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- <sup>2</sup>I am indebted to Mr. E. Alexander Bergstrom for the loan of Williamson's papers. *Massachusetts Institute of Technology, Cambridge, Mass.*

## THE TOPOGRAPHY OF A BIRD

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The regions used in the formal descriptions of the plumage of birds have been often illustrated. Much the same illustration will serve as general guide for field characters or for the study of museum specimens which lack much of the underlying structures. The bander is left at a loose end when he wishes to place with precision an abnormally colored feather or to state to which region the short new feathers on a molting bird pertain. For example, new feathers at the anterior edge of the rump may be covered by old feathers of the back. In the hope of assisting banders to record information about the plumage and molt of their birds I present a set of figures and definitions for an average passerine and some comments on birds of other orders.

Three intergrading types of feathers are significant to us. 1) Downs. The rachis or shaft is imperceptible beyond the calamus, the thickened portion inserted in the skin. The barbules have a particular microscopic structure which is also usual at the bases of feathers of the next two types. Briefly barbs and barbules are slender and flexible, the barbules without hooklets. 2) Contour feathers. The rachis is evident beyond the calamus. The barbs do not usually lock together to form a firm vane. These are the feathers of the head, body, legs, and bases of the wings. 3) Quill feathers. Similar to contour feathers but much larger and usually with firm vanes. The obvious quills are the primaries and secondaries (remiges) and the tail feathers (rectrices). On the basis of development, structure or behavior we might include here the greater primary coverts, the inverted secondary coverts on the underside of the wing and the upper tail coverts.

Most birds have the feathers springing from well-defined tracts (pterylæ) separated by unfeathered areas (apteria). The latter may produce downs. Among passerine birds the apteria are usually distinct and, hence, most pterylæ can be satisfactorily delimited. This is not true of some other orders. Unfortunately it is not possible in all cases to make out boundaries of regions in terms either of early development or of underlying structures. I have tried to use a minimum of arbitrary limits. The bander will be interested to notice the extent to which color boundaries follow the boundaries here described. The definitions are for the areas covered by the feather follicles with remarks on the extension of the feathers themselves beyond the stated limits.

The most complex area on a bird is the head (Fig. 1). It is quite clear that the feathering develops from a considerable number of centers.

Forehead: the dorsal, anterior portion of the head, bounded posteriorly by a line between the anterior edges of the eye openings and separated from the eye by the anterior end of the superciliary, below by a line from the dorsal edge of the nostril to the middle of the eye. The feathers are usually short and do not extend far beyond the given line along the posterior margin.

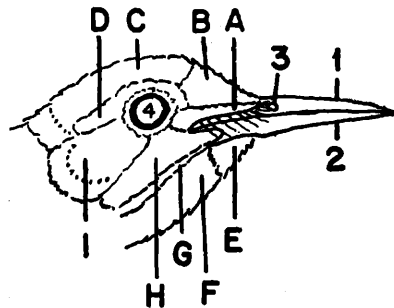
Crown: posterior to the forehead, bounded behind by the anterior end of the neck vertebræ and laterally by the superciliary. The tips of the hinder feathers extend somewhat beyond the posterior margin stated.

Superciliary: a narrow band of feathers passing from near the anterior point of the eye opening over the eye to near its posterior point, separated from the eye opening by the rimal feathering and the apterium of the upper eyelid. The more posterior superciliary feathers reach well behind the eye along the dorsal margin of the ear coverts.

Narial feathering: a small group of often bristly feathers projecting forward to more or less overhang the nostril. This feathering is particularly well developed in most Corvidæ and quite wanting in some other groups. The narials are not always clearly distinguishable from the forehead and the lores and may even grade into the rictal bristles.

Rimal feathering: two, or sometimes one, rows of small feathers on the eyelids close to the edge of the eye opening. When distinctively colored these form the true eye-ring. The rimals are sometimes bristly

Fig. 1. Side view of head. 1-maxilla, 2-mandible, 3-nostril, 4-eye, A-lores, B-forehead, C-crown, D-superciliary, E-chin, F-throat, G-malar stripe, H-malar area, I-auricular. The rictal bristles immediately below the lores and the rimals around the eye are not lettered.



(e. g. hornbills, Bucerotidæ). They are absent, as a group character, in pigeons, Columbidae, and very greatly reduced in extent in sandgrouse, Pteroclididae.

Lores: ventral to the forehead and superciliary, extending from the nariums, if present, to the eye, bounded below by the maxillary rhamphotheca or the rictal bristles, if present, and posteriorly by a line from the angle of the gape to the anterior point of the eye.

Rictal bristles: when present, a row of outwardly directed bristly feathers extending forward from the angle of the gape along the edge of the rhamphotheca of the maxilla and, sometimes, also of the mandible. Such a feather owes its peculiar character to the projection of the rachis beyond the outermost barbs.

Auriculars (ear coverts): the specialized feathers related to the ear opening, extending backward and downward from the posteroventral quadrant of the eye, bounded dorsally by the superciliary and crown and ventrally by the malar (cheek) area. The more anterior feathers (covering the ear opening) extend their tips somewhat beyond the insertions of the feathers posterior to the ear opening. The latter are suberect, stiff, narrow feathers in most groups of birds and wholly concealed by the more anterior auriculars.

Malar area: extending from the hind margin of the mandibular rhamphotheca posteriorly, ventral to the rictal bristles, lores, eyelid, and auriculars and dorsal to the throat. This area extends about as far backward as the posterior end of the ear coverts. The portion of the malar adjacent to the eyelid together with the most anterodorsal part of the auriculars may sometimes be distinguished as the subocular pterygia and may be distinctively colored.

Chin: ventral feathering between the branches of the mandibular rhamphotheca.

With this area we consider the head feathering to be completed. The

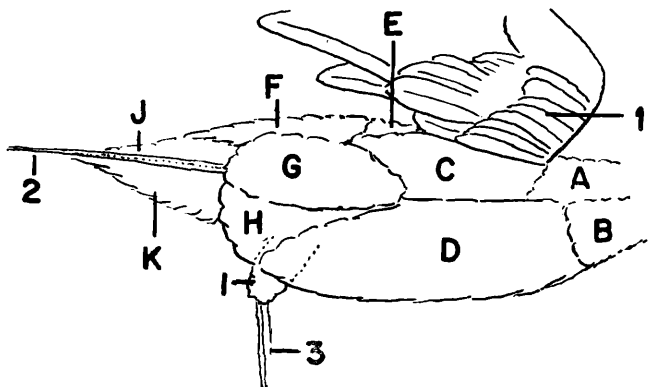


Fig. 2. Side view of body with wing raised. 1-base of wing, 2-edge of tail, 3-tarsus, A-nape, B-throat, C-side, D-breast, E-back, F-rump, G-flank, H-belly, I-crural feathering, J-upper tail coverts, K-under tail coverts.

remaining feathers fall into a ventral series of areas, a dorsal series, and a small number of lateral areas.

Throat: ventral feathering of the neck from the chin to the forking of the ventral feather tract, bounded dorsally mostly by the malar area (Figs. 1F, 2B). The lateral margin of the throat is sometimes distinctively colored and is then called the malar stripe.

Breast: ventral feathering posterior to the throat, extending over the breast muscles. (Fig. 2D) The tips of the feathers reach somewhat farther.

Side: The lateral portion of the breast feathering covering the side of the body up to the base of the wing and extending back to overlap the bases of the flank feathers. (Fig. 2C) In some groups of birds this feathering arises from a special lateral branch of the ventral pteryla.

Belly: posterior to the breast and reaching nearly to the vent. (Fig. 2H) The feathers extend past the anal pteryla and overlap the bases of the under tail coverts.

Anal pteryla: two (usually) rows of rather narrow, erect feathers surrounding the vent.

Under tail coverts (crissum): contour feathers behind the vent and covering the bases of the rectrices. (Fig. 2K)

Nape: dorsal feathering of the neck. (Fig. 2A) The feathers extend somewhat over the bases of the back feathers. This area is bounded ventrally by the throat and upper breast.

Back: feathering of the thoracic portion of the dorsum, bounded anteriorly by the nape, laterally by the bases of the wings (humeral feathering), and posteriorly by the rump. (Figs. 2E, 3A)

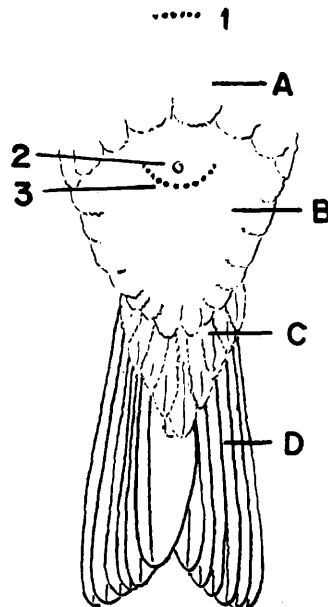


Fig. 3. Dorsal view of posterior body and tail. 1-insertions of most anterior rump feathers, 2-oil gland, 3-insertions of upper tail coverts, A-back, B-rump, C-upper tail coverts, D-rectrices.

Rump: feathering of the sacral portion of the back. (Figs. 2F, 3B) The most posterior feathers arise in front of the oil gland. This area is bounded laterally by the flanks and posteriorly by the upper tail coverts. The feathers usually extend far enough to overlap the bases of the tail feathers.

Upper tail coverts: a single, almost semicircular row of feathers arising behind the oil gland close to the rectrices, covering the bases of the latter. (Figs. 2J, 3C) These coverts may extend far beyond the rectrices, as in the Quetzal (*Pharomacrus*) and the Peacock (*Pavo*).

Humeral pteryla: extending across the base of the wing on its dorsal side from the vicinity of the shoulder joint parallel to the lateral edge of the back feathering. (Fig. 4G) It is bounded laterally by the wing coverts and tertiaries. This area is also referred to as scapular.

Flank: Feathering of the femoral (thigh) segment of the leg. (Fig. 2G) It is bounded anterodorsally by the side, dorsally by the rump, ventrally by the belly, and may, in some positions of the leg, meet the lower breast. The area is usually continuous with the next.

Leg (crural) feathering: the feathers covering the tibial (drumstick) portion of the leg. (Fig. 2I) It includes the feathering, if present, of tarsus and toes. In some groups even the lower part of the tibia is bare.

Tail: a single transverse row of quills (rectrices) on the margin of the anatomical tail (pygostyle). (Fig. 3D) The rectrices are wanting in grebes and some "ratite" birds and reduced in penguins.

The rectrices are paired and the number (rare individual exceptions) is constant within a sex and species and even, sometimes, throughout a whole order. Twelve appears to be most frequent. This number is found throughout the Passeriformes, except that the males of *Menura* have 16, *Cettia cetti* has 10, and the Australian sylviid-muscicapid genus *Stipiturus*, and perhaps some others, has 8. *Turdus aureus* is said to have 14. *Zeledonia* has 10. In the following the number is also 12: Trogoniformes, Strigiformes (except *Micropallas* with 10), and the suborder Lari. In the Piciformes the number is normally 12 but the Capitonidae, Rhamphastidae, and the indicatorid genus *Prodotiscus* have 10. The outermost rectrix is much reduced in Picidae. The Coraciiformes also have mostly 12 except for some Momotidae, the Upupidae, and Phoeniculidae where the count is 10. This later number appears to be uniformly found in Coliiformes, Apodiformes, and Caprimulgiformes. The Cuculiformes possess 10 except *Crotophaga* and *Guira* which have only 8. The Psittaciformes have generally 12 with 14 in *Oreopsittacus*. As we proceed downward in the scheme of classification, following Wetmore (1951) the numbers of rectrices become more diverse within the groups and the available information less full. In the suborder Columbae the number varies between 12 and 20, in the Alcae 12 to 18, in the Charadrii 10 to 28.

Restricting our attention from here on to American groups, we find the following recorded: Pelecanidae 22 to 24, Gaviidae 18 to 20, Heliornithidae 18, Spheniscidae 16 to 20, Anatidae 12 to 24, Sulidae 12 to 18, Procellariiformes 12 to 16 (14 in *Fulmarus*), Phaëthontidae 12 to 16, Phoenicopteridae 12 to 16, Phalacrocoracidae 12 to 14 (*P. carbo* 14, *P. aurita* and *P. olivacea* 12), Anhimidae 12 to 14, Fregatidae,

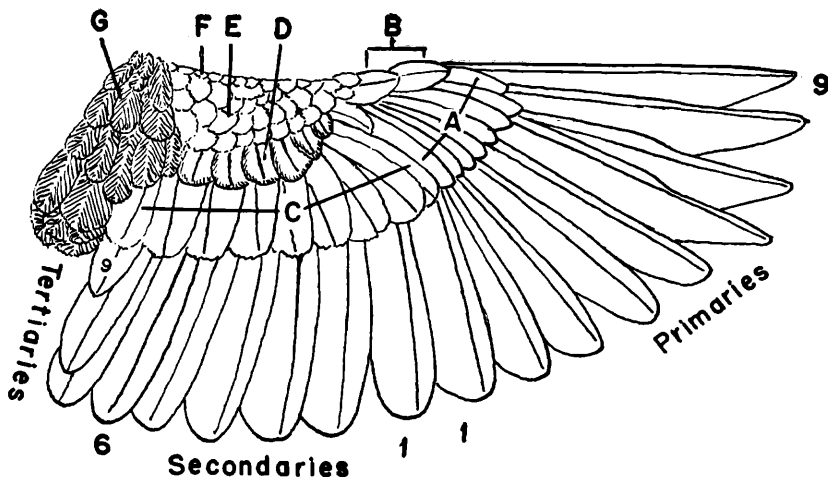


Fig. 4. Upper surface of wing. A-greater primary coverts, B-alula, C-greater secondary coverts, D-middle secondary coverts, E-lesser coverts, F-marginals, G-humeral area. The third tertiary is numbered as the ninth secondary.

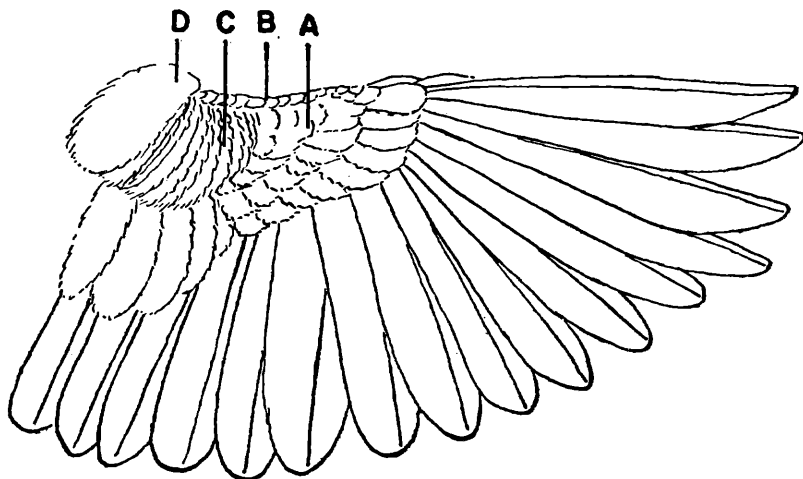


Fig. 5. Under surface of wing. A-under wing coverts, B-marginals, C-pteryla patagialis corridorii, D-axillars.

Cochleariidae, Ciconiidae, Falconiformes (14 in *Gymngyps*), Cracidae, Gruidae, Aramidae, Eurypygiidae, Cariamidae 12, Psophiidae 10 or 12, Opisthocomidae 10, Phasianoidea 8 to 32, Rallidae 8 to 14 (14 in *Fulica*), Tinamidae 8 to 12, Ardeidae 8 to 12 (8 in *Ixobrychus*, 10 in *Botaurus*). Rheidae and Colymbidae lack rectrices. The ostriches, *Struthio*, have the highest recorded count, 50 to 60.

It is customary to number the rectrices from the central pair outward. This follows the usual order of molt in passeriform birds. Even in this order there are exceptions. The creepers (*Certhia*) (and the woodpeckers) start with the second rectrices, proceed outward, and replace the central pair last. *Molothrus* and *Quiscalus*, at least in the postjuvenile molt, appear to show the order 5, 6, 4, 3, 2, 1. In other avian orders there is a variety of sequences. The Mayrs (1954) have discussed the owls. See also Heinroth (1898) and Friedmann (1930).

Wing: an assemblage of pterylae comprizing the coverts of the upper and lower surfaces, the axillaries, and the wing quills (remiges). (Figs. 4, 5)

The lesser coverts are a few rows of small feathers on the upper surface and largely confined to the anterior patagium. The lesser and middle coverts together are often popularly called the "shoulder" although this area extends approximately from the elbow to the wrist.

The middle coverts are (on the extended wing) a single row of larger feathers posterior to the lesser coverts. Their relation is mostly to the secondaries. The overlap of these feathers is reversed in certain groups of birds: Passeriformes, Picidae, Cuculidae, and perhaps others. In such cases the inner vane of one feather overlaps the outer vane of the next feather. When the overlap is normal (outer vane over inner vane) the middle coverts may not be distinguishable from the lesser coverts and are sometimes considered to be absent.

The greater coverts are a single row of feathers much larger than the middle coverts and posterior to the latter. Their overlap is normal. These coverts fall into two series. The more distal pertains to the primaries. Their number usually appears to be one less than that of the obvious primaries because the covert of the outermost large primary is very small and concealed. The proximal series usually consists of one covert feather for each of the secondaries (plus tertiaries).

In general the greater primary coverts have the structure of quills and each is normally molted when and if the corresponding primary is molted. The greater secondary coverts are structurally contour feathers and are molted nearly simultaneously at molts when the lesser coverts are replaced, regardless of molt of the secondaries. Quite commonly the greater coverts are shed before the middle coverts in the course of molt.

The fore edge of the wing from the body to the base of the outer primary is covered by a few rows of very small feathers called marginals which are related to the lesser coverts of both surfaces of the wing. They may be, in part, distinctively colored.

The under wing coverts are divisible into several parts. Close against the body and arising near the front of the wing are the few rather large axillaries. In some plovers they are quite elongate.

Next beyond the axillaries and arising immediately behind the marginals is a row of rather long, falcate feathers set with their planes parallel and nearly at right angles to the surface of the wing. These feathers make up the pteryla patagialis corridorii. They are one of the later parts of the juvenile plumage to appear.

Still further out are a few rows of small feathers similar to the lesser

coverts of the upper surface. These may be called the lesser under coverts.

Behind the feathers so far mentioned are the inverted under coverts. In passerines, those related to the primaries and about three of the outer secondaries are in two rows while the inner ones, related to the remaining secondaries, are in one row and elongate. The term 'inverted' refers to the fact that these feathers have their concave faces, which are toward the body in the case of other feathers, exposed. This comes about from their origin on the dorsal face of the wing and subsequent migration to the ventral surface.

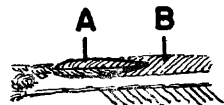
At the fore edge of the wing and attached at the wrist is the alula or bastard wing. This is mainly covered by small feathers which are probably lesser coverts. Except in some hummingbirds, it also bears one to four larger feathers which resemble short quills. Their exact homology with other wing feathers is uncertain. In the Red-eyed Towhee their behavior at the post-juvenal molt suggests that they may be middle coverts. Further observations on the behavior of the alular quills during molt are desirable. The alula is wanting as such in some flightless orders.

The only feathers remaining to be treated are the remiges. They are usually treated as two series, primaries and secondaries, but the latter series gives evidence of heterogeneity.

The quills related to the hand and digits (except thumb) are the primaries. The primitive number is not entirely certain but is most probably 12, which number is only exceeded (among living birds) in *Struthio* which has 16. The reduction in number comes about by reduction in size and eventual loss at the outer end of the series. The number of primaries in various groups is: Rheidae, Colymbidae, Ciconiae, Phoenicopteridae, 12; Gaviidae, Procellariiformes, Pelecaniformes, Ardeidae, Anseres, Falconiformes, *Grus*, Charadriiformes, Columbidae, Strigiformes, Alcedinidae, 11; Galliformes, Psittacidae, Cuculiformes, Caprimulgidae, Apodiformes, Trogonidae, Picidae, many Passeriformes (including all of suborder Tyranni), 10; some Passeriformes (at least the following families: Alaudidae in part, Hirundinidae, Motacillidae, Bombycillidae, Dicaeidae, Pardalotidae, Zosteropidae, Vireonidae in part, Coerebidae, Drepanididae, Parulidae, Ploceidae in part, including *Passer*, Icteridae, Tersinidae, Thraupidae, Catamblyrhynchidae, Fringillidae), 9; some flightless rails, 8; Dromaeidae 7; Apterygidae 4; Casuariidae 3.

The outer primary is reduced or very small in the following: Charadriiformes, Strigiformes, Alcedinidae, Picidae. A minute outer primary in addition to the above counts is present in *Coccyzus* and the 9-primaried passerines (Fig. 6). I have found what appears to be the eleventh primary in *Cyanocitta cristata* as did Miller (1928) in *Lanius ludovicianus*.

Fig. 6. Base of ninth primary of a fringillid. A-tenth primary, B-ninth primary.





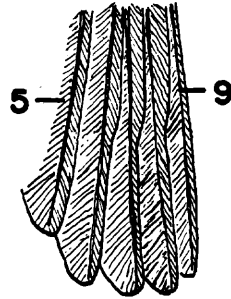


Fig. 7. Part of primaries 5 to 9.

It is not always possible to tell from the literature whether the counts of primaries include or exclude a rudimentary outer one or even whether it has been carefully looked for. Whether the outer one is short enough to omit may also be a matter of opinion as in the *Bombycillidae*. The ancient fossil, *Archaeopteryx*, may have had about 14 primaries.

The primaries are numbered from the innermost outward following the usual order of molt. The *Gaviidae*, *Colymbidae*, *Anhinga*, *Phoenicopteridae*, *Anseres*, *Gruiformes*, and *Alcidae* shed all the quills simultaneously. See Heinroth (1898).

Figure 7 illustrates the primary formula, a statement of the relative lengths of the longest primaries, in this case (*Carpodacus p. purpureus*) 5 to 9. This primary formula is: 7=8, 9, 6, 5. Note also that the outer vanes of primaries 6 to 8 are emarginate. Similar emargination may occur on the inner vanes or on some rectrices in certain groups of birds.

The secondaries are related to the ulnar (forearm) segment of the wing. There is still some debate as to which, if any, of the inner members of the series form a separate set of tertiaries. Some authors would restrict the latter term to the posterior humerals. The feathers are quite certainly not remiges. On the other hand there are a few inner quills which normally molt in the reverse direction from the outer secondaries. For our purposes we can consider all ulnar quills as secondaries, including similar feathers arising in the immediate vicinity of the elbow.

The number of secondaries is rather dependent on the relative length of the ulna. It varies from six to at least 37 among flying birds. *Gaviidae* have 22 or 23, *Colymbidae* 15 to 21. The larger procellariiform birds show the highest numbers, up to 33 in *Puffinus* and to, at least, 37 in *Diomedea*. The *Anatidae* have 15 to 24. The *Charadriiformes* have uniformly 11. *Columbidae* possess 11 to 15. In the *Strigiformes* there are 11 to 18, *Tyto* having 15. The *Caprimulgidae* have 12 to 14, with 13 in *Chordeiles*. The *Apodidae* have 8 to 11, while the *Trochilidae* have only 6 or 7. The *Alcedinidae* have 11 to 14 and the *Picidae* 11. The *Cuculidae* agree with the *Passeriformes* in having 9. *Menura* in the latter order has 10. In the 'ratite' orders the number of secondaries varies from 3 in *Casuaris* to 20 to 23 in *Struthio*.

The secondaries are numbered from the outer one inward. Their molt may start at more than one point. Only one of these points is essentially invariable, namely, the outer or first secondary. Other starting points are the fifth and the eighth, according to the group of birds.

In Passeres the first and eighth secondaries are often dropped about the same time. The molt progresses inward from both points and then outward from the eighth to the seventh or sixth. It is just because of this plurality of starting points and difference of direction that I consider the secondaries to be heterogeneous. The order of molt in the seventh to ninth secondaries seems to resemble that of some of the rows of coverts. Careful observations on the order of molt of all remiges at both postjuvinal and postnuptial molts are still desirable.

It should be noted that my views on which feathers are to be called humeral and which tertiary are rather different from those of Miller (op. cit.). A resolution of the differences will depend in large part on more detailed information with regard to their molting behavior.

With a few exceptions, the facts which I have brought forward can be observed and confirmed on the live bird in hand. In place of documentation for each individual statement I give below a literature list including most of my sources and which will help those who wish to go further.

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