

THE SKULLS OF THE CATHARTID VULTURES

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The New World vultures, family Cathartidae, form a heterogeneous group of large birds which is now limited in its range to the Americas. Only one member, the fossil *Plesiocathartes* of France, has been taken outside the Western Hemisphere. Including fossils, there have been at various times twelve genera and twenty species within the family. More than half of these are fossil; the oldest is from the Oligocene.

An earlier study (in press) of the appendicular skeleton and musculature of the Recent genera indicated that the modern forms are surprisingly diverse in spite of similarities in locomotion in the air and on the ground, which are correlated with similarities in appendages. Because it was believed that the skull, especially the cranial part, is a more "stable" part of the body and less subject to adaptive change than are the appendages, this region of the skeleton was selected as the basis for a study of relationships. In pursuing this investigation it has been necessary, however, to examine some other skeletal parts in order to clarify questions of taxonomy.

Materials. Recent.—Skull, including mandibles: South American Condor, *Vultur gryphus*, 6; California Condor, *Gymnogyps californianus*, 7; King Vulture, *Sarcoramphus papa*, 8; Black Vulture, *Coragyps atratus*, 10; Turkey Vulture, *Cathartes aura*, 18.

Fossil.—*Cathartes aura*, 5 crania, 2 incomplete rostra and 3 pairs of mandibles; *Coragyps occidentalis*, 81 crania, 18 rostra and 4 incomplete mandibles; *Sarcoramphus kernensis*, type humerus; *Gymnogyps amplus*, type tarsometatarsus, 127 crania, 67 rostra, 20 pairs of mandibles, and 100 tarsi; *Breagyps clarki*, 6 crania, 2 incomplete rostra and mandibular fragments.

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Measurements.—Often it is impossible for a subsequent student to make comparative measurements, because no description of method is included. For this reason I provide as precise a description of each measurement as is possible.

Body length. Straight line distance between anterior face of last cervical vertebra and acetabulum, when all bones are articulated.

Skull length. Distance from supraoccipital to tip of bill, when occipital condyle and tip of bill rest on beam of dial calipers.

Cranial length. Straight line distance from frontonasal hinge to dorsal lip of foramen magnum.

Cranial height. Vertical distance between anterior end of basitemporal plate and top of cranium, when one side of calipers is resting on condyle and tip of same side is on anterior end of plate.

Postorbital width. Smallest measurement across cranium immediately behind postorbital processes.

Temporal width. Distance between temporal fossae.

Hinge width. Greatest width of frontonasal hinge at level of posterior ends of premaxillaries.

Premaxillary length. Distance from hinge to tip of bill, when beam of calipers is parallel to dorsal surface of bill.

Premaxillary anterior to nares. Distance from anterior end of nares to tip of bill, when beam is parallel to dorsal surface of bill.

- Bill width. Distance between ventral surfaces of maxillaries at anterior end of nares.
 Bill depth. Distance between dorsal crest of premaxillaries and ventral edges of maxillaries, when one side of calipers rests on edges of both maxillaries.
 Narial length. Greatest longitudinal measurement of opening.
 Opisthotic width. Distance between lateral surfaces of opisthotic processes.
 Occipital width. Distance between lateral surfaces of occipital processes.
 Mandibular length. Greatest straight-line length of ramus from tip of mandible.
 Mandibular height. Greatest vertical measurement in posterior part of mandible.
 Symphyseal length. Greatest midline length of mandibular symphysis.

COMPARISON OF RECENT SPECIES

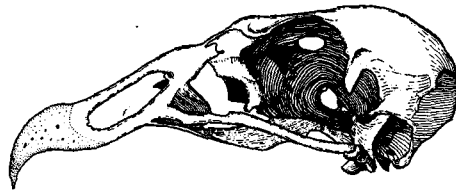
It is apparent from the drawings, and from the measurements in table 1 that the skulls of *Vultur* and *Gymnogyps* are approximately equal in length, as are those of *Sarcoramphus* and *Coragyps*. The skull in *Cathartes* is shorter than in any other cathartid. However, when the length of the skull is compared to body length, the ratios indicate that the skull is relatively shortest in *Vultur* and longest in *Coragyps* and *Cathartes*. The difference between the latter two is probably due to the lengthening in the rostral region in *Coragyps*; this lengthening is shown by the ratio of length of premaxillary to length of skull.

Absolute width of the posterior end of the skull exhibits striking variations; temporal width is practically identical in *Vultur*, *Gymnogyps* and *Sarcoramphus*, and it is almost equal in the two small vultures, *Coragyps* and *Cathartes*. Compared to skull length the temporal width is greatest in *Sarcoramphus*, intermediate in *Cathartes*, and least in the other three genera. Ratios concerning the length of the brain case follow almost the same pattern as do those of the width of the brain case. Thus the brain case is relatively largest in *Sarcoramphus*. When the height is compared to temporal width, one finds the highest ratios in *Coragyps* and *Vultur*, an intermediate condition in *Cathartes*, and low ratios in *Sarcoramphus* and *Gymnogyps*. Consequently, the brain case in *Sarcoramphus* may be described as the largest, widest and highest of any New World vulture; in *Cathartes* it is relatively smaller, narrower and somewhat lower than in *Sarcoramphus*; in *Gymnogyps* the brain case is lowest and smallest, and in *Coragyps* and *Vultur* it is low compared to skull length but highest compared to width (see tables 1 and 2 and figures 42 and 46).

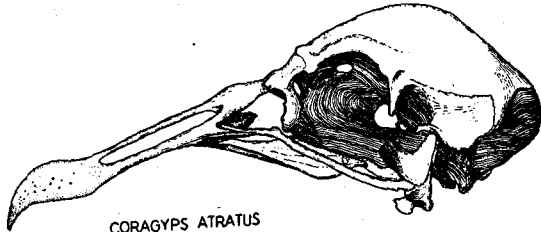
The top of the brain case is flattest in *Sarcoramphus* and shows little or none of the central, dorsal inflation which is most evident, among the cathartids, in *Coragyps*. *Vultur* possesses the next flattest skull. In *Gymnogyps* there is some slight inflation, but in *Cathartes* the brain case is nearly as rounded and inflated as in the Black Vulture. Pycraft (1902:278) found a prominent cerebellar dome in the cathartids but failed to mention the relative flatness in *Sarcoramphus* which is more nearly similar to that in accipitrine hawks.

When viewed from the dorsal side, the parietals and the supraoccipital are visible in *Vultur* and *Gymnogyps*. In *Coragyps* and *Cathartes* the posterior overhang of the brain case completely hides these bones in a dorsal view. In this regard *Sarcoramphus* is intermediate.

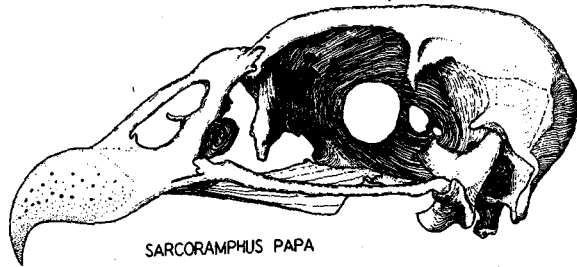
The lateral edges of the frontals, which form the supraorbital crests, exhibit constant differences of considerable magnitude. This border in *Vultur* describes a slight sigmoid curve with an excavation anterior to the postorbital process (fig. 45); in *Gymnogyps* the edge also describes a sigmoid curve, but it is widened out posteriorly and excavated anteriorly. The effect of this is to make the supraorbital area much narrower anteriorly in *Gymnogyps* than in *Vultur*. Well developed preorbital processes are not



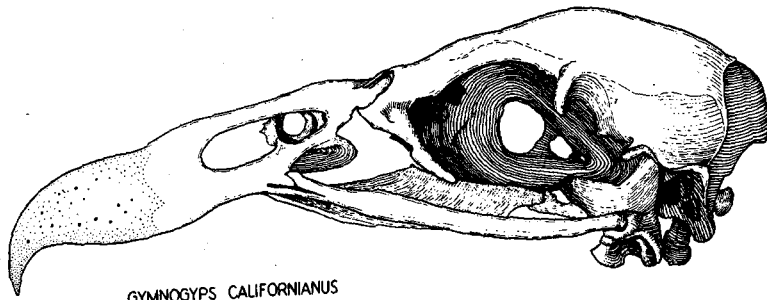
CATHARTES AURA



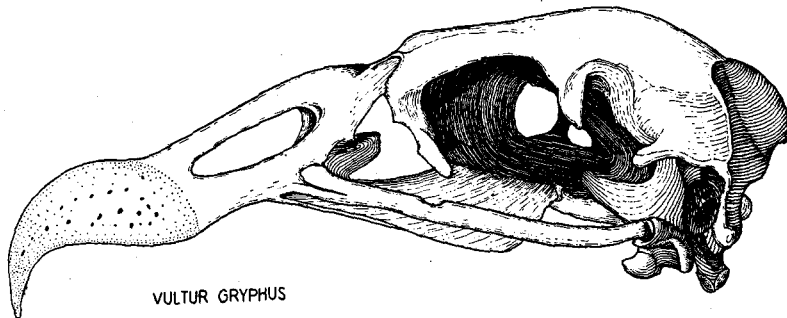
CORAGYPS ATRATUS



SARCORAMPUS PAPA



GYMNOGYPS CALIFORNIANUS



VULTUR GRYPHUS

Fig. 42. Lateral views of the skulls of Recent cathartids, $\times \frac{2}{3}$.

present in the condors and the King Vulture. In *Sarcoramphus* the supraorbital crest has a gentle outward bend in the middle of its length. The crest in *Coragyps* is almost a straight line, but it has the appearance of being excavated because of the presence of small processes at either end. In the Turkey Vulture the crest is very thin and is deeply excavated (fig. 44); the degree of excavation is somewhat variable, but in no case is it slight enough to confuse the outline with that in *Coragyps*. The preorbital processes are pronounced, due to the elimination of bone posterior to them.

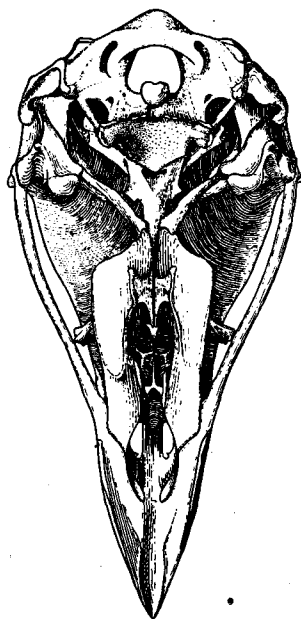
Sushkin (1905:21) found that the width of the supraorbital covering, the dimensions of the orbital socket, the shape and size of the postorbital processes, the shape of the orbital rim of the postorbital process and the base of the zygomatic process of the squamosal, and the degree of dorsal inflation of the brain case are specific and generic characters in the accipitrines; in only a few cases do several genera retain the same development of any of the above characters. Previously it has been shown that inflation of the brain case and width and shape of the supraorbital covering are probably generic characters in the cathartids. Size of the orbital socket is by far the greatest in *Sarcoramphus*, and it is relatively greater in *Cathartes* and *Coragyps* than in the condors.

The postorbital process in the Black Vulture is wider basally and much heavier throughout than in the Turkey Vulture. In both these vultures the process is also relatively longer than in the two condors; in all four the process does not extend farther laterally than the outer edge of the zygomatic process of the squamosal. The process in *Sarcoramphus* is sturdy as in *Coragyps* but in contrast to all other cathartids it flares laterally past the zygomatic process to a point dorsal to the union of the quadratojugal and the quadrate.

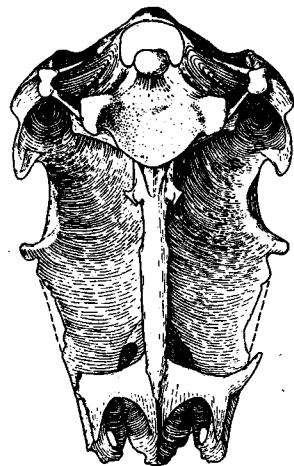
Shape of the orbital rim of the postorbital process is not a distinguishing feature among New World vultures; the variation in excavation of the supraorbital shelf tends to obscure differences in the process and is in itself a much better character for designating cathartid genera.

The zygomatic process of the squamosal is similar in *Coragyps* and *Cathartes*, and in *Vultur* and *Gymnogyps*; in *Sarcoramphus* it is much shorter and stronger than in the other genera. The posterior and ventral borders of this process vary with the size and development of the temporal muscles and consequently are of little use in studying cathartid relationships. Length of the process is not affected by the origin of the temporal muscles and is a good character. Sushkin divided the accipiters into two groups on the basis of length alone. In one group, the falcons, *Microhierax*, *Poliohierax*, *Polybori*, *Micrastur* and *Herpetotheres*, he found the length of the zygomatic process to be not less than two-fifths of the length of the long axis of the quadrate—this length being the distance from the outer articulation of the quadrate on the skull to the articulation of the zygomatic arch on the quadrate. In all other accipiters (as discussed by Sushkin) the length of the process is not more than one-fourth the long axis of the quadrate. The measurements are unsatisfactory, at least in the cathartids, but four members of the Cathartidae definitely fall in Sushkin's first group. *Sarcoramphus* is on the border line between the two groups.

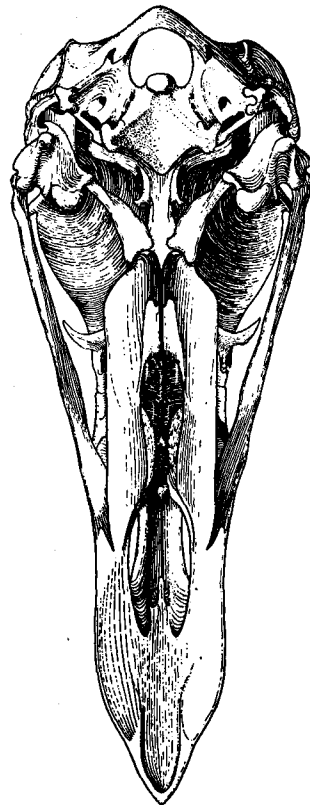
In profile (fig. 42) it may be observed that in *Vultur*, *Gymnogyps* and *Coragyps* the dorsal border of the rostrum, formed by the premaxillaries and frontals, is almost a straight line. In *Sarcoramphus* the line of the premaxillaries forms an acute angle of about 30 degrees with the dorsum of the frontals; in *Cathartes* the angle formed above the frontals is 12 to 18 degrees. This condition in *Sarcoramphus* along with the heavier



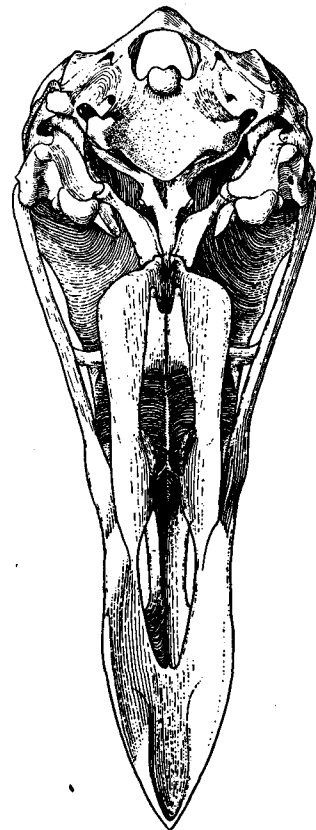
SARCORAMPHUS PAPA



GYMNOGYPS AMPLUS



GYMNOGYPS CALIFORNIANUS



VULTUR GRYPHUS

Fig. 43. Ventral views of cathartid skulls, $\times \frac{2}{3}$. Drawing of *Gymnogyps amplus* is from the plesiotype, No. B5415 in the Los Angeles County Museum.

Table 1
Average measurements and ranges in millimeters

	<i>Cathartes aura</i>		<i>Coragyps atratus</i>	<i>Coragyps occidentalis</i>	<i>Sarcoramphus papa</i>	<i>Gymnogyps californianus</i>	<i>Gymnogyps amplius</i>	<i>Vultur gryphus</i>	<i>Breagyps clarki</i>
	Recent	Fossil							
Body length	124	140	160	217	254
Length of skull	94.8	111	116	159	157
	92.6-98.0		108-113		114.2-119.2	150-163		151-164	
Length of cranium	52.0	49.9	51.9	54.4	64.3	82.0	84.5	79.5	80.3
	50.8-53.9	49.3-50.4	51.3-52.7	52.8-56.5	61.8-67	79.8-83.3	80.1-87.4	79.0-81.1
Height of cranium	29.8	29.7	32.1	34.5	40.4	41.0	41.8	45.9	44.2
	29.1-30.9	28.7-31.6	30.5-33.7	30.2-35.2	38.7-42.6	39.4-42.9	40.0-44.8	45.7-47.3	43.4-45.1
Postorbital width	35.8	34.6	36.2	39.5	49.0	41.7	43.7	48.6	49.9
	34.0-38.4	34.4-35.1	35.3-38.4	36.2-40.7	48.0-50.8	41.1-43.3	41.4-45.1	46.5-50.7	48.5-51.3
Temporal width	32.4	31.9	33.4	36.1	46.0	47.4	48.6	47.7	48.8
	31.2-33.9	31.5-32.8	33.0-35.1	33.2-37.9	44.6-48.1	46.2-49.0	45.8-49.8	45.6-51.4	47.9-50.0
Width of hinge	20.7	20.9	21.9	24.1	28.0	24.4	27.0	29.6	28.5
	19.1-21.7	21.5-22.3	22.8-26.0	26.6-29.0	23.4-25.1	25.5-28.4	28.3-31.4	27.8-29.0
Length premaxillary	49.3	50.9	63.8	70.0	62.6	86.5	93.5	91.2	112.2
	47.0-52.5	62.4-65.4	68.4-72.4	59.4-64.5	80.0-91.2	88.2-99.8	86.4-101
Length premaxillary anterior to nares	19.7	20.7	21.7	24.5	32.1	44.4	47.0	45.2	41.9
	18.0-22.6	20.1-21.3	20.5-22.8	23.0-25.7	29.3-33.6	42.1-46.5	43.9-51.3	43.3-46.6
Width of bill	14.0	14.9	13.4	15.2	20.4	23.8	25.2	25.2	25.1
	12.6-15.5	14.2-15.5	12.3-14.0	14.2-16.3	18.4-21.6	23.4-24.7	23.3-27.6	23.1-28.2
Depth of bill	9.65	11.1	7.4	7.9	16.1	17.4	17.0	15.4	14.8
	8.7-11.0	10.7-11.4	6.7-8.2	7.2-8.7	15.1-16.5	16.2-18.4	15.4-19.1	14.4-16.3
Length nares	17.6	18.7	25.9	31.2	18.3	25.5	25.8	28.3	47.6
	16.2-18.4	18.3-19.1	24.8-27.3	29.2-33.0	17.3-19.3	24.0-27.3	23.5-28.7	24.0-32.0
Opisthotic width	29.8	27.5	32.6	32.9	40.1	41.5	44.3	42.9	42.4
	28.6-30.8	25.4-29.2	31.7-33.2	29.0-35.1	39.2-41.0	39.8-44.0	42.2-48.5	42.7-43.2	37.8-44.8
Occipital width	13.0	12.9	16.2	17.4	20.8	23.7	27.2	31.1	26.9
	12.2-14.5	12.7-13.1	15.0-16.6	15.3-18.5	19.9-21.6	22.5-24.9	25.6-30.2	28.9-34.3	25.0-28.3
Length mandible	71.3	72.4	87.1	88.5	134	141	134
	69.1-75.4	71.6-73.2	85.7-88.6		84.9-91.4	128-139	134-145	124-136	
Height of mandible	9.4	9.6	11.1	13.6	18.2	19.9	19.9
	9.0-10.2	9.5-9.7	10.9-11.5		12.8-14.2	16.8-19.3	18.4-20.8	18.8-21.3	
Length symphysis	11.1	10.9	13.3	15.9	20.3	21.9	24.7
	10.2-12.3	10.1-11.4	12.1-14.2		15.0-16.8	19.4-21.3	21.0-24.2	21.3-27.1	

bill gives the skull a definite "predatory" aspect in contrast to the weak-billed, flat-topped condition found in the other cathartids.

The ratios in table 2 concerning the bill demonstrate that the bill is relatively widest and deepest in *Sarcoramphus*. It is narrowest and shallowest in *Coragyps*, next weakest in *Cathartes*, and only slightly stronger in the two condors. Another factor contributing to the appearance of weakness in the bill of *Coragyps* is the long nasal aperture which is almost one-fourth the length of the skull (tables 1 and 2); in comparison with skull length and length of premaxillaries the nares are by far the longest in *Coragyps*, intermediate in length in *Cathartes* and *Vultur* and shortest in *Sarcoramphus* and *Gym-*

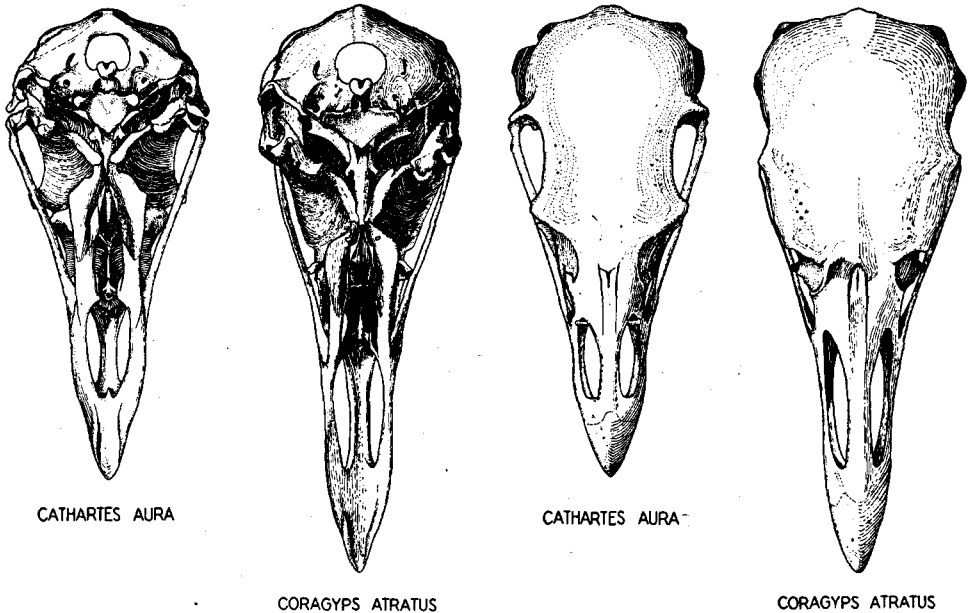


Fig. 44. Ventral and dorsal views of skulls of Recent *Cathartes* and *Coragyps*, $\times \frac{2}{3}$.

nogyps. The short bill together with short narial openings indicates strength in the bill of the King Vulture, *Sarcoramphus*. The hook on the bill is about equally developed in the various genera. The longitudinal axis of the naris is nearly parallel with the slope of the rostrum in *Vultur*, *Gymnogyps* and *Coragyps*; its anterior end is somewhat depressed in *Cathartes* and is depressed still further in *Sarcoramphus*. This character is further accentuated in the Turkey and King vultures by the depression of the entire rostral portion of the skull. Shape of the naris is constant for each genus and is a distinguishing feature. In *Coragyps* it is relatively narrow and long, and only a small part of the posterior end is occluded by a sharp nasal process. The opening is ovoid in *Cathartes* and more obstructed in the caudal area. In *Sarcoramphus* the opening is similar to that in the Turkey Vulture but is flattened, and the nasal processes form a shelf (figs. 42 and 43) on the ventral surface of the posterior half of the naris; the central tip on this shelf extends dorsally toward the premaxillaries in the midline and in one specimen formed a circlet as in *Gymnogyps*. The long, oval foramen in *Vultur* has little or no obstruction posteriorly. In *Gymnogyps* there is a ventral shelf as in *Sarcoramphus*, but it covers only a fourth to a third of the narial length. The medial process

of this shelf curves anteriorly and dorsally and then turns posteriorly to fuse with the premaxillaries. Thus a bony circle is formed in the posterior part of the nostril (fig. 42).

In *Gymnogyps* the nasal bridge is slightly shorter and from a third to a half wider anteriorly than in *Vultur*. *Sarcoramphus* displays a relatively wide and thick bridge; this contributes further to the appearance of strength in the rostral region. In actual measurements the nasal bridge in *Cathartes* is narrower than in *Coragyps*, but it is equal in thickness and considering its length is stronger.

Compared to trunk length (table 2) the premaxillaries are longest in *Coragyps* and approximately equal in the other genera. The high ratio of premaxillary length to skull length in *Vultur* is a result of the much shorter skull of *Vultur*, as shown by the ratios of skull length to trunk length. It is interesting to note that total premaxillary length and length of naris vary together, but that length of the premaxillary anterior to the nostril varies inversely to them.

In a posterior view of the skull (fig. 46) several characteristic features may be observed. In *Cathartes* and *Sarcoramphus* the suture of the frontals and parietals on either side forms an arc; the two inner ends form a definite V-shape in the midline. The junction of these bones in *Coragyps* and *Vultur* is a gentle arc from side to side with only a slight dip in the midline. In *Gymnogyps* the "V" is more pronounced than in *Vultur*, but in both condors the dorsolateral areas of suture lie farther dorsally and anteriorly. The squamosal-parietal suture is nearly vertical in the condors, but ventrally it flares out widely in the other cathartids.

The occipital condyle in the condors is a smooth, rounded surface with little or no trace of the sharp groove always found in the posterior edge in the Black and Turkey vultures. In *Sarcoramphus* the groove may or may not be present. Exoccipital processes are well developed in the condors, but are much longer and stronger in *Vultur* than in *Gymnogyps* and are larger in *Sarcoramphus* than in the small vultures. The processes are better defined in *Cathartes* than in *Coragyps* in which there is a sharp high ridge running medially from each process (fig. 44). Both *Cathartes* and *Sarcoramphus* show traces of this ridge, but in the South American and California condors the ridges run dorsomedially to the base of the condyle. When the skull is resting on the hook and the exoccipital processes and is on a flat surface, the opisthotic processes touch the surface in *Cathartes* and *Coragyps*. In this position the opisthotic processes are farthest from the surface in *Vultur*, next farthest in *Gymnogyps*, and closest to the surface in *Sarcoramphus*. The opisthotic processes are longer in the cathartids than in any other falconiform (Pycraft, 1902:279). In the Turkey, Black and King vultures the postero-medial surface of the opisthotic processes is either gently rounded or forms a ridge containing more than 90 degrees. In *Vultur* this surface is a ridge of about 90 degrees; in *Gymnogyps* the ridge contains about 60 degrees. Width and configuration of the hind wall of the ear (the opisthotic process) was found to be a generic character in the accipitrines (Sushkin). The cathartids as indicated above may be divided into two groups on the basis of this character, and the configuration is an aid in separating the two condors.

Those accipitrines with a thin posterior wall at the outer end of the auditory opening, by which I assume Sushkin (1905:23) meant the opisthotic process, were considered by him to be more primitive than those with thick, strong walls. He states that in the Cathartidae, as in Pelecaniformes, Ciconiiformes and Procellariiformes and in all birds closely or distantly related to the accipiters, this wall is only weakly developed and is thin. Within the Cathartidae I could find no major differences, but in the two condors

Table 2

Ratios* of measurements of cathartid skulls

	<i>Cathartes aura</i>		<i>Coragyps atratus</i>	<i>Coragyps occidentalis</i>	<i>Sarcoramphus papa</i>	<i>Gymnogyps californianus</i>	<i>Gymnogyps amplus</i>	<i>Vultur gryphus</i>	<i>Breagyps clarki</i>
	Recent	Fossil							
Skull length: trunk length	76	79	72.5	73	61.8
Cranial height: skull length	31.4	28.9	34.9	26.3	29.2
Cranial length: skull length	52.9	46.7	55.5	51.7	50.6
Cranial height: temporal width	92.0	93.1	95.2	87.9	88.0	86.0	96.2	90.5
Cranial height: cranial length	57.2	57.2	62.0	63.4	62.9	50.0	49.5	57.7	55.0
Cranial length: temporal width	155	156	164	150	140	173	174	167	165
Temporal width: skull length	34.2	30.2	39.7	29.9	30.4
Premaxillary length: skull length	52.1	57.5	54.0	53.3	58.1
Premaxillary length: trunk length	39.7	45.6	39.1	38.7	35.9
Premaxillary length: cranial length	94.5	102	123	129	97.5	106	111	115	140
Prenasal premaxillary: premaxillary length	39.9	40.6	34	35	51.2	51.5	50.2	49.6	37.4
Prenasal premaxillary: skull length	21.6	19.7	27.7	27.5	28.8
Postorbital width: cranial length	68.9	69.4	69.8	72.6	76.1	50.9	51.8	61.1	62.1
Bill width: skull length	14.7	12.2	17.6	15.1	16.1
Bill depth: bill width	69.0	74.4	55.1	51.9	79.0	75.8	67.5	61.1	59.0
Bill depth: skull length	10.2	6.7	13.9	11.3	9.8
Occipital width: cranial length	25.0	25.9	31.2	32.0	32.4	28.9	32.2	39.1	33.5
Opisthotic width: cranial length	57.3	55.1	62.8	60.5	62.4	50.6	52.4	54.0	52.8
Narial length: skull length	18.5	23.3	15.8	15.9	18.0
Narial length: premaxillary length	35.6	40.6	44.6	29.2	29.9	27.6	31.1	43.3
Hinge width: cranial length	39.8	41.9	42.2	44.3	43.5	29.8	32.0	37.3	35.5
Mandibular length: skull length	75.3	78.5	76.3	84.2	85.4
Mandibular height: mandibular length	13.2	13.3	12.7	15.4	14.2	14.1	14.8
Symphyseal length: mandibular length	15.6	15.1	15.3	18.0	15.1	15.5	18.4

*Figured from averages.

the wall is perhaps somewhat stronger and better-braced. The entire wall is weaker and less inflated in the New World vultures than in the accipiters.

In contrast to other falconiforms the cathartids do not have a well developed articular process on the squamosal. The process when present aids in holding in place the otic articulation of the quadrate. Absence or weakness of such a process and the consequent weakness in the connection of the quadrate probably contributes to the general weakness of the cathartid bill and forces these birds to subsist, for the most part, on soft foods. It is interesting to note in this connection that the articular process is present, though small, in *Sarcoramphus*, *Cathartes* and *Coragyps*. In *Sarcoramphus* it is a wide ridge and is more effective than in the two small vultures; it is larger in *Coragyps* than in *Cathartes*. Therefore, we have in this process another factor contributing to the effectiveness of the bill in *Sarcoramphus*, and to greater efficacy of the bill in *Coragyps* than in *Cathartes*.

The temporal fossa is relatively deep in *Cathartes* and *Coragyps*, intermediate in *Sarcoramphus* and shallow in *Vultur* and *Gymnogyps*. It is widest in *Coragyps* and *Sarcoramphus*. At the anterior end of the fossa the passageway is three-fourths encircled by bone in *Cathartes*, due in part to the better development of the postorbital process and the anterior extension of the ventral shelving of the squamosal. In the other vultures and the condors the passage is less enclosed by bone. When depth and width of the fossa and the area partly enclosed by the processes are considered, it seems probable that the temporal musculature is best developed in *Coragyps* and *Sarcoramphus* and weakest in *Gymnogyps*. As Sushkin (1905:21-22) has pointed out, the size and depth of the fossa is a specific character related to the manner of feeding and is useless for showing general relationships. However, shape and position are probably familial features; they are constant in the Cathartidae.

In lateral view the parietal and supraoccipital areas appear much inflated in *Vultur* and *Gymnogyps*. However, at least part of this appearance is due to the previously mentioned absence of a posterior overhang of the frontal bones in these genera. This posterior shelving is less in *Sarcoramphus* than in *Coragyps* and *Cathartes* and consequently the inflation seems greater in the King Vulture than in the two small vultures.

In all cathartids the basitemporal plate is triangular with the apex toward the front; in all except *Cathartes* the apex is consistently a sharp point. In approximately half the skulls of the Turkey Vulture the apex is blunted (fig. 44). Excavation of the posterior part of the sphenoidal rostrum is greatest in *Sarcoramphus* and *Vultur* and it extends forward half of the exposed length of the rostrum. In *Coragyps* and *Cathartes* the depth of the groove is intermediate and its length is two-fifths to one-half that of the exposed rostrum. In *Gymnogyps* the excavation is least and is confined to the posterior two-fifths of the rostral length. This excavation is not present in other falconiforms.

The position and the distance between the ventromedial ends of the bony eustachian canals are extremely variable within a genus because of the differences in the development of the thin, anterolateral wall of the canal.

The anteroventral wall of the auditory canal forms a sharp, shelf-like extension in *Coragyps*, *Cathartes* and *Sarcoramphus*; only vestiges of this shelf can be found in the condors. In all cathartids, except *Cathartes*, the auditory canal is complete, that is, it extends as a bone-encased aperture as far laterally as the ends of the pterygoids. In the Turkey Vulture, however, the canal is entirely open ventrally except where it passes dorsal to the sphenoidal rostrum! In only three specimens was it enclosed ventrally for as much as one millimeter on either side of the rostrum.

No differences were observed in the pterygoids, but the basipterygoid process of

the sphenoidal rostrum is strongest in *Sarcoramphus* and weakest in *Gymnogyys*. These processes are longest in *Gymnogyys* and shortest in *Sarcoramphus* and *Vultur*. Greater length in the pterygoid process tends to lessen the flexibility of movement since the pterygoid has a shorter distance in which to move, and strong processes give better support to movements of the bill. Pycraft (1902:280) found the basipterygoid process in all stages of development in his study of the falconiforms. He noted the stockiness of the process in *Sarcoramphus* and *Coragyys* and thought the slenderness of the bone in *Gymnogyys* and *Vultur* was a sign of the first stages of the disappearance of the bone.

Shape of the palatine bones exhibits no significant variation; at the posterior end the thin blade may be of various shapes, but these differences are not constant within a genus or species and must be attributed to individual variation in ossification which occurs so frequently in the free, attenuated ends of thin bones. The anterior ends of the palatines are nearly horizontal in *Coragyys* and *Cathartes*, and it is only in their posterior two-thirds that they begin to lie at a 45 degree angle (figs. 43 and 44). In the condors and the King Vulture they lie at about a 45 degree angle throughout their length. In the posterior third of their length, the palatines meet, or nearly do so, in the midline, and their medial edges turn ventrally to form the palatine processes. In no New World vultures do the palatine processes extend as far posteriorly as do the palatines. The medial edges of the palatines, which form the bases of the palatine processes, extend ventrally side by side and later flare out laterally in the condors and to a lesser extent in *Sarcoramphus*. A cross-section of the palatine processes thus has an inverted "Y" shape. In the Black and Turkey vultures the medial bases of the processes are more widely separated and extend straight down or begin to flare out laterally from the palatine itself; this produces an inverted "V". The posteroventral corners of the palatine processes are greatly variable within a genus, and yet it is possible to state that the corners extend farther caudally in the condors and the King Vulture than in the Black and Turkey vultures.

No significant differences were observed in the shape or relative length of the interpalatine opening. The length of the intermaxillary space, as would be expected, varies with the rostral length of the skull; the aperture is relatively long in *Coragyys* and is shortest in *Sarcoramphus*. As may be seen in figure 44, the opening is long, narrow and only slightly ovoid in *Coragyys*. In the condors (fig. 43) it is the same absolute length, but wider and more ovoid; in *Cathartes* it is approximately the same shape. The opening in *Sarcoramphus* is shorter and more circular than in any other cathartid.

The lachrymal process is wide, strong and long in the small vultures and the King Vulture; it extends straight ventrally and nearly touches the jugal. In the large condors the lachrymal is relatively thin and weak and runs posteroventrally (fig. 42). The upper ends of the lachrymal and the nasal form an acute angle (about 40 degrees viewed from the side) in *Sarcoramphus*; 75 to 85 degrees in *Coragyys* and *Cathartes* and about 90 degrees in *Vultur* and *Gymnogyys*. The lachrymal process in *Cathartes* differs from that in *Coragyys* in that it is much wider dorsally. In this respect *Cathartes* closely resembles the condors, and *Coragyys* is similar to *Sarcoramphus*. In all cathartids the lachrymal is completely fused to the frontals.

In all cathartids there is an imperfect frontonasal hinge; the flexibility of the prefrontals and of the posterior ends of the nasals is the limiting factor. The palatines can slide on the sphenoidal rostrum to a certain extent and thus offer no resistance to the action of the hinge. However if the zygomatic arch is an inflexible brace, the effect of the hinge is lost. In the cathartids the rigidity of the zygomatic arch is reduced in an interesting manner. The anterior end of the arch is split and the dorsal part articu-

lates with the maxillary (fig. 42). The ventral part is flattened in a horizontal plane and thus bends more easily in a vertical direction. Another factor contributing to the flexibility is a dorsal bend in the arch in the region of the lachrymal in *Cathartes* and *Coragyps* and to a lesser extent in *Sarcoramphus*. In the two large condors the arch is nearly, if not actually, straight.

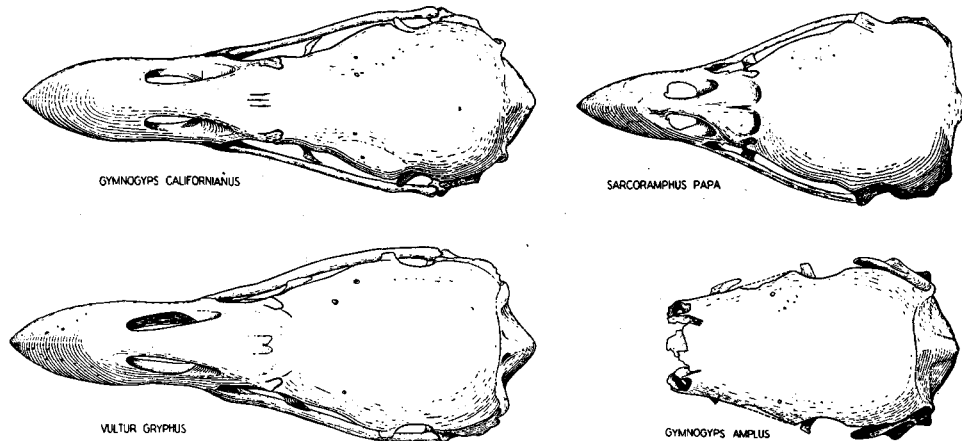


Fig. 45. Dorsal views of cathartid skulls, \times %. Drawing of *Gymnogyps amplus* is from the plesiotype, No. B5415 L. A. Mus.

The interorbital septum has a large central opening in the condors and the King Vulture which is separated by a thin pillar of bone from a smaller opening posterior to it (fig. 42); the smaller opening is continuous posteriorly with the foramen for the optic nerves on either side. No other fenestrae are present in the septum of these forms. In *Cathartes* and *Coragyps* the large central opening is consistently absent, but there is always an aperture 3 to 7 mm. long in the middorsal area of the septum in *Cathartes*. This dorsal aperture is usually, but not always, present in *Coragyps*; it is always smaller than in *Cathartes*. Formation of the dorsal opening in the two small vultures is the result of the breakdown of the lateral walls of the passageway for the olfactory nerves. Laterally the olfactory nerve canals are always open in the Black and Turkey vultures; in *Sarcoramphus* there may be small fenestrae in the lateral wall of the canal but in none of my specimens was the passageway completely open to the orbital socket in the middorsal region. No middorsal aperture is present in the septum in the condors and the canals for the nasal nerves are completely closed.

The posterior wall of the orbital socket and the interorbital septum furnish no characters useful in designating large groups of genera among the accipiters, according to Sushkin. However, he thought it might be possible to put the accipiters in two groups on the basis of the contour of the ventral border of the interorbital septum. After examining a number of accipiters and cathartids I came to the conclusion that the curvature was too slight in any case to be a reliable character; he also indicates in later studies that the differences are extremely small. It has been shown previously in this study that the fontanelles in the interorbital septum and the condition of the canal for the olfactory nerve in the orbit are constant generic features. Sushkin found that in "large buzzards" the canal was usually open and he followed Fürbringer in believing that the size of the fontanelles was in proportion to the size of the bird. In a general sort of way, the fonta-

nelles do follow this rule, but in *Sarcoramphus* the central fontanelle is nearly as large as in *Vultur* and *Gymnogyps* which weigh about three times as much as the King Vulture. The posterior fontanelle is larger in the Black Vulture than in the Turkey Vulture which is slightly heavier. The middorsal opening is often times twice as large in *Cathartes* as in *Coragyps*. Obviously the rule does not hold in the Cathartidae.

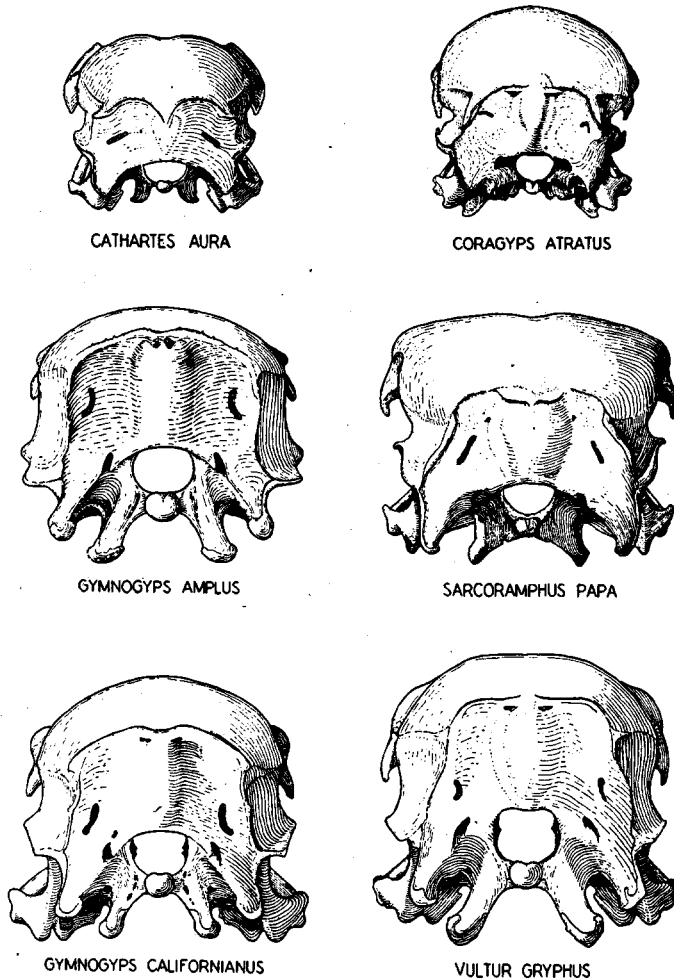


Fig. 46. Posterior views of cathartid skulls, $\times \frac{2}{3}$. Drawing of *Gymnogyps amplus* is of plesiotype, No. B5415 L. A. Mus.

The crest of the lateral or main articulating surface of the quadrate has in all the New World vultures the shape of a sigmoid curve. In the condors the posterior end of the surface is most medial; thus the axis is set about 20 to 30 degrees from the long axis of the skull. In the Turkey and Black vultures the long axis of the surface is about 45 degrees from the axis of the skull, and in *Sarcoramphus* it is about the same. In the latter the sigmoid nature of the area is obscured by inflation and enlargement of the entire surface. The larger articulating surface, the inflation, and the fewer restraining processes in this region make it possible for *Sarcoramphus* to open the bill more widely.

Then too, more lateral movement is possible. The angle to which the bill may be opened is approximately the same in the other cathartids, but the increased rostral length in *Coragyps* produces a greater gap between the tips of the mandibles than is present in *Cathartes* when the bill is opened to the maximum extent. Ability to open the bill more widely may be an adaptation in two ways. In grasping live, struggling prey a widely opened bill is an aid to securing and maintaining a strong hold. In the case of *Sarcoramphus* it probably aids in this manner as well as in enabling larger chunks of carrion to be swallowed. The latter adaptation is perhaps the more important in *Coragyps*, but here again the aid in grasping prey may be significant since McIlhenney (1939) has shown that Black Vultures attacking in groups kill skunks, o'possums and other small mammals.

The angle of the articulating surface and the sharp ridges bordering it in *Cathartes* and *Coragyps* preclude much anteroposterior movement. However, in the condors there is a possibility of some longitudinal movement. This longitudinal movement and a short up and down movement or snipping probably account for the method of feeding in the California Condor noted by Koford, Pemberton and others. In feeding, the condor inserts the bill in a soft part of the carcass and by short snipping movements which can be seen and heard literally scissoring its way into the soft carcass.

When the lower mandibles are set in proper articulating position with the quadrate, little or no generic difference can be noted in the relative lengths of upper and lower mandibles. Yet the ratios of mandibular length to skull length indicate relatively long mandibles in *Vultur* and *Gymnogyps*. This apparent anomaly is the result of the posterior bulging of the brain case in the small vultures and to a certain extent in the King Vulture, which increases skull length and thus decreases the relative mandibular ratio. No significant variation in length was noted, the length varying directly with increased rostral length, as found in *Coragyps*, or short rostral length, as in *Sarcoramphus*. Strength of the lower jaw as indicated by the height to length ratio, and the ratio of symphyseal length to mandibular length is greatest in *Sarcoramphus* and slightly less in *Vultur*. The lower mandible is apparently weakest in *Coragyps* and next weakest in *Cathartes*; *Gymnogyps* occupies an intermediate position in this respect. Shufeldt (1883:751) found the lower mandible more powerful in cathartids than in accipitrines.

The longitudinal axis of the articular surface of the lower mandible is nearly parallel to the long axis of the skull in the condors; its posterior end is more medial in the two small vultures and is most medial in *Sarcoramphus*.

DISCUSSION OF RECENT SPECIES

The skull of the cathartid vulture may be distinguished from the skulls of other falconiforms in the following ways: the external nares are perforated; the rostral area of the skull is elongated (except in *Sarcoramphus*); an imperfect frontonasal hinge is present; the lacrymals are completely fused to the frontals and are directed downward; the premaxilla is highly vaulted; the opisthotic processes are extremely long; the articular process of the squamosal is weak or absent; the sphenoidal rostrum is excavated in front of the basitemporal plate; the bones within the olfactory chamber are more completely ossified; the zygomatic arch is split anteriorly; and the skull is indirectly desmognathous.

It may be observed in table 3 that there are many characters dividing the Cathartidae into two main groups, with *Sarcoramphus* somewhere between. In the large condors, *Gymnogyps* and *Vultur*, the parietals and supraoccipitals are inflated and are vis-

Table 3
Comparison of skulls of modern cathartids*

	<i>Cathartes</i>	<i>Coragyps</i>	<i>Sarcoramphus</i>	<i>Gymnogyps</i>	<i>Vultur</i>
Relative skull length	1	1	2	2	3
Relative size of brain case	3	2	1	4	3
Parietals visible dorsally	no	no	intermediate	yes	yes
Lateral line of supra-orbital crest	deeply excavated	straight	gently rounded	sigmoid	reverse of <i>Gymnogyps</i>
Size of orbit	3	3	1	4	4
Zygomatic process of squamosal	a	a	c	b	b
Dorsal profile	12-18° bend	almost straight	30° bend	straight	straight
Bill strength	3+	3	1	4	4
Length naris	3	1	5	4	3
Shape naris	ovoid	long, narrow	ovoid, obstructed posteriorly	ovoid, bony cirlet	long, oval, little obstruction
Frontoparietal suture	a	b	a	c and d	b and d
Grooved condyle	yes	yes	in some	no	no
Development of exoccipital processes	3	3	2	1	1
Length of opisthotic processes	1	1	2	3	4
Posteromedial surface of opisthotic process	contains more than 90°	as in <i>Cathartes</i>	as in <i>Cathartes</i>	about 60°	about 90°
Articular process on squamosal	3	2	1	not present	not present
Depth of temporal fossa	1	1	2	3	3
Excavation of sphenoidal rostrum	3	3	1	5	2
Bony auditory canal complete	no	yes	yes	yes	yes
Shelf on anterior wall of canal	yes	yes	yes	no	no
Strength of basipterygoid	3	2	1	4	4
Length of basipterygoid	2	2	3	1	4
Anterior ends of palatines	horizontal	horizontal	45° angle	45° angle	45° angle
Cross-section palatine processes	inverted V	inverted V	intermediate	inverted Y	inverted Y
Shape of intermaxillary space	ovoid	long, narrow	nearly circular	ovoid	ovoid
Angle between nasal and lachrymal	75 to 85°	75 to 85°	40°	90°	90°
Lachrymal process	a and c	a and d	a and d	b and c	b and c
Fontanelles in interorbital septum	b and c	b and c	a and b	a and b	a and b
Olfactory nerve canal open in orbit	yes	yes	sometimes	no	no
Angle of articulating surface of quadrate	45°	45°	45°	20 to 30°	20 to 30°

*Increasing numbers indicate decreasing development of character. Each letter indicates a condition of the character in the left hand column. The same number or letter in more than one column indicates similarity of character.

ible from a dorsal position; in the small vultures, *Coragyps* and *Cathartes* these elements are relatively much smaller and are hidden from dorsal view by the overhanging frontals. In *Sarcoramphus* the inflation is more than in the small vultures, but is less than in the condors. In the condors the occipital condyle has no definite groove; in *Sarcoramphus* it is sometimes grooved and in the small vultures a large groove is always present. The temporal fossa is deepest in the small vultures, intermediate in the King

Vulture and shallowest in the condors. A cross-section of the palatines shows an inverted "V" in the small vultures, and an inverted "Y" in the condors and an inverted "V" with a short basal stem in *Sarcoramphus*. In the condors the canal for the olfactory nerve is closed; it is sometimes closed in *Sarcoramphus* but it is always open in *Coragyps* and *Cathartes*.

The King Vulture is similar to the small vultures, and different from the large condors in the following ways: the dorsal profile is not a straight line; the posteromedial surface of the opisthotic process is gently rounded; there is a definite articular process on the squamosal; the anteroventral wall of the auditory canal forms a sharp shelf, and the lachrymal process is robust and long and extends straight ventrally. In the development of the articular process on the squamosal and the lachrymal process, *Sarcoramphus* resembles *Coragyps* more than it does *Cathartes*. However, the King Vulture is nearer *Cathartes* than *Coragyps* in these characters: the dorsal profile is not straight; the frontoparietal suture forms a definite "V" in the midline; and the naris is short as is the intermaxillary space.

Similarity of *Sarcoramphus* to the two large condors is found in the rounded shape of the lateral edge of the supraorbital crest, the angle of the anterior ends of the palatines, and the fontanelles in the interorbital septum. In relative skull length, length of nares and length of opisthotic processes *Sarcoramphus* is closer to *Gymnogyps* than to *Vultur*, but in size of brain case, excavation of sphenoidal rostrum, and length of basiptyergoid processes, it is nearer *Vultur*; the characters showing similarity between *Sarcoramphus* and *Vultur* are, to my mind, less changeable and therefore more significant than those between *Sarcoramphus* and *Gymnogyps*.

In the general features of size, wing spread, pterylosis (Fisher, 1943:72), and perhaps even ecology the King Vulture is an intermediate form between the small vultures and the large condors.

Sarcoramphus is characterized by the following distinctive features: heavy skull and bill, large brain case, large orbit, depressed rostral region, strong bill, short nares, strong articular process on squamosal, deep excavation of sphenoidal rostrum, 40-degree angle between lachrymal and nasal, laterally flared postorbital process, frontoparietal suture with a median "V", wide temporal fossa, well developed basiptyergoid processes, and laterally expanded edge of the supraorbital crest.

Cathartes shows these diagnostic characters, by means of which its skull may be separated from that of any other cathartid: rostral part somewhat depressed, ovoid nostril only slightly occluded posteriorly, frontoparietal suture with deep "V", incomplete bony auditory canal, and deeply excavated supraorbital crest.

In *Coragyps* some of the more important generic characters are: long, narrow skull with long, weak bill and narrow nostril, frontoparietal suture a wide arc, sharp exoccipital ridge, wide temporal fossa and practically straight suborbital edge.

There are many characters which relate the two condors and separate them from the other New World vultures but few which may be used to distinguish them from one another. *Gymnogyps* may be distinguished from *Vultur* because of its sigmoid curve in the supraorbital edge, bony cirlet in the nostril, somewhat longer opisthotic processes, more angular posteromedial surface on the opisthotic processes and lesser excavation of the sphenoidal rostrum.

Because *Gymnogyps* and *Vultur* show so few fundamental differences it may be conjectured that they have separated rather recently compared to *Cathartes* and *Coragyps* which demonstrate major differences. If aberrancy (in the sense of differing greatly from related genera) is a sign of antiquity, as some believe, *Sarcoramphus* is the most

ancient of the living New World vultures. The fossil record apparently supports this theory for *Sarcoramphus kernensis* of the early Pliocene is the earliest cathartid known from the New World (Miller, 1942:212). No other cathartid genus represented by living members has yet been found until early or middle Pleistocene.

Not considered in this study is the musculature, certain features of which, namely the complete absence of *M. caudofemoralis* in *Sarcoramphus*, *Gymnogyps* and *Vultur*, link the King Vulture to the large condors. This muscle is present in the Black and Turkey vultures. It is highly unlikely that such a muscle would have evolved twice in the history of one group of birds; independent loss could be more easily understood.

DESCRIPTION OF FOSSIL SPECIES

CORAGYPS OCCIDENTALIS

The Black Vulture of the Pleistocene certainly represents a species distinct from *C. atratus* of Recent times. In table 1 it may be observed that in all measurements of the skull *occidentalis* is larger. In length of premaxillary, length of premaxillary anterior to the nares, length of nares, and width of bill the ranges of the measurements do not overlap. These same characters are emphasized by the ratios in table 2.

Thus the skull of *C. occidentalis* is significantly larger than that of *atratus* and the premaxillaries and nares are relatively longer. The ratios of temporal and postorbital width and cranial height to cranial length indicate that the Pleistocene vulture had a wider and somewhat higher brain case. The width at the frontonasal hinge is also greater, and bill depth is relatively less in *occidentalis*.

In many of the features just discussed it may be observed that the *Gymnogyps* group and the *Coragyps* group have paralleled each other in their development since the Pleistocene. For example, the premaxillaries have decreased in length, and the width of the cranium and of the hinge has decreased, but the depth of the bill has increased.

Aside from the quantitative characters there are important qualitative characters distinguishing *atratus* from *occidentalis*. In *occidentalis* the brain case is more inflated immediately anterior to the supraoccipital area; it is similar to *Cathartes aura* in this respect. The supraorbital edges are more excavated posteriorly and do not always form the characteristic straight line found in *atratus*. In some, the excavation approaches the depth found in *C. aura*. Because of the greater hinge width and interlachrymal width the crests are more nearly parallel in *occidentalis*.

The foramen magnum is larger and somewhat compressed vertically. The occipital processes are heavier, broader and smoother; this is reminiscent of those on *Breagyps*, but on a smaller scale. In *occidentalis* the pit on the postorbital process for muscle attachment is deeper and larger, and the posterodorsal corner of the masseter scar extends farther medially. The entire scar is deeper.

The proximal anterolateral surface of the lachrymal has only a very small opening compared to a large foramen in *C. atratus*. The nasal bridge is relatively heavier and the tip of the upper mandible is not hooked as much in *C. occidentalis*.

It may be noted from the preceding comments that *Coragyps occidentalis* shows fewer differences from *Cathartes aura* than does *Coragyps atratus* of our Recent fauna. Thus there has been considerable divergence of the two genera since Pleistocene times.

Because the open auditory canal is peculiar to *Cathartes*, among cathartids, a sub-adult *C. occidentalis* with open canals was especially interesting. This specimen, number 192/1939 HL-14, in the collection of Loye Miller, was taken from San Josecito cavern a Pleistocene deposit. All measurements of the cranium fell within the range of adult

C. occidentalis, but the ossification seemed incomplete and spongy. Examination with a magnifying glass indicated that the auditory canals had never been covered. The apparent significance of this similarity cannot be verified until developmental studies of the skull are made. However, it may be stated that in two skulls of *Coragyps atratus* known to be immatures, the canal was covered. Thus it may be that here is another link in the chain of relationship between *Cathartes* and *Coragyps*.

CATHARTES AURA

The Turkey Vulture of the Pleistocene varies only slightly from the Recent form. None of the measurements in table 1 show any significant differences in absolute size. Where there is an apparent difference as in the average depth of the bill and the length of the premaxillary, the ranges of the two groups merge; the difference in average measurements may be due to the few fossil specimens available. With the exception of the ratio of bill depth to bill width none of the ratios in table 2 demonstrate proportional differences between the Recent and Pleistocene specimens.

The upper mandible is significantly deeper in the fossil form as indicated by the absolute measurements and the ratio of depth to width. On the five fossil crania at hand the auditory canals are open as in the modern Turkey Vulture. The occipital processes are somewhat heavier and wider; in this respect *C. aura* of the Pleistocene approaches *Coragyps occidentalis* of the same period, as it does in the lesser excavation of the supraorbital crests. Because of this decreased excavation the preorbital processes appear shorter. The postorbital processes are somewhat shorter, heavier and more laterally directed than in the Recent *Cathartes*.

As stated in the discussion of *Coragyps* it is significant that the points of difference between *Coragyps occidentalis* and *Cathartes aura* of the Pleistocene are fewer than between *Coragyps atratus* and *Cathartes aura* of modern times. Although a second species of *Coragyps* may have evolved in perhaps that span of years *Cathartes aura* has also undergone some modifications which make it more distinct; there has been lightening of the basal processes and further excavation of the orbital covering.

GYMNOGYPS

Examination of some 107 crania, 67 rostra and 20 lower mandibles of the condor from the Pleistocene tar pits of Rancho La Brea in Los Angeles County, California, indicates that the fossil California Condor is a species distinct from the Recent *Gymnogyps californianus*.

Gymnogyps amplus (L. Miller, 1911) was named from a tarsometatarsus taken from the Pleistocene deposits of Samwel Cave in northern California. The name *amplus* refers to the width of the tarsus which at that time was regarded as extraordinary, due to the absence of a large series of related forms. Study of this type and comparison of it with both the Recent and the Rancho La Brea tarsi showed no qualitative differences. Further, all the measurements (table 4) show that the tarsus of *G. amplus* falls well within the range of the La Brea specimens. The only other condor bones which might, by time and place, be *Gymnogyps amplus* of northern California are fragments of a coracoid and a humerus from the Pleistocene Potter Creek cave. These fragments indicate larger size and probably are not *Gymnogyps californianus* although there are few characters by which to judge.

Consequently, because *amplus* is known only from a tarsometatarsus that exhibits no qualitative or quantitative differences from the *Gymnogyps* tarsi from Rancho La

Table 4
Average and extreme measurements of tarsus

	<i>G. californianus</i>	<i>G. amplus</i> —La Brea	<i>G. amplus</i> —Samwell Cave
Total length	115 (113-118)	123 (112-134)
Diameter through cotylæ	27.4 (25.6-28.0)	27.3 (25.3-31.2)
Diameter through trochleæ	30.2 (29.1-30.4)	31.9 (29.5-34.5)	32.5
Least transverse diameter of shaft	13.4 (12.8-13.8)	14.3 (12.8-16.1)	16.0
Anteroposterior thickness of middle of shaft	9.1 (8.8-9.3)	9.7 (7.8-11.7)	11.0
Transverse diameter inner trochlea	8.6 (8.0-8.9)	9.2 (8.4-10.2)	9.5
Transverse diameter outer trochlea	6.9 (6.8-7.0)	7.9 (7.1-9.0)	8.0

Brea it becomes necessary to designate the Pleistocene California Condor in the tar pits as *Gymnogyps amplus*. It is unfortunate that the tarsus is useless in separating *amplus* and *californianus*. It is true that the tarsus, as well as other elements, shows greater average measurements in *amplus*, but the ranges of all measurements overlap (table 4).

Since this study is chiefly concerned with the cathartid skull and because it is in the skull that the major distinctions between *G. amplus* and *G. californianus* have been found, I shall confine the discussion to this part of the skeleton. Later, it is hoped that the entire skeleton of the Pleistocene species may be studied statistically since large series of most bony elements are available. At that time it may be possible to add substantially to the differentiation of the two species.

For purposes of clarity and to aid future workers I wish to designate as plesiotypes of *G. amplus* in the collections of the Los Angeles Museum, cranium no. B5415, rostrum no. B6513 and lower mandible no. B7591; all are from the Pleistocene tar pits of Rancho La Brea.

The fossil species, compared to *G. californianus*, has greater absolute measurements throughout the skull, with the exception of the depth of the bill. The frontoparietal suture or crest marking the anterior extent of the cervical musculature is farther forward in the fossil (figs. 45 and 46) and the columnar swelling above the foramen magnum slopes dorsally and anteriorly. In *californianus* this swelling slopes slightly posteriorly at first and thus forms a larger shelf above the foramen. Consequently, in dorsal view more of the parietal is visible in *amplus*, and the suture between the parietal and the squamosal and frontal is more curved (fig. 45). In *amplus* the temporal fossa is slightly deeper, and, posteriorly, the temporal muscle attachment is deeper; both features apparently are due, at least in part to a greater flaring laterally of the ventral process of the squamosal in the fossil birds. The pit or muscle scar on the post-orbital process is deeper in *amplus*, and the process itself is usually longer and more laterally directed. The supraorbital crests do not always form a sigmoid curve as in the Recent species; sometimes they are almost as straight as in *Breagyps* or *Vultur*. Anteroposteriorly the base of the lachrymal, near the frontonasal hinge, is considerably wider in the fossil.

A major distinction is the great strength and spread of the occipital processes in *amplus*, in which the ends of the processes are wide and blunt. Measurements of occipital width (table 1) and the ratio of occipital width to cranial length (table 2) show significant differences, and in no instances do the ranges of either the measurements or the ratios overlap. To a lesser degree the opisthotic processes reflect the same distinctions.

In contrast to *Vultur* and *Breagyps* the posterior internal corners of the occipital processes are smooth in *amplus* as in *G. californianus*.

In addition to the qualitative differences there are a number of quantitative differences between the two species. The skull of *amplus* is larger in absolute dimensions (table 1), but certain parts are relatively larger than others when compared to *californianus*. If the various measurements of the Recent species be compared to those of the fossil species, as in table 1, it is demonstrable that the differences in size are greatest in occipital width, in width of frontonasal hinge, in height of mandible, and in the length of the premaxillaries and the symphysis. If interspecific ratios are calculated as in table 5, one finds that in *Gymnogyps amplus* the premaxillary length, the hinge width, and the opisthotic and occipital widths are relatively greater than in *Gymnogyps californianus*. Relative bill depth is less in *amplus* than in *californianus*.

That *Gymnogyps amplus* is not a subspecies of *G. californianus* is indicated by the absence of overlap in the ranges and ratios of certain characters in the relatively stable basitemporal region of the skull and by the major qualitative differences already discussed.

The great range of size found in many of the Pleistocene birds in the tar pits usually has been accepted as variation within a kind, that is, genus, species or subspecies. This is a result, I believe, of the unfortunate application of concepts of subspecies and species which have been designed for study of series of specimens collected within a relatively short time. Few collections of skins date farther back than 100 years and a series of a species in such a collection naturally shows relatively little variation as a result of progressive evolutionary change.

The taxonomist working with Recent material gives specific rank to those groups not showing intergradation, and relegates intergrading forms to subspecific status. These working definitions are sufficient for collections in which there has not been a long enough period between the collection of the first and the last specimens of a series for the stock to have changed appreciably. However, in a series of a fossil species collected in a tar pit during a half million years of the Pleistocene there has been time for the stock to change considerably. The first specimen trapped may have been of a subspecies that is now differentiated to the rank of a species, or perhaps the subspecies (and its species) was wiped out and another subspecies or species became the dominant form locally. Different contemporaneous subspecies of the same species may have been trapped in the same pit at different times owing to the shifting of ranges. Representatives of these several types of transitory populations may be deposited in the same pit without the possibility of exact chronological separation as is often possible with rock-borne fossils.

Therefore it seems plausible that we are dealing with a number of transitory populations of various subspecies and perhaps species in any discussion of Pleistocene forms from the tar pits. It is impossible to separate these populations because we have the intermediates! The result is that measurements taken on these "species" and "subspecies" show great variation. The usual feature of bimodality which serves to indicate different characters or populations is ineffective because we do not know the potentialities of age and sex differences.

It would appear reasonable to expect that populations of *Gymnogyps* of slightly different types inhabited the area of the tar pits at various times in the Pleistocene. It is unlikely that the population was any more established in a fixed location than are the populations of the modern species of cathartids; and within historical times the range of *G. californianus* has constricted greatly (Harris, 1941; L. Miller, 1931; Wet-

more and Friedmann, 1933; Wetmore, 1931a, and 1932). The Turkey Vulture is slowly extending its range northward, and the Black Vulture is changing its range. Wetmore (1935) found *Cathartes a. aura* in an excavation near Comstock, Texas. The only previously known record of this race was from the Pleistocene of Florida. Wetmore (1932) records *Coragyps atratus* from cave material near Carlsbad, New Mexico. If this is subRecent, it indicates a decreasing range for the Black Vulture, and it probably is not true Pleistocene, if *atratus*, and not *occidentalis*, is present.

Even though the same stock occupied the general area constantly during the million years of the Pleistocene, this stock might well have been split chronologically into one or more morphologically distinct populations. One must either assume that *Gymnogyps californianus* has evolved as a species since the Pleistocene, or that it has moved into the area since the Pleistocene.

In an attempt to find intermediates between *amplus* and *californianus* I examined all available cave and shell-mound material. Unfortunately the material was either too fragmentary or was of an element that showed no differentiation between the species. The only recorded bone that indicates the occurrence of *Gymnogyps amplus* outside of California is that reported by Wetmore (1932); he described a fragmentary premaxilla of *Gymnogyps* in deposits near Carlsbad, New Mexico. This premaxilla was found to be larger than in Recent specimens and it agreed closely with examples from Rancho La Brea. The premaxilla is one of the elements that is relatively large in *amplus*. However, some of the remains in the New Mexico deposit were associated with human elements and some were not. It is thus not feasible to judge the age of this premaxilla.

Gymnogyps amplus might well be considered the progenitor of *G. californianus*. Differences in the skulls of these two species are nearly paralleled by the differences between *Coragyps occidentalis* and *Coragyps atratus*, but the magnitude of the differentiation is greater in the Black Vultures.

BREAGYPS CLARKI

Found in the Pleistocene, *Breagyps* is the most generalized and primitive cathartid examined in this study. Yet, the rostral part of the skull presents few major characters except size to differentiate it from the specialized upper mandible of modern *Coragyps atratus*. I found only two structures in the skull of *Breagyps* that are peculiar to it; the opisthotic processes are heaviest and have their lateroposterior corners drawn out and produced posteriorly, and the external, ventral surface of the maxillopalatines is more deeply excavated and indented.

Compared to *Gymnogyps amplus* and *Gymnogyps californianus*, *Breagyps* has a wider and higher, but shorter brain case, a wider frontonasal hinge and a somewhat narrower ventral occipital area (tables 1 and 2). The crania of *Breagyps* and *Gymnogyps* may be separated only on the basis of the development of the occipital processes and the excavation of the maxillopalatines, aside from size differences. The most striking feature is the elongated rostrum. The premaxillaries are approximately 17 per cent longer than in *G. amplus*; the mandible is much weaker (15 per cent) and the nares are 50 per cent longer and have no bony circlet in them.

It is also difficult to distinguish the crania of *Vultur* and *Breagyps*. The postorbital margin is nearly straight as in *Vultur*, and the edges of the supraorbital covering form nearly a straight line, compared to the sigmoidal curve of *G. californianus*. Additional characters of the cranium that show similarity between *Breagyps* and *Vultur* are: wide frontonasal hinge, high brain case, and smaller and relatively narrower foramen mag-

num. The posterior shelf in the nares is most similar to that in *Vultur* and has no indication of a median process.

In the basitemporal area *B. clarki* exhibits major similarities to *Coragyps*, *Cathartes* and *Vultur*. The opisthotic and occipital processes are nearly equal in length. The occipital processes are much heavier and form nearly an acute V which is reminiscent of all modern cathartids except *Vultur* and *Gymnogyps*. Short, blunt and heavy occipital processes were present on all Pleistocene cathartids. They were never as strong relatively in *Cathartes* as in the other genera, and in this genus they have changed little. In *Coragyps* the processes are slightly slimmer and attenuated, compared to *Breagyps*, but this attenuation reaches its maximum in the two Recent condors, *Vultur* and *Gymnogyps*.

The posteromedial corner of the occipital processes in *Breagyps* are produced into an irregular ridge of knobs that extends medially almost to the midline. Such a crest is not present in any *Gymnogyps* and is represented only by a few nodules in some specimens of *Vultur*. This crest, designated as the occipital ridge in the discussion of the modern skulls, is easily visible in *Cathartes*, and is best developed in *Coragyps* (fig. 44).

Rostral similarity between *Coragyps* and *Breagyps* may be convergent adaptation, but the similar characters of the occiput are certainly significant phylogenetically. These occipital characters may be traced from *Breagyps* through *Coragyps occidentalis* to *Coragyps atratus*. Likewise, the above-mentioned features linking *B. clarki* to *Vultur*, *Gymnogyps* and *Cathartes* are important. Except in the occipital process and the occipital ridge the only link between *Breagyps* and *Cathartes* is the irregularly triangular aperture in the maxillopalatines immediately dorsal to their fusion with the palatine. I could find no pattern except the general cathartid structure to connect *Sarcoramphus* and *Breagyps*.

Table 5

Decrease in size in Recent species compared with Pleistocene species*

	<i>G. californianus</i> vs. <i>G. amplus</i>	<i>Coragyps atratus</i> vs. <i>Coragyps</i> <i>occidentalis</i>		<i>G. californianus</i> vs. <i>G. amplus</i>	<i>Coragyps atratus</i> vs. <i>Coragyps</i> <i>occidentalis</i>
Cranial length	3.0	4.6	Length nares	1.2	17.0
Temporal width	2.4	7.5	Postorbital width	4.5	8.3
Cranial height	1.9	7.0	Opisthotic width	6.5	1.0
Length premaxillaries	7.5	7.5	Occipital width	12.9	6.8
Length premaxillaries anterior to nares	5.5	11.4	Hinge width	9.7	9.1
Width bill	5.6	11.8	Mandibular length	4.3
Depth bill	-2.5	6.3	Mandibular height	8.5
			Symphyseal length	7.3

*Expressed in per cent of measurement of fossil species.

Broadly speaking *Breagyps* may be said to have the cranium of *Vultur* (which is little different from that of *Gymnogyps*) and the rostrum of *Coragyps*. As indicated previously *Breagyps* is a generalized and primitive New World vulture which appears to be near the line of descent of *Vultur* and *Gymnogyps*, if not actually the ancestral stock of these two.

DISCUSSION OF FOSSIL SPECIES

It has not been possible to obtain representatives of all fossil cathartids, and previous descriptions often are of little value in relation to this study. However, to attempt to trace lines of descent within the family it is necessary to review what evidence there is in the literature.

Plesiocathartes europaeus Gaillard (1908) from the Upper Eocene or Lower Oligocene of France is the oldest known species and it probably represents a straggler on the European continent. There seems to be no question that it is a cathartid, but whether it is a distinct genus is open to doubt. In the Cathartidae the tarsus is not a good element for taxonomic study, and unfortunately that bone is the most often preserved in the fossil record. *Plesiocathartes* is known only from one tarsus.

Phasmagyps patritus and *Palaeogyps prodromus* were named from the Oligocene of Colorado by Wetmore (1927) from tibiotarsi. *Phasmagyps*, Wetmore states, is similar to *Coragyps atratus*, but is at least fifty per cent larger. *Paleogyps* is similar to *Gymnogyps californianus* but more than one-third smaller. Size is apparently the chief distinguishing feature; some might question the erection of new genera on this basis.

Cathartidarum is the genus erected for a Pleistocene humerus from Lagoa Santa, Brazil, by Winge (1888). It is about the size of "*Cathartes atratus*."

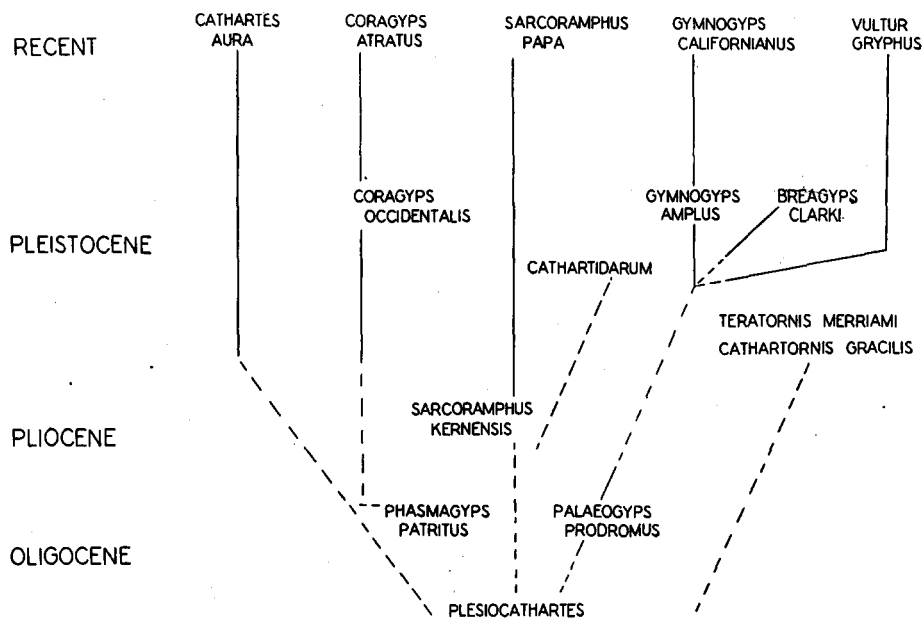


Fig. 47. A phylogenetic tree showing possible relationships of cathartid genera.

Sarcoramphus kernensis Miller (1931a) was named from a humerus found in the Kern River Pliocene of California. It is larger and more robust than in *S. papa*. Examination of the type shows that it clearly is a distinct species of cathartid, chiefly on the basis of size. Generic assignment is difficult because the pattern of the distal part of the humerus is disrupted by a fracture that destroys much of its character and because there is only slight generic difference between the cathartids in this region of the humerus.

Lönnerberg (1902) named *Vultur patruus* from a femur from the Pliocene of southwestern Bolivia. The chief difference from *V. gryphus* is size: *patruus* is intermediate in size between *gryphus* and *S. papa*, Lönnerberg states. However, if *Vultur* is as variable in size as *Gymnogyps amplus*, *patruus* probably is *V. gryphus*.

Vultur fossilis Moreno and Mercerat (1891) is similar to *V. gryphus* in size. Examination of the drawing (there is no description) showed no characters to distinguish *fossilis* from *gryphus*.

Three species of cathartids, *Psilopterus communis*, *P. australis*, and *P. intermedius* Moreno and Mercerat (1891) are placed by the authors near *Cathartes* and are considered intermediate or transitional toward *Sarcoramphus*. This material was so fragmentary it would seem impossible even to place it as to family, much less assign it to three different species.

Thus the literature gives little aid to the study of the inter-relationships of the genera and none to the relationships of the three major groups of cathartids as outlined in the study of the Recent species. The two species of *Sarcoramphus* stand as one group, intermediate to the small vultures and the large condors.

If *Cathartidarum* is valid it is the oldest member of the King Vulture group, and is probably a close relative of *S. papa* (Miller, 1931:71). *Phasmagyps patritus* and the two species of *Coragyps* constitute the Black Vulture line of the small vulture group. The position of *Phasmagyps* is uncertain, but *Coragyps occidentalis* appears to be near the ancestral stock of *Coragyps atratus*, if not the actual parent. *Cathartes aura* is the only representative of the Turkey Vulture line. The large condor group is also composed of two lines—*Gymnogyps* and *Vultur*. The former is made up of *Palaeogyps prodromus*, *Gymnogyps amplus* and *G. californianus*; *G. californianus* probably is a derivative of the *amplus* stock, but might be a relic stock that moved into this area in late Pleistocene or subRecent times.

Vultur gryphus is the only member of the *Vultur* line if *V. patruus* and *V. fossilis* are discarded. *Breagyps clarki* might well be included with *Vultur*, but it is intermediate in so many respects I prefer to place it between the *Gymnogyps* and *Vultur* lines as perhaps of stock ancestral to both.

The split of the *Cathartes-Coragyps* group probably occurred prior to the differentiation of the condor group because the genera of the small vultures are more distinct, and the *Coragyps* line has produced two well-defined species.

To express more graphically these views on the phylogeny of the Cathartidae I have prepared figure 47.

LITERATURE CITED

- Fisher, H. I.
1943. The pterylosis of the king vulture. *Condor*, 45:69-73.
- Gaillard, C.
1908. Les oiseaux des phosphorites du Quercy. *Ann. de l'universite de Lyon, Nouv. Ser. Sci. Med.*, 23:41-44, pl. 2, figs. 13-16.
- Harris, H.
1941. The annals of *Gymnogyps* to 1900. *Condor*, 43:1-55, 22 figs.
- Howard, H.
1929. The avifauna of Emeryville shellmound. *Univ. Calif. Publ. Zool.*, 32:301-394, pls. 1-4.
- Lönnerberg, E.
1902. On some remains of a condor from Bolivia. *Geol. Inst. Upsala*, 6:11, figs. 2, 4.
- McIlhenny, E. A.
1939. Feeding habits of black vultures. *Auk*, 56:472-474.
- Miller, L. H.
1910. The Condor-like vultures of Rancho La Brea. *Univ. Calif. Publ. Geol.*, 6:1-19, 2 pls.
1911. Avifauna of the Pleistocene cave deposits of California. *Univ. Calif. Publ. Bull. Dept. Geol.*, 6:385-400, 5 figs.
1931a. Bird remains from the Kern River Pliocene of California. *Condor*, 33:70-72, fig. 16.
1931b. The California condor in Nevada. *Condor*, 33:32.
1941. The passing of *Coragyps shastensis* Miller. *Condor*, 43:140-141.
- Moreno, F. P., and Mercerat, A.
1891. Catalogo de los pajaros fósiles de la Republica Argentina. *Ann. Mus. La Plata, Palaeont. Argent.*, 1:26, pl. 19, fig. 15 and pl. 20, fig. 19.

Pycraft, W. P.

1902. Contributions to the osteology of birds. Part 5. Falconiformes. Proc. Zoöl. Soc. London, 1:277-320, 3 pls., 5 figs.

Shufeldt, R. W.

1883. Osteology of the Cathartidae. Bull. U. S. Geog. Geol. Surv., 12:727-807, 10 pls.

Sushkin, P. P.

1900. Systematische Ergebnisse osteologischer Untersuchungen einiger Tagraubvögel. Zool. Anz., 23:269-277.

Winge, O.

1888. Fugle fra kinglehuler: Brasilien. E Museo Lundu, 2:5, 33-34, fig. 7.

Wetmore, A.

1927. Fossil birds from the Oligocene of Colorado. Proc. Colo. Mus. Nat. Hist., vii:1-14.

1931a. The California condor in New Mexico. Condor, 33:76-77.

1931b. The avifauna of the Pleistocene in Florida. Smithson. Misc. Coll., 85:1-46, 6 pls., 15 figs.

1932. Additional records of birds from cavern deposits in New Mexico. Condor, 34:141-142.

1935. The Mexican turkey vulture in the United States. Condor, 37:176.

Wetmore, A., and Friedmann, H.

1933. The California condor in Texas. Condor, 35:37-28

Museum of Vertebrate Zoology, Berkeley, California, March 15, 1944.