Recording the details of feather distribution presents certain difficulties. A three-dimensional system is hard to picture in words, and there is the problem of what to describe. The simple descriptions of pterylae used by Nitzsch (1867) are often as adequate as more detailed accounts. Similarly, the illustrating of feather arrangement is difficult. The figures of Nitzsch are simple outlines of the feather tracts, whereas those of Compton (1938) and Fisher (1943) show the position of each feather. In comparing these figures with specimens there are many points which are not clearly indicated, being lost in the flat projection of the three-dimensional surface.

In working with preserved materials there are several sources of error. The more muscular pterylae may shrink so that the positions of the feathers are altered, or fat in the pterylae may accentuate them. A plump, rounded specimen presents a different appearance than an angled one. An improperly stored specimen may have the feathers pushed aside. Lastly a specimen may have been molting or may have lost feathers in preparation. Because of such distortions, freshly taken specimens were clipped and prepared for examination before injection and, after injection, wrapped in cloths soaked with preservative and laid on a flat surface until hardened.

The figures used in this account show each feather in its relationship to the others and to the important contours of the body. This has been done by using a ventrolateral view rather than a ventral one. In such a figure certain distortions seem necessary to reproduce the general appearance of the specimen. The figures were drawn from specimens on which reference feathers were stained or on which a grid of lines was drawn. It is my opinion that the details of feather arrangement (number of rows along the body, the relationship of the axillary and sternal divisions of the ventral tract) will prove of value.

Since the word feather applies to any of the various forms observed, it is not always an exacting term. As usually conceived, there are four types of feathers: pennaceous contour feathers, which will be called plumes in order to present consistency in terminology; semiplumes, which intergrade in form between the plumes and the plumules; plumules, downy structures with or without a short rachis; and filoplumes, small hair-like forms with a few barbs on the tip of the shaft. Powder down is a fifth type. The morphology of each of these types may show some variation. Plumes are modified into eyelashes, rictal bristles, and into nuptial or decorative plumes (the usual connotation of the term). The first three types are independent units of the feather cover, while the fourth, the filoplume, is associated with their follicles (figs. 7-10, 40-41).

Terms are needed to indicate areas of study; three are introduced here. The first is ptilomorphology, a study of feather structure, both macro- and microscopic. One aspect to be considered is adaptive ptilomorphology; the differences in gross structure of feathers from different points on the adult body (Chandler, 1914). The second is ptilogenesis, which deals with the development of feathers from the appearance of the follicle to the achievement of the adult type. Lastly there is

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ptilodianomography, the description of feather distribution. Ptilodianomography deals with the details of arrangement of downs and contour feathers and, thus, is more inclusive than pterylography. However, because of its long use, some may wish to retain the term pterylography and expand its meaning.

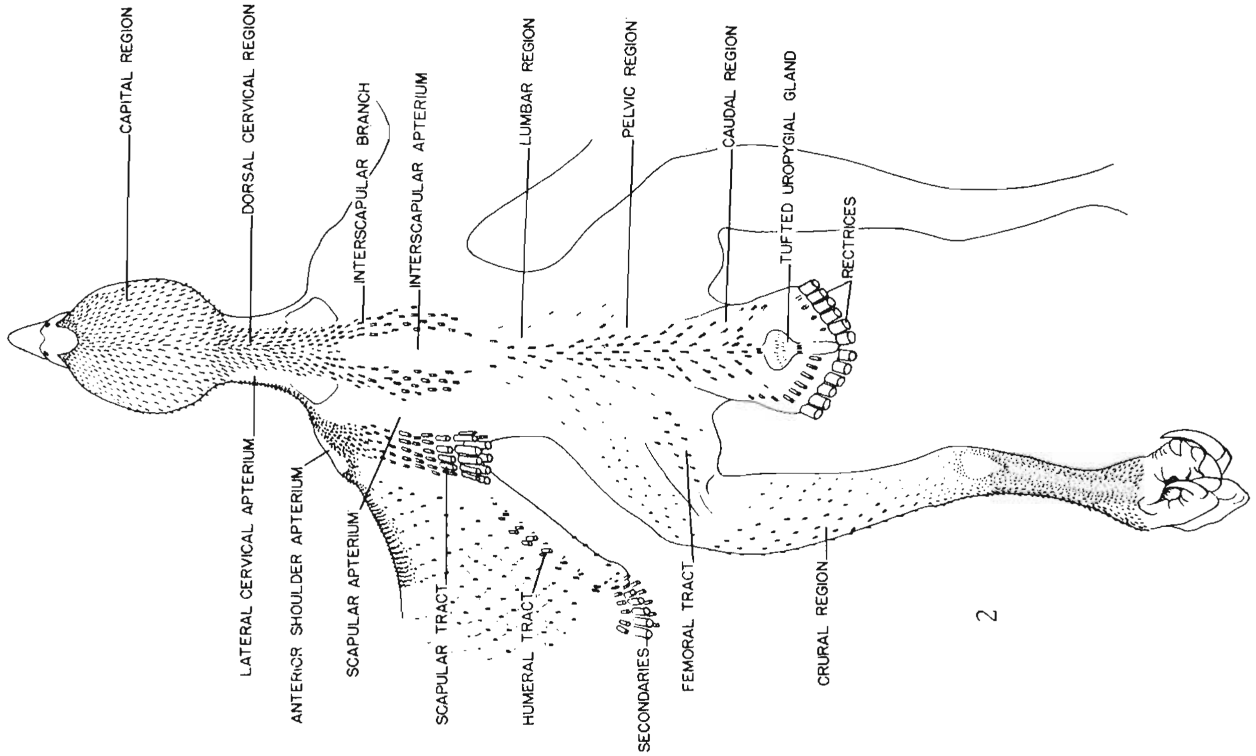
The terminology of the feather tracts and regions is largely that of Compton (1938). I have deviated somewhat for purposes of consistency (figs. 1 and 2). The main alteration suggested is the use of *scapular tract* for what is ordinarily called the humeral tract (*see* Wetherbee, 1957). The reason for this change is that the feathers of this tract are identified as scapulars when one considers the topography of the bird. Also, that part of the spinal band lying between the scapular tracts is called the interscapular region in current usage. It is true that the scapular tract does not overlie the scapula, although it does parallel that bone; it is not oriented along the humerus either. Freeing of the term humeral makes it available for application to a tract (tertiaries) lying along the humerus. I have altered the name submalar to submandibular for topographic accuracy. I have limited the use of the word tract, preferring to identify many parts of the feather cover as regions.

Ptilodianomography and Ptilogenesis of a Hawk

The ptilodianomography of the adult means little until the ontogeny of the plumage is considered. The order of appearance of the feathers and tracts has not yet been studied for any member of this array (Burt, 1929; Gerber, 1939, Lucas and Stettenheim, 1972). In figures 3 and 4 the natal plumage of the golden eagle is shown. The figures, showing a chick removed from the egg just before hatching, were compared with the skin of a newly hatched eagle (2757 of the Ralph Ellis Collection in the Museum of Vertebrate Zoology). The units of the natal plumage are arranged along *A* and *B* lines (figs. 6,7) and essentially cover the body. The order of appearance is briefly from the dorsal tracts, ventrally around the body. The large contour feathers appear earlier than the smaller ones in any region. The relative size of the natal down is indicated both by the width and length of line.

Comparisons of these figures with those of the fully grown individual (figs. 1,2) show that the larger natal down feathers correspond to the contour feathers. That down which occurs on the apteria of the chick (i.e., covering the crop area, the furcular apterium, and forming strips on either side of the sternal keel) is represented in the adult by semiplumes or down feathers. In natal specimens of *Buteo* and *Pandion* the ventral medial strips of down are continuous with the pterylae.

Examination of both eagle chicks under a binocular dissecting scope showed no indication of down within the pterylar tracts, but in clearing the preserved specimen with potassium hydroxide and glycerin the buds of the secondary cover (metategmen--new term) could be discerned among the larger follicles of the primary cover (protegmen--new term). The units of the natal cover do not form a perfect pattern of rows, indeed, laterally, no rows are apparent. Loss of pattern appears to be due to the shifting of follicles to form the denser pterylae and to differences in relative area



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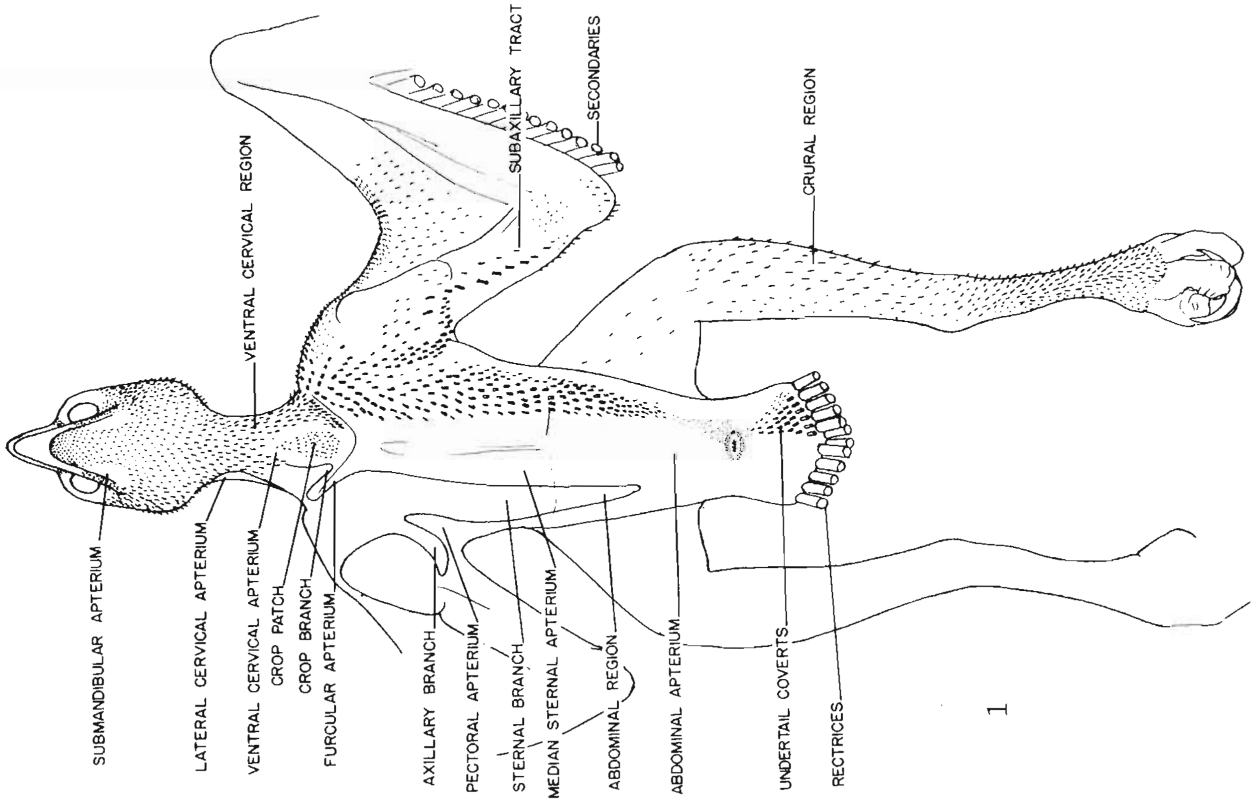

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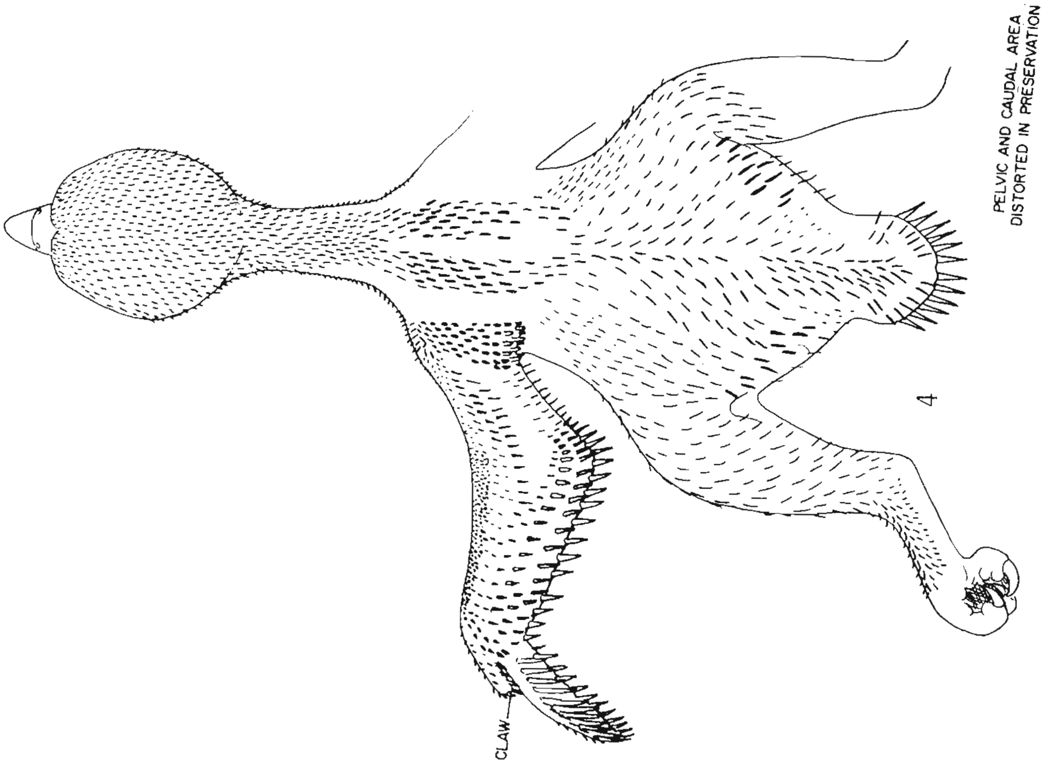
Fig. 1. Ventral view of an adult golden eagle (*Aquila chrysaëtos*).

Fig. 2. Dorsal view of an adult golden eagle.



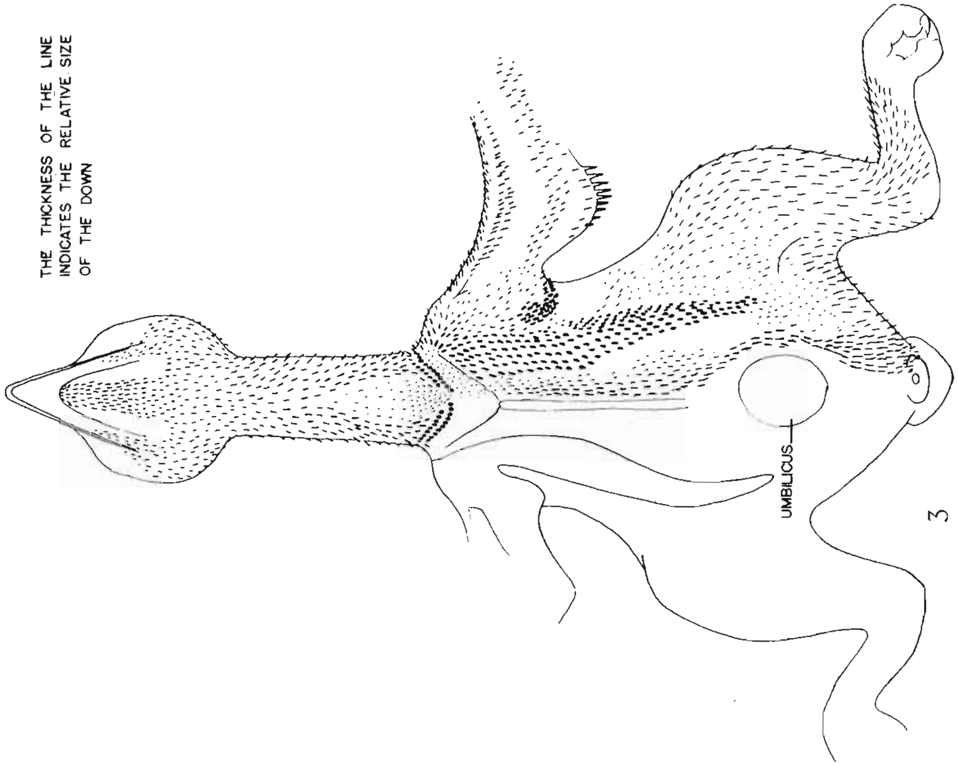


Fig. 3. Ventral view of a natal golden eagle.

Fig. 4. Dorsal view of a natal golden eagle.

caused by the contours of the body. The buds of the secondary cover are irregularly spaced among the follicles of the natal, or primary cover and are not grouped into feather complexes. There are two to five units in the secondary cover for each of the primary ones.

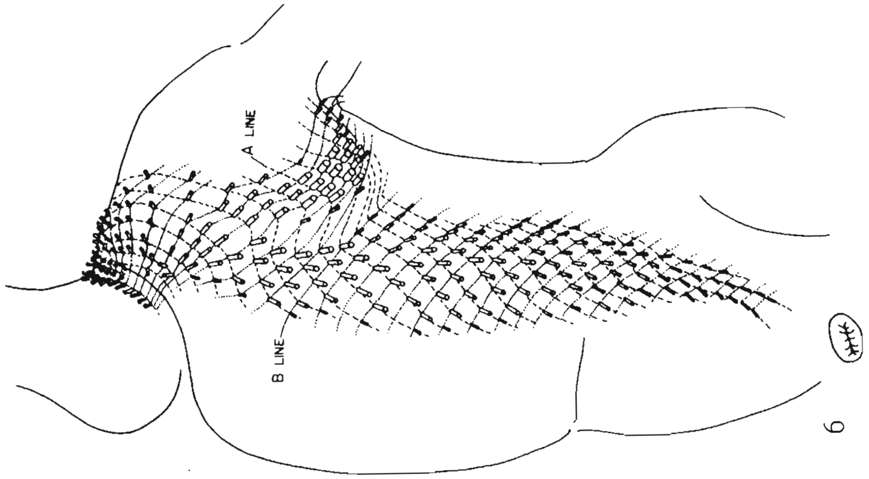
The details of the ptilodianomography of the nestling (2½ weeks old) and adult red-tailed hawk support the observations on the golden eagle (figs. 5,6,7). The pterylae of the young and adult are comparable in many details. The pterylae increase in width by the addition of feathers medially and laterally; there is some increase in length with the addition of new rows posteriorly. On the Figures (6 and 7) comparable *A* and *B* lines are labeled to aid in comparisons. In the adult (fig. 5), downy feathers continue, roughly, the contour feather spacing towards the ventral midline. These down feathers have a heavier shaft as contrasted with the intrapterylar plumules and they have filoplumes associated with them (fig. 9). Some of them, in *Aquila*, have a well developed rachis and are true semiplumes. The apteria of the nestling (fig. 8) are densely covered with an irregular scattering of downs of both the primary (with filoplumes at their bases?) and secondary covers. Apparently much of the secondary cover is not represented in these areas in the adult. There is a heavy shedding of down by young just out of the nest, much of which is not replaced, or is periodically replaced (in response to season?--figs. 8,9,10,11).

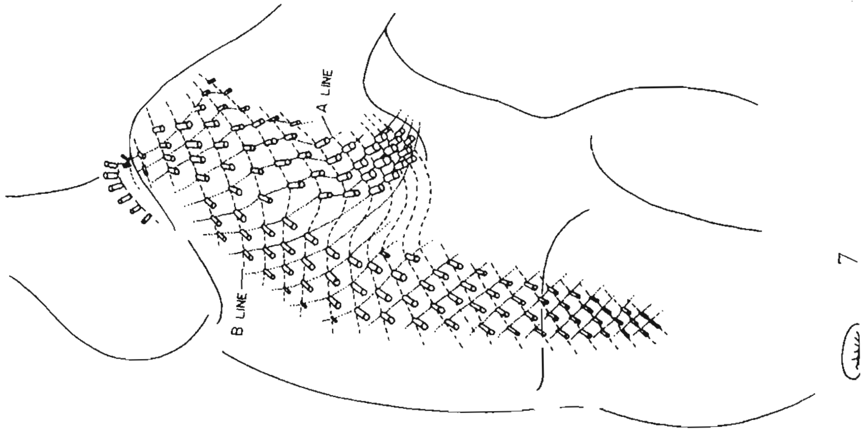
Comparison of the eagle with the chicken suggests that the natal plumage represents the primitive, nearly continuous, protegmen of the ancestral bird. As there is no clean-cut structural line between downs and pennaceous feathers, the conclusion is that the pterylar tracts have been derived by increased size and concentration of some of the units of the primitive coat, the remainder develop as downs and, at the edge of the pterylae, some show the transitional semiplume structure. The chicken is described as having down only on the apteria. A more accurate description would be that a chicken has only a primary cover of proptilae (new term); those feathers of the apteria, and an occasional crowded unit in the spinal pteryla, develops as down.

In the eagle, an extensive metategmen develops about the sixth day after hatching. This down (metaptilae--new term) appears among the natal feathers of pterylae and apteria.

Verheyen (1953) suggested that the feather rows are segmental; he equates the number of rows with the number of spinal nerves. This may be true in the hawk except on the head and the anterior margin of the wing where there appears to be at least a doubling of the number of rows (polyisomerism--this can be observed on the head of the chicken where at 28 days of age downy precursors about equal the number of feathers bursting from quills). Like the other areas, there is down among the plumes of the hawk's head. There appears to be two down feathers (metaptilae) for each plume in the red-tailed hawk (very few down feathers in *Gampsonyx*). The down (metaptilae) of the head and neck in *Gypaëtus* has become semiplumes.

In development, the feather may be preceded by a downy





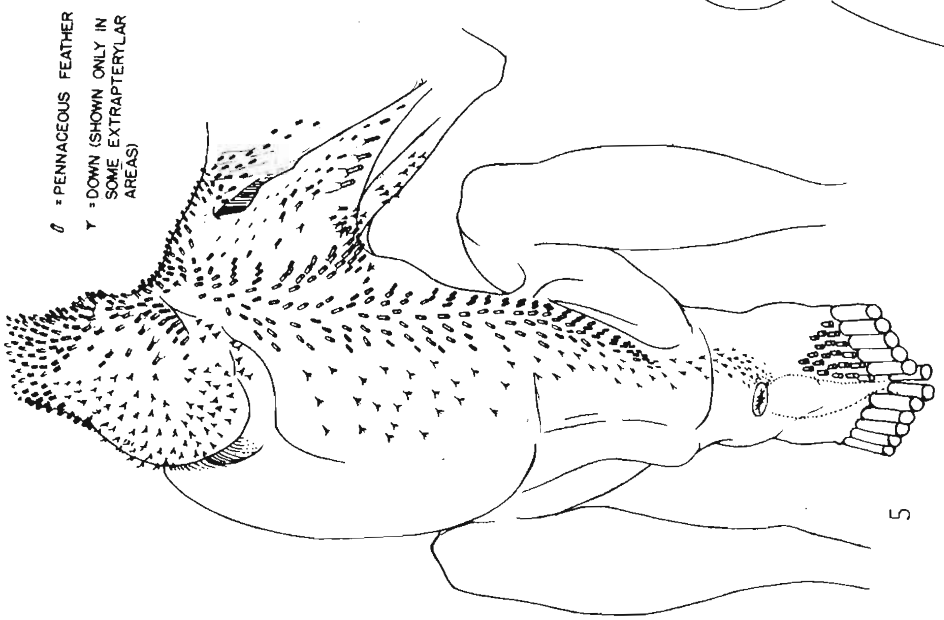
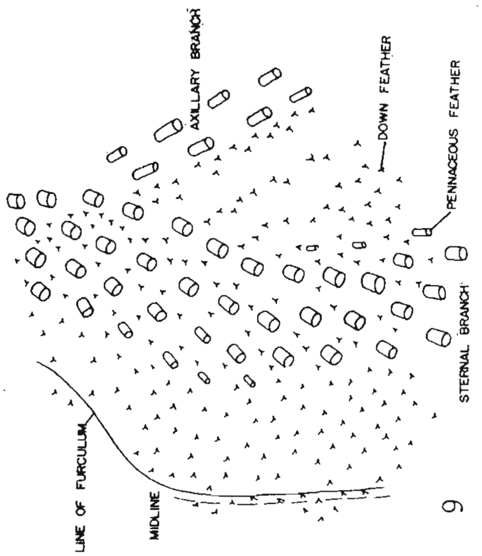
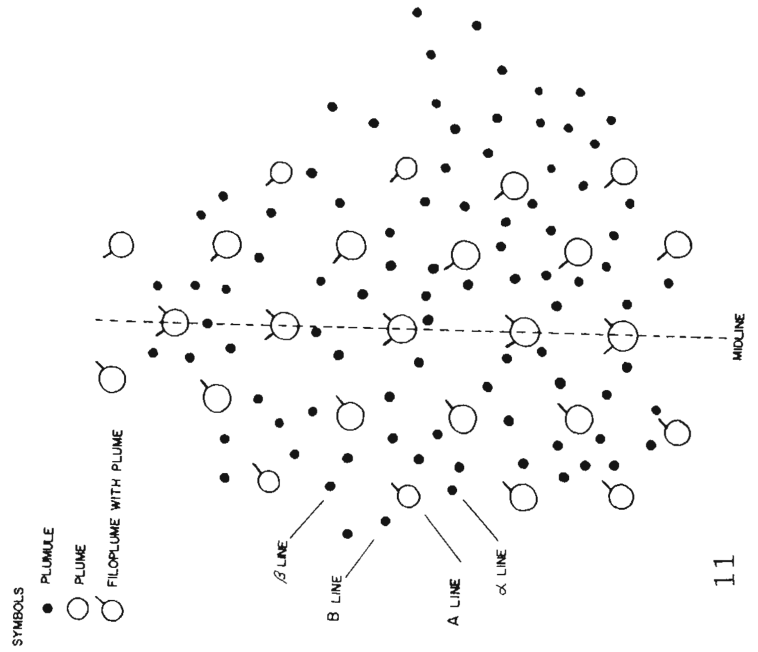


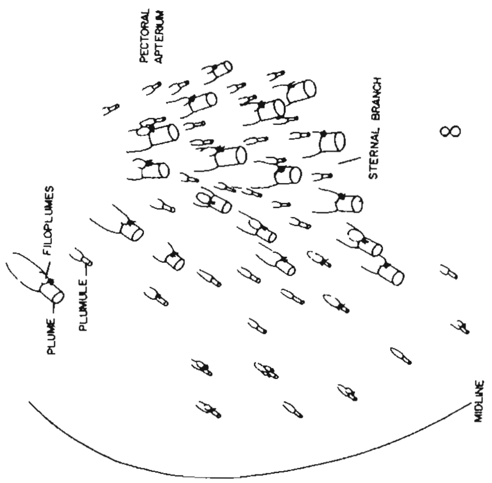
Fig. 5. Ventrolateral view of the protegmal cover of an adult red-tailed hawk (*Buteo jamaicensis*).

Fig. 6. Details of spacing of the contour feather cover of an adult red-tailed hawk.

Fig. 7. Details of spacing of the contour feather cover of the breast and abdomen of a 2½-week-old, nestling red-tailed hawk.







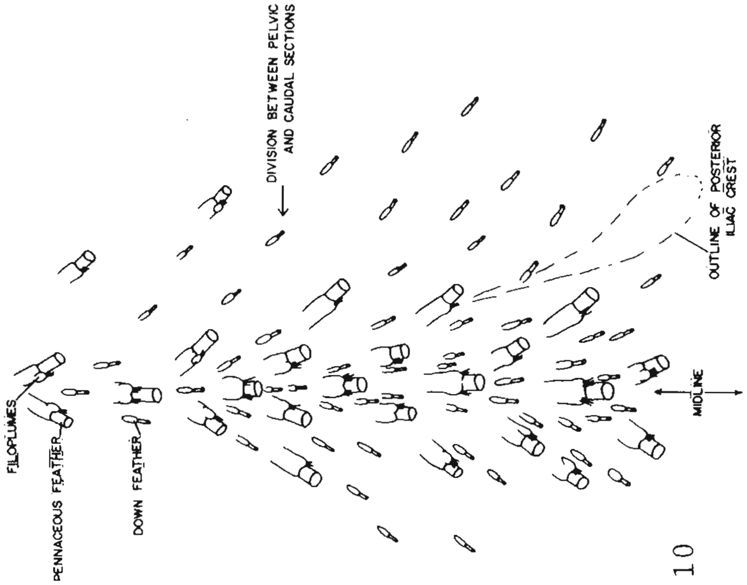


Fig. 8. Details of spacing of the plume and plumule cover of a section of the breast of an adult red-tailed hawk.

Fig. 9. Details of spacing of the plume and plumule cover of a section of the breast of a 2½-week-old, nestling red-tailed hawk.

Fig. 10. Details of spacing of the plume and plumule cover of a section of the pelvic region of the dorsal tract of an adult red-tailed hawk.

Fig. 11. Details of spacing of the plume and plumule cover of a section of the pelvic region of the dorsal tract of a 2½-week-old, nestling red-tailed hawk (diagrammatic).

structure (protoptile). At the time of hatching or shortly thereafter growth within the follicle is modified and a pennaceous or downy structure is produced bearing the down precursor on its tip (fig. 12). This tufted condition does not support the contention that two generations of feathers occur (Dwight, 1900a, 1900b; Friedmann, 1930; Leopold, 1943), or that even three generations are sometimes indicated (Ingram, 1920) (fig. 12 E, F, G).

A study of feather growth and its anomalies helps in understanding the production of such tufts (Riddle, 1908a, 1908b). Any reduction of nutriment to the follicle, whether from starvation or shock, can disturb feather growth sufficiently to produce aberrations. Great horned owls and red-tailed hawks, captured at the time of nest leaving, may have growth completely interrupted, drop the entire tail, and then grow a new one. One day's excitement during the molt is sufficient to cause a "fault bar" on a growing feather even in tame birds.

There is no doubt that a disturbed nutritive state, caused by reorganization of growth of the feather papilla at, and shortly after, the time of hatching accounts for the constriction between the natal down and the basal structure and also for any downlike filaments on the barbs at the tip of a feather. The faster-growing feathers show a greater constriction (figs. 12E, 12H).

In the golden eagle the natal down of the pterylar tracts shows a complete constriction, with cessation of barb production. Outside the pterylae the natal barbs are continuous with those of the later protegmal down feather; no constriction of any kind is noticeable. The preplumulae (i.e., metaptilae) develop without tufting. The metaptilae undergo a postnatal molt in falconiforms while the primary cover does not.

Comparative Ptilology

In order to compare the four families of the Falconiformes, each will be described and the variation within the family indicated. Because of its many peculiar features *Pandion*, which has been viewed as belonging to a distinct family or suborder by different taxonomists, will be considered separately. The order of description will be: cathartid, sagittariid, accipitrid, pandionid, and falconid.

The Cathartid Type (figs. 13 - 16)

Descriptions and figures of all living members of this group have been published by Compton (1938), Miller and Fisher (1938), and Fisher (1943). I have examined *Cathartes* (figs. 13-14 illustrate ventral and dorsal aspects--*see* Compton's figures 6 and 12) and *Coragyps*.

The head and neck is covered only by reduced feathers and downs and appears largely naked as in some genera of the Aegypiinae. The dorsal cervical band arises sharply near the base of the neck and forms a ruff, which is continuous ventrally with "lateral parts" of the ventral cervical tract. A small lateral cervical apterium appears at the shoulder in *Cathartes* (but in none of the others) and extends anteriorly for just a short distance where it narrows to a point. The midline of the neck

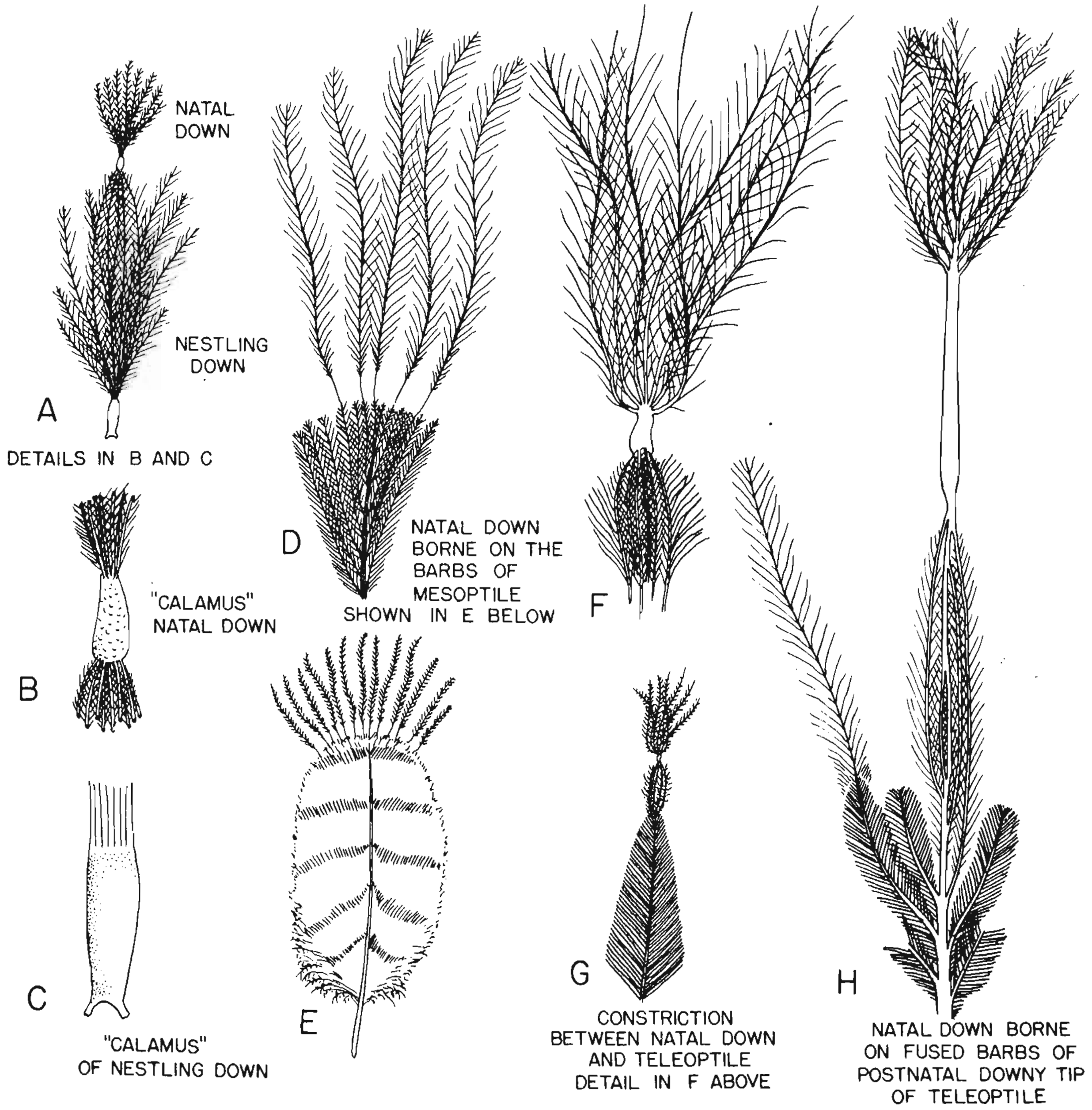


Fig. 12. Relationships between developmental stages of feathers. A. Down feather from the knee of a nestling of *Falco sparverius*. B. Detail of constriction between protoptile and nestling down of feather shown in A. C. Detail of calamus of nestling down shown in A. D. Filaments of protoptile down borne on tip of nestling feather of great-horned owl (*Bubo virginianus*) shown in E. F. Tip of developing (teleoptile) feather from crown of head of nestling golden eagle; entire vane of feather shown in G. H. Tip of tail feather of nestling golden eagle showing tuft of protoptile barbs, basal structure, transition barbs and teleoptile.

and crop, ventrally, is bare with brightly colored skin (narrower in *Coragyps* as compared with *Cathartes*), while the lateral parts of the ventral cervical region extend across the furcular depression at the shoulder (on the lateral cervical patagium) to continue as the sternal portion of the ventral tract.

The pectoral portion of the ventral tract of *Cathartes* has an indistinct apterium (feathers smaller and more widely separated). *Coragyps* has a distinct pectoral apterium while *Gymnogyps* has a large one (Miller and Fisher, 1938). The abdominal portion ends just in front of the anus and near the midline. On the body, the ventral tract shows relatively fewer *A* lines (15 in *Cathartes*, fig. 13).

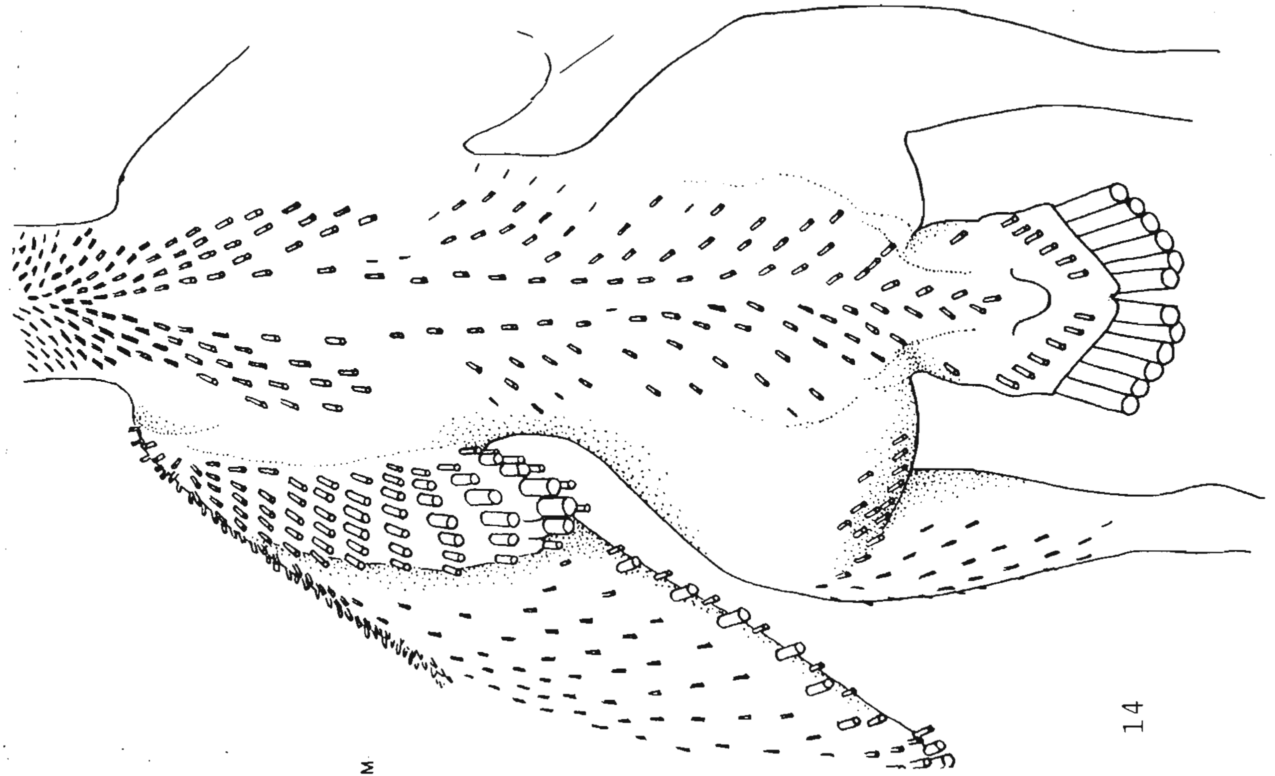
Dorsally there is a long spinal apterium extending from the shoulder to the caudal region. *Coragyps* differs in having a more distinct row of median feathers in the caudal region (fig. 15). The interscapular region is only slightly differentiated from the lumbar bands, the spinal tract spreads out somewhat in the pelvic and caudal regions. The femoral region is distinct and continuous with the crural cover. The scapular tract shows fairly clear transverse lines of feathers and is relatively wide. The humeral band is well developed. There is a small anterior shoulder apterium partially visible from below (fig. 13).

The alar tract (fig. 16) is distinctive in lacking the carpal remex although the covert is present; the secondaries do not have a patagium between them. There are eleven primaries, the eleventh vestigial, and a varying number of secondaries, from 18 (*Cathartes* and *Coragyps*) to 25 (in *Vultur*, according to Fisher, 1943:72). The wing is diastataxic.

In the tail region, the oil gland is naked except in some specimens of *Coragyps*, which have a small tuft. The spinal tract ends caudally as a pair of feathers in both *Cathartes* and *Coragyps*. The rectrices number 12 and each has a greater dorsal covert. (Beddard, 1898:473, recorded 14 rectrices for "*Rhinogryphus californianus*," indicating perhaps an abnormal specimen or an error as on p. 481 he allows only 12 for the entire group.) The rectrices, just as the remiges, are not set in a patagium. The lesser undertail coverts are greatly reduced in number; there are 12 greater undertail coverts, and one or two rows of lesser coverts.

Down feathers occur over the entire body. On the head unpigmented brushlike feathers (down) occur irregularly among pigmented feathers of similar form. On the neck and body the down feathers outnumber the contour feathers about three or more to one. The feathers on the apteria, both of the pro- and metategma, are more irregularly spaced than in the dorsal and ventral tracts proper. Even in the latter, asymmetry is evident. Distinct feather complexes could not be defined although certain relationships are common and suggest a basic pattern of α and β (parallel *A* and *B* lines respectively) which may be more evident in the nestling.

The natal chick is peculiar in that it has a bare head. The natal plumage is entirely protegmental and gives rise to both pennaceous contour feathers and apterylar down (the latter is frequently pigmented). The metaptilae appear shortly after



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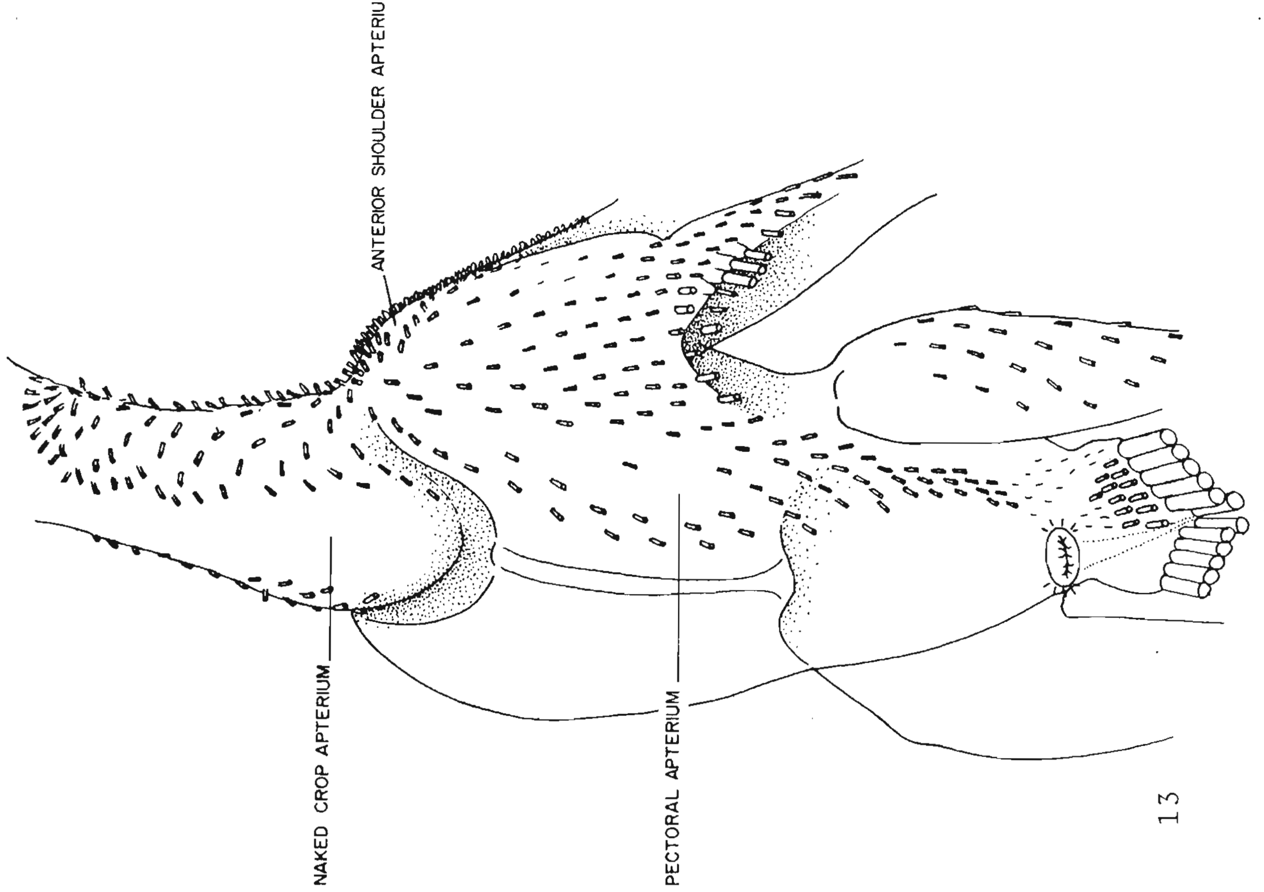

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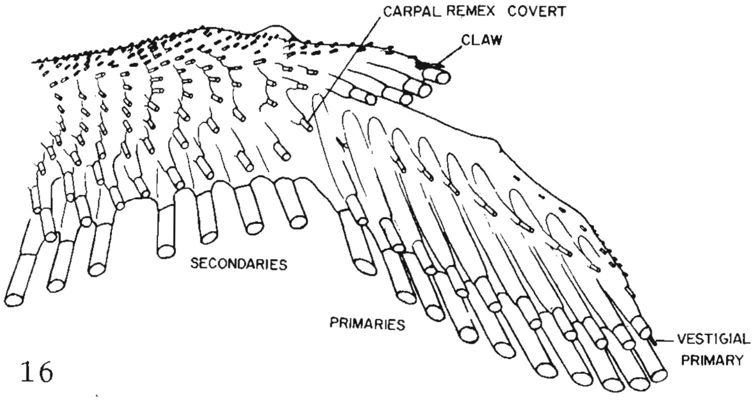
Fig. 13. Ventrolateral aspect of body of specimen of *Cathartes aura*.

Fig. 14. Dorsal aspect of body of specimen of *Cathartes aura*.



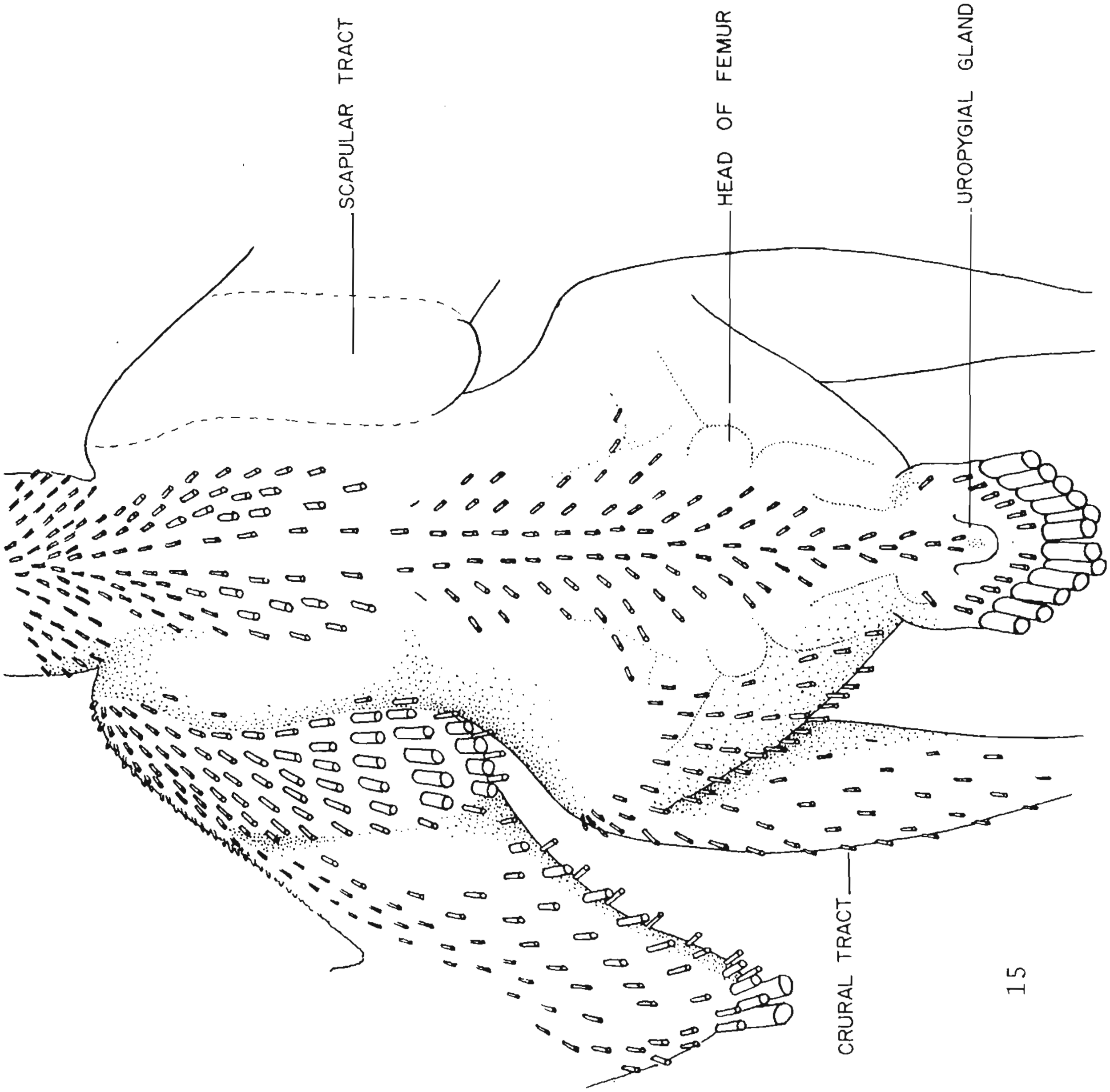


Fig. 15. Dorsal aspect of body of specimen of *Coragyps atratus*.

Fig. 16. Dorsal aspect of distal part of wing of specimen of *Cathartes aura*.

hatching. Both natal and nestling downs are white.

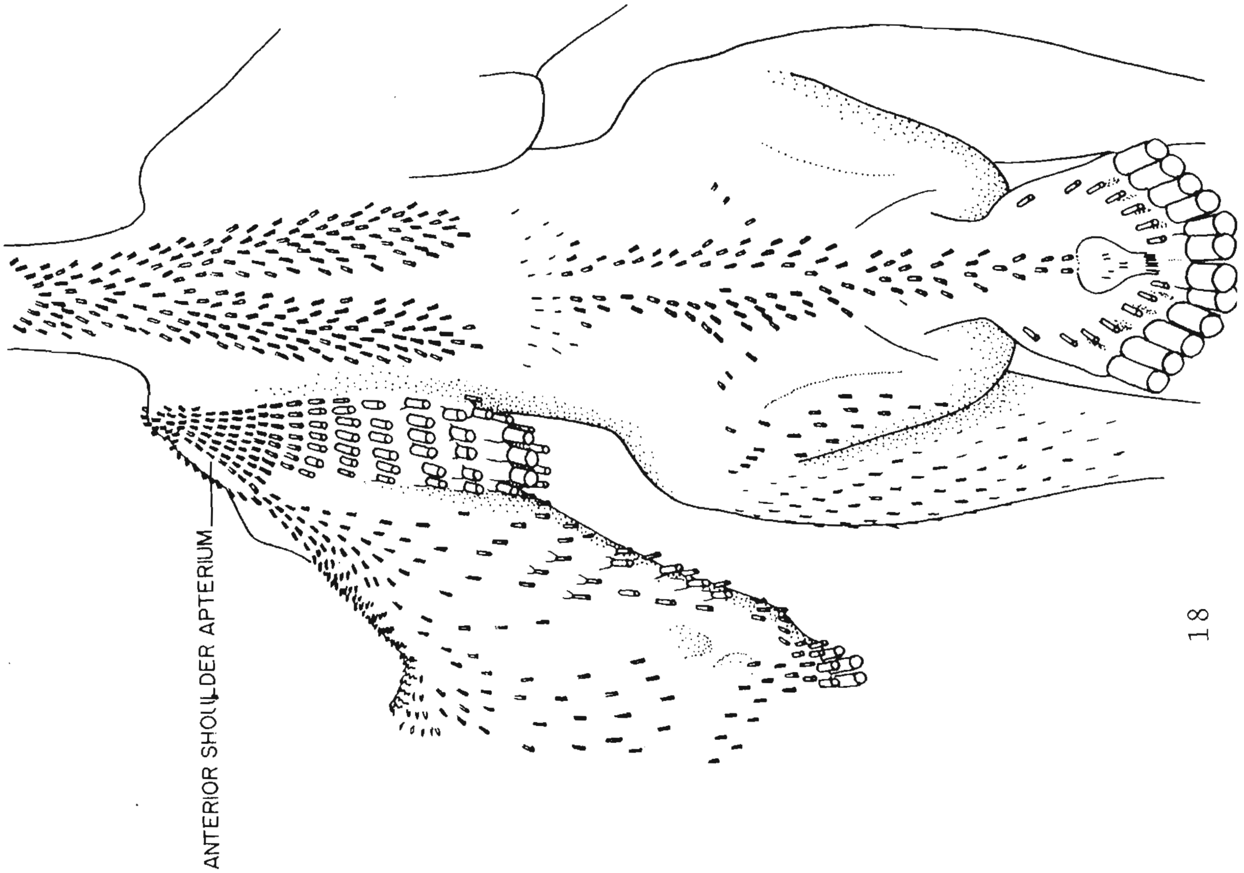
The cathartid type as defined by Compton (1938:206-207) is not acceptable. Fisher (1943:73) has shown that the pterylosis of this group varies considerably and has characterized it as follows: "absence of a submalar [=submandibular] apterium, vestigal or obsolete lateral cervical apterium, wide dorsal cervical region, presence of a ruff, continuous dorsal (i.e., interscapular) and pelvic regions, fused sternal, axillar and subaxillar areas, a definite sternal (pectoral) apterium, a femoral tract consisting of 5 to 7 longitudinal rows of lanceolate feathers on the posterior margin of thigh, 4 alular quills, absence of a patagium about the bases of the rectrices, an essentially nude oil gland and a reduced number of lower tail coverts." To this can be added the division of the neck ruff by the ventral cervical apterium, which extends forward past the mid-point of the neck, the reduced number of *A* lines covering the body ventrally, the lack of a patagium for the remiges, the absence of an aftershaft throughout the plumage, and the "bare" head of the natal chick. The reference to 4 alular quills can be deleted since it is not distinctive in itself or in combination with other features.

The Sagittariid Type (figs. 17-19)

Ventrally, the head region has distinct submandibular apteria, and the lateral cervical apterium of either side extends to the angle of the jaw and below the ear opening. The ventral cervical band is narrow and forks at the midpoint of the neck to form the ventral cervical apterium which widens over the crop and then narrows to the sternal apterium (fig. 17). The ventral cervical tract has a crop branch, composed of two lines of feathers on a fold of skin, which distally connects with the sternal region and thus isolates a small furcular apterium.

On the breast there are distinct axillary and sternal divisions. The sternal band narrows abruptly at its posterior end, and there may be a distinct gap between it and the abdominal one. There is a short recurrent branch projecting anteriorly and laterally from the abdominal region. The configuration of the pectoral area is similar to that of the cathartid, but the outer bounding line of the pectoral apterium has been lost. The axillary division of the ventral tract is continuous with the subaxillary tract along the underside of the humerus, the ventral aspect of the shoulder is covered only with down. The narrow abdominal band sweeps around the abdominal apterium; posteriorly, it approaches the midline, on the pubis, just in front of the anus. There are about 26 *A* lines on the ventral aspect of the body from the angle of the shoulder to the anus but these are hard to follow while the *B* lines are strongly marked.

The head has a large bare area around the eye which is surrounded by bristle-like feathers. The eyelids have long lashes, and the loral bristles are reduced in number. Dorsally, the head is fully covered, the feathers becoming much enlarged and elongate on the nape and upper neck to form the crest plumes. The dorsal cervical band is fairly broad and ends



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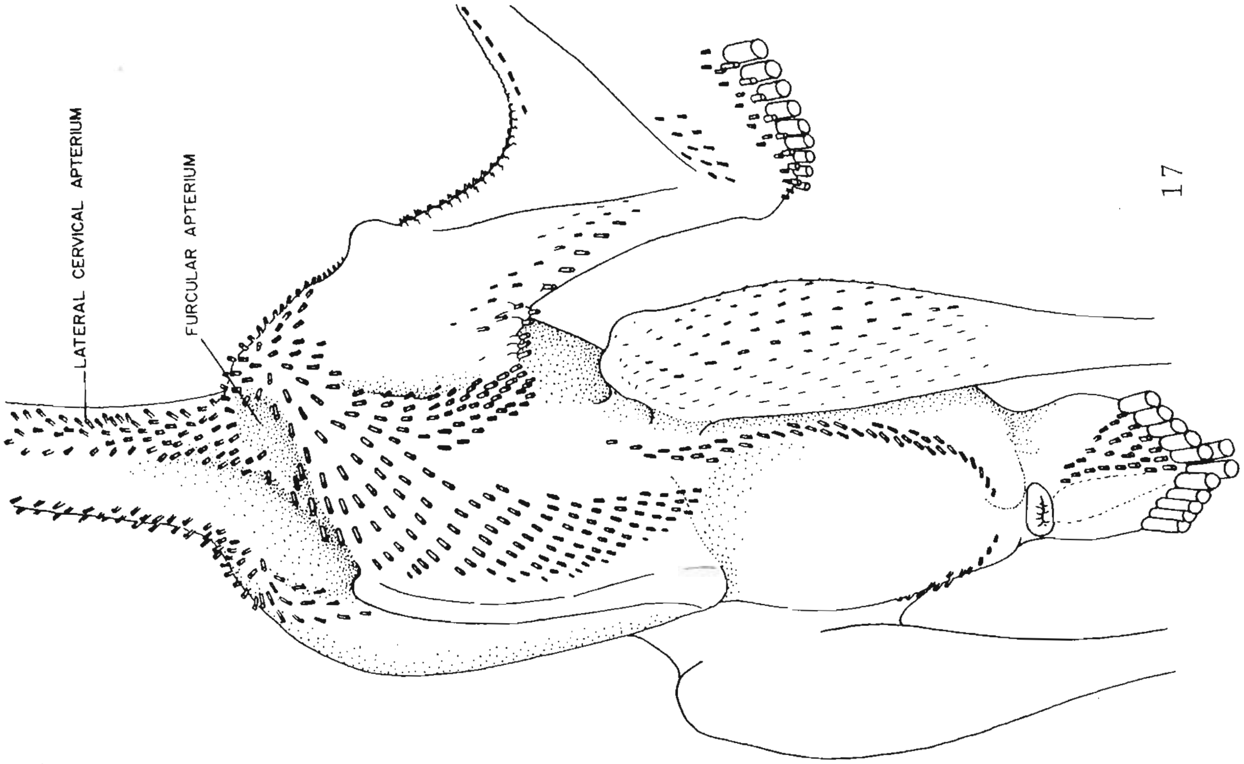

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Fig. 17. Ventrolateral aspect of body of specimen of *Sagittarius serpentarius*.

Fig. 18. Dorsal aspect of body of specimen of *Sagittarius serpentarius*.

posteriorly in the separated interscapular bands (fig. 18). The latter are dense aggregates, quite different from those of the other falconiforms. Posteriorly the interscapular bands end abruptly, with a distinct gap separating them from the lumbar region. The lumbar feathers are much reduced and grade into the pelvic region. The spinal apterium extends from just behind the level of the shoulder to well into the caudal region.

Compton (1938:187), working from a skin, described a median row for the pelvic region. In the two specimens I examined there was none, and Nitzsch (1867) did not observe it. A skin was examined in order to check the possibility of determining the presence or absence of such a row, but it was too difficult keeping track of the individual feathers encased in down.

The scapular tracts are strongly developed with marked transverse rows of feathers; a small anterior shoulder apterium is visible from above (fig. 18).

Eleven primaries are usually present (fig. 19), the 11th vestigial but sometimes as large as 1 3/4 inches in length. There are 20 secondary remiges set in a wide patagium, and the wing is diastataxic. The carpal remex is well developed (3 inches) and has a nearly full-sized greater covert (5 inches). Four large alular feathers are present while a 5th (proximal) covert is discernable. The alular digit bears a claw. The dorsal aspect of the wing is peculiar in having an apterium between the most posterior row of lesser coverts and the more anterior ones.

There are 12 rectrices set in a weak patagium. The number of coverts above is like the cathartid while below the series is continued forward through seven transverse rows to the anus.

This type is lightly covered with down, which occurs within the pterylae as well as on the apteria; many of the feathers of the primary cover appear to be reduced to down. No natal chick was available for examination.

The sagittariid type can be characterized by the large ocular apteria, the large eyelashes and ocular bristles, presence of a submandibular apterium, the broad anterior end of the lateral cervical apterium reaches up under the angle of the jaw and below the ear, the continuous ventral cervical and sternal regions, with a small furcular apterium, presence of a pectoral apterium, narrow abdominal bands ending on the pubis near the midline, large number of *A* and *B* lines dorsally and ventrally, well-developed undertail coverts, broad interscapular regions with many small units, broad scapular tracts, medial feathers present only in the caudal part of the spinal tract, and possession of a dorsal alar apterium.

Speculation is in order at this point which stems from a comparison of the ventral tracts of the cathartids and *Sagittarius*. In *Cathartes* the pectoral apterium is poorly developed while through *Coragyps* and *Sarcoramphus* it reaches its peak of development in *Gymnogyps* and *Vultur*. This apterium increases in size coincident with the reduction of feathers. *Sagittarius*, shows a superficial resemblance to *Gymnogyps*, but the apterium appears to be the result of a split with the feathers being moved to either side of the apterium as in the accipitrid or falconid.

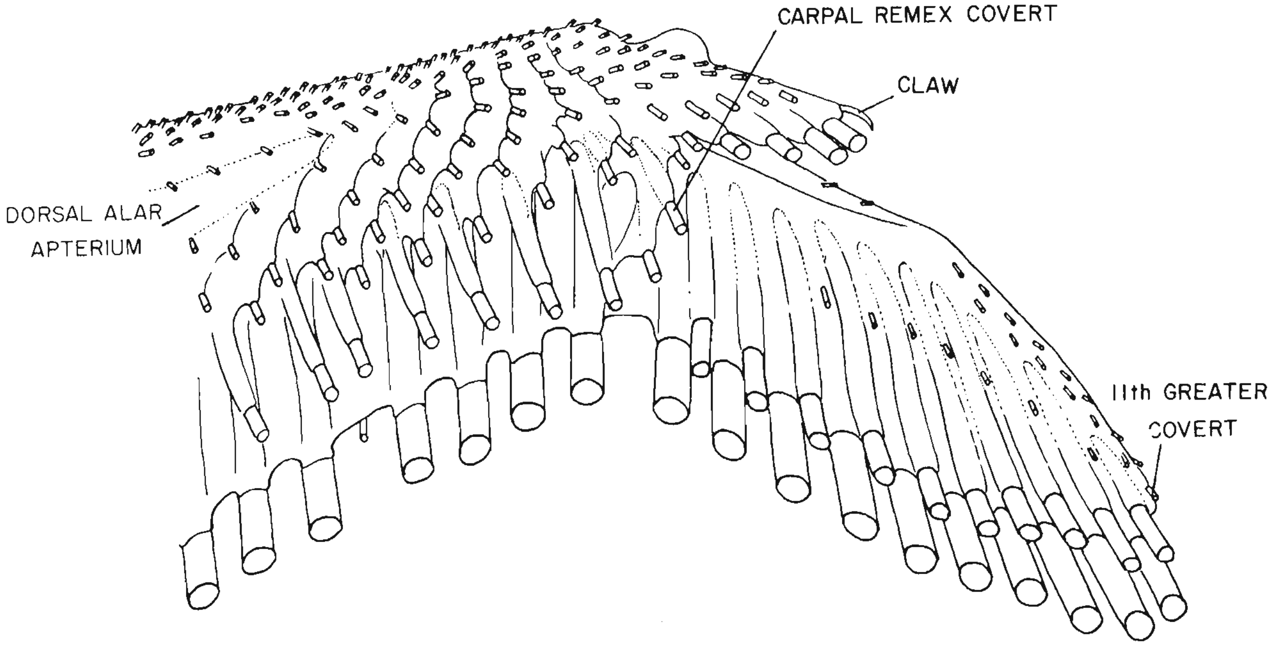

Fig. 19. Dorsal aspect of distal part of wing of specimen of *Sagittarius serpentarius*.

The Accipitrid Type (figs. 1 - 11, 20 - 29)

Ventrally there is a submandibular apterium (fig. 20), except in *Necrosyrtes* where the skin of the throat is thickened, wrinkled, and dotted with scattered bristles. The ventral cervical band bifurcates well up on the neck and connects with the sternal region only at the shoulder by a narrow band of feathers on the cervical patagium. In *Torgos* and *Necrosyrtes* this band is missing as a recognizable entity, the latter genus has but a single well-developed plume at the shoulder to represent it (fig. 23). The lateral divisions are present in *Pseudogyps* and *Neophron* (fig. 21). In most accipitrids the ventral cervical band ends on the crop in a posteromedially directed strip, the crop branch. The size and development of this branch varies, and in some hawks it is identified more by the furcular apterium than anything else. In *Aquila* the furcular apterium is spanned by semiplumes.

The crop area is usually covered by down, but in the aegypiin vultures and some of the aquilin genera* the crop area is densely covered with short, appressed, pennaceous feathers. In the aegypiins the crop patch is particularly well developed and without interspersed down; anteriorly it is cut off sharply along the line

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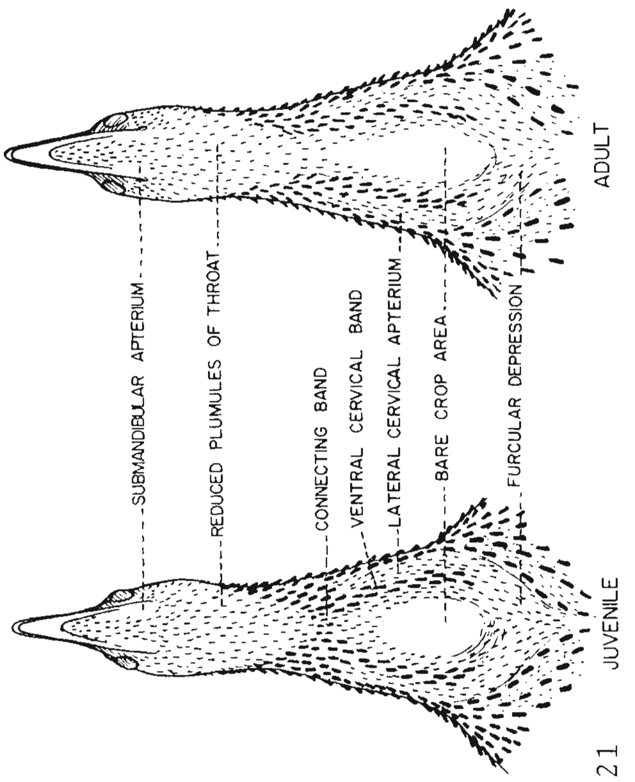
* Aegypiin vultures--*Aegypius, Torgos, Trigonoceps, Sarcogyps, Gyps, Pseudogyps,* and *Necrosyrtes*.

Aquilin genera--eagles with the tarsus feathered all around: *Aquila* (+*Uroaëtus*), *Ictinaëtus*, *Hieraaëtus*, *Spizaëtus*, *Oroaëtus*, *Spizastur*, *Lophaëtus*, *Cassinaëtus*, *Stephanoaëtus*, *Polemaëtus*.



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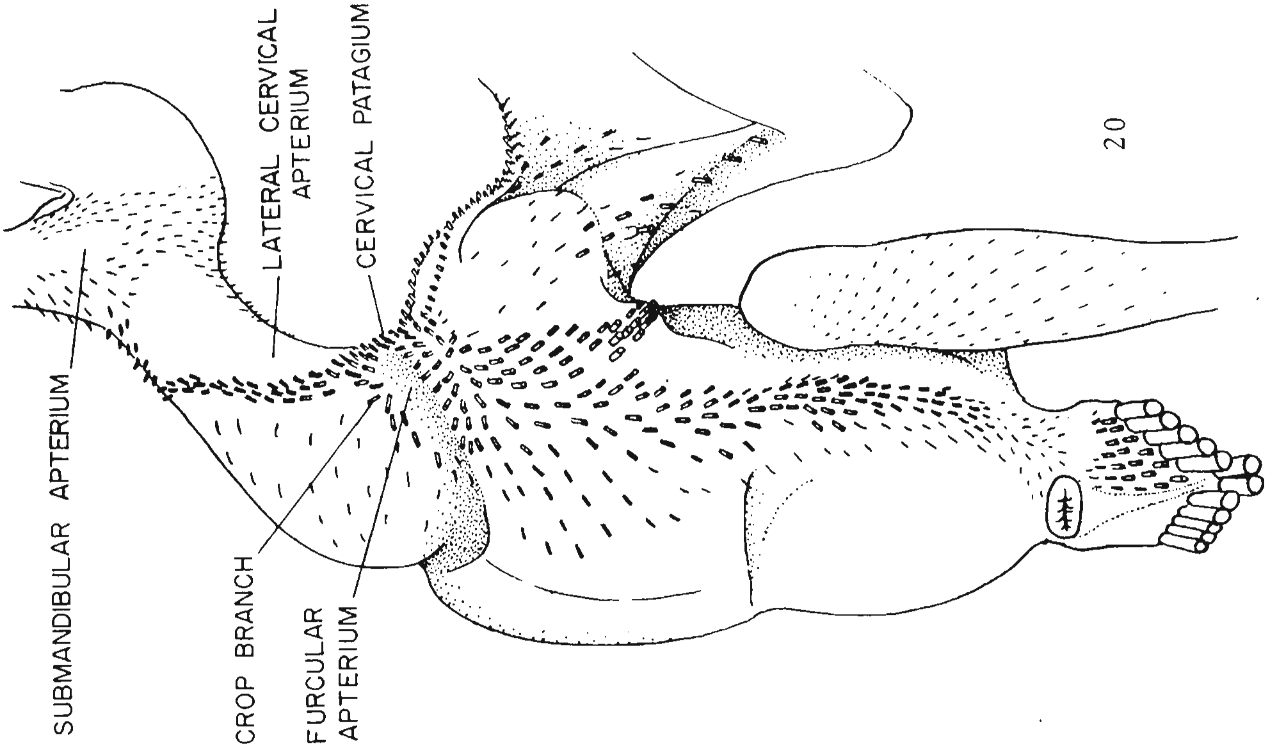

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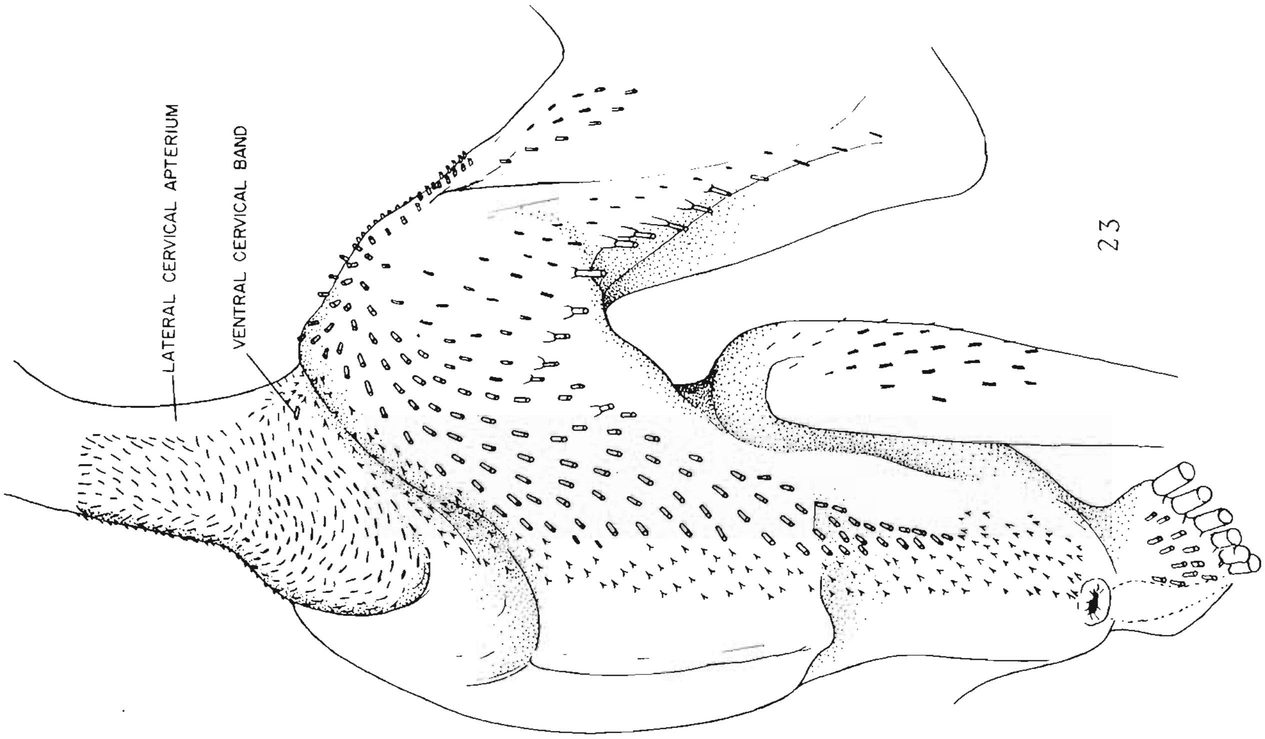
Fig. 20. Ventrolateral aspect of body of specimen of *Gampsonyx swainsonii*.

Fig. 21. Ventral view of throat region of adult (A) and immature (B) specimens of *Neophron perenopterus*.



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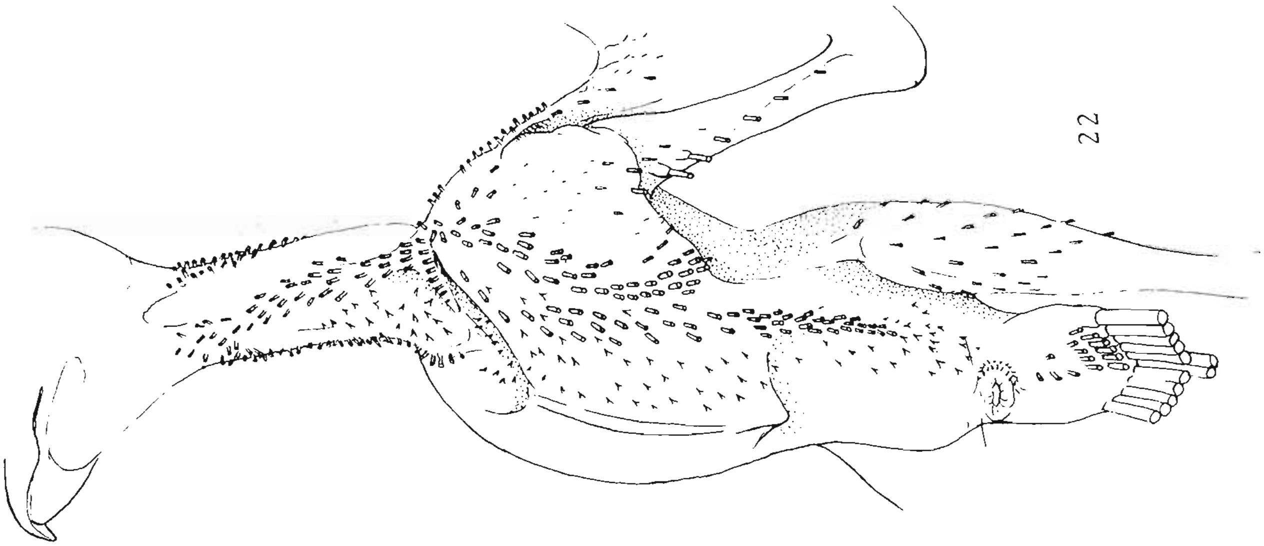

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Fig. 22. Ventrolateral aspect of body of specimen of *Aviceda subcristata*.

Fig. 23. Ventrolateral aspect of body of specimen of *Necrosyrtes monachus*.

of the reduced head feathering. In the aegypiins (except *Pseudogyps*) the lateral divisions of the ventral cervical band are not developed. In the aquilins the patch has down amongst the plumes and the patch is separated from the lateral divisions of the ventral cervical band by a distinct gap. Down also occurs on this isolating gap. The crop patch is poorly developed in most species of *Aquila* but is large in *A. verreauxi* and in *Stephanoaëtus* and *Oroaëtus;* in these it approaches the condition found in the aegypiin. In *Neophron*, the midline of the crop area is bare, the skin highly colored (fig. 21).

The development of the ventral cervical band is related in part to the lateral cervical apterium. This apterium varies in size according to the contours of the shoulder and the length of the neck. It usually extends forward nearly to the head while in the long-necked vultures it extends more ventrally.

On the breast (the pectoral region), the ventral tract may be undivided or show every gradation of division to distinct sternal and axillary parts. The division is achieved not by way of repression of feather development in the intermediate region, as in the cathartid, but by a longitudinal split with subsequent medial and lateral movement of the feather rows (the split does not follow the *B* lines). The axillary portion of the ventral tract ends posteriorly at the margin of the pectoral muscle mass and angles outward (and dorsally) along this margin. This band is separated from the subaxillary feathers of the humerus by a varying gap. In *Buteo* (fig. 5) or *Aquila* (fig. 1) this gap is narrow, being due to the loss of one or two rows of feathers; in *Accipiter* a much wider gap appears, while in *Torgos* there is none. Each feather row is represented in *Circus*, but not at a single level; thus, the gap is purely an arbitrary one (it is arbitrary in any case if one considers the continuity of the protegmen).

The sternal band is separated from the keel by a wide medial sternal apterium that widens somewhat on the abdomen. Semiplumes and downs extend medially from the sternal band to cover much of this apterium, the mid-ventral line is bare (figs. 9, 20). The abdominal continuation of the ventral tract ends well before the pubis. Although the width of the ventral tract varies on the sternum and abdomen, its relative position is constant throughout the group. The number of *A* lines varies from about 16 (*Aviceda*, fig. 22, and *Necrosyrtes*, fig. 23) to 25 (*Buteo, Aquila*).

Some notion of the range of variability of the ventral tract is shown by comparing *Necrosyrtes* (fig. 23) with *Aviceda* (fig. 22). It is of interest to note the great reduction in the number of both extrapterylar down and contour feathers in the latter. The intrapterylar down scarcely numbers more than the contour plumes in *Aviceda* and there are probably fewer than one half the number of plumules and plumes as compared with *Necrosyrtes* (Hutt and Ball, 1938). Reduction of the number of *A* lines on the undersurface of the latter is apparent, the loss being in the abdominal rows. This would appear to be a neotenic situation (figs. 6, 7).

The capital feathering in this family shows irregular variation. The aegypiins are usually considered as "naked" headed but in reality show a dense growth of reduced feathers, especially on the crown and at the nape. Reduction is most extreme laterally, at the throat, and around the neck just before the ruff and crop patch. On bare faces (around the eyes and the lores) there are hairlike feathers; such faces are found in *Gymnogenys*, *Terathopius*, and *Haliaeetus*. Among the aegypiins (*Torgos*) the submandibular apterium is continuous with a lateral mandibular one. *Necrosyrtes* has only the mandibular apterium. The facial ruff of *Circus* (fig. 24) resembles that of the owls; such eagles as *Spizaëtus*, *Lophaëtus*, and *Harpia* have crests or "ear" tufts. The variations of the capital feathering indicate that this area is extremely plastic.

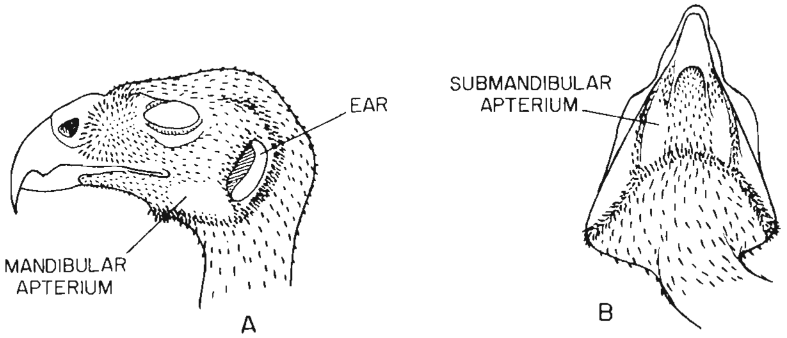
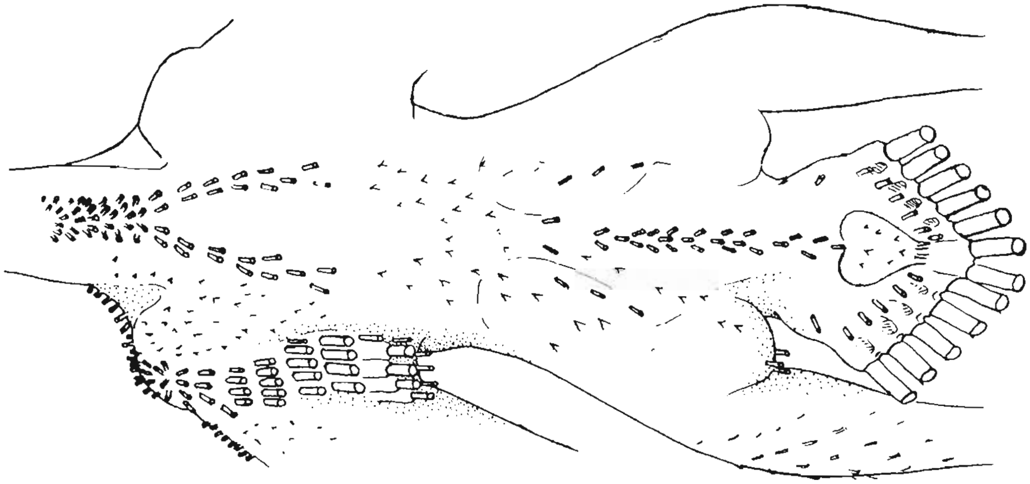


Fig. 24. Lateral (A) and ventral (B) views of head of a specimen of *Circus cyaneus*.

The dorsal cervical band is poorly developed anteriorly and forms a ruff about midway on the neck of such vultures as *Torgos* or *Necrosyrtes*. In all accipitrids it bifurcates at the body to form bilateral interscapular bands (figs. 25, 26, 27, 28). These extend posteriorly the length of the scapulae; although they are usually narrow, they reach a substantial width (five feathers) in *Torgos*. The interscapular portion of the spinal tract connects with the lumbar region by means of a few almost bilaterally arranged feathers. Posteriorly the spinal tract is more strongly developed and has median feathers in both the pelvic and caudal regions. One specimen of *Torgos* largely lacked a median row while another had it (figs. 28 a and b). Laterally the pelvic area connects with the few feathers of the femoral region.

Paired feathers occurred just before the oil gland in two specimens of *Aquila chrysaëtos* while two specimens of *Uroaëtus* had single median feathers. Paired feathers were also observed in *Elanus* and *Circus*. Two of three red-tailed hawks showed but a single terminal feather while the other had a tandem pair, the last at the base of the oil gland. The presence of small semiplumes in this region indicates the possibilities for individual variation.

The scapular tract is well developed with transverse lines of feathers. The tract connects anteriorly with the dorsal and ventral cervical tracts; connection with the latter is by means of the strip of feathers on the margin of the cervical patagium.



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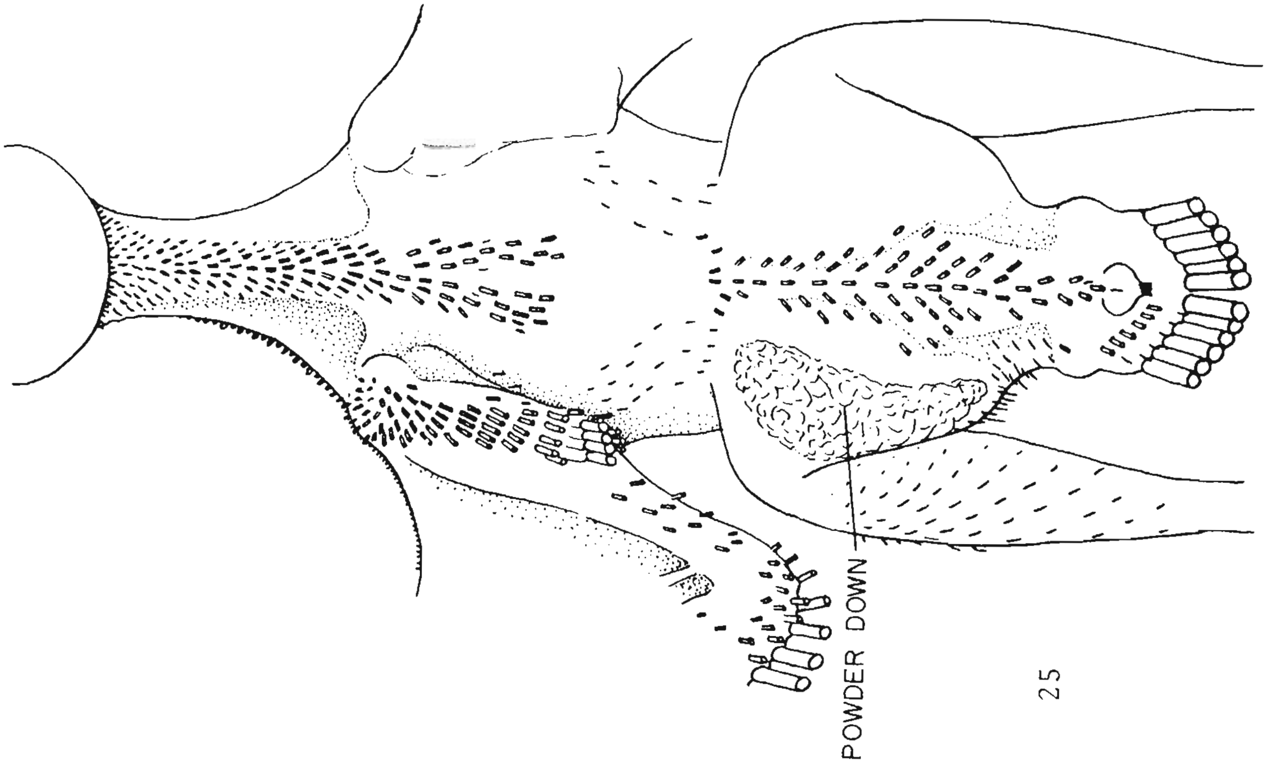

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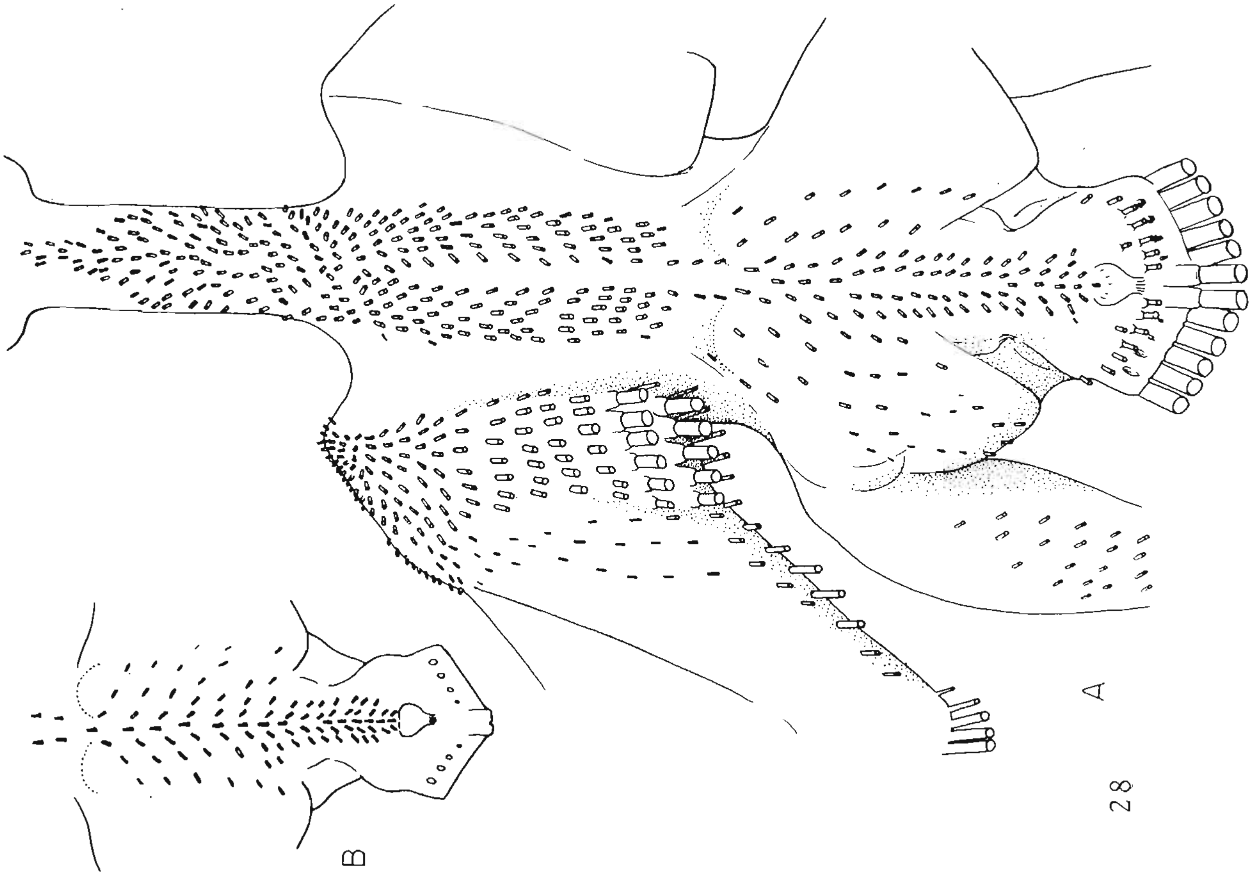
Fig. 25. Dorsal aspect of the body of a specimen of *Gampsonyx swainsonii*.

Fig. 26. Dorsal aspect of the body of a specimen of *Aviceda subcristata*.



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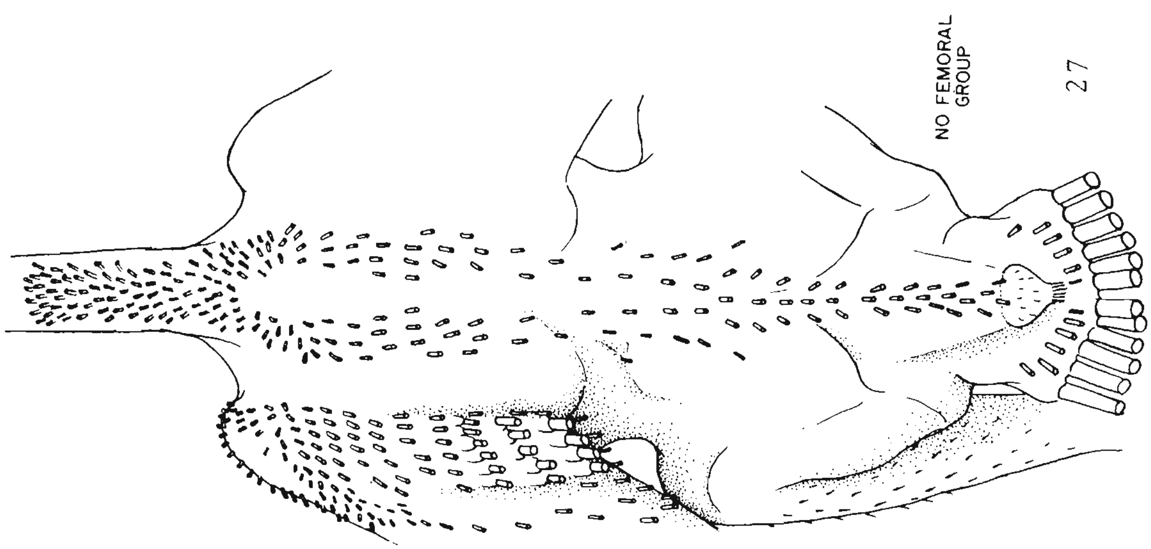

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Fig. 27. Dorsal aspect of the body of a specimen of *Necrosyrtes monachus*.

Fig. 28. Dorsal aspect of the body of a specimen of *Torgos tracheliotus* (A); (B) pelvic region of a second specimen.

There is a small anterior shoulder apterium visible from above.

Compton's "lateral scapular region" does not appear in *Aquila* (+*Uroaëtus*), *Torgos*, *Aviceda* (most of the accipitrids), but it is of questionable significance in any case. A group of feathers which might bear this name is well developed in owls (figs. 45-48).

The alar tract (figs. 29 a, b, c) has a carpal remex with a well-developed covert. Eleven primaries are usually present; the outermost may be extremely reduced or missing as in one specimen of *Pseudogyps* (deWitt Miller, 1924a:314) and several of *Accipiter cooperii*. The number of secondaries is: 14 in *Aviceda*, 15 in *Circus*, 19 in *Aquila*, 23 in *Pseudogyps*, and 24 in *Terathopius* and *Torgos*.*

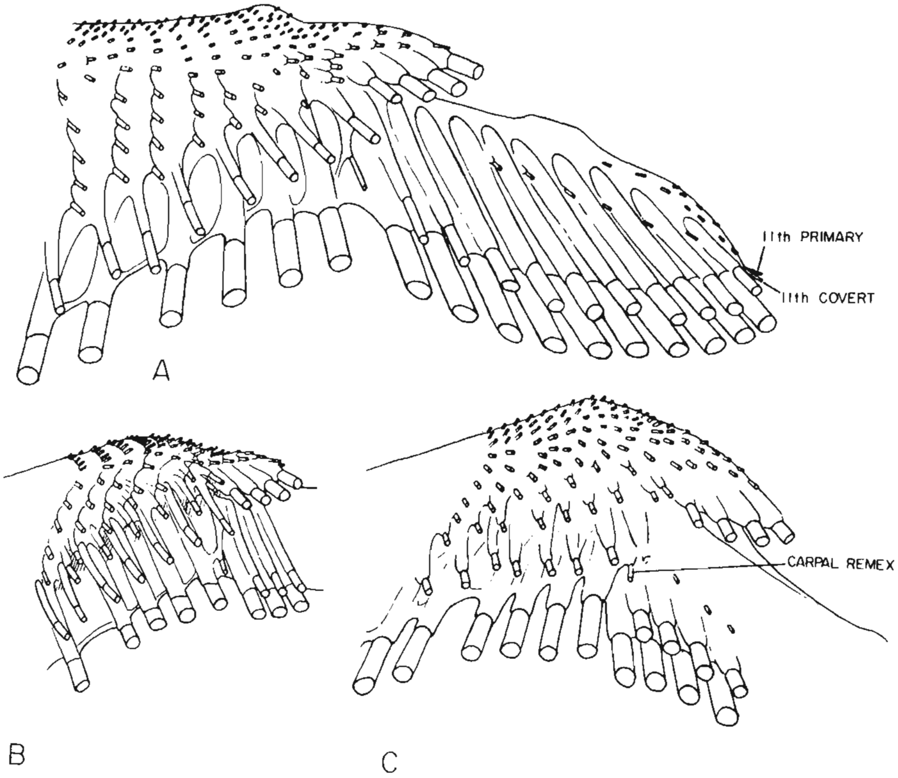


Fig. 29. Dorsal aspect of the distal part of the wing of (A) *Aquila audax*, (B) *Buteo jamaicensis*, and (C) *Torgos tracheliotus*.

* *

* Nitzsch (1867) gave 26 as the number for *Gyps*, 25 for *Aegypius* and 23 for *Terathopius*, while Chapin (1932) commented that "The number of secondaries possessed by *Terathopius ecaudatus* is the greatest found in any bird of prey. Mr. W. deW. Miller counted twenty-five in one specimen, and twenty-six in another. Only in *Gyps coprotheres* did he ever find as many as twenty-five..." In contrast to deWitt Miller's result, I counted 23 plus 1 inconspicuous proximal feather in *Terathopius*. The counting of either primaries or secondaries is extremely difficult and arbitrary in that the terminal feathers grade into the coverts in such a way that one is often not quite sure where to stop unless the specimen has been clipped.

The wing is diastataxic and the secondaries are set in a wide patagium, which is most reduced in such long-winged forms as *Torgos* (fig. 29 c). A dorsal, intercovert apterium is lacking. Frequently there is a claw on the alular digit.

The pattern of lapping of the wing feathers was studied by Goodchild (1886:202), who noted that it was fairly uniform in all of the hawks except *Pernis*. Several stuffed specimens of the latter had the posterior row of cubital coverts lapping distally, somewhat as in the ciconiine birds (storks) or in *Crax* (a gallinaceous bird).

The number of tail feathers is usually 12, but *Gyps*, *Neophron*, and *Haliaeetus pelagicus* have 14 rectrices. One greater covert is present for each tail feather. The tail feathers are usually set in a patagium (fig. 26), but this is lacking in such genera as *Elanus*, *Gampsonyx* (fig. 25), or *Necrosyrtes* (fig. 27). There are four to six transverse rows of undertail coverts; with six being the usual number.

The crural tract shows some variation. Reduction in the size of feathers is greatest among the aegypiins. Only a few appear along the posterior lateral margin of the legs of *Torgos*. Otherwise the tibia is heavily covered with down.

The lower leg (tarsometatarsus) is feathered in some genera, but in most it is scaled. A feathered "tarsus" may have little taxonomic significance as both feathered and scaled tarsometatarsi can be found within the same genus (*Buteo*) or even within the same species, as in *Buteo hemalasius* (Portenko, 1929) and *Haliaeetus pelagicus* (Robinson, 1924). Two types of feathered tarsometatarsi occur in the accipitrids; one has a row of large plates (scutes) extending up the posterior aspect (*Buteo*), and the other is feathered all around (the aquilin, as defined p. 30. figs. 1, 2).

The tarsal feathering of *Aquila* is of interest in that the feathers are largest along the anterior aspect of the leg and most reduced (down-like) posteriorly; there is a fairly well defined intermediate zone laterally. When only a few feathers occur in the various species of *Buteo*, they are along the anterior aspect. Scales are lacking among the feathers of these tarsometatarsi and appear only on the margins of the feathered area. In *Uroaëtus* the bare, scaled heel pad extends as a narrow line down the tarsus for two-thirds of its length.

The distribution of down has already been mentioned in the case of the capital feathering of *Gypaëtus*, and the crop patch of the aquilin and aegypiin. *Gypaëtus* is the only bird in which the plumules of the metategmen have been converted to semiplumes. Generally, down occurs over the entire body, on the head, in the pterylae and on the apteria. In the case of *Buteo* or *Aquila*, there are, on the top of the head, about two down feathers for each contour feather; in *Gampsonyx* there is only an occasional plumule on the crown. Units of the primary cover give rise to a part (or most, if not all in *Gampsonyx*, fig. 20) of the down on the apteria. The natal chick has been figured (figs. 3, 4).

The accipitrid type is definable more in the relative positions of its parts than in their presence or absence. There is generally a submandibular apterium; a forked ventral cervical band with a down covered crop, or a plumed crop area with no distinct ventral cervical band; the furcular apterium is well developed, the ventral cervical band and pectoral region are joined at the shoulder; the median ventral apterium is wide in the pectoral region; this tract is usually divided into axillary and sternal branches, the latter continues onto the abdomen where it ends about midway. There are at least three transverse rows of undertail coverts; the lumbar area of the spinal tract is usually repressed, leaving a gap in the dorsal tract. There is a medial row of feathers in both pelvic and caudal regions, the oil gland is tufted. The most distinctive feature is the termination of the ventral tract midway on the abdomen.

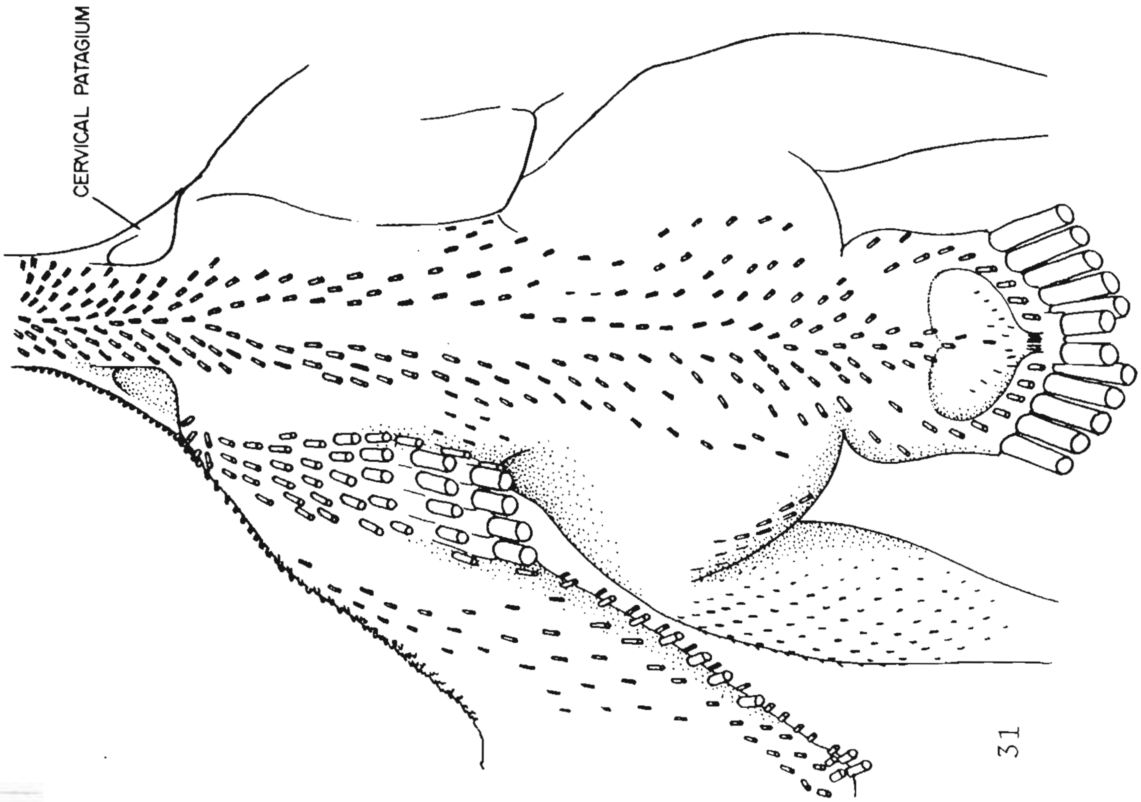
The Pandionid Type (figs. 30, 31)

The osprey (*Pandion*) is generally assumed to have a ptilosis adapting it for its habit of plunging into water to catch fish. Compton (1938) has described the pterylosis of this type and has compared it with that of the cathartid.

The throat region lacks a submandibular apterium; this is due to lack of upfolding of skin medial to the ramus of the mandible, a situation matched in the cathartids and some accipitrids. The ventral cervical band extends posteriorly undivided, over the crop area (fig. 30). The crop feathers are mixed with down and are separated from the pectoral region by a transverse, triangular, furcular apterium which is heavily downed. The ventral cervical band is connected by a narrow strip of feathers along the cervical patagium to the pectoral region just as in other accipitrids. The lateral cervical apterium is triangular, the apex forward, and is much reduced in size as compared with that of the typical accipitrid. The pectoral region is covered uniformly with feathers of one size, and there is only a slight, lateral, axillary condensation. The spacing of feathers is much like that of *Torgos*, and a similar vestigial break can be observed between the axillary and sternal divisions. The median ventral apterium is relatively narrow. The ventral tracts end bluntly in the middle of the abdomen. There are about 24 *A* rows on the ventral aspect of the body.

Dorsally (fig. 31) there is a resemblance to the cathartid in that the spinal apterium extends from the shoulder to the caudal region and in that the interscapular region is not sharply differentiated from the lumbar region. The scapular tract is distinct in that strong transverse rows of feathers are not shown. There is a small anterior shoulder apterium. The number of crural contour feathers is large; there are nearly as many plumes as plumules.

The alar tract has 11 primaries and 22 secondaries; there is a carpal remex with a covert, and four large alular quills with coverts. A claw is at the tip of the alular digit. The wing is diastataxic, and the secondaries are set in a patagium. Like *Sagittarius*, there is a narrow dorsal alar apterium between the bulk of the lesser coverts and the most posterior row. Goodchild (1886:202) noted that the lapping of coverts in the osprey was somewhere between the style of the pygopodes (Alcidae)



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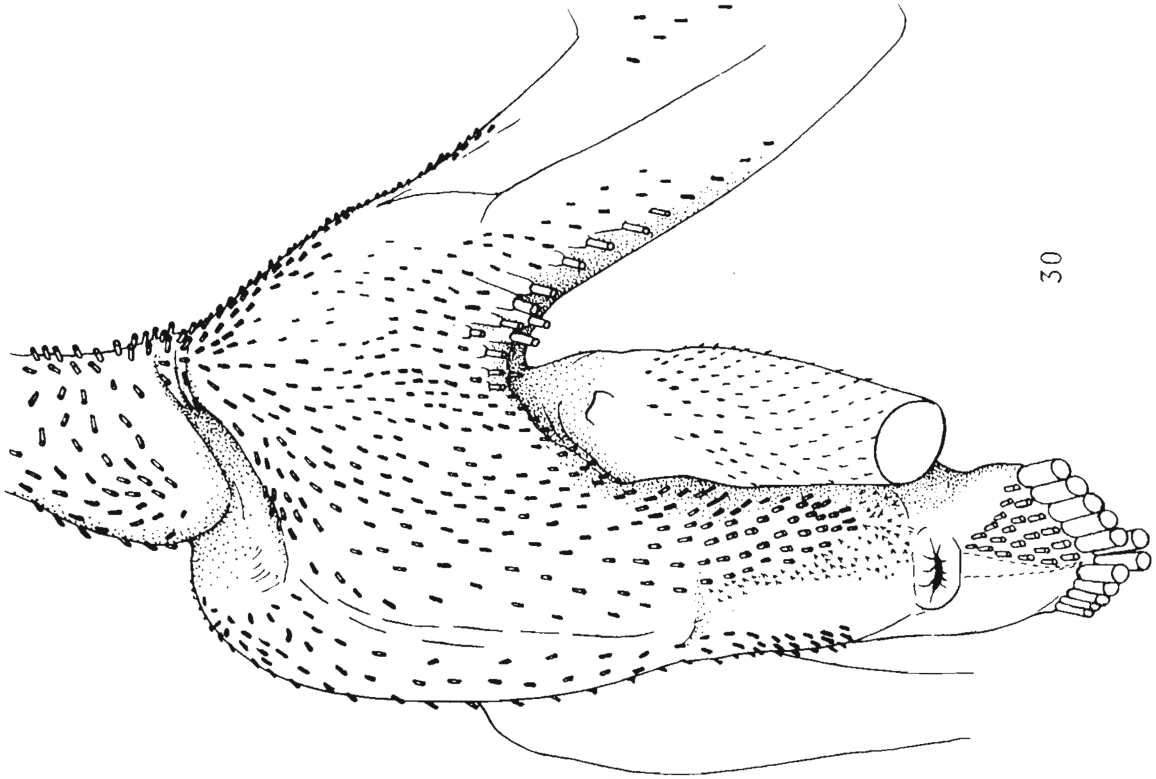

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Fig. 30. Ventrolateral view of body of a specimen of *Pandion haliaetus*.

Fig. 31. Dorsal view of body of a specimen of *Pandion haliaetus*.

and the Accipitres. There are 12 rectrices, not set in a patagium. Each has a greater covert. There are six transverse rows of undertail coverts as in the Accipitridae.

The plumes of the osprey are narrow and lanceolate and form a dense cover over the entire body. "It has long been supposed that...the feathers are without an aftershaft, and time and again ...this alleged character [has] been cited as diagnostic of the *Pandionidae* among the typical *Accipitres*...I was, therefore, surprised to find a perfectly distinct aftershaft with stiff, elastic shaft, on the feathers of the interscapulum, rump and crissum...The plumage of the underparts in general has no aftershaft." (deWitt Miller, 1915:139-140). The body is covered with down. On the top of the head the number of plumules about equals that of the contour feathers; on the body there are irregular α and β rows, much as in *Cathartes* or *Aquila*.

The natal chick, a specimen collected shortly after hatching, has both protilae (prototegmen) and metaptilae (metategmen) in its natal cover. As a result, the body is covered more-or-less evenly with down, which is somewhat longer above than below. The down is very short everywhere compared with that of accipitrids. There is some admixture of shorter down (metaptilae) among the proptilae. No pattern of pterylae and apteria is discernable. The osprey is distinct in that the natal chick has a striped color pattern.

The pandionid type can be characterized by its small, hard-textured, appressed feathers, which have a reduced aftershaft or none; lack of a submandibular apterium; undivided ventral cervical band which continues down over the crop area; reduced size of the lateral cervical apterium, basically undivided pectoral region with only a slight axillary condensation; ventral tract ending about midway back on the abdomen; relatively narrow median sternal apterium; spinal apterium extending most of the length of the dorsal aspect of the body; and a very large number of feathers in the crural tract.

Compton's (1938) comparison of the osprey with the cathartid is unfortunate. The importance of any modification of the capital feathering is questionable; reduction can modify the entire area in closely related groups (*Circaetinae--Aegypiinae*). The size of the ocular apterium is related to the overhanging brow and that of the submandibular apterium with the infolding of skin inside the ramus of the mandible.

Pandion differs from the cathartid type in the following ways: it lacks the bare median ventral cervical and crop strip; the ventral cervical region is not broadly continuous with the pectoral region; there is no pectoral apterium, reduction of the capital feathering, or neck ruff; the ventral tract ends well in front of the anus; the oil gland is not nude; the undertail coverts are not reduced in number; the carpal remex is present, while the secondaries are set in a patagium; some feathers have an aftershaft. Dorsally a resemblance might be assumed, but here again a detailed comparison is more favorable with the accipitrid.

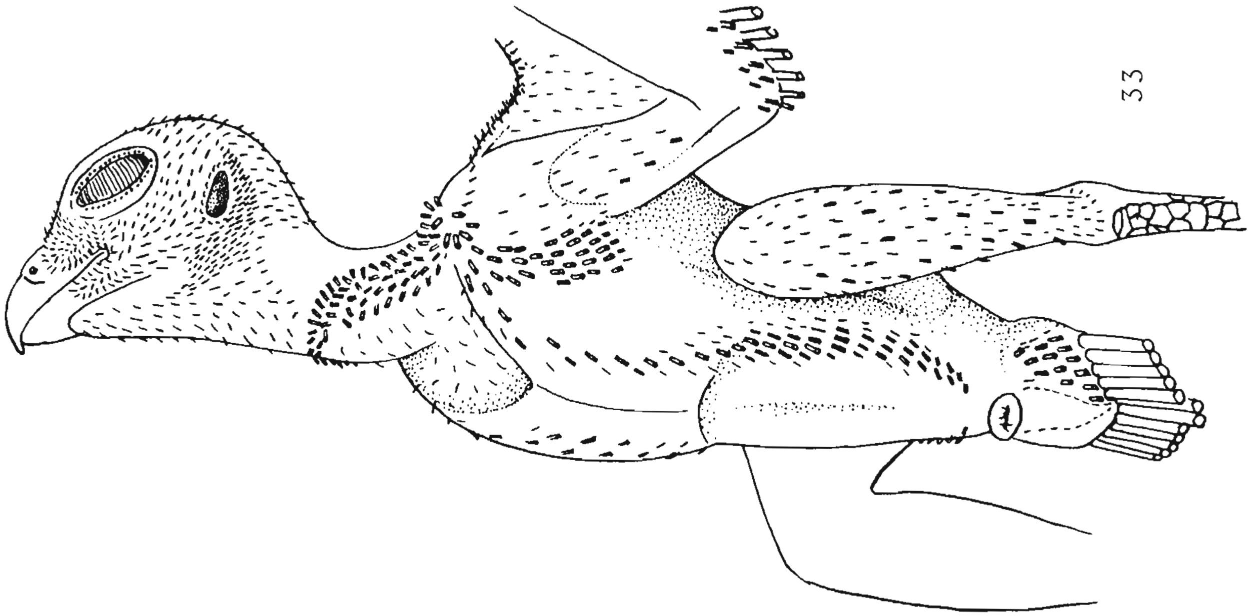
The cathartid type differs from the accipitrid in much the same way. The crop area in *Neophron* resembles that of the cathartid in being bare and the reduced capital feathering and ruff of the aegypiins is somewhat similar. The lateral cervical apterium is large in the accipitrid, small in *Pandion* or *Cathartes* and lacking in most cathartids. On the basis of all comparisons *Pandion* is more like the accipitrid; particularly so in matters of the number of rows of feathers on the ventral aspect of the body, in the termination of the ventral tract midway on the abdomen, in the number of undertail coverts, and in having a carpal remex.

The Falconid Type (figs. 32 - 39)

Ieracidea berigora is described as representative of this type. It compares well with *Falco mexicanus* (Compton, 1938, figs. 5 and 11). There are no significant differences other than those explainable as inaccuracies of illustrations. As in the Accipitridae, the small species, *Polyhierax*, *Micrastur ruficollis*, and *Falco sparverius*, show a great reduction in the number of contour feathers and downs.

There is a submandibular apterium. The ventral cervical band of *Polyborus* or *Daptrius* has a crop branch as in some accipitrids. A crop branch is lacking in the other falconids. The crop is naked and the skin colored in the *Polyborus*, *Daptrius*, and *Herpetotheres* while in the others it is covered with down. The ventral tract (figs. 32-35) is widely divided into sternal and axillary bands. The axillary division is broad and made up of a large number of feathers; it extends posteriorly beyond the margin of the axilla of the wing, ending relatively close to the thigh. It extends into the axilla in some. Its posterior margin is truncated with an angle at the medial and lateral margins. The medial angle is directed posteriorly or posteromedially. Only in *Herpetotheres* is there a distinct gap between the axillary division and the subaxillary tract. *Polyborus* shows a reduction in size and number of feathers at the anterior end of the sternal band, due to the separation of crop branch. The sternal band lies close to the keel; there is no down (some anteriorly) between it and the bare portion of the median ventral apterium. It extends posteriorly, shifting laterally around the abdominal apterium, and ends just anterior to the anus, on the pubis and near the midline. In *Herpetotheres* the abdominal portion of the ventral tract is broader than the sternal band with the result it forms a recurrent division much like that of *Sagittarius* (fig. 17). This recurrent division nearly connects with the axillary division and the crural tract of the leg. There are from 20 to 30 *A* rows on the body.

The spinal tract (figs. 36-38) varies in that the interscapular portion may be undivided (*Micrastur*, *Polihierax*) or divided (*Falco*--only slightly in *Falco sparverius*, *Ieracidea*, *Polyborus*). In the lumbar region there tends to be a gap in the bilateral series. A median row of feathers does not appear until the caudal region, although a couple of median feathers may mark the gap between the ilia anteriorly. A juvenal of *Polyborus* had a median line of small feathers in the pelvic area. *Milvago* is the



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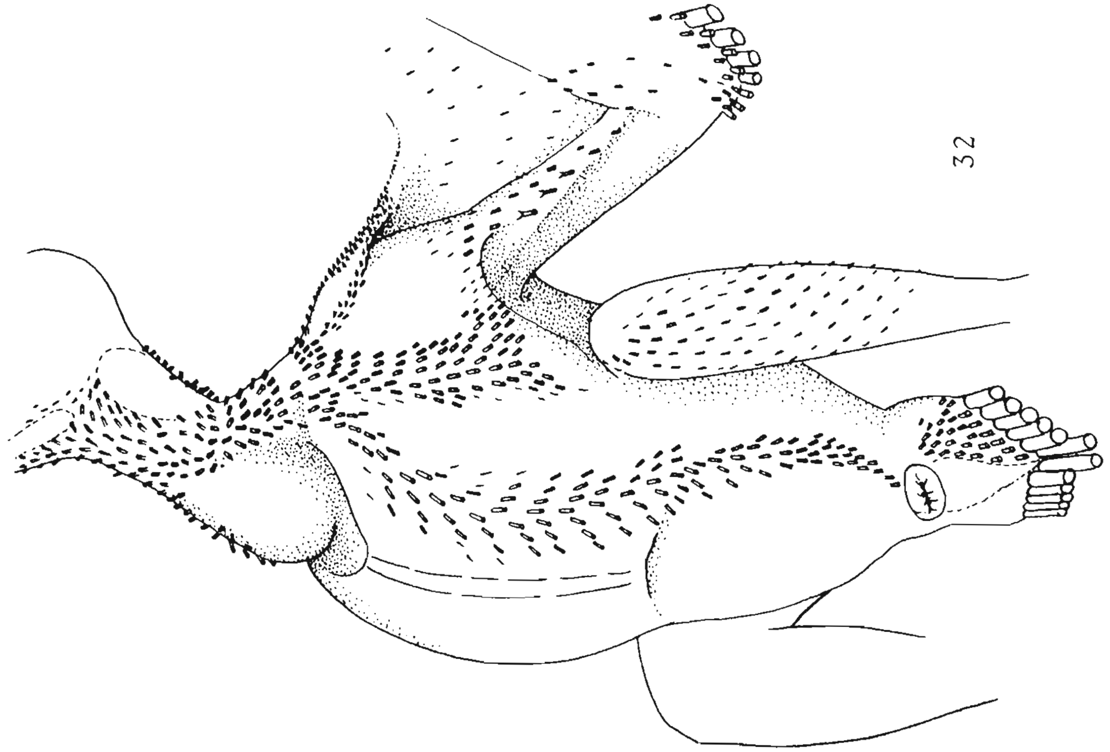

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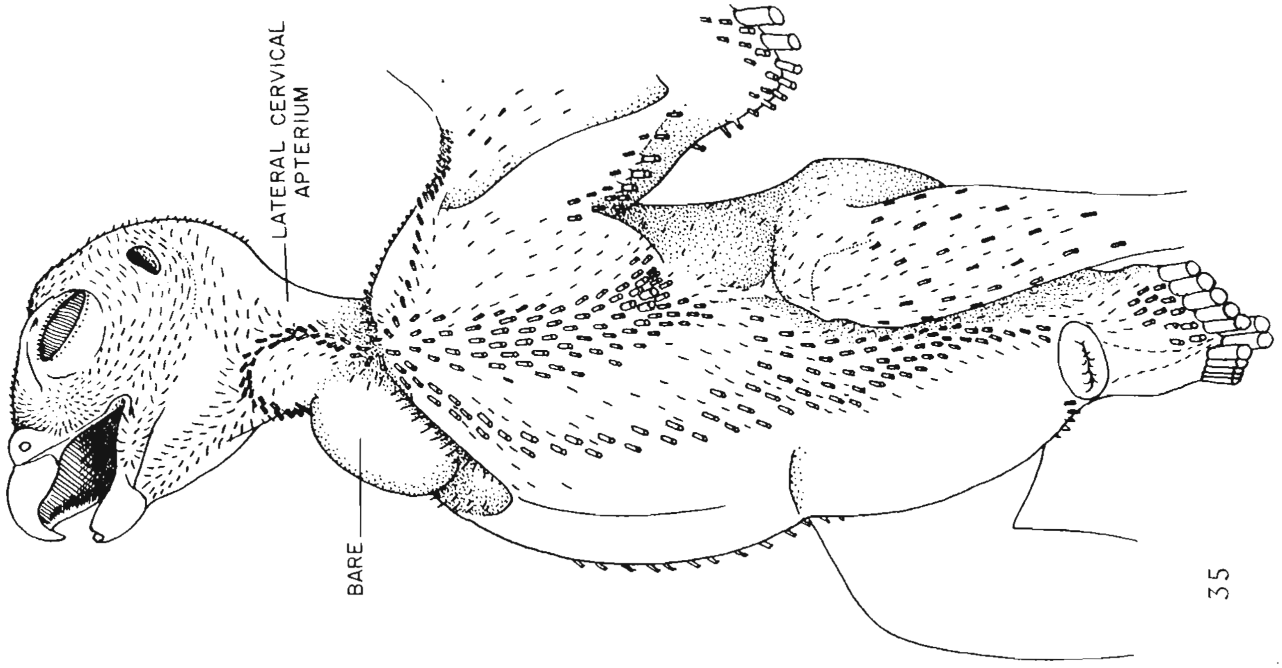
Fig. 32. Ventrolateral view of body of a specimen of *Ieracidea berigora*.

Fig. 33. Ventrolateral view of body of a specimen of *Micrastur ruficollis*.



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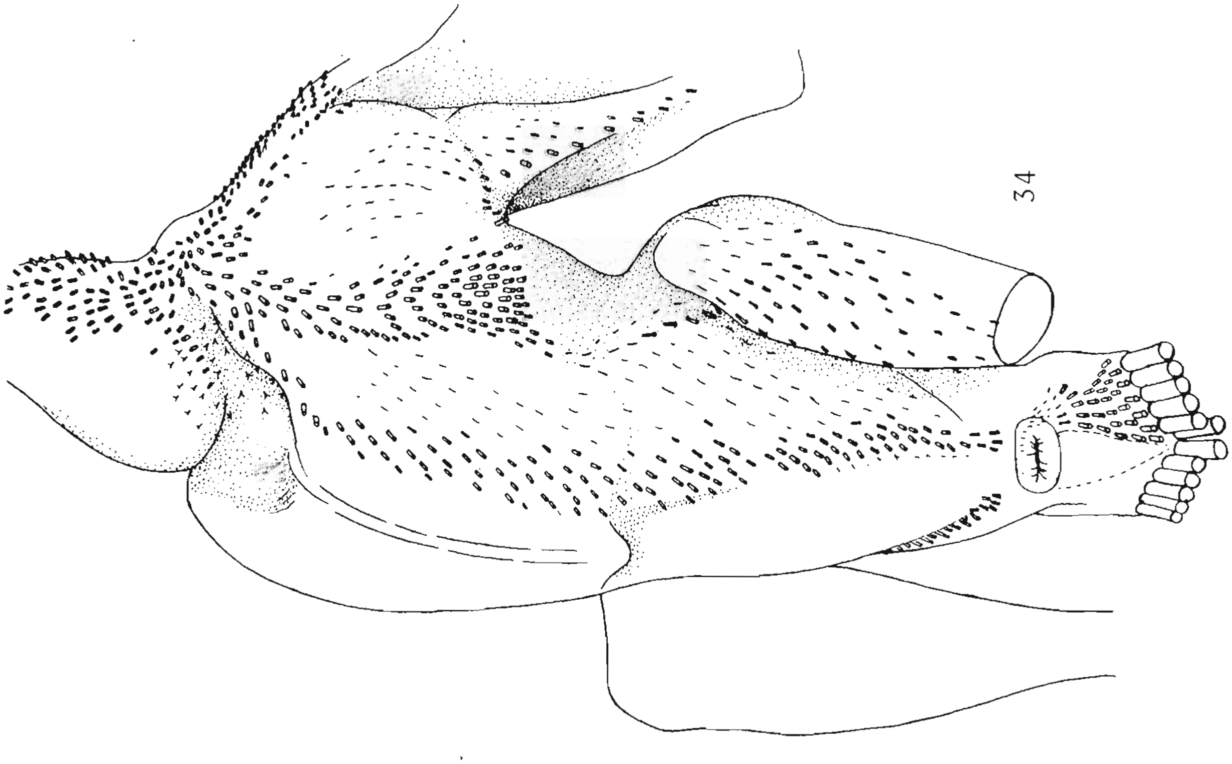
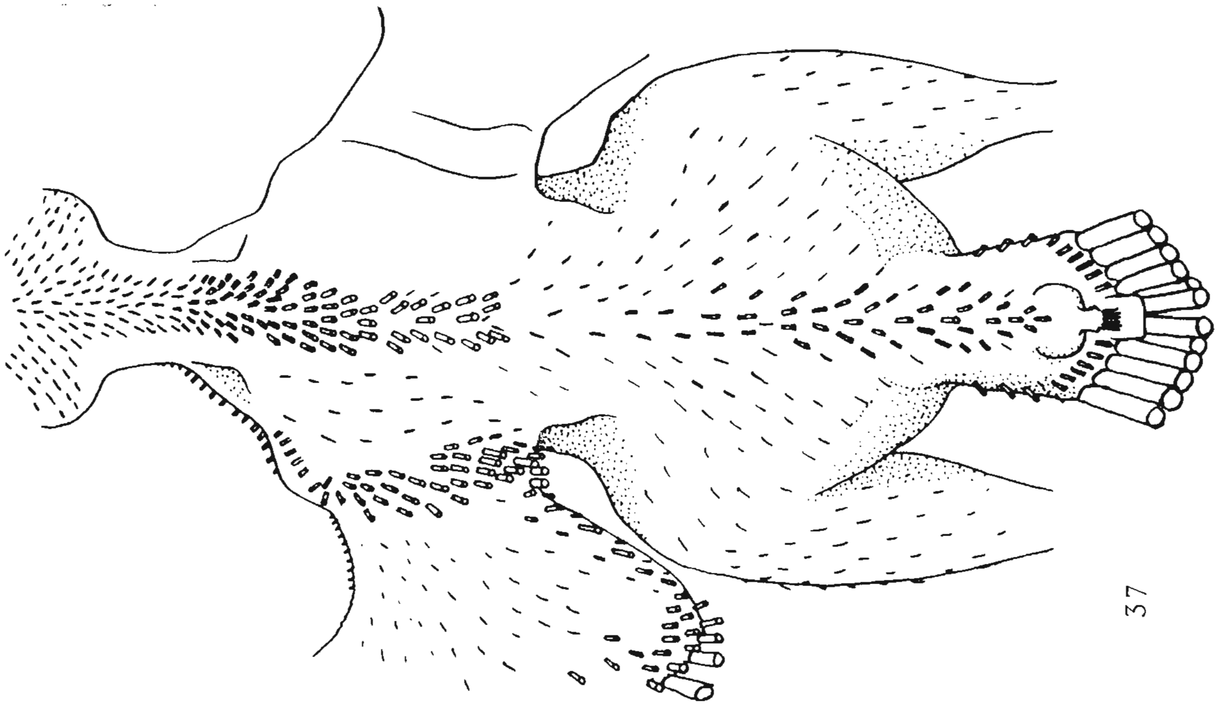


Fig. 34. Ventrolateral view of body of a specimen of *Polyborus cheriway*.

Fig. 35. Ventrolateral view of body of a specimen of *Herpetotheres cachinnans*.



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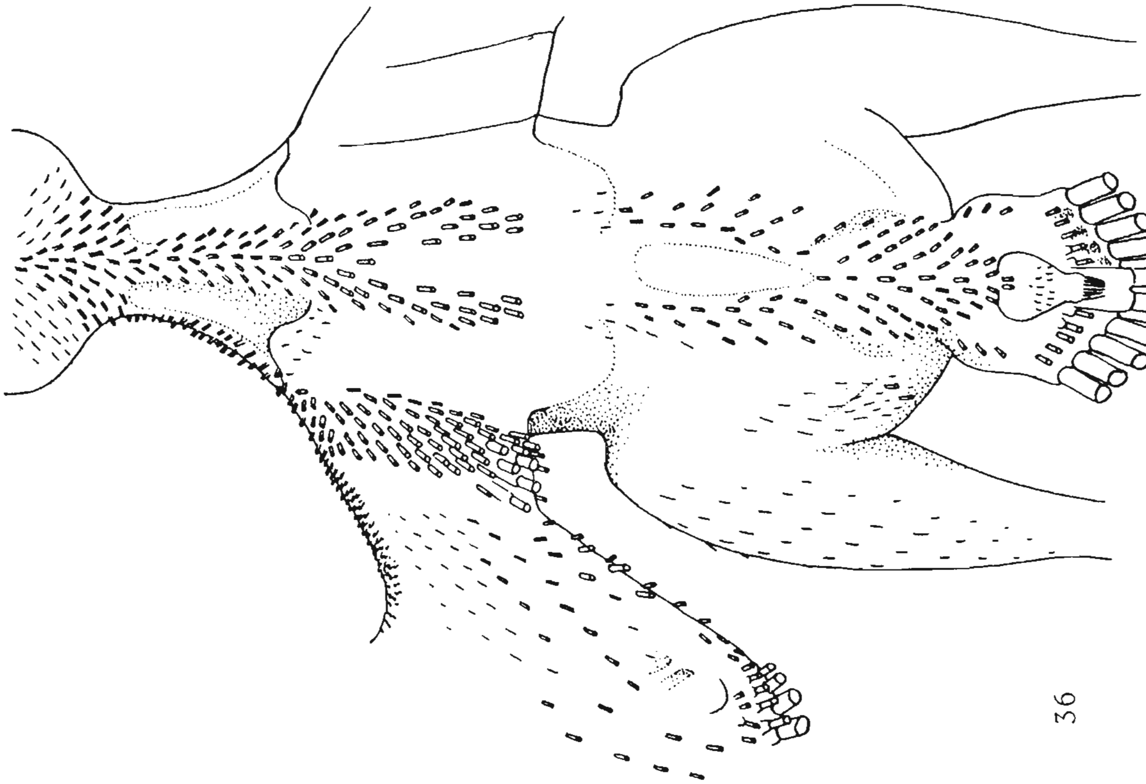

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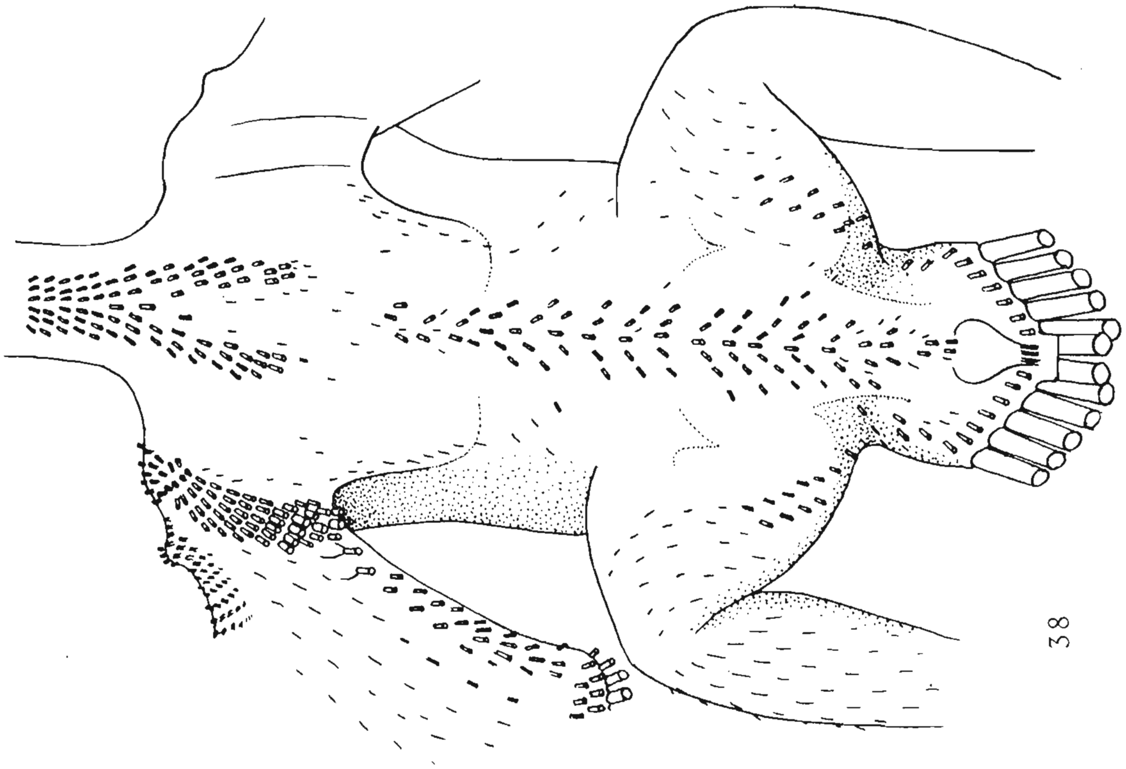
Fig. 36. Dorsal view of body of a specimen of *Ieracidea berigora*.

Fig. 37. Dorsal view of body of a specimen of *Micrastur ruficollis*.



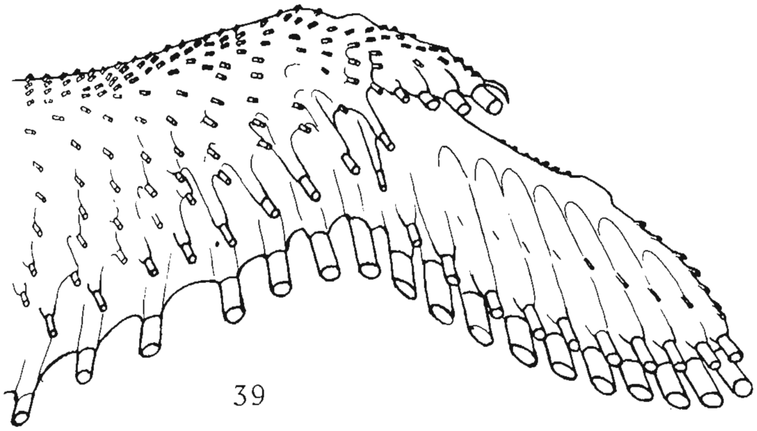


Fig. 38. Dorsal view of body of a specimen of *Milvago chimachima*.

Fig. 39. Dorsal view of distal part of wing of *Polyborus cheriway*.

extreme with a medial row of feathers in the caudal and pelvic regions.

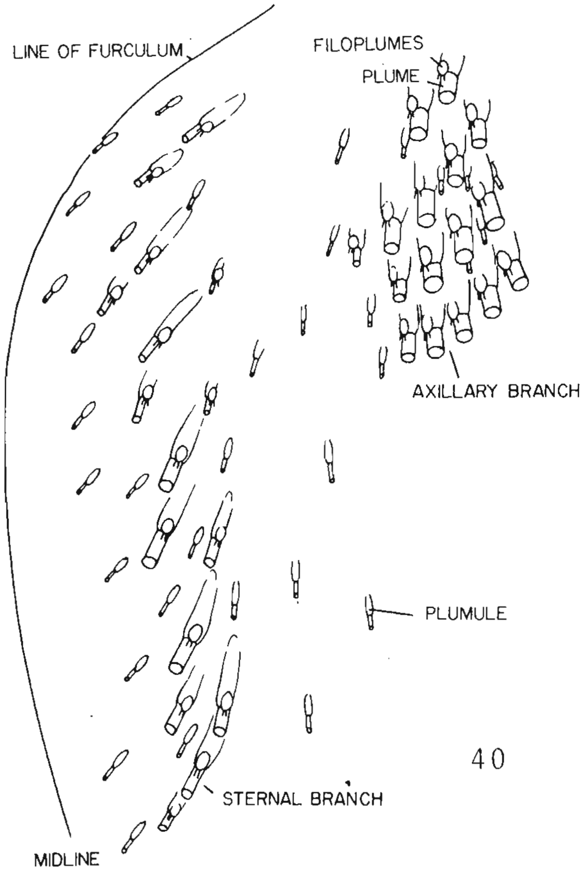
The scapular tract is distinctive, with the exceptions of *Daptrius* and *Milvago*, in its lack of well-defined transverse rows of large quills. At the shoulder a band of feathers, which connects the ventral tract with the marginal wing coverts, extends out on the tensor patagii muscle to separate off a well marked, anterior shoulder apterium. In the accipitrid type, this line of feathers is weakly developed and separates a poorly defined apterium, located more on the anterior aspect of the shoulder so that it is visible dorsally. In *Cathartes* this muscle does not show through the skin nor is it marked with feathers; the apterium is present though small. In *Pandion* the apterium is poorly defined, although feather enclosed, as in the accipitrids.

The alar tract (fig. 39) has 11 primaries, except in *Polyborus* which has 10; as in the other families, the 11th is vestigial when present. The carpal remex and its covert are present, there are four alular quills and a terminal claw, the secondaries are set in a patagium and number 15 except in *Polyborus* which had 18.

There are 12 rectrices, set in a weak patagium in most forms (*Falco, Ieracidea, Micrastur*); a patagium is lacking in *Polihierax, Herpetotheres, Daptrius,* and *Polyborus*. The oil gland is tufted in all except *Microhierax*. The number of undertail coverts may be reduced, they vary from six rows (*Ieracidea*) to three rows (*Herpetotheres*).

The body in the adult, with the exception of the top of the head (occasional tufts in *Herpetotheres*), is covered with down, but the number of plumules does not exceed the number of plumes in the pterylae (figs. 40, 41). *Herpetotheres* and *Micrastur* have the greatest number of units in the down cover while *Polyborus* and *Daptrius* have the least. In the latter genera, only an occasional down feather is found in the pterylae, and all the down feathers have filoplumes associated with them. The spacing of the plumules on the apteria is that of proptilae, rather than metaptilae (fig. 34).

The paucity of plumules in the adult is not as one would expect from the developmental picture for the peregrine falcon (based primarily on Witherby, 1921:108). The chick when hatched is thinly covered with short creamy-white down A(proptilae). There are bare areas around the eyes, at the sides of the neck, and on the crop. Very short tufts of white down B (metaptilae) are present amongst down A. When the nestling is about 10 days old it has become very thickly covered with a coarse, long down C (second stage metaptilae, the nestling down), which is pale buff-grey on the upper parts and pale cream on the under parts. Down C replaces down B, which can be seen clinging to its tips, but it also grows in many parts where there was no previous down. Down C occurs on the head but numbers little more than down A. Down C when fully grown almost conceals down A. About the time that C appears, pennaceous contour feathers begin to sprout in the pterylae and these replace down A, which adheres



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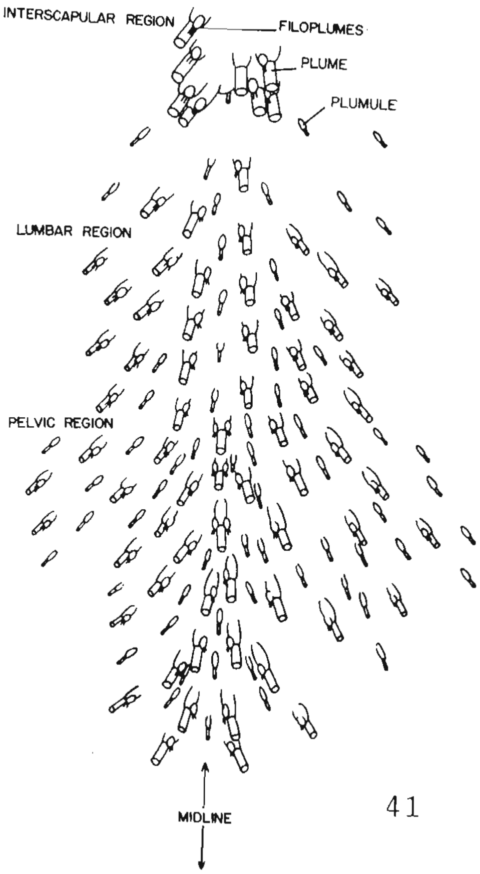

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Fig. 40. Details of spacing of the plume and plumule cover of a section of the breast of an adult specimen of *Micrastur ruficollis*.

Fig. 41. Details of spacing of the plume and plumule cover of a part of the pelvic region of the dorsal tract of an adult specimen of *Micrastur ruficollis*.

to the tips of the feathers, in the feather tracts. Down A on the apteria develops as plumules. Down C is shed when the contour feathers are almost fully grown. The plumules of the grown bird are of finer and more silky structure than the nestling down and develop from some of the follicles of down A (on apteria) and C (in pterylae).

Apparently much of down C is not replaced in the fully grown individual, a situation which occurs in the accipitrid but is carried even further in the falconid where no down was observed amongst the head feathers of the adult. The caracara (*Polyborus*) is peculiar in that the chick has a well-developed color pattern of stripes.

The falconid type can be characterized as having a submandibular apterium; the ventral cervical band is narrow but not separated from the pectoral region by a furcular apterium except in *Polyborus*; the sternal and axillary bands are widely separated; the axillary band is made up of a large number of feathers strongly condensed; the sternal band lies close to the midline but sweeps laterally on the abdomen to end on the pubis just in front of the anus; the scapular tract usually does not show strong transverse lines of feathers, the spinal apterium usually extends posteriorly to the caudal area, and metategmal down is only poorly represented in the adult, usually there is none among the feathers on the top of the head. The independent occurrence of a crop branch in *Polyborus* or *Daptrius* indicates the probable origin of this strip of feathers by the formation of a furcular apterium as a result of the folding of the skin produced by the bulging crop.

The pterylosis of the falconid raises the question of the homology of the feather bands of the ventral tract. Figure 42 indicates diagrammatically my views regarding this matter. The bifurcation of sternal and axillary bands in *Falco* lies far forward as compared with the accipitrid in which this split is rather indistinct. The split between these bands appears to have occurred more medially, but in the same manner, certainly the sternal band of the falconid has shifted medially. The abdominal portion of the ventral tracts of the various falconiforms seems to be comparable, except for extension to the tip of the pubis.

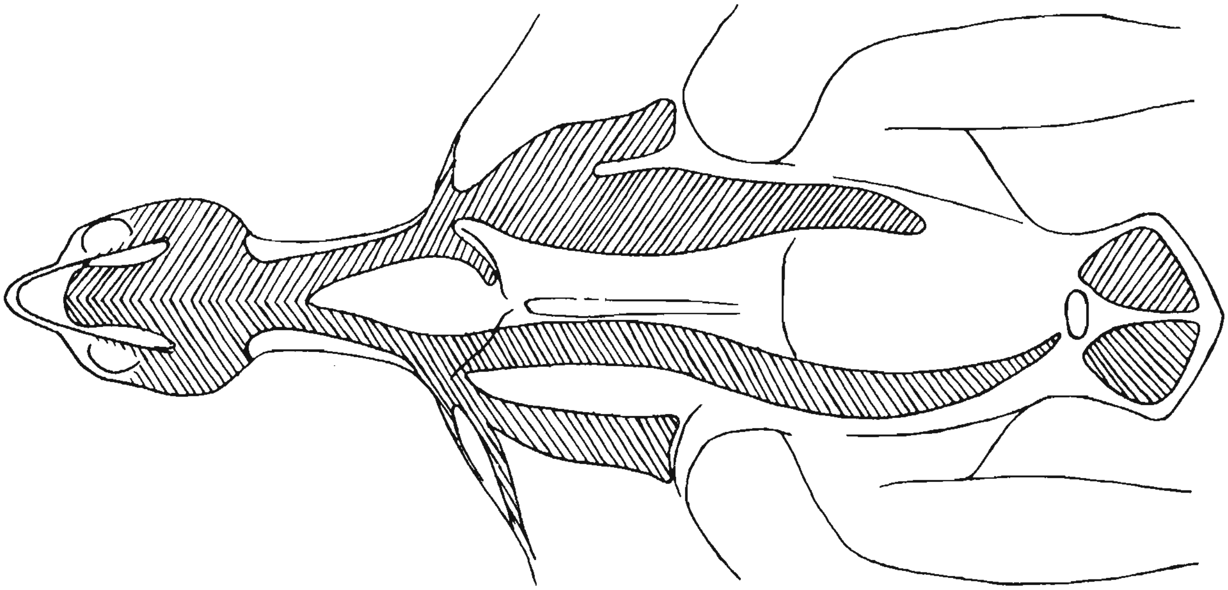

Fig. 42. Outline comparison of ventral tracts of Accipitridae (right) and Falconidae (left).

Summary and Conclusions

The ptilosis (plumage) of the bird is made up, in some types at least, of two covers, which can be identified by the terms protegmen (first cover) and metategmen (later cover). The former is assumed to represent the primitive cover of the ancestral bird because the units of the protegmen (proptilae) are larger than those of the metategmen (metaptilae); they appear earlier in the developmental process and show a stronger tendency to be arranged in rows similar to the rows of scales on the reptile or fish. The metategmen is less regular in its distribution but consists of a larger number of smaller units.

The protegmen is usually represented by the natal plumage, but units of this cover may not yet have appeared at the time of hatching or units of the metategmen may already be present. There does not appear to be any fixed relationship between units of these two covers as suggested by Gerber (1939). Rather, there is a relationship based on the space involved. Excessive crowding of papillae may reduce a unit of the primary cover to an apparent unit of the secondary one, as in the case of the down feathers of the spinal tract of the chicken. A large area between units of the primary cover will frequently have a larger number of down feathers than a smaller area, in any given region. The relationship holds within either pterylae or apteria, but because of the less active growth in the latter the two regions cannot be directly compared.

The arrangement of units of the protegmen is fairly regular, especially toward the ventral or dorsal midline, and to a lesser extent laterally. The *A* and *B* rows of this cover probably have a segmental relationship as suggested by Verheyen (1953), but it is possible for a segment to give rise to two rows or perhaps more (e.g. penguins). Multiplication of rows occurs on the head and the anterior margin of the wing.

The protegmen is more clearly differentiated in the nestling than in the adult. Only the protegmen undergoes pterylization, the metategmen is continuous in the nestling but is reduced in the adult and has a midventral apterium. Pterylosis is an evidence of specialization, which was achieved not later than the time of the common ancestor of living orders of birds. The pterylosis of this ancestor can be assumed to have been maintained with little change in some of the living birds. No single species, or group, can be selected as being least modified with time, but a composite of many such groups, usually assumed to be least specialized can be described. In this, the dorsal and ventral tracts are bilateral bands on the body, the ventral tract is not dividing on the breast into axillar and sternal divisions. Posteriorly it sweeps around the midventral apterium of the abdomen and ends on the pubis near the midline. The spinal apterium extends from the base of the neck to the caudal region.

From this type, reversion to a more evenly distributed cover could have occurred as a specialization for an aquatic existence as in the case of penguins; or conversion to a soft, loose plumage in the cursorial palaeognaths; or for the acquisition of a body cover composed of relatively small units as in the Anhimidae. It is assumed that adaptive modification has affected this cover, in whole or in part, in all birds.

Specialization in the falconiforms is best marked by the reduction in number of units in the plumage when comparing small species with those of medium or large size. In many of the largest species the number of units in their cover is greater than in smaller forms suggesting that more of the prototegmen has been used and that multiplication of metaptilae occurred. Beyond this type of variation, modification of the feather cover has been limited within the families of the falconiforms.

Pandion is frequently considered as having a specialized cover. The main modification for immersion in water is the reduction in size of the individual feathers, and in changing their texture to repel water. The even distribution of the contour feathers over the breast resembles that of aquatic species also. In other features, except the lack of bilateral division of the ventral cervical band over the crop region and the lack of an aftershaft, the osprey remains fairly comparable to the accipitrid. The loss of the aftershaft can be related to the reduction in size of the feathers.

The aftershaft is a variable structure showing several stages of development to complete absence within a taxonomic group. The general trend in birds appears to be toward reduction. In this detail the osprey can be viewed as the most specialized accipitrid.

The styles of ptilosis differentiating the families of this assemblage probably represent responses to changes in size and body proportions coupled with thermal and protective needs. A well-developed spinal apterium occurs in the cathartid, *Sagittarius*, the osprey and the falconid. For this reason it is assumed to be the primitive condition, while the short spinal apterium of the accipitrid is a modification, achieved as a result of medial movement of the bilateral bands--a movement which finds some support in the natal chick (fig. 4). The spinal tract of the accipitrid may be little more than a measure of the narrowness of the body coupled with the development of strong legs.

Ventrally the accipitrid appears to have a less-modified condition in contrast to the wide separation of the sternal and axillar bands of the falconid or *Sagittarius*. A separation is lacking in *Cathartes* but is developed in the more modified condors. Certainly there is doubt as to the ancestral condition of this tract, and the starting point used here may be in error. In the case of the accipitrid, modification has been from the undivided (Aegypiinae, *Pandion*) to the divided ventral tract in the "more specialized" species, a change which suggests that the typical accipitrid style is an intermediate between the primitive bird and the more widely separated type of the falconid.

The pectoral region in the cathartids suggests that this group was derived from one in which a more even distribution of feathers had been achieved (perhaps an aquatic association). Then, secondary reduction in the number of feathers occurred by substitution of larger and softer units. The progressive development of the sternal apterium indicates that the largest species are the more modified in this feature. This is a sequence which one would expect on the basis that the primitive bird was not large but tended toward a medium size in terms of living types. *Cathartes* and *Coragyps* are closer to this size; the former indicates its primitive condition by retention of the lateral cervical apterium.

It is probable that *Sagittarius* and falconids have specialized patterns produced by further movement apart of the sternal and axillary divisions (fig. 42). This hypothesis finds no support within the Falconidae where the ventral pattern is consistent throughout the group.

The independent modification of parts of the feather cover is well shown by the falconids. *Polyorus* is one of the largest species and appears to be a terminal specialized form in all respects. As such, it resembles the accipitrid in having a crop branch. This structure is indicated in *Milvago* and well developed in *Daptrius*, a sequence which supports the terminal position of *Polyborus* and the primitive position of *Milvago*. In terms of size, *Milvago* could be selected as the most primitive member of the subfamily yet it lacks the spinal apterium in the pelvic and much of the lumbar region, thus marking the extreme in modification. The scapular tract also probably represents a modified state related to the same consolidating force observed in the narrowed spinal tract. *Daptrius* is intermediate, so that again the presumed phylogenetic sequence is reversed.

Species of similar habit may show anatomical adaptive convergence. Among the falconiforms there are three vulturine groups: the Cathartidae, Aegypiinae, and Polyborinae, representatives of three of the types described here. In each of these groups there is reduction of the head feathering, but here the similarity ends. The bare throat and crop area of the cathartid is found among the accipitrids only in *Neophron* and in the falconid in *Polyborus*, *Daptrius*, (? *Phalcoboenus*) and *Herpetotheres*. In contrast to *Neophron* the aegypiins have a dense crop cover of small feathers. There is a neck ruff in the cathartid and the aegypiin, but the two differ in detail. The cathartid has lost the lateral cervical apterium while the aegypiin has repressed the ventral cervical tract. In the latter the trend appears to be toward the development of an evenly spaced pectoral cover. In the cathartid, although there is a parallelism in size and shape of plumes, there is the tendency for the development of a pectoral apterium--the breaking up of a continuous pectoral cover and the development of separate sternal and axillar bands. The pectoral cover of the caracara is similar to that of other falconids.

Many details in the several types of the falconiforms appear to be functional responses to form. For example, the submandibular apterium is related to folding of the skin on the inside of the mandibular ramus, the crop branch is related to a deep furcular infolding of skin (the furcular apterium) produced by a bulging crop. The supraocular apterium is related to the extension of the brow. The appearance of a feathered crop patch in some of the large eagles suggests the need of thermal protection for this region which is externally exposed when the crop is inflated with food. These details can be differentiating features or species peculiarities.

The taxonomic value of the observed patterns in the falconiforms has to be determined. The usual evaluations, based on Nitzsch (1867), or an examination of the system in a restricted group, cannot be accepted as final, rather they must be revised continually and supplemented with new materials. Various views have been expressed as to the value of ptilology. Forbes (1882:14) pointed out that the procellariiforms "seem to be, on the whole, very uniform throughout, both in the form of the tracts and in structure of the feathers." Sushkin (1905:64) dismissed ptilology as useless for the differentiation of families or higher catagories but useful at the generic or subfamilial level. Burt (1929:441) concluded that the pterylosis of the woodpeckers was a useful means of distinguishing the order but not for catagories below this level. As regards microptilomorphology, Chandler (1916:385) concluded that it is as valuable as osteology, myology, or the systematic morphology of any other organ or system of organs of the body. He did not clearly indicate that this system, on the basis of his own report, suffers the same limitations as others and cannot be used to the exclusion of the others.

The present lack of faith in ptilology is due in part to the work of Compton (1938) who concluded, in part, that the osprey was related to the cathartid because of the "similarity" in pterylosis. Further, a survey of the available accounts, and reference to Nitzsch, suggests that there are relatively few patterns of pterylae, and, therefore, criteria for critical differentiation may be lacking; however, expansion of pterylography to ptilology should add many useful new features. Last of all there is the fact that adaptive modification can alter any feature of this cover. The many differences in detail, particularly in the head region, indicate this potential.

There is no real evidence, available as yet, of any real basic disagreement between forms assumed to be closely related. The one exception that might be cited is in the association of *Pluvianus* with the other charadriiforms (Lowe, 1931, fig. 29). This situation should be investigated further. In any case, the charadriiform aggregation is such a large one and has such divergent parts that it is not in the least surprising that this one extreme case occurs.

Agreement within genera (where two or more species were available in the study materials--*Accipiter*, *Buteo*, *Aquila*, *Falco*) is very marked, individual feathers can frequently be compared from one species to another, the range of variation between species being only slightly more than within any one species. Closely related genera (*Falco--Ieracidea*, *Buteo--Accipiter*, *Elanus--Gampsonyx*, or *Buteo--Kaupifalco*) are thus "identical" in most respects.

Within each of the cathartid, accipitrid, and falconid types there is a marked range of variation, the greatest being found in the accipitrid, which has the largest number of species (and shows the widest range of adaptations). The inclusion of *Pandion* with the accipitrid is quite proper since variations within the subfamily Aegypiinae bridge much of the gap. The accipitrid assemblage thus suggests the limits of variation to be expected or tolerated within a family (fig. 43).

Where the range within a family is wide, ptilology may be useful in characterizing subfamilies or generic complexes. For example, the aegypiins, which are at present part of the subfamily Aegypiinae, can be characterized. The head feathers are much reduced and there is some sort of neck ruff formed from the dorsal cervical band. The ventral cervical apterium is covered by a crop patch of pennaceous feathers which have no down among them (i.e., down crop patch of typical accipitrid--formed of metaptilae). *Necrosyrtes* shows a few fairly large feathers along the anterior line of the crop patch and *Torgos* has some down in this same region suggesting a remnant of the ventral cervical band. Laterally a string of plumes, the ventral cervical branches, may connect the crop patch with the pectoral region (*Pseudogyps*). This connection is reduced in *Gyps* and only suggested in juvenals of the other genera; it is probably always lacking in *Torgos*.

The furcular apterium may be naked next to the crop patch (*Pseudogyps*). The pectoral region of the ventral tract is made up of evenly scattered feathers with a relatively narrower medial apterium than in the typical accipitrid (fig. 43A). In *Torgos*, gaps in the pectoral feather arrangement indicate the vestigial break between the sternal and axillary divisions. Such gaps may be indicated in other aegypiins.* The breast feathers are reduced in size and are lanceolate in shape, particularly in the axillary region. The abdominal portion of the ventral tract is relatively broad and ends halfway to the anus. The large vultures show reduction of the number, as well as of size, of the body feathers and, especially, of the leg feathers. Dorsally the spinal apterium appears to extend further posteriorly.

Differing in various degrees from this basic plan are the other genera of the subfamily Aegypiinae. *Gypohierax* appears to be just like the typical accipitrid in every feature and may even show a division of the pectoral region into axillary and sternal divisions; this could not be determined from skins. Reduction of feathering has occurred in the loral region and also on the inner side of the shank of the leg.

Neophron shows distinct reduction of the head and throat feathering like the aegypiins (fig. 21). It is distinctive in that the adult shows a bare patch of colored skin along the midline of the otherwise down-covered crop region. Like the aegypiins, *Neophron* lacks a connection at the shoulder between the branches of the ventral cervical band and the sternal region.

Gypaëtus is peculiar in the development of the "beard" around the base of the bill (fig. 202). The head feathers of the

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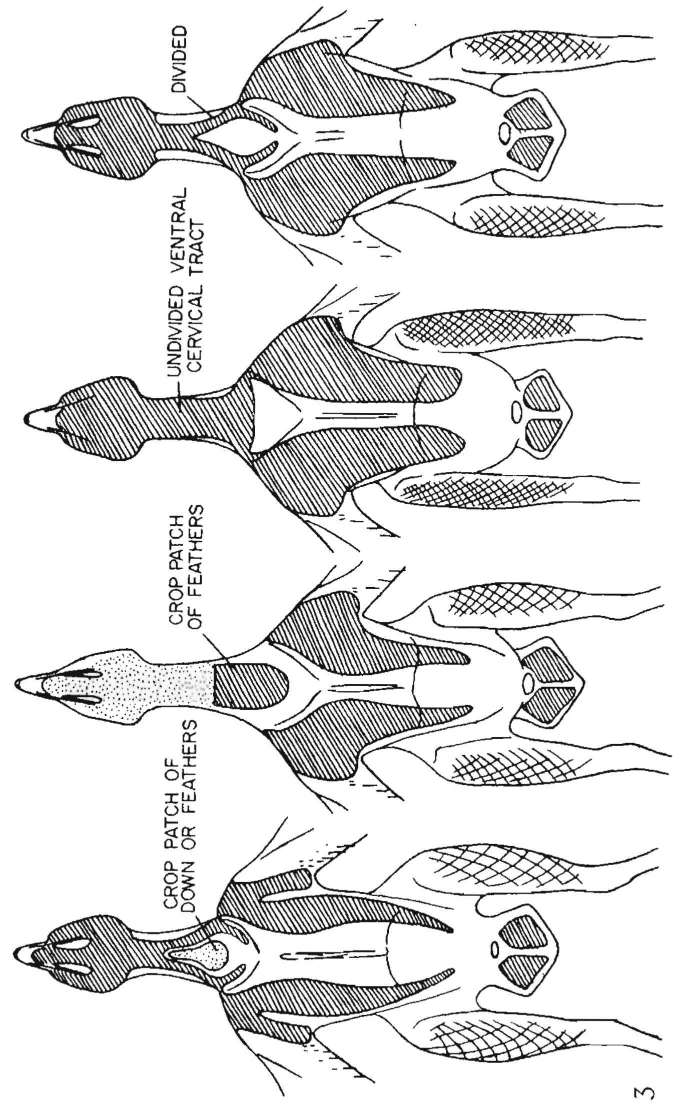
* Beddard (1898:473) described the ventral tract of *Gyps fulvus* as divided into an outer and inner branch on the breast; however, no such division was observed on skins of *Gyps ruppellii*.



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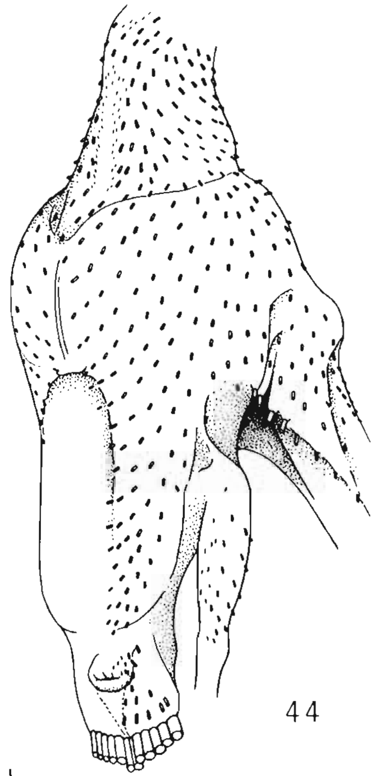

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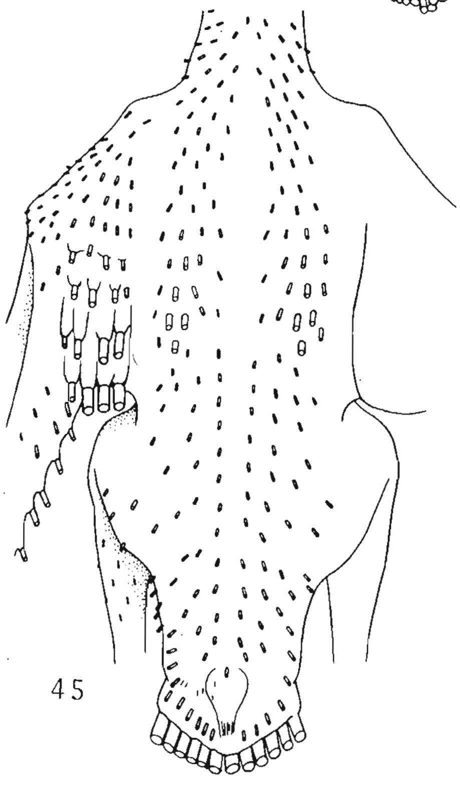

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Fig. 43. Outline of styles of ventral tract observed in the accipitrid type. A. Basic style. B. Aegypiin C. *Pandion haliaetus*. D. *Terathopius ecaudatus*, or *Gypaëtus barbatus*.

Fig. 44. Ventrolateral view of body of specimen of *Fregata magnificens*

Fig. 45. Dorsal view of body of specimen of *Fregata magnificens*.

primary cover are reduced to black bristle-like plumes, which contrast with the cream-colored, downy semiplumes of the metategmen. The semiplumes are the more obvious covering of the head and upper neck while, further down, on the upper chest and back, the lanceolate plumes of the primary cover take over and the semiplumes grade into the usual secondary cover of down. The adults show the strongest modification of the capital feathering. The crop is down covered and, like *Aquila*, it is nearly enclosed by the crop branches of the ventral cervical tract. The adult, unlike the juvenal, lacks the connective between the ventral cervical band and the undivided pectoral region.

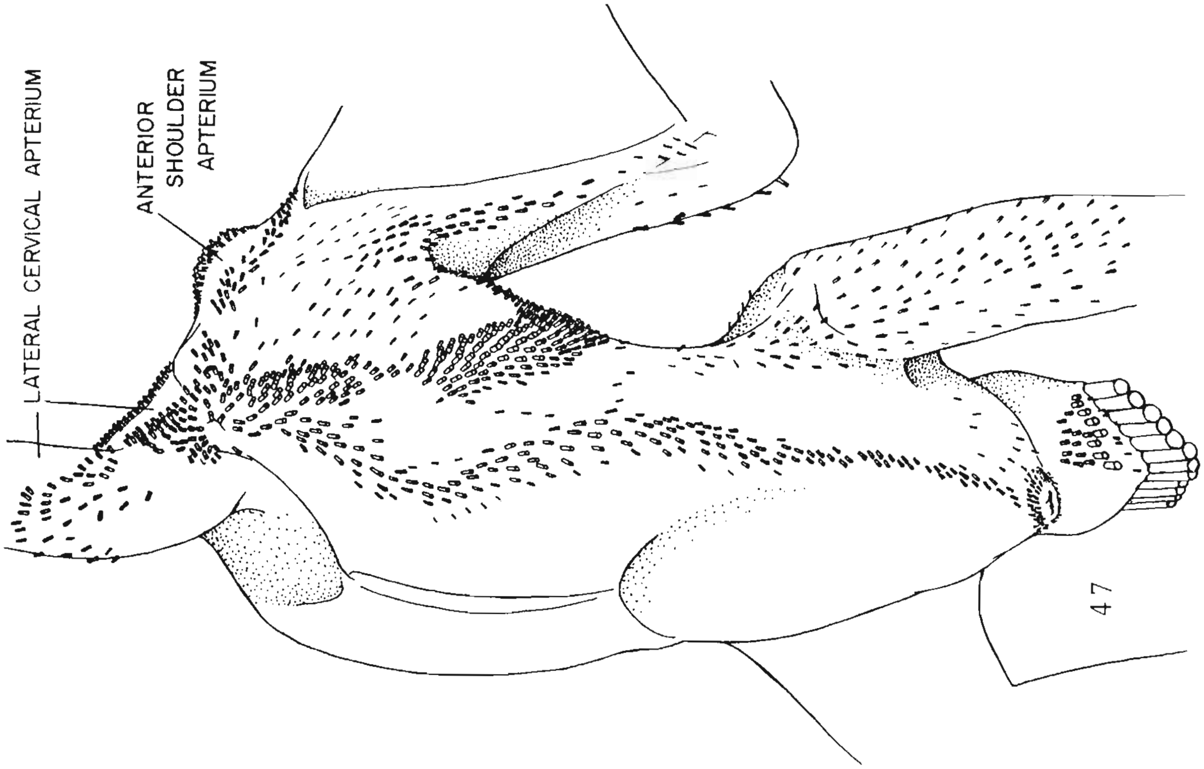
Terathopius can best be described as like the typical accipitrid in every way except for the lack of distinguishable sternal and axillary divisions in the pectoral region. The down on the crop is peculiar in being blackish (a remnant or precursor of the crop patch?).

With the exclusion of *Pandion* and the aegypiins, the remainder of the Accipitridae are remarkable homogeneous. Subdivision of the other falconiform families is not possible on the basis of pterylosis; although individual genera may differ from the basic plan.

Agreement in ptilosis between supposedly unrelated forms poses a problem. For example, *Fregata* (figs. 44 and 45) agrees well with the cathartid in lacking an aftershaft throughout its plumage (a fringe of barbs is present in both--*see* deWitt Miller, 1924b, fig. 7), in lacking a patagium for the quills of the rectrices and remiges, in the general distribution of feathers over the body, in lacking a lateral cervical apterium, and in having a reduced number of undertail coverts. It differs in having an unmodified capital tract (the thoat is bare), in lacking a neck ruff, in having a carpal remex, in having a group of feathers lateral to the anus, and in having a tufted oil gland (as does *Coragyps* occasionally). These differences seem not too great for tolerance within an order. Other pelicaniforms have a much larger number of contour feathers (and rows of feathers), i.e., a specialization for their more aquatic habit. This limitation of value, indicated by comparison of the cathartid and pelicaniform, on further analysis may be due more to adherence to traditional thought than to failure of this system to indicate relationship.

Some notion of the degree of difference to be expected between related families can be gained by a comparison of the two families of owls, the Strigidae and Tytonidae (figs. 46-49--although surely it is not to be assumed that all families must show a similar level of difference). The ptilosis of these families agrees in great detail (*see* Shufeldt, 1889 on *Spheotyto*; Pycraft, 1903, *Photodilus*; Lucas and Stettenheim, 1972, *Bubo virginianus*). They do not show differences comparable to those indicated above for *Fregata* and the cathartid. If one assumed that the owls were related to the Caprimulgidae (including Nyctibiidae and Aegotheliidae), Podargidae, and Steatornithidae, as members of a single order, then comparable differences might be said to exist (not thoroughly studied as yet).

Comparison of the owl with any one of the falconiform types gives nothing like the degree of similarity shown by comparison



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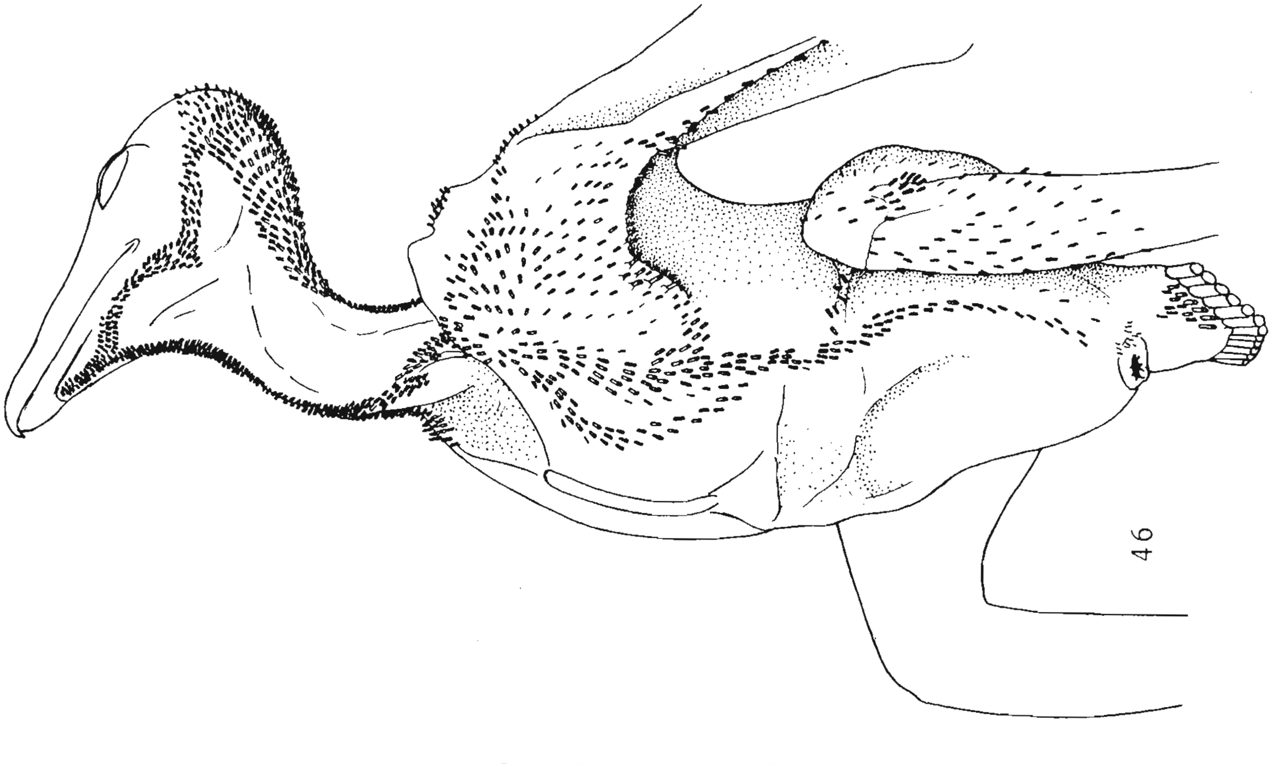

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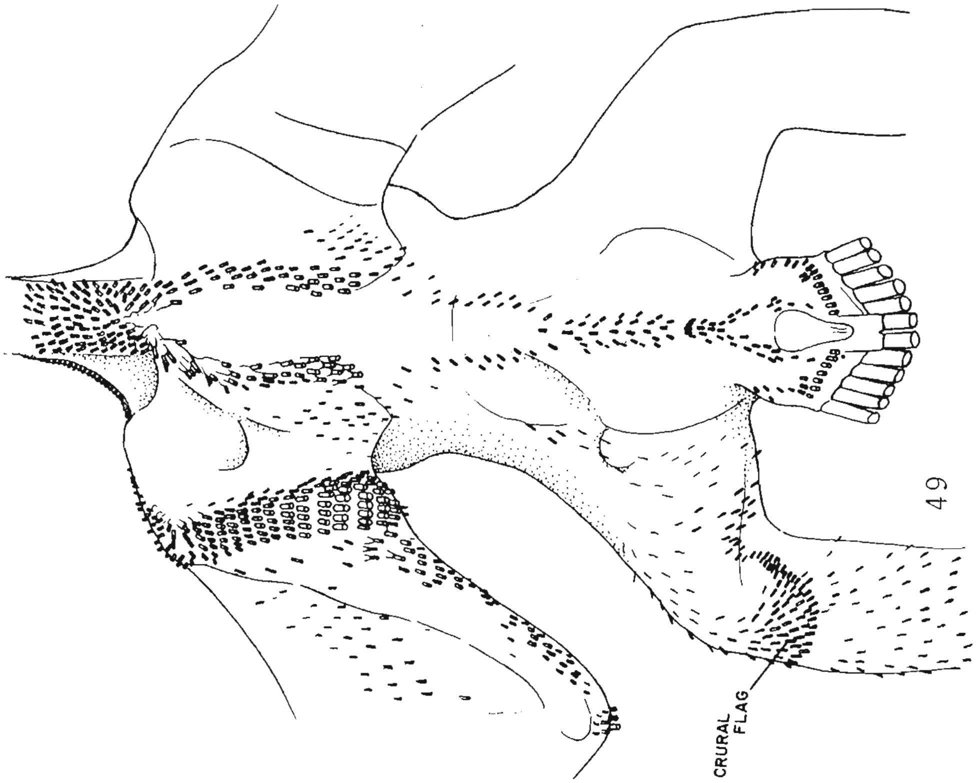
Fig. 46. Ventrolateral view of body of specimen of *Tyto alba*.

Fig. 47. Ventrolateral view of body of specimen of *Bubo virginianus*.



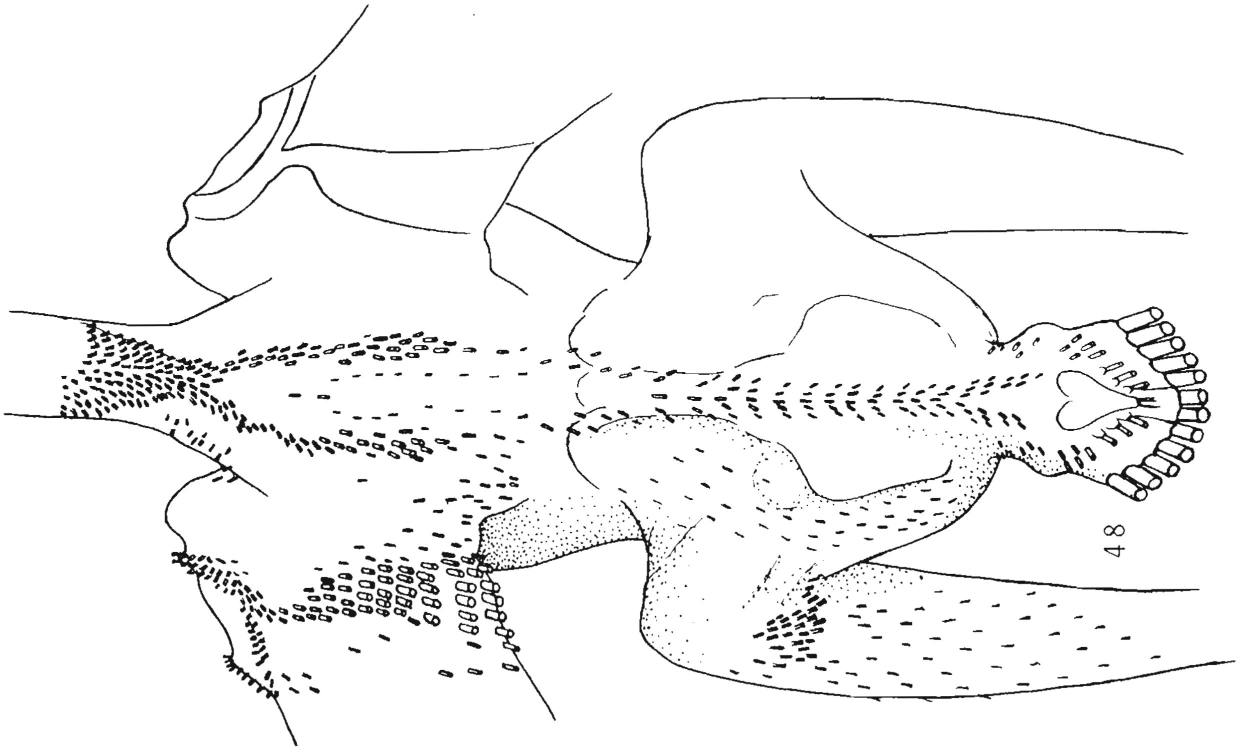


Fig. 48. Dorsal view of body of specimen of *Tyto alba*.

Fig. 49. Dorsal view of body of specimen of *Bubo virginianus*.

of the cathartid and *Fregata*. The degrees of difference shown by the several falconiform types and the owl range from a minimum of agreement in the case of the cathartid to a maximum in the case of the falconid (these are arbitrary evaluations with which the reader might not agree), yet in the latter case the agreement cannot be considered as indicative of any relationship.

Comparisons between the falconiform types does not result in anything as positive as the Tytonidae--Strigidae or *Fregata*--*Cathartes* comparisons, but lack of interagreement between these types is not as marked as between any one of them and the owl. An important point is that these types do not appear to be stages of some sort of continuum. The sagittariid agrees as well with the cathartid as with the falconid, indeed one might be inclined to place it closer to the latter. The accipitrid is not a connecting link between the cathartid and the others. In short there is no evidence of any close (ordinal) interrelationship between these groups, they appear to represent divergent lines from the ancestor of living birds identifiable at least as separate orders.

The ptilology of the falconiforms supports the contention that developmental aspects and adult ptilosis may be of value in determining taxonomic relationships at the family level and sometimes at both higher and lower levels.

OSTEOLOGY--GENERAL

Review of Literature

The osteology of birds has been more throughly investigated than any other anatomical system. Being made up of many individual parts, each with numerous details, the skeleton offers more evident possibilities for study than other systems. Bones also make up most of the fossil evidence.

Study of the bird skeleton got off to a well known start through Belon's (l'Histoire des Oyseaux, Paris, 1555) comparison of the bird and human skeletons. Each of the various descriptions of bird anatomy produced in the early period included a figure or a superficial description of the skeleton of the species under consideration. This descriptive period ended with the encyclopedic compilations of figures of articulated skeletons produced by D'Alton and D'Alton (1838), Eyton (1867-1875) and Meyer (1879-1897). Many additional illustrations of this type were supplied by Milne-Edwards and Grandidier (1879-1881).

A more detailed and comparative analysis of the skeleton began with Nitzsch's (1811) remarks on sesamoid and accessory bones. Brandt (1839) summarized knowledge of certain accessory bones and compared skeletons of different orders. The first comparative study of a single element involved the variations of the sternum (Merrem, 1812; DeBlainville, 1821; l'Herminier, 1827; St. Hilaire, 1833--for references *see* Fürbringer, 1888:1027). Cornay (1844, 1847) commented on the variations in shape of the palatine bone, but it was not until Huxley (1867) called attention to the possible value of several palatal features that current knowledge of this area developed. Although there has been some debate (McDowell, 1948; Hofer, 1955, Jollie, 1958, 1962; Bock, 1963), we have accepted from Huxley the primitive nature of the dromaeognathous (palaeognathous) type of palate.

The types described by Huxley were elaborated on by Parker, (1866 to 1890) who described in detail the anatomy and development of the skull. He commented (1879:133) that, "The study of the modifications produced by metamorphism of the primordial face (of the bird) is of the utmost importance to taxonomists...and the vomer alone is, in this respect, worth more than all Mr. Garrod's muscles put together." Parrington and Westoll (1941) decided the homology of the prevomer with a part of the premaxilla so that this term need no longer be confused with the vomer. Garrod (1873) pointed out the holorhinal-schizorhinal condition of the nasal bones. Fürbringer (1888) described the shoulder area and reviewed knowledge of this system.

Blanchard (1860) began a survey of the osteology of birds, a topic which was also considered by Milne-Edwards (1867-1871) who was particularly interested in the identification of fossil bones. The phylogeny of the class was the basic target of Pycraft in a series of papers describing the comparative osteology of various orders (1902 for the falconiforms). Sushkin (1899a, 1905) systematized much of the information concerning the falconiforms, and his paper served as a model for this study. Shufeldt (1878 to 1922) described the skeletons of many species of birds including comparative studies of the cathartids and some of the accipitrids.

Recent contributions to osteology include Fisher's (1944 to 1947) papers on the cathartids, particularly the morphology of the skull. McDowell (1948) and Bock (1963) evaluated the palates of palaeognaths, and Oliver (1945) used details of the vomer along with other osteological features as important criteria in the classification of birds. Hofer (1945, 1949, 1955) described as functional certain aspects of the palate and commented on the significance of the schizorhinal or holorhinal condition of the nasals in terms of adaptation for movement of the upper jaw. Howard (1929 to 1947), Loye Miller (1909 to 1937), Wetmore (1923 to 1960) and Brodkorb (1963) have made extensive use of osteology in the identification of fossils.

Past work indicates that the skull and tarsus have been considered most important; the former in the comparison of living forms, the latter because of its common occurrence in fossils. The sternum has been viewed with some doubt, but its modifications have been used. The presence or absence of any bone is considered worthy of note (i.e., clavicle) as is any strong modification of form, usually indicative of adaptive modification. Detailed comparisons of form and proportion have been used in identification of fossils. The differences between living and fossil species have not always been fully evaluated (a situation similar to that described for the study of human fossil remains by LeGros Clark, 1955).

In spite of the elaborate terminology that has been evolved and the frequent references to osteological details, one cannot escape the feeling that our present knowledge of the bird skeleton is at best superficial. Studies of adaptive modification have not shown what features of the bones can be used or how; rather they leave the impression that no feature can be trusted.

Material and Methods

Seventy-five of the 89 genera of falconiforms listed by Peters (1931) have been examined (Table 4). For many species,

* *

Table 4. Skeletal material examined as to Museum and catalog number. The Museum initials are identified on p. 64. Additional specimens were available for some species. * Indicates fossil forms.

Species	Museum	Number	skull	mandible	tarsus	coracoid	pelvis	sternum	furculum
Cathartid									
Cathartes aura teter (ser. 10)	MVZ	65174	X	X	X	X	X	X	X
Cathartes urubitinga	AM	1264	X	X	X	X	X	X	X
	USNM	227374	X	X	X	X	X	X	X
Coragyps atratus (ser. 4)	MVZ	78681	X	X	X	X	X	X	X
Sarcoramphus papa	MVZ	85526	X	X	X	X	X	X	X
*Sarcoramphus kernensis	type humerus								
Gymnogyps c. californianus	MVZ	74888ad.	X	X	X	X	X	X	X
	MVZ	23459ad.	X						
	MVZ	? jv.	X	X	X				
*Gymnogyps c. amplus	UCMPal	(20 crania)	X		X	X	X	X	X
*Breagyps clarki	UCMPal	(4 crania)	X		X				
	LAM misc. specimens								
Vultur gryphus	LM	218jv.	X	X	X	X	X	X	X
	LM	1734ad.	X						
*Teratornis merriami	UCMPal	12101(type)	X	X	X	X	X	X	X
		skull-mis. pts.							
	LAM	(2 composite)	X						
Neocathartes grallator	Carnegie Museum		X	X					
Sagittariid									
Sagittarius serpentarius	AM	4006	X	X	X	X	X	X	X
	AM	505jv.	X						
	USNM	346684	X	X	X	X	X	X	X
	LM	1988	X	X	X	X	X	X	X
Accipitrid									
Pandion haliaetus (ser. 10)	MVZ	47824	X	X	X	X	X	X	X
	MVZ	85556	X						
Elanus caeruleus	USNM	319982	X	X	X	X	X	X	X
Elanus leucurus	MVZ	45528	X						
	MVZ	79327	X	X	X	X	X	X	X
Gampsonyx swainsonii	AM	2018	X	X	X	X	X	X	X
	AM	1340	X	X	X	X	X	X	X
	USNM	345789	X	X	X	X	X	X	X
Machaerhamphus alcinus anderssoni	AM	3911	X	X	X	X	X	X	X

Species	Museum	Number	skull	mandible	tarsus	coracoid	pelvis	sternum	furculum
Elanoīdes forficatus	LAM	Bi-221	X	X	X	X	X	X	X
	USNM	289686	X	X	X	X	X	X	X
Aviceda cuculoīdes	AM	4716	X	X	X	X	X	X	X
Pernis apivorus	USNM	343983	X	X	X	X	X	X	X
	MCZ	253	X	X	X	X	X	X	X
Leptodon palliatus	MVZ	85527	X	X	X	X	X	X	X
Chondrohierax uncinatus	MVZ	85528	X	X	X	X	X	X	X
	USNM	289785	X	X	X	X	X	X	X
Harpagus bidentatus	USNM	344062	X	X	X	X	X	X	X
	USNM	344563				X	X	X	X
Ictinia misisippiensis	MVZ	60938	X	X	X	X	X	X	X
Ictinia plumbea	AM	4342	X	X	X	X	X	X	X
	USNM	322983	X	X	X	X	X	X	X
Rostrhamus sociabilis	USNM	227376	X	X	X	X	X	X	X
	AM	4341	X	X	X	X	X	X	X
Milvus milvus	USNM	17837	X	X	X	X	X	X	X
Milvus migrans	AM	4009	X	X	X	X	X	X	X
	USNM	346405	X	X	X	X	X	X	X
	USNM	291444	X	X	X	X	X	X	X
Milvus lineatus	USNM	319226	X	X	X	X	X	X	X
	USNM	319227	X	X	X	X	X	X	X
	USNM	319228	X	X	X	X	X	X	X
Lophoictinia isura	AM	3857	X	X	X	X	X	X	X
Haliastur indus	AM	2997	X	X	X	X	X	X	X
	USNM	347306	X	X	X	X	X	X	X
Haliastur sphenurus	AM	1943	X	X	X	X	X	X	X
Accipiter striatus	MVZ	58478	X	X	X	X			X
	MVZ	17039	X				X	X	
Accipiter badius	USNM	343987	X	X	X	X	X	X	X
Accipiter cooperii	MVZ	62394	X						
	MVZ	16691	X	X		X	X	X	X
	MVZ	16696			X				
Accipiter gentilis	MVZ	63058	X	X	X	X	X	X	X
	MVZ	77815	X						
Accipiter melanoleucus	USNM	291786	X	X	X	X	X	X	X
Meliërax gabar	USNM	290384	X	X	X	X	X	X	X
Meliërax musicus	USNM	291207	X	X	X	X	X	X	X
Heterospizias meridionalis	MVZ	94066	X	X	X	X	X	X	X
	MVZ	319440	X	X	X	X	X	X	X
Urotriorchis macrourus	USNM	292348	X	X	X	X	X	X	X
Buteo (Geranoaëtus) melanoleucus	LM	233	X	X	X	X	X	X	X
Buteo galopagoensis	USNM	18472	X	X	X	X	X	X	X
Buteo jamaicensis (ser. 10)	MVZ	66668	X	X	X	X	X	X	X
	MVZ	66669	X	X	X	X	X	X	X
Buteo lineatus	MVZ	77236	X	X	X	X	X	X	X
	MVZ	81616	X		X				
Buteo ridgwayi	USNM	226132	X	X	X	X	X	X	X
	USNM	226133	X	X	X	X	X	X	X

Species	Museum	Number	skull	mandible	tarsus	coracoid	pelvis	sternum	furculum
Buteo swainsoni	MVZ	68691	X	X	X	X	X	X	X
	MVZ	68832	X						
Buteo lagopus	MVZ	57116	X	X	X	X	X	X	X
Buteo regalis (ser. 4)	MVZ	41225	X	X	X	X	X	X	X
	MVZ	84650	X	X	X	X	X	X	X
Buteo magnirostris	MVZ	85535	X	X	X	X	X	X	X
	MVZ	85537	X						
Buteo albonotatus	MVZ	27708			X	X	X	X	X
Buteo (Asturina) nitida	MVZ	78684	X	X	X	X			X
	MVZ	74854					X	X	
	MVZ	85539	X						
Parabuteo unicinctus	MVZ	74748	X	X	X	X			X
	MVZ	74749	X						
	MVZ	55024					X	X	
Leucopternis albicollis	LM	1771			X	X	X	X	
	USNM	344057	X	X	X	X	X	X	X
Kaupifalco monogrammicus	MCZ	217	X	X	X	X	X	X	X
	USNM	322456	X	X	X	X	X	X	X
Butastur indicus	USNM	223986	X	X					
Hypomorphnus urubitinga	MVZ	85542	X	X	X	X	X	X	X
	USNM	345775	X	X	X	X	X	X	X
Hypomorphnus fragilis	LAM	misc. pts.	X		X	X	X	X	X
*Wetmoregyps daggetti	LAM	misc. pts.			X				
Buteogallus anthracinus	MVZ	85545	X	X	X	X	X	X	X
	MVZ	85547	X						
Busarellus nigricollis	MVZ	85550	X	X	X	X	X	X	X
	USNM	345773	X	X	X	X	X	X	X
Morphnus guianensis	AM	1376	X	X	X	X	X	X	X
	USNM	18468	X	X					
	LM				X				
*(Morphnus) woodwardi	LAM	misc. pts.	X		X	X	X	X	X
Harpia harpyja	USNM	345669	X	X	X	X	X	X	X
	LM	2203	X	X	X	X	X	X	X
	MCZ	333	X	X	X	X	X	X	X
	AM	2041	X	X	X	X	X	X	X
Pithecophaga jefferyi	LM	1730	X	X	X	X	X	X	X
	USNM	226900	X	X	X	X	X	X	X
Harpiopsis novaguineae	AM	6252	X						
Spizastur melanoleucus	USNM	321507	X	X	X	X	X	X	X
	USNM	345787	X	X	X	X	X	X	X
Spizaëtus ornatus	MVZ	85551	X	X	X	X	X	X	X
	MVZ	85554	X	X	X	X	X	X	X
Spizaëtus tyrannus	USNM	344051	X	X	X	X	X	X	X
Spizaëtus cirrhatus	USNM	344616	X	X	X	X	X	X	X
Spizaëtus nipalensis	AM	2004	X	X	X	X	X	X	X
Polemaëtus (Spizaëtus) bellicosus	AM	2028	X	X	X	X	X	X	X
	AM	493	X	X	X	X	X	X	X
Stephanoaëtus coronatus	AM	4263	X	X	X	X	X	X	X
	AM	3909	X	X	X	X	X	X	X

Species	Museum	Number	skull	mandible	tarsus	coracoid	pelvis	sternum	furculum
Lophaëtus occipitalis	AM	497	X	X	X	X	X	X	X
	AM	4160	X	X	X	X	X	X	X
	USNM	291451	X	X	X	X	X	X	X
*Spizaëtus grinnelli	UCMPal and LAM	misc. pts.	X		X	X	X	X	X
Hieraaëtus fasciatus	MCZ	211	X	X	X	X	X	X	X
*Neogyps errans	UCMPal and LAM	misc. pts.	X		X	X	X	X	X
Aquila chrysaëtos (ser. 16)	MVZ	61231	X	X	X	X	X	X	X
	MJ	Mule Creek	X	X	X	X	X	X	X
	LM	675jv.	X		X				
*Aquila (La Brea)	UCMPal and LAM	misc. pts.	X		X	X	X	X	
Aquila (Uroaëtus) audax	AM	2774	X	X	X	X	X	X	X
	AM	3850	X	X	X	X	X	X	X
	LM	1286	X	X	X	X	X	X	X
	USNM	346461	X	X	X	X	X	X	X
Aquila verreauxii	AM	1375	X	X	X	X	X	X	X
Aquila rapax	AM	495	X	X	X	X	X	X	X
	AM	4052	X	X	X	X	X	X	X
Aquila pomarina	AM	3917	X	X	X	X	X	X	X
Aquila (Spizaëtus) gurneyi	AM	5147				X		X	X
(Aquila) wahlbergi	AM	3906	X	X	X	X	X	X	X
Haliaeetus palagicus	USNM	226265	X	X	X	X	X	X	X
Haliaeetus albicilla	USNM	292774	X	X	X	X	X	X	X
Haliaeetus leucocephalus	MVZ	8326	X	X	X	X	X	X	X
Haliaeetus leucogaster	AM	2024	X	X	X	X	X	X	X
	AM	3552	X	X	X	X	X	X	X
	LAM	Bi-1503	X	X	X	X	X	X	X
Haliaeetus vocifer	AM	3582	X	X	X	X	X	X	X
Icthyophaga (ichthyaëtus)	USNM	224807	X	X	X	X	X	X	X
Pseudogyps africanus	USNM	19991	X	X					
	USNM	19992	X	X					
Trigonoceps occipitalis	AM	3908	X	X	X	X	X	X	X
	USNM	320859	X						
Sarcogyps calvus	AM	623	X	X	X	X	X	X	X
	LM	232	X	X	X	X	X	X	X
Aegypius monachus	AM	1939	X	X	X	X	X	X	X
	USNM	289569	X	X	X	X	X	X	X
Torgos tracheliotus	AM	2990	X	X	X	X	X	X	X
	USNM	320977	X	X	X	X	X	X	X
Necrosyrtes monachus	AM	4893	X	X	X	X	X	X	X
	USNM	291443	X	X	X	X	X	X	X
Gyps fulvus	LAM	Bi-1730	X	X					
	MCZ	1412	X	X	X	X	X	X	X
Gyps coprotheres	AM	5378	X	X	X	X	X	X	X
(Labelled Gyps indicus) considered Pseudogyps bengalensis	LAM	Bi-226	X	X	X	X	X	X	X

Species	Museum	Number	skull	mandible	tarsus	coracoid	pelvis	sternum	furculum
Neophron perenopterus	LAM	mounted skel.	X	X	X	X	X	X	X
	MCZ	213	X	X	X	X	X	X	X
	AM	502	X	X	X	X	X	X	X
*Neophrontops americanus	LAM and								
	UCMPal	misc. pts.	X	X	X	X	X	X	X
Gypohierax angolensis	AM	494	X	X	X	X	X	X	X
	AM	2005	X	X	X	X	X	X	X
	USNM	18892	X	X	X	X	X	X	X
	MCZ	215	X	X	X	X	X	X	X
Gypaëtus barbatus	AM	5279	X	X	X	X	X	X	X
	LM	263	X	X	X	X	X	X	X
	CM	67941				X	X	X	X
	MCZ	329	X	X	X	X	X	X	X
Circus cyaneus	MVZ	65111	X	X	X	X			X
	MVZ	65112	X						
	MVZ	66596					X	X	
Circus aeruginosus	USNM	34419	X	X	X	X	X	X	X
Circus cinereus	USNM	321772	X	X	X	X	X	X	X
Geranospiza nigra	MVZ	85555	X	X	X	X			X
	MVZ	74747	X				X	X	
Geranospiza caerulescens	MVZ	94068	X	X	X	X	X	X	X
Gymnogenys typicus	USNM	292399	X	X	X	X	X	X	X
Terathopius ecaudatus	AM	4306	X	X	X	X	X	X	X
	AM	2324jv	X						
	AM	2973	X						
	USNM	292912	X						
Circaëtus gallicus	LM	147	X		X				
Haematornis cheela	USNM	343985	X	X	X	X	X	X	X
	LAM	Bi-1498			X				
	MCZ	271	X	X	X	X	X	X	X
Falconid									
Herpetotheres cachinnans	MVZ	85557	X	X					
	MVZ	85559			X	X	X	X	X
	USNM	289775	X	X	X	X	X	X	X
Micrastur semitorquatus	MVZ	85561	X	X	X	X			X
	MVZ	85560					X	X	
	LM	669	X	X	X	X	X	X	X
	USNM	245788	X	X	X	X	X	X	X
Daptrius americanus	USNM	67878	X	X	X				
	USNM	13491				X	X	X	X
Daptrius ater	USNM	344059	X	X	X	X	X	X	X
Milvago chimachima	USNM	321503	X	X	X	X	X	X	X
Milvago chimango	USNM	318387	X	X	X	X	X	X	X
	MVZ	?	X	X	X	X	X	X	X
Phalcoboenus megalopterus	LM	764	X	X	X	X	X	X	X
Polyborus cheriway	MVZ	83996	X	X					
	MVZ	74750	X		X	X	X	X	X
Polyborus lutosus	USNM	19916	X	X	X	X	X	X	X
Spiziapteryx circumcinctus	USNM	227499	X	X	X	X	X	X	X

Species	Museum	Number	skull	mandible	tarsus	coracoid	pelvis	sternum	furculum
Polihiërax semitorquatus	AM	3601	X	X	X	X	X	X	X
	USNM	292920	X	X	X	X	X	X	X
	USNM	322698	X	X	X	X	X	X	X
Microhierax caerulescens	USNM	343197	X	X	X	X	X	X	X
Falco mexicanus (ser. 6)	MVZ	79002	X	X	X	X			X
	MVZ	68694					X	X	
Falco biarmicus	USNM	322046	X	X	X	X	X	X	X
	MCZ	254	X	X	X	X	X	X	X
Falco rusticolus	USNM	344415	X	X		X	X	X	X
	USNM	345380			X				
Falco jugger	MCZ	294	X	X	X	X	X	X	X
Falco peregrinus	MVZ	77260	X	X	X	X			X
	MVZ	41228					X		
	MVZ	45019						X	
Falco cuvierii	USNM	18963	X	X	X	X	X	X	X
	USNM	18964	X	X	X	X	X	X	X
Falco albigularis	MVZ	78687	X						
	MVZ	85564		X	X	X	X	X	X
Falco columbarius	MVZ	15631	X						
	MVZ	79023		X	X	X	X	X	X
Falco sparverius	MVZ	62587	X	X	X				
	MVZ	67546					X	X	
	MVZ	63320			X	X			X
Falco punctatus	MCZ	2354	X	X	X	X	X	X	X

* *

only a single specimen is listed whereas several were available. Fossil species are indicated with an asterisk. Not seen were examples of *Chelictinia, Henicopernis, Helicoleste, Hamirostra, Erythrotriorchis, Harpyhaliaëtus, Urubitornis, Oroaëtus, Cassinaëtus, Ictinaëtus, Dryotriorchis, Eutriorchis, Neohierax,* and *Ieracidea.* (*Ieracidea* has been described as similar to *Falco* by Condon, 1951.) Some genera (*Harpyopsis, Breagyps,* etc.) are incompletely known. The source and catalog number of representative specimens of each species examined is indicated in the table. The collections referred to are the Museum of Vertebrate Zoology (MVZ) and the Museum of Paleontology (UCMPal) of the University of California at Berkeley, the American Museum of Natural History (AM), the United States National Museum (USNM), the Museum of Comparative Zoology at Harvard (MCZ), the Chicago Museum (CM), the Los Angeles County Museum (LAM), and the private collection of Dr. Loye Miller (LM) of the University of California at Los Angeles.

Most of the genera, assumed to show the greatest divergences, were examined. Sushkin saw slightly fewer genera (12) but had examples of *Ieracidea, Ictinaëtus* and *Harpyhaliaëtus.*

In addition to living forms, several fossil species (10) have been intercalated, and, as the individual elements could not be cited by catalog number, these have been lumped and the source identified. Some fossil forms were not available for examination and, like several modern genera, are known only from published figures and descriptions. Table 5 lists the species and elements figured in different reference sources.

* *

Table 5. Osteological figures of various falconiforms in the literature. *Indicates fossil forms.

Cathartid	
Cathartes aura	
skull	Fisher 1944 figs. 42,44,46.
vent. view skull	Beddard 1898 fig. 230, p.483.
vent. and lat. sternum	Fisher 1946 Pl. 2, fig. c; Pl. 4, fig. a.
coracoid front and back	Fisher 1946 Pl. 5, fig. e.
tarsometatarsus	Fisher 1946 Pls. 1-13.
dorsal view pelvis	Pycraft 1902, text-fig. 36, p.303.
Coragyps atratus	
skull	Fisher 1944, figs. 42,44,46.
shoulder articulation	Shufeldt 1909, fig. 17, p.37
3/4 view sternum	Schiøler 1931, Tafl. II.
vent. and lat. sternum	Fisher 1946 Pl. 2, fig. b; Pl. 4, fig. b.
coracoid front and back	Fisher 1946 Pl. 5 f.
*Phasmogyps patritus	
end of tibiotarsus	Wetmore 1927
*Palaeogyps prodromus	
end of tibiotarsus	Wetmore 1927
Sarcoramphus papa	
skull	Fisher 1944 figs. 42,43,45,46.
vent. and lat. sternum	Fisher 1946 Pl. 1, fig. d, Pl. 3, fig. d.
coracoid front and back	Fisher 1946 Pl. 5, fig. d.
tarsometatarsus	Fisher 1946 Pls. 1-13.
tarsometatarsus	Milne Edwards 1867-71 atlas II, Pl. 179, figs. 15-18.
Gymnogyps californicus	
skull	Fisher 1944 figs. 42,43,45,46.
vent. and lat. sternum	Fisher 1946 Pl. 1, fig. b; Pl. 3, fig. b.
coracoid front and back	Fisher 1946 Pl. 5. fig. a.
tarsometatarsus	Fisher 1946 Pls. 1-13.
dorsal view pelvis	Pycraft 1902 text-fig. 35, p.302.
*Gymnogyps c. amplus	
cranium	Fisher 1944 figs. 43,45,46.
*Breagyps clarki	
skull	Miller and Howard 1938 Pl. 2.
skull	Miller 1925 Pl. 4.
tarsometatarsus	Miller 1925 fig. 12a and b.
Vultur gryphus	
skull	Fisher 1944 figs. 42,43,45,46.
vent. and lat. sternum	Fisher 1946 Pl. 1, fig. a; Pl. 3, fig. a.
coracoid front and back	Fisher 1946 Pl. 5b.
tarsometatarsus	Fisher 1946 Pls. 1-13.
whole skeleton	Eyton 1867-1875 Pl. 1 Z

*Neocathartes grallator	
skull	Wetmore 1944 Pl. III
mandible	Wetmore 1944 figs. 1,2.
frag. tarsometatarsus	Wetmore 1944 Pl. V, fig. 5.
misc. frag. parts	Wetmore 1944 Pl. IV, Pl. V, figs. 3-10.
*Teratornis merriami	
skull	Miller 1909 Pl. 1.
skull	Miller 1925 Pl. 1.
palate	Miller 1925 fig. 17.
furculum	Miller 1925 Pl. 2, A-B
sternum	Miller 1925 Pl. 2, D-E, Pl. 3, A.
pelvis	Miller 1925 Pl. 3, B.
humerus	Miller 1925 Pl. 3, C-D.
tarsometatarsus	Miller 1925 fig. 14a and b, Pl. 4.
*Plesiocathartes europaeus	
tarsometatarsus	Gaillard 1908 fig. 6, p.42. Cracraft and Rich 1972 fig. 4.
*Diatropornis (Tapinopus) ellioti	
tarsometatarsus	Gaillard 1908 fig. 8, p.49. Cracraft and Rich 1972 fig. 2.
tibiotarsus	Cracraft and Rich 1972 fig. 3.
Amphiserpentariid	
*Amphiserpentarius schlosseri	
distal end tibiotarsus	Gaillard 1908 fig. 7, p.46. Cracraft and Rich 1972 figs. 5,6,7.
Sagittariid	
Sagittarius serpentarius	
skull	D'Alton and D'Alton 1838, Pl. IV.
vent. view skull	Beddard 1898 fig. 228, p.481.
vent. view skull	Pycraft 1901 Pl. XXXI, fig. 7.
dorsal view skull	Pycraft 1902 Pl. XXXII, fig. 2.
lat. view rostrum	Pycraft 1902 Pl. XXXII, fig. 11.
sternum 3/4 view	Schiøler 1931, Tafl. I.
sternum	Eyton 1867-1875 Pl. 1.
vent. view pelvis	Schiøler 1931 fig. 4, p.13.
body skeleton	Pycraft 1902 text-fig. 33, p.297.
tarsometatarsus	Milne Edwards 1867-1871, atlas II, Pl. 179, figs. 19,20,21,22.
whole skeleton	Shufeldt 1909, Pl. I.
whole skeleton	Eyton 1867-1875 Pl. 2A.
*Amynoptilon (Amphiserpentarius) robustum	
tarsometatarsus	Milne Edwards 1867-1871, atlas II, Pl. 186, figs. 1,2,3,4,5,6. Cracraft and Rich 1972 figs. 8,9,10.
Accipitrid	
Pandion haliaetus	
shoulder articulation	Ridgway 1875, Pl. XI, fig. 5.
sternum, 3/4 view	Schiøler 1931 Tafl. II.
dorsal view pelvis	Pycraft 1902 text-fig. 36, p.305.
tarsometatarsus	Milne Edwards 1867-1871, atlas II Pl. 179, figs. 5,6,7,8,23,24.
whole skeleton	Eyton 1867-1875 Pl. 1.
Elanus caeruleus	
vent. view skull	Pycraft 1902 Pl. XXXI, fig. 2.

Elanus leucurus	
dorsal view skull	Shufeldt 1909 p. 85.
shoulder articulation	Ridgway 1875 Pl. XI, fig. 7.
Machaerhamphus alcinus	
skull	Milne Edwards and Grandidier 1879-1881 Pl. 25,26.
whole skeleton	
Elanoïdes forficatus	
dorsal view of skull	Shufeldt 1909 fig. 38, p.85.
dorsal view of skull	Ridgway 1875 Pl. XIII, fig. 7.
shoulder articulation	Ridgway 1875 Pl. XI, fig. 6.
Aviceda madagascarensis	
skull	Milne Edwards and Grandidier 1879-1881 Pl. 20,21.
whole skeleton	
Pernis apivorus	
vent. view skull	Sushkin 1905 fig. 6, p.30.
sternum 3/4 view	Schiøler 1931 Tafl. II
tarsometatarsus	Milne Edwards 1867-1871, atlas II Pl. 179, figs. 12,13,14.
Harpagus bidentatus	
dorsal view of skull	Ridgway 1875 Pl. XIII, fig. 8.
lat. view rostrum	Ridgway 1875 Pl. XII, fig. 8.
Ictinia misisippiensis	
dorsal view skull	Shufeldt 1909 p.85, fig. 38.
dorsal view skull	Ridgway 1875 Pl. XII, fig. 6.
lat. view rostrum	Ridgway 1875 Pl. XIII, fig. 8.
shoulder articulation	Ridgway 1875 Pl. XI, fig. 8.
Rostrhamus sociabilis	
shoulder articulation	Ridgway 1875 Pl. XI, fig. 9.
Accipiter hiogaster etorques	
whole skeleton	Meyer 1879-1897 Pl. CCX.
Accipiter cooperii	
coracoid front and back	Fisher 1946 Pl. 5, fig. i.
misc. parts	Fisher 1946 Pls. 1-13.
Accipiter francesi	
whole skeleton	Milne Edwards and Grandidier 1879-81, Pls. 33,34.
Accipiter madagascarensis	
whole skeleton	Milne Edwards and Grandidier 1879-81, Pl. 36.
Accipiter gentilis	
coracoid front and back	Fisher 1946 Pl. 5, fig. h.
lat. view sternum	Fisher 1946 Pl. 4, fig. d.
sternum 3/4 view	Schiøler 1931 Tafl. II.
misc. parts	Fisher 1946 Pls. 1-13
Accipiter nisus	
sternum, 3/4 view	Schiøler 1931 Tafl. II.
Melierax musicus	
whole skeleton	Meyer 1879-1897 Pl. CLIX
(body is of Falco peregrinus)	
*Palaeastur atavus	
distal end tarsus	Wetmore 1943 fig. 63, p.230.
Buteo jamaicensis	
shoulder articulation	Ridgway 1875 Pl. XI, fig. 10.
vent. and lat. sternum	Fisher 1946 Pl. 2, Fig.a, Pl. 4, fig. c.

coracoid front and back	Fisher 1946 Pl. 5, fig. g.
Buteo buteo	
lat. and post skull	Schiøler 1931 Tafl. III.
sternum, 3/4 view	Schiøler 1931 Tafl. II
whole skeleton	Meyer 1879-1897 Pl. CXLVII
Buteo lagopus	
lat. and post. skull	Schiøler 1931 Tafl. III.
sternum, 3/4 view	Schiøler 1931 Tafl. II.
*Buteo ales	
tarsometatarsus	Wetmore 1926 Pl. XXXVIII.
Hypomorphnus urubitinga	
whole skeleton	Meyer 1879-1897 Pl. CCIX
Hypomorphnus *(Urubitinga) fragilis	
cranium	Howard 1932 Pl. 1, figs. 1, 1^a.
lat. and vent. rostrum	Howard 1932 Pl. 1, figs, 2, 2^a.
dorsal view mandible	Howard 1932 Pl. 1, fig. 3.
furculum	Howard 1932 Pl. 1, figs. 4, 4^a.
coracoid	Howard 1932 Pl. 2, figs. 2, 2^a, 2^b, 3, 3^a.
sternum	Howard 1932 Pl. 2, figs. 1, 1^a.
pelvis	Howard 1932 Pl. 5, figs. 1, 1^a, 1^b.
tarsometatarsus	Howard 1932 Pl. 6, figs. 1, 1^a, 1^b.
misc. parts	Howard 1932 Pls. 1,3,4,5,6.
Busarellus nigricollis	
whole skeleton (feet?)	Meyer 1879-1897 Pl. CLIV
*Titanohierax gloveralleni	
tarsometatarsus	Wetmore 1937 figs. 5,6,7.
*Calohierax quadratus	
tarsometatarsus	Wetmore 1937 figs. 1,2,3.
*Wetmoregyps daggetti	
coracoid	Howard 1932 fig. 1, p.15.
tarsometatarsus	Howard 1932 Pl. 13, figs. 2, 2^a.
tibiotarsus	Howard 1932 Pl. 13, figs. 1,1^a.
*Palaeoborus umbrosus	
rostrum	Cope 1877 Pls. 67-68.
coracoid	Cope 1877 Pls. 67-68.
pelvis	Cope 1877 Pls. 67-68
tarsometatarsus	Cope 1877 Pls. 67-68
misc. parts	Cope 1877 Pls. 67-68
*Palaeoborus howardi	
dist. end tarsus	Wetmore 1936 fig. 13, p. 74.
*Palaeohierax gervaisi	
tarsometatarsus	Milne Edwards 1867-1871, atlas II Pl. 183, figs. 1-10.
*Paleoplancus sternbergeri	
rostrum and mandible	Wetmore 1933 fig. 1, p.2.
tarsometatarsus	Wetmore 1933 fig. 15-16, p.6.
misc. parts (frag.)	Wetmore 1933 figs. 2-19.
*Aquilavus hypogea	
tarsometatarsus	Gaillard 1908 fig. 1, p.28.
*Morphnus woodwardi	
cranium	Howard 1932 Pl. 7, figs. 1, 1^a.
lat. and vent. rostrum	Howard 1932 Pl. 7, figs. 2, 2^a.

dorsal view symphysis of mandible	Howard 1932 Pl. 7, figs. 3.
furculum	Howard 1932 Pl. 7, figs. 4, 4^a.
coracoid	Howard 1932 Pl. 7, figs. 5, 5^a.
sternum	Howard 1932 Pl. 8, figs. 1, 1^a.
pelvis	Howard 1932 Pl. 11, figs. 1, 1^a.
tarsometatarsus	Howard 1932 Pl. 12, figs. 2, 2^a, 2^b.
misc. parts	Howard 1932 Pls. 8-12.
Stephanoaëtus coronatus	
whole skeleton	Meyer 1879-1897 Pl. CLVI.
Spizaëtus grinnelli	
cranium	Howard 1932 Pl. 14, figs. 1, 1^a, 1^b.
lateral and ventral rostrum	Howard 1932 Pl. 14, figs. 2, 2^a.
dorsal view of mandible	Howard 1932 Pl. 14, figs. 3
furculum	Howard 1932 Pl. 14, figs. 4, 4^a.
sternum	Howard 1932 Pl. 15, figs. 1, 1^a.
coracoid	Howard 1932 Pl. 15, figs. 2, 2^a, 2^b.
lat., vent. and dorsal pelvis	Howard 1932 Pl. 18, figs. 2, 2^a, 2^b.
tarsometatarsus	Howard 1932 Pl. 19, figs. 2, 2^a, 2^b.
misc. parts	Howard 1932 Pl. 19, figs. 15-19.
Hieraaëtus bonelli	
tarsometatarsus	Milne Edwards 1867-1871 atlas II Pl. 187, figs. 12-14.
Hieraaëtus fasciatus	
whole skeleton	Meyer 1879-1897 Pl. CLV.
Aquila chrysaëtos	
skull and disarticulated skeleton	Milne Edwards 1867-1871, atlas II, Pl. 2-6.
shoulder articulation	Ridgway 1875 Pl. XI, fig. 11.
sternum, 3/4 view	Schiøler 1931 Tafl. II.
vent. and lat. sternum	Fisher 1946 Pl. 1, fig. c; Pl. 3, fig. c.
coracoid front and back	Fisher 1946 Pl. 5, fig. c.
tarsometatarsus	Fisher 1946 Pls. 1-13.
Aquila rapax	
body skeleton	Pycraft 1902 text-fig. 34, p.299.
*Aquila depredator	
coracoid	Milne Edwards 1867-1871, atlas II, Pl. 186, figs. 11, 12.
tarsometatarsus	Milne Edwards 1867-71, atlas II, Pl. 184, figs. 5,6,7,8 9,10,29.
*Aquila prisca	
tarsometatarsus	Milne Edwards 1867-1871, atlas II Pl. 184, figs. 1,2,3,4.
*Neogyps errans	
cranium	Howard 1932 Pl. 20, figs. 1, 1^a.
lat. and vent. rostrum	Howard 1932 Pl. 20, figs. 2, 2^a.

dorsal view mandible	Howard 1932 Pl. 20 fig. 4.
furculum	Howard 1932 Pl. 20, figs. 3, 3^{a}.
sternum	Howard 1932 Pl. 21. figs. 1, 1^{a}.
coracoid	Howard 1932 Pl. 21, figs. 2, 2^{a}.
pelvis	Howard 1932 Pl. 24, figs. 1, 1^{a}, 1^{b}.
tarsometatarsus	Howard 1932 Pl. 24, figs. 2, 2^{a}.
misc. parts	Howard 1932 figs. 21,22,23,25.
*Harpagornis moorei	
skull	Hamilton 1892 Pl. 7,8.
skull	Hamilton 1893 Pl. 23, fig. 1.
sternum	Hamilton 1893 Pl. 23, figs. 2, 3.
whole skeleton	Oliver 1930 fig. opp. p. 392.
*Harpagornis haasti	
dorsal skull, lacrimal missing	Oliver 1945 Pl. 10, fig. 46.
Necrosyrtes monachus pileatus	
whole skeleton	Meyer 1879-1897 Pl. CLI.
Gyps fulvus	
skull	Meyer 1879-1897 Pl. CLI.
skull	Shufeldt 1909 Pl. III, IV.
skull	D'Alton and D'Alton 1838 Pl. V. figs. a, b, c, d, e.
sternum 3/4 view	Schiøler 1931 Tafl. II.
whole skeleton	Meyer 1879-1897 Pl. CXXI.
Pseudogyps bengalensis	
skull	D'Alton and D'Alton 1838 Pl. VII.
vent. view skull	Pycraft 1902 XXXI, fig. 5.
Torgos tracheliotus	
skull	D'Alton and D'Alton 1838 Pl. VII.
Neophron peranopterus	
skull	D'Alton and D'Alton 1838 Pl. II. figs. e, d.
lat. view skull	Shufeldt 1909, v, vi, x, xii, xiv.
shoulder articulation	Shufeldt 1909 fig. 18, p. 37.
whole skeleton	Meyer, 1879-1897 Pl. CLII.
*Neophron vestuta	
distal end humerus	Wetmore 1943 fig. 62, p.229.
*Neophrontops americanus	
cranium	Howard 1932 Pl. 26, figs. 1, 1^{a}.
dorsal view ramus mandible	Howard 1932 Pl. 26, fig. 3.
rostrum	Howard 1932 Pl. 26, figs. 2, 2^{a}.
furculum	Howard 1932 Pl. 26, figs. 5, 5^{a}.
sternum	Howard 1932 Pl. 26, figs. 4, 4^{a}.
coracoid	Howard 1932 Pl. 27, fig. 1
pelvis	Howard 1932 Pl. 29, figs. 1, 1^{a}.
tarsometatarsus	Howard 1932 Pl. 29, figs. 4, 4^{a}.
misc. parts	Howard 1932 Pl. 27, 28, 29.
Gypaëtus barbatus	
vent. view skull	Pycraft 1902 Pl. XXXI, fig. 6.
dorsal view skull	Shufeldt 1909
sternum	Shufeldt 1909
tarsometatarsus	Milne Edwards 1867-1871, atlas II, Pl. 179, figs. 1,2,3,4.

Circus aeruginosus	
vent. view skull	Schiøler 1931 Tafl. III.
sternum, 3/4 view	Schiøler 1931 Tafl. II.
Gymnogenys typicus	
skull, whole skeleton	Milne Edwards and Grandidier 1879-1881, Pl. 17, 18.
Terathopius ecaudatus	
sternum	Shufeldt 1909 Pl. XI.
Haematornis cheela	
whole skeleton	D'Alton and D'Alton 1838 Pl. III.
Haematornis rufipectus	
whole skeleton	Meyer 1879-1897 Pl. CLVII.
Circaëtus gallicus	
vent. view skull	Pycraft 1902 Pl. XXXI, fig. 4.
vent. view skull	Sushkin 1905 fig. 7, p.30.
Falconid	
Herpetotheres cachinnans	
skull	Sushkin 1905 Tafl. IV, figs. 86-89.
mandible, lat. view	Sushkin 1905 Tafl. IV, fig. 93.
lat. view rostrum	Pycraft 1902 Pl. XXXIII, fig. 4.
shoulder articulation	Ridgway 1875 Pl. XI, fig. 4.
shoulder articulation	Sushkin 1905 Tafl. IV, fig. 99.
furculum	Sushkin 1905 Tafl. IV, fig. 98.
sternum	Sushkin 1905 Tafl. IV, fig. 95,96,97.
pelvis	Sushkin 1905 Tafl. IV, figs. 100, 101, 102.
tarsometatarsus	Sushkin 1905 Tafl. IV, fig. 103, 105, 106, 107.
Micrastur ruficollis	
skull	Sushkin 1905 Tafl. IV, figs. 75,76,77.
sternum	Sushkin 1905 Tafl. IV, figs. 81,82,83.
prox. end tarsometatarsus	Sushkin 1905 Tafl. IV, fig. 85.
Micrastur semitorquatus	
skull	Sushkin 1905 Tafl. III, figs. 52, 53, 54.
lat. view mandible	Sushkin 1905 Tafl. III, fig. 58.
shoulder articulation	Sushkin 1905 Tafl. III, fig. 65.
furculum	Sushkin 1905 Tafl. III, fig. 63.
sternum	Sushkin 1905 Tafl. III, fig. 61, 62, 64.
pelvis	Sushkin 1905 Tafl. III, fig. 66, 67, 68.
prox. end tarsometatarsus	Sushkin 1905 Tafl. III, figs. 70, 71, 72, 73.
Daptrius americanus	
shoulder articulation	Ridgway 1875 Pl. XI, fig. 2.
Milvago chimango	
skull	Sushkin 1905 Tafl. II, figs. 30, 31, 32.
lat. view rostrum	Pycraft 1902 Pl. XXXIII, fig. 3.
whole skeleton	Meyer 1879-1897 Pl. CLIII.
Phalcoboenus australis	
lat. view skull	Sushkin 1905 Tafl. 1, fig. 36.
palatines	Sushkin 1905 Tafl. 1, fig. 37.

skull	Sushkin 1905 Tafl. II, figs. 33, 34, 35.
sternum	Sushkin 1905 Tafl. 11, figs. 40,41.
whole skeleton	Meyer 1879-1897 Pl. CXLIX
Polyborus cheriway	
skull	Sushkin 1905 Tafl. II, figs. 38,39.
lat. view rostrum	Pycraft 1902 Pl. XXXIII, fig. 5.
Polihierax	
dorsal view of skull	Sushkin 1905 Tafl. I, fig. 29.
Microhierax fringillarius	
skull	Sushkin 1905 Tafl. 1, figs. 15,16, 17.
lat. view mandible	Sushkin 1905 Tafl. 1, fig. 20.
shoulder articulation	Sushkin 1905 Tafl. 1, fig. 24.
furculum	Sushkin 1905 Tafl. 1, fig. 22.
sternum	Sushkin 1905 Tafl. 1, fig. 21.
pelvis	Sushkin 1905 Tafl. 1, figs. 25,26.
pts. of coracoid	Sushkin 1905 Tafl. 1, fig. 23.
tarsometatarsus	Sushkin 1905 Tafl. 1, fig. 28.
Falco rusticolus	
skull	Schiøler 1931 Tafl. III.
lat. view of rostrum	Pycraft 1902 Pl. XXXIII, fig. 1.
sternum, 3/4 view	Schiøler 1931 Tafl. II.
Falco concolor	
whole skeleton	Milne Edwards and Grandidier, 1879-1881, Pl. 12, 12A.
Falco novaezealandica	
lat. view rostrum	Pycraft 1902 Pl. XXXIII, fig. 2.
Falco peregrinus	
vent. view skull	Eyton 1867-1875 Pl. 4, fig. 3.
shoulder articulation	Ridgway 1875 Pl. XI, fig. 1.
tarsometatarsus	Milne Edwards 1867-1871, atlas II, Pl. 179, fig. 9,10,11.
whole skeleton (body is that of Melierax musicus)	Meyer 1879-1897 Pl. CLVIII.
whole skeleton	Eyton 1867-1875 Pl. 3A.
Falco tinnunculus	
tarsometatarsus	Sushkin 1905 fig. 18, p. 46.
dist. end tibiotarsus	Sushkin 1905 fig. 16, p. 45.
*Falco ramenta	
dist. end tarsus	Wetmore 1936 fig. 14, p. 76.
*Falco swarthi	
tarsometatarsus	Miller 1927 fig. 54, p. 151.
Cariamid	
Cariamid	
whole skeleton	Eyton 1867-1875, Pl. 3K.

* *

The method used in this survey consisted of having the individual bones from the different skeletons placed together so that, for example, a feature of the skull could be traced through the entire order with a minimum of effort. The osteological series were referred to again and again as points arose which needed verification.

A study of the osteology of the falconiforms means little until it is fitted into the general picture of birds. Uniting (or separating) *Sagittarius* with *Cariama* can only be significant when comparisons with all types of birds have been made and when the similarities and dissimilarities can be properly evaluated--superficial agreement may not necessarily be indicative of relationship as such agreement can be found with members of several orders.

The preliminary survey of the osteological materials disclosed the same basic groups defined by ptilology. Therefore, in describing the different elements of the skeleton these same groups will be used wherever possible. The cathartid type, as referred to in this section, includes the Neocathartidae and Teratornithidae. *Pandion* is included in the accipitrid type, although some workers view it as belonging to a separate family. Where there is little comparative information or the materials are insufficient for independent treatment, the several types will be discussed together.

The figures have been sketched directly from the specimens; they are not designed to present exact dimensions or proportions (which can only be appreciated with the materials in hand). The figures give an impression of the particular structure described and any significant relationships which it might have.

Many measurements were made and these have been used whereever possible. Most measurements were useless because of individual variation, overlapping in comparing one species with another (related or unrelated), irregular variation within the group, and lack of distinctive reference points when comparing one group with another. The conclusion was reached that a mathematical analysis of the falconiforms was impossible at the moment. (This phase of the study was completed in 1956 before the advent of "numerical taxonomy" and multivariate analysis.)

OSTEOLOGY--THE HEAD SKELETON

Definition and Orientation

The avian skull and mandible have featured largely in systematic accounts (e.g., Brandt, 1853; Huxley, 1867; Barnikol, 1952, 1953a) and have engaged much attention as to function (e.g., Lakjer, 1926; Hofer, 1945, 1949, 1950).

Study of the avian head skeleton rests in part on developmental stages, as in the adult few suture lines are retained. Some phases of development of this area has been treated by W. K. Parker (1866 to 1890), Magnus (1871), Gadow and Selenka (1891), Newton and Gadow (1893-1896), Stresemann (1927-1934), Marinelli (1946), deBeer (1937), Schinz and Zangerl (1937), Parker and Haswell (1940), Erdmann (1940), and Grassé (1950). The falconiforms have been investigated by W. K. Parker (1873--*Accipiter nisus*), Sushkin (1899b--*Falco tinnunculus*), and Chomjakoff (1901--*Buteo buteo*).

In spite of numerous accounts, there is some doubt as to the homology of various bones. An example of this involves a figure of Heilmann (1926, fig. 3). He showed the opisthotic as forming the posterior margin of the tympanic cavity in the goose

(*Anser*), while Stresemann (1927-1934, fig. 53), using the same drawings, united the exoccipital and the opisthotic and labeled the combined bone the exoccipital. Ihle (1947, fig. 227), again using this same figure, introduced some new labels. Further some of the usual concepts of bone origin are not necessarily accurate (*see* Smith, 1947; McLean and Urist, 1955).

In order to resolve these difficulties, a study of the development of the chicken head skeleton was undertaken (Jollie, 1957a) and served as a base for understanding the head skeleton of hawks. Figure 50, A-H, shows several views of a specimen of *Accipiter cooperii* taken just before hatching. Figure 51 of a half-grown nestling red-tailed hawk shows a later state of development, but the exoccipitals have not yet grown out to the tympanic margin (which they do by the time of nest leaving). Also, the mesethmoid extends back to the brain capsule and down to the parasphenoid to complete the interorbital septum, except for a central fenestra.

Certain aspects of the adult skull are as vaguely understood as the developmental picture. Particularly difficult are the fenestra and foramina of the *basis cranii* (*see* Kesteven, 1915), which are shown in figures 52 and 53. The terminology of this region has been modified to agree with the findings of my studies (1957a, 1962).

Comparative Anatomy

The Cathartid Type*

Shufeldt (1878, 1909), Pycraft (1902), and Sushkin (1899a, 1905) have enumerated the features of the cathartid head skeleton and speculated upon their taxonomic importance. Fisher (1944) figured and compared the skulls of the recent forms and discussed their interrelationships; he appears to have followed the terminology suggested by Howard (1929).

The fossil genera have been described in various accounts: Loye Miller (1909, 1925), Miller and Howard (1938) and Wetmore (1944). Figure 54 shows several views of the skull of *Teratornis*, drawn from the type cranium with rostrum subsequently attached and three fairly complete skulls in the Los Angeles County Museum (L.A.M. B1367, B1382, and one referred to by Miller, 1925, as number 13, now L.A.M. B1381). The cranium of *Breagyps* is illustrated (fig. 55-56) along with that of the fossil *Gymnogyps* (*G. amplus* of Fisher) and modern *Gymnogyps californianus*. Because of the close similarity of these forms the mention of *Gymnogyps* can be assumed to include *Breagyps* unless otherwise stated. The remains of *Neocathartes* (Wetmore, 1944, 1950) from the upper Eocene, include a nearly complete skull and mandible (fig. 57).

No study has been made of the development of the cathartid skull, but the anatomy of this type is partially revealed by the skull and mandible of a nestling California condor (*Gymnogyps*

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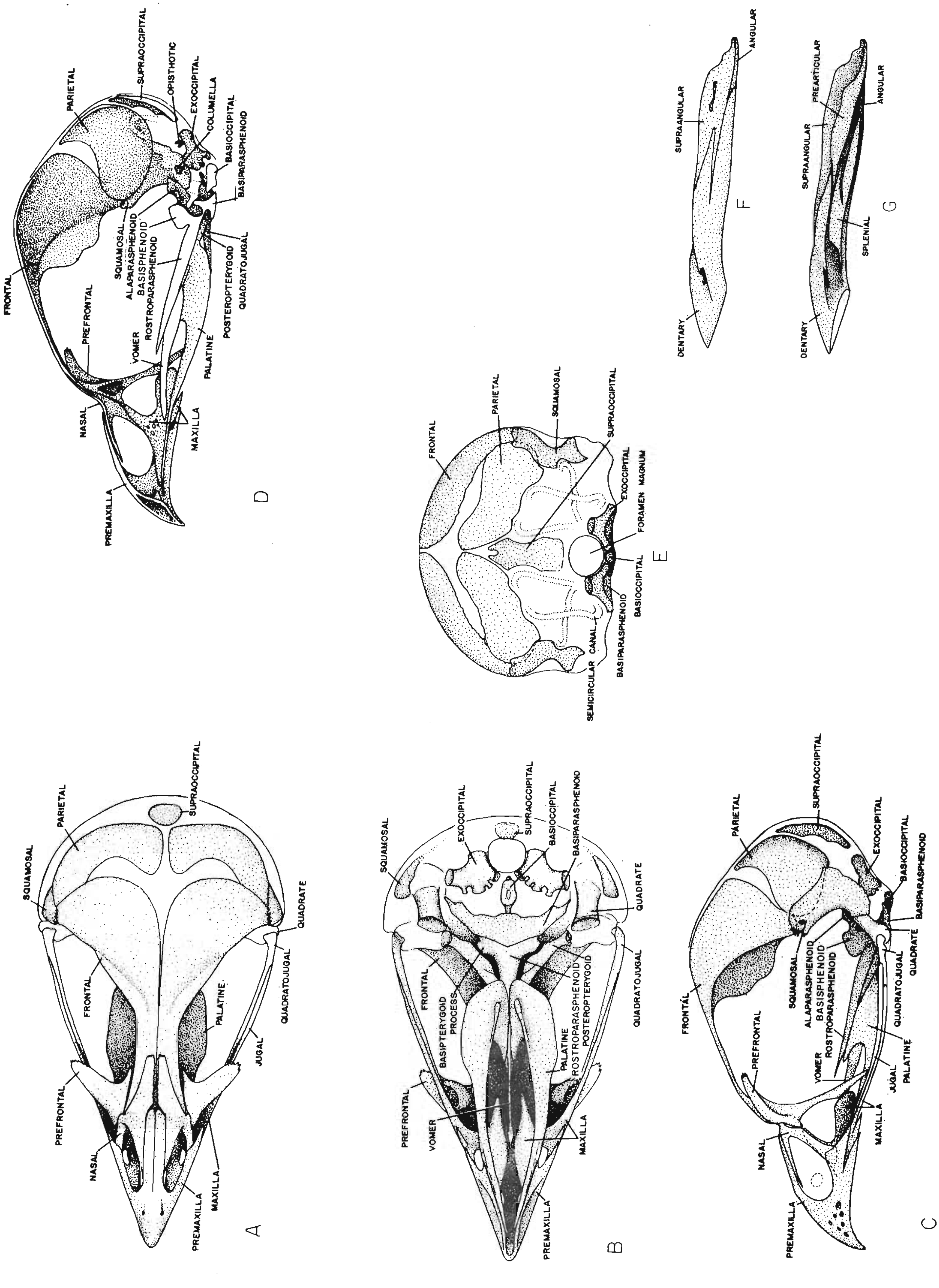
* Because of the basic agreement in form, the aberrant genera *Neocathartes* (Neocathartidae) and *Teratornis* (Teratornithidae) are discussed along with the living and fossil members of the Cathartidae as members of the cathartid group. The cathartid type, thus, becomes a cathartoid type, however, the former term is retained to preserve the uniformity of the types being compared.


A
SUPRAOCCIPITAL
PARIETAL
SQUAMOSAL
QUADRATE
QUADRATOJUGAL
FRONTAL
PALATINE
JUGAL
PREFRONTAL
NASAL
MAXILLA
PREMAXILLA
MAXILLA
B
SQUAMOSAL
EXOCCIPITAL
SUPRAOCCIPITAL
BASIOCCIPITAL
BASIPARASPHENOID
QUADRATE
QUADRATOJUGAL
FRONTAL
BASIPTERYGOID PROCESS
PALATINE
ROSTROPARASPHENOID
POSTEROPTERYGOID
PREFRONTAL
VOMER
MAXILLA
MAXILLA
PREMAXILLA
C
PARIETAL
SUPRAOCCIPITAL
EXOCCIPITAL
BASIOCCIPITAL
BASIPARASPHENOID
QUADRATE
FRONTAL
SQUAMOSAL
ALAPARASPHENOID
BASISPHENOID
ROSTROPARASPHENOID
QUADRATOJUGAL
QUADRATOJUGAL
PALATINE
PREFRONTAL
VOMER
JUGAL
PALATINE
NASAL
MAXILLA
PREMAXILLA
D
PARIETAL
SUPRAOCCIPITAL
OPISTHOTIC
EXOCCIPITAL
COLUMELLA
BASIOCCIPITAL
BASIPARASPHENOID
BASIPARASPHENOID
FRONTAL
SQUAMOSAL
ALAPARASPHENOID
BASISPHENOID
ROSTROPARASPHENOID
POSTEROPTERYGOID
QUADRATOJUGAL
PREFRONTAL
VOMER
PALATINE
NASAL
MAXILLA
PREMAXILLA
E
FRONTAL
PARIETAL
SQUAMOSAL
SUPRAOCCIPITAL
EXOCCIPITAL
FORAMEN MAGNUM
BASIOCCIPITAL
BASIPARASPHENOID
SEMICIRCULAR CANAL
F
ANGULAR
SUPRAANGULAR
DENTARY
G
PREARTICULAR
ANGULAR
SUPRAANGULAR
SPLENIAL
DENTARY

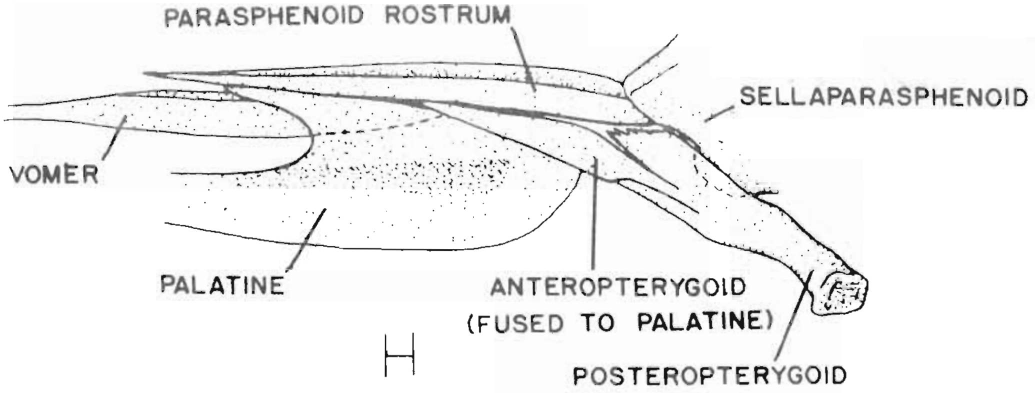


Fig. 50. Skull and mandible of chick of *Accipiter cooperii* taken from egg just before hatching. A. Dorsal, B. ventral and C. lateral views of skull. D. Medial view of right half of skull. E. Posterior view of skull. F. Lateral and G. medial views of mandible. H. Dorsolateral view of pterygoid-palatine relationship.

californianus) (fig. 58), found dead at the time of nest leaving. The specimen* shows the composition of the rostrum and the relationships of the prefrontal bones; the cranium is already well-ossified. The nasal septum is partly ossified and the "alinasal" connections with the maxilla are not formed. The posterior part of the interorbital septum is incomplete as is also the olfactory capsule. The relationship between the ectethmoid and mesethmoid portions of the olfactory capsule is shown. The passage of the olfactory nerve is open as is the eustachian tube and the anterior tympanic recess. The bird skull is peculiar in that the eustachian tube is usually enclosed by the parasphenoid. In ontogeny it proceeds from an open groove to a closed one, suggesting that this has been its phylogeny.

The basipterygoid processes of this nestling condor are well developed. The anteropterygoid articulates with the posteropterygoid and is partially fused to the palatine. The various processes of the skull are somewhat undeveloped, especial-

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* Assumed to be the property of Dr. Telford Work, it was for a time at the University of California at Berkeley.

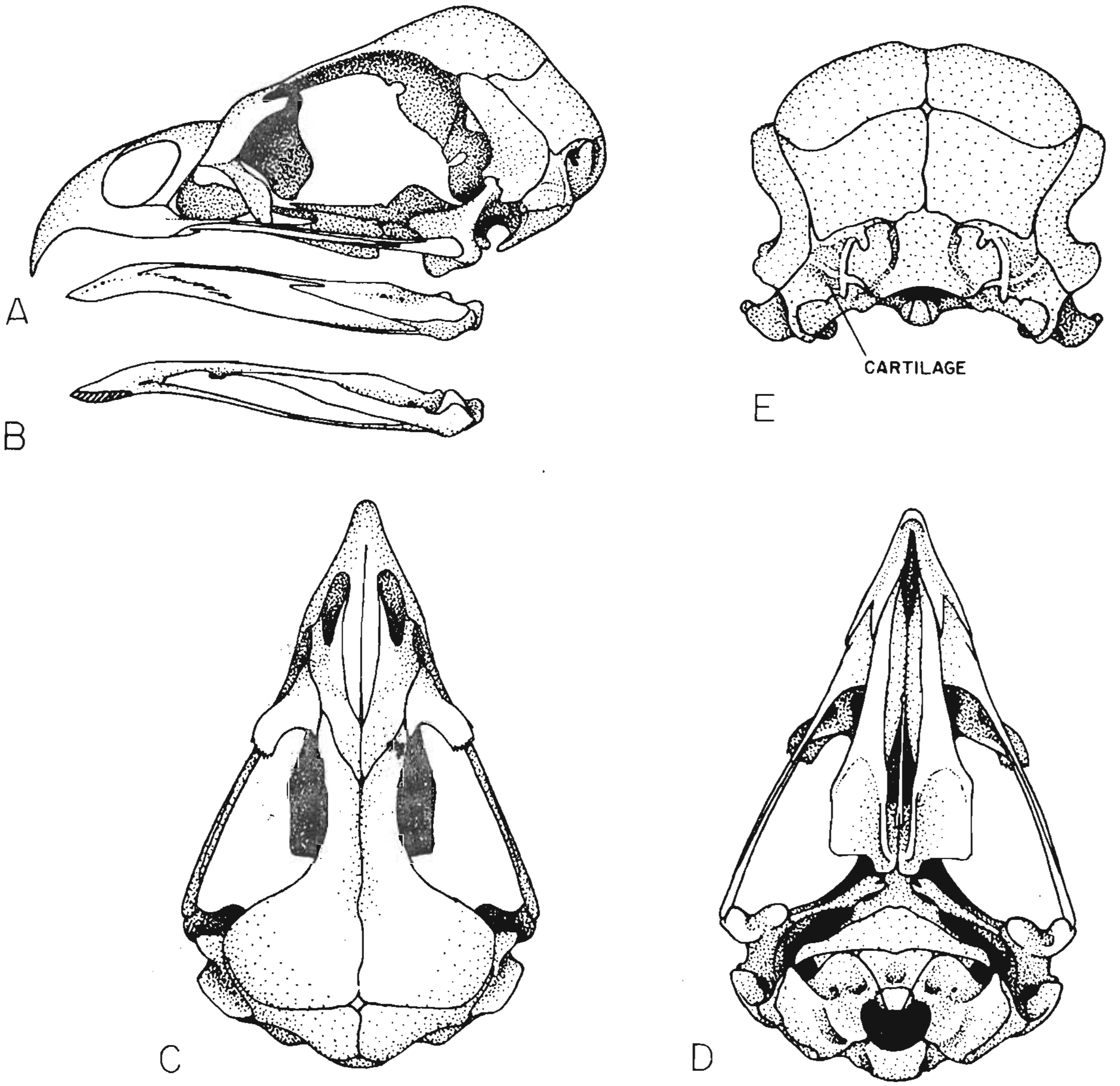
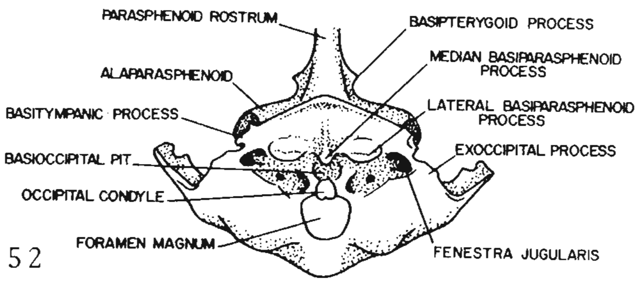


Fig. 51. Skull and mandible of nestling *Buteo jamaicensis* 2½ weeks old. A. Lateral view of skull and mandible. B. Medial view of mandible. C. Dorsal, D. Ventral, and E. Posterior views of skull.



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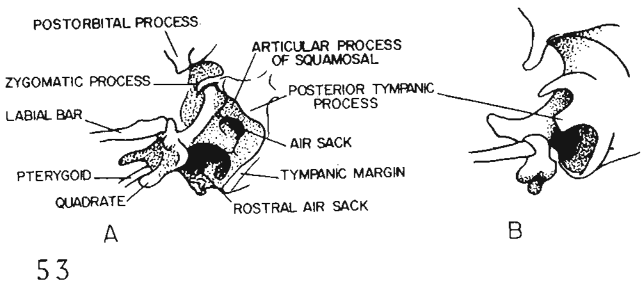

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Fig. 52. Base of the skull of *Aquila chrysaëtos*.

Fig. 53. Ventrolateral view of tympanic area of A. *Aquila chrysaëtos*, B. *Polyborus cheriway*.

Fig. 54. Skull of *Teratornis merriami*. A. Dorsal, and B. bentral views of skull. C. Diagrammatic X-section through the rostrum in the nasal region to show the nasal capsule ossifications. D. Lateral, E. posterior views of skull. F. Medial view of the anterior part of the right half of the rostrum. G. Tip of the rostrum seen in X-section along line G. H. Rostral septum as seen from behind. I. X-section of rostrum along line I to show contour of palatal surface.
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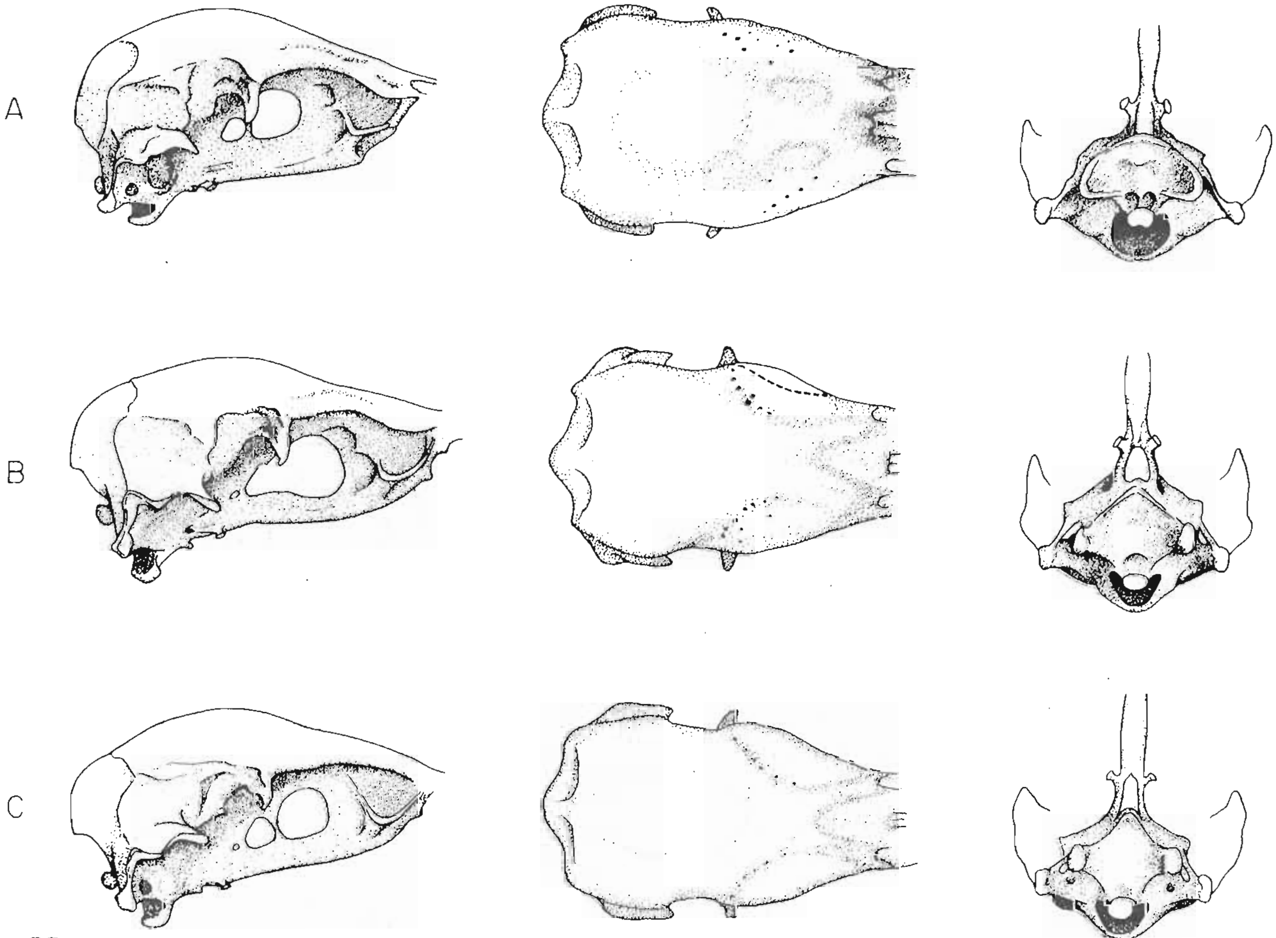

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Fig. 55. Comparative sketches of crania of A. *Breagyps clarki*, B. *Gymnogyps californianus*, and C. *Gymnogyps amplus*. Lateral view at left, dorsal view middle, ventral view at right.

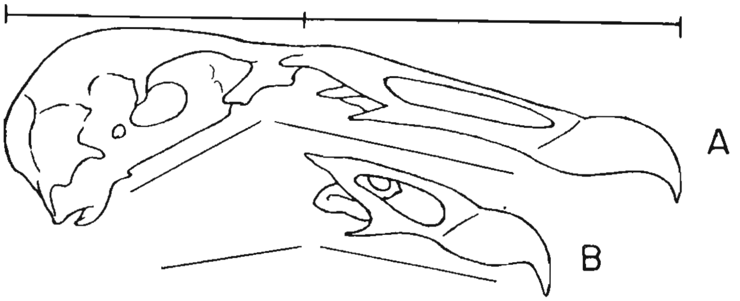


Fig. 56. Lateral view of skull of *Breagyps*, A, showing craniorostral angle and relative lengths of rostrum and cranium (line above). Rostrum of *Gymnogyps californianus*, B, with craniorostral angle indicated.

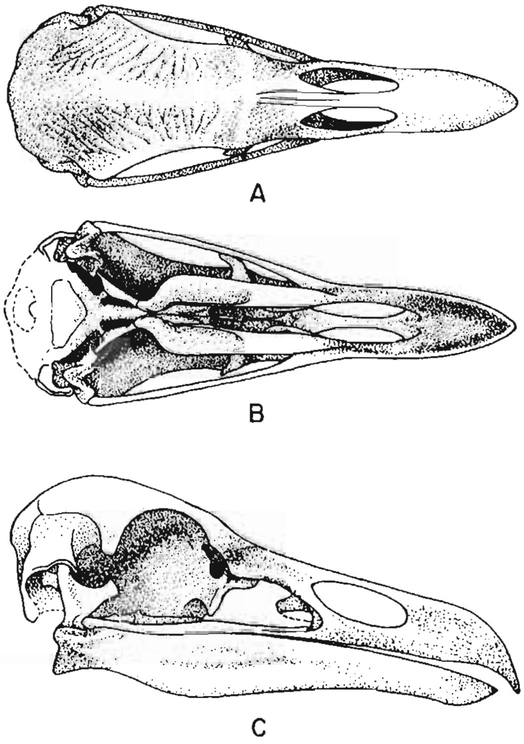


Fig. 57. Skull and mandible of *Neocathartes grallator*. A. Dorsal, and B. ventral view of skull. C. Lateral view of skull and mandible.

ly anteriorly.

The cathartid palate (see figures 54, 57, 58, 59) is distinctive in that it has a large anterior palatal fossa which separates a "floored" premaxillary portion from the medial projecting palatal processes of the maxillae (for convenience these can be called the maxillopalatines). The premaxillary palate (fig. 54F, G), which underlies the tip of the rostrum, appears to have been produced from a midline ossification in the prenasal cartilage fused with medial (palatine) processes of the premaxilla. This premaxillary floor is joined by a median

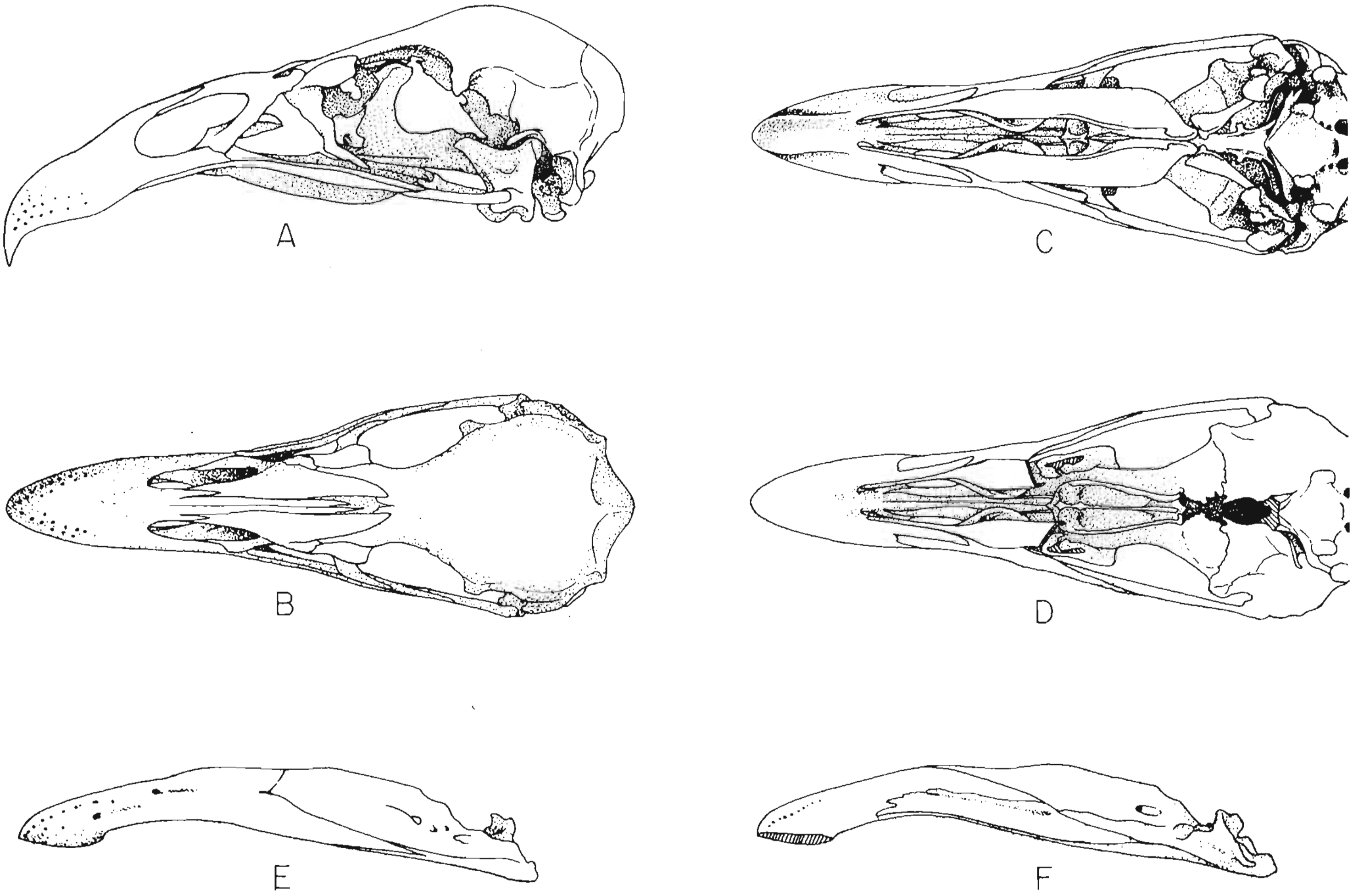


Fig. 58. Skull and mandible of fully grown nestling *Gymnogyps californianus*. A. Lateral, B. dorsal, and C. ventral views of skull. D. Ventral view with parasphenoid rostrum and part of palate cut away. E. Lateral, and F. medial views of mandible.

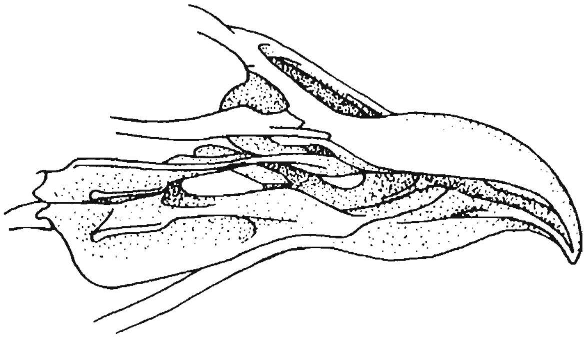


Fig. 59. Ventrolateral view of rostrum of *Sarcoramphus papa* to show anterior end of palatine in the anterior palatal fossa.

bony septum to the dorsal wall of the premaxilla as is shown in the cutaway section (fig. 54F). The septum appears to be made up of lateral components which in *Teratornis* may be separated ventrally, thus giving the appearance of an inverted Y (fig. 54H).

As the premaxilla is largely hollow, its cavity connects with the anterior palatal fossa by means of openings lateral to this septum. As the palate becomes more vaulted (arching dorsally), the dorsal and palatal walls come to lie in closer proximity, the median septum becomes heavier and the lateral openings become more restricted. The inflated beak of *Teratornis* marks one extreme, the other is *Coragyps*. In the latter the lateral openings are much reduced, allowing only the passage of the palatine nerves and blood vessels, the palatal surface lies nearly in contact with the upper wall of the premaxilla.* In one specimen of *Gymnogyps* a bit of nasal septum appeared as a short ridge extending posteriorly from the premaxillary septum (Fisher, 1944, fig. 43).

The anterior portion of the premaxilla has shallow lateral depressions along the down-curving margin of the bill tip (fig. 54B, D, I). The premaxilla has a long posterior palatal process; This process later fuses to the maxilla, and, to a lesser extent with the palatine, except in *Sarcoramphus* where the anterior end of the palatine remains free (fig. 59). In *Teratornis* the posterior palatal process of the premaxilla is probably fused with the palatine (fig. 54B). The nasal processes of the premaxilla are exceptionally narrow when contrasted with most falconiforms, and in the adult are fused to the cranium and overlaid with bone so that their posterior ends are

* *

* Pycraft (1902:286) made a comment concerning this portion of the palate: "The *Cathartae* differ markedly from all the other *Falconiformes* in the form of the palatal surface of the premaxilla. In these last the body of the premaxilla is very highly pneumatic, a section thereof revealing a mass of cancellated tissue between two dense plates of bone. This increase of pneumatic tissue brings the palatal surface down close, or very near to, the level of the tomium. In the *Cathartae* this pneumatic tissue is almost wanting, so that the palatal surface comes to form a vaulted chamber."

hidden; they are distinct for only a short distance in the region of the frontonasal hinge.

The surface of the premaxilla, which underlies the horny bill sheath, shows irregular vascular foramina and distinct grooves for superficial blood vessels. The vascular perforations tend to be larger along a line just above the margin of the tomium.

The maxilla forms a part of the jaw margin and palate. (It is largely overlain by the palatal process of the premaxilla, which fuses with it.) The palatal processes of this bone are flat to spoon-shaped, opening outward or downward and extending medially behind the large palatal vacuity. These processes never meet along the midline, although in *Teratornis* they are almost in contact (may be in some specimens). The maxilla has a long well-developed labial process which forms a part of the labial bar.

The palatines (fig. 88) are fairly characteristic of the group. Just posterior to the point of the palatal process of the premaxilla, the palatines (unknown in *Teratornis*) widen and extend posteriorly with little change in width, they are widest posteriorly and narrowest opposite the internal nares. They are variously rotated, the medial margin up as much as 45°. Their lateroposterior margins are gently rounded (irregular in *Cathartes*). Along the medial border at the level of the posterior end of the internal nares, the margin is bent ventrally (choanal ridge); lateral to this ridge is the palatal fossa which in life is occupied by the palatal muscle. The lateral border may also be somewhat bent downward. The anteropterygoids are fused to the median dorsal margins of the palatine (thus forming a pterygopalatine--fig. 58A).

A bony vomer is lacking but the membranous nasal septum in which it ordinarily lies is similar to that of species having this bone (fig. 60). It can be assumed that reduction in ossification of this bone has lead to its loss.

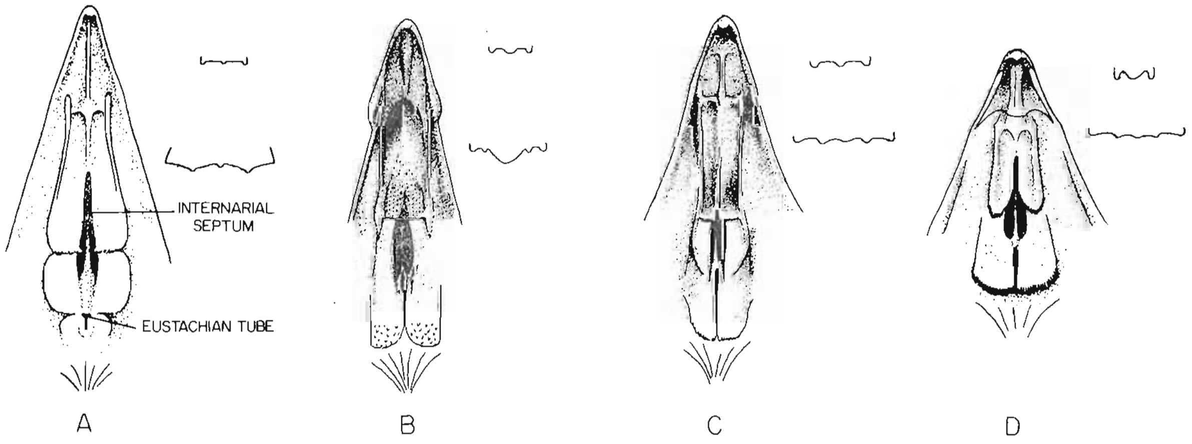


Fig. 60. Palatal surface of the rostrum, as seen in the flesh, of A. *Sagittarius serpentarius*, B. *Cathartes aura*, C. *Aquila chrysaëtos*, and D. *Falco sparverius*.

The rostrum might be characterized by the large, elongated, ovoid nasal opening. *Teratornis* has proportionally the largest such openings as would be expected in view of the enormous rostrum. Wetmore (1944:69) used the large narial opening as a feature of his Family Neocathartidae. The nasal opening of *Neocathartes*, however, is proportionally little larger than that of the turkey vulture and is much smaller than that of *Teratornis* (approximate proportion of length of narial opening to length of skull in *Cathartes* 18.5%, *Neocathartes* 20%, *Teratornis* 33%).

Nasal septum and nasal capsule ossifications are not completely lacking among the cathartids. A portion of the nasal septum, just posterior to the level of the posterior margin of the narial opening, ossifies in all of them and is connected by a bony band (alinasal), in the floor of the nasal passage, with the dorsal surface of the palatal process of the maxilla (fig. 54C). A slight ossification in the dorsal wall of the nasal vestibule also occurs at the level of the septum and is sometimes visible externally in the dorsoposterior angle of the narial opening (fig 64; *see* Miller and Howard, 1938, in *Breagyps*). The ossification of the nasal septum may include a circlet of bone surrounding the internarial perforation (in *Gymnogyps* and one specimen of *Sarcoramphus*, fig. 61). The cathartids are the only falconiforms which display such ossifications, and which have, in the flesh, a perforated internarial septum (fig. 67).

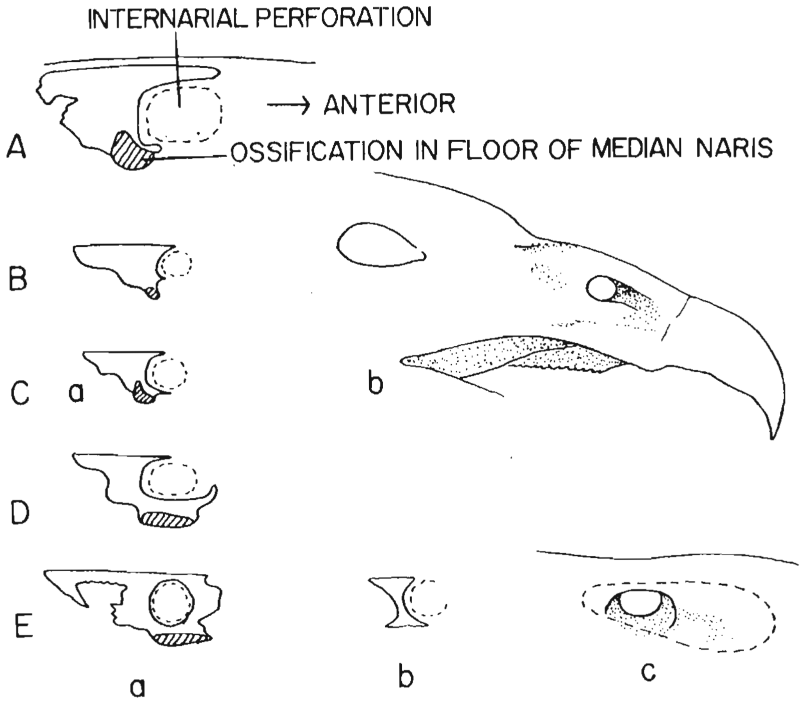


Fig. 61. Ossified nasal septum of A. *Teratornis merriami*; B. *Coragyps atratus*; C, a and b *Cathartes aura*, b. external naris in flesh; D. *Sarcoramphus papa*; E, a-c *Gynmogyps californianus* adult, b. fully grown nestling, c. external naris in flesh, with outline of bony external opening dashed.

The external nares are not comparable to those of other falconiforms; they are little more than the open vestibular chamber (fig. 68). The median naris, which opens between the nasal vestibules and the posterior nasal passages (olfactory and turbinal chambers), is readily seen from the outside and, functionally it is the "external naris." The median naris is elyptical in form, faces directly forward and lies just behind the internarial perforation. It is margined laterally and ventrally by the posterior wall of the vestibule (fig. 70).

The shape of the cathartid rostrum is plastic; usually the length, anterior to the prefrontal, exceeds 50% of the total length of the skull (fig. 56). *Sarcoramphus* has the shortest, stoutest rostrum while that of *Cathartes* is next. Elongation takes place in the narial region while the prenarial portion remains of fairly normal proportion as compared with other falconiforms. The rostrum of this group, with the exception of *Neocathartes*, shows a distinct downward projecting axis as related to the line of the base of the skull (axis of the cranium). A corresponding angle occurs between the ventral line of the upper mandible and the labial arch (fig. 56).

The form of the prefrontal is useful in characterizing the cathartid skull. Primitively this bone is free as it is in the nestling condor (fig. 58B). The supraorbital process is small (not large as suggested by Pycraft, 1902:279) and the medial margin is in contact with the supraorbital rim of the frontal; anteriorly it contacts the nasal. The orbital process is well developed and descends nearly to a point of contact with the labial arch to which it is joined by a ligament; in the adult it is fused to the lateral ethmoid plate (fig. 69D). The form of the prefrontal is discernable in one specimen of *Coragyps atratus* (MVZ 78681) where the bone is still separate (fig. 62). Its shape in a fully grown cathartid is obscured by fusion with the frontal and with the outward extension of the supraorbital margin of the frontal behind it. The supraorbital margin of the nestling can be roughly defined by a row of foramina (compare dorsal views of nestling and adult, figs. 58B, 65; also Pycraft, 1902:279). The orbital process may extend ventrally as in *Teratornis*, *Sarcoramphus*, *Cathartes*, *Coragyps*, or *Neocathartes*; or curve posteriorly as in the condors. This bone is peculiar in that small anterior and posterior processes, separated by a small

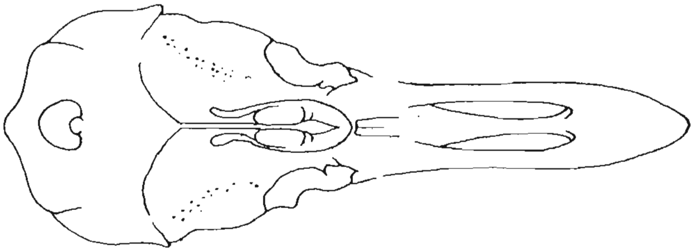


Fig. 62. Ventral view of skull of *Coragyps atratus* (MVZ 78681) with parasphenoid rostrum and palate removed.

gap, underlie the frontal (fig. 58D).

The brow of both *Cathartes* and *Coragyps* has a peculiar fold which extends transversely out to the tip of the prefrontal (fig. 63). Anterior to this is a shallow fossa, while posteriorly there is also a slight depression. Dissection of *Cathartes* and *Coragyps* shows the anterior depression occupied by spongy connective tissue.

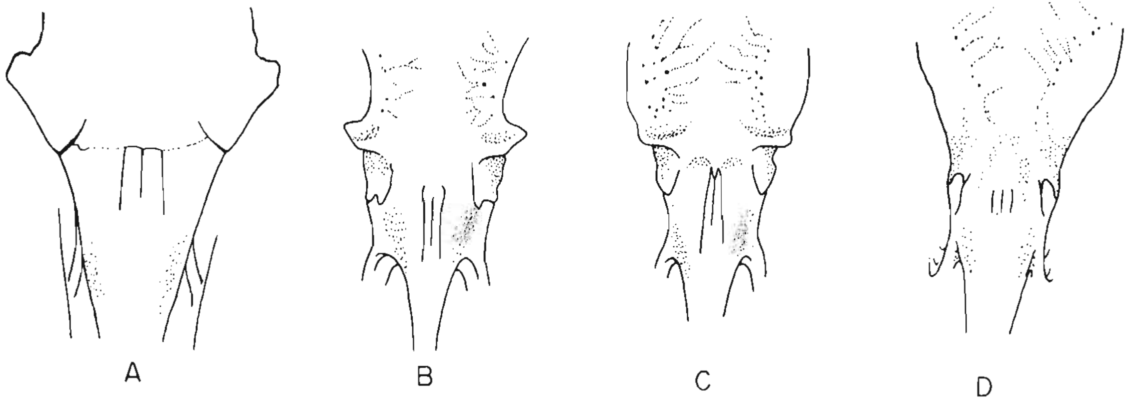


Fig. 63. Dorsal views of frontonasal hinge of A. *Teratornis merriami*, B. *Cathartes aura*, C. *Coragyps atratus*, and D. *Gymnogyps californianus*.

Rostral movement (*see* Kripp, 1933; Engels, 1940; Beecher, 1951; Hofer, 1955) is made possible by the presence of the frontonasal hinge between the rostrum and the cranium. Bending along this hinge is facilitated by the fact that the anterior ends of the frontals are not fused to the overlying frontal processes of the nasals. At this hinge no superficial ossification of bones occurs and the medial margin of the nasal remains free from the nasal processes of the premaxilla for a short distance; dorsally this appears as an anteroposteriorly oriented, crack. The cathartid frontonasal hinge (not known for *Neocathartes*), is peculiar in that the lateral margin of the nasal, at the hinge, abuts transversely against the anterior margin of the prefrontal or it may project posteriorly into a socket of the prefrontal (fig. 64). This lateral projection, is least in *Teratornis*, *Cathartes*, and *Coragypes*; it is most extreme in *Gymnogyps*. Such a hinge is by no means peculiar to this group, inasmuch as it is found also in the pelicans.

The hinge between the rostrum and the labial arch is noteworthy. Beddard (1903) figured and discussed this character while Fisher (1944:282-283) used the split nature of the anterior end of this arch (identified as the "zygomatic arch") to characterize the cathartid skull. Pycraft (1902:290) pointed out that, "In *Cathartes* (*C. aura*) this bar, when it reaches the middle of the lachrymo-nasal fossa, splits into a long inferior dorso-ventrally depressed lamella and a superior shorter rod-shaped portion, which extends forward to within a short distance

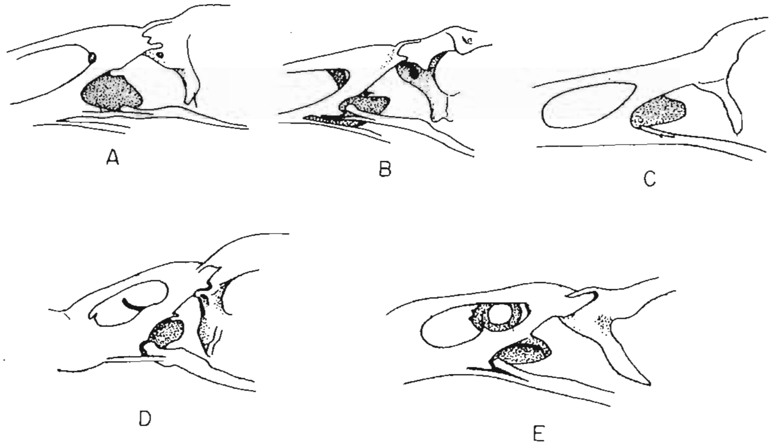


Fig. 64. Lateral views of rostral articulations with cranium and labial bar in A. *Cathartes aura*, B. *Coragyps atratus*, C. *Neocathartes grallator*, D. *Sarcoramphus papa*, and E. *Gymnogyps californianus*.

of the maxillary process of the premaxilla....These features may be traced through a series of stages gradually increasing in complexity, and associated with a gradually developing fronto-nasal hinge." Thus, the labial arch hinge is distinctive in that the premaxilla lacks a well-developed, dorsal labial process, and, in most forms, the anterior end of the jugal is bluntly expanded and articulates in an exteriorly exposed socket of the nasal (fig. 64).

Whereas the structural features of the rostrum seem to be fairly constant, those of the cranium are variable. In comparing the crania of nestling and adult California condors, a superficial ossification covers that of the latter producing grooves in which the surface blood vessels lie (figs. 58B, 65).

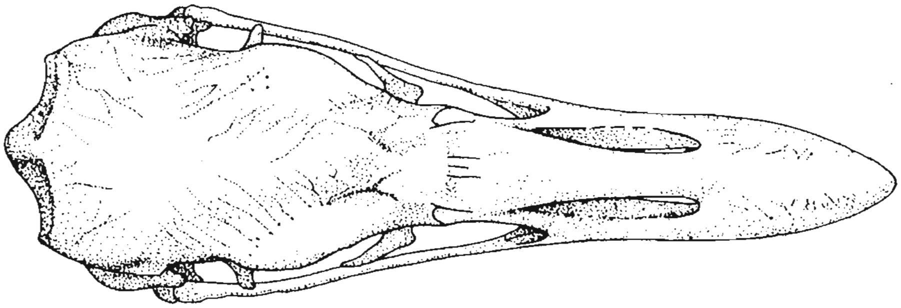


Fig. 65. Dorsal view of the skull of an adult *Gymnogyps californianus*.

This bony layer and venation is distinctive of the group. The venation is characterized by a series of small vessels converging toward the center of the cranium from a line of foramina, which mark the orbit margin of the nestling skull. The superficial ossification of the cranium appears to be correlated with extension of the frontal bones over the orbit.

Extension of the frontal bones over the orbits is least in *Teratornis* and *Neocathartes*. Nestling specimens of the living genera have this region undeveloped, full growth being achieved probably by the time of nest leaving. Whereas in some genera the mature orbital margins curve out beyond the margin of the prefrontal, in others this is not the case. *Cathartes* has distinct prefrontal projections and incurved subraorbital margins. *Teratornis* has large prefrontals with truncated tips and deeply incised (rounded) margins. *Neocathartes* lacks a jutting prefrontal and has a gently incurving margin, which is distinctive within the group. Within most species these margins are consistent; however, a series of La Brea condors showed marked differences in outline as seen from above.

The cranium may have a highly rounded outline, as in *Coragyps*, or flat one, as in *Gymnogyps*. The cathartid is distinctive in the even rounded surface of the cranium and the lack of modeling in the form of cerebral bulges with guttering medially (indicated slightly in *Cathartes* and *Sarcoramphus*) or along the posterior orbital margins (*see* Pycraft, 1902). A slight sagittal ridge occurs in most. The rounding of the cranium may produce a posterior bulge, which extends beyond the dorsal margin of the foramen magnum or this margin may be on the same plane as the back of the skull.

Fisher (1944:273) believed that the dorsal line of the cervical muscle scars marked the fronto-parietal suture. Although the young condor studied did not clearly show cranial sutures dorsally, the posterior limit of the frontal, as indicated in the orbit, is much anterior to the dorsal edge of the cervical scars, as it is in other birds. These cervical muscle scars (nuchal line) mark rather the supraoccipital-parietal suture.

In the well-rounded skulls, the occipital muscle scars lie on a plane facing posteroventrally (the supraoccipital thus being concealed from above in *Coragyps* and *Cathartes*), while in the flatskulled genera the plane of muscle scars is nearly vertical (fig. 66). Parelleling this situation is the orientation of the the plane of the foramen magnum. The angle of this plane with the base of the skull is least in the rounded types and greatest in the flat ones (ranges from approximately 45° in *Teratornis* to 72° in *Vultur*, fig. 67--(*Breagyps* was not measured for this angle, which might exceed *Vultur*). Although there is not a perfect correlation, a high-angled foramen magnum is accompanied by a low flat cranium.

The postorbital process is variously developed, ranging from the massive broad type of *Teratornis* to the horn-like one of *Gymnogyps* (figs. 54, 55). The temporal muscle scar covers a good part of this process in all of the cathartids, with the exception of *Teratornis* where it covers only the posterior edge.

The zygomatic process of the squamosal shows little variation;

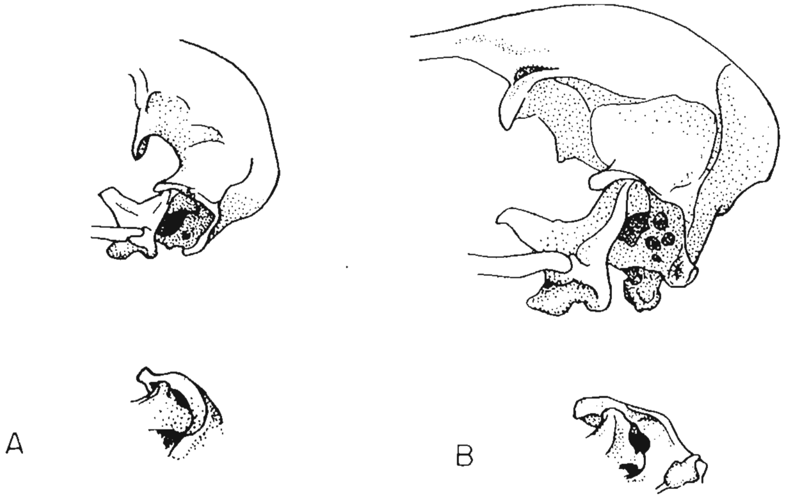


Fig. 66. Lateral views of tympanic area of crania of A. *Cathartes aura*, B. *Gymnogyps californianus*. Ventrolateral view of this area shown below.

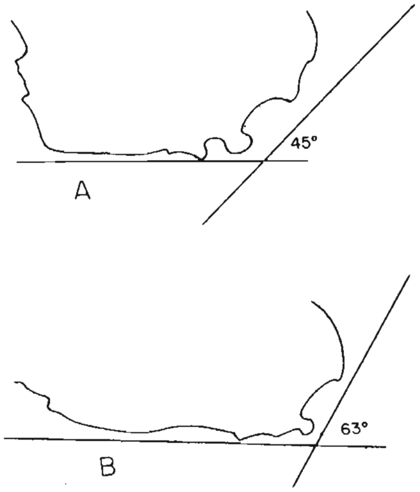


Fig. 67. Median sagittal outline of interorbital septum and back of cranium of A. *Teratornis merriami*, B. *Gymnogyps californianus*. Lines below indicate the angle between the base and the back of the cranium.

it is a truncated, anterior projection above the tympanic cavity (fig. 66). Fisher (1944: 275) cited Sushkin's use of this process and attempted to orient the cathartids among the falconiforms on the basis of it.*

* *

* According to Sushkin (1905:22) the Aquilidae differ from the Falconidae in the relative length of the zygomatic process

The articular process of the squamosal is reduced to a vestige in most cathartids (*Neocathartes* appears to have it well developed, fig. 57C); but is not lacking as Pycraft (1902:283) indicated. The general appearance of the tympanic area differs when one compares the rounded skull of *Cathartes* with the elongated skulls of *Breagyps* and *Gymnogyps* (fig. 66). In the former, the tympanic margin curves posteriorly to an angle then down and forward to the exoccipital process (opisthotic process of Fisher, 1944). In the latter, the squamosal portion of the tympanic rim meets the exoccipital portion at a much more open angle. The tympanic area is not distinctive for the group beyond the weak development of the articular process of the squamosal.

Of more importance in this region is the relationship of the dorsal margins of the lateral cervical musculature (*rectus capitis lateralis*) and the ventral margin of the *masseter et temporalis* (fig. 68). In the cathartid, the line of contact extends out nearly to the edge of the tympanic rim, where the squamosal and exoccipital come in contact. Here the muscle scars diverge to form a limited, somewhat triangular area (fig. 66B--the obscure character of this line is shown for *Teratornis* in fig. 54D). The *depressor mandibulae* arises from this triangular area, from the line of contact between the *masseter et temporalis* and the cervical muscles and from the tympanic rim below the triangular area.

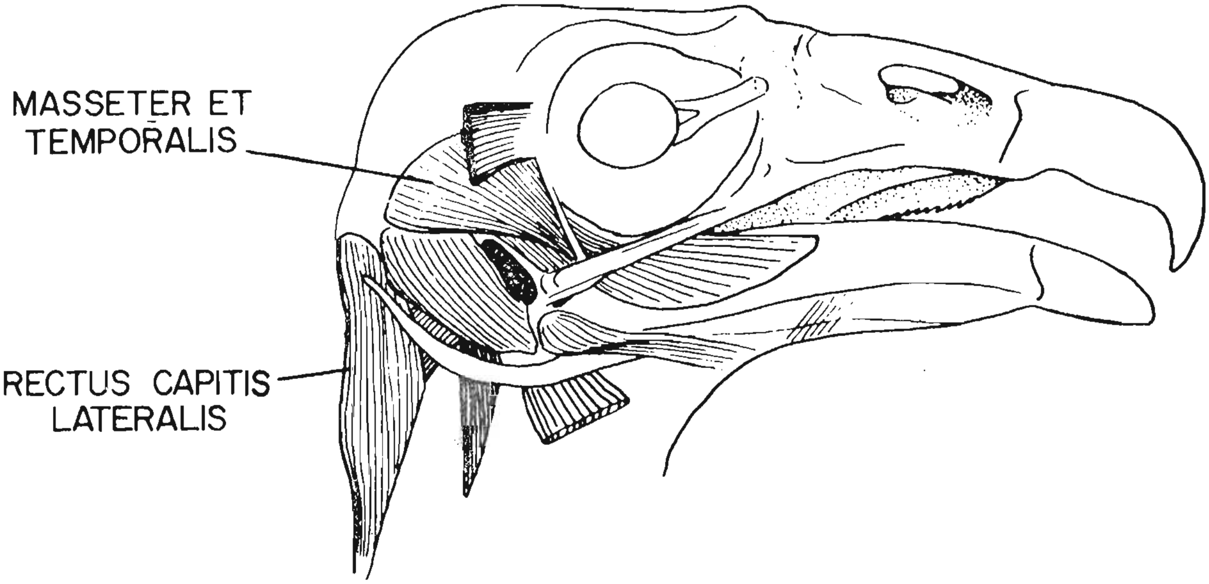


Fig. 68. Lateral view of jaw and neck musculature of *Cathartes aura*.

On the base of the skull (fig. 52 for orientation) both the

* *

as compared with the axial length of the quadrate. For the cathartids, Fisher said that the measurements are unsatisfactory, but four members of the Cathartidae definitely fall in Sushkin's first group; *Sarcoramphus* is on the border line between the two.

lateral basiparasphenoid (exoccipital or occipital process of Fisher, 1944) and exoccipital processes in *Cathartes* and *Coragyps* are weakly developed while in *Vultur*, *Gymnogyps*, and *Breagyps* they are large and project ventrally; *Sarcoramphus* tends to be intermediate. The base of the skull of *Neocathartes* is unknown, while that of *Teratornis* is unlike the others. In the latter the lateral basiparasphenoid processes are prominent, rounded ridges projecting outward and somewhat posteriorly. The exoccipital processes are well developed but of an entirely different form than those of *Gymnogyps*.

A small, median basiparasphenoid process is seen in *Coragyps* and *Teratornis*; in *Cathartes* this is separated into two small projections. Among the condors this process is absent. The basioccipital pit is present in all except modern *Gymnogyps* (present to absent in *Gymnogyps amplus*) and *Vultur*. The situation in fossil *Gymnogyps* is of interest in that some have a distinct pit whereas others show the transition to no pit.

The ventromedial margin of the tympanic cavity is entire (not notched). The eustachian tubes show no significant variation; they are closed in all except *Cathartes* while the condition in *Neocathartes* is in doubt. The basipterygoid processes are well developed and functional in all.

The interorbital septum (fig. 69), composed of the orbitosphenoid, parasphenoid, and mesethmoid, is imperforate but thin in *Cathartes* and *Coragyps*; it has a large fenestra in the condors and *Sarcoramphus*. The septum of *Neocathartes* is not known; that of *Teratornis* is thick and imperforate.

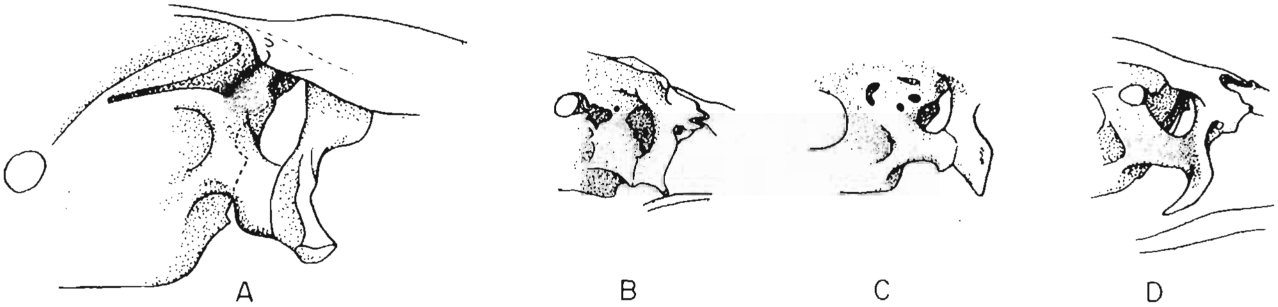


Fig. 69. Orbital views of A. *Teratornis merriami*, B. *Cathartes aura*, C. *Sarcoramphus papa*, and D. *Gymnogyps californianus*.

The nasal passages should be described here, since their form influences certain bony features (fig. 70). In birds this passage is fairly constant in its structure (*see* Gegenbaur, 1873; Technau, 1936) being made up of three main parts: vestibule, nasal passage, and olfactory chamber. The vestibule is open and a fold (or turbinal) is lacking. The median naris opens into the laterally compressed nasal passage in which there is a simple, rolled nasal turbinal. The turbinal is attached along a line beginning anteriorly on the roof of the nasal passage, a

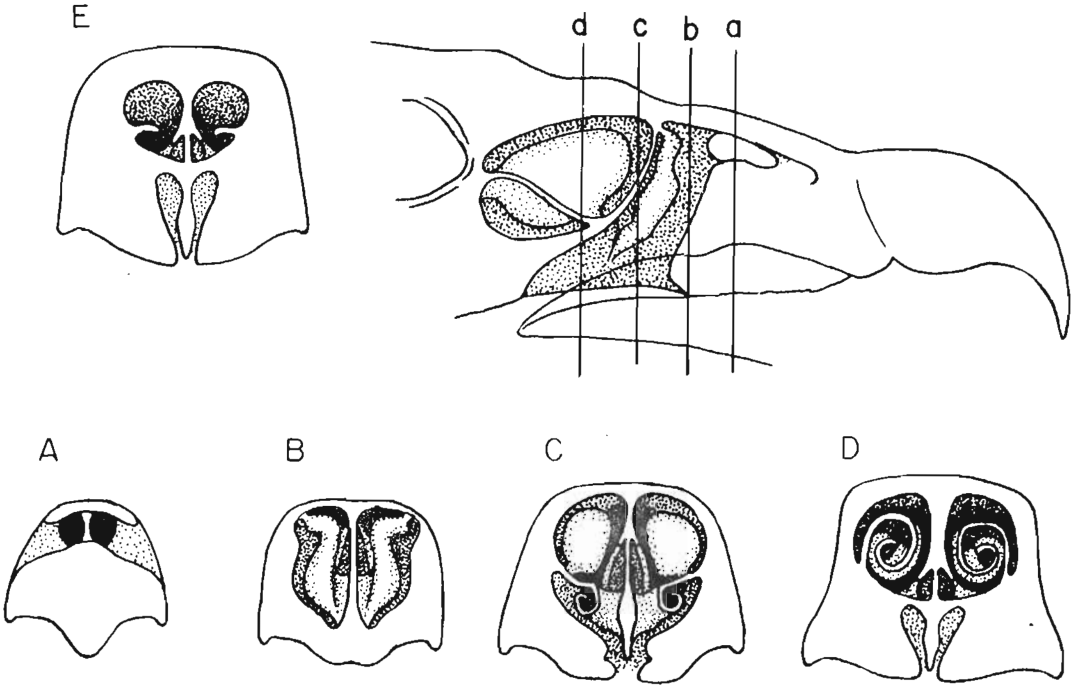


Fig. 70. Nasal passage of *Cathartes aura*. A. X-section of rostrum as seen with end of bill cut off along line a, showing median nares in black. B. X-section of rostrum as seen with end of bill cut off along line b, showing nasal turbinal and opening into olfactory chamber (black). C. X-section of rostrum as seen with bill cut off along line c, showing section of nasal turbinal, olfactory turbinal, and pockets on nasal septum. D. X-section of rostrum with bill cut off along line d, showing section of olfactory turbinal and septal pockets. E. Section similar to D, showing olfactory turbinal and septal pockets in *Coragyps atratus*.

short distance back from the median naris, and extending almost directly ventrad to end upon the nasal septum below the olfactory capsule. At the point where the turbinal ends posteriorly and ventrally, a small pocket opens directly into the suborbital space by a short tube. The olfactory capsule opens into the passage medial to the turbinal and lies above and behind it. The highly vascular olfactory turbinal nearly fills the ovoid olfactory capsule.

The olfactory turbinal of *Cathartes* makes two turns or more, whereas that of *Coragyps* is but a shelf-like projection extending medially from the lateral wall of the capsule. The median septum of the two dissected genera has a small fold, which extends into the opening of the olfactory capsule and isolates a small septal pocket. This fold acts as a baffle to air entering the olfactory capsule. Such a fold is lacking in the other falconiforms.

Returning to the bony structure associated with the nasal passages, the mesethmoid and lateral ethmoid form a large triangular (as viewed laterally) olfactory capsule (also remarked by Pycraft, 1902). Figures 58D and 62 show this area as seen with the more ventral parts removed. The olfactory capsule reaches posteriorly in the orbit nearly to the anterior end of the brain cavity and the olfactory nerve lies within the ethmoid (fig. 69). *Teratornis*, in sharp contrast to the others, has only a small, ovoid olfactory capsule, lying well anterior to the brain cavity, and the olfactory nerve lies in a groove in the interorbital septum; the capsule lacks the ventral cupping of the other cathartids (*Neocathartes*?). The anatomical evidence supports the contention that the olfactory sense of these birds is well developed. The form of the olfactory capsule of *Teratornis* indicates that it lacked an olfactory turbinal.

The outline of the ventral margin of the parasphenoid rostrum and the craniofacial fissure margin of the mesethmoid vary widely (fig. 67).

The quadrate (fig. 54, 66, 103) of the cathartid is not distinctive except that, as viewed ventrally, it has a saddle-shaped surface on its medial articulation and a relatively narrow lateral flange. This grooved articular surface is usually characteristic of the group; it is weakly developed in *Cathartes* and absent in *Teratornis*. Fisher (1944:284) described the sigmoid shape of the outer, distal, articular surface, but this does not seem to be characteristic of the group.

Sushkin (1905:37) used the details of the articular surface of the mandible, the shape of the mandibular bones and the fenestration of this structure in characterizing different groups. The features of the articular surface and the posterior view of the articular area of the mandible of the cathartids are more effectively illustrated than described (fig. 104). The component bones of the mandible are known for *Gymnogyps* (fig. 58) but not for the others. A point to note is the depth of the ramus proximally, a situation common to the group. A small posterior mandibular fontanelle is usually present (? *Neocathartes* and *Teratornis*).

The hyoids of the living cathartids show basic similarities (fig. 71). In the California condor the basihyal is deeply

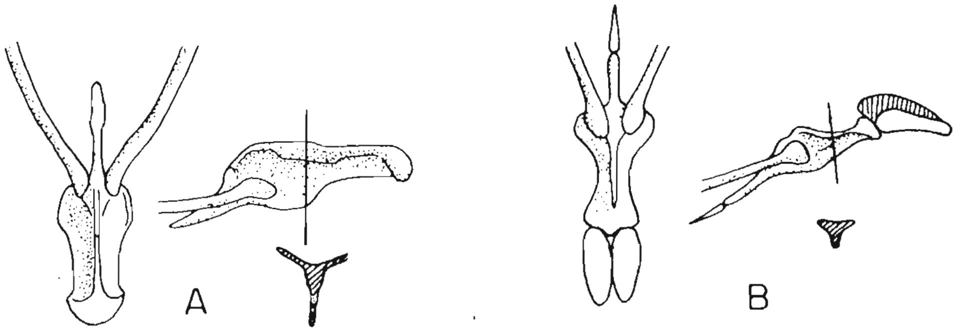


Fig. 71. Lateral, X-sectional, and ventral views of hyoids of A. *Gymnogyps californianus*, B. *Cathartes aura*.

keeled and the dorsal portion is drawn out into lateral wings, i.e. has a Y-shaped cross section. The entoglossal articulations are positioned anteriorly and reduced to rounded surfaces. The entoglossal ossifications are flattened, ovoid pieces extending dorsolaterally and forward from their articulations. There is no distinct postarticular process. It cannot be assumed that the more aberrant fossil members, *Teratornis* and *Neocathartes*, had similar hyoid apparatuses.

The variations of the cathartid skull fall into four groups: *Teratornis*, *Neocathartes*, *Cathartes--Coragyps*, and *Sarcoramphus--Gymnogyps--Breagyps--Vultur*. The first differs markedly from the others in almost every detail of the cranium. The second (so far as is known) differs only in the development of the prefrontal and orbital margins. The last two differ only in minor details, particularly the shape of the cranium and the morphology of its basal processes.

Taxonomically, the last two groups are very close, whereas the second could easily have been derived from them. The first however, represents a wide divergence (or a superficial convergence), which may not be allowable within a single family--there is little doubt of its highly specialized nature, at least, in regards to size.

If we include all four groups in a single characterization we have the following: the palate is schizognathous with large, anterior palatal fossa behind which the spoon-like palatal processes of the maxilla approach (or even touch at) the midline, there is no vomer; the nasal aperture tends to be large and ovoid; nasal capsule ossifications (alinasal) encircle the median nares and include a small median septum, which lies behind or is perforated by the internarial fenestra; the rostrum, as viewed laterally and as measured from the anterior point of the prefrontal, exceeds 40% of the total length of the skull; the fronto-nasal hinge is more complex than in the other falconiforms; the prefrontal is fused to the frontal and usually to the lateral ethmoid; its supraorbital process is short and there is no supraciliary bone; the cranium is variable in shape, its processes range from well developed to rudimentary; a low rounded sagittal ridge usually occurs in place of a median gutter between cerebral bulges; the articular process of the squamosal is usually vestigial; the basipterygoid processes are well developed and functional; the ramus of the mandible is of great depth in its posterior half, and there is usually a small posterior mandibular fenestra; the basihyal is usually keeled below.

If the association of these four groups is a natural one, we can assume that details of the olfactory capsule and the shape and processes of the cranium are plastic, whereas those of the rostrum and palate are conservative.

The Sagittariid Type

Because of the similarity of the sagittariid and accipitrid skulls only the special features of the former need description. A nestling skull (AM 505), in fragmentary condition and incomplete, gives some clues to the rostral and cranial structure.

Figure 72 shows a dorsal view of this skull as it may have appeared; the shape of the prefrontals is speculative.

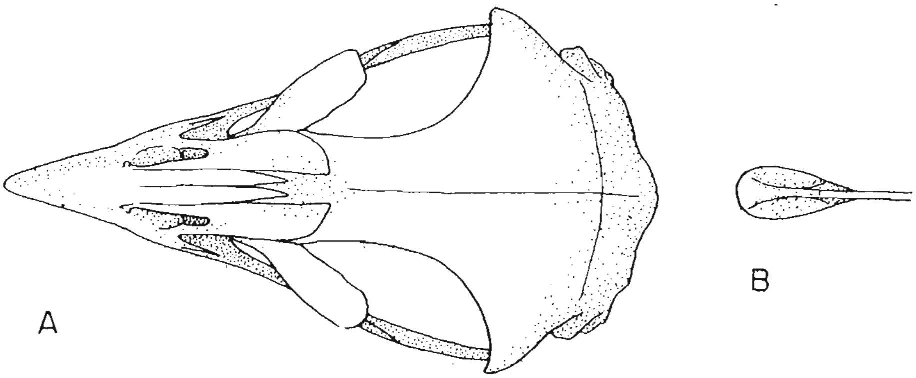


Fig. 72. A. Dorsal view of skull of nestling *Sagittarius serpentarius*; the shape of the prefrontal is speculative. B. Ventral view of anterior end of the interorbital septum.

The palate of this type is desmognathous (fig. 73). The anterior palatal fossa is reduced to small foramina and contact sutures between the palatal processes of the premaxillae and the

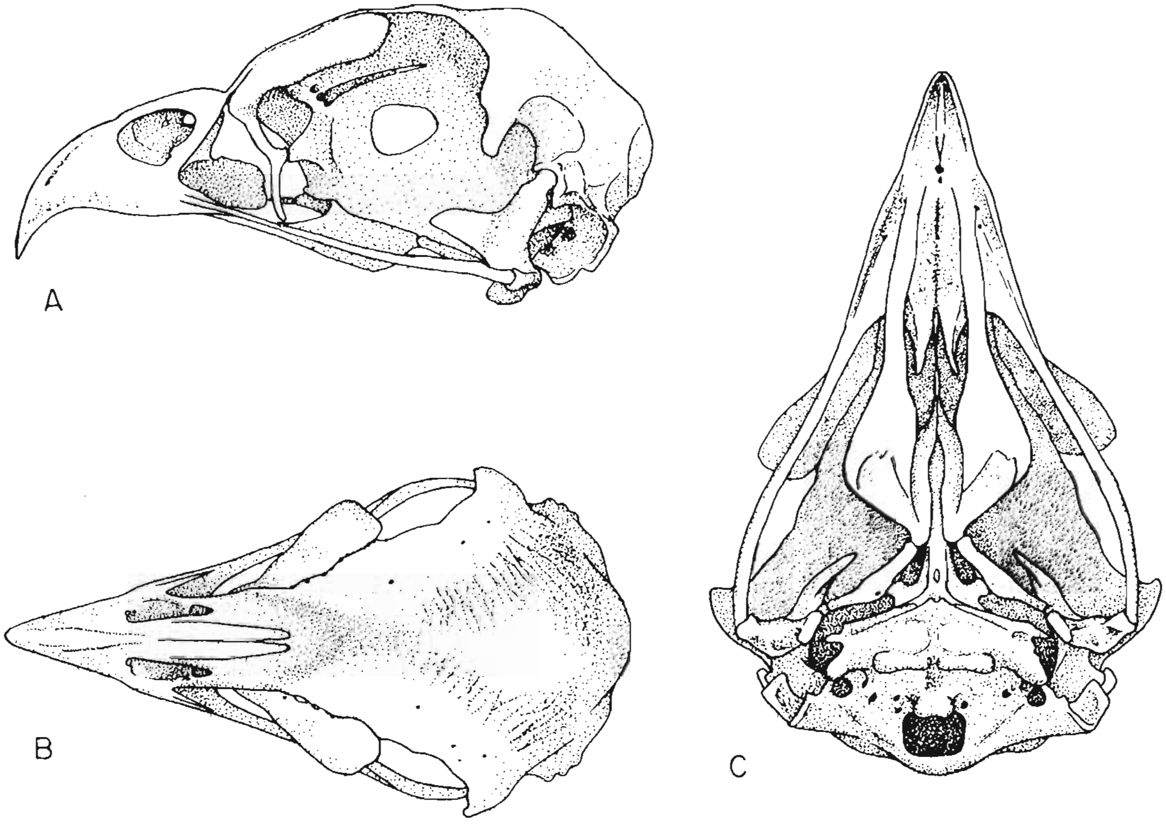
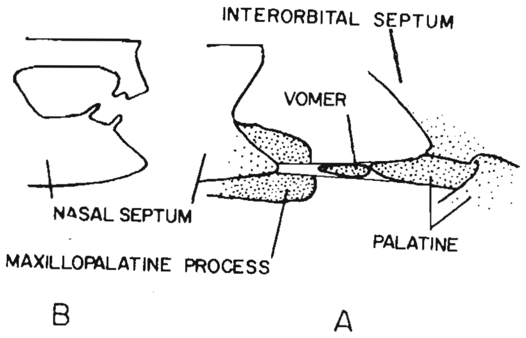


Fig. 73. Skull of *Sagittarius serpentarius*. A. lateral, B. dorsal, C. ventral views.

ossified ventral margin of the nasal septum. The ossified ventral septal bar extends forward from the anterior tip of the sliver-like vomer to the tip of the bill (fig. 74). In the juvenal, the palatal processes of the maxillae lie in contact (along the midline) but are not fused and, anteriorly, the vestiges of the anterior palatal fossa appear as narrow cracks between the processes of the premaxillae and the median bar. The palatal processes of the maxillae are spongy structures, laterally compressed posteriorly and open on their lateral aspects.



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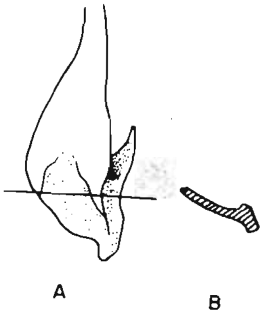

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Fig. 74. A. Lateral view of posterior part of vomer *Sagittarius* lying in a connective tissue band between tips of palatines and nasal septum. B. Outline of posterior part of nasal septum of second specimen; septal perforation extends through posterior margin.

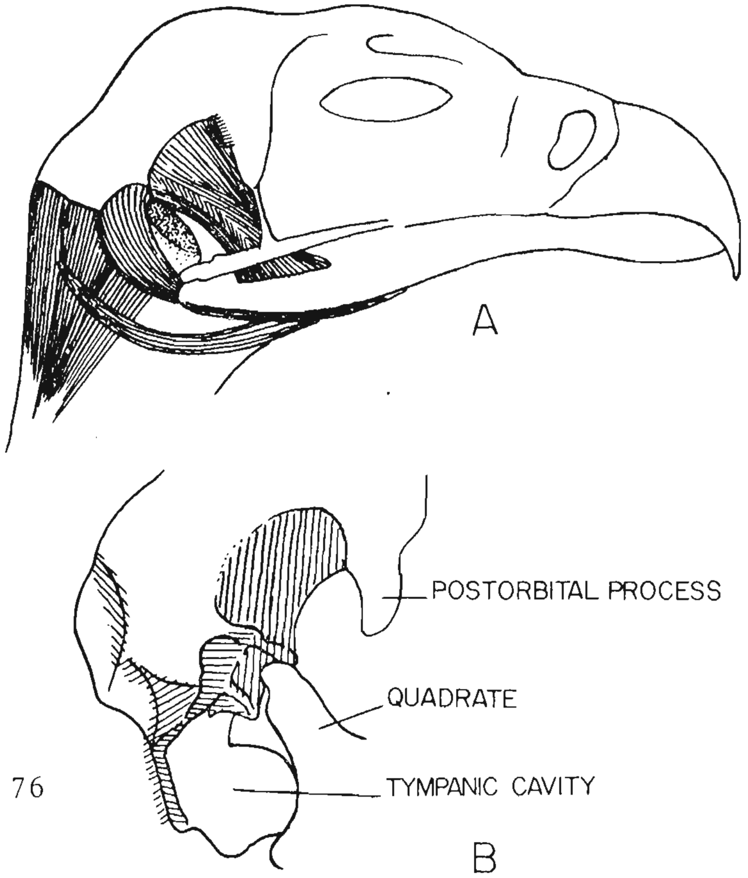
Fig. 75. Palatine (pterygopalatine) of *Sagittarius* seen A. in ventral aspect, B. X-section, dorsal side down.

The palatines are distinctively shaped. Anteriorly each is narrow and of irregular width, and, posterior to the maxillopalatines, each widens out to reach a maximal width beneath the orbit, then tapers to the pterygoid process, which is actually the anteropterygoid fused to the palatine. The palatine fossae are shallow excavations, not bounded medially by a distinct choanal ridge (*see* x-s, fig. 75). The palatines lie in contact only at the anterior ends of their parasphenoid (rostral) processes. The anteropterygoids are presumably well developed since the pterygopalatines clasp the parasphenoid rostrum.

The form of the rostrum is accipitrid-like. The nasal septum is irregularly perforate and its posterior margin is notched, or incomplete (fig. 74). Dorsally the nasal is fused with the frontal and does not show a lateral crack for movement of the frontonasal hinge. The labial bar differs in that the jugal does not extend forward to contact the nasal.

The supraorbital margin of the adult cranium is extended out and contacts the medial margin of the prefrontal, which is well developed and free. The large supraorbital process of the prefrontal extends posteriorly and laterally and has an almost truncated tip. There is no superciliary bone. The orbital process is thin and rounded (figs. 73A, 79).

The ear area is easily characterized. The *depressor mandibulae* has an extensive origin beginning lateral and posterior to the squamosal articulation of the quadrate (fig. 76). The *masseter et temporalis* scar is small, well separated from the cervical muscle scars, and does not seem to extend ventrally below the level of the zygomatic process of the squamosal; actually the origin overlies that process and extends down onto the articular process of the squamosal. The zygomatic process is short and blunt. The articular process is exposed in the flesh at the edge of the tympanic cavity. It is large and has a distinct, lateral ridge (ventral margin of *masseter et temporalis* origin), which gives it a triangular X-section (fig. 77).



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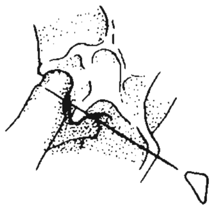

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Fig. 76. A. Muscles of the head of *Sagittarius* viewed laterally. B. Origins of jaw muscles in relation to contours shown in Figure 77.

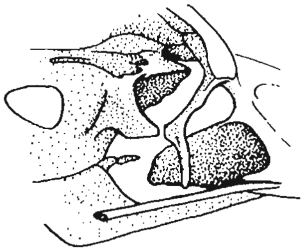
Fig. 77. Lateral view of tampanic area in *Sagittarius*; articular process of squamosal in cross section along line to left.

The base of the skull differs in being inflated; the parasphenoid bulges ventrally to either side of the midline. The occipital condyle is exceptionally wide and has a median, posterior, and ventral groove. The basiparasphenoid area is not as triangular as in the accipitrid. The lateral basiparasphenoid processes are low, rounded ridges extending out to either side;

they are separated medially by a small median basiparasphenoid process. Posterior to the latter and anterior to the condyle, the basioccipital bone has the form of a low ridge instead of a pit.

The tympanic articulations (figs. 52, 73C) are well developed, the eustachian tubes are partly (variably) open and the anterior wall of the anterior tympanic recess has a blunt, hornlike alaparasphenoid process. The basiptergoid processes are developed and articulate with the posteropterygoids.

The interorbital septum is perforate as in most falconiforms. The olfactory capsule, which encloses the olfactory nerve, is narrow (fig. 78). The olfactory chamber is accipitrid-like.



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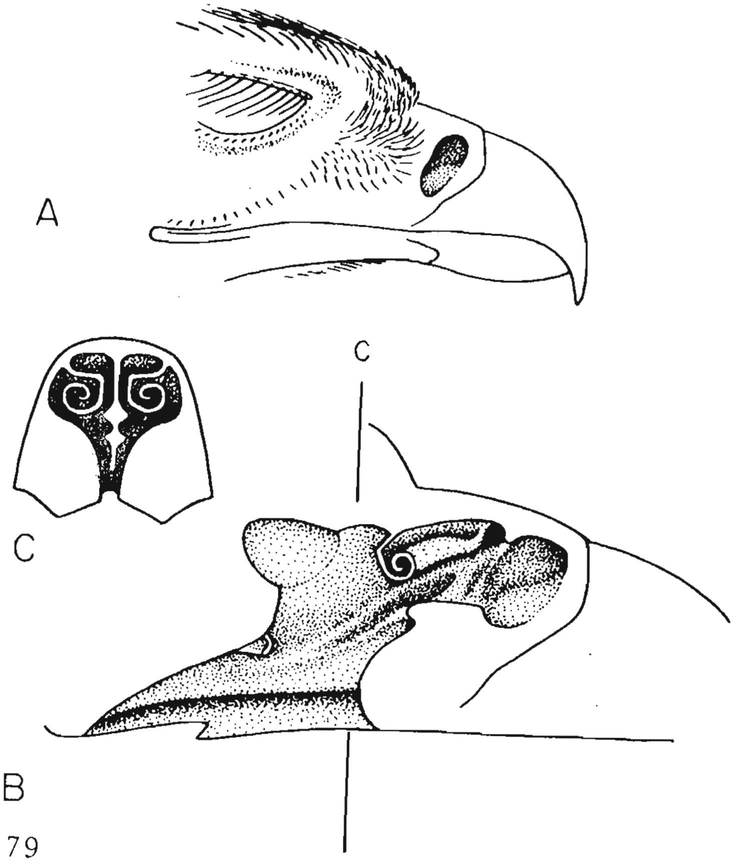

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Fig. 78. Orbital view of mesethmoid-lateral ethmoid structure of *Sagittarius*.

Fig. 79. Nasal passage of *Sagittarius*. A. Lateral view of rostrum, in flesh, showing external naris. B. Sagittal section through nasal passage, middle portion of nasal turbinal removed to show contours of nasal septum. C. X-section of rostrum as seen with tip of bill cut off along line c.

Fürbringer (1888:1073), following Gegenbauer, remarked that the membranous turbinals of *Sagittarius* differ from those of the other accipitres, but the only real difference is the lack of the vestibular fold, a situation shared with some of the accipitrids (fig. 79).

The outline of the ventral margin of the parasphenoidal rostrum and the craniofacial fissure is not characteristic (fig. 80). The distal articular surfaces of the quadrate, viewed ventrally, are simpler and more widely separated than in the other (fig. 103), and the articular surface of the mandible is likewise distinct (fig. 104). The mandible appears to be generally like that of the accipitrid, but study of its development may reveal distinctive features. The hyoid is like that of the accipitrid (fig. 105A).

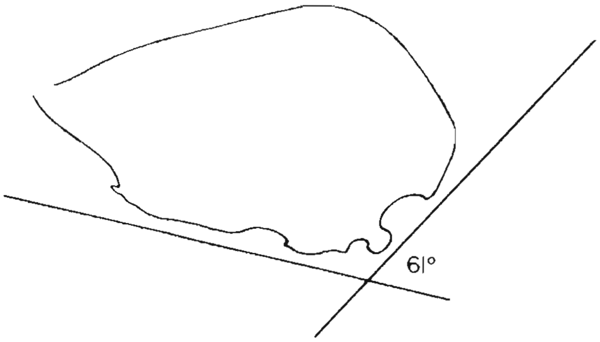


Fig. 80. Median sagittal outline of interorbital septum and back of cranium of *Sagittarius*. Lines below indicate the angle between the base and the back of the cranium.

The sagittariid head skeleton can be characterized as follows: like the accipitrid in most respects but having fully developed and functional basipterygoid processes; the superorbital process of the prefrontal large but without a supraciliary; vomer much reduced with no evidence of bilateral structure; palatines with small shallow palatine fossae, which extend forward only a short distance and lack a medial choanal crest; palatines lie in contact only along their rostral processes and sometimes in the region of the anteropterygoids; zygomatic process of squamosal rudimentary, articular process triangular in section; articular areas of both quadrate and mandible distinctive.

The Accipitrid Type

In describing the head skeleton of this group only the extremes will be cited. The general anatomy of this type is shown in figures 50, 51; its development is only partially known.

The palatal aspect of the rostrum of the sagittariid, accipitrid, and falconid have the tip of the premaxilla braced by ossification of the ventral margin of the nasal septum (figs. 73, 83, 106); this can be called the septal bar. The palatal vacuity is vestigial and divided by this bar; it may be reduced to mere lines of contact or irregular foramina by expansion forward and inward of the palatal processes of the maxillae (fig. 81). Among the accipitrids the development of this brace ranges from that of *Elanus* (fig. 85) in which the maxillopalatines are widely separated to that of *Haliaeetus* (fig. 87) in which contact and fusion of these maxillary processes has crowded out the septal bar and reduced it to a fibrous vestige.

The palatal surface of the tip of the rostrum has a charac-

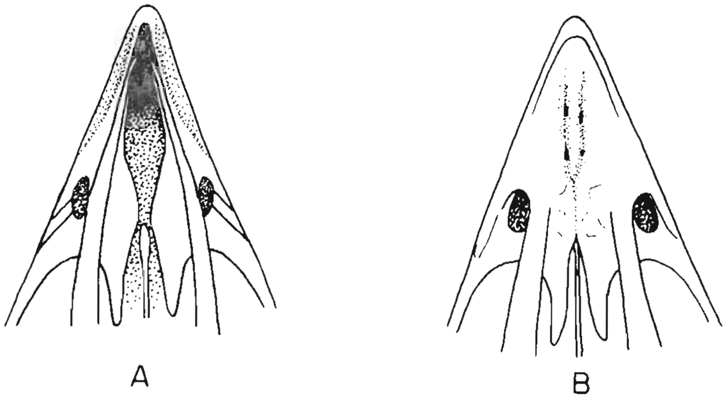


Fig. 81. Bony palate of A. natal *Accipiter cooperii*, and B. adult of this species.

teristic median grove formed by the difference in level of the palatine processes of the premaxilla and the septal bar. In this groove lies a median ridge formed by the septal bar (figs. 83C). The median ridge obliterates this hollow in some of the kites (*Ictinia, Harpagus, Leptodon*, and *Chondrohierax*), which thus resemble the falconid (figs. 82, 107).

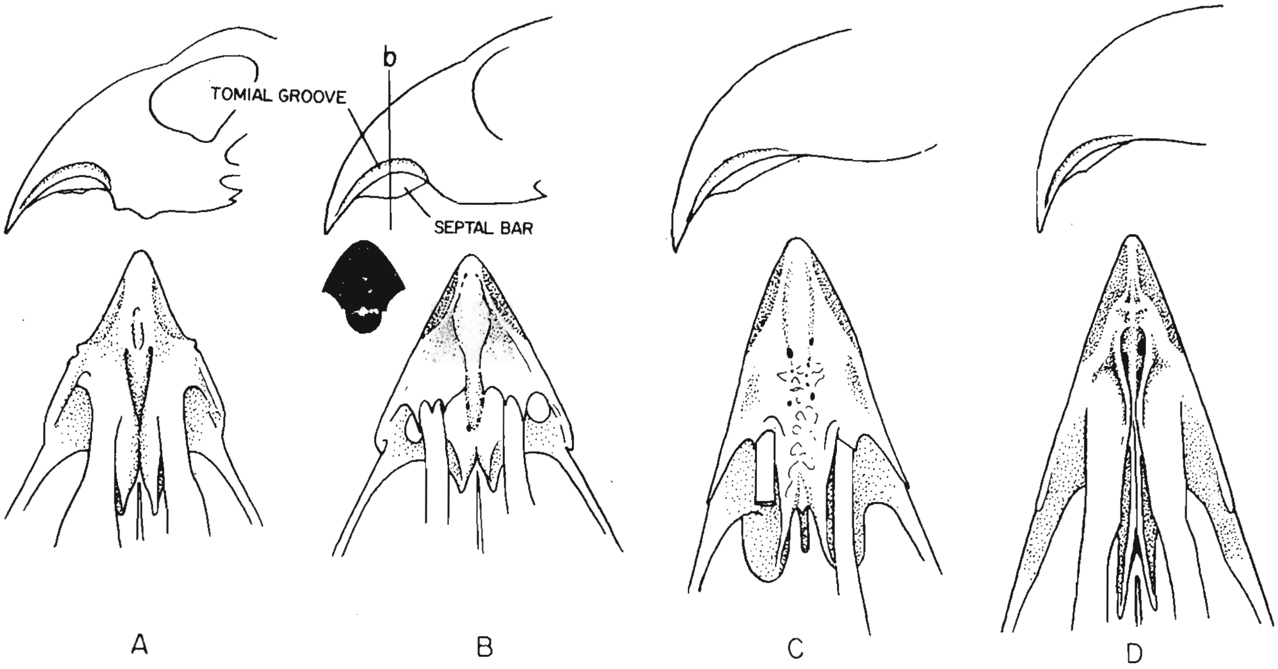


Fig. 82. Falconid-like rostra of accipitrids as seen in lateral (above) and ventral views (below). A. *Harpagus bidentatus*; B. *Ictinia misisippiensis*, X-section along line b in black; C. *Leptodon palliatus*; D. *Chondrohierax uncinatus*.

The tomial margin of the premaxilla is grooved in the region of the hook (figs. 82, 83A, C). These grooves appear to be sites of growth for the tip of the horny sheath. The tomial

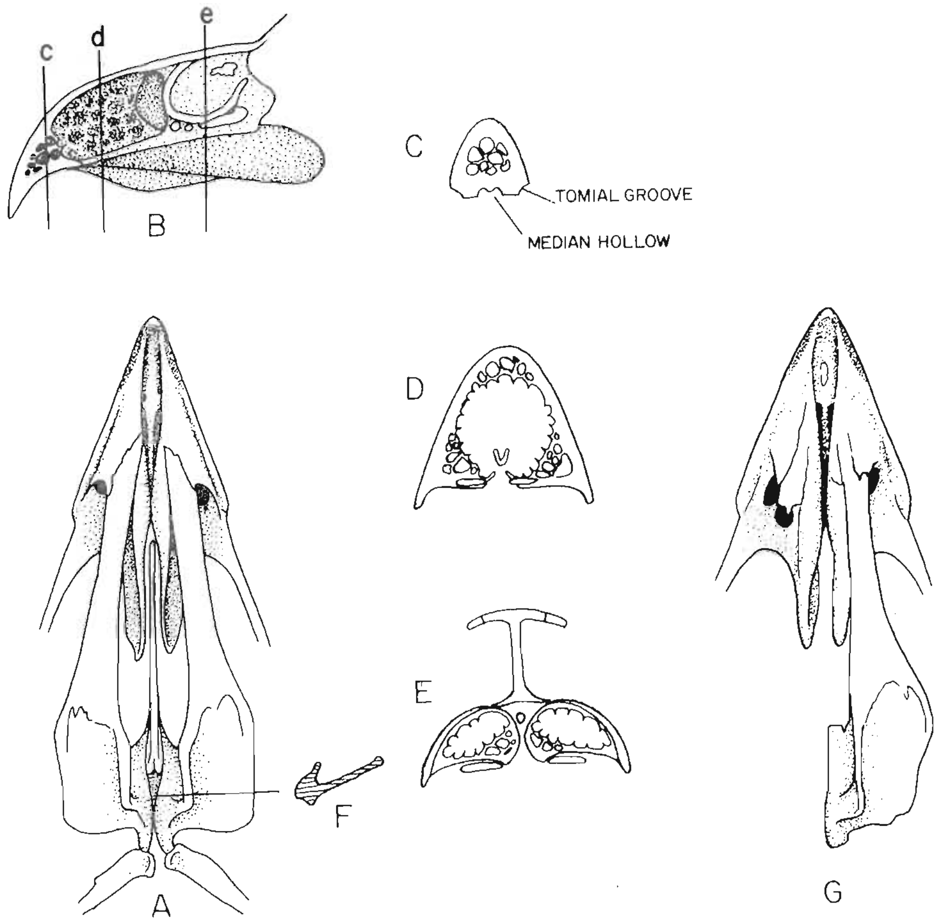


Fig. 83. Rostrum of *Aquila chrysaëtos*. A. Palatal view, B. median sagittal view of right half, C. X-section along line c, D. X-section along line d, E. X-section along line e, F. X-section of palatine, dorsal aspect down. G. Palatal view of Rancho La Brea *Aquila*.

margin of the premaxilla is festooned posterior to this groove; viewed laterally, it presents an evenly, somewhat sigmoid, curved outline with only an irregular (?) toothing in *Harpagus* (*see* Ridgway, 1875:pl. XII, fig. 8). The "toothing" of the accipitrid tomium is not comparable to that of the falconid.

The posterior palatal process of the premaxilla is weakly developed in most (long in young of *Gyps*); it lies lateral to the anterior end of the palatine. In the adult, the anterior splint of the palatine and the outline of the palatal process of the premaxilla becomes obscured by a superficial bony cover.

The maxillopalatine processes may be well separated or show every stage between this and complete fusion, with obliteration of the median line of contact (fig. 84). The shape of this process is variable; generally it is inflated and becomes laterally compressed posteriorly. It ends bluntly, well separated from its mate. The posterior part may be incompletely ossified on the outer and dorsal aspects, thus exposing the weblike confusion of criss-crossed fibers of bone (cancellous) in its

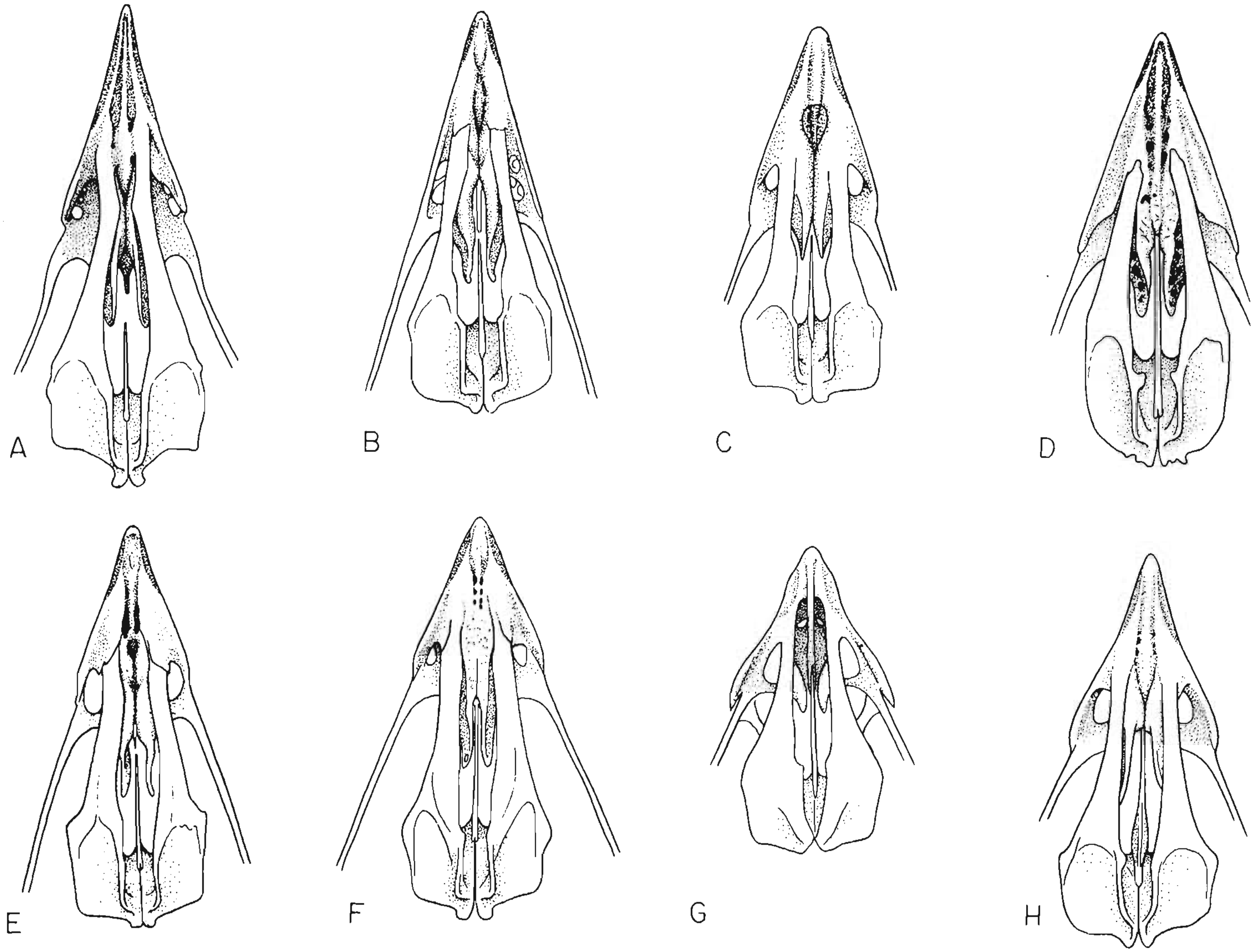
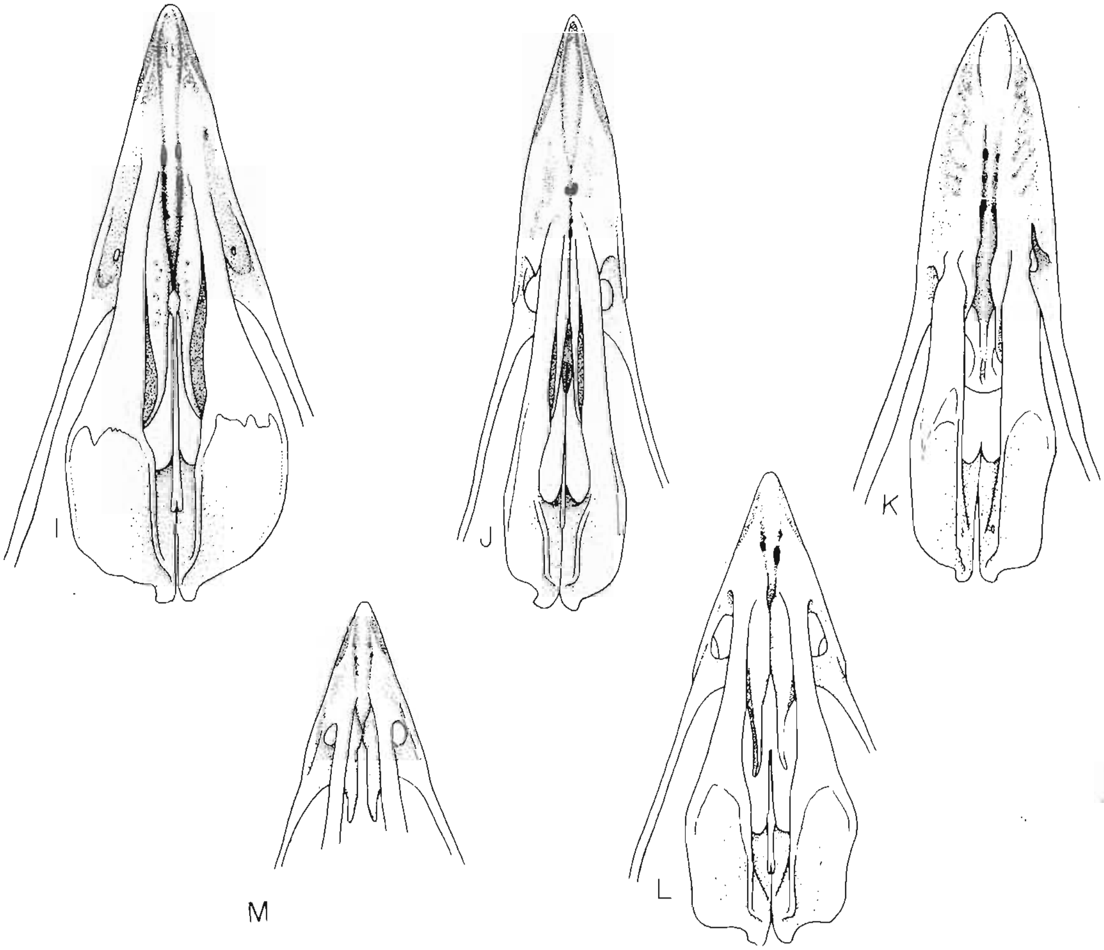
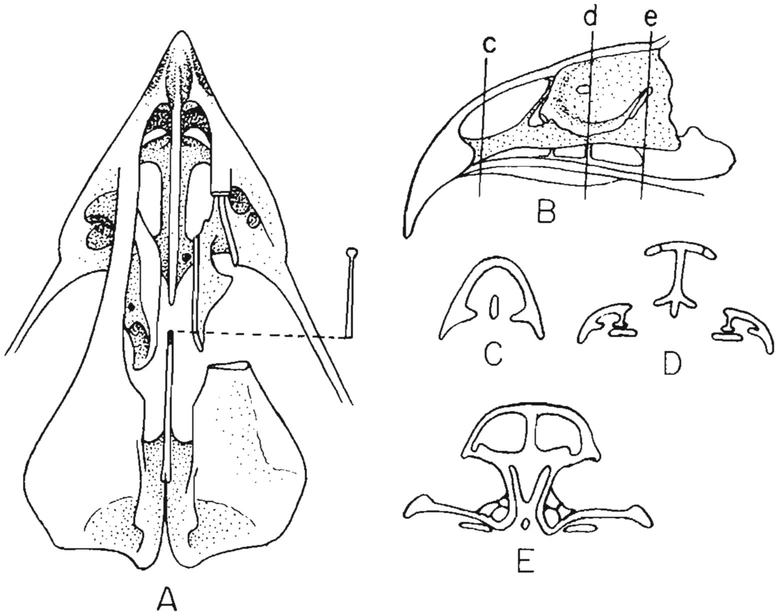


Fig. 84. Palatal views of rostra of A. *Rostrhamus sociabilis*, B. *Gymnogenys typicus*, C. *Haliastur sphenurus* (atypical), D. *Pandion haliaetus*, E. *Geranospiza nigra*, F. *Buteo jamaicensis*, G. *Gampsonyx swainsonii*, H. *Elanoïdes forficatus*, I. *Gypaëtus barbatus*, J. *Gypohierax angolensis*, K. *Gyps coprotheres*, L. *Terathopius ecaudatus*, M. *Circus cyaneus*.



interior. These processes may fuse dorsally with the ventral wall of the vestibule; usually they form the outer part of the vestibular floor along the ventral margin of the narial opening.

Well separated palatine processes of the maxillae, approaching those of the schizognathous palate, are found in *Gyps*, *Pseudogyps*, *Aegypius*, *Neophron*, *Elanus*, *Gampsonyx*, *Pernis*, *Aviceda*, and *Circaëtus* (fig. 84). In *Lophaëtus* and some specimens of *Aquila chrysaëtos*, and all fossil *Aquila* from La Brea and Carpenteria, these processes are separated by a narrow chink (fig. 83G). The tip of the vomer may bridge this gap as in *Gypaëtus*. *Elanoïdes*, and *Gymnogenys* have these processes in contact for a short distance but not fused, whereas *Geranospiza*, *Rostrhamus*, *Ichthyophaga*, and *Terathopius* display an intermediate condition as compared with *Leptodon*, *Ictinia*, *Accipiter*, *Hypomorphnus*, *Heterospizias*, *Busarellus*, *Buteogallus*, *Milvus*, and *Pandion* in which complete fusion occurs along with obliteration of the line of contact (figs. 82-87).



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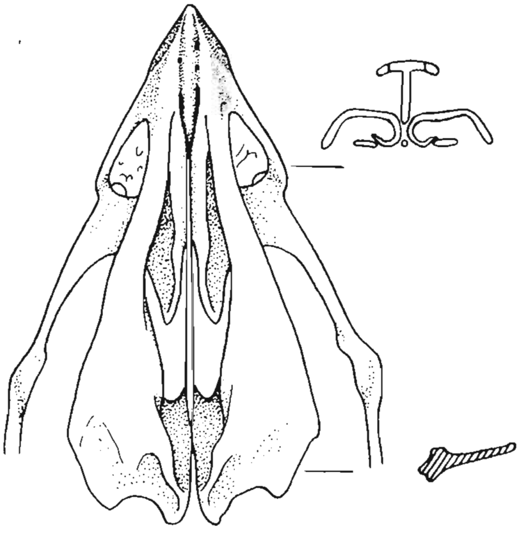

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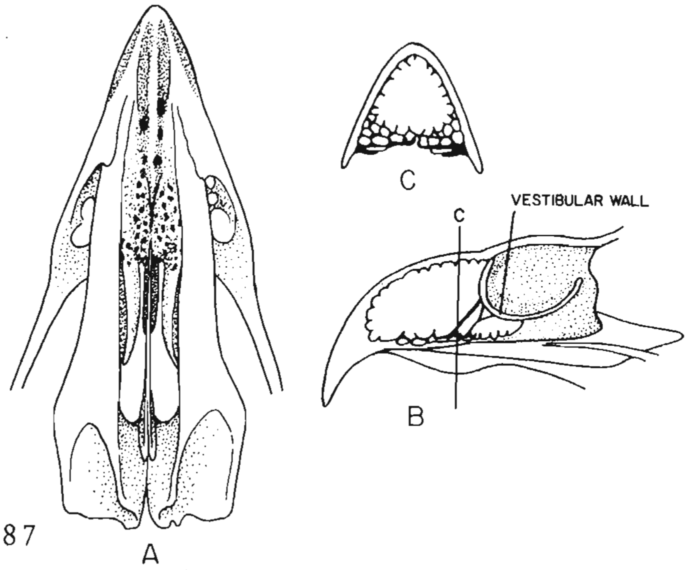

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Fig. 85. The rostrum of *Elanus leucurus*. A. Palatal view, anterior end of vomer set to right; B. sagittal view of right half cut just to the left of the midline; C. X-section along line c; D. X-section along line d; E. X-section along line e.

Fig. 86. The rostrum of *Machaerhamphus alcinus*. Palatal view; X-sections of rostrum and palatine bone at levels indicated by lines.

Fig. 87. The rostrum of *Haliaeetus leucocephalus*. A. Palatal view; B. Sagittal view of right half cut just to the left of the midline; C. X-section along line c.

Extreme variations are not limited to differences between

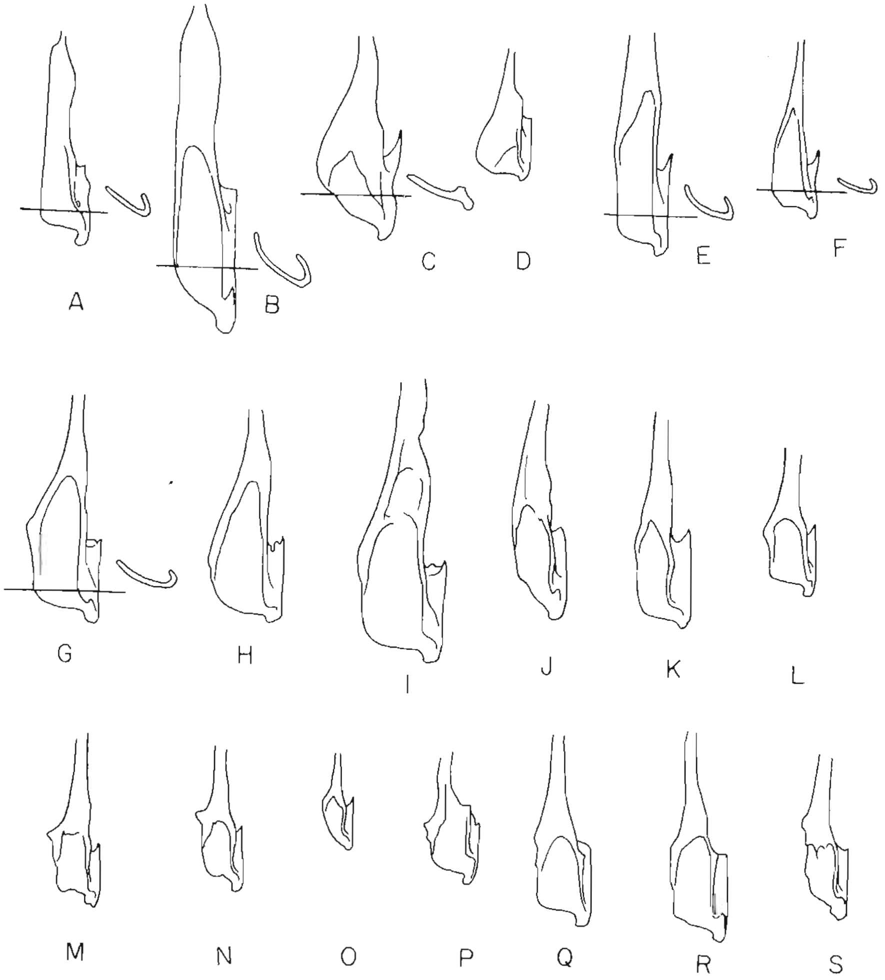

Fig. 88. Ventral views of palatines (actually pterygopalatines-anterior ends not shown) some with X-sections to right. A. *Cathartes aura*, B. *Gymnogyps californianus*, C. *Sagittarius serpentarius*, D. *Elanus leucurus*, F. *Necrosyrtes monachus*, G. *Sarcogyps calvus*, H. *Trigonoceps occipitalis*, I. *Aegypius monachus*, J. *Spizaëtus coronatus*, K. *Spizaëtus bellicosus*, L. *Buteo jamaicensis*, M. *Heterospizias meridionalis*, N. *Buteo magnirostris*, O. *Accipiter striatus*, P. *Falco peregrinus*, Q. *Milvago chimachima*, R. *Polyborus cheriway*, S. *Herpetotheres cachinnans*.

genera. Within such genera as *Buteo* and *Haliaeetus* (to a more limited extent in *Aquila*) these processes range from being in loose contact to completely fused. The fact that such variation also characterizes the development of the individual (fig. 81) suggests that the words "schizognathous" and "desmognathous" have only the most general descriptive value (Parker's 1879:112, subtypes of desmognathism are useless and arbitrary).

One remarkable palate which has been much discussed is that of *Elanus* (which includes *Gampsonyx swainsonii* and probably *Chelictinia riocourii*). In *Elanus leucurus* (fig. 85), the maxillopalatines are well separated, and the median bar is exceptionally well developed. Reduction of ossification appears to have occurred leaving only a delicate framework for the rostrum.*

The exposed anterior parts of the palatines are irregular to the level of the lateral maxillary fenestra. This irregularity is caused by the overlapping of the medial edge and the posterior palatal process of the premaxilla. The palatines then extend posteriorly for a short distance retaining a fairly constant width. Behind this level, they widen variously and are of maximal width beneath the anterior part of the orbit. The posterior end may be rectangular with an almost square posterolateral angle, or taper to a pterygoid process (fig. 88). The pterygoid process is formed from the anteropterygoid, which is fused with the palatine. The palatine fossa is usually well excavated and is bounded medially by a strongly developed choanal ridge. The exception to this is *Machaerhamphus* which resembles *Sagittarius* in having the fossa limited to the most posterior part of the palatine and in having no real choanal ridge (fig. 86).

The vomer is formed of lateral components (figs. 84,89), as is indicated by a slight posterior median bifurcation. Among the accipitrids this bone is generally a thin, laterally compressed, splint lying in the septum between the internal nares. Reduction of ossification may occur at the anterior end; a separate segment may be isolated in the crevasse between the palatine processes of the maxillae (synonymous in part with the median septo-maxillar of Parker, 1879). In some genera an anterior knob lies in the posterior angle of juncture of the maxillopalatines. The midsection may have an irregular fenestra. Generally, the dorsal and ventral margins are thickened and the latter may show a median crevasse.

The most singular vomer is that of *Elanoïdes*; it is inflated and nearly tubular toward its posterior end. An ossified vomer is apparently lacking in the aegypiins; i.e., *Aegypius*, *Torgos*, *Sarcogyps*, *Trigonoceps*, *Gyps*, *Pseudogyps*, and *Necrosyrtes*. One specimen of *Gyps coprotheres* has a small point separated from the median rostral processes of the palatines, which might be a portion of the vomer. In some specimens, of almost any species, the vomer appears to be fused to the rostral processes of the palatines. It shows variation in form or in degree of ossification from one genus to the next and, to some extent, within species. Sushkin (1905:35) has suggested that the posterior part

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* Sushkin (1905:31) noted that "Bei *Elanus coeruleus* bleibt der Boden der Vorhofskapseln in seinem, dem Nasenseptum anliegenden Teile, zeitlebens bindegewebig, wodurch auch die Gaumenforsätze mit dem Septem durch keinerlei Knochensubstanz verbunden sind,--kurz, *der Schädel bleibt zeitlebens auf einem schizognathischen Stadium*...Innerhalb der Gattung *Elanus* ist aber auch eine Form zu finden, bei welcher der Desmognathismus, so zu sagen, erst anfängt, nämlich bei *El. hypoleucus*. Wir sehen hier, dass vom hinter-unteren Winkel des Vorhofsseptum eine knocherne Brücke zum nächsten Punkte der Dorsalseite des Proc. palatinus maxillae sich erstrecht."

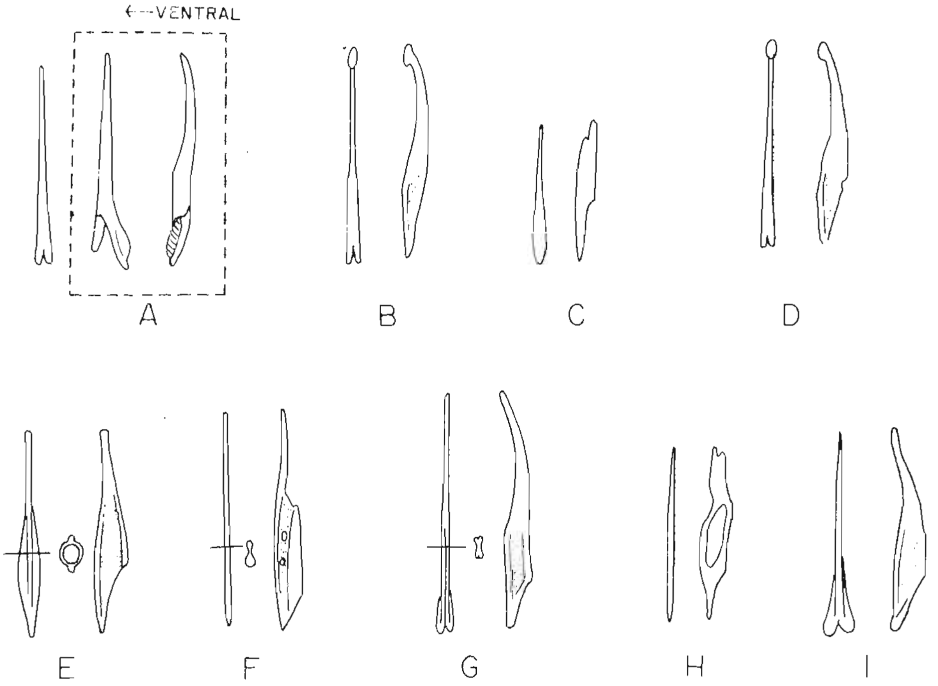

Fig. 89. Ventral and lateral aspects of the vomer, ventral view to left. A. *Neophron perenopterus*, ventral and lateral views after Parker enclosed by dashed line; B. *Gypaëtus barbatus*; C. *Gypohierax angolensis*; D. *Elanus leucurus*; E. *Elanoïdes forficatus*; F. *Machaerhamphus alcinus*, G. *Aquila* or *Haliaeetus*; H. *Haematornis cheela*; I. *Harpia harpyja*.

shows the greatest stability, but this does not agree with the variations described.

The vomer is associated with the anteroptergoids (fig. 50H) which, in the adult, are indistinguishably fused to the palatines. In the majority of accipitrids the vomer appears to be rooted to the anteropterygoids by fibers. In those genera in which the anteropterygoids are known to occur, the pterygopalatines (posteropterygoids) of the adult distinctly clasp the parasphenoid rostrum, whereas in those supposedly lacking them the palatines do not. In *Necrosyrtes* (and the other aegypiins) and *Terathopius*, no particular clasping is noticeable; the palatine-parasphenoid relationship is like that of the falconids, but they may not lack an identifiable anteroptergoid as does the latter.

The last element of the palate is the posteropterygoid, which articulates anteromedially with the palatine (through the anteropterygoid), and posterolaterally with the quadrate. This portion of the pterygoid is subject to much individual as well as generic variation. Pycraft (1902:290) commented that, "In *Pandion* the anterior end of the pterygoid is Y-shaped, the external fork of the Y articulating with the external posterolateral angle of the palatine. This is, so far as I am aware, a quite unique feature; but nevertheless a quite secondary character, and in no way com-