and adults are also seen in other passerines.

The general types of differences that occur among species, genera, families, etc. are discussed; these include the possible effects of body size and climatic adaptation. The functional significance of pterylographic variation is speculated upon. It is clear that climate, especially temperature, has an effect on the pterylosis of certain species, but the type of reaction varies. Pterylosis does not react in any single or simple way to selective pressures.

Pterylosis is uniquely avian. No other land vertebrate has an epidermal system quite like it, and (contrary to many statements in the literature) all birds show a pterylosis. As a basically avian phenomenon, therefore, it should offer an important anatomical complex for use in taxonomic studies. The range of differences in pterylosis patterns encountered within the Passeriformes, as well as the lack of individual or subspecific variation, indicate that pterylosis is both remarkably consistent and evolutionarily conservative. As such, the pattern differences observed among taxa should be highly significant indications of relationships, especially at higher taxonomic levels.

Two types of pterylographic differences may be important to taxonomists: variations in pattern, including the presence, location, and length of rows and apteria; and major differences in feather numbers within similar patterns. Pattern differences in the saddle of the dorsal tract and the flank element of the ventral tract seem to have the greatest significance, but variations in the other elements may also be important.

Pterylosis varies on two taxonomic levels: minor differences (especially in feather counts) occur among closely related forms, and major differences (primarily in patterns) are seen among higher categories. In a few instances pattern variations appear among well-differentiated subfamilies, but they are most often found among families or groups of families.

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