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PTERLYOGRAPHY AND MOLT OF THE ALLEN HUMMINGBIRD

By ELMER C. ALDRICH

Knowledge concerning pterylography of any avian species is a necessary part of an effort to study its plumages and molts. The increasing attention given matters of aging according to plumage criteria and to the phenomenon of sexual dimorphism also calls for precise background information concerning pterylography. Furthermore, this aspect of external morphology continues to serve in examinations of phylogenetic relationships.

Among hummingbirds, there is information on pterylography available for only one species, the Giant Hummingbird (Patagona gigas) of South America, provided by Thompson (1901). Certain critical details were, however, not considered by Thompson, and in any event the size and diversity of the family Trochilidae is such that a number of species representing different sections of the family must be examined to ascertain the basic features of feather-tract patterns among its members. It is therefore the objective of this paper to describe the pterylography of the Allen Hummingbird (Selasphorus sasin), a species occurring primarily in coastal California but representing a genus with eight members distributed over western North America and southward to Panamá. Certain facts concerning molt are also reported, but these must be regarded as only preliminary results because the series of specimens available at the time of the study was relatively small and not representative of all seasons.

ACKNOWLEDGEMENTS

The studies reported here were carried out in 1937–38 under the direction of the late Joseph Grinnell as part of a thesis investigation (Aldrich, 1939). A portion of the thesis concerned with nesting of the Allen Hummingbird has already been published (Aldrich, 1945). That this additional part is now prepared for publication is largely due to the interest and assistance of Dr. Frank A. Pitelka and Mr. Francis S. L. Williamson, to whom I express my appreciation. For assistance in the preparation of the drawings, I am indebted to Mrs. Alice Aldrich Labellarte.

MATERIALS AND METHODS

Specimens of three males and two females used for the study of pterylography were taken in the San Francisco Bay region between the dates of March 4 and May 25, 1938. Drawings were made from these birds after their feathers were clipped and while the birds were fresh. Feathers were cut near their bases, usually one at a time, and never more than about three at one clipping. All feathers were segregated according to tracts and placed in labelled envelopes so that the total number of feathers for each specimen examined might be obtained. Clipped birds were kept moist with wet cotton to facilitate mapping of the feathered areas. The larger feathers of the wing, the primaries, secondaries and their greater coverts, were not clipped, but the webs were sheared from the shafts. This procedure was essential to retain, for drawing, the angles of insertions of the feather bases in the skin.

The most intensive work was done on female specimens. This was rechecked with study of three males, and differences between sexes were noted. Most of the differences in shapes of tracts were a result of the differences between sexes in size and proportions. Drawings and descriptions are based on females. However, where differences occur in the the extent of a tract or in types of feathers within that tract these are mentioned in the remarks on the tract in question.

The nomenclature here used for the regions of the tracts (figs. 1 and 2) is essentially that employed by Boulton (1927) and Miller (1931). No effort is made to provide a

detailed textual description; rather the objective is to present drawings with text serving as a supplement that will stress certain general features and provide comment on relevant published work.

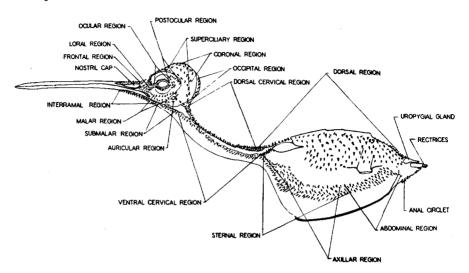


Fig. 1. Pterylography of Selasphorus sasin, lateral view, approximately $\times 2$.

Capital tract.—The frontal region extends from the base of the bill above and anterior to the cap covering the nostril posteriorly to an imaginary line running between the middle of the orbits (figs. 1 and 2). Laterally the frontal region is separated from the loral region anteriorly, and from the supercilliary region more posteriorly, by the superciliary apterium, which begins at the base of the nostril cap, courses posteromedially to the dorsal border of the orbit, and extends to the posterior end of the coronal region. The frontal region encloses the frontal apterium, a narrow space 6 mm. long and 1 mm. wide. This apterium occupies a longitudinal depression between the dorsal borders of the orbits.

Thompson (1901) finds a similar frontal apterium in the Giant Hummingbird (Patagona gigas). He notes, however, that in this species the space continues forward to the culmen, whereas in the Allen Hummingbird, there is a 3-mm. feathered interval between the apterium and the base of the exposed culmen. In other respects it is quite similar. Nitzsch (1867:87) failed to note this apterium in Trochilus moschitus. Shufeldt (1890), however, states, "This [apterium] is well marked in all species [of hummingbirds] which I have thus far examined, moreover, it is absent in the Swifts and Swallows." Other birds found to have the median frontal apterium seem to be in closely related orders as well as in groups farther distant. Thompson (1901:315) found it in Caprinulgus macriurus, and he refers to Clark's (1894) account of it in Phalaenoptilus nuttallii, both members of the Caprimulgiformes, an order closely related to hummingbirds. Miller (1931) describes the frontal apterium of the Loggerhead Shrike (Lanius ludovicianus) and attributes its presence to the elevation of the maxillaries and nasals into a median crest coincident with the production of a raptorial bill. Burt (1929:433) describes in detail the frontal apterium of woodpeckers and correlates this space with the extension of the hyoid apparatus which perhaps causes pressure on the skin beneath, not permitting feathers to grow. This seems a reasonable correlation in woodpeckers as he found the frontal apterium of Ceophloeus pileatus asymmetrically placed and deviating to the right, immediately above the extended hyoid.

The occurrence of the frontal apterium in the Allen Hummingbird is difficult to link with any of these associated structural arrangements even though the hyoid processes are long as in woodpeckers. The ends of the ceratobranchial bones extend into the frontal apterium a relatively short distance (about 1 mm.). Burt found a similar situation in Sphyrapicus where the apterium was present beyond

the termination of the hyoids, and he attributes this condition to an evolutionary reduction in the length of the hyoids. The only place in the Allen Hummingbird where feathers occur in the skin overlying the ceratobranchials is just posterior to the frontal apterium where there is a band of feathers about 2 mm. wide; such overlap is not found in *Sphyrapicus*. Posterior to this band of coronal feathers, those of the occipital region seem to lie in rows parallel with the ceratobranchials over the skull. The frontal apterium, since it occupies a depression, is easily covered in the adult bird by surrounding feathers. The skin of the frontal apterium is thin and closely adherent to the skull.

Nearly all the feathers of the occipital, coronal, and frontal regions possess the same general color and structural pattern. Exceptions to this are the dense, short anterolateral feathers of the frontal region in the adult male which are similar to the orange feathers of the loral region in color and structure. The feathers of the frontal region are placed in no apparent order whereas those of the occipital and coronal regions are in single rows with the feathers less dense than are those of the frontal region.

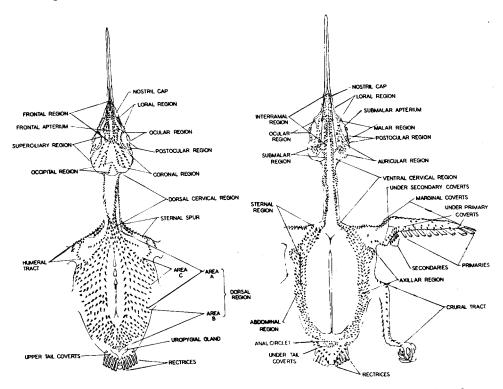


Fig. 2. Pterylography of Selasphorus sasin, dorsal view at left, ventral view at right; approximately $\times 2$.

The feathers of the posterior part of the head possess a relatively larger downy basal portion than do those anteriorly. The short feathers above the nostril have a downy portion less than one-tenth the total feather length, whereas those of the occipital and coronal regions may be one-half downy. On some feathers there was an aftershaft, consisting of three or four filaments branching distally, which was one-half the length of the main shaft. These appeared to be essentially the same morphologically as the downy portion of the feather proper.

Spinal tract.—To simplify description, this tract will be subdivided into two regions only (cervical and dorsal) instead of the customary four (cervical, interscapular, dorsal, and pelvic). The cervical region is essentially a single row of feathers connecting the auricular and superciliary regions posteriorly with the dorsal tract. On the neck proper, they are inserted on a longitudinal fold in the

skin that occupies a dorsal position on each side of the neck. Anteriorly near the base of the skull the dorsal and ventral cervical regions come close together and fuse. This is one of the two places in the Allen Hummingbird where the dorsal and ventral tracts meet, the other place being at the fusion of the malar and submalar regions below the ear.

The dorsal region is a large area of feathers that are inserted on the back from the shoulders to the base of the tail (area A). This region spreads laterally behind the wings (areas B and C) and nearly merges with the posterior tip of the abdominal region of the ventral tract; but at that point it remains distinct because of the white, downy character of the feathers of the latter tract. The dorsal region encloses the dorsal apterium, which extends anteriorly between the wing bases and posteriorly to a bony knob of the synsacrum. The apterium is about $2\frac{1}{2}$ mm. wide, tapering at both ends, and about 17 mm. long. A similar apterium occurs in many kinds of birds in widely separated orders, and it is of no ordinal significance. In the Allen Hummingbird, however, the presence of this apterium may be correlated with the presence of hard, bony structures immediately below the skin. Three of the vertebrae anterior to the synsacrum form a hard and sharp ridge. There is a similar but unjointed ridge extending back from them, ending in a rounded point over the center of the synsacrum.

Ventral tract.—In the interramal region, the feathers display a marked sexual dimorphism, as is true of most hummingbirds, since these are the feathers forming the gorget of the adult male. In the adult male of Selasphorus sasin, the iridescent gorget feathers are smallest anteriorly where they may be 0.5 mm. in length; the longest, reaching 12.5 mm., occur posteriorly and laterally, in the "tails" of the gorget on the sides of the neck.

All the gorget feathers of the male have the same color and structural pattern except those shorter than 2 mm. These lack the gray, downy base, whereas the larger ones more posteriorly have a downy base which is at least one-half the feather length. The tips of nearly all the gorget feathers are iridescent, and because of their imbrication, the gray bases and intermediate buffy portions of successive feathers are concealed. The gorget area, then, appears as a solid area made of "scales" of varying shades of red. The predominant color seen on this area in bright sunlight is yellowish red or copper. Close examination with different angles of light may reveal shades of greenish-yellow or purplish red. The color of the tips in transmitted light is brownish gray.

Structural colors of the Allen Hummingbird are not here discussed in detail; reference may be made to Allen (1896), Mallock (1911), Strong (1903a, 1903b, 1905), Gadow (1882), and Newbigen (1896). In figure 6 the character of the refracting structure of the naked part of the barbule is shown. It is the recurved tip of the barbule with hooks that tends to hold the adjacent barbs together, and the greater part of the barbule serves as a color-producing surface. The structure of the iridescent barbs will be discussed in the section on molt and wear.

The interramal area of the adult female has a few iridescent feathers which are similar to those of the male. The number of these occurring on the throat of adult females is highly variable (from one to twenty-two feathers recorded), and for field work on nesting birds the amount of red was used to distinguish individual females. Surrounding the red gorget feathers of the adult female are feathers of similar pattern but with the terminal band smaller and iridescent green instead of red. The numbers of these are also highly variable. The intermediate band of the individual throat feathers of the female is usually pure white instead of deep buff, as in the adult male; this gives a white background for the gorget feathers. The gorget feathers of all Allen Hummers have buffy tips when new, but these tips are worn away rapidly.

Immediately posterior to the interramal region is the submalar region which merges indistinguishably with the malar region below the ear opening and marks a union of the dorsal and ventral tracts. Extending posteriorly from the submalar region to the sternal region is the ventral cervical region which is a group of feathers inserted in folds of the skin of the neck. Posteriorly the ventral cervical region unites with the sternal region at the anterior base of the large pectoral muscle mass. At the point of union there is a branch of the ventral tract that merges eventually with the marginal coverts of the wing, which are different in color. Feathers of this small group I have termed the sternal spur. They are similar to those of the axillar region but smaller.

The sternal region along nearly its entire length is contiguous with the feathers of the axillar region which are characterized by a different color pattern and by their angle of insertion. The feathers of the sternal region are inserted acutely to the skin and are directed anteromedially, serving to

cover the large naked place over the bulging sternum and pectoral muscles. There is a protrusion under the wing of the axillar area; the feathers of this region are inserted posteromedially and cover the posterolateral part of the bird.

The posterior ends of the axillar and sternal regions merge with the markedly different feathers of the abdominal region. These latter feathers are inserted in the same fashion as those of the axillar region and cover the base of the tail. When the bird is flying or perched, the feet are drawn into this downy mass.

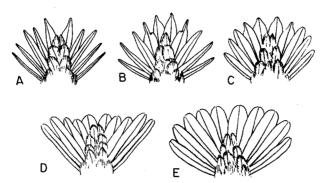


Fig. 3. Ventral views of spread tails of western American hummingbirds showing sexual dimorphism in size and form of rectrices. A, Selasphorus sasin, male; B, Selasphorus rufus, male; C, Selasphorus sasin, female; D, Calypte anna, male; and E, Calypte anna, female.

Caudal tract.—The rectrices are ten in number and are among the most specialized feathers found in this order of birds (fig. 3). They are specialized for the production of sound in the course of rapid movements during flight displays. The rectrices are inserted at the end of the uropygium which is broadly pointed at an angle of about 95 degrees. On the dorsal side at the point of insertion there are one or two filoplumes which are tufted at the tip with a few barbs. These filoplumes average about 6 mm. in length and lie along the dorsal surface of each rectrix. The purpose of these is obscure.

All rectrices have a rachis and vane that is curved to a greater or lesser degree. This curvature evidently helps to make possible some of the noises produced by the tails of hummingbirds. Measurements given in table 1 show the relative sizes and shapes of the plucked rectrices of an adult male and female taken in good plumage in March, 1938. The bend of the rachis is measured as the distance in millimeters from the center of the rachis to a straight line (chord) from the tip of the calamus to the inner tip of the rachis.

Table 1

Size and Relative Bending of Rectrices of the Allen Hummingbird 1

	Length		Maximum width		Bend of rachis	
Rectrix	Male	Female	Male	Female	Male	Female
1st	7.7 mm.	7.6 mm.	8.0 mm.	8.8 mm.	0.3 mm.	0.4 mm.
2nd	6.3	7.5	6.2	6.0	0.7	1.0
3rd	6.5	7.2	3.2	4.5	0.7	1.6
4th	3.7	5.1	2.4	3.4	1.5	1.9
5th	2.4	3.3	2.2	2.6	2.1	2.1

¹ In assessing differences between sexes here measured, the reader should remember that females of S. sasin are slightly larger than males in both weight and linear dimensions (Pitelka, 1951).

The rectrices of an Allen Hummer vary in size with the sex and age of individuals. These differences are shown in figure 3. The bases of the vanes of all the rectrices are slightly downy and the color of the shafts corresponds to the color of the adjacent vanes. In the following descriptions the rectrices are numbered from the center to the outside.

Rectrices of adult female: Rectrix 1 rounded, spear-shaped, and slightly broader than that of male, tending when worn late in summer to be more sharply pointed; rachis and vanes slightly bowed ventrally (fig. 3). Ventral bowing typical only of first rectrix and to lesser degree of second. All other rectrices of both sexes lie approximately in horizontal plane. Terminal 9 mm. of rectrix iridescent black; rest of feather orange. Rectrix 2 elipse-shaped, becoming slightly pointed in late summer. Markings approximately same as rectrix 1 but in some females small and indistinct white edging occurs. In adult females this edging occurs more frequently on inner vane. Rectrix 3 bent, narrow, ovalshaped, tending to be slightly broader distally. White tip measures on rachis about $4\frac{1}{2}$ mm. long and is wider on inner vane. Proximal to white tip, rectrix 3 has black band measuring 7 mm. on the rachis. It differs from white tip in being broader on outer vane. Remainder of feather orange. Rectrix 4 of similar shape to 3 but relatively narrower. Color markings also similar to rectrix 3 but boundaries between color areas more perfectly transverse. Rectrix 5 same as 4 but smaller, more bent, and relatively narrower.

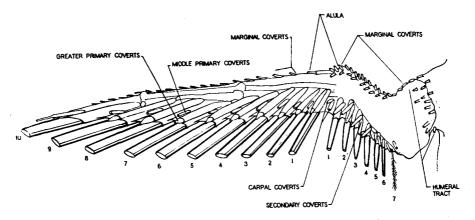


Fig. 4. Pterylography of the wing of Selasphorus sasin, dorsal view, approximately $\times 5$.

Rectrices of adult male: The rectrices of the male differ greatly in color from those of the female, all the orange areas being darker. Rectrix 1 about same length and breadth as that of adult female, the widest portion basally, and tapering to tip. With wear, tip may become constricted and thus sharper. A black marking (about 10 mm. long) of varying shape present, running longitudinally to tip. Boundaries of this mark well defined. Remainder of feather dark orange. Rectrix 2 a smaller duplicate of 1 but with relatively broader and larger black marking at tip. Rectrix 2 of adult male of S. rufus has characteristic notch near tip on inner web. Rectrix 3 about same length as 2 but distinctly narrower with nearly parallel sides. Tip of outer vane black for 12 mm., inner vane for about 5 mm. Rectrix 4 smaller and relatively narrower than 3, and more bent medially. Black markings similar, but with boundaries less distinct. Rectrix 5 smallest, narrowest and most bent of all the rectrices. Very sharp terminally; this accentuated by wear in late summer. Outer vane extremely narrow and black distally for nearly three-fourths its length; inner vane black distally but for one-fourth its length. It is rectrix 5 that produces most of the noise in the power dive.

Rectrices of immature individuals: After young leave the nest, and before the postjuvenal molt, the rectrices of both sexes of the young resemble closely those of the adult female. I have detected no age difference in the rectrices of the females, but the outer rectrices of the immature males are narrower and the orange color is darker, resembling the color found in the adult male.

Alar tract.—The first six primaries are attached to the fused metacarpals and are situated on the dorsal side (fig. 4). Primary 1 is inserted nearly perpendicular (75°) to the fused metacarpal bone, but progressing distally, the primaries are inserted more acutely until number 6 is at an angle of about 15°. Primaries 7, 8, and 9 are inserted against the posterior border of the bone of the third digit. These all come off at an angle of about 20°. The tenth primary is inserted along the entire posterior border of the second phalanx of the second digit and is bound parallel to it. All the primaries are held

together with a slightly flexible webbing which extends into the region of the secondaries, decreasing in width proximally.

Primary 9 is the longest (33.6 mm. in a male, 31.0 mm. in a female), and in adults of both sexes and in immatures the ninth and tenth protrude an equal distance to form the point of the wing. The wing is more rounded in the females and immature individuals than in adult males, partly because the last three primaries are more curved than those of males and partly because primaries 4 to 8 are relatively longer and thus round out to a greater extent the posterior margin of the wing.

Primaries 1 to 6 have a nearly straight shaft. Primaries 8 to 10 are tapered more or less symmetrically. The others are not so pointed, but are truncate and so conform to the trailing edge of the wing. The shaft is broadest in primary 10; the outer vane of this primary is relatively narrow and, in the adult male, is scarcely visible. This provides a sharp cutting edge, which contributes to the

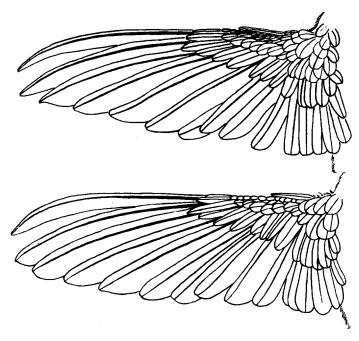


Fig. 5. Outspread wings of Selasphorus sasin to show sexual dimorphism in form and size of remiges; male above, female below; primary 10 pulled forward slightly beyond normal position to show its form and size more clearly; ×2.

rattling noise in the flight of the adult male. The shaft is also coarser near the tip of the outer primary of the adult male. Also assisting in the flight sound is the sharper point on the tenth primary of the adult male. In figure 5 the tenth primary of the adult male is shown to be narrower than that of the female.

The secondaries are six in number. The presence of a greater and lesser carpal covert without a corresponding secondary leads one to suggest that a carpal remex was lost in the course of evolution. The individual on which most of the wing study was made had a vestigial seventh secondary (fig. 4), which had a narrow shaft, lacked barbicels, and was plumaceous and nearly white. A corresponding covert was noted that was larger than the vestigial secondary. The secondaries are inserted at about a 60° angle on the posterodorsal border of the ulnar bone. The feathers and their quill bases are largest distally and decrease in size proximally to the last one.

The alula or first digit is not free from the adjacent skin and bears three or four feathers. The largest feather is 6 mm. long, 1 mm. wide, and is appressed along the anterodorsal edge of the wing.

It is the same color as the primaries, dark brown, and thus stands out amongst the green marginal coverts. The other feathers of the alula are indistinguishable from the marginal coverts.

The greater primary coverts begin proximally as tubes solidly bound to the bases of the primaries. They run parallel to the primaries and fill spaces between them. The middle primary coverts are bound basally to the bases of the greater primary coverts, although they do not always run parallel to them.

The under wing coverts of the primaries are in two rows (fig. 2). The under greater coverts are rigidly attached as are the upper greater coverts between the bases of the primaries; they lie proximal to their corresponding remiges. The under middle primary coverts are all attached on the inserted ends of the corresponding primaries.

The secondary coverts are more loosely bound to their respective feathers than are the primary coverts. A greater and lesser carpal covert are present between the bases of the primaries and secondaries. Secondary 1 has a single covert, whereas secondaries 2 and 3 have two. From the fourth to the seventh, the coverts are arranged in confusing manner. There is evidence of a state of diastataxy between the fourth and fifth secondaries. There appear to be three coverts arranged in no order at the base of secondary 4, one of which may belong to a secondary that has been "lost." Secondary 5 has a covert attached to its base; the covert of secondary 6 is placed proximally to one side. There is a seventh covert regardless of the presence or absence of the corresponding aberrant secondary.

Because of the congested condition in the region of the secondaries the relation of the coverts to them is obscure; here the rows of greater and lesser coverts cannot be distinguished clearly. The cause for this confusion probably lies in the extreme evolutionary reduction that has taken place in the proximal structures of the wing. During this adaptation for a highly specialized flight, the feather rows have probably shifted in relation to one another and have lost their original arrangement.

The under secondary coverts are less confusing than are the upper ones. The two rows remain distinct, but the relation of each covert to its secondary is difficult to make out. There are several additional feathers on the under side of the wing proximal to the under secondary coverts.

The marginal coverts are small distally and larger proximally where they blend with those of the humeral tract and with the sternal spur.

The humeral tract is a single row of feathers running anteroposteriorly along the humerus. The feathers are very similar to those adjacent on the dorsal region of the body.

The feathers of a male and a female were counted. Those of the male totalled 1,459 and those of the female, 1,659.

NOTES ON MOLT AND FEATHER WEAR

The molt of the Allen Hummingbird was not studied intensively because of the limited number of specimens available. Young were kept in captivity with the hope that they would display the complete postjuvenal molt, but the longest period they survived after leaving the nest was three months. This aided materially, however, in providing information on the immature plumage. Most of the facts concerning molt and wear reported here were gleaned from museum skins. Selasphorus rufus and Selasphorus sasin were studied together on the assumption that there is little or no difference in the molt cycles of the two species; 164 specimens of rufus and 57 specimens of sasin were available in 1938, in the Museum of Vertebrate Zoology.

Fade and wear of feathers.—Most of the species of hummingbirds in the United States have large iridescent green areas on the upper parts, at least in females. The shades of these greens differ among the species, and of the common hummingbirds in California, sasin may be distinguished from all except rufus by the coppery or golden cast to the green. The golden cast is due in part to the character of the tips of the barbs and to the structural color of the green portion of the feather tip. The iridescent feathers, when new, have buff tips that are loose because of the small number of barbules and barbicels present. These tips are more susceptible to wear and thus serve as an aid in determining the age of the plumage. The buff tips when examined from a distance seem to assist in producing the golden-green appearance and as the tips wear, some of the golden cast is lost. The golden color of the green portion of the feather in time may fade,

leaving a purer green with a slight bluish tint. Evidence of this fading can be seen by examining a well worn feather. The more terminal portion of the green that is exposed to the surface and that is not covered by part of another feather is pure green, whereas that portion of the feather that is concealed by overlap remains golden green.

Wear and molt in the males.—Time of acquisition of the adult plumage is not known, but it is probably assumed sometime in the early part of the calendar year while the birds are on their winter range. Most work was done on a series of 64 adult male rufus; but unfortunately these specimens were all taken between February 29 and July 29, and there is thus a critical gap in the data needed to describe the plumage cycle.

A great variation was found in the degree of wear and fading exhibited by individuals at the same time of year. This may be a result of differences in environment or in activity of individuals rather than a difference in time of molt. However, further study is required on this point.

The green crowns of the adult males were examined for new incoming feathers and none was found, which probably indicates that the crown feathers of adult males are obtained some time between dates that are not represented by the specimens examined. Fourteen specimens representing the period from February 29 to April 7 had crown feathers classed as "new." Specimens obtained after this date, and up to June 6, comprised a heterogeneous group of 37 specimens. In this group occurred individuals with new as well as with partly worn crowns. Eleven specimens from June 6 to July 29 had crowns either partly worn or badly worn. The 17 adult male specimens of sasin taken between March 3 and July 31 exhibit crowns all of which are partly worn.

It is apparent from these data, then, that the chief and perhaps only molt of adult males of *rufus* and *sasin* occurs but once a year and some time between July 31 and February 29, which would be while they are on their winter range.

The gorget, because of its structure, serves better as a criterion of wear than any other feather area. It is necessary at this time to describe the structure of these feathers in order to give a basis for the account of molt and wear.

The iridescent gorget feathers are about one-half their definitive length before they break through the sheaths. The terminal portion that produces the red iridescence occupies but one-third the total length of the feather. Because of the imbrication of these feathers, a mass effect of this brilliant color is produced. The rachis of the gorget feather does not extend to the tip, but the axis of the feather is taken over by the two terminal barbs which are parallel, thus forming the tip of the feather (fig. 6). The terminal part of these feathers is blunt and rounded. The iridescent color of the gorget feathers is produced by the proximal parts of the barbules. This part in each barbule is smooth and rod-like and is devoid of barbicels. Distal to the specialized, color-producing part is a tip (pennulum) that is curved nearly at right angles to the basal part of the barbule. Barbicels occur on the pennula only and serve to hold together the barbules on one side of a barb, but they do not unite the barbules of two adjacent barbs.

In studying the wear of gorget feathers, three stages were recognized: stage 1 (new), stage 2 (slightly worn), and stage 3 (worn). These are shown in figure 6.

All feathers of the gorget may not be in the same stage of wear at one time. Some parts wear more rapidly than others. This is caused not by differences in structure but is a result of the position of attachment in the gorget area. The feathers of the "tail," or elongated posterolateral part, wear more rapidly than feathers of any other part. This is correlated with the movement of the neck of the bird. These "tails" are long enough to abrade on the bends of the wings during the almost constant turning of the head of the adult males when perched. In most individuals, the gorget "tails" have reached stage

3 by the time the rest of the gorget is at the beginning of stage 2. Most central gorget feathers are worn to stage 3 by late April and early May.

Feathers of the gorget also may fade. This fading makes the gorget slightly more yellowish. The portion of the red tip that is covered by the overlap of another gorget feather remains its original color. A plucked worn feather therefore exhibits an iridescent part that is bicolored. Fading of the gorget feathers can be noticed only on a few specimens that were taken in May, June and July.

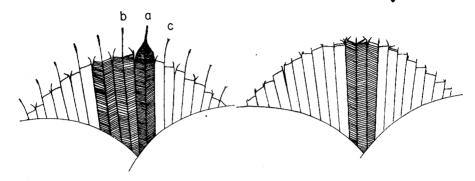


Fig. 6. Portions of two iridescent gorget feathers of Selasphorus sasin, unworn at left, worn at right; stages of wear shown at left are (a) new feather, (b) and (c) intermediate stages of wear; at right, feathers with broken barb shafts are shown in an advanced stage of wear.

Tracing wear and molt in the feathers of regions other than the gorget and crown is more difficult. With age the orange on the breast and belly becomes slightly lighter and less brilliant. The primaries lose their slight metallic sheen and become brownish, and the tips, especially that of primary 1, become ragged and wear to a sharper point. Parts of the barbs break away from the rachis leaving a narrower structure which theoretically should make a flight sound louder than that of unworn feathers.

Fading, wear and molt in females.—Females on their northward migration appear to be growing new feathers. Adult females of rufus and sasin taken in early March have new iridescent red gorget feathers that are in stage 1 or early stage 2 of wear. The throat areas of these same birds also show some gorget feathers that are badly worn and are in stage 3. Moreover, the finding of pin feathers on throats of adult females taken in the summer indicates that there is a slow but continuous molt of feathers of this area while the birds are still on their breeding range or in migration.

With this apparent continuous change in the feathers of the throat area in adult females, there is also a change in its markings. Adult females at the beginning of the year have more red iridescent feathers than later. As molt progresses there is a tendency for the adult to acquire throat patterns resembling those of the immature females. More of the new incoming feathers have small green tips than red ones, and in the series of specimens of *rufus* taken in July and August, it is difficult to distinguish adult from immature females on the basis of throat characters.

Females arriving on breeding grounds have green upper parts which appear fairly worn, and those specimens positively identified as adult females in August and September show greater wear than immature individuals of the same sex.

Postjuvenal molt and acquisition of the adult male plumage.—Because of the similarity between immature and adult females, accurate information concerning the postjuvenal molt could be obtained from study of the males only. Virtually no information

concerning molt is present in the literature, and the time and sequence of changes is not fully known. All immature male specimens in the collection up to October 15 show no sign of normal postjuvenal molt. The period of the postjuvenal molt is therefore not known, but it probably occurs while the birds are on their winter range.

Four male specimens of *rufus* taken between March 21 and April 17 in southern and central California are in a molt which is tentatively considered to be a first prenuptial molt because of the timing relation to breeding. Rectrices of all three are like those of adult males, but one specimen possesses only four adult rectrices (the two central pairs) while the others are immature, with pinkish white terminal spots.

Feathers of the upper parts are new on all four specimens, with the exception of those at the base of the bill and on the forehead. Here the old feathers are very worn and dull brown in color. Numbers of old forehead feathers present vary, and replacement of these apparently is not closely correlated with the general advance of molt on other areas. One of the four specimens that is otherwise farthest advanced in molt actually has more old feathers on the forehead than any of the other three.

Remiges of all four specimens appear to be immature in character, with the two outer primaries broad. They are also noticeably faded to a light brown, and no metallic sheen is present. Males in such transition plumage make a low humming sound characteristic of the females and immature individuals, and not the loud rattle produced by the sharp outer primary of the adult male.

The under parts of all four specimens are in an advanced stage of molt. All show the orange under tail coverts, the orange sides and the pure white lower neck area characteristic of the adult male. One retains some of the whitish feathers characteristic of the central belly of the immature.

Most of the feathers of the throat are like those characteristic of the immature but appear faded due to the loss of much of the green on the feather tips. This makes for a more buffy appearance of the throat. In three of the specimens there are present both new and old iridescent red gorget feathers, and one has four of the old gorget feathers and none of the new. All four specimens, however, have new gorget feathers still sheathed. The new feathers usually appear first on the posterocentral portion of the gorget area.

Of interest is a fifth male of *rufus* taken on April 16, 1904, at Pasadena, California, that also is in the prenuptial molt. It is typical of adult males in all respects, including the sharp outer primary, but the gorget area appears new, and there are many pin feathers in it. Replacement in the gorget area, therefore, probably occurs first centrally and posteriorly, and then proceeds anteriorly.

Still another male of *rufus* observed on April 7, 1938, in Berkeley, California, indicates the occurrence of the first prenuptial molt. It was observed closely at a distance of eight feet and appeared to be coming into first breeding plumage and hence was similar to the specimens just described. Noticeable was the well worn patch of feathers on the forehead and crown. These feathers were grayish brown contrasting with the green present more posteriorly. The throat appeared to be almost solid light buff. The flight sound was distinctly like that of females, and this fact was strengthened by the contrast noted between it and an adult male hovering five yards away.

Thus, while there appears to be a single annual complete molt in adult males, molt in females and particularly first-year birds of both sexes appears to be more protracted, complex, and diffuse. For *rufus*, which has a larger and more northern distribution than *sasin*, there is evidence for a fairly intensive prenuptial molt in first-year birds. This could conceivably be the last phase of a protracted and interrupted postjuvenal molt.

SUMMARY

The pterylography of the Allen Hummingbird (Selasphorus sasin) is described and comparisons are made with one other hummingbird species and also with a few passerines and woodpeckers for which adequate information is available. Frontal and dorsal apteria occur; the former may be characteristic of the Trochilidae and other closely related groups. The rectrices, 10 in number, are specialized in form and structure to serve in production of flight sounds and they are sexually dimorphic. This is also true of the primaries, which are 10 in number. An irregularity in the serial relations of secondaries and their coverts suggests evolutionary loss of some secondaries and a considerable degree of modification in this sector of the wing.

Successive degrees of plumage wear are described and the possible uses of these characteristics as criteria of sex and age are suggested. Certain observations on molt based on specimens of *Selasphorus sasin* and *Selasphorus rufus* are presented. Postjuvenal molt occurs some time after mid-October. In *rufus*, at least, a first prenuptial molt (possibly the last phases of a protracted postjuvenal molt) occurs in first-year males, but otherwise there is no evidence for more than one complete annual molt. This occurs between October and February on the wintering grounds. In females there are local body areas, such as the throat, which appear to molt over a longer period and in a more diffuse manner than in males.

LITERATURE CITED

Aldrich, E. C.

1939. Natural history of the Allen hummingbird (Selasphorus alleni). M.A. thesis, University of California, Berkeley.

1945. Nesting of the Allen hummingbird. Condor, 47:137-148.

Allen, I.A.

1896. Alleged changes of color in feathers without molting. Bull. Am. Mus. Nat. Hist., 8:13-44. Boulton, R.

1927. Ptilosis of the house wren (Troglodytes aedon aedon). Auk, 44:387-414.

Burt, W. H.

1929. Pterylography of certain North American woodpeckers. Univ. Calif. Publ. Zool., 30:427-442.

Clark, H. L.

1894. The pterylography of certain American goatsuckers and owls. Proc. U.S. Nat. Mus., 17:551-572.

Gadow, H.

1882. The coloration of feathers as affected by structure. Proc. Zool. Soc. London, 1882:409-421.

1911. Notes on the iridescent colors of birds. Ann. Rept. Smithsonian Inst., 1911:425-432.

Miller, A. H.

1931. Systematic revision and natural history of the American shrikes (*Lanius*). Univ. Calif. Publ. Zool., 38:11-242.

Newbigen, M. I.

1896. Observations on the metallic colours of the Trochilidae and the Nectariniidae. Proc. Zool. Soc. London, 1896:283-296.

Nitzsch, C. L.

1867. Nitzsch's pterylography, translated from the German, edited by P. L. Sclater (Ray Society, Robt. Hardwicke, London).

Pitelka, F. A.

1951. Ecologic overlap and interspecific strife in breeding populations of Allen and Anna hummingbirds. Ecol., 32:641-661.

Shufeldt, R. W.

1890. Studies of the Macrochires, morphological and otherwise, with the view of indicating their relationships and their several positions in the system. Jour. Linn. Soc., 20:299-395.

Strong, R. M.

1903a. Iridescent feathers. Science, 17:483-484.

1903b. Metallic colors of feathers from the neck of the domestic pigeon. Mark Anniv. Vol., pp. 263-277 (Henry Holt Co., New York).

1905. The evolution of color producing structures in birds. Science, 21:380-381. Thompson, D'A. W.

1901. On the pterylosis of the giant hummingbird (Patagona gigas). Proc. Zool. Soc. London, 1901:311-324.

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