

THE PTERYLOSIS OF THE CALIFORNIA CONDOR

WITH FIVE ILLUSTRATIONS

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The vultures of the New World show their distinctness from other diurnal birds of prey in a number of ways. Recently, their pterylosis has been compared with that of other falconiforms by Compton (Univ. Calif. Publ. Zool., vol. 42, 1938, pp. 173-212). He showed that the feather arrangement in the Falconiformes falls naturally into three types, known as the accipitrid, falconid, and cathartid patterns. Of the species which he dissected, the Turkey Vulture (*Cathartes aura*) and the Osprey (*Pandion haliaetus*) showed the cathartid arrangement. This led to the conclusion that the Osprey belongs to the suborder Cathartae. Manifestly it is desirable to determine how uniform the pterylosis may be among the New World vultures (family Cathartidae) and to test the applicability of Compton's definition of the cathartid type.

The opportunity to study the feather tracts of the California Condor (*Gymnogyps californianus*) came about through the efforts of Mr. J. R. Pemberton and Mr. Perry Sprague. On January 1, 1937, Mr. Sprague came upon an adult condor that was gorged with food, unable to fly, and apparently sick. This was on the Tejon Ranch east of Bakersfield. The bird was taken to ranch headquarters and fed upon meat and squirrels, but it disgorged everything it ate and became weaker. Finally it died on January 10, the nature of its infirmity as yet undetermined. Mr. Pemberton learned of its death and took immediate steps to send the bird to the Museum of Vertebrate Zoology at Berkeley. Upon its arrival it was embalmed, thus assuring a chance to study the anatomy of this vanishing species. We are greatly indebted to Mr. Pemberton and Mr. Sprague for the essential parts they played in making this study possible and for the opportunities for further investigations that lie before us.

To facilitate reference to Compton's work, we follow his nomenclature and plan of description. At the end of the discussion of each feather tract is a summarized comparison of *Gymnogyps* and *Cathartes*. Doubtful points relative to the pterylosis of *Cathartes* have been rechecked by examination of alcoholic specimens.

Capital tract.—The head feathering, though much reduced, is unequally developed in different regions. There is a transverse band of small plumaceous feathers, 6-12 mm. long, that occupies the frontal, anterior superciliary, and loreal regions. The frontal and rostral regions are well feathered from slightly in front of the nostril to the level of the posterior margin of the eye along the median line. Laterally, the feathered area is restricted and sparser, passing ventrally as a band between the eye and the nostril to merge with the loreal region. In parts of the frontal region the feathers almost completely obscure the skin. The feathers of the rostrum are arranged in a whorl which centers between the anterior ends of the nostrils.

The feathers of the loreal region are directed posterodorsally in the upper section near the eye, but posteroventrally in the lower section. The loreal region is connected at its ventral margin with another, triangular area beneath the eye. This latter is occupied by more reduced feathers, 4-5 mm. in length, intermediate between those of the loreal region and the vestigial hair-like feathers of the other parts of the head. This area below the eye occupies part of the anterior auricular region and the upper margin of the malar area (see Compton, *op. cit.*, fig. 1, p. 181).

The posterior auricular region consists of a ring of fairly heavy bristles about the meatus, not directly connected with the anterior auricular area. The ring is well developed anteriorly and dorsally.

The coronal region is bare except for two patches of weak bristles, about 2 mm. in length, on either side near its posterior boundary. These are separate from the occipital, postauricular and submalar regions. The similar, sparse bristles of these latter regions form a continuous zone that meets the anterior and posterior auricular regions. The interramal and ocular regions are entirely bare.

Compared with *Cathartes aura*, the capital tract is less uniformly feathered. In both, the loreal region is relatively well feathered, but no feathers are plumaceous in *Cathartes*. *Gymnogyps* lacks eyelashes and many other parts are entirely naked (fig. 65). In *Cathartes* only the normal apteria about the eye, the anterior interramal region and the rostrum are bare, and the vestigial feathers of other areas are less widely spaced.

In the reduction of head covering in the Condor, the boundaries of regions that commonly are recognized in pterylography have been transgressed. Some new delineations have appeared. However, the auricular ring and the loreal region preserve an arrangement typical of falconiforms with normal head plumage.

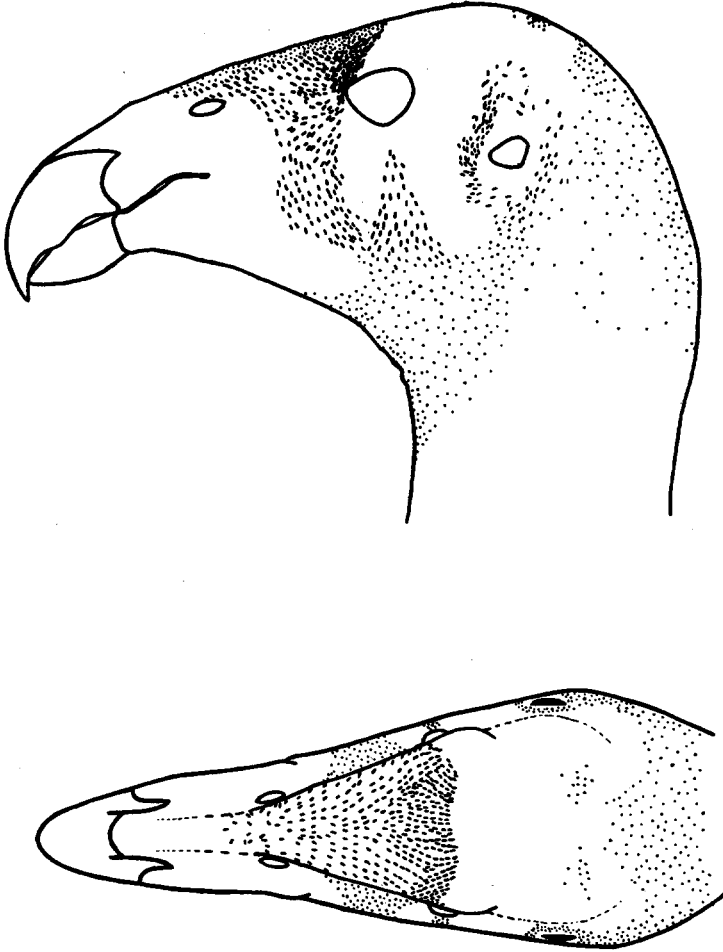


Fig. 65. Drawings of lateral and dorsal surfaces of head of California Condor, approximately $\times \frac{1}{2}$, showing distribution of feathers.

Spinal tract.—The anterior dorsal cervical region is sparsely feathered with vestigial bristles. Dense feathering begins abruptly and forms a ruff whose margin slants posterolaterally from a dorsal anterior apex. The skin for 5 cm. behind the apex is covered with lanceolate feathers. These feathers are set in a whorl with the center on the middorsal line about 4 cm. from the apex. Thus, the lanceolate feathers of the ruff project forward and laterally over the essentially bare neck. Behind the ruff the feathers in the dorsal cervical region are closely set, and increase gradually in length posteriorly. A short distance in front of the shoulder a narrow lateral cervical apertium appears that separates the humeral and ventral cervical areas from the dorsal cervical region.

The interscapular region is continuous with the dorsal cervical region; there is no abrupt change in feather type. At the level of the anterior margin of the shoulder a small median apertium is discernible; it remains narrow posteriorly. The largest feathers of the interscapular region occur in the central posterior section of the region on each side. Each division narrows posteriorly. The

rows of feathers are irregular and the two sides of the region unequal in total number of feathers. Similar irregularity and asymmetry are apparent on many regions of the body. There is no lateral scapular region.

The dorsal region consists of irregularly placed feathers, one or two on either side of the midline at any given level. These are distinctly smaller than those of the interscapular area, but blend with those of the pelvic region which is continuous posteriorly.

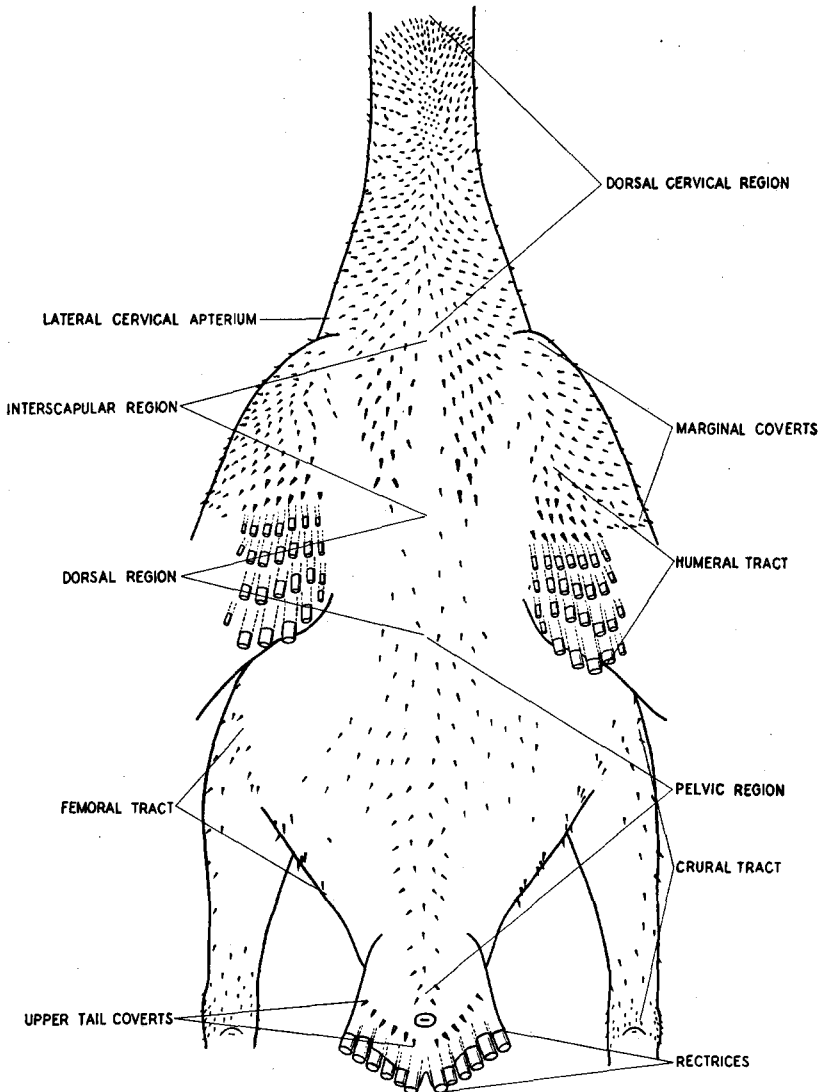


Fig. 66. Tracts and regions of dorsal surface of the California Condor, $\times \frac{8}{11}$.

The pelvic region is a broad irregularly arranged field (fig. 66), which at its maximum width consists of five longitudinal rows on either side of the midline. There are no feathers inserted directly on the midline in front of the free caudal vertebrae. Yet, there is no marked median apterium, the median space being no greater than the normal space between feather rows laterally. Occasional feathers adjoining the midline are inserted so as to extend across the line. The pelvic tract narrows to three feathers at the posterior end of the pelvis and continues as a narrow line of feathers to the

base of the oil gland. Behind the broadest points of the pelvic region are single feathers that connect it with the femoral tract. There is no lateral pelvic region. The feathers of the pelvic region increase in size posteriorly, approximately doubling in length.

Throughout the spinal tract there is heavy down between the contour feathers. Down also covers the apteria lateral to the interscapular and pelvic regions.

The spinal tract of *Gymnogyps* contrasts with that of *Cathartes* in the following points: pronounced ruff; somewhat narrower apterium between the two parts of the interscapular region; interscapular region more gradually tapered; greater irregularity of feather placement (at least in specimen studied); broader, less axial, pelvic region and less distinct median space in this region. The posterior extension of the tract along the base of the tail is closely similar in the two genera. The interscapular apterium is more like that of *Buteo* or *Pandion* than like that of *Falco* or *Cathartes*. In general, however, the tract conforms to the cathartid type, including *Pandion*, as defined by Compton.

Ventral tract.—Posterior to the submalar region there are a very few vestigial feathers in the ventral cervical region, but behind these, there is an area 2 cm. in length that is entirely bare. The feathers of the ruff or collar extend over the sides of the neck from the dorsal cervical region, but the collar is incomplete ventrally. Fairly compact down feathers, 1 cm. long, that perhaps represent reduced contour feathers, occupy the ventral cervical apterium between the ventral ends of the collar and behind the completely naked apterium of the anterior ventral surface. Still farther posteriorly the ventral cervical apterium is devoid of down. The contour feathers of the ventral cervical region are lanceolate, widely spaced, and three or four rows next to the ventral apterium are directed antero-ventrally, although the shafts of some curve posteriorly.

At the shoulder the ventral cervical region is continuous with the humeral tract. The sternal region is continuous ventrally. Anteriorly there is no demarcation of sternal and axillar regions, the feather covering, except for the median apterium, being continuous out on to the ventral surface of the humerus as the subaxillar region (see Compton, p. 191). A short distance from the shoulder the marginal coverts become separated from the subaxillar region by an apterium.

A row of large feathers extends laterally from the axillar region into the axilla proper and on to the arm posterior to the subaxillar rows. At this same level on the body the axillar region becomes separated from the sternal region by an apterium that is entirely enclosed by the ventral tract (fig. 67). This apterium is bounded posterolaterally by a single row of feathers.

All the feathers of the sternal region are to varying degree lanceolate. The feathers in the eighth to tenth longitudinal rows lateral to the midventral apterium at the base of the wing are of almost normal form and some are white on the outer webs. Usually there are two or three such rows of black and white feathers, and then the tract narrows into the two subaxillar rows which consist of feathers that are white except for their shafts. The feathers of the posterior row of the subaxillar region are greatly elongated, maximum 23 cm.; those of the anterior row are no longer than 8 cm. The two terminal members of the row that extends from the axillar region into the axilla proper are elongated, nearly pure black, and not lanceolate. The most posterior row of marginal coverts of the under surface of the humerus is partly white. The downs, which are abundant all through the ventral tract, enclosed sternal apterium, and lateral apteria become gray or whitish in the subaxillar area.

In the abdominal region the ventral tract narrows to a single line of feathers that ends in front of the anus. All the feathers are lanceolate.

The ventral tract of *Gymnogyps* corresponds in most essentials with Compton's cathartid pattern. The extension of a row of axillars through the axilla to the humerus is identical with the condition in *Cathartes*. The major point of difference in *Gymnogyps* is the prominent sternal apterium enclosed between axillar and sternal regions. This apterium, described by Nitzsch (1867, p. 51) as an insular space, was not found by Compton in *Cathartes*. Nitzsch reported it as prominent in the King Vulture (*Sarcoromphus papa*) and as small in the Black Vulture (*Coragyps atratus*). He found it "not particularly perceptible" in the Andean Condor (*Vultur gryphus*) and apparently not particularly distinct in *Cathartes*. Nitzsch had skins only for examination, except for *Sarcoromphus*.

Caudal tract.—The twelve rectrices insert in the uropygium without a patagium. Loye Miller (Condor, vol. 39, 1937, p. 161) reports an abnormal number, seven, on one side of the pygostyle. There are twelve upper tail coverts in a single row. Except for the outer two on each side, these are inserted lateral to the corresponding rectrix, but are directed somewhat laterally. There is no postpelvic region. The oil gland is without feathers of any kind.

There are twelve major under tail coverts, each of which inserts lateral to the base of the corresponding rectrix, except at the outer ends of the series. All tend to be directed laterally to cross the bases of the rectrices. The central coverts are largest.

The single row of minor under tail coverts has three feathers on each side, irregularly placed relative to the major coverts. There are single feathers on either side, representative of another series

of under tail coverts. These lie between the outer members of the series of minor coverts and the anal region.

Similar feathers occur in *Cathartes*, although they were not shown by Compton.

The anal circling is complete and outside it there is a second partial circling on the posterior and lateral sides.

Over the ends of the pubes, anterior and lateral to the anus, are a few reduced feathers, some of them difficult to distinguish from downs. These constitute a weakly developed postventral region.

Gymnogyps differs from *Cathartes aura* in lacking a postpelvic region and in the possession of a poorly developed postventral region. In *Cathartes* the anal circling is incomplete and there is no outer circling, and the minor under coverts number six instead of three on each side.

Important resemblances in *Cathartes* and *Gymnogyps* are: Lack of patagium at the base of the rectrices; reduction of under tail coverts; nude oil gland.

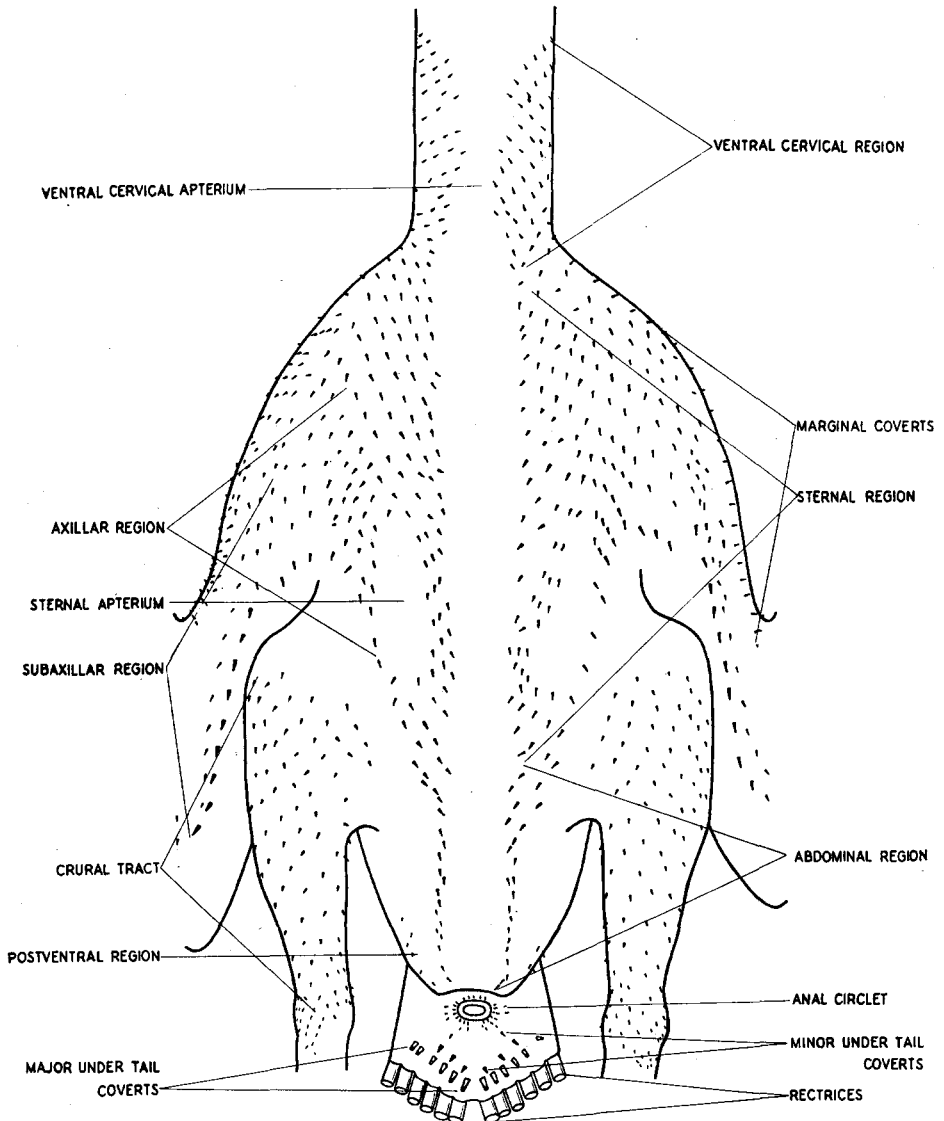


Fig. 67. Tracts and regions of ventral surface of California Condor, $\times \frac{9}{11}$.

Humeral tract.—This tract begins at the anterior angle of the shoulder where it is connected with the ventral cervical region. The feathers are arranged in diagonal rows that anteriorly are continuous with rows of marginal coverts on the anterodorsal aspect of the humerus. Posteriorly the rows are transverse. Only the five posterior rows are entirely separate from the marginal coverts. The feathers of the tract increase in size posteriorly, attaining a length of 38 cm. in the last row. In the last row, the central feathers, four in number, are longer than the terminal members of the row. In each of the four rows preceding the last there are five large feathers.

Gymnogyps differs from small falconiforms only in the greater numbers of large feathers in the posterior transverse rows. In other falconiforms there are usually three or four such feathers per row.

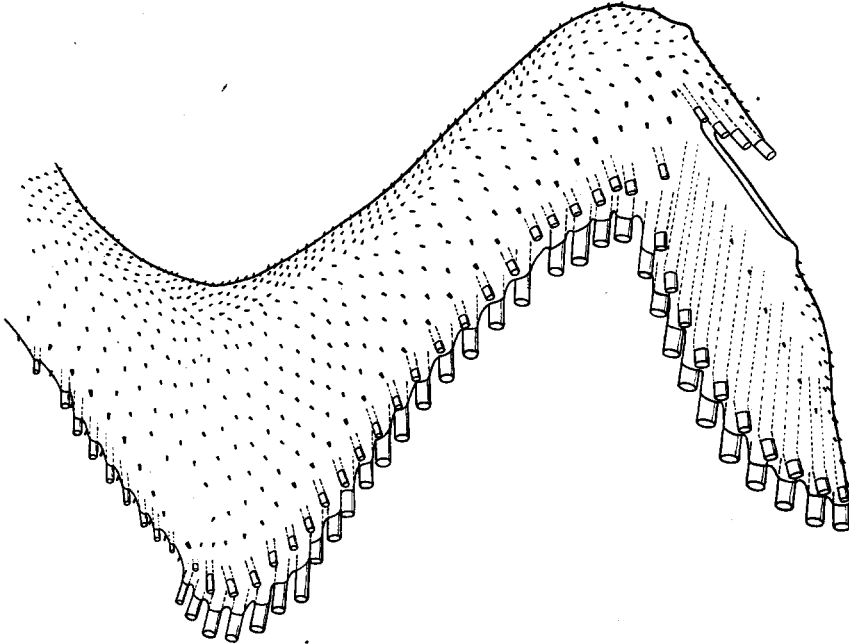


Fig. 68. Dorsal surface of wing, $\times \frac{8}{11}$.

Alar tract. Dorsal surface.—There are 10 tertiaries (9 in *Cathartes*), the largest ones being in the center of the series (fig. 68). The most distal member is inserted on the joint, is much smaller than the others, and is in line with the middle upper coverts of the forearm (not the lesser upper secondary coverts as stated by Compton, p. 202). The most proximal tertiary is separated from the others by a greater interval than that between other members of the series. Proximal to it is still another feather, in line with the tertiaries, that is much smaller. It also is in line with a row of lesser coverts that runs across the axis of the humerus. It seems to be best considered one of this latter group.

The secondaries number 22, the inner two being smaller than the others, and the last little more than half the length of the eighteenth secondary. No patagium joins the secondary quills, and a carpal remex is lacking.

There are 10 well developed primaries and a vestigial eleventh primary distally that is no larger than the adjacent coverts.

Coverts on the humeral segment consist of one row of 8 enlarged feathers inserted above and between the nine proximal tertiaries. These are separated at the elbow from the lesser coverts of the forearm.

Greater secondary coverts, as usual, are inserted on, or proximal to, the bases of the secondaries to which they correspond, but cross over to lie in the space distal to their respective remiges. The wing is diastataxic and hence there are 23 greater coverts. The first five (distal) coverts are set lower on the surface of the wing than the proximal ones and suggest the embryonic continuity with the more proximal secondaries which Steiner (*Jenaische Zeit. für Naturwissenschaft*, vol. 55, 1917, pp. 221-496) has demonstrated. A carpal covert is set in line with the greater secondary upper coverts, but it is separated by a relatively large interval from the first secondary covert. Proximally, the greater upper

secondary coverts are continuous with the first row of under coverts of the tertials. Middle secondary coverts are inserted between the greater coverts and also occur proximal to the last and distal to the first greater covert. Thus, the series consists of 24 feathers. There is a corresponding middle carpal covert. Five axial rows of lesser coverts overlie the radius and ulna. These and the row of middle coverts are deflected at the diastataxic break so that the rows may be thought of as either curving upward here (the embryonic rows) or, with an irregularly set feather, continuing along the axis of the arm. Distal to the diastataxic point there are six rows of lesser coverts.

The bases of the secondaries, especially the outer webs, are gray or dull white. Secondaries 1 to 4 show little of this. The greater upper secondary coverts are gray basally and whitish distally, especially on the exposed outer webs. Extreme development of white and gray occurs in the middle of the series, the terminal members being nearly black.

The dorsal coverts of the patagium and of the humeral surface are continuous with the lesser upper secondary coverts and with the marginal rows. The four anterior rows of marginals are more closely set than are the lesser coverts and distally on the forearm contrast sharply with them.

The coverts of the hand consist of 10 greater upper coverts, and 7 (8 in *Cathartes*) middle coverts, beginning distal to greater covert 4 and continuing to the margin of the wing. The greater coverts are bent distally across the bases of the primaries as described by Loye Miller (*op. cit.*, p. 160). Three rows of marginal coverts begin at the base of primary 8. The most posterior row might be considered lesser coverts.

The alula bears 4 main feathers and coverts in rows that are continuous over the wrist with the marginals and lesser coverts of the forearm. The claw on the pollex is curved and is 14 mm. long on one wing, 23 mm. on the other.

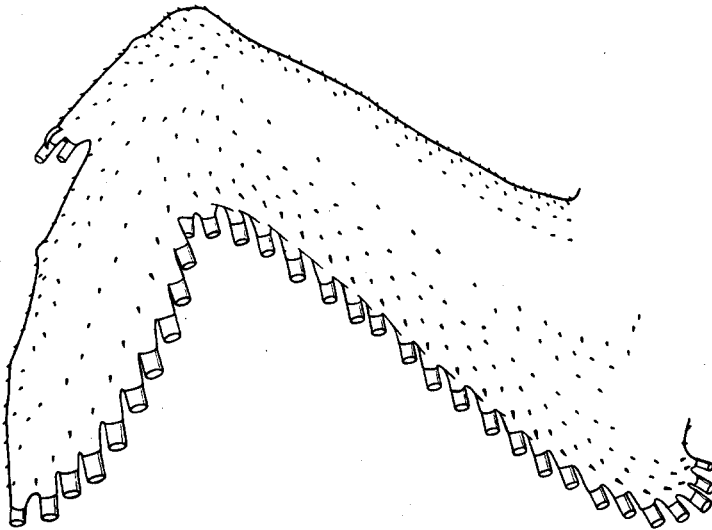


Fig. 69. Ventral surface of wing, $\times \frac{8}{11}$.

Under surface.—Under coverts of the tertials consist of one row of 9 feathers, each inserted between two tertials (10 in number). These coverts are continuous at the elbow with the greater upper secondary coverts. Although there are no middle under tertiary coverts, a series of downs may represent them. The under tertial coverts are whitish basally and the tertiarials are slightly gray basally. On the posterior ventral aspect of the humerus is an entirely bare area.

The 22 greater under secondary coverts are set between the bases of the secondaries, with two between secondaries 4 and 5 (fig. 69). Middle under coverts are set anterior and only slightly distal to the greater coverts. There are two between secondaries 4 and 5 and 24 in all, for the row continues proximally around the elbow beyond the secondaries. All these coverts are blackish, but the middle coverts are less intensely pigmented.

Two rows of lesser under secondary coverts lie posterior to the ridge of the ulna. These rows are shorter than the rows of middle and greater coverts, not extending so far around the elbow. They merge with rows on the under surface of the hand across the carpal region. All are white except for their shafts. Anterior to the ulna is a single row that runs from the marginals at the base of the alula

to the anterior side of the elbow. Here two additional rows appear and the area connects with the subaxillary region of the under humeral surface. These feathers are white, as are those behind them, and of about the same size. At the wrist they are bicolored and the extra rows at the elbows are not entirely white.

The 11 greater under primary coverts lie between the bases of the primaries, there being one proximal to the first primary and another distal to the last. Anterior and proximal to the first greater under covert is a small feather in line with the middle under secondary coverts that may represent a carpal covert. It is not associated with the first secondary. The greater under primary coverts are black.

The middle under primary coverts are a continuation of the posterior row of lesser under secondary coverts, and are white proximally, becoming black on the outer vane distally.

The lesser under hand coverts consist of one principal row and a short second row on the skin above the intermetacarpal space. The lesser coverts are continuous with the anterior row of lesser under secondary coverts behind the ulna. They are white, or partly white, but distally may be entirely black. Marginal coverts of the under surface of the hand and alula are entirely black.

Three rows of marginal coverts of the humeral and ulnar segments occur on the under wing surface. The posterior row is chiefly pure white, with black shafts, but bicolored feathers occur at shoulder and wrist. The middle row is partly white in the center of the patagium and the anterior row is entirely black.

The pterylosis of the wing corresponds with that of *Cathartes* in detail. It conforms to the general cathartid type as described by Compton in having four enlarged alula feathers, narrow propatagium, and a claw on the pollex. However, the claw is curved, not straight. Both *Cathartes* and *Gymnogyps* lack the carpal remex. The number of secondaries and, accordingly, the number of coverts are less in *Cathartes* (see Compton, p. 201).

Femoral tract.—This tract consists of 6 or 7 diagonal rows of 3, rarely 4, long normal, or slightly lanceolate, feathers. This is the typical cathartid condition. The two distal rows merge with the rows of the crural tract. The middle of the tract is connected with the pelvic region of the spinal tract by a single feather.

Crural tract.—The leg below the knee is not densely set with feathers, but is fairly continuously covered except dorsomedially. In dorsal aspect only two or three rows show, these being on the dorso-lateral surface. In *Cathartes* two additional rows occur on the dorsomedial surface. At the heel the feathers are much reduced. The feathers in *Gymnogyps* are short and normal medially and proximally, but laterodistally they are weakly lanceolate, forming a poorly developed tuft or flag.

In comparing the pterylosis of the Condor and the Turkey Vulture, one is impressed with a fundamental similarity in plan. From such a comparison a sense of values emerges as to the importance of the various aspects of feather arrangement.

In these two vultures the alar tracts are remarkably similar. Details of the feather spacing, numbers of rows, and manner of insertion in the skin correspond closely. This is not merely a reflection of the general stability of alar pterylosis, for many of these details are not the same in other falconiforms. The greater number of feathers in the rows of the forearm of the Condor results in no difference in arrangement. It seems that feathers have been gained or lost in the center of the forearm series in these vultures without disruption of the complex patterns at elbow and wrist.

The humeral, femoral, and crural tracts show few significant differences in *Gymnogyps* and *Cathartes*. But, the arrangement of the femoral tract in the *Cathartae* is a feature of special significance, distinguishing this group from others of the order.

In the spinal tract, the difference in breadth of the pelvic area suggests that extent of this region should not be given great weight in phylogeny. The absence of feathers on the midline and the confluency of dorsal and pelvic regions, in which the two vultures are alike, are characters of more importance.

On the ventral surface, the general continuity of feather areas and the arrangement of rows in the axilla are fundamental likenesses, but presence of an insular apterium within the ventral tract overlying the sternum varies strikingly among the New World vultures.

The caudal areas in the two vultures show basic resemblances in the lack of patagia about the quills of the rectrices, in the reduction of under tail coverts (although the details differ), and in the lack of feathers on the oil gland. Differences in the anal cirlet and in the weakly developed postpelvic and postventral regions seem more evanescent.

The capital tracts of the Condor and Turkey Vulture do not correspond closely. It is difficult to point to significant similarities other than the general tendency to reduction of feathering and the preservation of normal patterns in loral and auricular areas.

The items in Compton's (*loc. cit.*) diagnosis of the cathartid pattern (including the Osprey) that must be abandoned because of nonconformity in the California Condor are: ventral tract extended over entire ventral surface; and straight (rather than curved) claw on pollex. Further items which still may be valid, but which appear to us to be of minor importance are: reduction of certain capital apteria; spacing of feathers in, and width of, humeral tract. Otherwise, his diagnosis seems significant, and the resemblance of the Osprey to the cathartids is substantiated. It is only natural that there are many characters of pterylosis common to *Cathartes* and *Gymnogyps* that are not shared by the related, yet distant, *Pandion*.

Museum of Vertebrate Zoology, University of California, Berkeley, September 10, 1938.