RELATIONSHIPS OF THE CATHARTID VULTURES

BY J. DAVID LIGON

THE PHYLOGENETIC affinities of the New World vultures, Family Cathar-
tidae[1], have been questioned for many years. Upon examination of
many anatomical and other characters of this and other groups, I have
concluded that the Cathartidae are not at all closely related to the
remainder of the Falconiformes, that they share a great many features
with the storks, Ciconiidae, and that the storks and herons are dis-
similar. None of these conclusions is original (Garrod, 1873; Friedmann,
1950:5; Jollie, 1953; Cottam, 1957:54).

The purpose of this paper is to summarize the evidence bearing on
the interrelationships of the storks and New World vultures, and to
emphasize the differences between the Cathartidae and Accipitridae
as well as between the Ardeidae and Ciconiidae. Other families of the
orders Ciconiiformes and Falconiformes, as they are presently consti-
tuted, are not considered here.

REVIEW OF CATHARTID CLASSIFICATION

Gadow (1893) stated that Illiger in 1811 was the first to separate the
New World vultures from other diurnal birds of prey, giving them
familial rank equal in his system to that of all other diurnal birds of
prey combined, and that Vieillot in 1816 and Nitzsch in 1840 also
recognized the differences between the New World vultures and other
groups. Garrod (1873) separated the Cathartidae entirely from the
Accipitres and placed them next to the storks. His order Ciconiiformes
was arranged in the following sequence: Pelargi, Cathartae, Herodiones,

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[1]Brodkorb (1963, 1964) has shown that the proper familial name of the New
World vultures is Vulturidae rather than Cathartidae, and that the ordinal names
Ciconiiformes and Falconiformes were preceded by Ardeiformes and Accipitriformes,
respectively. However, in order to avoid confusion, I will retain the current
nomenclature.

Steganopodes, and Accipitres. Gadow (1893), in discussing the relationships of the birds of prey, stated that it is of great taxonomic significance that the diurnal birds of prey cannot be well defined. He concluded that the nearest relatives of the Falconiformes are to be sought in the Ciconiiformes. In discussing the conclusions of the leading taxonomists of the day, he stated further that Garrod emphasized the great differences between the Cathartidae and Accipitres, but went much too far, placing the Cathartidae between his Pelargi and Herodiones and separating them entirely from the Accipitres and that Forbes followed him in this, but spoke for relationships of the Cathartae with the Tubinares; also, Fürbringer missed in the other extreme, in which he gave the Cathartidae only family rank. Gadow concluded that there is agreement that the Falconiformes are related to storks and cormorants and are linked through the Cathartae. Chandler (1916) felt that the structure of the feathers showed a relationship between the Cathartae and *Plotus* [= *Anhinga*], and suggested the possibility of regarding the Cathartae as direct descendants of the Steganopodes [= Pelecaniformes and Ciconiiformes], from a group not far removed from *Anhinga*. Compton (1938) attempted to demonstrate a relationship between *Pandion* and the cathartids. From his myological studies of the "heterogeneous order Falconiformes," Hudson (1948), in speaking of the cathartids and typical Falcones [= Accipitridae, Pandionidae, and Falconidae] concluded: "It hardly seems likely that such wide differences developed from the same line of descent. It is quite possible that the American vultures have no more natural affinity with the hawks and falcons than the owls which were ousted by systematists from the order Falconiformes many years ago." Friedmann (1950), while recognizing that the American vultures are quite distinct from the Falcones, stated that their relationships are somewhat complex. He concluded that they are not distantly related to the Ciconiiformes, Pelecaniformes, and Procellariiformes. Jollie (1953) stated that the cathartids differ strongly in every way from the other Falconiformes: "Their affinities are with a pelecaniform-procellariiform group which I would identify as an order, with each of these as a suborder." This conclusion is based on anatomical studies not described. Verheyen (1959a, 1959b) retained the orders Ciconiiformes and Falconiformes as they are presently constituted, with four suborders in each group. On the basis of studies of egg-white protein, Sibley (1960) and Peakall (1963) reached very different conclusions regarding the relationships of the cathartid vultures and other falconiforms. Sibley felt that the

cathartids were related to the accipitrids while Peakall felt that they were not.

Recent classifications of birds of the world (Mayr and Amadon, 1951; Wetmore, 1951; and Storer, 1961) have placed the Cathartidae in the order of Falconiformes, separating them at the subordinal or superfamilial level.

It is apparent that there is little unanimity of opinion supporting the position of the cathartids in the order Falconiformes. Why then have the New World vultures been retained in this group? Both Beddard (1898) and Jollie (1953) provide answers to this question. Beddard (1898:485) stated: "The only group which has the distinctive characters of the Cathartidae (besides of course the present group) is that of Herodiones. There only do we find birds with ambiens and expansor secundariorum, without biceps slip, holorhinal, and with rudimentary or absent caeca. The Steganopodes also are not far off. It really comes to the beak and claws, the ceroma, and to the presence of various structures (e.g., the peculiar palate, the basipterygoid processes) which forbid their association with the Herodiones. The several groups are not far off, but on the whole the American Vultures are more like the remaining birds of prey than like the stork tribe." This statement is made by Beddard despite his demonstration that the cathartids differ from other falconiforms in all of eight major characters listed by him. Jollie (1953) thought that the main reason the order has not been broken up is one of convenience. "To separate the different groups of the Falconiformes would necessitate setting up each fragment as a distinct order or associating the fragments as parts of other orders. Both actions have been looked upon as repugnant, and the order has been left intact."

METHODS

In attempting to show relationships between groups which appear to be ancient, one must be careful not to over-emphasize any one character or set of characters which the groups involved may have in common; at the same time he must realize that related species or groups often exhibit one or more strikingly different features. Two examples illustrate these dangers. On the basis of their osteology and myology the Old World vultures are unquestionably accipitrids, but their tarsi, feet, and heads are amazingly similar to those of the cathartids. Both groups have an elevated hallux, strong webbing between the toes, reticulate tarsi (other accipitrids have an incumbent

hallux, little webbing between the toes, and have the tarsus reticulate, scutellate, booted, or feathered), a bare head or one tending towards bareness, and a cere. A single genus in the family Accipitridae, *Elanus,* is schizognathous, while all other genera are desmognathous.

Taxonomically pertinent characters of the herons, storks, New World vultures, and accipitrids (hawks, eagles, kites, and Old World vultures) are described and contrasted below. These four families are well defined and thus, to an extent, generalizations about each can be made. I have examined skeletons of representatives of each of the four families and the osteological descriptions are my own. Terminology follows that of Howard (1929). Genera examined include: Ardeidae *(Ardea, Casmerodius)*; Ciconiidae *(Ibis, Sphenorhynchus, Euxenura, Jabiru, Ciconia, Mycteria)*; Cathartidae *(Coragyps, Cathartes, Sarcoramphus)*; and Accipitridae *(Necrosyrtes, Haliaeetus, Buteo)*. Osteological characters of a bone or region, such as the skull, have usually been treated in tabular form for ease of comparison.

Without knowledge of the functional significance of the various osteological characters one cannot be certain of their relative importance in a study of phylogeny, and I concede this to be a weakness of this study. My feeling has been, however, that very few of the several really striking similarities between ciconiids and cathartids could be attributed to convergence, while characters that are common to herons and storks, and to vultures and accipitrids more certainly could be.

Other characters are discussed in what I consider to be a decreasing order of importance. Friedmann (1950: 4–6) may be consulted for some additional cathartid characters and a discussion of the relationships of this family to other groups.

<div align="center">OSTEOLOGY</div>

SKULL (Fig. 1).—The cathartids are unique among the birds examined in having the maxillopalatines unfused. They and the storks alone have: (1) the alinasals, located dorsal to the maxillopalatines, fused; (2) the lacrymals fused to the frontals; (3) functional or vestigial basipterygoid processes; (4) a slender ectethmoid; (5) the pterygoids stocky and twisted; and (6) the palatines relatively short and deep, extending only to the middle of the orbital region. These and other characters are summarized in Table 1.

There is a foramen in the mandible of the storks and vultures, but not in the herons or hawks.

STERNUM.—The sternum does not yield much information on relationships of the groups considered here. Table 2 summarizes some of the sternal features of the four groups.

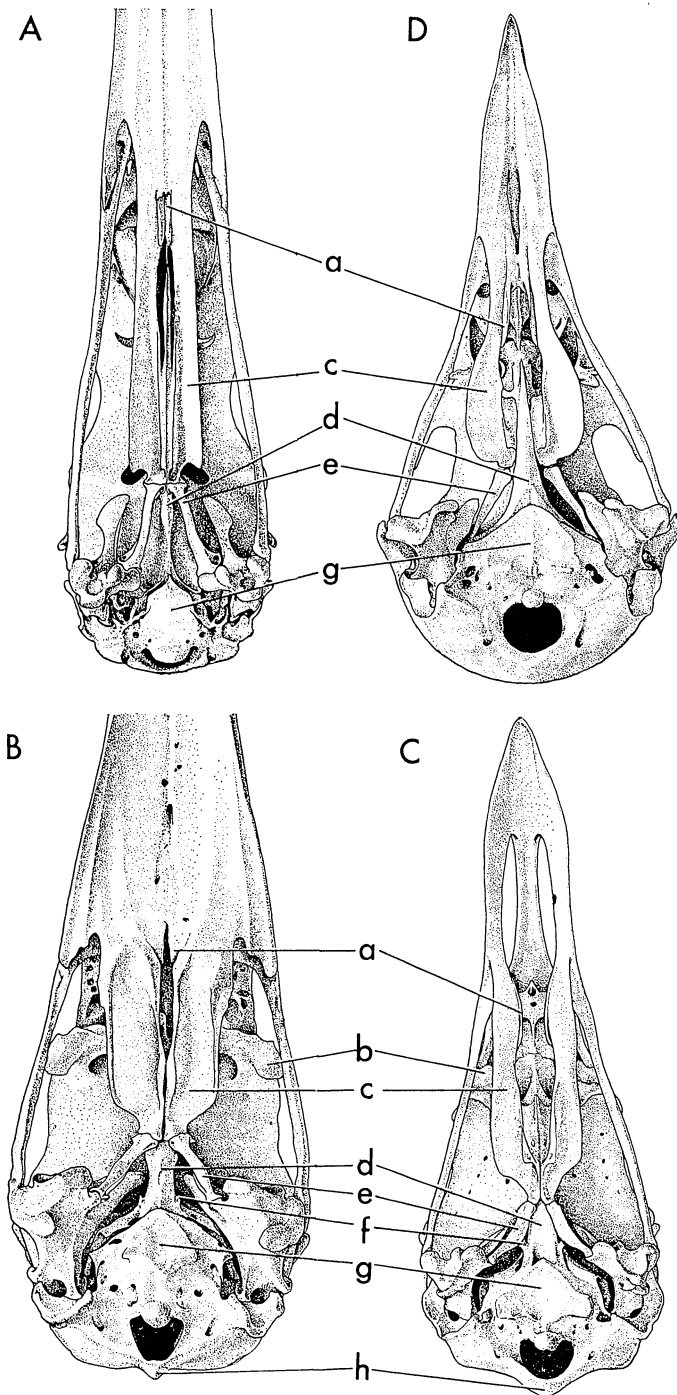PELVIC GIRDLE (Fig. 2).—Table 3 summarizes some characters of the pelvic girdle.

FIG. 1. Ventral views of the skulls: A, *Ardea herodias;* B, *Ibis leucocephalus;* C, *Coragyps atratus;* and D, *Necrosyrtes monachus.* a, maxillopalatine; b, lacrymal; c, palatine; d, sphenoidal rostrum; e, pterygoid; f, basipterygoid process; g, basitemporal plate; h, supraoccipital.
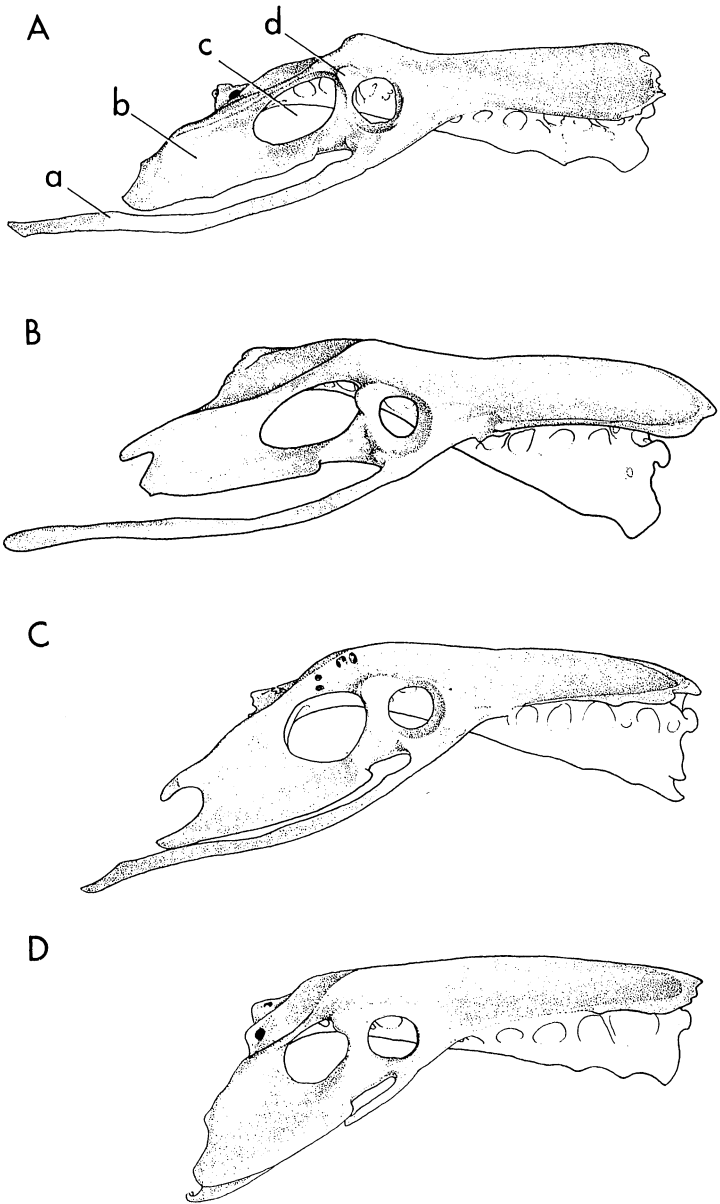
FIG. 2. Lateral views of pelvic girdles: A, *Ardea herodias;* B, *Mycteria americana;* C, *Coragyps atratus;* D, *Necrosyrtes monachus.* a, pubis; b, ischium; c, ilio-ischiatic fenestra; d, antitrochanter.

FURCULUM.—In the ardeids the clavicles are long and weak with no large articulating areas; the hypocleideum is long and pointed dorsally. The ciconiid furculum is much more robust, with a large articulating surface at the symphysis, and is pneumatic. The furculum is also robust in the vultures, but is very light and strongly bowed. There is a pneumatic fossa on the lateral side of each clavicle; the hypocleideum is pointed anteriorly; the dorsal region is greatly expanded. The accipitrid clavicle is flattened with an articulating surface on the dorsolateral side; the hypocleideum is pointed posteriorly; the dorsal region is greatly expanded.

CORACOID.—The ardeid coracoid is very distinctive: no coracoidal fenestra; shaft long and furcular facet small and only slightly slanted; procoracoid long and curved upward. The coracoidal fenestra is absent in the storks; procoracoid process long and curved upward; the anterior end may be pneumatic. A coracoidal fenestra is present in the cathartids; the procoracoid process is short and extends at right angles from the shaft; the distal end is pneumatic. The accipitrids possess a coracoidal fenestra; a downward-pointing brachial tuberosity; the furcular facet is somewhat curved; the sternocoracoidal process is pointed.

CERVICAL VERTEBRAE.—The herons possess 18–20 cervical vertebrae; the storks, 17–18; the vultures, 15–17; and the hawks, 13–14.

HUMERUS.—The major characters of the humerus of these groups are given in Table 4. That of the ardeids is most unlike the others, while those of the ciconiids and cathartids appear most alike.

CARPOMETACARPUS.—Superficially, the carpometacarpus of the herons and storks, and vultures and accipitrids appear to be similar. However, upon close examination one finds distinct similarities between storks and vultures, and strong differences in these groups from herons and hawks, respectively. Although I feel that the carpometacarpus provides some of the best postcranial osteological evidence for a relationship between storks and vultures, this element did not prove to be suitable for illustration. Table 5 gives the major distinguishing characters of this element.

FEMUR (Figs. 3 and 4).—The femora of the storks and vultures are similar. Both are highly pneumatic, stocky bones with rounded heads, short necks, and with a rounded trochanter, when viewed medially. Distally the external condyle, internal condyle, intercondylar fossa, and flexor attachments are similar and quite different from those of the herons and accipitrids.

TIBIOTARSUS (Fig. 5).—Although the proportions of the groups considered here vary widely in the two distal long bones of the leg, the articulating ends show several characters of possible phylogenetic significance. Table 6 summarizes these.

TARSOMETATARSUS (Fig. 6).—Some characters of this element are summarized in Table 7.

MYOLOGY

The order Falconiformes has probably received more careful myological study than any other major group. The work done by Fisher (1946) on the cathartids is one of the few that deals with all the genera of a well-marked higher taxon. Hudson's (1948) study of the pelvic
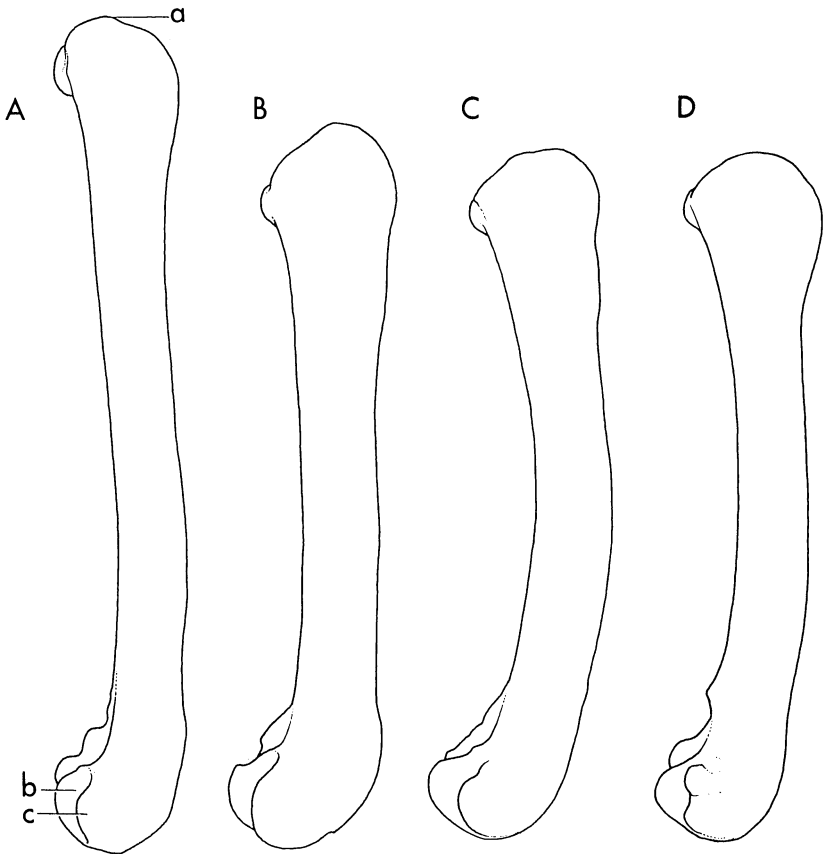
FIG. 3. Lateral views of the right femora: A, *Ardea herodias;* B. *Mycteria americana;* C, *Coragyps atratus;* D, *Necrosyrtes monachus.* a, trochanter; b, external condyle; c, fibular condyle.

appendages of the members of this order demonstrated great dissimilarities in the Falconiformes. Rather than listing these, I simply point out that he found 20 "important differences" between the cathartids and typical Falcones and only nine "important similarities."

The great pectoral muscle, Pectoralis major, is double in storks and vultures, single in herons and accipitrids (Garrod, 1874). In the Ardeae the Peroneus longus is fairly large, but has only a superficial origin; the P. brevis is well developed. The P. longus is large and strong in the storks with no deep origin; the P. brevis is absent. The P. longus is strong with a deep origin in the cathartids, while the P. brevis is

very slender and arises from the distal two-thirds of the fibula. In the
Falcones both peroneals are present, but the P. brevis is the more
powerful and the P. longus tends to be reduced to only its deep origin.
The expansor secundariorum is absent in the Accipitridae but is
present in the others (Mitchell, 1913).

Beddard (1898:482) stated: "In *Gyparchus* [= *Sarcoramphus*] *papa*
the tendons of the patagium are somewhat complicated. The brevis
consists of a separate anterior and posterior section, of which the latter
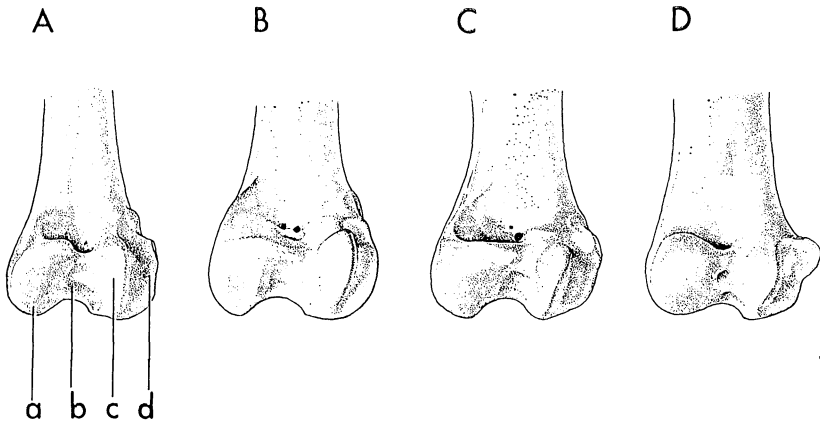is thinner and more diffuse. The anterior tendon divides into two, of

A   B   C   D

Fig. 4. Posterior distal views of femora: A, *Ardea herodias;* B, *Mycteria ameri-
cana;* C, *Coragyps atratus;* D, *Necrosyrtes monachus.* a, internal condyle; b, inter-
condylar fossa; c, external condyle; d, fibular condyle.

which the foremost gives off a slip to the longus. There is no *biceps
slip.* The tendons, in fact, are thoroughly stork-like, as are those of
the condor *(Sarcoramphus)* [= *Gymnogyps*] and *Cathartes.* In this
character the family is very uniform."

Garrod (1873, 1874) developed the thigh muscle formulae for birds.
The femoro-caudal is represented by A; the accessory femoro-caudal
by B; the semitendinosus by X; the accessory semitendinosus by Y;
and the presence or absence of the ambiens by a plus or minus sign.
Parentheses indicate the absence of a muscle in one or more genera.
According to Garrod, the catharids are (A)XY+; the storks (A)XY±
(ambiens absent in one genus); herons AXY—; and hawks A+. Hudson
(1948) presents the thigh muscle formulae of the cathartids and other
falconiforms in greater detail, further emphasizing their differences.
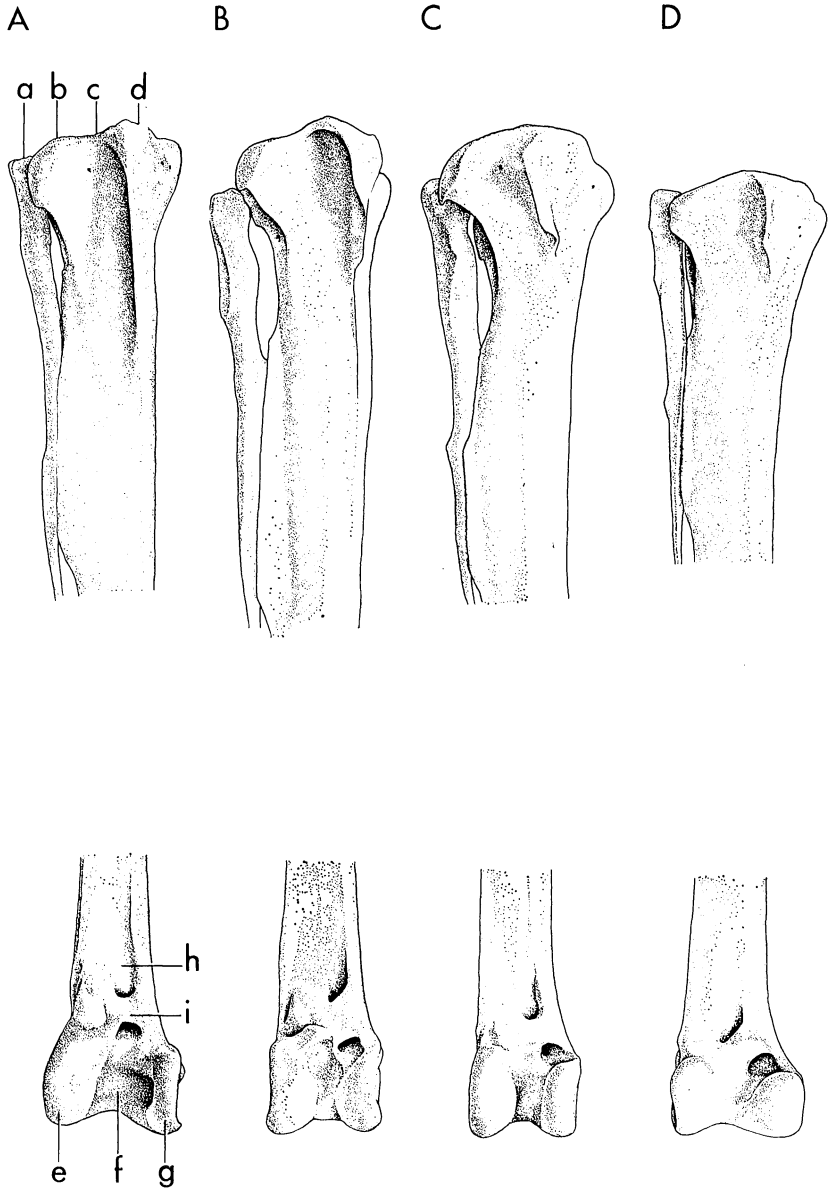
Fig. 5. Proximal and distal anterior views of right tibiotarsi: A, *Ardea herodias;* B, *Mycteria americana;* C, *Coragyps atratus;* D, *Necrosyrtes monachus.* a, fibula; b, outer cnemial crest; c, intercnemial ridge; d, inner cnemial crest; e, external condyle; f, anterior intercondylar fossa; g, internal condyle; h, tendinal groove; i, supratendinal bridge.
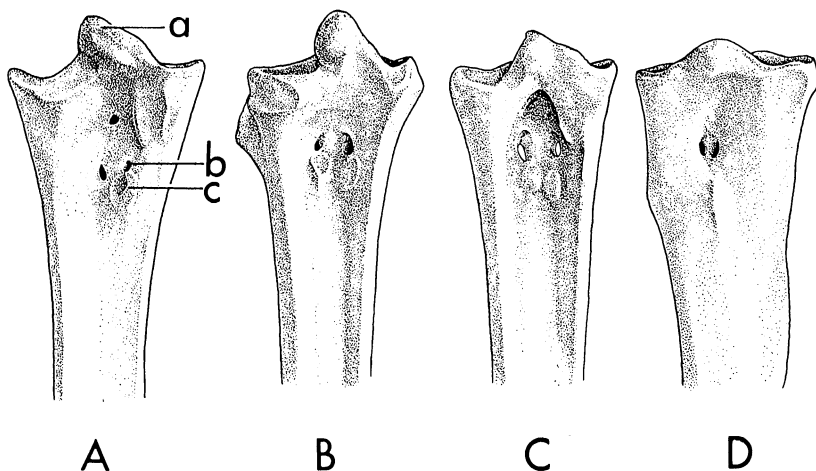
Fig. 6. Proximal anterior views of tarsometatarsi: A, *Ardea herodias;* B, *Mycteria americana;* C, *Coragyps atratus;* D, *Necrosyrtes monachus.* a, intercotylar prominence; b, proximal foramen; c, tubercle for tibialis anticus.

The myology strongly indicates that the cathartids are not closely related to the accipitrids, and, to a lesser degree, that the cathartids and ciconiids are related.

NESTLING PLUMAGE

Nestling cathartid vultures, incorrectly said by Gadow (1893) to be hatched naked, possess two downy plumages prior to development of the juvenal plumage (see Finley, 1906: 140–141, and Koford, 1953, pls. 25–28). I have examined downy chicks of the Black and Turkey vultures. They are hatched with a coat of down covering the entire body except the lores, orbital region, and throat. In the Turkey Vulture the down is white, and the ventral side of the throat is naked down to the breast. The first coat in the Black Vulture is a buffy brown, and its throat is covered up to the gular region. The second down is darker in both species.

Van Tyne and Berger (1959) state incorrectly that storks are hatched naked. The Wood Stork is hatched with a sparse gray down which is replaced after about ten days with a very dense, woolly white second down (Kahl, 1962). Bent (1927) described the downy plumage of the Jabiru (*J. mycteria*): "In the downy young the lores and the spaces around the eyes are naked; and there is a naked space encircling the

TABLE 1
COMPARISON OF SKULL CHARACTERS

Character	Ardeidae	Ciconiidae	Cathartidae	Accipitridae
Palate	Desmognathous	Desmognathous	Indirectly desmogna-thous, no fusion of maxillopalatines	Desmognathous
Alinasals	Not fused	Fused	Fused	Not fused
Lachrymals	Not fused	Fused to frontals	Fused to frontals	Not fused
Interorbital septum	Completely open	May have small opening	May be open	May be open
Palatines	Long and shallow	Short and deep	Short and deep	Flattened and shallow
Basipterygoid process	None	Vestigial or absent	Well developed	None
Pterygoids	Long and straight	Short, stocky, and twisted	Short and twisted	Long and slender
Opisthotic	Does not extend below articulation of quadrate	Extends far below articulation of quadrate	Extends far below articulation of quadrate	Extends slightly below articulation of quadrate
Ectethmoid	Broad and flattened dorsally	Slender	Slender	Somewhat broadened and flattened dorsally
Sphenoidal rostrum	Ridged	Cylindrical	Cylindrical	Cylindrical
Basitemporal plate	Not separated from occipital condyle	Well separated from occipital condyle and tri-angular in shape	Well separated from occipital condyle with strong lateral project-tions; triangular in shape	Less well separated from occipital condyle and without lateral wings
Vomer	Laterally compressed and largely double	Single	Absent	Single and not expanded
Supraoccipital	Does not protrude in ventral view	Protrudes posterior to rim of skull	Protrudes posterior to rim of skull	Does not protrude pos-terior to rim of skull

TABLE 2
COMPARISON OF STERNAL CHARACTERS

Character	Ardeidae	Ciconiidae	Cathartidae	Accipitridae
Ventral manubrial spine	Extends beyond apex of carina	Short, notched, blunt, with carinal apex extending anterior to it	Short, blunt, notched; carinal apex posterior to it	Short, asymmetrical; external apex even or posterior to it
Coracoidal sulci	Deeply crossed	Uncrossed or very slightly crossed	May show slight tendency towards crossing	Crossed in either direction
Sternocoracoidal processes	Pointed	Pointed	Reduced and rounded	Pointed
Costal processes	Four in number	Five	Four to six	Six or seven
Sternal notches	One pair	One pair	One or two pairs	One pair of manubrial fenestrae
Posterior xiphial area	Squared	Somewhat squared	Rounded or slightly pointed	Reduced

TABLE 3
Comparison of Pelvic Girdle Characters

Character	Ardeidae	Ciconiidae	Cathartidae	Accipitridae
Posterior ischium	Unnotched	Notched	Notched	Unnotched
Ilioischiatic fenestra	Elongate	Elongate	Rounded	Slightly elongate
Anterior iliac crest	Does not overlie antitrochanter	Overlies antitrochanter	May or may not overlie antitrochanter	Does not overlie antitrochanter
Pubis and ischium	Separate	Separate	Separate	Mid-portion or entire posterior portion of pubis gone; anterior and posterior portions (when present) fused to ischium
Curvature of girdle	Slightly curved posteriorly	Slight angle above antitrochanter	Slight angle above antitrochanter	Bends at 45° angle above antitrochanter

TABLE 4
COMPARISON OF HUMERAL CHARACTERS

Character	Ardeidae	Ciconiidae	Cathartidae	Accipitridae
Shaft	Long and straight	Stocky and sigmoid	Stout, may be strongly sigmoid and highly pneumatic	Often slender, as compared with the cathartids
Deltoid crest	Small	Prominent	Long and conspicuous, with a knob at its distal termination	Long with sharp angle at its midpoint; without distal knob
Bicipital crest	Much reduced	Expanded and forms right angle to shaft	Prominent, joins shaft at almost right angles	Well-marked, joins shaft more gently than previous two families
Pneumatic fossa	Small	Larger relatively than in the herons	Prominent	Prominent foramen on shaft distal to pneumatic fossa, absent in other groups
Head	Somewhat pointed	Rounded	Rounded	Rounded, external tuberosity weak as compared with the other groups
Brachial depression	Shallow, extending well up on shaft	May be deep, not extending far up on shaft	Deep, not extending far up on shaft	Very shallow
Attachment of anterior articular ligament	Almost parallel to palmar side of shaft	Almost at right angle to palmar side of shaft	At 45° angle to palmar surface of shaft	Weakly developed

TABLE 5

COMPARISON OF CARPOMETACARPAL CHARACTERS

Character	Ardeidae	Ciconiidae	Cathartidae	Accipitridae
Shaft of metacarpal II	Long, straight, with slight indication of tendinal groove	Less slender and with a fairly well-marked tendinal groove	Stocky, tendinal groove well marked	Relatively long and slender, tendinal groove well marked
Carpal trochlea	Small	More expanded	Rather rounded from lateral or medial view	Less rounded than in cathartids
Process of metacarpal I	Thin and pointed	Rounded	Chunky, rounded at its termination	Short and squared
Metacarpals II and III	M. III is weak and slightly bowed, lying close to M. II	M. II and III are attached for a greater distance along their lengths than in the herons	M. III thick and strongly bowed, flaring out from M. II	M. III is not attached to M. II along its shaft and is rather slender, especially at its distal end
Pollical facet	Smooth, without distinctly separated articulating surfaces	Three distinct articulating surfaces	Three distinct articulating surfaces	Two distinct articulating surfaces
Indentations	None between pollical facet and process of M. I, nor between process of M. I and carpal trochlea	Present between pollical facet and process of M. I and carpal trochlea	Deep indentations between pollical facet and process of M. I and between M. I and carpal trochlea	No real indentations between pollical facet and process of M. I or between process of M. I and carpal trochlea
Distal facets	Facet of digit III separated by shallow depression from that of digit II	Facet for digit III separated by deep depression from facet of digit II	Facet for digit III separated from digit II by deep depression	Facet for digit III extends distad to facet for digit II; groove between facets for digits II and III is shallow

TABLE 6

COMPARISON OF TIBIOTARSAL CHARACTERS

Character	Ardeidae	Ciconiidae	Cathartidae	Accipitridae
Interarticular surface	Protuberance present	Protuberance slight or absent	Protuberance slight or absent	No protuberance
Inner cnemial crest	Reduced and merges gradually into shaft	Elevated and joins shaft abruptly	Slightly elevated and joins shaft abruptly	Somewhat elevated, the portion adjacent to the shaft is small and joins the shaft gently
Outer cnemial crest	Articulating surface at right angle to crest	Articulating surface at slight angle to crest	Articulating surface at slight angle to crest	Articulating surface almost at right angle to crest, as in herons
Intercnemial area	No pronounced ridge	Elevated ridge	Ridge present	Ridge present
Condyles	Internal much smaller, depression on anterolateral side of internal condyle	Unequal in size, both project into anterior intercondylar fossa; distally both condyles terminate in something of a point	Unequal in size, both project into anterior intercondylar fossa; posterior ridge of internal condyle sharp, as in storks	May be equal or unequal in size
Condylar area	Triangular ridge above external condyle	Large protuberance lateral to the supratendinal bridge and there may be a ridge dorso-lateral to it	No protuberance lateral to the supratendinal bridge, a slight ridge dorsomedial to the external condyle	Anterior intercondylar fossa wide, as opposed to the narrowness of the fossa in storks and vultures; may or may not have protuberance dorsomedial to external condyle
Ligamental prominences	Reduced or absent	Internal well marked	Reduced	Internal conspicuous

TABLE 7
COMPARISON OF TARSOMETATARSAL CHARACTERS

Character	Ardeidae	Ciconiidae	Cathartidae	Accipitridae
Hypotarsus	Complex, large inner ridge, two smaller ridges and one or two canals	Simple and weakly U-shaped	Simple and almost square posteriorly	Simple
Intercotylar prominence	Large and pointed laterally	Large and pointed laterally	Less well developed than in herons or storks	Knob is reduced
Tibialis anticus	One tubercle	One or two tubercles of tibialis anticus	Two tubercles	One tubercle
Trochleae	Nearly on a plane, trochlea IX most proximal, and rounded	Strongly curved posteriorly, second trochlea slightly shorter than fourth; facet for first metatarsal long and narrow, outer ridges of trochleae two and four extend posterior to internal ridges	Somewhat curved posteriorly, second trochlea slightly longer than fourth, outer ridges of trochleae two and four extend posterior to internal ridges	Curved posteriorly, second trochlea much lower than fourth and with a prominent lateral wing, outer ridges of trochleae two and four extend posterior to internal ridges

central part of the neck. Below this naked space the lower neck and the entire body is completely covered with short, thick white down, locally tinged with yellowish, the top and back of the head are thickly covered and the sides of the head and upper neck are scantily covered with greyish white or yellowish white down."

A downy young accipitrid (*Buteo jamaicensis*) possesses a complete downy coat covering the entire head region. Down feathers are longest on the head, in contrast to the cathartids and storks in which it is shortest in this region. Hawks have two downy coats, while herons at hatching are sparsely covered with a long thin down and acquire their juvenal plumage while still small (Bent, 1937; Palmer, 1962).

In summary: the natal plumages, both in covering and sequence, are similar in the storks and vultures. They differ strongly from those of the herons and to a lesser degree from those of the accipitrids.

SYRINX

The ardeids possess a tracheobronchial syrinx with intrinsic muscles, as do the Falconiformes, except the cathartids. Storks have a poorly developed tracheal syrinx, but no intrinsic muscles. Cathartids have neither syrinx nor intrinsic syringeal muscles. The membrana tympaniformis may be present or absent in this group (Beddard, 1898).

Both storks and vultures are voiceless, or nearly so, giving hisses or grunts. The storks have utilized their large beaks to offset this deficiency, and clacking of the mandibles may replace the voice.

PTERYLOGRAPHY

Fisher (1943) summarized the pterylography of all genera of cathartids. Unfortunately, no such concise treatment appears to be available for the other groups. Features distinguishing cathartids from other falconiforms include: absence of a submalar apterium; vestigial or obsolete lateral cervical apterium; wide dorsal-cervical region; presence of a ruff; continuous dorsal and pelvic regions; fused sternal, axillar and submalar regions; a row of large feathers in the posterior subaxillar area; a definite sternal apterium, a femoral tract consisting of five to seven long rows of lanceolate feathers on the posterior margin of the thigh; four 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.

Chandler (1916) lists the following characters distinguishing the Ciconiae from the Ardeae: (1) absence of powder down; (2) even dis-

tribution of plumules in both pterylae and apteria, as in the cathartids; (3) feathered lores; (4) wide pterylae.

The aftershaft is absent in the cathartids, present in other falconiforms (except *Pandion*), present in the ardeids, and may be present, rudimentary, or absent in the Ciconiae.

The cathartids have 12–14 rectrices; the storks 12; herons 10–12; and hawks 12–14. All four groups have 10 functional primaries.

EGG-WHITE PROTEINS

Sibley (1960), utilizing electrophoretic separation, concluded that the cathartids are related to the accipitrids, and that herons and storks also are related. Later (letter, Sept. 13, 1966), on the basis of both egg-white proteins and hemoglobin data he stated "that the storks and herons are not especially close and neither are the New World vultures and typical hawks." Also, the resemblances, in both systems, between the Cathartidae and Ciconiidae are not convincing. Peakall (1963) concluded that the cathartids are not closely related to the other falconiforms. Conclusions to be drawn from the protein evidence are well stated by Sibley (1960: 232): "The possible relationships of the Ciconiiformes to diurnal birds of prey (Mayr and Amadon, 1951) is not opposed by the egg-white evidence but neither is it strongly supported."

DEEP PLANTAR TENDONS

Garrod (1875) found that the arrangement of the deep plantar tendons of the cathartids was unique among birds possessing an ambiens muscle. He concluded: "The arrangement observed in the Cathartidae is in no way allied to any of these, and adds another important point to the many now known to separate them off entirely from the Accipitres verae."

The herons, storks, and hawks have an arrangement somewhat similar to each other and of little worth in separating them.

FOSSIL RECORD

The fossil record of the storks and vultures has not revealed information concerning their relationships either to each other or to the herons and hawks, respectively. *Neocathartes* (Wetmore, 1941) of the Eocene of Wyoming is of interest, showing that within the evolutionary history of the cathartids there have been forms with rather stork-like proportions of the legs.

TEMPERATURE REGULATION

Kahl (1963) showed that the Wood Stork cools itself by excreting a very dilute substance on the legs, thus facilitating heat loss by evaporation. He stated that this habit appears to be widespread among storks of the world and that he has also seen Black Vultures excrete on their legs. I too have noted this behavior in Turkey Vultures. The functional significance of this habit has not been experimentally studied in the cathartids.

EXTERNAL MORPHOLOGY

In the ardeids the nostrils are linear and slightly perforate. They are perforate in the ciconiids and cathartids and are imperforate in the hawks.

The tarsus of the herons is scutellate in front, at least proximally. It is reticulate in the storks and vultures and usually scutellate in the hawks, although in the latter it may be reticulate, booted, or feathered.

The hallux is incumbent in the herons and typical hawks and is elevated in the storks and vultures.

The middle claw is pectinate in the herons only, among the groups here considered.

The bases of the toes are strongly webbed in the storks and cathartids, and in the Old World vultures (Accipitridae). The herons and some accipitrids have a strong web between the third and fourth toes only.

The oil gland is tufted in all except the cathartids, in which it is naked. In the Black Vulture, down is often present on the oil gland (Fisher, 1943).

The ramphotheca is simple in all.

FORAGING AND FEEDING

Cathartids typically soar while searching for food, either singly or in groups. Storks also are great soarers, and this is used as a foraging technique. In the Wood Stork, soaring is the primary means of movement from the nesting to the feeding grounds. The change from soaring to gliding flight is marked by a conspicuous change in the shape of the wings similar to that described for the Black Vulture (Kahl, 1964:103).

Both storks and vultures are opportunistic feeders. Some storks feed primarily on carrion, others on fish, but in a manner completely

different from that of the herons (Bent, 1927; Kahl, 1964), while others, such as the White Stork, *Ciconia ciconia,* feed on a wide variety of items (Haverschmidt, 1949). New World vultures may feed on vegetable as well as on animal matter. Squash, pumpkins (Bent, 1937) and opened coconuts (pers. obs.) having been recorded as food items. It should be noted that the Vulturine Sea Eagle (*Gypohierax angolensis*) of the family Accipitridae also is omnivorous, eating kernels of the oil palm in season (Bannerman, 1930).

MISCELLANEOUS CHARACTERS

Additional characters that were investigated, but which yielded little information concerning the phylogenetic affinities of the groups under consideration include: carotid arteries (Glenny, 1955); vestigial wing claws (Fisher, 1940); the sclerotic ring (Curtis and Miller, 1938); the tongue (Garner, 1925), although the tongues of herons and storks are extremely different; mallophagans (Clay, 1951); intestinal convolutions and caeca (Beddard, 1910); egg color and clutch size; incubation and nestling periods; courtship behavior; and plumage color and patterns, although in the storks and vultures there are basically only two plumage colors, black and white.

DISCUSSION

The groups here considered may represent some of the more striking examples of convergence to be found in the class Aves. The two orders involved are quite likely polyphyletic, each perhaps being composed of three or four groups. Cottam (1957) stated: "The Ciconiiformes is basically a less uniform group than the Pelecaniformes. Osteologically, it seems to be a collection of unrelated groups which, superficially, only have long beaks, long necks and long legs in common." Jollie (1953), in discussing the Falconiformes, concluded: ". . . it is made up of four undoubtedly unrelated groups (Cathartidae, *Sagittarius,* Accipitridae-Pandionidae and Falconidae) and perhaps a fifth (Pandionidae)."

The major pieces of osteological evidence indicating a relationship between storks and vultures include characters of the skull, humerus, carpometacarpus, femur, tibiotarsus, and tarsometatarsus. The primary non-bone characters further indicating this relationship are: tendons of the patagium, thigh muscle formulae, nestling plumage, poor development or absence of a syrinx, and absence of intrinsic syringeal muscles. The extreme anatomical dissimilarities of herons

and storks, and of vultures and accipitrids force one to conclude either
that anatomy does not reflect phylogeny or that these members of the
orders Ciconiiformes and Falconiformes are not at all closely related.
Most of these differences have been known for many years, but their
significance has not been faced and the problem has been resolved by
placing these convergent but basically very different groups in different
suborders within the same order. Both the statements of Beddard (1898)
and Jollie (1953), quoted earlier, demonstrate the overriding effect
that external or superficial appearances have had on higher bird
classification. Cottam's (1957) proposal that *Balaeniceps* is allied to the
pelecaniforms rather than to the Ciconiiformes is an example of a
recent attempt to rectify this situation.

<center>CONCLUSIONS</center>

From the evidence presented here, I conclude that the following
taxonomic arrangement more accurately expresses the relationships of
the groups here considered than those in general use today. The posi-
tion of the other families of the Ciconiiformes and Falconiformes as
presently constituted, as well as the orders Pelecaniformes and Pro-
cellariiformes, should be re-examined before being included in this
system.

Order Ardeiformes
   Suborder Ardeae
      Family Ardeidae
Order Ciconiiformes
   Suborder Ciconiae
      Family Ciconiidae
   Suborder Sarcoramphi
      Family Vulturidae
Order Accipitriformes
   Suborder Accipitres
      Family Accipitridae

<center>SUMMARY</center>

1. Although it has long been known that there are many basic differ-
   ences between the Cathartidae and Accipitridae, and between the
   Ardeidae and Ciconiidae, they have been retained in the same
   orders, Falconiformes and Ciconiiformes, respectively.
2. The many and often striking anatomical similarities of the New
   World vultures and storks, coupled with other lines of evidence,

indicate that they are more recently derived from a common ancestor than are vultures and accipitrids, or storks and herons.

3. Evidence supporting this conclusion includes: osteological characters, especially of the skull and several of the long bones, natal plumages, myology, patagial tendons, and absence of syringeal muscles in both groups.

4. Extreme cases of convergence are indicated by the superficial similarity, especially in proportions, of the herons and storks, and of Old and New World vultures. As stated above, anatomical investigations do not support these apparent similarities.

5. A taxonomic arrangement that more nearly shows the phylogeny of these groups would place the herons and storks in separate orders, the vultures and accipitrids in separate orders, and the storks and vultures in the same order, being separated at the subordinal level.

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