

The coracoid sulci are peculiar in their depth and narrowness. The dorsal margins of the sulci have distinct, anteriorly facing coracoid pads, correlated with the reduced posterior flange of the coracoid.

In *Herpetotheres* there are large, separate, lateral processes, while *Micrastur*, *Milvago*, *Polyborus*, and some species of *Falco* have these processes moved toward the midline; a single median dorsal spine is found typically in *Falco* (fig. 166). These processes are produced by ossifications in the origins of the *supracoracoideus* muscles. Small lateral processes are indicated in *Spizapteryx* along with a median one.

The sternocoracoid processes jut upward, out, and forward and end bluntly. The sternocoracoid fossa is like that of the accipitrid. The costal margin has five to six distinct rib articulations separated by pneumatic fossae (fig. 167). The

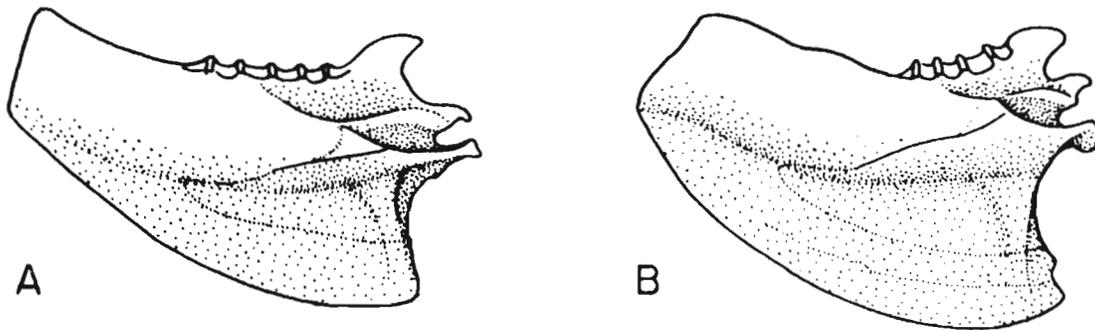


Fig. 167. Lateral views of sterna of A. *Falco mexicanus*, B. *Herpetotheres cachinnans*.

sternal plates are cupped anteriorly for the viscera but are flat posteriorly. The posterior margin is square; it may be complete, or have a pair of fenestrae or notches (fig. 168).

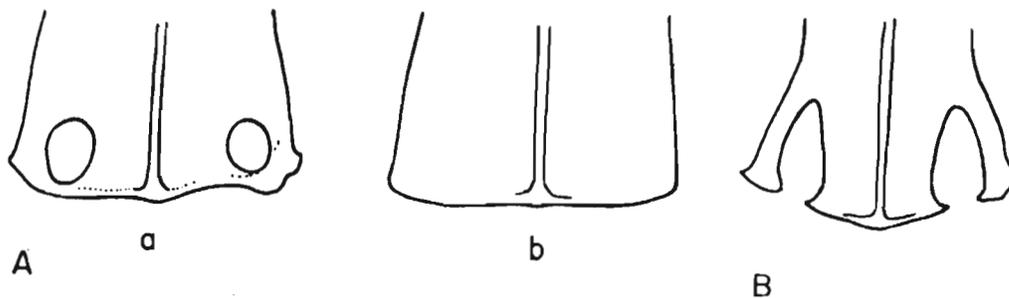


Fig. 168. Ventral views of posterior part of sterna of A. *Falco mexicanus*, two specimens (a and b); B. *Microhierax caerulescens*.

The keel is thin; it is usually deepest along its anterior pillar. In outline it is roughly triangular with the anterior margin jutting slightly or distinctly forward and showing only a

slight curve along the line of junction of the carina and lateral plates. It tapers to its terminus on the posterior margin. *Herpetotheres* and *Micrastur* show an uptilting of the anterior end of the keel like that of the accipitrid.

The *supracoracoideus* scar is regular in outline and extends from one-half to three-fifths of the length of the sternum. Its ventral margin is well separated from that of the keel (thick pectoralis muscle). The outer tip of the coracoid is not braced by a ligament as in the other groups; therefore, at the point where the sternocoracoid fossa and the lateral line of the *supracoracoideus* muscle intersect there is a distinctive, scarless, triangular area (fig. 167).

The falconid sternum can be characterized as follows: anterior dorsal margin with a single medial dorsal process, or two lateral ones, incompletely or slightly separated; coracoid sulci deep and narrow and extensively lapped; coracoid pads reduced to anteriorly facing contact lines; ventral margin of the sternocoracoid fossa lacking a ligament scar; a delimited triangular area between the sternocoracoid fossa and the *supracoracoideus* scar. Subgroups cannot be characterized.

#### Summary and Conclusions

The sternum, like the shoulder area, shows such irregular variations from group to group that one wonders whether adaptive or phyletic features are involved. Since the form of the thorax and the pectoral musculature molds the overall shape of this bone, there is little doubt that adaptation is a causative mechanism. However, the consistency of overall body form within a family, and often throughout an order, gives this bone some phylogenetic value. Thus, the differences in myology, tendinal attachments, and ligamental bindings, which differentiate the sterna of the falconiforms appear to correlate as well with ancestry as with adaptive modification.

The cathartid type is not exactly matched in any other bird, but certainly it resembles that of the pelecaniforms, some ciconiiforms, and procellariiforms. If *Teratornis* is assumed to be a highly modified cathartid, then the likeness with these other orders is strengthened. Fisher (1945:728) was aware of the similarity of the sternum of *Teratornis* and *Diomedea* but overlooked the point-by-point agreement with *Fregata*. Not only the sterna but also the coracoids and, to a lesser extent, the entire skeletons of these genera are similar. Such similarity suggests some element of common ancestry rather than adaptive modification for a particular style of flight. (No one would assume that they did, in fact, have a common style of flight.)

The sternum of *Sagittarius* is matched fairly well by that of *Cariama*, but comparison with procellariiforms, pelecaniforms and storks seems more likely. Comparison with the cathartid suggests common ancestry of much the same antiquity as that of the other orders mentioned.

The Accipitrid sternum cannot be used for the identification of subgroups although there have been such attempts in the past. Here again it is necessary to consider the writings of Howard and

Loye Miller in regard to the Aegyptiinae. Howard (1932:49) noted that, "The characters of the sternum of the modern vultures, as distinguished from the eagles, are as follows: (1) broad ventral manubrial spine; (2) low carina; (3) short and broad sternocoracoidal impression."

Figure 169 shows a view of the sternum of *Neogyps* and several of the Aegyptiinae. The coracoid sulci are widely

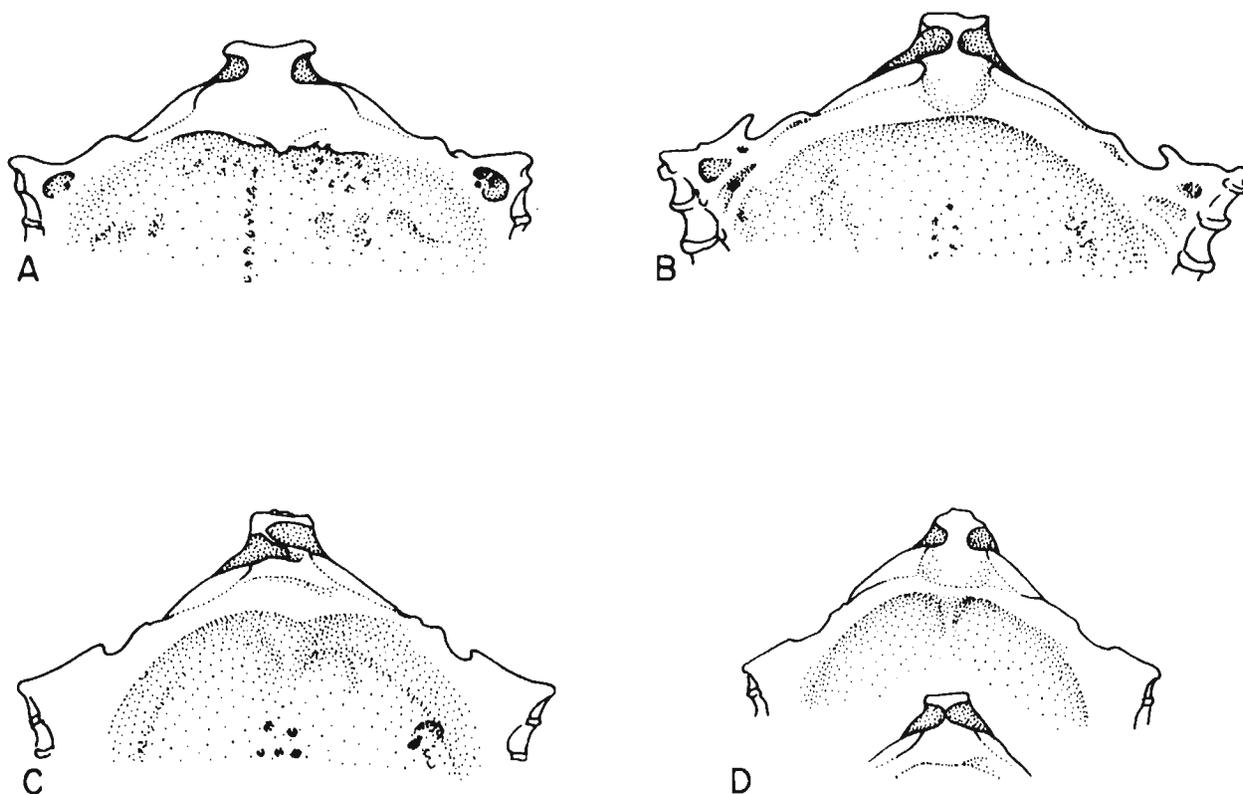


Fig. 169. Dorsal views of anterior part of sterna of A. *Gypaëtus barbatus*, B. *Aegyptius monachus*, C. *Gyps coprotheres*, D: *Neogyps errans* (2 specimens).

separated on the manubrial spine in *Neogyps* (range from well separated to in contact) and *Gypaëtus*; those in *Torgos* and *Aegyptius* are nearly in contact; *Trigonoceps*, *Sarcogyps*, *Neophron*, *Necrosyrtes* show incipient lapping while in *Gyps*, *Pseudogyps*, and *Gypohierax* they are distinctly lapped. *Terathopus* agrees with *Torgos* and *Aegyptius* in this detail. Most accipitrids show well lapped sulci, but in some specimens of *Buteo* and *Leptodon*, they are only slightly lapped. In fossil sterna of *Aquila* it was noted that some showed no lapping and every transitional phase to that found in the modern species. On the bases of breadth of manubrial spine and small size of the anterior inner process on the

sternocoracoid process *Leptodon* compares well with the aegyptin.

The relative depth of the carina is difficult to evaluate. That of *Neophron* or *Gypohierax* can be included in the range of variation found among the typical accipitrids, whereas that of *Aquila* is definitely lower than in the majority of genera. *Neogyps* is like *Aquila* in this respect and it resembles that genus in almost every way.

Howard's last point on the relative size of the sternocoracoid impression overlooks the very small fossa of *Pandion* and the overlapping series from *Aquila* through *Necrosyrtes*, *Gypohierax*, *Neophron*, and *Neophrontops* to that of the large aegyptins.

A more characteristic feature of the sternum of the Aegyptiinae is the form of the *supracoracoideus* scar. This is lobed along its posterior lateral margin, and the ventral (medial) margin lies close to the edge of the keel. The shape of the scar in *Torgos* is determined in part by the *pectoralis* muscle. *Neophron* tends toward the aegyptin outline, whereas *Neophrontops* and *Gypohierax* are similar to the typical accipitrid; i.e., they lack the lobe. *Terathopius* agrees with the aegyptins in this character as does also *Sagittarius*. A type of sternum, limited to the subfamily Aegyptiinae, cannot be characterized by any one feature or combination of features, unless the species content of that subfamily is altered. The latter step would necessitate removal of *Neogyps*.

The falconid sternum superficially resembles that of the accipitridae, and it does not find a better comparison elsewhere. However, this does not require a common ancestry for these two families as the comparison is still poor. The sternum of these two families, thus, gives no clue to their ancestry, at least at this reading.

#### OSTEOLOGY--MISCELLANEOUS SKELETAL PARTS

Under this title the vertebral column, pelvis, humerus, ulna, manus, tibiotarsus, fibula, and foot will be considered, more by discussing features reported in the literature than in attempting to delineate and evaluate new ones. Since any of the above can be described rather briefly the types characterizing the families of the falconiforms will be discussed together.

##### Vertebral Column

According to Beddard (1898:115), the total number of vertebrae in the spinal column of birds varies from 39 to 64, counting the pygostyle as one (based upon Giebel, 1866). According to Parker (1890:17), "More than half of the *twelve thousand* species known have, on an average, only *forty* vertebrae, even in the embryo. The African ostrich has *fifty-six*, and the common swan, *sixty-three*. Numerical law is not very strict in birds; yet those six thousand species just mentioned have in a great majority just *fourteen* cervicals....*Twelve* also is a common number for the *avian sacrum* in the small high-type birds; and from ten to twelve vertebra in the caudal region is as a rule the number in the embryo." The total number of vertebrae in the falconiforms,

not including the pygostyle, varies from 39-41 among the cathartids, from 37-41 (usually 40) among the accipitrids, 40 in *Sagittarius*, and 39-41 (usually 40) among the falconids.

Ordinarily the vertebral column is divided into a series of artificial segments: cervical, thoracic, lumbar, sacral, and caudal (fig. 170). The cervical vertebrae are those of the neck region, which extend posteriorly to (but not including) the vertebra bearing the first complete rib. Thoracic vertebrae begin with the first complete rib and extend posteriorly to that vertebra bearing the last (floating or vestigial) rib. The lumbar bear no ribs and continue the series to the sacrals, which purportedly support the pelvic girdle. The caudals extend posteriorly from the sacrals (but may be indistinguishable from them) to the tip of the tail, the terminal caudal vertebrae fuse into a pygostyle. Part of the thoracic series, the entire lumbar, and sacral series and part of the caudal vertebrae are fused into the synsacrum (Table 12, fig. 173).

Information on the brachial and pelvic plexuses supplies an approach to comparisons of the segments of the body in the different falconiforms. Figure 171 shows diagrammatically the distribution of the brachial roots in relation to the cervical and thoracic vertebrae as based on ribs; Figure 172 indicates the roots of the pelvic plexus. Homologizing nerve roots necessitates criteria such as thickness, main apparent pathway of fibers, and detailed similarities between related forms. Using these criteria, comparable roots have been blackened in the figures and the resulting segments of the body have been summarized in Table 13.

*Sagittarius*, the Accipitridae, and the Falconidae are found to agree in having 14 vertebrae in front of the brachial root and nine between this root and the pelvic one--the exceptions among the accipitrids being highly specialized forms in which these numbers are modified. One can conclude that the number of cervicals, based on the position of the brachial nerves, is 14. Modification of the number of cervicals involves displacement of the pectoral appendage posteriorly (a relatively longer neck and shorter body) or an increase or decrease in the number of cervical vertebrae produced during embryonic segmentation (see Goodrich, 1930:137-142); the former is the more probable.

Among the accipitrids there are one to three incomplete cervical ribs; the usual number is two. In most species the first cervical rib is a short, triangular segment with both tubercular and capitular articulations. Occasionally this vestige may be fused to the vertebra and thus removed from the list of ribs; such may be the case in *Gymnogenys* and *Elanus*. The second cervical rib is well developed, tapering distally to a point. In *Gymnogenys* the second rib (assuming the above) is a small, triangular nubbin like the first cervical of other accipitrids. The first thoracic rib of several specimens of *Ictinia* was incomplete. It is possible that other specimens may have this rib complete.

The cathartids have five or six complete ribs, plus an

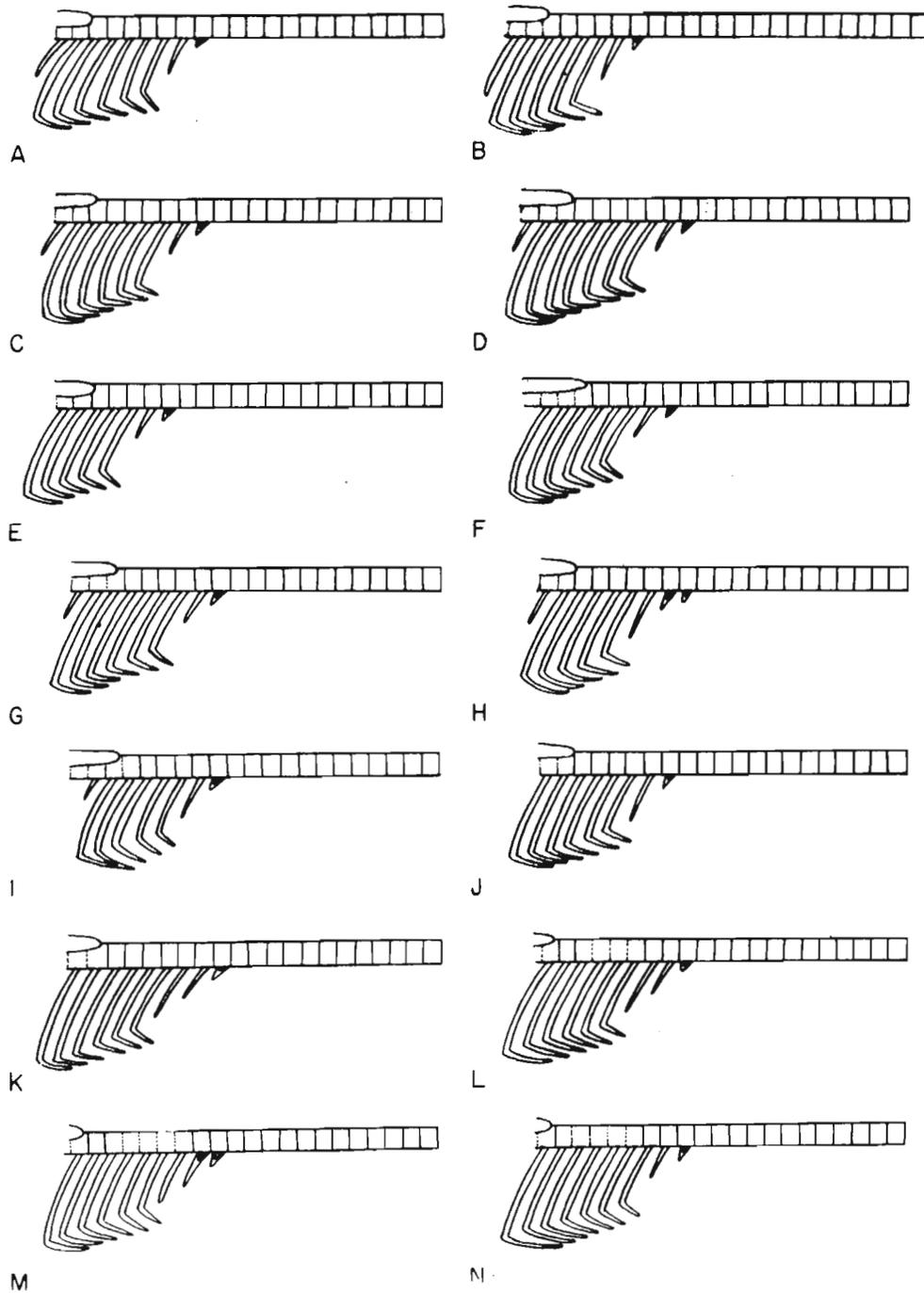


Fig. 170. Segmentation of the prepelvic portion of the vertebral column in A. *Cathartes aura*, B. *Gymnogyps californianus*, C. *Sagittarius serpentarius*, D. *Aquila chrysaëtus* (*Buteo*, *Haliaeetus*, *Busarellus*), E. *Gyps coprotheres*, F. *Torgos tracheliotus* (*Aegyptius*, *Pithecophaga*), G. *Elanoidea forficatus* (*Neophron*), H. *Ictinia mississippiensis*, I. *Chondrohierax uncinatus*, J. *Pandion haliaetus* (*Pernis*, *Harpia*), K. *Herpetotheres cachinnans* (*Micrastur*), L. *Ieracidea berigora* (*Polyborus*, *Milvago*, *Microhierax*, most species of *Falco*), M. *Falco columbarius*, N. *Falco columbarius* (MVZ 15631).

Table 12. The number of segments in each region of the vertebral column for selected species of each of the basic types. In some cases there is a range of variation, the more common number is underlines

	number of cervicals	number of cervical ribs	complete thoracic ribs	number of segments in synsacrum	number of synsacral ribs	number of ribs articulating with sternum	number of free caudal vertebrae	total segments
Cathartid								
Cathartes aura	15	2	4	14- <u>15</u>	<u>1</u> -2	5	<u>5</u> -6	39
Cathartes urubitinga	15	2	4	14	<u>2</u>	5	<u>6</u>	39
Vultur gryphus	17	2	3		2-3	5-6	<u>5</u> -6	
Gymnogyps californianus	18	2	3	14- <u>15</u>	<u>2</u> -3	5-6	<u>5</u> -6	41
Sagittariid								
Sagittarius serpentarius	15	2	3	15-16	2-3	6	5-6	39
Accipitrid								
Pandion haliaetus	15	2	4	15	2	6	6	40
Aviceda cuculoïdes	14		4	13			7	38
Pernis apivorus	15	2	4		2	6	7	
Chondrohierax uncinatus	14	2	3	13	<u>2</u> -3	4	7	37
Leptodon palliatus	13	2	4	13	2	5	7	37
Elanoïdes forficatus	14	2	5	14	2	6	6	39
Elanus leucurus	14	2	5	13	1	6	7	39
Ictinia missippiensis	15	3	4	13	<u>1</u> -2	5	7	39
Rostrhamus sociabilis	14	2	5		2	7	6-7	
Gymnogenys typicus	14	1	5		2	6	7	
Machaerhamphus alcinus	14	2	5	14	2	7	7	40
Milvus migrans	14	2	5	14	2	7	7	40
Haliaeetus leucocephalus	14	2	4-5	14-15	2	7	7	40
Gypohierax angolensis	15	2	4-5		1	6	7	

Gypaëtus barbatus	15	2	4	14	2	6	5-7	
Neophron perenopterus	14	2	4		<u>2-3</u>	6		
Haematornis cheela	14	2	5	14	2	7	7	40
Terathopius ecaudatus	15	2	4	16	<u>2-3</u>	6	6-7	
Torgus, Aegyptius	15	2	3	15-16	3	6	6	40
Gyps, Pseudogyps	17	2	3	15	2	5	5-6	41
Necrosyrtes monachus	15	2	4	14	2	6	5-6	
Harpia harpyja	15	2	4	15	2	6	7	41
Pithecophaga jefferyi	14	2	4		3	7	7	
Aquilins and Buteonins	14	2	5	14	2	7	7	40
Falconid								
Herpetotheres cachinnans	15	3	4	14	2	6	6	40
Micrastur semitorquatus	15	3	4	13	2	6	7	39
Milvago chimachima	15	3	5		1	6	7	
Polyborus cheriway	15	3	5	13	2	5	7	40
Microhierax caerulescens	15	3	5		1	5	7	
Falco mexicanus	15	3	5	12-13	1	6	7	39-40
Falco columbarius	15	3	5		1-2	6	7	
Falco columbarius	14	2	5		<u>1-2</u>	7	7	

\* \* \* \* \*

additional vestigial rib posteriorly. The number of thoracic ribs not included in the synsacrum ranges from three in *Gymnogyps* and *Vultur* to four in *Cathartes*. The last genus has two full synsacral ribs and the former genera have two or three. All may have an additional vestigial rib.

*Sagittarius* has two cervical and five or six complete thoracic ribs; there is a vestigial seventh rib in some specimens. Two of the normal complement of thoracic ribs, plus any vestigial seventh, articulate with the synsacrum. *Sagittarius* resemble the large aegyptiins (and *Cariama*) in its thoracic structure.

Usually the accipitrid has seven complete thoracic ribs, two of which articulate with vertebrae fused into the synsacrum. Occasionally there is an eighth (posterior) rib, and it may be complete or vestigial. The extreme is reached in *Buteogallus* (MYZ 85546), which has a ninth, vestigial costal segment and *Busarellus* (MVZ 85549), which has both vertebral and costal segments of that rib. The number of ribs is reduced among the aegyptiins, certain kites, *Pandion* and *Harpia* (see Table 12). Reduction reaches its extreme in *Gyps*, which has but five full ribs; two of these articulate with the synsacrum.

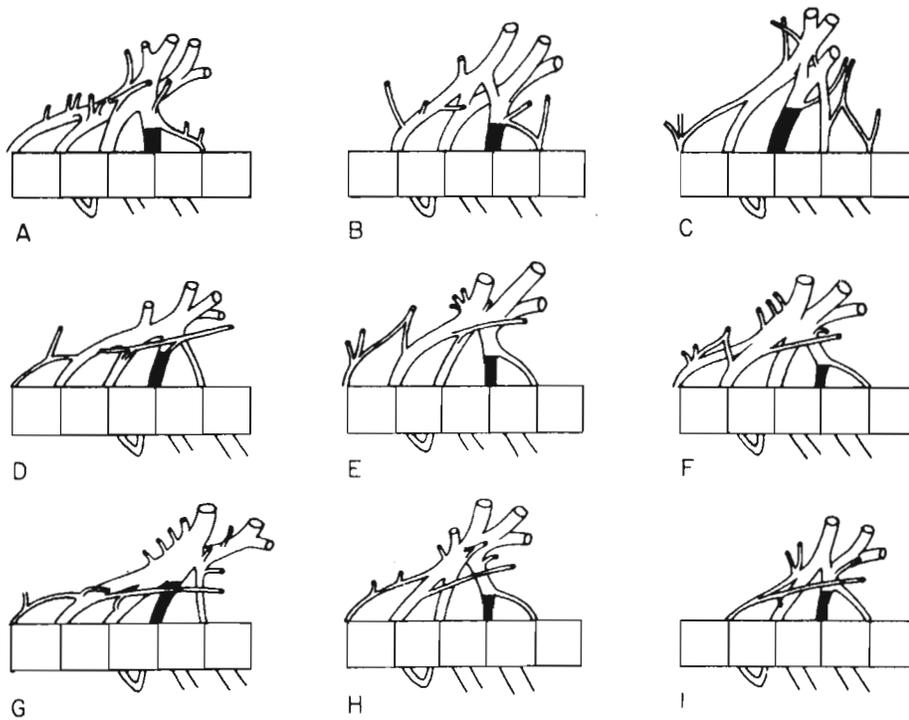


Fig. 171. Roots of the brachial plexus of A. *Cathartes aura*, B. *Coragyps atratus*, C. *Sagittarius serpentarius*, D. *Aviceda subcristata*, E. *Buteo jamaicensis*, F. *Torgos tracheliotus*, G. *Pandion haliaetus*, H. *Polyborus cheriway*, I. *Falco sparverius*. Key root shown in black.

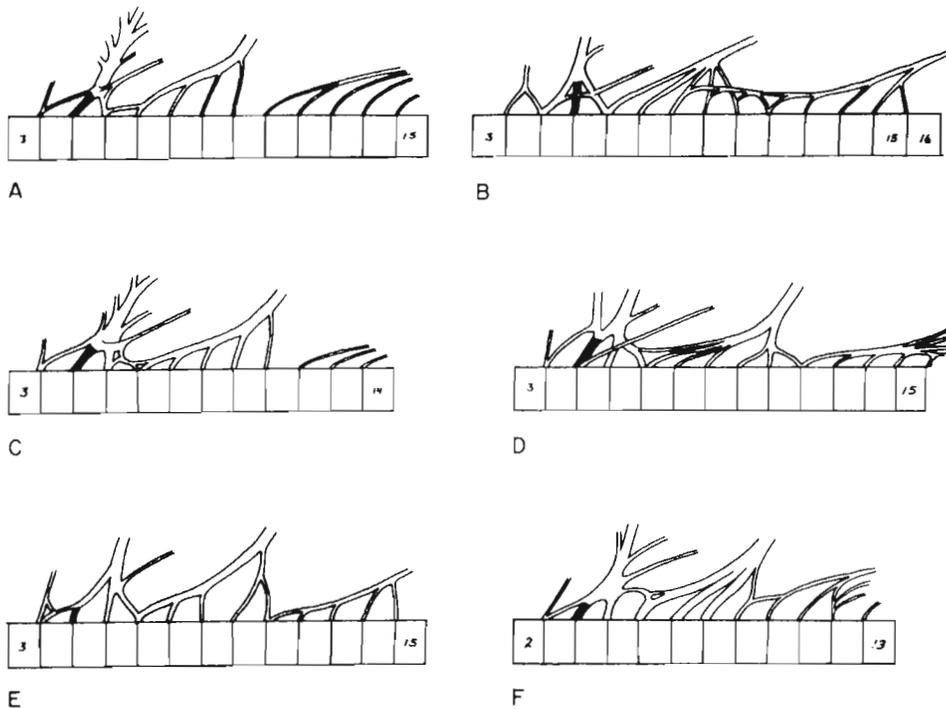


Fig. 172. Roots of the pelvic plexus of A. *Cathartes aura*, B. *Sagittarius serpentarius*, C. *Buteo jamaicensis*, D. *Torgos tracheliotus*, E. *Pandion haliaetus*, F. *Falco sparverius*. Key root shown in black.

Table 13. The number of segments in each region of the column for selected species of each of the basic types, based on the position of the main brachial and femoral nerves. In one case there is a range of variation, the more common number is underlined.

	number of vertebrae anterior to main brachial nerve	number of vertebrae between main brachial and main femoral nerve	number of vertebrae posterior to main femoral nerve
Cathartid			
Cathartes aura	15	8	16- <u>17</u>
Coragyps atratus	15	8	<u>16</u>
Sagittariid			
Sagittarius	14	9	16
Accipitrid			
Pandion	14	9	17
Aviceda			
subcristata	13	8	16
Chondrohierax			
uncinatus	14	8	16
Buteo			
jamaicensis	14	9	17
Haliaeetus			
leucocephalus	14	9	17
Necrosyrtes	15	8	17
Torgos	15	8	17
Falconid			
Falco			
sparverius	14	9	17
Polyborus			
cheriway	14	9	17

\* \* \* \* \*

The falconids have three cervical ribs (actually two true cervicals and one thoracic as indicated in Table 13). The total number of complete ribs is generally six or seven. Eight ribs occur in a few specimens of *Falco*, but in one specimen of *Falco mexicanus* a ninth, vestigial rib was noted.

Sushkin (1905:38) pointed out that in the falconid the gap between the transverse processes of the thoracic vertebrae is equal to or less than the width of the processes, whereas in the accipitrid the space is more than double the width of the processes. Measurements, summarized in Table 14, indicate that his views are largely true. The particular specimen of *Micrastur* cited has the widest gap of the falconids examined, whereas *Spizaetus ornatus* is peculiar in the great width of its transverse processes. Further, the falconids, with the exception of *Herpetotheres* and *Micrastur*, have four (or five) of the thoracic vertebrae fused. There is some variation as to which vertebrae are involved and their relationship to the pelvis (fig. 170).

Among the accipitrids and falconids there are usually seven free caudals (exclusive of the pygostyle); occasionally five or

Table 14. Relative widths of the transverse processes of thoracic vertebrae in the accipitrid and falconid.

	a	b	a/b
	width of transverse process in mm.	gap width between processes in mm.	
Herpetotheres			
cachinnans	3.5	4.0 - 4.5	77.7 - 87.5
Micrastur			
semitorquatus	3.8	5.0 - 5.2	73.0 - 76.0
Spizaetus ornatus	4.3	6.6 - 6.8	63.2 - 65.0
Aquila chrysaetos	4.3	10.0 - 12.0	35.8 - 43.0
Heterospiza			
meridionalis	2.7	7.2 - 7.7	35.0 - 37.5
* * * * *			

six are found or rarely eight. The number of free caudals varies because of the inclusion of one in the syncacrum or fusion with the pygostyle. This is particularly marked in the cathartids where if there are 14 segments in the syncacrum, there will be six free caudals (one may be fused to the pygostyle); if there are fifteen syncacra, there will be five caudals. *Sagittarius* is like the cathartid in the number of free caudals.

The pygostyle is made up usually of five units, the last three of which cannot be detected in the adult bone; the first two units may be clearly marked. A caudal vertebra may be partially or almost completely fused to this structure.

Associated with the pygostyle in most falconids is an accessory ossification at the insertion of the *depressor coccygis* muscles (see Table 18). According to Sushkin (1905:74) this ventral coccygeal sesamoid is found in all of the falconids except the polyborinae, Polihieracinae and "Harpie" [*Falco novaeseelandiae*]. Sushkin believed that this sesamoid is correlated with the strong tail musculature needed for "steering" among the falconids. Pycraft (1910:339) viewed it as a brace for the tail feathers when they are used to check the rush of flight. Among the accipitrids and cathartids the amount of connective tissue here is much less than in the falconids and no ossification takes place.

The development of the free caudal vertebrae, and pygostyle corresponds with the use of the tail. Minimal development is observed in *Terathopius* where the tail is short and small.

Beddard (1898:115) concluded that, "The number of vertebrae...is not of the faintest use for the systematic arrangement of existing forms," however, the cervical or caudal number have some value--although it is probably never a sharp or absolute one. In the case of the falconiforms the falconid type is differentiated on the basis of the number of "cervicals" and the fusion of thoracic vertebrae anterior to the pelvis. The cathartid is marked by the increased number of cervicals, which is matched only in aberrant genera of the accipitrid. The sagittariid is like the cathartid in the apparent number of cervicals but like the accipitrid and falconid in the true number. It differs from the latter in the number of "cervical" ribs.

### Pelvis

The pelvis is formed by the fusion of a number of vertebrae, the synsacrum, with the bones of the pelvic girdle. The segments of the synsacrum are exceedingly difficult to count in some adult birds, but the number of spinal nerves observed in the flesh makes such a count simple (fig. 173). In the natal or early nestling the segments are well marked, fusion occurring late in the growth period. The pelvis may undergo a degree of folding during development, which tends to obliterate any ventral trace of certain segments. The number of vertebrae in the synsacrum in the cathartids is usually 14, but a fifteenth can be added from the caudal series. The accipitrids usually have 14, some kites have 13, and some of the aegyptiins and *Pandion* have 15. *Sagittarius* has 15 or 16, depending on the inclusion of a caudal. Among the falconids, *Falco* and *Microhierax* have 12 (*Falco sparverius*, MVZ 54386, appears to have 11) or 13; the Polyborinae have 13, and *Herpetotheres* is alone in having 14. Variation in number in the cathartids and the aegyptiins involves not only the inclusion of a caudal but also forward extension of the ilia to add a thoracic. Normally the anterior margin of the ilium is even with the anterior face of the first synsacral, but in these vultures this margin extends to the middle of the added vertebra, which may be firmly fused into the synsacrum or remain free.

The synsacrum is functionally equivalent to the sacrum of the mammal, although it is made up of a much greater number of units, some of which bear ribs. The attempt to distinguish parts of this series as thoracics, lumbar, "sacrals," and caudals can be viewed only as artificial. In the development of this structure there is no clue as to the presence of "true" or "primary" sacrals. The entire structure is involved in support of the pelvic girdle with the exception only of partially included, unfused, thoracic or caudal vertebrae.

Viewed ventrally the segments of the synsacrum show varying development of the transverse processes; this is related in part to the kidney. The strongest transverse supports lie anterior to the acetabulum, and the kidney, with secondary supports behind. The latter, usually identified in part as the sacrals, lie embedded in the kidney. Posterior to the kidney are strong supports for the posterior margin of the innominate bone of either side. The supports in the region of the acetabulum may show asymmetric development or reduction.

The number of ribs (i.e., thoracic vertebrae) articulating with the synsacrum varies; it is not uncommon in any species to find one more than the usual number.

In the developing pelvis there is a fenestra between each of the transverse processes. Anteriorly these tend to become covered by medial extension of the ilia; posteriorly they may be closed by bone growing inward from the margin. Closure appears to result from the downward rotation of the posterior part of the innominate bones and the consequent shift in origin of the *levator coccygis* and *levator caudae* muscles. The strongly fenestrated pelvis has a straighter dorsal outline of the innominate bones and the anterior ends of these muscles reach forward beneath the

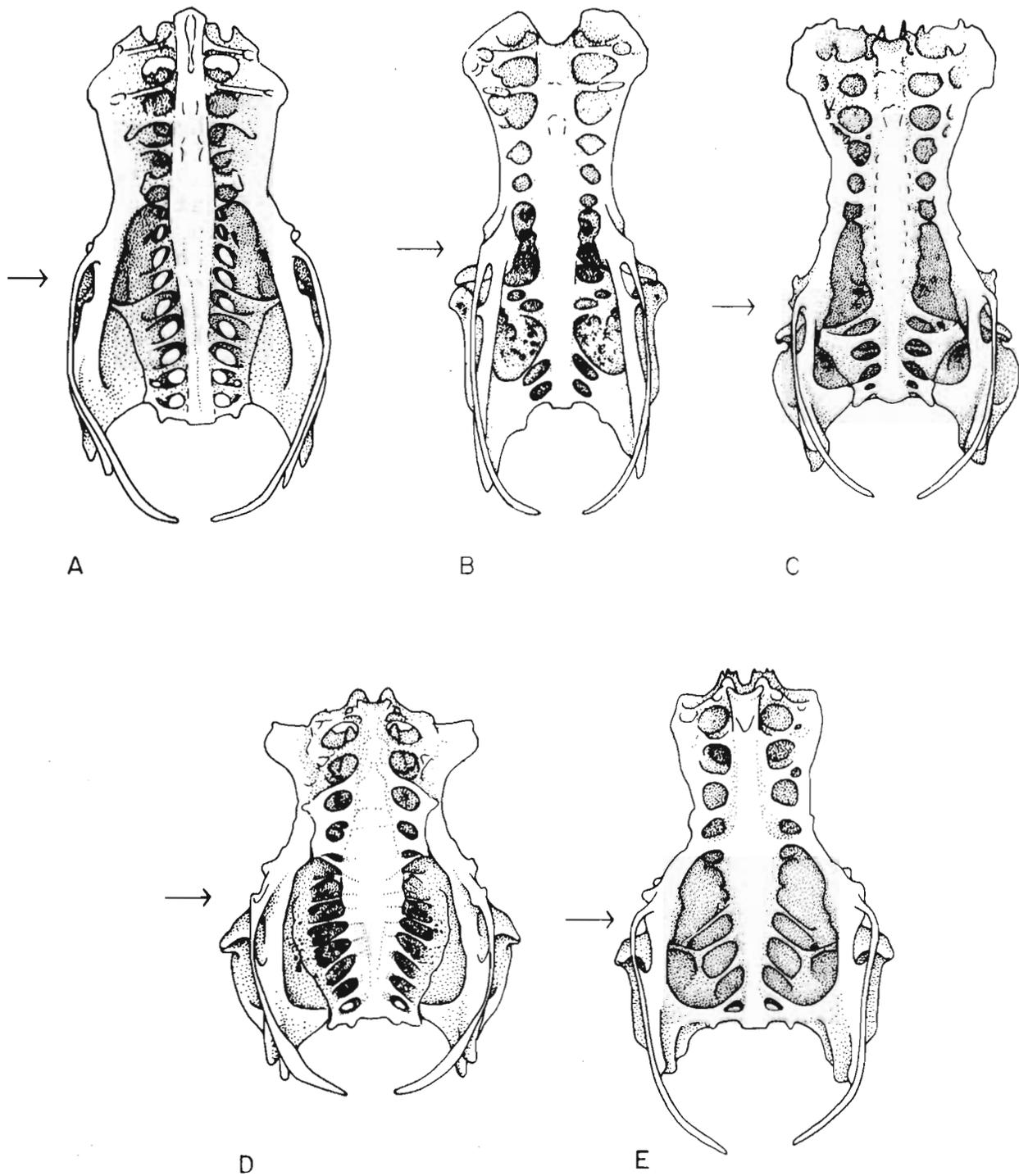


Fig. 173. Ventral views of pelves of A. *Cathartes aura*, B. *Sagittarius serpentarius*, C. *Buteo jamaicensis*, D. *Pandion haliaetus*, E. *Falco mexicanus*. Arrow indicates level of center of acetabulum.

anterior plates of the ilia (*Coragyps* and *Elanus*--fig. 174).

The "primitive pelvis," that with openings particularly in the posterior half, is found in each group of the falconiforms. Fenestrae range from large (*Machaerhamphus*) to small (*Torgos*, *Aviceda*, *Leptodon*, *Chondrohierax*, *Ictinia*, *Gymnogenys*, and *Geranospiza*) among the accipitrids, although usually they are lacking as most species have a strong downward curve of the axis. Far posterior pairs of fenestrae may be found in practically any species as a correlate of age or the degree of ossification reached in the individual. Fenestrae are usually lacking in the falconid but appear in *Polyborus*, and some species of *Falco*.

According to Fisher (1946:641), "The height of the (synsacral) vertebrae in the Cathartidae diminishes rapidly posteriorly. The decrease in the height is much more gradual in the hawks and eagles." *Chondrohierax* equals the reduction shown in *Cathartes*, whereas the synsacrum of some of the aegyptiins or *Sagittarius* may exceed it (fig. 175).

Lying lateral to the synsacrum, and showing varying degrees of fusion with it, are the innominate bones formed by the fusion of the ilia, ischia, and pubes. The ilium lies dorsally and extends the entire length of the pelvis. Anteriorly it is a thin spoon-shaped plate lying at an angle. This anterior hollow is the area of origin of the *gluteus medius* muscle, while the dorsal crest marks the origin of the *tensor fascia latae* (see section on myology for muscle names). Posteriorly the dorsal crest has been drawn out as the line of origin of the *iliofibularis*; it overhangs the ilioischic fossa from which the *obturator internus* arises. This fossa is margined anterodorsally by the antitrochlearis mass and anteriorly by the column of the fused acetabular portions of the ilium and ischium.

In the anterior half of the pelvis the ilia meet for a short distance along the midline above the synsacrum. Viewed laterally the dorsal outline in this region of meeting is flat, but in the genus *Aquila* and other powerful forms (*Spizaëtus*) it is distinctly arched (fig. 176). Arching of this crest reaches its extreme in *Sagittarius*, *Spizaëtus*, and *Micrastur*; in the last two genera the form of the crest may be correlated with a narrow pelvis. In *Sagittarius* it appears to be associated with the cursorial habit. Posteriorly the dorsal margin of the ilium angles downward. This slope is strongest in the powerful predators and least in the kites and scavengers.

Posteriorly, the ilium may not be fused to the synsacrum. The cathartids (with the exception of *Vultur*) and accipitrids have a distinct crack along this line of junction (fig. 174). *Sagittarius* shows complete fusion here as do also the falconids.

Viewed from above, the lateral outline of the posterior iliac crest varies due perhaps to the influence of the *iliofibularis* muscle. Among the accipitrids the lateral margin is distinctly S-shaped. It curves over the ilioischic fossa, abruptly in at the posterior tip of the ilium, and then out slightly as the margin of the ischium. Lateral extension of the margin is greatest in *Pandion*, which has an extremely broad pelvis; it is least among some of the Aegyptiinae (especially *Neophron*) and in *Leptodon* and

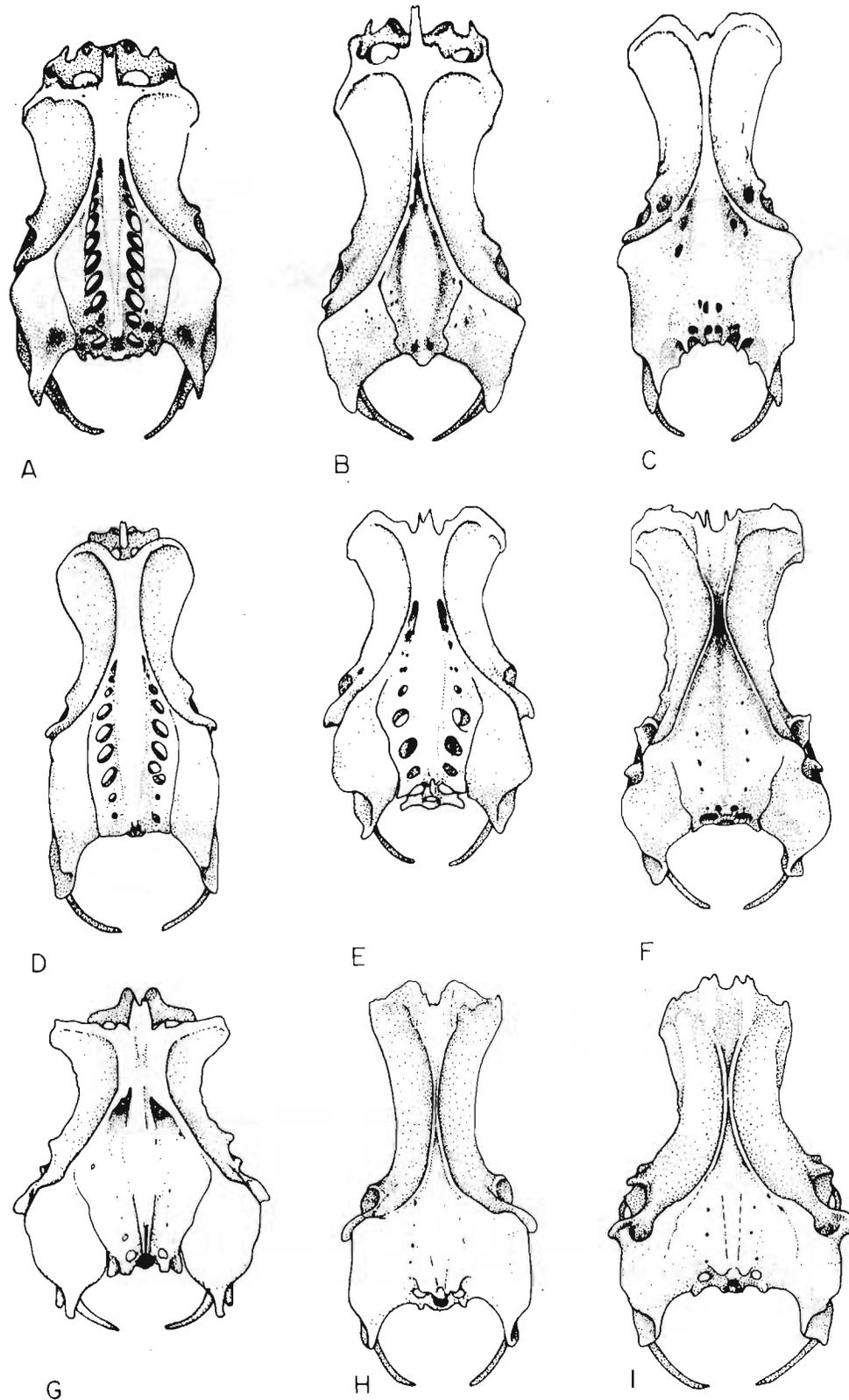


Fig. 174. Dorsal views of pelves of A. *Cathartes aura*, B. *Gymnogyps californianus*, C. *Sagittarius serpentarius*, D. *Neophron perenopterus*, E. *Elanus leucurus*, F. *Buteo jamaicensis*, G. *Pandion haliaetus*, H. *Micrastur semitorquatus*, I. *Falco mexicanus*.

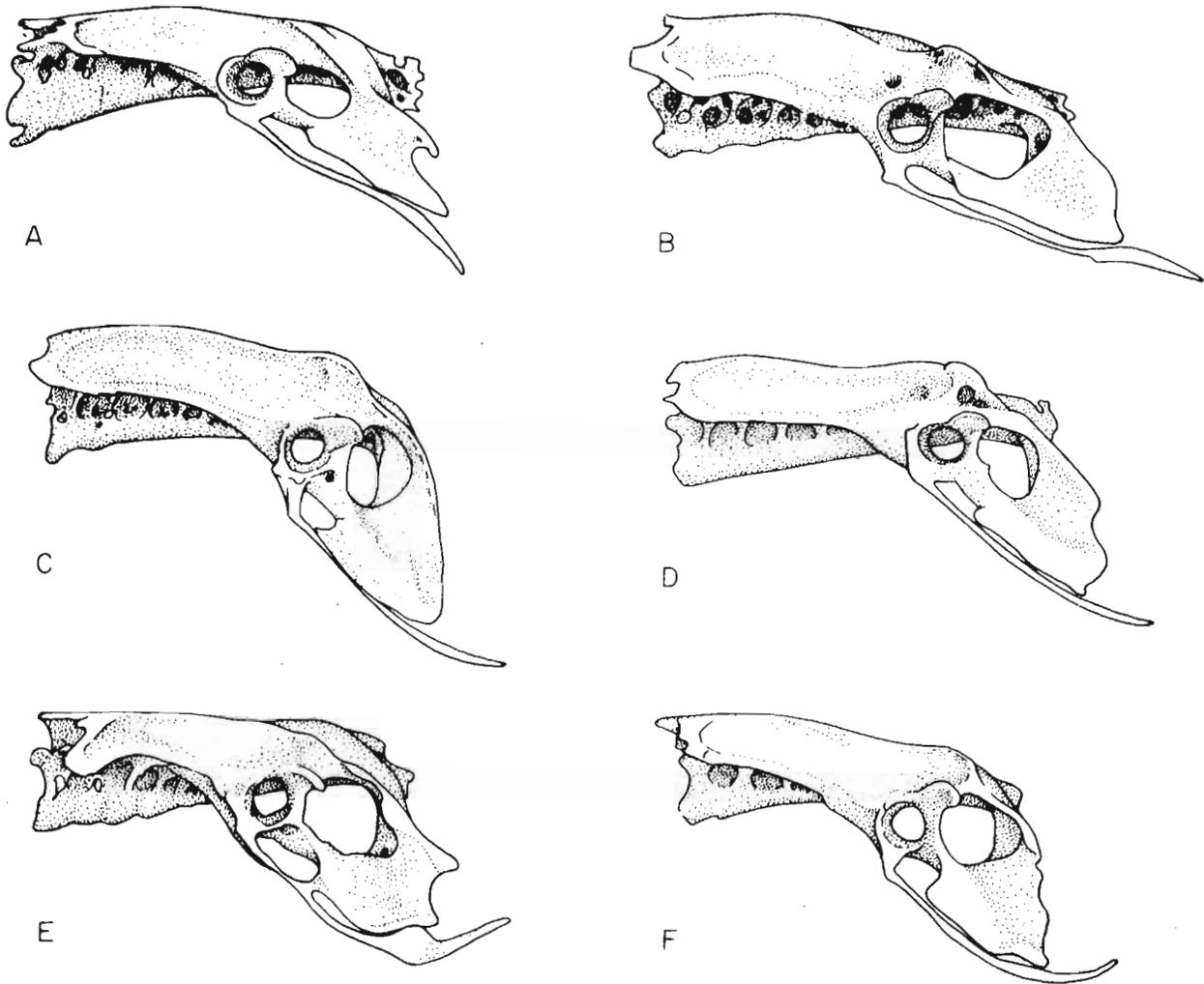


Fig. 175. Lateral views of pelves of A. *Cathartes aura*, B. *Sagittarius serpentarius*, C. *Buteo jamaicensis*, D. *Leptodon palliatus*, E. *Pandion haliaetus*, F. *Falco mexicanus*.

*Chondrohierax*. In these accipitrids the margins are nearly straight and parallel as in the cathartids. Among the falconids the margins are slightly outcurved with the exception of *Herpetotheres*, where they are parallel. *Sagittarius* is unique in that, although these margins are like those of the aegyptiins, they extend far out over the ilioischial fossae.

The depth of the ilioischial fossa is variable; it is deepest in some accipitrids where the posterior dorsal crest of the ilium has been drawn out. It is least developed in the cathartids, aegyptiins, kites, and falconids. *Sagittarius* is peculiar in the overhanging iliac crests (fig. 177).

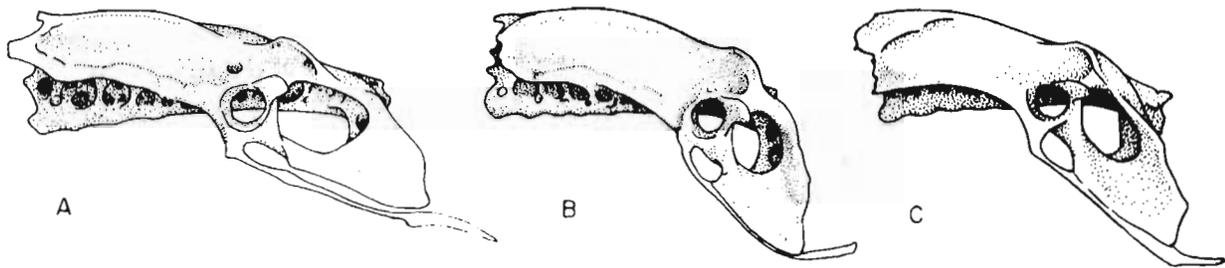


Fig. 176. Lateral views of pelves of A. *Sagittarius serpentarius*, B. *Spizaetus ornatus*, C. *Micrastur semitorquatus*, showing arching of dorsal iliac crest.

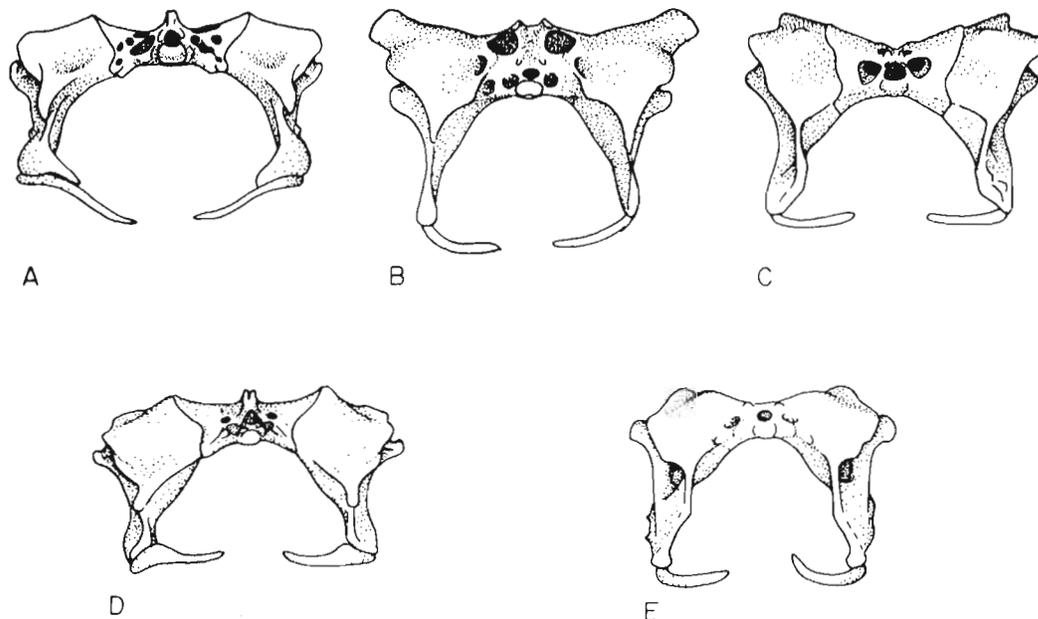


Fig. 177. Posterior views of pelves of A. *Cathartes aura*, B. *Sagittarius serpentarius*, C. *Buteo jamaicensis*, D. *Pandion haliaetus*, E. *Falco mexicanus*.

The ischium arises as a stout backward-projecting pillar at the acetabular circlet and then spreads out as a thin plate, which fuses with the ilium behind the large round ilioischial (ilioischialic or ischiadic) fenestra. Ventrally the ischium lies in contact with or close to the pubis. In most accipitrids, and in some specimens of *Sagittarius*, the fused plate of the ilium and ischium, as viewed laterally, tapers to a rounded point, which

lies next to the pubis (fig. 175). In some specimens of *Sagittarius*, some of the large aegyptiins and in *Leptodon*, *Chondrohierax*, and *Pandion* the posterior margin has a distinct notch. This margin is truncated in the falconid, although certain members of *Falco* may show a wedged form similar to that of the accipitrid. The cathartids stand apart from the others by virtue of a deep irregular notch here.

The pubis is much reduced and appears as a long, ventro-posterior projecting splint attached below the acetabulum. The pubis may be fused or closely bound with the ischium behind the ovate obturator foramen, or these bones may be separated by a puboischiadic gap or fissure (cathartids, *Sagittarius*, *Microhierax*). In some falconiforms a segment of the pubis lying behind the obturator fenestra is lost. *Pandion* is unique in having an extremely widened region that contacts the posterior ventral angle of the ischium, although a somewhat broadened pubis occurs in *Herpetotheres*, *Gyps*, and *Sagittarius*. The posterior tip of the pubis in *Coragyps* is spatulate.

The sagittariid pelvis can be characterized, although it is matched in many details by that of *Cariama*. It resembles the typical aegyptiin in some respects, differing in the arching of the anterior dorsal iliac margins and the overhanging of the posterior margin (or medial movement of ischial and pubic components). The number of vertebral segments exceeds that in the other families (not always the case).

The cathartid series is continuous with the accipitrid but tends to differ in the following ways: weak transverse processes at the posterior limit of the acetabulum, pouched posterior margin of the ilioischiac fenestra (which is either pneumatic or unpouched in the accipitrid), heavy rectilinear form with straight lateral margins to the posterior part of the ilium, and a distinct deep notch along the posterior margin at the junction of the ilium and ischium. The pelvis of the cathartid is most closely approached by those of some kites and aegyptiins.

The accipitrid series is discontinuous and varied. The cathartid-like pelvis of kites and aegyptiins, the narrow pelvis with sweeping lateral curves of the more powerful members, and the broad perforated type of *Pandion*, *Elanus*, and *Machaerhamphus* tend to confuse rather than clarify. The most peculiar pelvis is that of *Pandion*, which can be included in the accipitrid series only in the most general way; it is as distinctive as the sagittariid or falconid.

The falconid pelvis resembles the accipitrid, differing only in the type of postacetabular transverse processes and the fusion of these with the posterior extension of the ilium. The number of segments is generally less than that of the accipitrid.

The form of the pelvis appears to be correlated in some cases with adaptive modifications. Those forms which are more cursorial (or use the legs in diving) have relatively narrow pelvises of rectilinear outline (lacking strong curves). This shape also can be partly correlated with powerful, grasping feet--the preacetabular portion is proportionally longer and narrower, whereas the

posterior margins are broad and strongly incurved. Those which are less cursorial have very broad pelves, even though the legs may be powerful as in *Pandion* (see Pycraft, 1910:390-392. The tinamou pelvis does not fit into the above; nor does the similarity of the pigeon pelvis to that of the tinamou help in understanding the variations of this bone.

Since these correlations are not very exact, the pelvis can be of taxonomic value only at the extremes of the taxonomic hierarchies. At one extreme, it is possible that the separation, or near separation of the ilium, from the ischium identifies the palaeognaths (palaeopelves) in contrast to the neognaths (neopelves) in which these bones are always broadly fused. At the other extreme, closely related genera or species should share similar pelves. At the family or order level only suggestive similarities supporting interrelationship are wanting.

#### Humerus

It has been suggested that the humerus of the bird might be of taxonomic value (Simpson, 1946), but as yet a study of its variation has not been made (McDowell, in Mayr and Amadon, 1951:9, has based broad taxonomic conclusions on it, see also Berger, 1957:240, 266-267). Some fossils have been described on the basis of this bone.

The type specimen of the Pliocene cathartid, *Sarcoramphus kernensis*, is a somewhat crushed fragment of a humerus (Miller, 1931). The specimen certainly resembles this bone of the modern species, *S. papa*, particularly in the possession of a prominent rounded tubercle at the distal end of the deltoid crest. In the living species this tubercle is the point of insertion of a strong tendon of the superficial layer of the *pectoralis* muscle. A similar tubercle is found on the humerus of *Chauna chavaria*.

The shape of the humerus is fairly consistent in each of the falconiform groups, but it is unlikely that this bone could be used in an effective characterization of them. *Pandion* is unique among the accipitrids in that there is a deep pit on the anterior aspect of the bone between the distal condyles. The functional significance of this pit is unknown; the *brachialis* muscle arises from it in the same fashion as in the others.

#### Ulna

Howard (1932) attempted to characterize the ulna of the Aegyptiinae and to ally *Neogyps* with it. Regarding *Neogyps*, it is pointed out (p. 53) that, "This similarity is noted particularly in the narrowing of the palmar side of the shaft near the proximal end, and in the relatively short external condyle at the distal end."\*

A comparison of the ulnae of the various genera of the Aegyptiinae reveals no cogent features. The measurements given in Table 15 differ from those made by Howard but indicate the same

\* \* \* \* \*  
\* Howard's terminology differs from that of Fisher (1946); in the figures and text "palmer" and "anconal" are anterior and posterior aspects, "external" and "internal" are dorsal and ventral.

Table 15. Various proportions of the proximal and distal articulations of the ulna and a comparison of the total length of the ulna to the length of the body as measured from the anterior end of the first thoracic vertebra to the anterior margin of the acetabulum.

	Greatest depth through dor. process of prox. end/length of ulna	Width anterior aspect, base of dorsal proc., flat of art./greatest depth through dor. process of prox. end	Width dorsal aspect distal end, across condyle/length of ulna	Width across art. sur- face from vent. proc./ width dorsal aspect distal end, across condyle	Width dorsal aspect distal end, across condyle/length of art. surface	Body length/length of ulna
Neophron perenopterus	10.1	75.5	7.84	87.3	95.0	51.0
Necrosyrtes monachus	9.64	75.3	6.8	106.8	100.7	51.0
Gyps fulvus	8.72	78.4	6.37	99.0	108.8	47.7
Trigonoceps occipitalis	8.33	76.3	6.17	92.0	95.8	47.4
Aegyptius monachus	9.21	76.0	7.18	87.2	95.0	51.2
Gypaëtus barbatus	10.0	72.7	7.1	95.0	114.7	57.2
Terathopius ECAUDATUS	9.2	70.5	6.28	92.0	100.0	59.0
Gypohierax angolensis	9.5	74.0	6.8	92.7	110.0	61.1
Haematornis cheela	10.33	71.4	8.48	95.5	100.0	63.7
Pernis apivorus	11.4	69.2	7.81	100.0	93.8	75.0
Leptodon palliatius	11.2	73.6	8.67	91.8	111.8	80.7

Chondrohierax uncinatus	12.05	8.52	70.7	8.52	97.4	107.2	62.9
Elanoides forficatus	10.25	7.58	73.9	6.78	118.3	89.4	57.2
Ictinia mississippiensis	10.23	7.83	76.5	7.47	100.0	100.0	67.5
Accipiter cooperii	11.13	8.28	74.3	8.86	88.7	103.3	92.8
Circus hudsonius	9.7	7.25	74.7	7.45	98.7	101.3	72.5
Haliaeetus leucocephalus	9.8	6.83	69.7	6.87	92.7	100.5	61.7
Ichthyophaga ichthyaetus	9.32	6.99	75.0	6.85	96.0	103.1	63.0
Aquila chrysaetos	10.27	7.75	75.4	7.97	88.2	98.3	64.8
Aquila audax	10.00			7.33			59.0 - 60.7
Neogyps errans				6.45			

relationships of which she speaks. From these data and the bones themselves, one can say that the ulnae of the Aegypiinae are usually very large, fairly straight, and relatively longer as compared with trunk length (from anterior end of first thoracic vertebra to anterior margin of acetabulum) than those of other accipitrids. However, *Terathopius* must be included in the Aegypiinae, whereas *Gypohierax* does not conform.

*Aquila audax* has the longest ulnae of the typical accipitrid group and approaches the Aegypiinae, just as does the fossil genus *Neogyps*. Assuming that the trunk of *Neogyps* was approximately of the same length as that of the golden eagle, but the wing was 10% longer (as based on a reconstruction at the Los Angeles County Museum) the ratio of body length to ulna length would be from 55-61% or the same as that of *Aquila audax*.

The ulnae of *Necrosyrtes* and *Terathopius* show a distal tapering, which is not shared with the other genera of the Aegypiinae. *Trigonoceps*, *Aegyptius*, and *Sarcogyps* have a proximal pneumatic pit on the ventral (inner side); this is developed in *Gyps* and *Necrosyrtes*. Another fossa, at the base of the proximal dorsal process (= the external condylar process), is found in *Gyps*, *Aegyptius*, *Sarcogyps*, *Trigonoceps*, and *Necrosyrtes*. *Terathopius* agrees with *Aquila* in showing only a shallow impression. The shape of the external condylar process tends to be more squared and less drawn forward among the Aegypiinae although *Necrosyrtes* and *Terathopius* bridge any gap that might exist here. The form of the ridge that runs distally from this process is distinct in the larger aegyptiins, but again the group lacks agreement among all of its members.

The distal end of the ulna of the Aegypiinae shows a tendency for pneumatic foramina, just as does the proximal end, although here too the variability is too great to serve for characterization of the group. On every count the Aegypiinae overlap the typical accipitrid. The ulnae of the kites show a genuine resemblance to those of the large vultures.

The ulna of *Neogyps* may resemble that of some members of the Aegypiinae, but this is not evidence of relationship because of the heterogeneity of that subfamily and its intergradation with the other accipitrids. The resemblance of *Neogyps* to one of the large vultures is no better than to the eagles.

*Palaeoborus rosatus* was described by A. Miller (1944) from a fragment of the ulna and was included in the subfamily Aegypiinae.

#### Manus

There is a small bone in the wrist of the accipitrid which articulates with the "radial" (fig. 178). This bone was first illustrated by Milne-Edwards (1867-71) in a drawing of the wing myology of *Aquila (Uroaëtus) audax*. Mivart (1873) also used this illustration and called the element a sesamoid bone. Alix (1874b) identified it as the "os prominens" or "epicarpium" in the kestrel; in 1881 Shufeldt used this name for a bone in the wrist of *Circus cyaneus*. Shufeldt also noted its occurrence in several species of hawks, including *Pandion*. Lucas (1882)

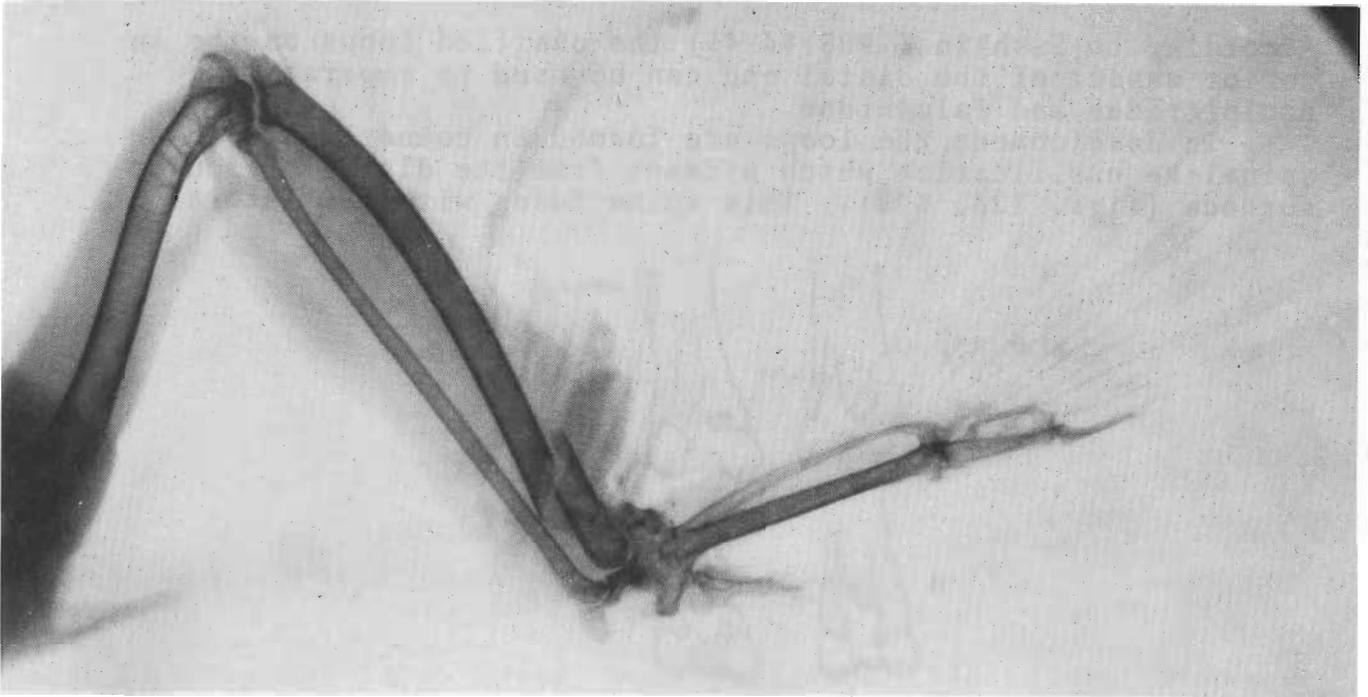


Fig. 178. X-ray of left wing of specimen of *Accipiter cooperii* (ulna broken distally) showing os prominens on anterior aspect of wrist (arrow).

described and figured an *os prominens* in *Bubo virginianus* and noted its absence in *Strix*. He noted its presence in *Sarcogyps* and its absence in *Polyborus* and *Milvago*. Shufeldt (1909) agreed with Lucas in all details and, on page 129, suggested its presence be used as a character of the superfamily Falconoidea. After this brief flurry nothing more was said concerning this bone until 1939 when Holmgren commented that it answered the description of the true radial rather than the fused centralia now identified by that name.

Shufeldt's (1881) description of the *os prominens* is definitive. It should be stressed, however, that in the accipitrid this bone is not of the usual sesamoid character. Rather it is elongated and acts in holding out the *extensor patagii* tendon from the wrist joint. It has a distinct articulation with the end of the radius. When the wing is closed this ossicle is folded against the underside of the manus, and when the wing is opened it rotates outward and forward.

A bone of the usual sesamoid type is described by Lucas (1882) for the great-horned owl. A "sesamoid" was observed by the writer in this species and also in the wing of *Sagittarius*; none was found in *Falco* (as described by Alix, 1874b). The typical *os prominens* is found only in the Accipitridae, although it varies considerably in size; that of *Pandion* is little more than a sesamoid.

#### Tibiotarsus

The distal end of the tibiotarsus is frequently fossilized.

According to Sushkin (1905:44-45) the ossified loops on the anterior aspect of the distal end can be used to separate the Accipitridae and Falconidae.

In development, the loops are formed in connection with a spinelike ossification which ascends from the distal articular surface (figs. 123, 179). This spine fuses with the lateral

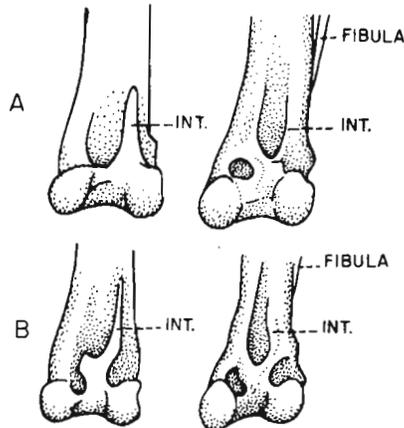


Fig. 179. Anterior aspect of distal end of left tibiotarsus of adult (right) and nestling (left) A. *Milvus migrans*, B. *Falco tinnunculus* (after Sushkin, 1905: figs. 15, 16).

margin of the shaft and may isolate a lateral opening. An osseous loop develops over the *extensor digitorum communis* tendon to form the medial opening. The spine has been homologized with the intermedium (Morse, 1872).

Among the cathartids (fig. 180) the lateral opening is absent; a remnant of it is indicated by a pit in *Gymnogyps*. The tibiotarsus of *Neocathartes* (Wetmore, 1944, Pl. V, fig. 1) does not show a loop structure. The tibiotarsus of *Sagittarius* has a small opening in some specimens. The width of the osseous loop is a suggestive feature of this type. The accipitrids lack a lateral opening, although a fossa here appears in many forms. The falconids usually have a well-developed lateral opening, but in *Herpetotheres* this may be reduced to a small hole (MVZ 85557). In *Micrastur* it is little more than a pit showing perforations.

Howard (1932:57) pointed out that, "The supratendinal bridge is more horizontally placed in the Aegypiinae than in the eagles," however, that of *Necrosyrtes* is directly comparable with the normal accipitrid angle. The only really peculiar loop is that found in *Geranospiza* and *Gymnogenys*; in these it is almost exactly horizontal in position. These two genera agree closely in the form of the tibiotarsus (as in other limb elements), the bone having nearly parallel sides. One specimen of *Leptodon* was peculiar in having an incomplete loop--an anomalous condition.

Other features of the distal end have been cited. Howard (1932:57) noted that, "The distal end of the tibiotarsus in the Aegypiinae differs from the Aquilinae and Buteoninae in greater

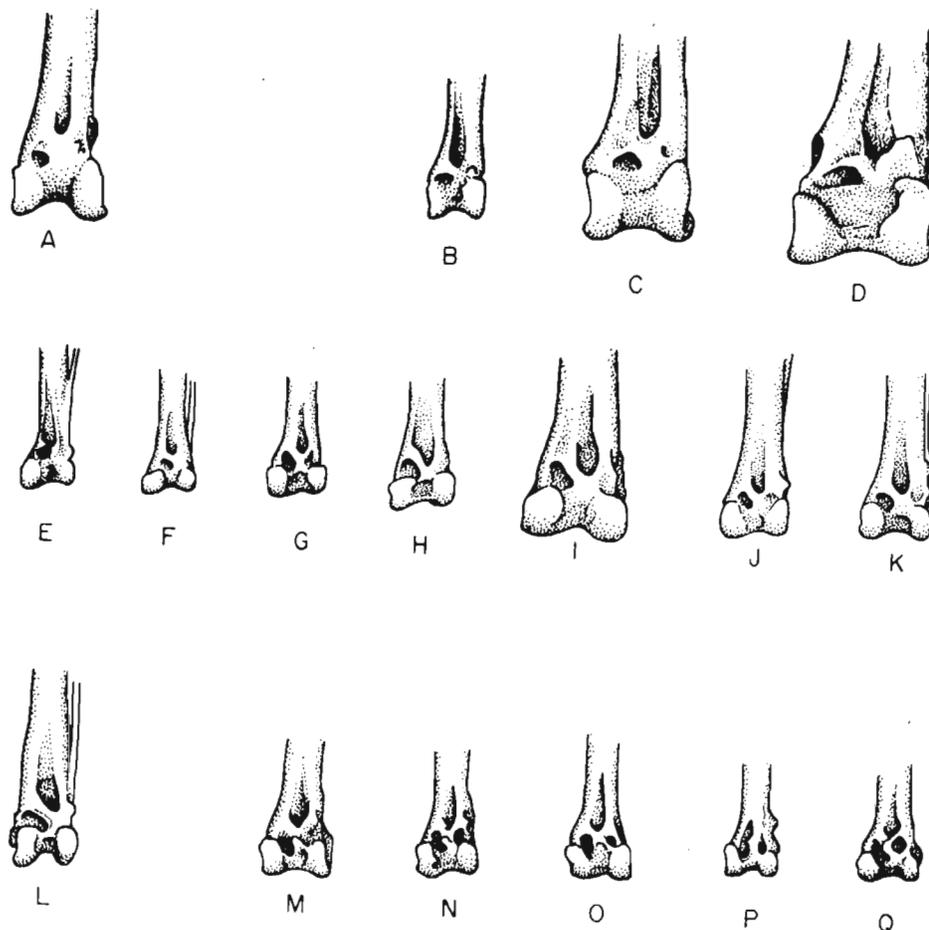


Fig. 180. Anterior aspect of distal end of right tibiotarsus of A. *Sagittarius serpentarius*, B. *Cathartes aura*, C. *Gymnogyps californianus*, D. *Teratornis merriami*, E. *Leptodon palliatus*, F. *Chondrohierax uncinatus*, G. *Accipiter cooperii*, H. *Busarellus nigricollis* or *Elanus leucurus*, I. *Aquila chrysaetos*, J. *Necrosyrtes monachus*, K. *Terathopius ecaudatus*, L. *Pandion haliaetus*, M. *Herpetotheres cachinnans*, N. *Micrastur semitorquatus*, O. *Polyborus cheriway* or *Milvago chimachima*, P. *Microhierax caerulescens*, Q. *Falco peregrinus*.

depth relative to breadth." A comparison of some ratios (Table 16) shows that the vultures do not differ materially from other accipitrids. Deep articulations are usually typical of a cursorial type of leg such as is found in *Sagittarius* or a cathartid. The largest percentages among the accipitrids are found in some of the Aegypiinae and such genera as *Accipiter*, *Circus*, *Haliaeetus*, *Busarella*, and *Pandion*. The distal articulations of *Pandion* are peculiar in every respect and certainly the leg is not cursorial. The falconids show a range of from 70 to 87% which places them in the same category as the accipitrid.

Other characters as the length of the tibial crest are unsatisfactory criteria, as they cannot be accurately measured.

Table 16. Percentage proportion of the depth of the distal end to the width of the distal end of the tibiotarsus.

	Distal end of Tibiotarsus			Howard's values
	A--width of distal end	B--depth of distal end	B/A	
Cathartid				
Cathartes aura	13.7	12.8	93.5	
	12.0	11.6	96.7	
Coragyps atratus	13.3	12.8	96.3	
	12.6	13.1	104.0	
Sarcoramphus papa	19.3	17.7	92.0	
Gymnogyps californianus	24.3	22.3	95.7	
Sagittariid				
Sagittarius serpentarius	21.7	21.3	97.8	
Accipitrid				
Pandion haliaetus	14.4	13.9	96.5	
Pernis apivorus	11.0	7.8	70.8	
Chondrohierax uncinatus	10.5	7.2	68.6	
Leptodon palliatus	8.6	5.7	66.3	
Elanoïdes forficatus	9.0	5.8	64.4	
Elanus leucurus	9.6	6.7	69.8	
Ictinia missippiensis	6.8	4.4	64.7	
Accipiter cooperii	7.4	5.8	78.4	
Circus cyaneus	7.7	6.5	84.4	
Haliaeetus leucocephalus	15.6	12.5	80.2	71.6
Gypohierax angolensis	14.5	10.5	72.4	
Gypaëtus barbatus	22.4	17.5	78.2	79.0
Neophron perenopterus	20.0	13.7	68.5	
Torgos tracheliotus	24.5	19.5	79.7	
	23.7	20.0	84.5	
Buteo jamaicensis	13.7	8.8	64.2	
Busarellus nigricollis	12.7	9.6	75.6	
Falconid				
Herpetotheres cachinnans	12.1	10.0	82.6	
	11.5	10.0	87.0	
Micrastur semitorquatus	11.8	9.6	81.4	
Polyborus cheriway	12.7	10.2	80.3	
	12.3	10.2	83.0	
Falco peregrinus	11.0	8.1	73.6	
Falco (5 species)			70.3-80.8	

\* \* \* \* \*

Tibiotarsi are poor indicators of relationship and at best are usable only at the generic or specific level. Thus the distal end

of this bone does not effectively separate the several types of falconiforms. The intermediate condition of *Herpetotheres* (note peculiar external condyle) between accipitrid and falconid appears to be a convergence.

Two fossil cathartids, *Phasmagyps patritus* and *Palaeogyps prodromus*, were described by Wetmore (1927) on the basis of tibiotarsi from the Oligocene of Colorado. These tibiotarsi appear to be cathartids but conceivably could belong to species in several present orders, determination of their exact relationship being dependent upon the other elements of the skeleton. Cracraft and Rich (1972) associated *Diatropornis elliotti* and *Amphiserpentarius schlosseri* with the cathartids on the basis of the distal end of the tibiotarsus (and the tarsometatarsus in the case of the former). Their opinion may be justified, but I would prefer to know more elements of these species.

#### Fibula

The fibula is best developed among the kites and aegyptiins; it may extend nearly the length of the tibiotarsus. The most complete example--there is considerable individual variation--is found in *Pandion* and *Terathopius*. In these genera the fibula has a distinct articulation with the tibial bone. In most genera, it ends well above the lateral condyle as a small lump fused with the tibia. The presence of the extended distal end in the kites and some aegyptiins is probably indicative of a more generalized state. *Gymnogenys*, which resembles *Geranoospiza* in many details, has the longer, better developed fibula of a kite.

#### Foot

The foot of the typical accipitrid is developed for grasping, and this specialization has resulted in strengthening of the claws and in the shortening of various segments of the toes. The extreme is achieved in *Harpia*, *Stephanoaëtus*, and *Pithecophaga*. Most accipitrids have strong feet, but some kites have a weak foot which resembles that of a chicken. Feet of a weak type, perhaps useful in walking, are found in the cathartids (fig. 181).

On the structure of the foot the falconiforms can be divided into three groups (fig. 204): cathartid, sagittariid, and an accipitrid-falconid group. The first has long front toes, a very short hind toe, the claws of all digits are relatively short and straight, and the second and third phalanges of the fourth digit are relatively long. The second group has relatively short toes, the hind toe approximates the second digit in length, and the claws are fairly long and curved. In the first two groups the basal phalanx of the second digit is as long as the distal phalanx, and the basal phalanx of the fourth toe is as long or longer than the terminal phalanx of that digit. The last group tends to have longer, sharper claws, the basal phalanx of the second digit is distinctly shorter than the distal one, and the basal phalanx of the fourth is distinctly shorter than the terminal phalanx. The foot of *Pandion* is peculiar in that the outer toe (IV) is longer than the middle one (III) and is semi-reversible like that of an owl. In addition all of the claws are equally

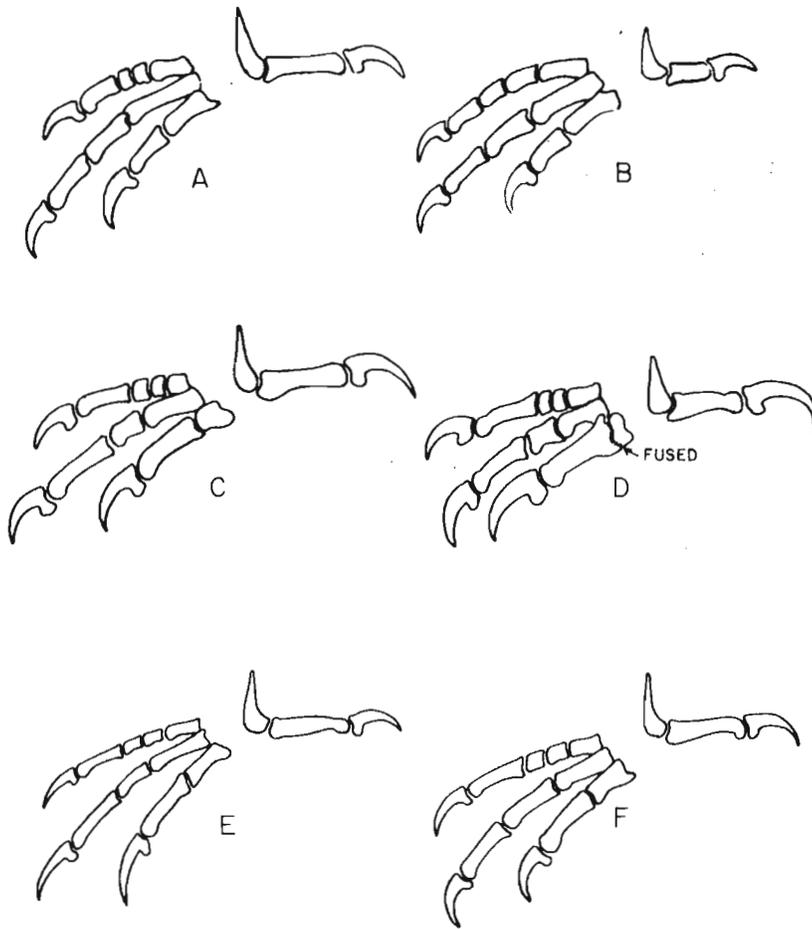


Fig. 181. Bones of the right foot of A. *Sagittarius serpentarius*, B. *Cathartes aura*, C. generalized accipitrid (including *Pandion*), D. *Ichthyophaga ichthyaëtus*, E. *Aviceda cuculoides* or *Elanoïdes forficatus* or *Gymnogenys typicus*, F. generalized falconid.

developed as contrasted to the preferential development of the hind and index claws in the other accipitrids.

The aegyptian foot outwardly resembles that of the cathartid in scalation and the blunt claws but has the typical accipitrid bone structure. *Gypohierax* has well-developed claws, whereas *Terathopus* resembles the aegyptian.

The claws of the various accipitrids range from the enormous curved weapons of the large eagles through the short blunt talons of the aegyptians, to the slender, elongated tips of *Pernis*, *Gymnogenys* or the extremes, *Rostrhamus* and *Ictinaëtus*.

Of the feet examined only those of *Milvus*, *Ictinia*, *Haliaeetus*, and *Ichthyophaga* showed fusion of the basal and distal phalanges of the second digit. Shufeldt (1891b) observed such fusion in specimens of *Ictinia* and *Haliaeetus*. The fusion in *Haliaeetus* may be incomplete with only the under surface involved, whereas

the joint appears more or less normal above.

### Summary and Conclusion

The miscellaneous skeletal parts have value when detailed agreement is involved (at species or genus level). Lack of close similarity cannot be interpreted as more distant relationship because of adaptive radiation. Any level of relationship, or lack of it, is possible under these circumstances. The three groups indicated by the foot seem to have relevance since there is no real overlap between them and rather basic agreement within each style.

### OSTEOLOGY--SUMMARY AND CONCLUSIONS

There has never been great doubt as to the intrinsic value of the skeleton in taxonomy. It has been used to support the association of different species as well as to demonstrate lack of interrelationship. It has generally played a supporting role to relationships based on external features. However, questions remain as to its value when species which are now considered as belonging to separate orders closely resemble each other in a particular area or when species presume to belong to the same order differ markedly. In the case of the falconiforms we are more involved with the latter than the former, but both are encountered and decisions must be reached regarding them.

An example of the first situation is the similarity of the cathartid to *Catharacta*, *Macronectes* or *Fregata*. The association with *Macronectes* finds further support by the similarity of *Teratornis* to *Diomedea* in many features. This similarity of form is not complete since many details, such as the ossification of the nasal passage area, the orbital gland impressions, and the tarsometatarsus, can be used in their separation. However, we are comparing specialized end species rather than basic archetypes for each of the represented orders. As represented in the living fauna, the procellariiform type is quite distinct from the cathartid, viewed in terms of the total mosaic of features, as is certainly the pelecaniform. However, the similarity of these terminal genera with the cathartid cannot be dismissed since an explanation based on adaptive convergence demands far too much.

Somewhat less marked is the similarity of body and limb structure shared by the storks and *Sagittarius*. Again there appears to be more than adaptive convergence involved. One can arrive at the assumption that there was some common ancestral type from which the cathartid, sagittariid, procellariiform, pelecaniform, and ciconiiform (and perhaps other groups as well) arose. From this stem type all of these highly specialized lines developed; yet each retained a great deal of its common heritage. Just as probable is the view that they underwent parallel changes (basically chargeable to increase in size) so as to arrive at their present state of sharing many features in common. The nature of the shared features suggests that they are a result of independent evolution rather than common heri-

tage, and this is further supported by their absences in the otherwise similar charadriimorph type (complex containing the Gruiformes and Charadriiformes of Wetmore, 1960).

Recognition of functional modification is difficult since so many facets must be examined. Parallel changes might be charged to a number of general factors (increase in size), but demonstration of correlation would be difficult, whereas more specific responses to needs, such as the relationship between a long neck and vulturine habits, are more apparent.

On the basis of the more obvious functional features, it might be assumed that the skull, the tarsometatarsus, and foot show the most adaptive modification whereas the body (shoulder girdle, sternum, and pelvis) is more conservative. The plasticity of the skull is explained through use of the bill as a feeding device. This in turn necessitates changes in the palate, prefrontal region, nasal passages, and olfactory area for movement or for bracing the bill, modification of the eye and ear regions in response to the visual and auditory needs of securing food, and remolding of the cranium as a result of brain alterations, and changes in the neck and jaw musculature required for the new behavior patterns and movements.

The weakness of this line of thought lies in the idea that the design of the body is not particularly affected by changed feeding habits (but is affected by locomotor changes). It is certainly open to question which has been changed more in such groups as the anseriform or the loons, the head or the body. It could be argued that once a particular specialized style of bill and feeding is achieved it is selectively "fixed" and undergoes only limited modification, while the body, which still serves a wide range of functions may specialize along any one of several lines.

Here the question can be raised whether the bill of the stork could be modified into that of *Sagittarius* in response to its predatory habit. This is improbable for two reasons. First, the stork bill should be viewed as a specialized end form (see below) and, second, some of the storks are vulturine in habit and yet have lost none of their heritage. This type of bill, as well as the body form, is a dead end. It is unlikely that the foot of *Sagittarius* has been derived from that of the stork on similar grounds. It is more probable that a predator (bill and foot type fixed) developed long legs and a cursorial style of feeding.

Whereas the bill of the stork is an extreme and distinctive structure that of the predator (like that of the charadriimorph complex) is of a supraordinal nature. The bill of the primitive avian had a hook at the tip and needs only to be shortened and strengthened to be transformed (at least in its superficial outline) to that of a hawk or owl. Thus, in the case of predators one might assume that the body structure can be more distinctively affected by adaptive modification than the head. As can be observed, the bills of predators may differ at the finer levels of structure, but these differences are of the same order and kind as observed in the body.

When bill forms are comparable, the skull can be utilized for ordinal differentiation only by directing attention to what otherwise might be considered as rather minor details. For example, the skull of a bustard differs most markedly from that of a charadriiform in its holohinal nasal opening and in lacking supraorbital fossae for the nasal glands; the cathartid differs from the fulmar or albatross in its vestibular (alinasal) ossifications and lack of a bony vomer. That such differences are occasionally unimportant does not mean that they are always so. In the situations cited it can be assumed that these details (correlated with other dissimilarities throughout the skeleton) are of real value. In the case of the parrot perhaps even such details have been effaced by modification of the bill; yet the fact that the parrot bill is only plastic within limits is attested to by the ease of its identification and the wide range of food habits which it serves.

A peculiar case, where the bill form might be considered comparable and yet there is almost total disagreement in its aspect, is that of the ibis and stork. These two essentially agree only in being "desmognathous." A much better comparison of bill form exists between the ibis and the scolopacid than between the ibis and stork. The major disagreement is that the scolopacid is schizognathous. I doubt whether the condition of the palate is worthy of recognition in this particular case, the scolopacid being more like the ancestral source of the ciconiiforms in terms of bill structure.

A consideration of the variations of the skull, which should be plastic to adaptive modification, tells little. The bill, as the most responsive part, tells least. Yet in spite of this, the skull suggests that there are four types of falconiforms, and these show little or no "intergradation" or phylogenetic inter-relationship. If these four types of crania could be adequately characterized the continuing discussion of the makeup of this order would cease, but they cannot. Thus the answer to the riddle must be sought elsewhere.

The mandible of the bird has never been thoroughly studied since, in its fused adult form, few useable features can be detected. The mandible of the falconiform gives hints but nothing more. One is cautioned by the possible parallelism in form of that of the Sphenisciformes, Gaviiformes, Procellariiformes, Pelecaniformes, and Ciconiiformes.

The tarsometatarsus, like the skull, should be quite responsive to adaptive changes in the foot dictated by its use, but the number of comparable points is restricted. The four styles of the falconiforms support this view, and the fact that any one of these is not well matched in any other order gives added significance. In contrast some types of tarsometatarsi (those of the charadriimorphs) can only be considered as supraordinal.

The falconiform tarsometatarsi share only one feature: the middle trochlea does not project as strongly as it does in most birds. This similarity is of little import, since there is lack of agreement in detail, and the general type is matched in

some non-falconiform groups; it might have functional meaning rather than close relationship. There is some agreement in that the hypotarsal structure is seldom perforated by tendinal canals as it is in many other kinds of birds. There does not appear to be any functional correlation; this lack of canals appears to be a primitive feature shared with many other kinds of birds.

Other elements of the skeleton, being simpler, or more constant, in form are less useful than the skull or tarsometatarsus. The sternum, which is frequently ignored, seems to be of value in the identification of a columbiform-galliform complex. (The similarity of the pigeon and the chicken does not appear to be convergence, although it could be interpreted as such.) In contrast, the sternum does not support the union of the gruiforms and charadriiforms; in the former it is a long narrow structure, whereas in the latter it is short and broad. The elongated form is probably a specialization achieved by the ancestor of both the cranes and rails. Intermediate forms do not connect these two types; rather other species with elongated sterna appear to represent modifications in the same direction as that taken by the ancestral gruiform (i.e. parallelisms).

Whereas the sterna of some groups (orders) are strongly differentiated those of others are not. Within an order, the passeriforms or cuculiforms for example, two styles of posterior margins occur with some intermediate species or individuals. Among the ciconiiforms one finds both styles but no identifiable intermediates. Among the charadriiforms there is general agreement with some quite distinctive variants (*Philohela*, *Scolopax*, Burhinidae, Parridae, Rostratulidae, Alcidae, Thinicoridae).

The pelvis has a limited number of comparable features, which appear to be quite plastic. Particularly interesting are the close agreement of pelvises of diving types. Although the pelvis has little value among the existing birds, it appears to support the early dicotomy of birds into the Palaeognathae and Neognathae.

Summarizing the case of the falconiforms, the skull is somewhat suspect as to value, particularly the form of the rostrum. In contrast, the sternum and shoulder region more accurately reflect the heritage of the four types described. The tarsometatarsus and some of the features of the skull support the evidence provided by the body.

The cathartid resembles some species of the procellariiforms, pelecaniiforms, and ciconiiforms. The resemblance is not exact enough to demand union into a single group; each is equally distinct from the others. These groups are each composed of highly specialized species in terms of size and habit, and the entire assemblage shows many common features with a less specialized type, which can be represented by *Catharacta skua*, a member of the charadriiform complex. The closer similarity between the extreme species (*Teratornis* to *Diomedea*) in each of these groups is as much parallelism as anything. There can be little doubt that each of these orders represents a primary line of radiation from the ancestral bird. Comparing the cathartid with the other falconiforms produces no evidence of any closer tie than being birds.

The sagittariid type, on the basis of its body skeleton, appears to be like the storks. There is some agreement with *Cariama*, but this is more likely convergence. If one disregards the presumed convergent features there is little evidence of stork affinity. One can assume that this aberrant genus does, in fact, represent a product of a pre-accipitrid line, but such a speculation finds no osteological support. To argue that this type comes closer to the accipitrids than any other and, therefore, that this implied similarity is evidence of relationship, disregards the possibility of convergence. The question then follows whether the long legs of *Sagittarius* preceded the hawk-like bill, whether the reverse is true, or whether these features were developed simultaneously. I have concluded that the bill and feet, as parallel developments to the accipitrid, preceded the long legs.

The accipitrid is one of the most distinctive types among birds, yet it has always been linked with the falconid. Its individuality suggests that, like the sagittariid, it is an independent line of development from a very basic stock. Similarities in shoulder girdle to the storks (or cathartids and sagittariid) mean little when viewed in respect to the total variation in these structures and are as attributable to functional value as to common ancestry.

*Pandion* appears to be an aberrant accipitrid and as such is useful in testing criteria. It differs consistently from the typical accipitrid in every feature, but the nature of these differences is such that interrelationship can be assumed. Compared with the cathartid or sagittariid it is apparent that a different degree of differentiation is involved. For example, the accipitrid tarsometatarsus is defined by the separation of the hypotarsus into medial and lateral calcaneal processes. *Pandion* comes as close to this as some of the kites, but the other types do not even approximate it.

*Teratornis merriami* has a similar relationship to the cathartids, since, as a highly specialized species, it is not so different from the typical cathartid as to demand separate consideration. It is like comparing a pelican to other pelecaniforms or an albatross to other procellariiforms. Using the aberrant-genus method of measure, each of the types described takes on greater significance.

The falconid type is most distinctive on the basis of its shoulder girdle. The sternum and tarsometatarsus are markedly different. Their closest approach is to the owls, or parrots, but even here the level of agreement is low. *Herpetotheres* is the most accipitrid-like, but it appears to represent convergence rather than an intermediate form. Its affinities are entirely falconid; in no detail is it truly accipitrid. Although the falconid might be assumed to be less specialized than the accipitrid, there is no agreement with the sagittariid or cathartid.

## MYOLOGY

### Introduction

There is need for a revised system of names for the muscles of birds. The general treatises, those by Stresemann (1927-1934), Grassé (1950), and George and Berger (1966), do not satisfy this need because like the older account of Gadow and Selenka (1891), they are not in harmony with my view that a system more nearly like that of the mammal is desirable. I believe that a basic system of muscles, developed in the origin of the amphibia, has been modified in each of the derived classes (Jollie, 1962) and that the individual muscles can be identified with N.A. (Nomina Anatomica) terms. The utilization of names compounded from origins and insertions, as advocated by comparative anatomists of the last century, results in a different system of names for each class and makes comparative study difficult, if not impossible. The assumed impropriety of comparing muscles of two classes has been based in part on innervation. It is now apparent that the nerve supply may be no more reliable than the muscles themselves. Since homology cannot be irrefutably demonstrated it should be sufficient to look for a less exacting correspondence of parts, in agreement with their evolution from a common (or nearly common) ancestral pattern.

There is little question that "homologous muscles" in different vertebrates vary in their interrelationship from exact correspondence to rough resemblance or no resemblance at all. The use of a system such as I advocate does not imply exact correspondence of parts, but it does imply some level of correspondence in agreement with the taxonomic separation of the groups. Such a system does not compromise exact scientific procedure, but rather it facilitates by increasing the ease of comprehension and communication. By abandoning rigid and meaningless concepts of homology, less time is needed for argument on terminology and more time is available for the exploration of variation within groups. Certainly little is to be gained by detailed comparison of the muscles of different classes with the goal of demonstrating their dissimilarities instead of their evolutionary continuity and adaptive specialization.

Studies of the myology of birds are few in number. Several of the older treatises are those of Owen (1849) for *Apteryx*, Macalister (1864-1866) on the ostrich, Alix (1874a) on a timamou, Perrin (1875) on the hoatzin, Watson (1883) on penguins, Shufeldt (1890) on the raven, Marshall (1905) on the poorwill, Chamberlain (1943) on the chicken, and Fisher and Goodman (1955) on the whooping crane. Summaries of the myology of birds have been presented by Owen (1866), by Alix (1874b), Gadow and Selenka (1891), Beddard (1898), Stresemann (1927-1934), Grassé (1950) and George and Berger (1966). Several authors have dealt with restricted portions of the muscular system and these include Garrod (1873-1874; thigh), Fürbringer (1888, 1902; shoulder and breast), Buri (1900; wing), Lakjer (1926; jaw muscles), Banzhaf (1929-1930; wing), Hudson (1937, 1948; Hudson and Lanzilloti 1955; thigh and wing), Fisher (1946; wing and leg), Beecher (1950, 1953; jaw muscles) and vanden Berge (1970; appendicular muscles of ciconiiforms).

Materials

The homologies (often tentative) implied by the names used in this account were determined by dissection of more than 30 genera of birds, three of reptiles, and three of mammals plus a review of a part of the literature on the myology of these classes. The illustrations will assist the reader in identifying the muscles described with the names used by other writers. Comparisons within the falconiforms are based on 24 genera dissected as indicated in Table 17. The source of supplementary information is also indicated in that table. Table 18 lists the muscles of the bird and the assumed corresponding muscle of the human when one is present. Some of the muscles of the human are not found in the bird and this also is indicated in the table. Only those muscles starred are discussed in the following section; the others are not as yet known to show useable variations, although some of them may.

\*\*\*\*\*  
 Table 17. Falconiforms dissected for this study or described in the literature.

Symbols: A - Alix, 1874b; B - Beddard, 1898 and 1903; b - Berger, 1956b; F - Fisher, 1946; f - Fürbringer, 1888; G - Garrod, 1873, 1874; H - Hudson, 1948; M - Milne-Edwards, 1867-1871; N - Nitzsch, 1863, 1866. The species personally investigated are indicated with a J.

	Column I	II	III	IV	V	VI
	Locomotor muscles or total myology	Shoulder region	Patagial region	Posterior limb	Thigh	Syrinx
Cathartid						
Cathartes aura	J F	f		H		B J
Coragyps atratus	J F	F		H	G	J
Sarcoramphus papa	F				G	B
Gymnogyps californianus	F					
Vultur gryphus	F					B
Sagittariid						
Sagittarius serpentarius	J	f	B	H B	G	
Accipitrid						
Pandion haliaetus	J	f	B	H		J
Elanus caeruleus	J					J
Ictinea plumbea	J					J
Aviceda (cuculoïdes)				B		
Aviceda subcristata	J					J
Chondrohierax uncinatus	J					J
Gymnogenys typicus	B			B		B
Milvus milvus					G	

	I	II	III	IV	V	VI
Milvus migrans	J					B
Haliaeetus vocifer					G	
Haliaeetus albicilla		f	B		G	B
Haliaeetus leucocephalus		J				J
Gypohierax angolensis			B			B
Gypaëtus barbatus	N		B			B
Neophron perenopterus					G	
Dryotriorchis spectabilis			B			B
Circaëtus (gallicus)						B
Haematornis cheela					G	
Terathopius ecaudatus			B		G	B
Aegyptius monachus			B			B
Torgos tracheliotus	J		B		G	B J
Gyps fulvus	N		B		G	B
Necrosyrtes monachus	J					J
Morphnus guianensis						B
Harpia harpyja			B		G	B
Harpyhaliaetus coronatus			B			
Accipiter striatus	J					
Accipiter nisus		f				
Accipiter fasciatus			B			
Accipiter cooperii	J			H		
Accipiter gentilis					G	
Melierax musicus			B			B J
Circus cyaneus	J			H		
Circus aeruginosus					G?	
Circus pygargus					G	B
Circus maurus			B		B	
Kaupifalco monogrammicus	J		B		G	J
Hypomorphnus urubitinga						B
Leucopternis (albicollis)						B
Buteo fuscescens						B
Buteo buteo		f	B		G	B
Buteo jamaicensis	J			H		J
Buteo swainsoni				H		
Buteo lagopus					G	B
Buteo nitida						B
Hieraeetus fasciatus						B
Spizaëtus sp?						B
Lophaëtus occipitalis			B			
Aquila rapax					G	
Aquila heliaca			B			
Aquila chrysaëtos	J			H		B J
Aquila audax	J M	f			G	J
Falconid						
Herpetotheres cachinnans	J					B J
Micrastur ruficollis	J					J
Milvago chimachima	J		B			B J
Milvago chimango			B			B
Daptrius ater	J					J
Polyborus plancus			B		G	
Polyborus cheriway	J					B J

	I	II	III	IV	V	VI
Polihierax semitorquatus	J b					J
Microhierax caerulescens			B			
Falco peregrinus				H	G	B
Falco rusticolus						B
Falco columbarius			B	H		B
Falco biarmicus					G	
Falco jugger						B
Falco mexicanus				H		
Falco subbuteo			B		G	G
Falco sparverius	J			H		J
Falco tinnunculus	A	f	B		G	B
Falco vespertinus						B
Ieracidea berigora	J					B J
* * * * *						

Table 18. The homologies of bird and human muscles. Those marked with an \* are described in the text.

Bird	<i>Skeletal Muscles of Head</i> Muscles of Eye	Human
rectus inferior		rectus inferior
rectus medialis		rectus medialis
rectus lateralis		rectus lateralis
obliquus superior		obliquus superior
obliquus inferior		obliquus inferior
orbicularis oculi		orbicularis oculi
rectus superior		rectus superior
quadratus nictitantis		lacking
pyramidalis nictitantis		lacking
levator palpebrae		levator palpebrae superioris
depressor palpebrae		lacking
pars ventralis		
pars posterior		
Jaw and Throat Muscles		
*masseter et temporalis		masseter, temporalis
pars temporalis et quadratis		
pars orbitomandibularis posterior		
pars orbitoquadratis		
pars quadratomandibularis		
pars orbitomandibularis anterior		
pterygoideus		pterygoideus externus, pterygoideus internus, tensor tympani
pars dorsalis		
pars intermedia		
pars ventralis		
pars pterygoideus		
*depressor mandibulae		?lacking
ceratomandibularis		?lacking
?lacking		diagastricus



lacking	corugator cutis ani, sphincter ani externus, sphincter ani internus
*transversus perinei	lacking
<i>Skeletal Muscles of Vertebral Column</i>	
longissimus dorsi	longissimus dorsi
longissimus cervicis et capitis	longissimus cervicis, longissimus capitis
spinalis dorsi	spinalis dorsi
spinalis cervicis et capitis	spinalis cervicis, spinalis
pars cervicis et capitis	capitis, (splenius capitis)
pars spinalis cervicis	
pars cervicalis anterior	
pars cervicalis posterior	
rectus capitis posterior major	rectus capitis posterior major
rectus capitis posterior minor	rectus capitis posterior minor
lacking	obliquus capitis inferior, obliquus capitis superior
multifidus et semispinalis dorsi	multifidus, semispinalis dorsi
semispinalis cervicis	{ semispinalis cervicis, rota- tores, iliocostalis cervicis, splenius cervicis
obliquo transversales	
semispinalis capitis	
iliocostalis lumborum	semispinalis capitis iliocostalis lumborum, iliocostalis dorsalis
longus lateralis	intertransversares
intertransversares	
longus colli	longus colli
pars thoracicus	
pars cervicalis	
longus capitis et rectus capitis anterior	longus capitis, rectus capitis anterior
rectus capitis lateralis	rectus capitis lateralis
interspinales	interspinales
<i>Skeletal Tail Muscles</i>	
levator coccygis	{ coccygeus levator ani
lateralis caudae dorsalis	
*depressor caudae	
pars superficialis	
div. levator cloacae	
div. retractor cloacae	
pars profundus	
lateralis caudae ventralis	
pars depressor coccygis	
pars infracoccygis	
<i>Skeletal Body Wall Muscles</i>	
quadratus lumborum	quadratus lumborum
scaleni et levatores costarum	scalenus anterior, scalenus medius, scalenus pos- terior, levator costarum

intercostales externi	intercostales externi
intercostales interni	intercostales interni,
pars vertebralis	subcostales
pars sternalis	
pars internus	
*sternocoracoideus	lacking
pars sternalis	
pars costalis	
costisternalis	lacking
lacking	serratus posterior su-
	perior, serratus
	posterior inferior
obliquus externus abdominis	obliquus externus ab-
	dominis
obliquus internus abdominis	obliquus internus ab-
	dominis, cremaster
rectus abdominis	rectus abdominis, py-
	ramidalis
transversus abdominis	transversus abdominis
costopulmonarii	(? diaphragm)
	<i>Skeletal Superficial Muscles of Pectoral Limb</i>
rhomboideus	rhomboideus major,
pars superficialis	rhomboideus minor
pars profundus	
serratus anterior	serratus anterior
pars superficialis anterior	
pars superficialis posterior	
pars profundus	
lacking	levator scapulae
*latissimus dorsi	latissimus dorsi
pars anterior	
pars posterior	
	<i>Skeletal Dorsal Muscles of Upper Arm</i>
*teres major	teres major
*subcoracoscapularis	subscapularis, (sub-
pars subcoracoscapularis	clavius)
pars scapularis anterior	
pars scapularis posterior	
*deltoideus	deltoideus
pars clavicularis	
insertion longus, insertion brevis	
pars scapularis	
*teres minor	teres minor
pars externus	
pars internus	
*triceps brachii	triceps brachii
pars externus	
pars internus	
pars axillaris	
anconaeus	anconaeus

*Skeletal Ventral Muscles of Upper Arm*

*pectoralis	pectoralis major, pectoralis minor
pars superficialis	
pars profundus	
pars patagialis	
*supracoracoideus	supraspinatus, infraspinatus
coracobrachialis brevis }	
*coracobrachialis longus }	coracobrachialis
*biceps brachii	biceps brachii
pars biceps brachii	
pars propatagialis	
brachialis	brachialis

*Skeletal Dorsal Muscles of Forearm*

lacking	brachioradialis
extensor carpi radialis brevis	extensor carpi radialis brevis
extensor carpi radialis longus	extensor carpi radialis longus
supinator	supinator
extensor digitorum communis	extensor digitorum com- munis, extensor digiti quinti proprius
pars anterior	
pars posterior	
extensor indicis	extensor indicis proprius
abductor et extensor pollicis	abductor pollicis longus, extensor pollicis longus, extensor pollicis brevis
extensor carpi ulnaris	extensor carpi ulnaris

*Skeletal Ventral Muscles of Forearm*

pronator teres	pronator teres
flexor carpi radialis	flexor carpi radialis
flexor digitorum superficialis	flexor digitorum sublimis, palmaris longus
flexor digitorum profundus	flexor pollicis longus, flexor digitorum profundus
pars anterior	
pars posterior	
pars ulnaris	
flexor carpi ulnaris	flexor carpi ulnaris
pars anterior	
pars posterior	
lacking	pronator quadratis

*Skeletal Dorsal Muscles of Manus*

interossei dorsales	interossei dorsales
pars abductor digiti II	
pars extensor digiti II	
pars extensor metacarpi	
pars interosseus dorsalis	
pars flexor metacarpi	
pars flexor digiti IV, flexor brevis digiti IV	

lacking		abductor pollicis brevis opponens pollicis flexor pollicis brevis adductor pollicis palmaris brevis abductor digiti quinti flexor digiti quinti brevis opponens digiti quinti lumbricales (part of) interossei volares
interossei volares pars interosseus palmaris		
	<i>Skeletal Ventral Muscles of Manus</i>	
metacarpal flexores pars flexor digiti II pars adductor digiti II pars abductor digiti III pars abductor brevis digiti III		lacking
	<i>Skeletal Dorsal Muscles of Thigh</i>	
sartorius		sartorius
*tensor fascia latae		tensor fascia latae
iliofibularis		(short head of) biceps femoris
	proximal deep layer	
*gluteus maximus		gluteus maximus
gluteus medius		gluteus medius
gluteus minimus		gluteus minimus
*piriformis		piriformis
iliopsoas		psoas major, psoas minor, iliacus.
lacking		pectineus
	distal deep layer	
*rectus femoris		rectus femoris
*vastus lateralis		vastus lateralis
*vastus intermedius		vastus intermedius, articularis genu
*vastus medius		vastus medius
	<i>Skeletal Ventral Muscles of Thigh</i>	
*biceps femoris et semimembranosus pars lateralis (biceps femoris) pars medialis (semimembranosus)		(long head of) biceps femoris, semimembranosus
*semitendinosus		semitendinosus
*gracilis et adductor longus pars gracilis pars adductor longus		gracilis adductor longus
*adductor brevis et magnus		adductor brevis, adductor magnus, (adductor minimus)
obturator internus		obturator internus
lacking		gemellus superior, gemellus inferior, quadratus femoris.

obturator externus	obturator externus
pars internus	
pars externus	
*caudiliofemoralis	lacking
pars caudatus	
pars iliacus	
	<i>Skeletal Flexor Muscles of Shank</i>
*gastrocnemius	gastrocnemius
pars lateralis	
pars medius	
*plantaris	plantaris
pars accessorius	
pars tibialis	
*soleus	soleus
*flexor digitorum superficialis	lacking
pars perforans et perforatus digiti II	
pars perforans et perforatus digiti III	
pars perforatus digiti IV	
pars perforatus digiti III	
pars perforatus digiti II	
popliteus	popliteus
*flexor hallucis longus	flexor hallucis longus
*flexor digitorum longus	flexor digitorum longus
lacking	tibialis posterior
	<i>Skeletal extensor Muscles of Shank</i>
*tibialis anterior	tibialis anterior
*peronaeus longus	peronaeus longus
lacking	extensor hallucis longus
peronaeus brevis	peronaeus brevis
*extensor digitorum longus	extensor digitorum longus, peronaeus tertius
	<i>Skeletal Tarsal Muscles</i>
*extensor digitorum brevis	extensor digitorum brevis
pars hallucis	
pars abductor digiti II	
pars extensor digiti III	
pars adductor-extensor digiti IV	
lacking	{ abductor hallucis, flexor digitorum brevis, abductor digiti quinti, quadratis plantae, ad- ductor hallucis, flexor digiti quinti brevis, interossei dorsales
*interossei plantaris	interossei plantaris
pars abductor digiti IV (pars adductor-flexor digiti IV)	
pars adductor digiti II	
*flexor hallucis brevis	flexor hallucis brevis
pars externus	
pars internus	
*lumbricales	lumbricales

## Comparative Anatomy

*Masseter et Temporalis (adductor mandibulae)*

The jaw muscles of birds have been studied in detail by Lakjer (1926), Starck (1940), Beecher (1951, 1953), Barnikol (1953b) and Starck and Barnikol (1954). These studies have not convinced me of the usefulness of Lakjer's terminology or the taxonomic value of the subdivisions of the main adductor. The parts identified here are equivalent of Lakjer's (1926) names as follows: *pars temporalis et quadratis* = *adductor mandibulae (externus and posterior)*, *pars orbitomandibularis* = *pseudotemporalis superficialis*, *pars orbitoquadratis* = *protractor quadrati*, *pars quadratomandibularis* = *pseudotemporalis profundus*.

Starck and Barnikol (1954) studied the jaw musculature in *Cathartes (aura?)*, *Sarcoramphus papa*, *Accipiter gentilis*, *Accipiter nisus*, *Buteo buteo*, *Haliaeetus leucocephalus*, *Torgos tracheliotus*, *Gyps fulvus*, and *Falco tinnunculus*. There is fundamental agreement among all of the genera examined by these writers and myself, the main differences being in proportions. For example the *pars orbitomandibularis* of *Elanus* is small and tapers to a thin insertion tendon whereas in other falconiforms this muscle is bulky. It may or may not taper to a tendon.

*Depressor Mandibulae*

In *Cathartes* and *Coragyps*, the origin of the *depressor mandibulae* extends over the ventral portion of the preceding muscle (figs. 68, 76, 94, 114). *Circus* shows a separation of this muscle and the *temporalis*, which are in contact in most species. This separation appears to be the result of the enlarged and protruding tympanic margin.

*Ceratoglossus*

The position of the *ceratoglossus* (fig. 182) and its relationship with the *transversus hyoideus* varies as indicated under that muscle. In the cathartid, sagittariid, and some accipitrids (*Elanus*, *Pandion*), it arises along the lateral and ventral margins of the proximal end of the ceratobranchial lateral to the insertion of the *transversus hyoideus* (the posterior division of that muscle). The muscle of the typical accipitrid or falconid lies below the *transversus hyoideus* insertion and arises more from the ventral aspect of the ceratobranchial. The size of this muscle varies considerably, possibly reflecting a functional response.

*Transversus Hyoideus*

The *transversus hyoideus* of the cathartid is proportionally more massive than in the accipitrid (except *Elanus*) or falconid and in addition only the medial insertion is present (fig. 182). *Sagittarius* is like the cathartid but the muscle is smaller. In the typical accipitrid (*Accipiter* or *Buteo*), only the lateral insertion is present and the belly is relatively slender; in *Ictinia* it is broad and well developed. Only the medial insertion is found in *Elanus* or *Gampsonyx*, and it is well developed as in the cathartid. Both parts are present in *Aviceda*, *Necrosyrtes*, and *Pandion*. Among the falconids, only the lateral insertion is present.

*Constrictor Colli*

The *pars transversus articularis* of this muscle (fig. 182)

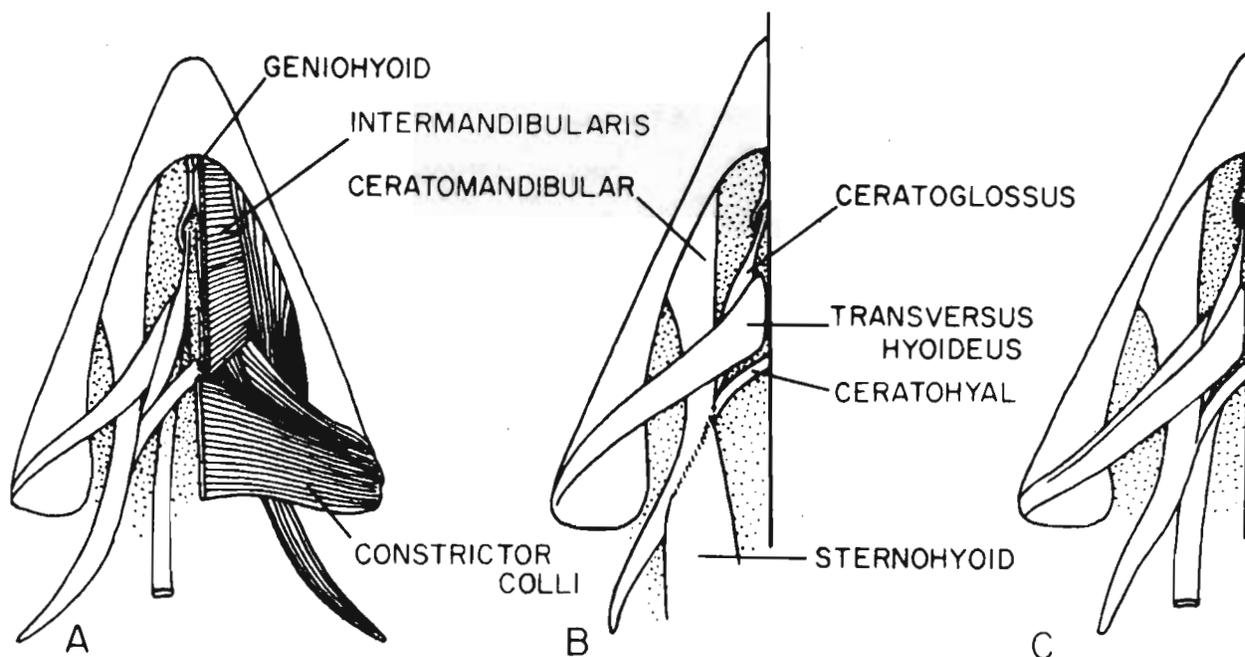


Fig. 182. Ventral view of hyoid musculature of A. generalized accipitrid and falconid, B. cathartid, C. *Pandion haliaetus*, *Aviceda suberistata* or *Necrosyrtes monachus*.

is best developed in the cathartid, the vulturine species of the accipitrid, and *Polyborus* as a corollary to the extensibility of the throat which normally is more pouch-like than in the other falconiforms. However, it is equally well developed in *Herpetotheres* and *Micrastur*. In *Coragyps* and *Milvago*, some of its fibers (*platysma myoides* of Owen, 1866) attached to the fascia lying medial to the hyoid cornus. This part of the muscle, and particularly its posterior part, is least developed in *Falco*. It is continuous posteriorly with the rest of the *constrictor* (or *sphincter*) *colli* of the neck.

The *pars colli* is best developed in the cathartid (fig. 183), and somewhat less developed in *Torgos* or *Necrosyrtes*. It is distinctive in *Herpetotheres* and *Micrastur*, particularly just behind the head. This layer is present in all, but sometimes it is hard to observe being but one layer of fibers thick and with the fibers sometimes widely spaced and adhering closely to the skin.

#### *Sternocleidocapitalis*

In the cathartid, the *sternocleidocapitalis* (fig. 184) is best developed as a continuous layer serving the entire area of the neck. This layer of muscle is well developed in all of the falconiforms and in all the *pars temporalis* and *pars clavicularis* are continuous through a part of their fibers. The *pars trapezius* is present in all and a true trapezius appears to be present in

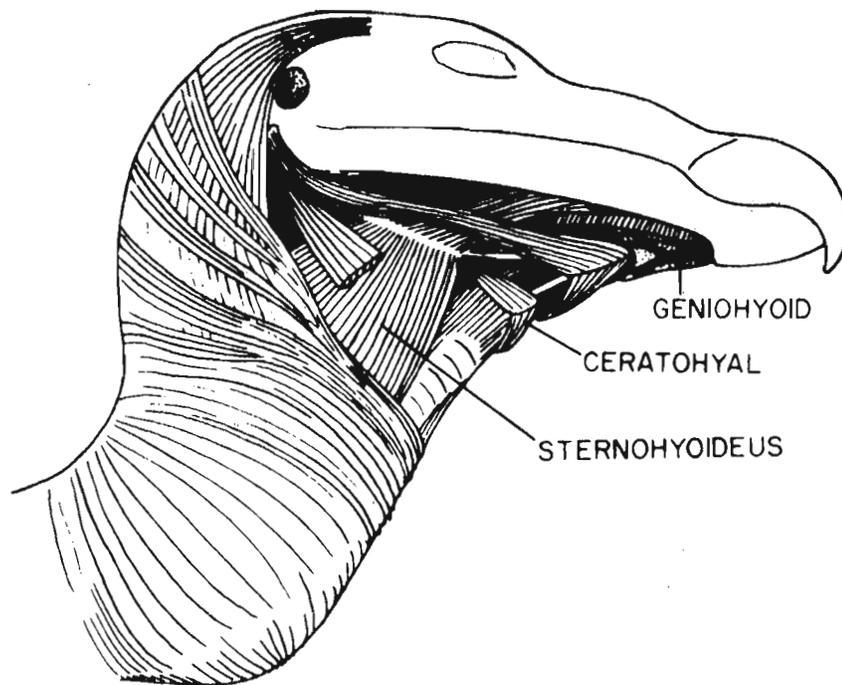


Fig. 183. Ventrolateral view of throat musculature of *Cathartes aura*.

some. It is weakest among the accipitrids where only a few fibers attach to the head of the clavicle. The *pars propatagialis* is only weakly developed (the skin of the shoulder region strongly bound to the underlying muscles) and difficult to identify in this group (observed in *Circus*, *Falco*, and *Ieracidea*). In none of these do the muscle fibers extend to the *tensor patagii* tendon. The *pars spinalis* is not present in any of the falconiforms.

#### *Dermocervicalis*

The *dermocervicalis* is best developed in *Necrosytres* (fig. 184) where a series of bellies arise from the fifth to the ninth or the tenth cervicals. This muscle is present in all falconiforms but usually has only one or two slips to a side.

#### *Sternohyoideus*

The *sternohyoideus* is best developed in the cathartid (figs. 183, 184), large in the vulturine accipitrids, *Sagittarius*, *Herpetotheres* and *Micrastur*, and least developed in the typical accipitrids and falconids. In *Cathartes* and most falconiforms, its origin underlies partially that of the *sternocleidoccipitalis*; such is not the case in *Coragyps*. The belly fans out over the skin of the neck then tapers to the insertion. In the cathartid, the insertion is along the hyoid cornua with occasionally an asymmetric bundle attaching at the posterolateral margin of the thyroid cartilage. In *Sagittarius*, there is a lateral insertion on the hyoid cornus and a narrower medial one on the posterolateral margin of the thyroid cartilage. The accipitrid and falconid agree in having a dispersed insertion along the lateral margin of the thyroid cartilage which extends forward to the basihyal in common

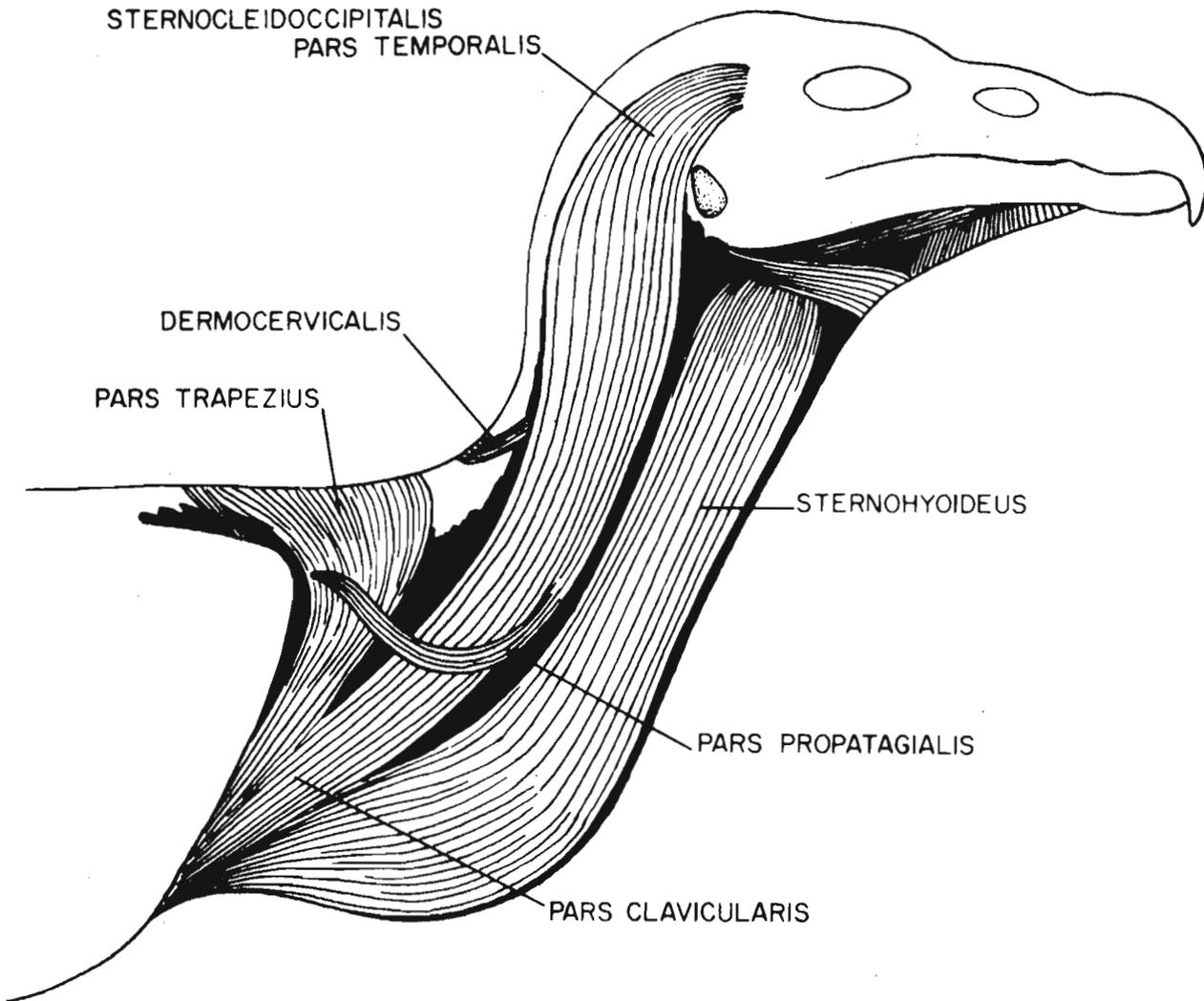


Fig. 184. Neck dermals of falconiforms, based primarily on *Cathartes aura* which actually lacks the *pars propatagialis* shown here.

with the thyreohyoideus.

#### *Sternotrachealis*

In the cathartid the *sternotrachealis* arises on either side of the midline from the dorsal margin of the sternum. The two bands are in contact medially and pass forward and dorsally to the ventral aspect of the trachea (still in contact, fig. 200). They blend with the *trachealis* of one side. In the accipitrid the origin is somewhat more lateral from the connective tissue overlying the sternocoracoid muscle (indirectly from the margin of the sternum, fig. 189). In *Pandion* these muscles insert upon the trachea asymmetrically but in contact one with the other.

The muscles of the falconid or sagittariid arise laterally from the anterior margin of the tip of the sternocoracoid process of the sternum (as in the majority of birds) rather than from the sternal margin behind or medial to the coracoid. The bands in-

sert laterally on the trachea and blend with the *trachealis*.

*Tracheobronchialis*

Among the falconiforms, the *tracheobronchialis* does not show any subdivision but there are variations in the syringeal insertion which have been described by Beddard (1898:475-476). The cathartids differ from the others in lacking a distinct syrinx and *tracheobronchialis* muscle (fig. 200).

The syrinx of *Sagittarius* is more boxlike than that of the accipitrid and the muscle inserts upon the second bronchial semiring. In the accipitrids the oval gap between the second and third semirings, occupied by the interannular membrane, is much reduced and the muscle inserts on both of these semirings or on only the second.

In the falconid the interannular membrane is large. The *tracheobronchialis* of *Falco* inserts on the interannular membrane (on a transversely elongated cartilaginous bar, not observed in *Falco sparverius*) between bronchial semirings 2 and 3 (see Sushkin 1905:62, fig. 23). The various species of *Falco* are alike, except for the bar, and agree with *Polyborus*, *Daptrius*, *Milvago*, *Ieracidea*, and *Polihierax*. In *Herpetotheres* the insertion is on the second bronchial semiring, and slightly on the first, whereas *Micrastur* is intermediate with a part of the insertion on the interannular membrane.

*Cutaneous Maximus*

The *pars latissimus* of the *cutaneous maximus* is present in most falconiforms--vestigial in *Herpetotheres* and *Micrastur* (not absent in *Polihierax* as suggested by Berger, 1956b:327). It may be present or absent (extremely vestigial?) in what may be considered related genera--*Coragyps-Cathartes*, *Necrosyrtes-Torgos*. *Necrosyrtes* is peculiar in that this muscle arises over the anterior part of the posterior slip of the latissimus dorsi (also the case in *Sagittarius*). *Gymnogyps* differs in having this muscle divided into two parts inserting with the two parts of the *pars metapatagialis*. *Sagittarius* differs in the transverse orientation of the belly (usually directed anterolaterally).

The *pars metapatagialis* arises by two to four narrow heads from ribs three and four or from each of the first four ribs (in *Falco* or *Gampsonyx* an aponeurosis adds ribs five and six). The origins are below those of the *serratus anterior pars superficialis*. *Herpetotheres* is peculiar in the origin of this muscle from two ribs and in its insertion extending from the underside of the scapular tract of feathers almost to the midline (insertion nearly matched in *Gampsonyx*).

The *pars axillaris* and *pars abdominalis* are apparent only in the falconid (fig. 185). In *Falco* or *Ieracidea*, the *pars axillaris* arises from the outer end of the deltoid crest, at the outer margin of the insertion of the *pectoralis*; the axillary connective tissue brace is only slightly developed. In the other falconids, the origin is somewhat more posterior from the connective tissue and fascia of the *pectoralis* margin between the *pectoralis* and *biceps*. The axillary connective tissue brace is stronger with the result that the belly extends first posteriorly to the brace and then ventrally to its insertion on the underside of the posterior

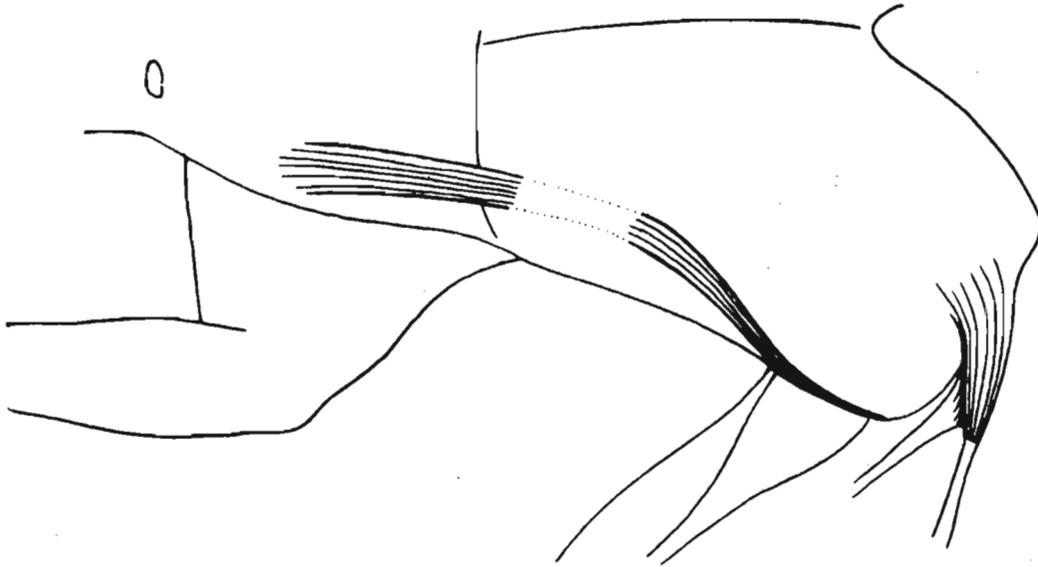


Fig. 185. Ventral view of body of *Falco sparverius* showing *pars axillaris* and *pars abdominalis* of the *cutaneous maximus*.

end of the axillary division of the ventral tract of feathers. Reduction of this part is greatest in *Herpetotheres* and *Micrastur* where only the posteriorly directed part of the belly is present--no ventrally directed fibers were observed in the connective tissue brace. The *pars abdominalis* is weakly developed in all falconids; it is vestigial in *Herpetotheres* and *Micrastur*.

In the other groups, the skin is usually closely bound to the *pectoralis* muscle in this region thus eliminating the apparent function of these muscles. A vestigial *pars axillaris* was observed in *Kaupifalco* but in no other accipitrid.

#### *Expansor Secundariorum*

The *expansor secundariorum* (see discussion in Berger, 1956a, and Jollie, 1957b) is well developed in *Sagittarius* and the falconid (fig. 188). In these a connective tissue brace (tendon) is associated with the muscle and extends from the axilla nearly to the elbow. Most of the muscle fibers arise from this brace whereas others may arise (falconid) from the skin nearby. These fibers insert along the outer three tertiaries and the inner secondaries. Other "bellies" of this complex serve the other tertiaries. In the falconid, the bracing band (tendon) is anchored in the axilla by the general connective tissue around the nerves and blood vessels. Usually at least two bands converge here to form the brace. The main one passes through the group of blood vessels and nerves and anchors broadly over the inner aspect of the *subcoracoscapularis* to the angle of the coracoid and scapula. The other extends inward along the path of the blood vessels and nerves and disappears on their surfaces. A third band from the margin of the head of the biceps is usually identifiable. In *Sagittarius* the main attachment is to the posterior margin of the *subcoracoscapularis pars scapularis posterior*.

The cathartid is much like the falconid but the belly and its

bracing tendon is much reduced. In the accipitrid the reduction is even greater, a connective tissue brace being absent but replaced functionally by more diffuse connective tissue binding of the skin to the axilla.

*Transversus Perinei*

The *transversus perinei* (fig. 186) is variable within groups

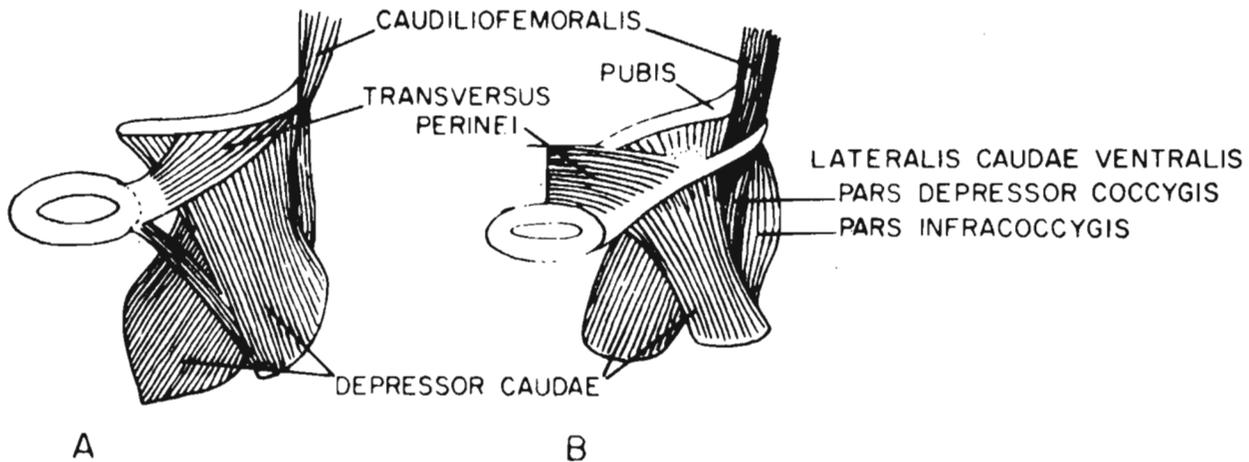


Fig. 186. Ventral view of cloacal aperture area of A. *Cathartes aura*, B. *Pandion haliaetus*.

particularly as to the site of origin and the size of the belly. The cathartid differs in that the main origin is fleshy from along the posterior margin of the tip of the pubis and the insertion is tendinous on the cloacal aperture mass. *Sagittarius* is like the accipitrid (including *Pandion*) and falconid in that the origin is usually from the posterior angle of the ilium above the *caudiliofemoralis* muscle. The origin may be diffuse as in *Gampsonyx* where it is more from the general connective tissue in this region than from any single point. *Herpetotheres* is similar. The falconids show about the same range of variation as the accipitrids.

*Depressor Caudae*

The *depressor caudae* shows some variation. In the cathartid (fig. 186) a separate slip inserts on the cloacal sphincter mass: this slip is the division *levator cloacae*. In *Falco*, *Buteo*, and *Sagittarius*, a connection between the sphincter fascia and the medial margin of this muscle occurs but a separate "*levator cloacae*" has not developed. Such a fascial connection allows both retraction and levation of the aperture.

*Lateralis Caudae Ventralis*

The *pars depressor coccygis* is a separate muscle in the falconid, accipitrid, and sagittariid; it is combined with the *pars*

*infracoccygis* in the cathartid (fig. 186).

*Sternocoracoideus*

In the cathartid, the *pars sternalis* of the *sternocoracoideus* arises from the dorsal, anterior margin of the sternum adjacent to the coracoid and extends as a thin sheet to the dorsal margin of the sternocoracoid fossa of the coracoid. In the falconid (and *Sagittarius*) the origin includes the anterior margin of the sternocoracoid process of the sternum (fig. 189). The accipitrid and sagittariid differ in that the origin in the later includes the area of the sternocoracoid fossa of the sternum beneath the posterolateral part of the coracoid.

The *pars costalis* occurs in all falconiforms although it is almost, if not entirely, lacking in *Pandion* and vestigial in *Torgos*. This part is relatively small and arises from the surface of the sternal segments of the ribs just posterior to the sternocoracoid process of the sternum. Its fibers pass forward and downward and insert by a distinct tendon on the truncated tip of the sternocoracoid process of the coracoid in the sagittariid, accipitrid, and cathartid (fig. 191). Among the falconids, the insertion is by a broad membrane along the rounded lateral margin of the coracoid. In *Pandion* or *Torgos*, this insertion is largely or entirely taken over by the *pars sternalis*.

*Obliquus Internus Abdominis*

The internal oblique of *Sagittarius* is peculiar in that the belly is restricted to the anterior half of the abdomen whereas in the others it extends, on its medial margin, posteriorly to the pubis (fig. 187).

*Rectus Abdominis*

The *rectus abdominis* is best developed in the cathartid (fig. 187). The belly extends posteriorly nearly to the pubis and laterally it is continuous, or nearly continuous with the internal obliquus.

*Transversus Abdominis*

In the sagittariid and cathartid, the fibers of this layer run nearly transversely (fig. 187). This condition is approached in *Pandion* and the pernin genera.

*Latissimus Dorsi*

The *latissimus dorsi* is fairly uniform throughout the falconiforms. Its *pars anterior* and *pars posterior* bands are most powerful in the large species (cathartids, *Torgos*), and narrowest among the falconids (fig. 190). Associated with the posterior band is the dermal *pars latissimus* of the *cutaneous maximus*. When this cutaneous muscle is lacking, the posterior part of the latissimus is closely bound to the skin. The over-all aspect of this region in *Sagittarius* is distinctive in that the very broad anterior part of this muscle and the well-developed *pars latissimus* of the *cutaneous maximus* nearly conceal the *pars posterior*.

*Teres Major (proscapulohumeralis)*

Among the falconiforms, this muscle (fig. 188) is perhaps best developed in *Polihierax* (not absent as indicated by Berger, 1956b) and *Micrastur*. *Polyborus* has a thin round muscle like the accipitrid or cathartid. *Sagittarius* is peculiar (possibly an individual variation) in that this muscle is divided into two

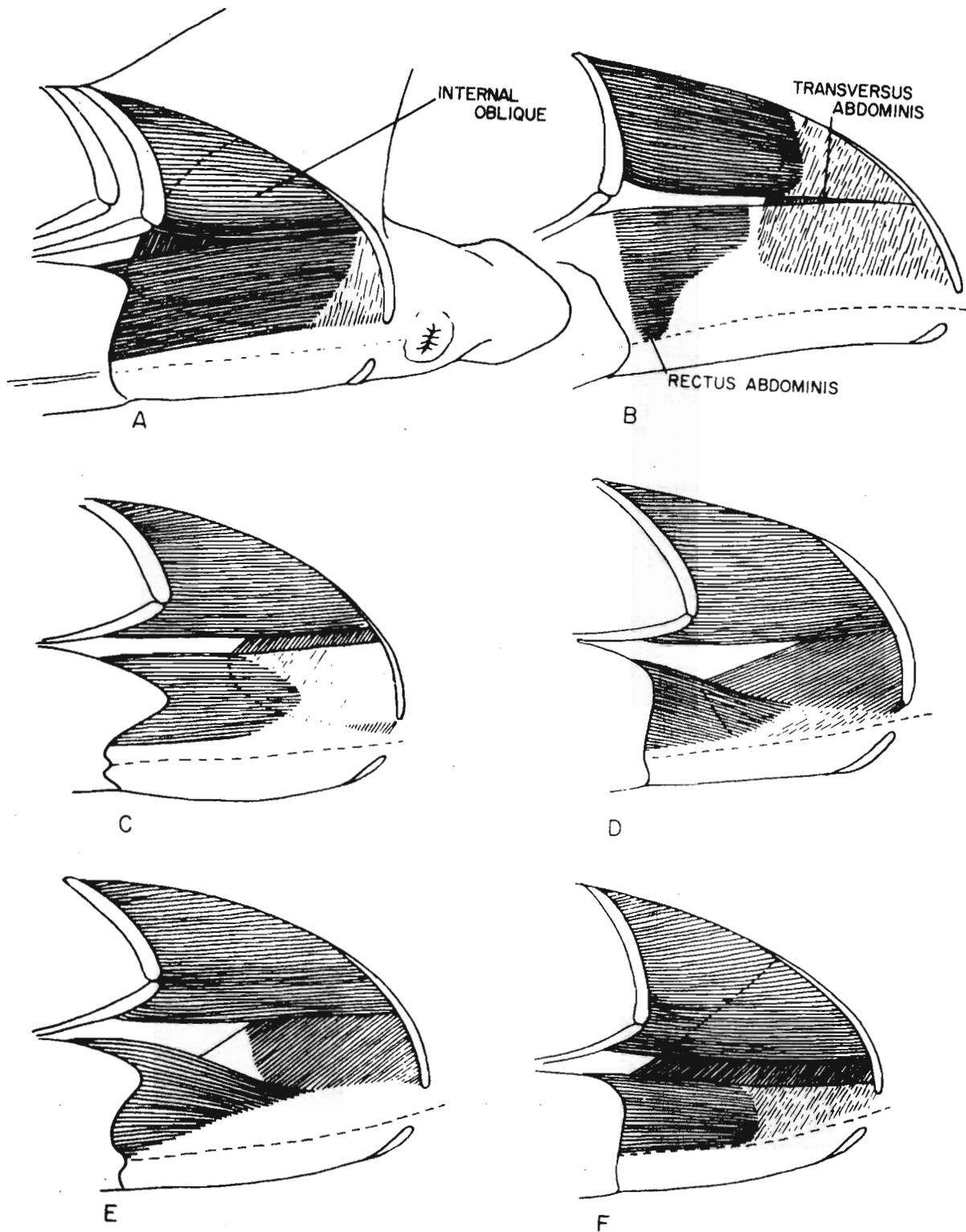


Fig. 187. Ventrolateral view of abdominal muscles, leg raised, of  
 A. *Cathartes aura*, B. *Sagittarius serpentarius*, C. *Pandion*  
*haliaetus* or *Gampsonyx swainsoni*, D. *Buteo jamaicensis* or  
*Accipiter cooperii*, E. *Elanus caeruleus*, F. *Polyborus cheriway*  
 or *Falco sparverius*.

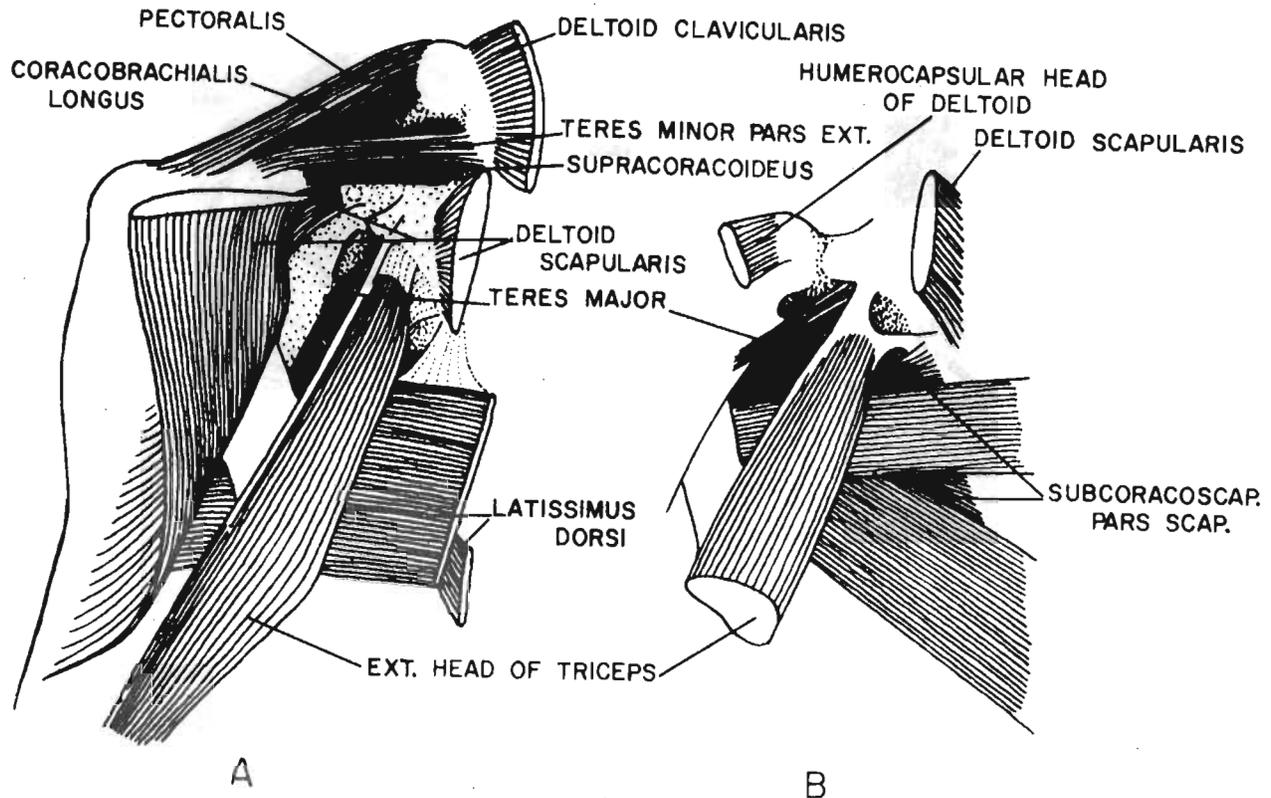


Fig. 188. Dorsal view of head of the *pars externus* of the triceps and adjacent structures in A. *Sagittarius serpentarius*, B. *Coragyps atratus*.

separate parts (bellies and insertions), which lie close together. *Subcoracoscapularis* (includes *dorsalis scapulae*)

The *pars subcoracoscapularis* has three surface subdivisions: *pars scapularis posterior*, *pars scapularis anterior*, and *pars coracoideus*. The falcons differ in that the coracoid division is completely separated from the others at its origin and throughout most of its belly (fig. 189); its origin extends down the shaft of the coracoid medial to the insertion of the *sternocoracoideus*. *Polyborus* and *Herpetotheres* are like the cathartid in showing a massive, closely-connected, coracoid division, but in the cathartid the *sternocoracoideus* is concealed medially (lies under the ligamentous sheet attaching the coracoid to the sternal margin).

The coracoid division in the accipitrid and *Sagittarius* is much smaller and closer to the angle while the anterior and posterior scapular divisions are hardly separable. *Sagittarius* has the smallest coracoid division and there is a large gap between

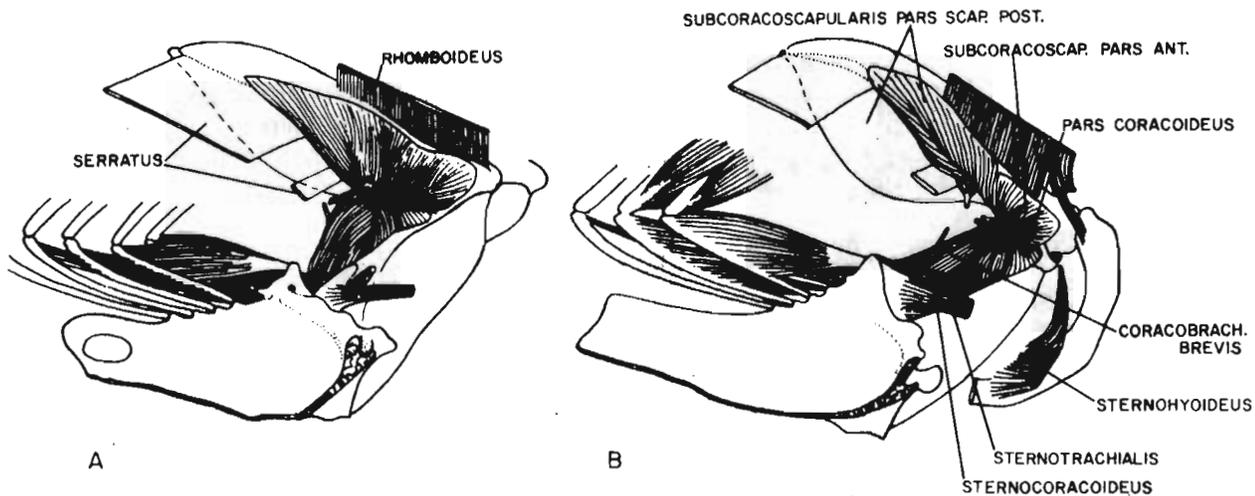


Fig. 189. Medial view of the shoulder region of A. *Buteo jamaicensis*, B. *Herpetotheres cachinnans*.

its area of origin and that of the *coracobrachialis brevis*.

The *pars scapularis posterior* (*dorsalis scapulae*) is constant in its form and relationships, although in *Vultur* the insertion tendon bifurcates slightly (Fisher, 1946:586).

#### *Deltoideus*

The *pars clavicularis* gives rise to both the *tensor patagii longus* and *tensor patagii brevis* tendons (fig. 190). In the falconiforms, a distinct slip from the *sternocleidoccipitalis* is lacking although a vestigial one may be found in the cervical patagium. A slip from the *pectoralis* is common to all. The patterns of the *tensor patagii* tendons is somewhat distinctive. The *brevis* tendon of *Sagittarius* has an outer accessory division which separates before the midpoint and joins a brace from the *longus* tendon. Also the *brevis* tendon spreads out distally so that the insertion is more diffuse and with less well-marked braces. A connective between *longus* and *brevis* tendons also occurs in the cathartids, *Gypaëtus*, *Pandion*, and *Gypohierax*; it is indicated in *Torgos* and some falconids.

Among the cathartids, according to Fisher (1946), the *brevis* is a wide band in *Coragyps* and *Sarcoramphus* whereas in *Cathartes*, *Gymnogyps*, and *Vultur* there are several subdivisions of this tendon which insert at different points. From my dissections, *Coragyps* is much like *Cathartes*, although the bands are closely connected to the patagial skin in all and difficult to separate.

The accipitrid and falconid may have a single narrow *brevis* tendon or one that bifurcates. The tendons of these two groups are better defined (do not fade into the adjacent connective tissue). In *Pandion* the *brevis* fans out distally and is indis-

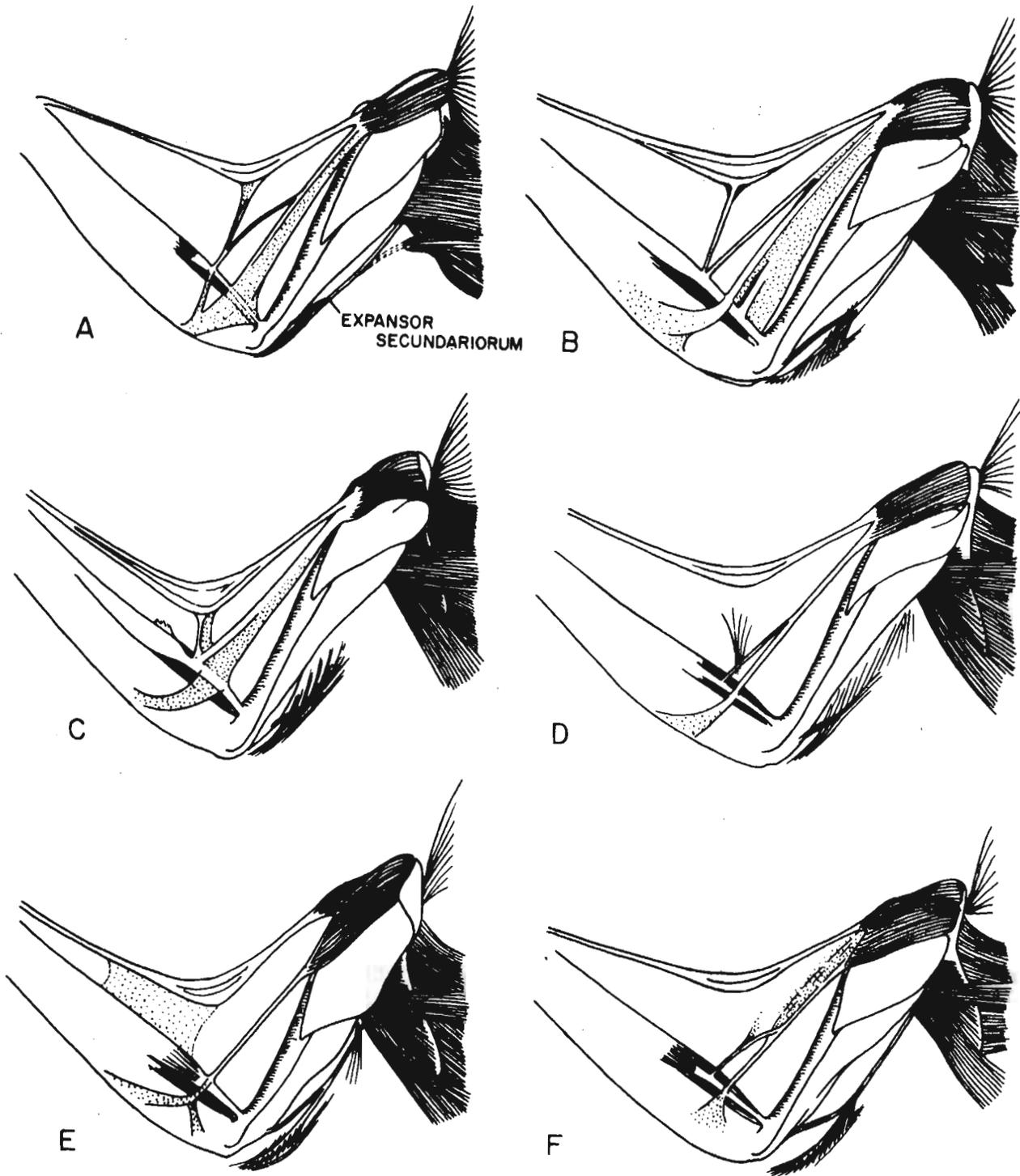


Fig. 190. Dorsal view of shoulder muscles and tensor patagii area of wing in A. *Sagittarius serpentarius*, B. *Cathartes aura*, C. *Pandion haliaetus*, D. *Buteo jamaicensis*, E. *Falco sparverius*, F. *Polyborus cheriway*.

tinct in its middle section.

The *pars scapularis* of the *deltoideus* distinguishes the cathartid in that the origins of the two heads are continuous and the *os humerocapsularis* is lacking. The sagittariid, accipitrid, and falconid have two distinct heads, the deeper one from an *os humerocapsularis* (fig. 188).

#### *Teres Minor*

The *pars externus* (fig. 188) is well developed in the cathartid and arises along the outer aspect of the tip of the head of the clavicle; its deeper division arises from the acromion process and the anterior, outer margin of the scapula. These two divisions insert separately in *Cathartes* (slightly fused), *Gymnogyps*, and *Vultur*. In *Sarcoramphus*, the deeper division is more or less lacking. (*Fregata* lacks it.) Only the deeper division appears to be present in the sagittariid, accipitrid, and falconid. The accipitrid, including *Pandion*, differ in that the belly inserts along the posterior margin of the tendon of the *supracoracoideus* for most of its length. In the sagittariid and falconid, the belly is free and its insertion is confined to the point of insertion of the *supracoracoideus* and beyond.

The *pars internus* occurs only in the cathartid. It arises from the manubrial region of the sternum and the medial edge of the coracoid; the belly overlies the medial aspect of the *supracoracoideus* and extends out through the triosseal canal along with that muscle. The broad tendon of insertion overlies that of the *supracoracoideus* and attaches in common with the *pars externus*. This part is innervated along with the *externus* and is thus not a part of the *supracoracoideus* (see Fürbringer, 1902, footnote p. 535).

#### *Triceps Brachii*

The triceps of the cathartid differs in that the *pars externus* (long head) has two separate and distinct tendons of origin, one at right angles to the other (fig. 188). The first continues the axial line of the belly and attaches to the scapula just behind and above the glenoid process; this is the main and typical origin. The second is a brace which extends medially from the anterior end of the belly to attach to the dorsal aspect to the scapula below the anterior margin of the *pars scapularis posterior* of the *subcoracoscapularis*. In this group the brace to the humerus is broad and strong.

The scapular origin is widest and entirely tendinous in *Sagittarius*, but there is a broad brace suggesting the cathartid. In the other falconiforms, the glenoid origin is the only one and consists of a strong round tendon (as in the cathartid) and dorsomedially there may be a thin tendinal or fleshy continuation.\*

\* Beddard (1898:474) commented on the variations of origin of the *pars externus*, "The *anconaeus* arises in *Polyboroides* [= *Gymnogenys*] and in some other types by a single head from the scapula, which is partly fleshy and partly tendinous. In *Vultur* [= *Torgos*] *auricularis*, on the other hand, the muscle arises by two completely tendinous heads, so that the muscle has not that

The muscle of the accipitrid and falconid are much the same except that in the former the origin tends to be broadly tendinous and a humeral brace is better developed. Further distally a broad connective tissue band braces the belly of this part to the humerus in all.

The *pars internus* is well developed in all, and a *pars axillaris* is present but sometimes extremely minute in the falconid and cathartid (fig. 190). This part arises off the tendinous band of the *expansor secundariorum*.

#### *Pectoralis*

The *pectoralis* of the cathartids is completely divided into a *pars superficialis* and a *pars profundus*. In the other groups the belly may show some division but the layers do not seem to correspond to the parts of the cathartid. *Sagittarius* (fig. 191)

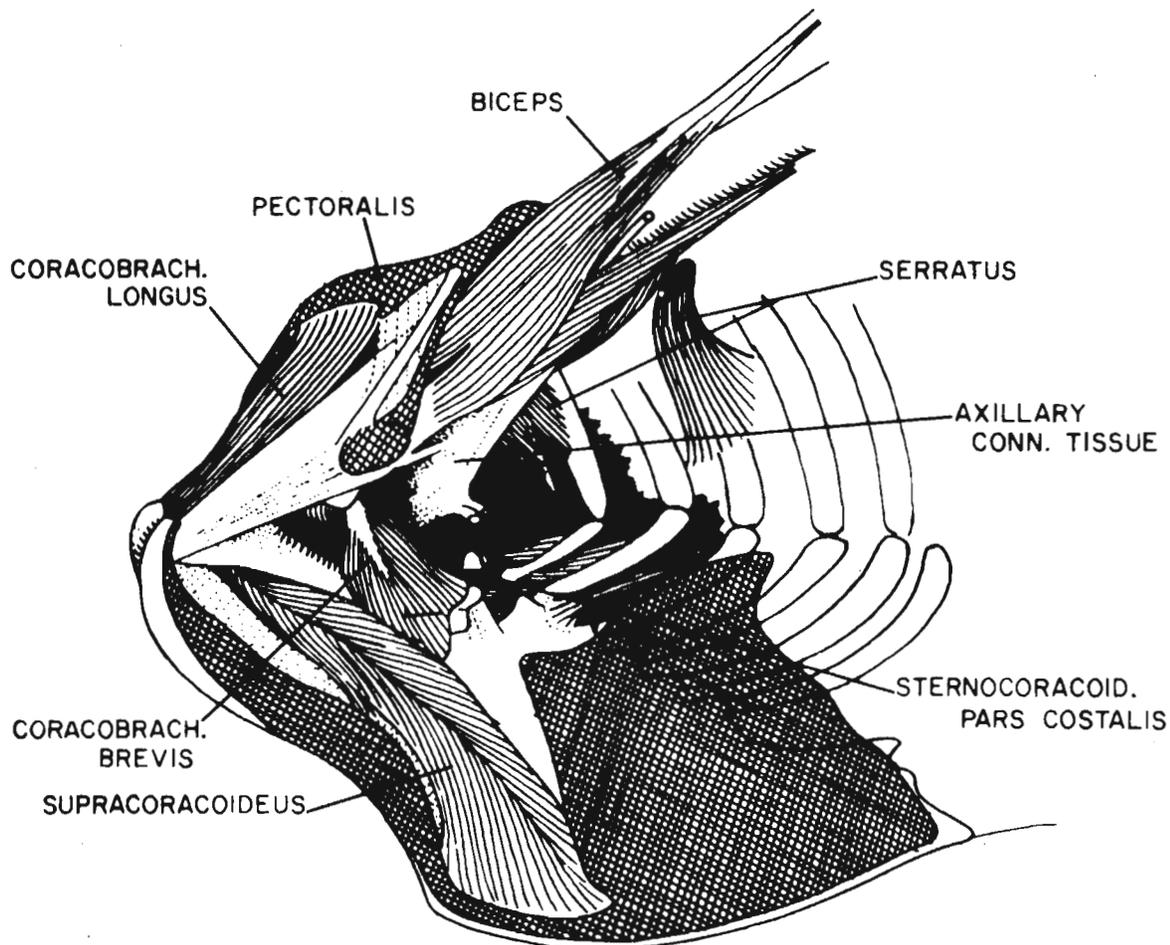


Fig. 191. Lateral view of body, wing raised, and pectoralis muscle removed of *Sagittarius serpentarius*. Origin and insertion of the pectoralis are cross hatched.

\*\*\*\*\*  
 value in the classification of the *Accipitres* that I at one time thought."

has a greater area of origin for this muscle beyond the margin of the sternum than any other falconiform, this correlates with the shortening of this bone. A *pars patagiialis* occurs in all but presents no useable information.

*Supracoracoideus*

The *supracoracoideus* is largest in the cathartid (excluding *Teratornis*--fig. 191), its origin extending nearly to the posterior end of the sternum (fig. 160). In the accipitrid, falconid, *Sagittarius*, and *Teratornis*, it is limited to the anterior half.

*Coracobrachialis Brevis*

In the falconid, the *coracobrachialis brevis* (*posterior*) arises off the coracoid and an adjacent area of the sternum. As a result the tip of the sternocoracoid process of the coracoid is concealed whereas in the other falconiforms it is exposed and braced by a strong ligament to the sternum (fig. 191).

*Biceps Brachii*

The *biceps* of *Sagittarius* is different in that the bellies of the coracoid and humeral origins are slightly separated and soon fuse (fig. 191). The insertion tendon gradually divides and attaches to both the radius and ulna. The insertion tendon shows a slight subdivision in some accipitrids (*Milvus*, *Pandion*).

*Tensor Fascia Latae*

In the cathartid, the *tensor fascia latae* arises along the entire iliac crest from the posterior margin of the *sartorius* to near the posterior end of the ilium. The belly, near its insertion, is braced to the outer aspect of the shank by a fascial binding. The preacetabular part inserts by an aponeuroses over the *vastus lateralis* as in the other falconiforms while the postacetabular part, thick and fleshy in *Coragyps* and *Sarcoramphus* and proportionally smaller in *Cathartes* and *Gymnogyps*, inserts along the posterior margin of the *vastus lateralis* and the anterior part.

The other falconiforms lack the postacetabular division of this muscle. In *Sagittarius* the two slips indicated in the accipitrid or falconid muscle are separated (fig. 192). *Herpetotheres* and *Micrastur* approach *Sagittarius* in differentiation of these slips.

*Iliofibularis*

The anterior proximal margin of this muscle is not fused to the *tensor fascia* sheet in the cathartid as it is in the others (fig. 192).

*Gluteus Maximus (piriformis)*

*Pandion* is peculiar among the falconiforms in that the *gluteus maximus* is fused with the *gluteus medius* (*gluteus profundus*). Hudson (1948:103) did not record this fusion for his specimen. It may be that there is some individual variation in the species.

*Piriformis (iliotrochantericus medius)*

The falconiforms can be divided into two groups on the basis of the fusion of the *gluteus minimus* and *piriformis* (fig. 192). In the accipitrid, *Pandion*, falconid, and *Sagittarius* these muscles are nearly or completely fused, and the line of fusion is indicated by the point of penetration of the superior gluteal nerve. In the cathartid these two muscles are separated and distinct as, for example, in the crow.

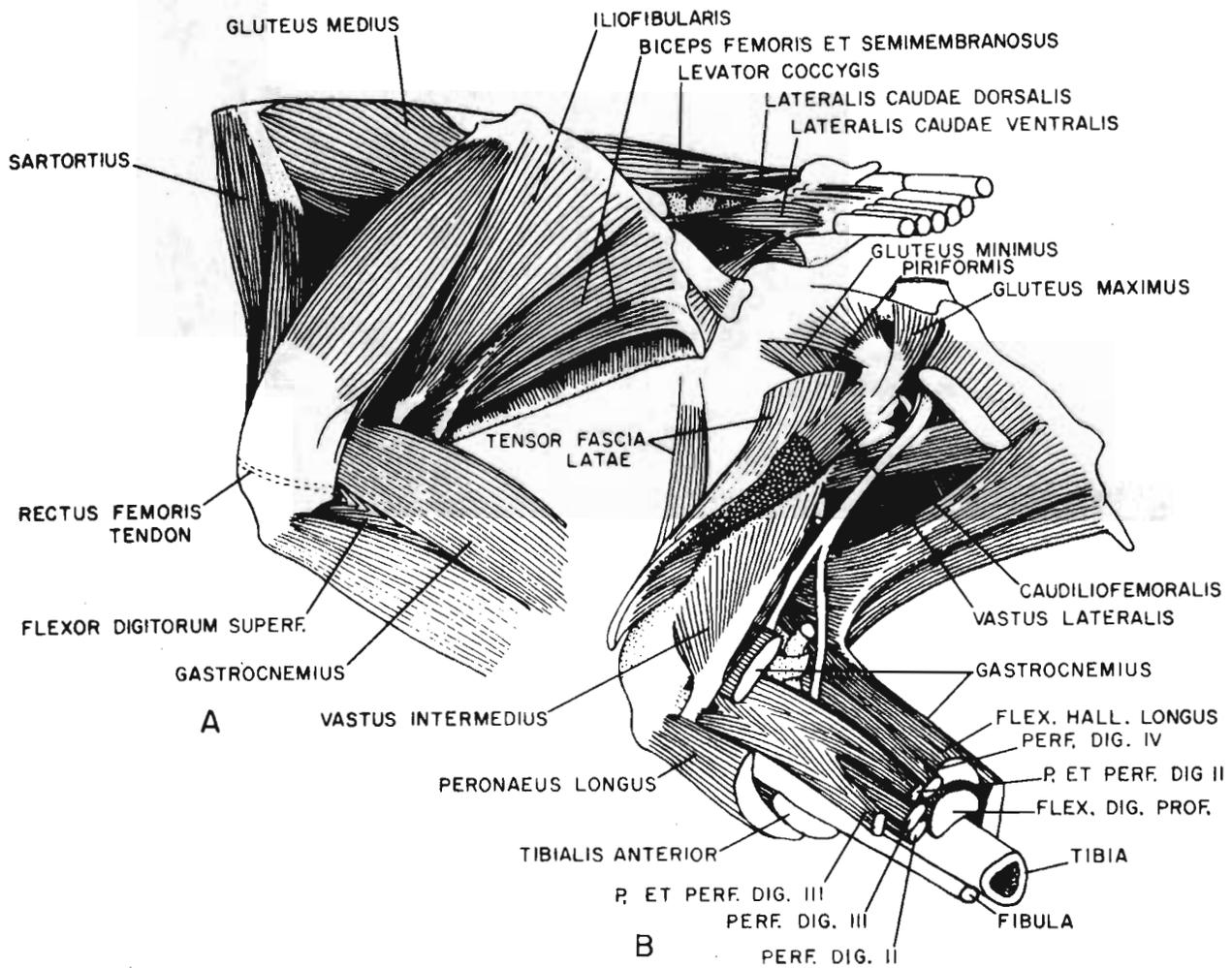


Fig. 192. Lateral view of thigh and upper shank of *Sagittarius serpentarius*. A. External layer, B. deeper layer (*extensor digitorum longus* not shown).

*Rectus Femoris (ambiens)*  
The belly of the *rectus femoris* (fig. 193) is present and

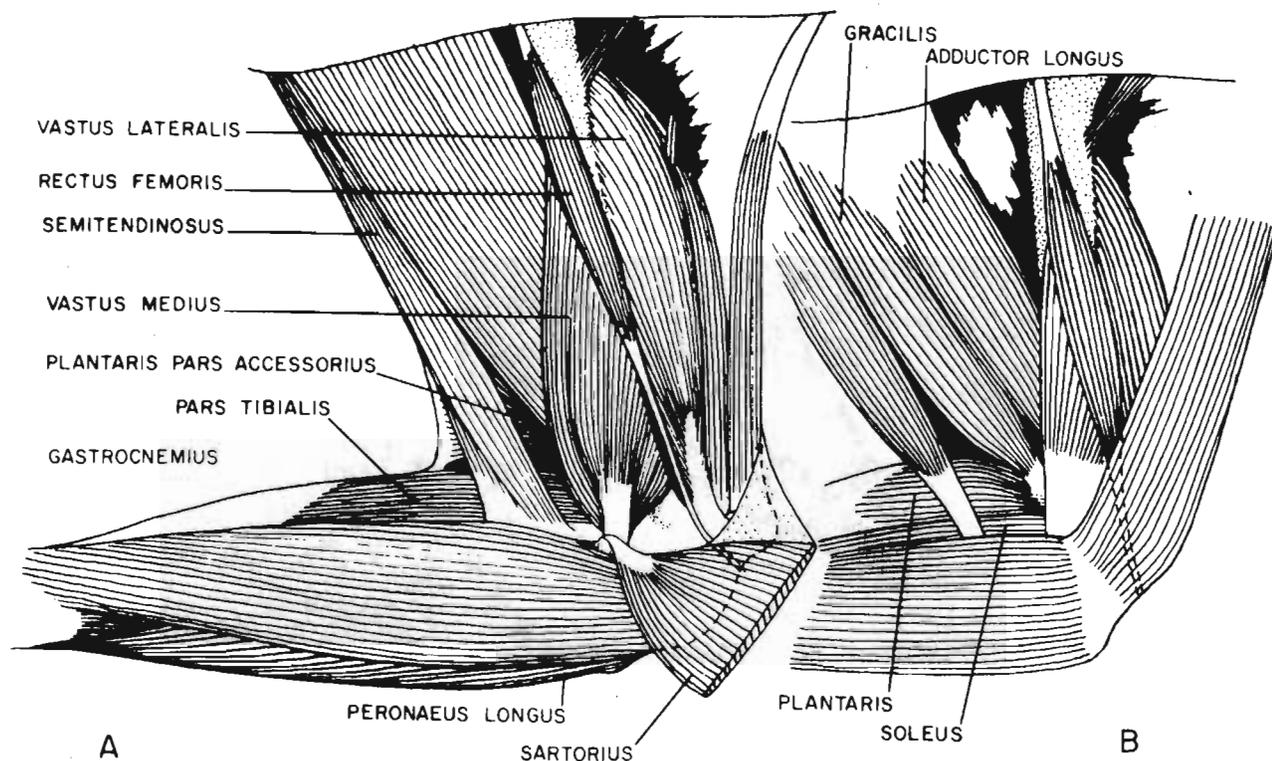


Fig. 193. Inner aspect of thigh of A. *Sagittarius serpentarius*, B. *Pandion haliaetus*.

constant in its form in all of the falconiforms with the exception of the pernin kites (only *Aviceda* and *Chondrohierax* dissected). Here, it is lacking although the tendon is present in the shank. In *Chondrohierax* the tendon arises deep to, and from, the fibular attachment of the *iliofibularis* frenula or the lateral condyle of the femur and acts as an origin for the *flexor digitorum superficialis* muscle. In *Aviceda*, it acts mainly as an origin for the *pars perforatus digiti II* as in the typical accipitrid. In these kites, the remnant of the tendon passes lateral to the insertion of the *iliofibularis*. *Elanus* (and *Gampsonyx*) is the only accipitrid in which this muscle is fully developed. Yet the tendon passes lateral to the *iliofibularis* insertion and acts as a general origin for the entire complex of the superficial digital flexor. *Pandion* has a relatively broader *rectus* than most accipitrids. The tendon passes medial to the *iliofibularis* insertion

and acts as the only medial origin for the superficial flexor complex.

The falconid differs from the other falconiforms (with the exceptions cited above) in that the tendon of this muscle usually passes lateral to the *iliofibularis* insertion (Hudson, 1937:16; 1948:104) and serves as a common origin for the parts of the superficial digital flexor (as in *Elanus*). (The tendon usually ends on the belly of the *pars perforatus digiti III.*) *Polihierax* is an exception (Berger, 1956b:320); here the tendon passes medial to the *iliofibularis* insertion. *Sagittarius* and the cathartid are like the typical accipitrid.

#### *Vastus Lateralis*

In the falconiforms, the *vastus intermedius* and *vastus lateralis* are not separable. The *vastus lateralis* is somewhat divisible into outer and inner parts at the point of penetration of the nerve (fig. 193A). Here, superficial layers of muscle fibers are evident (the division *lateralis*), but, when seen in section, there is no separating membrane present. The insertion tendon of the internal division is poorly marked in accipitrids, falconids, and cathartids; it is stronger in *Pandion* and well marked in *Sagittarius*.

#### *Vastus Medius (femoritibialis internus)*

There is some variation in the form of this muscle in the accipitrids. In *Buteo* it appears to have two parts whereas in most genera only one part is evident. *Necrosyrtes* is similar to *Buteo*; here, the proximal end of the muscle is partially divided. *Aquila* shows only a surface tendon in the position of the tendons of *Buteo* whereas *Pandion*, *Circus*, *Accipiter*, *Ictinia*, *Elanus*, *Aviceda*, and the falconid genera have a thin surface fascia, which condenses distally and along the posterior margin to form a superficial part of the insertion tendon. This type of muscle corresponds only to the medial division of *Buteo*. The muscle of *Pandion* has a median superficial fissure that does not correlate with any deep tendon and its significance is questionable. In *Sagittarius* several bundles form the belly and converge to the insertion (fig. 193A). *Cathartes* shows distinct medial and internal divisions, but *Coragyps* has only the central tendon of two such (unseparated) parts. The internal division of *Cathartes* is very small compared with the muscle of *Buteo* but otherwise resembles it. The variations of the *vastus medius* appear to have little, if any, taxonomic value and cannot be correlated with size or function.

#### *Vastus Intermedius*

*Sagittarius* is unique in that there is a separate and distinct *vastus intermedius* (fig. 192B).

#### *Biceps Femoris et Semimembranosus*

The *pars lateralis (biceps femoris)* is present in *Sagittarius* (fig. 192) and the cathartid, it is missing in the accipitrid and falconid. This muscle is associated with a part of the *plantaris* (the accessory head) and is further identified by its origin and its position lateral to the nerve of the *semitendinosus*. The insertion of this muscle on the "accessory" is characteristic (except in *Dryobates pubescens*, a woodpecker, where it inserts like

the *pars medialis*).

The *pars medialis (semimembranosus)* is found only in the falconid. It arises in common with the *semitendinosus* and lies medial to the nerve of that muscle, (*Falco*, *Ieracidea*, and *Poli-hierax*) or the nerve passes through its belly. It is further identified by its insertion near the *semitendinosus*.

#### *Semitendinosus*

*Sagittarius* differs in that the *semitendinosus* inserts nearer the head of the tibia than in the other types.

#### *Gracilis et Adductor Longus*

The cathartid differs from the others in that this superficial adductor layer, the *gracilis et adductor longus* fused, more or less in different genera, to the deeper adductor except near the origin of the *pars adductor longus*. The *pars gracilis* is indistinguishable (weak line of separation in *Coragyps* and *Gymnogyps*) from the posterior margin of the deeper layer in my specimens, but Fisher (1946:668) described it (also Hudson, 1948:106) as distinct. Fisher's description of the form of the *pars gracilis* as "A thick spindle-shaped posterior part" is not applicable to my specimens. In most accipitrids and falconids the *pars gracilis* is distinguishable by the length of its fibers and separate insertion on the origin of the *plantaris* (fig. 193B). In *Sagittarius*, the cathartids, some accipitrids (*Ictinia*, *Aviceda*, *Elanus*, *Necrosyrtes*) and some falconids (*Polyborus*) it is, at best, only poorly marked.

#### *Adductor Brevis et Magnus*

The *adductor brevis et magnus* of the cathartids tends to be fused with the superficial adductor layer. In the others this layer is free. The muscle of *Pandion* arises by a relatively narrow, strap-like tendon just anterior to the origin of the *semitendinosus*. The belly fans out from this origin to its thick and fleshy insertion along the distal third of the shaft of the femur. In the remainder of the falconiforms, the muscle arises along the ventral edge of the ischium for some distance and inserts as in *Pandion*.

#### *Obturator Externus*

The *obturator externus* is constant throughout the falconiforms with the exception of *Sagittarius* where the *pars internus* arises from the inner surface of the posterior, lateral part of the ilium, as well as from the inner aspect of the ischium and pubis. A situation similar to *Sagittarius* is found in the chicken. In the large cathartids (*Sarcoramphus*, *Gymnogyps*, *Vultur*), this muscle has two tendons, the more dorsal one being the longest; these fuse at the distal end of the belly to insert as one. The dorsal belly of the *pars externus* is lacking only in *Pandion* (Hudson, 1948:106).

#### *Caudiliofemoralis*

The *pars caudatus* of the *caudiliofemoralis* is absent in *Sagittarius*, *Gymnogyps*, *Sarcoramphus*, and *Vultur* but present in *Coragyps* and *Cathartes* and other falconiforms. Both the origin and insertion are tendinous when this muscle is present in the cathartid. Its loss in the condors is an indication of their specialization from the ancestral condition shown by the smaller species. Among the accipitrids the origin is usually by a short flat tendon and the insertion is tapered and tendinous. However,

the length and width of the origin tendon varies as does that of the insertion. In *Pandion*, *Torgos* and *Necrosyrtes*, the insertion is by a long and thin tendon. In *Circus* and *Ictinia* it is broad and fleshy. *Milvus* shows a more or less intermediate condition. The falconid resembles the small cathartids and some of the accipitrids in having a long thin tendon of origin and a short, fairly broad insertion tendon. *Sagittarius* is the only falconiform which has the *pars iliacus* (fig. 192B).

#### *Gastrocnemius*

The pattern of the *pars lateralis* and *pars medialis* of the *gastrocnemius* (fig. 194), as well as that of the *plantaris* and *soleus*, differentiates the sagittariid and cathartid from the other falconiforms. The cathartid and *Sagittarius* agree in having the medial part arise in part from the patellar fascia. *Sagittarius* resembles the accipitrid in having strong tendons for both parts. These tendons are just distinguishable from the general sheet in the cathartid. In the falconid the medial tendon is only slightly marked (strongest in *Herpetotheres* and *Micrastur*).

#### *Plantaris*

The cathartid and *Sagittarius* are distinctive in having both a *pars accessorius* and a *pars tibialis*. In the cathartid, the *pars tibialis* inserts with the lateral part of the *gastrocnemius* rather than separately or with the medial part. The falconid and accipitrid are similar.

#### *Soleus*

The *soleus* is lacking in *Sagittarius* (and *Chondrohierax* among the accipitrids). It is a separate entity only in the falconid and cathartid. In the cathartid, the belly is very short (less than one-fourth the length of the tibia), and the tendon is long and slim. In the falconid, the belly may extend two-thirds or more of the length of the tibia and is partly exposed posteriorly below the margin of the medial part of the *gastrocnemius*. The extreme in the falconid group is found in *Herpetotheres* and *Micrastur* where the distal part of the belly is fused with the medial part of the *gastrocnemius*; the insertion tendon is separate. In *Polihierax*, the belly has a small slip which inserts with the *plantaris*. The muscle otherwise is like that of *Falco* (may be individual variation--not reported by Berger, 1956b). In the accipitrid, the *soleus* is always vestigial and fused distally with the *gastrocnemius*. It is lost in *Chondrohierax*. The proximal end of the belly (lateral to the insertion of the *semitendinosus*) is most distinct in some of the kites and vultures and in *Pandion* (fig. 193B). It was also well developed in a specimen of *Accipiter striatus*.

#### *Flexor Digitorum Superficialis*

The *flexor digitorum superficialis* has five parts in birds (fig. 192B) which share common origins but which usually insert separately, across the heel and down the posterior aspect of the tarsometatarsus, on the toes. The configuration of the parts of this muscle distinguish each of the groups of the falconiforms.

The *pars perforans et perforatus digiti II* lies entirely exposed laterally in the falconid; its origin is from the margin of the *tibialis anterior* (or *peroneus longus*) proximally and from

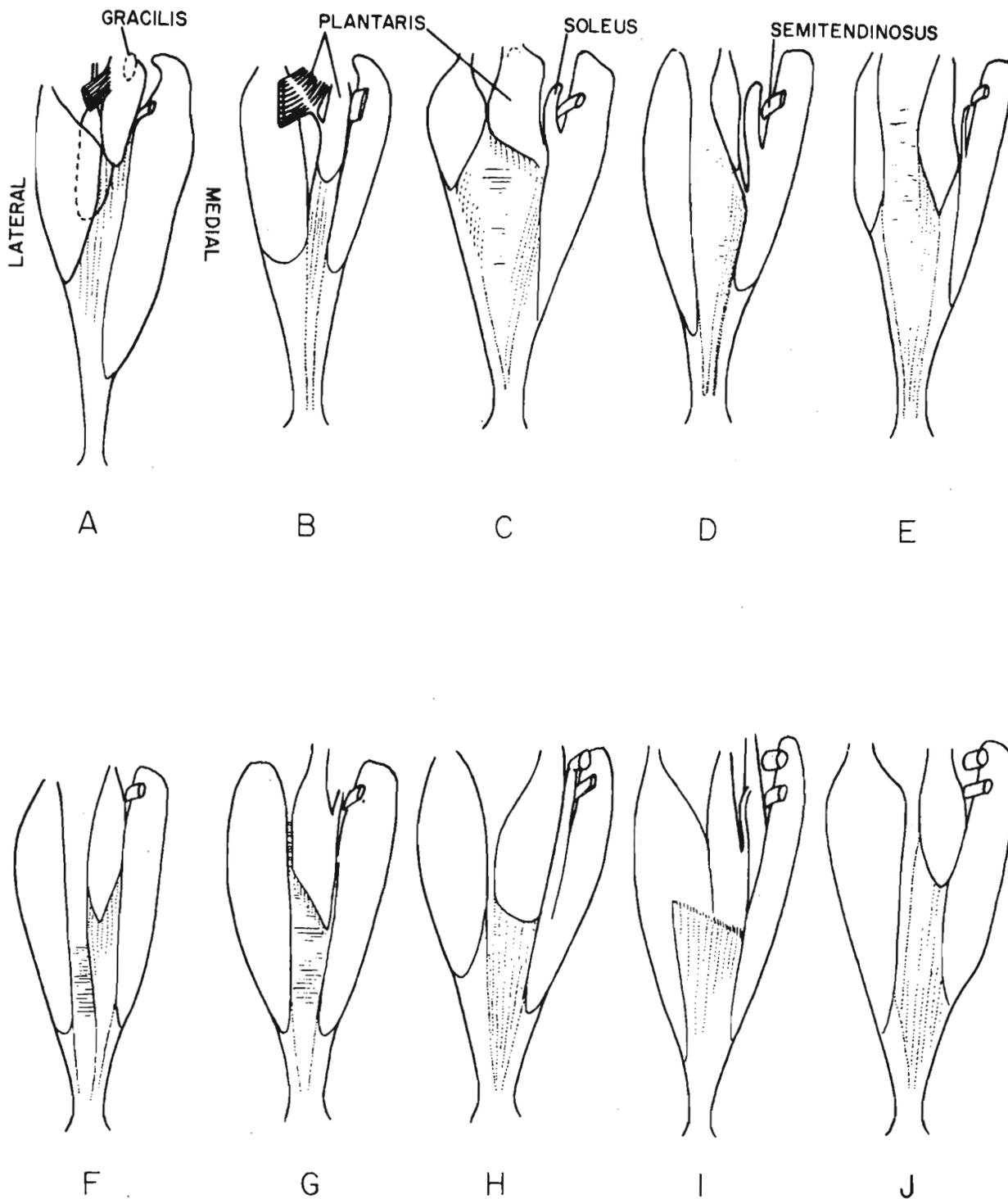


Fig. 194. Semidiagrammatic dorsoposterior views of gastrocnemius-plantaris pattern in A. *Cathartes aura*, B. *Sagittarius serpentarius*, C. *Pandion haliaetus*, D. *Elanus caeruleus*, E. *Ictinia plumbea*, F. *Milvus migrans*, G. *Necrosyrtes monachus*, H. *Micrastur ruficollis* or *Herpetotheres cachinnans*, I. *Polihierax semitorquatus*, J. *Polyborus cheriway*.

the fibula distally. The other groups agree in having the anterior origin from the margin of the *perforans et perforatus digiti III* (the *rectus femoris* tendon possibly involved here in most falconids and some accipitrids) and the belly is partly or entirely (in *Sagittarius*) concealed by the lateral part of the *gastrocnemius*. In *Pandion* the tendon of this part and that of the *pars perforatus digiti II* fuse in the calcaneal region, and throughout their tarsal length, and insert in common on the base of digit II. Correlated with its restricted function, the belly of this muscle in *Pandion* is proportionally smallest.

The *pars perforans et perforatus digiti III* of the falconid is concealed by the previous part. In most of this group (except *Polihierax*) and in some accipitrids (*Avideda*, *Chondrohierax*, *Elanus*, *Gampsonyx*) it arises in part from the *rectus femoris tendon* along with the *pars perforans et perforatus digiti II* and the *pars perforatus digiti IV*). The cathartid has a distinct fibular origin along the line of contact with the *tibialis anterior* whereas the other groups have little if any direct origin from that bone, except at the extreme proximal end. The origin, from along the margin of the *tibialis anterior* (or *peronaeus longus*), is restricted or even lacking in the accipitrid but extensive in the falconid and in *Sagittarius*.

The *pars perforatus digiti IV* has both lateral and medial origins, one or the other of which may be developed to the near exclusion of the other. The medial head of the cathartid is large and fleshy (arises by a very short round tendon) whereas the lateral head is a broad aponeurosis as well as an attachment to the bellies of the previous parts (in *Cathartes* and *Coragyps*). *Sagittarius* differs in having fleshy heads from both the lateral head and a tendinous, or largely tendinous, medial one. *Gampsonyx* and *Elanus* lack a distinct lateral head and have a large fleshy medial one for this part. *Pandion* is peculiar in lacking a distinct medial tendon; this origin is entirely replaced by the *rectus femoris tendon*. The falconid differs from the accipitrid in that the lateral head arises near or at the proximal end of the shank and, in part, from the *rectus femoris tendon* (see above) whereas in the latter the aponeurosis of origin extends to the middle of the belly of the *pars perforans et perforatus digiti II*. In those accipitrids in which the *rectus* tendon passes lateral to the *iliofibularis* insertion (see above), this tendon serves as the only lateral origin. The medial head is tendinous in the falconid, or, as in *Polyborus*, is represented by a few, fleshy fibers from the medial tendon which also acts as a part of the origin of the *pars perforatus digiti III*.

The *pars perforatus digiti III* typically has two separate heads of origin. In *Elanus* and *Gampsonyx*, these are completely separated and their tendons do not fuse until they pass over the calcaneal mass. A strong vinculum connects the tendon of this part with that of the *pars perforans et perforatus digiti III* near the distal end of the tarsometatarsus in *Sagittarius* and the cathartid. In *Vultur* (Fisher, 1946:679), a vinculum occurs between the tendon of this belly and that of the *pars perforatus digiti IV*.

The *pars perforatus digiti II* in the cathartid and *Sagittarius*

arises mainly from the medial origin from below the belly of the *par perforatus digiti IV* whereas in the accipitrid, *Pandion*, and falconid the lateral head gives direct origin. The *rectus* tendon acts as a secondary origin in each instance; it is more involved in the accipitrid and cathartid and less involved in the falconid and *Sagittarius*.

The relative positions of the tendons in the calcaneal region is constant in all members examined, the flexors for digit II being deep and somewhat separate from the other tendons. The genus *Falco* has an ossified tibial cartilage lying over the hypotarsus in this area (see fig. 143), which is lacking in the other falconids.

The insertions of the various parts of this complex are variable (fig. 195) but do not show any correlation as to group.

Each of the several groups of the falconiforms can be characterized on the basis of this muscle and each type appears to be completely independent of the others. The greatest variation is found among accipitrids with which *Pandion* can be associated as the most aberrant style. *Elanus* and *Gampsonyx* differ in many ways from the other accipitrids and show some similarity to the pernins (*Chondrohierax* and *Aviceda*).

*Flexor Hallucis Longus*

The origin of the *flexor hallucis longus* differs in *Pandion* from that of the accipitrid and falconid in that it arises laterally by a powerful tendon. The cathartid differs in that there is both a lateral and medial origin from the femoral condyles between which the femoral origin of the superficial flexors arises (*pars perforatus digiti IV*). The double area of origin is higher on the femur in *Sagittarius* than in the other groups. In the cathartid, the two areas of origin are continuous below the medial head of the *flexor digitorum* complex. The belly of this muscle is much smaller in the cathartid than in the other falconiforms (less than one-half the length of the tibia), and it is largely concealed by the superficial flexor mass.

The nature of the vinculum between the tendons of the *flexor hallucis* and *flexor digitorum longus* is described by Beddard (1898: 475) as of three types, one of which, ascribed to *Aviceda* (*Baza*), lacks a recognizable division to the second digit. This genus (fig. 196C) is peculiar in that instead of a single branch, serving digit II, passing through the vinculum, two distinct branches occur. The first of these serves digits II and III and the second, lying above the first, serves digits III and IV. In no other accipitrid examined is there a distinct branch to digits III and IV.

*Chondrohierax* is peculiar in that it shows no branches to the front digits associated with the vinculum, or elsewhere, and thus matches Beddard's third type. The concurrence of vinculum and branch to digit II is not limited to *Aviceda* but occurs in most accipitrids. *Torgos* is peculiar in the length of the vinculum which extends nearly one fifth the tarsal length of the deep flexor tendons.

In general the insertion of this muscle in the falconid is like that of the accipitrid except that the tendons are ossified. *Pandion* and the cathartid are similar in that the tendon of the *flexor hallucis* fuses for nearly half its tarsal length with that

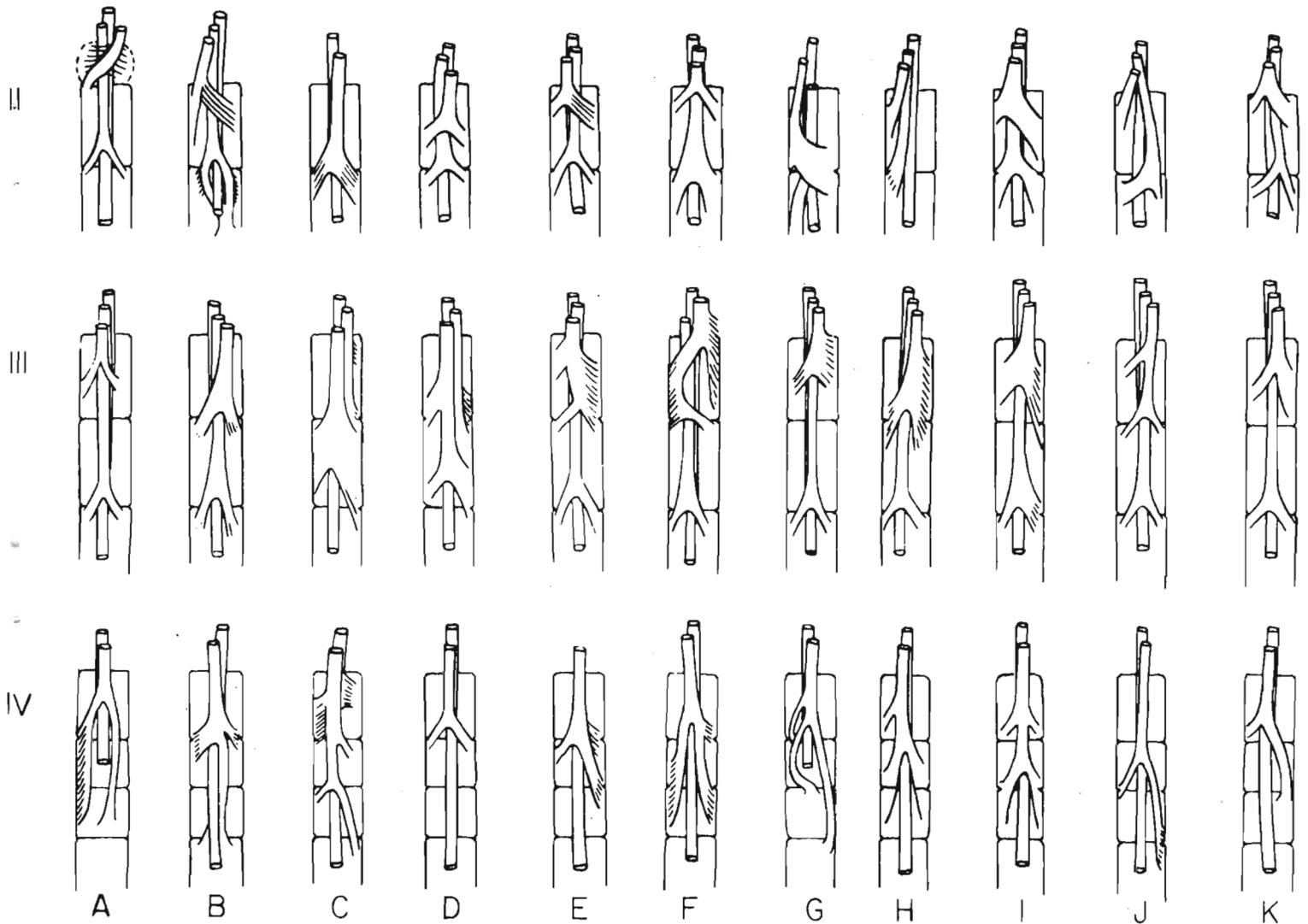


Fig. 195. Ventral view (semidiagrammatic) of insertions of tendons of the superficial flexor complex on the phalanges of the toes of A. *Sagittarius serpentarius*, B. *Cathartes aura*, C. *Pandion haliaetus*, D. *Elanus caeruleus*, E. *Aviceda subcristata*, F. *Chondrohierax uncinatus*, G. *Circus cyaneus*, H. *Buteo jamaicensis*, I. *Necrosyrtes monachus*, J. *Falco sparverius*, K. *Polyborus cheriway*.

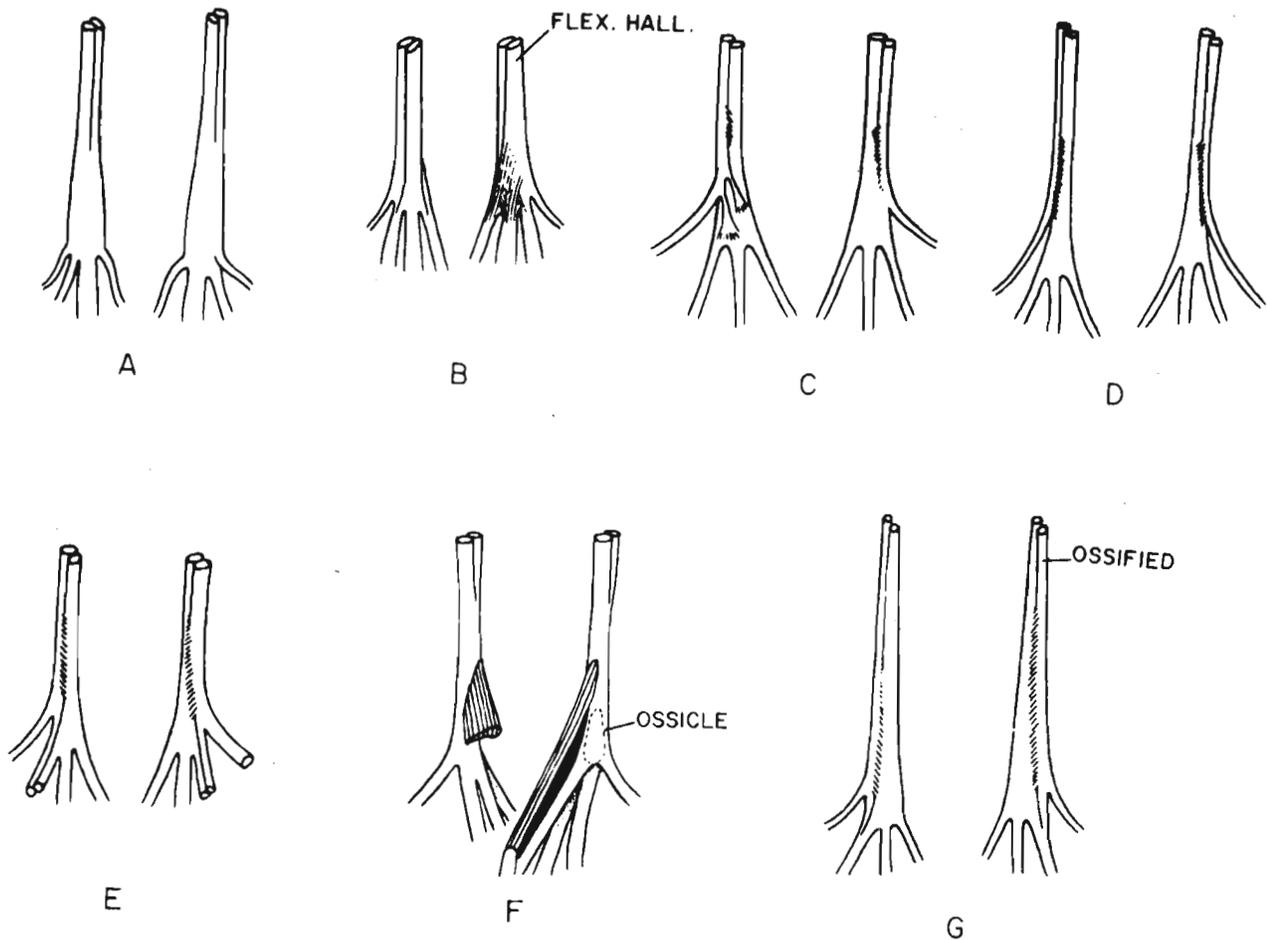


Fig. 196. Deep flexor tendons, viewed from in front (left) and behind (right) of A. *Coragyps atratus*, B. *Sagittarius serpentarius*, C. *Aviceda subcristata*, D. *Chondrohierax uncinatus*, E. *Buteo jamaicensis*, F. *Pandion haliaetus*, G. *Falco sparverius*.

of the *flexor digitorum longus* so that fibers from this muscle serve all four toes (as they do to a lesser extent in *Aviceda*). As a result of the relationship between these two deep tendons, the *flexor hallucis* of *Pandion* or the cathartid lies somewhat more laterally in the calcaneal region than in other falconiforms. In *Sagittarius*, these tendons blend just above the digital branches.

#### *Flexor Digitorum Longus*

The relative size of the belly of this muscle varies in different groups, that of the cathartid is smallest. In the accipitrid and *Pandion*, it is usually exposed on the lateral aspect of the shank between the *peronaeus longus* and the superficial parts of the *flexor digitorum superficialis*. In *Aviceda*, it is nearly concealed whereas in *Elanus* it is very prominent. This muscle is exposed only at its extreme posterior end in the other

groups due to variations in size and interrelationships of the different muscles.

*Tibialis Anterior*

In the accipitrid, the *tibialis anterior* is a superficial muscle of the shank whereas in the cathartid and *Sagittarius* it is covered by the *peronaeus longus*. The falconid may have this muscle covered (Polyborinae, *Micraster*) or entirely exposed. When exposed the lateral margin is bound to the margin of the *flexor digitorum superficialis* and the underlying *peronaeus longus*. In the cathartid, where this muscle is covered, the lateral line of attachment is reduced (*Polyborus* is like the cathartid). Like the others, the cathartid has a medial membranous origin from along the tibia (contrary to Hudson, 1948:106), but it is reduced and present only distally. *Sagittarius* has a similar origin medial to the *extensor digitorum longus*.

The insertion tendon of the cathartid and sagittariid bifurcates to attach to the two closely associated tubercles on the anterior aspect of the proximal end of the tarsometatarsus. That of the other falconiforms is undivided and attaches to the single tubercle. The accipitrid (not *Pandion*) and some falconids (not Polyborinae) have a secondary tendon (or two) inserting into the surface fascia of the tarsometatarsus.

*Peronaeus Longus*

The *peronaeus longus* covers the lateroanterior aspect of the shank in the cathartid, sagittariid, and some falconids (also *Neophron* according to Berlin, 1963, J. Animal Morph. and Phys. 9:11). It is much reduced in size in the others and is lacking only in *Pandion*. In *Falco*, *Ieracidea*, *Polihierax*, and *Herpetotheres*, this muscle is like that of the accipitrid; in *Micrastur*, it has a strong aponeurotic origin which covers the *tibialis anterior* and in *Milvago* and the other Polyborinae muscle fibers cover much of that muscle.

The form of this muscle in the cathartid, sagittariid, and the Polyborinae appears to be the primitive type (occurs in most birds--Hudson, 1937:33). Reduction of this muscle is correlated with a more powerful clenching foot. The extreme is *Pandion* and the owl in which it is lacking.

*Peronaeus Brevis*

In *Pandion*, the origin of the *peronaeus brevis* extends proximally, as compared with the others, to include the greater part of the length of the fibula.

*Extensor Digitorum Longus*

Although the muscle itself shows no real variation the frenula associated with its tendon does. It is on the joint or the rim of the tarsometatarsus in the falconid, whereas in the others it is on the proximal end of the tarsometatarsus. In *Pandion*, this frenula is ossified. In most species, it is a distinct fibrous band, but in *Torgos* and *Sagittarius* it is a long, indistinct, enclosing sheath. In *Cathartes*, it is a very narrow band set in a well-developed sheath.

The distribution of the extensor tendons to the toes is quite irregular. In *Cathartes* and *Coragyps*, the tendon bifurcates just above the third trochlea and the branches extend down onto the

second and third trochleae. The lateral branch is the wider, and, between the third and fourth trochleae, it divides into tendons which go to these digits. The main tendon of the accipitrid bifurcates one fifth of the length of the tarsometatarsus above the toes; the tendon for digit III tends to arise from fibers from the lateral division (from the medial division in *Circus*) but becomes distinct only at the base of the third digit within the fibrous connecting sheet between the two primary divisions (also in *Sagittarius*). *Pandion* and *Torgos* have distinct branches from both the medial and lateral divisions contributing to the tendon of the third toe. The falconid is like the accipitrid; only *Polyborus* differs in that the tendon for digit III arises largely from the medial division (but receives a distinct contribution from the lateral one).

*Extensor Digitorum Brevis*

The *pars hallucis* of the *extensor digitorum brevis* (figs. 126, 128, 130, 141 *extensor hallucis*) is simplest in the cathartid, or *Sagittarius*, where it arises along the line of fusion of metatarsals II and III for most of their length. In both, the origin extends across the face of metatarsal II to a position above the first metatarsal. In *Sagittarius*, there is a slight bifurcation of the proximal end of the muscle to either side of the *tibialis anterior* insertion.

This muscle is most variable in the accipitrid where it arises from several heads. The medial head, usually the largest, includes the proximal rim of the medioanterior face of the shaft of the tarsometatarsus, the frenula of the *extensor digitorum longus* and a variable length of the shaft below these. A second head, lateral to the first, attaches to the anterior ligament of the tibiotarsal-tarsometatarsal joint and the general fascia of this joint. This middle head may fuse, in the area below the *extensor digitorum longus* frenula, with the medial head; it is missing as a distinct entity in *Torgos*, although a bundle of fibers arises from the shaft in its position (like the falconid). The middle and medial heads are grooved for the passage of the *extensor digitorum longus* tendon (slight groove in *Pandion* and the medial head may overlap that tendon (*Aquila*, *Buteo*, *Accipiter*, *Circus*). Lateral to the *tibialis anterior* insertion, a third head may arise (lacking in *Torgos*) from the same general region as the second. This head may be large or small depending on the presence of a fourth head from the lateral rim of the tarsometatarsus above the origin of the *pars adductor-extensor digiti IV*. This last head is lacking in *Accipiter striatus* and *Pandion*. The various bellies unite distal to the *tibialis anterior* tubercle and the thick wide tendon extends down around the medial margin of the tarsometatarsus to the upper surface of the hallux where it inserts upon the ungual phalanx.

The falconid muscle has two heads (corresponding to the first and fourth of the accipitrid), both of which arise below the proximal rim, on either side of the *tibialis anterior* tendon, from a variable length of the shaft (matched by *Torgos*). The lateral head is usually the larger. These heads unite at the level of the *tibialis anterior* tubercle and taper down to a tendon at, or

above, the level of the middle of the tarsometatarsus.

It might be assumed that the muscle of the accipitrid is the more specialized in that its origin has crept upward on to the joint and several distinct heads have appeared.

The *pars abductor digiti II* may arise either proximally, distally, or from both areas within a group. Among the cathartids, its origin is distal. It is largest in *Sarcoramphus*, arising as far laterally as the face of metatarsal III. In *Vultur*, the muscle has two heads; one from the face of the tarsus and a smaller second head from the first metatarsal. Such a state is indicated in *Cathartes*. In *Sagittarius*, the origin is distal, from the anterior face, and bindings, of the first metatarsal and the adjacent part of metatarsal II.

Among the accipitrids, this muscle usually arises proximally to either side of the *tibialis anterior* insertion. The lateral origin is restricted to the proximal margin whereas the medial one extends down the face of the tarsometatarsus past the *tibialis anterior* tubercle--including the medial and distal aspects of this tubercle--for a varying distance (just past it in *Circus* or *Accipiter* and nearly to the proximal end of the first metatarsal in *Aquila* and *Buteo*). *Aquila* has both origins well developed; *Buteo* lacks the lateral one and the medial one extends more proximally. *Circus* has both heads well developed although the lateral one connects membranously to the medial one beyond the *tibialis anterior* tubercle. *Accipiter* has the lateral head reduced to a narrow, fleshy band and the medial one restricted to an area extending from the level of the *tibialis anterior* tubercle to a short distance distal to this tubercle.

There is no distinct proximal origin in *Ictinia* or *Aviceda*. The muscle arises along a line from the *tibialis anterior* nearly to the distal end of the bone and from the adjacent margin of the first metatarsal. In *Torgos* and *Necrosyrtes*, only the distal origin is present, including a part of the surface of the first metatarsal. In *Pandion*, the muscle is even more distally restricted.

In *Micrastur*, this muscle extends much of the length of the tarsometatarsus and has both proximal and distal origins which are slightly separated. The first extends for one half the length of the tarsometatarsus, its proximal portion underlying the medial head of the *extensor hallucis*. The distal belly is very small and does not extend onto the first metatarsal. In sharp contrast, *Herpetotheres* has a powerful distal part which does include the anterior margin of the first metatarsal in its origin. In the other falconids, only the distal part occurs; it is very small, but includes the margin of the first metatarsal in its origin.

The *pars extensor digiti III* is present in all. It is very small in *Sagittarius* and the falconid, arising just above the middle trochlea. In the cathartid, it is also minute but *Gymnogyps* and *Sarcoramphus* (Fisher, 1946:688) have an additional small tendon from a proximal origin. In the accipitrid, this muscle ranges from somewhat better developed than in the cathartid (*Accipiter*, *Circus*, *Buteo*, *Torgos*) to strongly developed, the origin extending up the shaft to the *tibialis anterior* insertion

or beyond (*Aquila*, *Pandion*, *Aviceda*, *Chondrohierax*, *Elanus*, *Gampsonyx*). The belly may show some subdivision. There are two heads in *Pandion* but these do not correspond to those of *Aquila* where both arise along a line on the shaft up to the tibialis anterior tubercle rather than side by side. *Chondrohierax* shows a partial longitudinal division, deep fibers arising separately which soon join the more superficial and medial belly.

The *pars adductor-extensor digiti IV* of the cathartid arises along the line of fusion of metatarsals III and IV, from the level of the *tibialis anticus* tubercle to just above the distal foramen. The origin expands abruptly distally, fibers arising even from the face of metatarsal II. There is little variation among the cathartids, but the muscle is least developed in the condors. The muscle of *Sagittarius* is weakly developed. It arises by two thin heads which are confined to the distal third of the long tarsometatarsus. The accipitrid and falconid are similar in that this muscle extends the length of the tarsometatarsus. It arises lateral to or underneath the belly of the *extensor hallucis longus* for a varying distance. The insertion tendon, like the belly, may be very long or short.

#### *Interossei Plantaris*

The *pars abductor digiti IV* of the cathartid is well-developed both proximally and distally but is not two parted. The point of insertion varies from the margin to a short distance out on the first phalanx (basal phalanx). In *Sagittarius*, there are proximal and distal bellies joined by a long tendon (Hudson, 1948:108, described only the distal belly). The falconid is like the accipitrid but always has a partial origin from the calcaneal fascia and usually a shorter belly (restricted to proximal third). In *Herpetotheres* or *Torgos*, the origin extends nearly the length of the bone. Where the tendon is long (accipitrid, falconid), it is closely bound to the lateral margin of the tarsometatarsus above the trochlea. The insertion is on the proximal end of the basal phalanx.

The *pars adductor digiti II* is present in all of the groups and is similarly developed in all. It has a small proximal belly lying in the flexor groove and a long thin tendon extending to the insertion. The size of the belly varies but without apparent significance. The exact position of the belly and its relationships to the *flexor hallucis brevis* or *abductor digiti IV* appear to be a functional variable. Sushkin (1905:54) said that only the most distal part of the tendon of this muscle was present in *Milvus* but my specimen had this muscle typically developed (as in *Buteo* or *Aquila*). Nitzsch (1866:156) noted that this muscle is missing in *Gypaëtus*.

#### *Flexor Hallucis Brevis*

The *flexor hallucis brevis* is single or two-parted in the accipitrid and falconid; the two parts insert separately when present. In these groups, the origin is proximal, more so in the latter than the former. Usually, in the accipitrid, there are two tendons and the bellies are fused (separate only in *Torgos*). The tendon of the *pars externus* of the typical accipitrid inserts broadly across the base of the phalanx, the

tendon fanning out somewhat just before inserting. The tendon of the *pars internus* is somewhat lighter in weight and inserts narrowly on the medial side of the base of the digit. In *Elanus* and *Gampsonyx*, the *pars internus* has the wider tendon whereas in *Chondrohierax* and *Aviceda* the tendons are of about equal width. *Pandion* is like *Necrosyrtes* in having only the *pars internus* present.

In *Falco*, *Ieracidea*, or *Polihierax*, only the *pars externus* is present whereas in the other falconids both parts are well developed and the bellies are entirely separate (*Polyborus*) or fused proximally.

In the cathartid, this muscle arises along nearly the entire length of the second metatarsal and the belly is wider both proximally and distally. The insertion usually covers the proximal end of the hallux phalanx and, in some, the adjacent connective tissue. The proximal part of the belly gives rise to a tendon which inserts laterally. More distal fasciculae insert on this tendon throughout most of its length, but the most distal ones insert upon the medial tubercle of the base of the phalanx and even across the ventral aspect of the deep flexor tendon on the lateral tubercle as a perforate insertion.

Perforation of this insertion occurs in some accipitrids. In *Chondrohierax*, both tendons of this muscle enclose the deep tendon at their insertion, the lateral one inside the medial one.

*Sagittarius* has only the *pars internus*, the belly is limited to the proximal half.

#### *Lumbricales*

The *lumbricales* is best developed in *Pandion*, but it is present in all of the falconiforms. *Cathartes* differs from *Coragyps* in that this sheet inserts directly on the pulley of trochlea III, secondarily on the pulley of IV, and partially on the pulley of II. In *Coragyps* the main insertion is on pulley IV, a weaker one on pulley III and no apparent insertion on the pulley of II as in the other falconiforms. This muscle is thin in *Coragyps* and fairly thick in *Cathartes*, it is smallest and bandlike in *Vultur* and *Sarcoramphus*. In *Herpetotheres*, only the slip to IV is well developed, that of III vestigial. *Pandion* is unique in that there is an insertion on the posterior, lateral wing of trochlea IV as well as on pulleys IV and III.

#### Summary and Conclusions

The interpretation of myological variations is contingent upon conclusions regarding their value. Such conclusions can be reached only after a consideration of the opinions of the various contributors to the subject and a resynthesis of our knowledge.

Garrod's wide (but unsystematic) experience with the comparative anatomy of birds is summarized in his articles of 1873 and 1874. He considered the thigh musculature simplest for analysis because of the variation in the presence or absence of a group of five muscles. He used a letter to represent each of four muscles and a plus or minus to represent the fifth (the *rectus femoris* of this account, Garrod's *ambiens*), and he thus characterized the thigh of each species by means of a formula.

On the basis of the presence (at least in some members of a group) or absence (in all members of a group) of the *rectus femoris*, he divided birds into two main groups. Beyond this he utilized variations of formula as indicative of relationship or lack of relationship within groups. He pointed out (1874:112-113) that on the basis of his formula species show no individual variation in their myology (ignoring obvious anomalies and considering only the presence or absence of the formula muscles); that genera show no variation among their species, or only very slight variation involving a minor variation of formula, except where species have been lumped into unnatural genera; that families show no, or only minor, variation in the myology of their genera, variation which involves only one element of the typical formula. He considered that any greater variations than these require further separation in a natural arrangement. In his view (p. 114), "An inspection of Plate XVII is sufficient to show that the formula of a bird is not of direct value in estimating ordinal characters..." but by means of his formula and other anatomical characters (caeca and oil gland tuft) the known groups of birds were rearranged.

Fürbringer (1888) laid stress not only on presence or absence of a muscle but on its form, relative development, and relationships to others. His system lacked any means of simple expression, like that of Garrod's, and because of this can be utilized only after exhaustive comparisons. Fürbringer considered the myology of the shoulder and breast most valuable and useful for the determination of relationships.

Beddard (1898:77) listed 17 muscles which show significant variation in birds, most of which are in the thigh. He pointed out (p. 76) that, "The muscular system of birds is remarkably constant for the species, the number of variations being apparently, comparatively speaking, but slight...The muscular system too is apt to be very constant for a given genus or even a larger division." Like his predecessors, Beddard made little real use of muscle differences.

Hudson (1937) reinvestigated the thigh musculature of the bird and extended the formula of Garrod so as to include other muscles and structural features of the hind limb, which show variations. His work indicated the possibilities for success offered by careful, comparative studies. He corrected many errors of Garrod and indicated that the taxonomic value of myology is largely "yet to be determined."

As a first attempt at utilization of hind limb musculature in determining the relationships within an order and in differentiating orders, Hudson (1948) gave an analysis of the falconiforms. His conclusions are similar to those of Garrod (1874:113-114), differing only in that he separated *Pandion* as a suborder distinct from that which contains the Accipitridae and Falconidae.

Fisher and Goodman (1955:123-124) cast some doubt on the value of Garrod's formula and Hudson's modification of it, at least in the cranes, where both individual and species variation in the presence and development of the two parts of the *caudilio-*

*femorialis* occurs.

Historically speaking, no one has as yet successfully established taxonomic value for myology, although many have expressed faith in its possibilities. Myological characters have so far been of purely secondary importance.

From my own dissections it is apparent that total similarity of myology (based upon presence and absence of muscles, shapes, sizes, and interrelationships depends upon the closeness of relationship, general body proportions, and similarity of life habit (behavior). It is to be assumed that as divergence of species in time takes place the differences in myology, as of any morphological character, tend to increase. Where convergence has occurred the superficial similarities should be betrayed by differences in basic pattern.

Generally speaking muscular structure is as conservative as (but no more than) bone structure since the two are interrelated. Because evolution is not a predictable process, two families of a group may be closely similar in the structure of the limb, and a third may be different. The actual time of divergence between the three might be the same, but on the basis of myology it would appear otherwise. The absence of a particular muscle, or other minor changes, does not necessarily indicate a lack of relationship or even lack of close relationship (*see* Fisher and Goodman, 1955:123-124).

Fürbringer (1888:1055) cited a hypothetical instance where myology could be utilized to demonstrate relationship when the underlying bones differed strikingly. I doubt if such a situation actually exists. Here we encounter the difficulties of interpretation. One must define the basis upon which a similarity or dissimilarity is said to exist. It is possible that the osteology of two species might be thought more dissimilar than their myology, and yet when approached by a different set of criteria, the reverse might seem to be the case (i.e. problem of *Fregata-Cathartes* relationship).

In terms of myology, conservation and adaptation are well represented. The distal wing musculature is conservative, since most birds fly and utilize relatively similar motions. These movements vary in rate and style of flapping as well as the propensities for soaring or sailing. Variations in the distal parts of the wing (not so much the presence or absence of muscles but their relative size, form of belly, modifications of origin and insertion, and general patagial pattern) do occur and can be correlated with the shape and use of the wing. Two species, even though closely related, will differ in detail if different proportions have been developed.

Less conservative and more indicative of basic lines of specialization is the shoulder and breast musculature. Within the falconiforms there are the basically different patterns of the cathartid and aegyptian. Both are adapted for soaring and in general there is a similarity in body proportions and in behavioristic adaptations of feeding (the same situation described by Steinbacher, 1935, for the foot). It is interesting to note in this regard the detailed anatomical similarity of the raven

and crow but the difference in their flight habits. These cases indicate that the same muscle system can be used effectively in different ways and different muscle plans can be adapted to the same type of movements. Agreement in detail is not complete--for example the angle at which the wings normally are held may differ.

The hind limb musculature probably shows more adaptational modification than any other region. This limb may be scarcely used (*Trochilidae*, *Fregatidae*, *Caprimulgidae*), powerfully developed for grasping prey (hawks, owls) or for climbing (parrots), elongated for wading (herons), well developed for running and walking (galliforms), modified for swimming (Gaviiformes, Anseriformes) or for perching and foraging on the ground and in trees (passerines).

The trunk and vertebral column muscles will show some variation because detailed movements demand specific modification in any region. Boas (1929) described differences in the cervical musculature and correlated these with the length of the neck and the feeding movements of the head. Similarly the muscles of the jaws show modifications following those of the form of the bill and its use. These modifications of trunk and head, however, are generally of a detailed nature.

The differences observed in the falconiforms cannot be ascribed to adaptive radiation, since the common habits of this array should produce parallel similarities. There is as wide a range of habits among the accipitrids as within the falconids, and yet there is basic agreement in myological detail within groups but not between groups. Thus, the evidence presented by the falconiforms suggests that the several myological patterns observed were developed in the first radiation of the avian type and that these have secondarily become adapted for a predatory or vulturine existence with little or no actual convergence.

Among the falconiforms over 50 muscles, or their parts, are observed to show usable variation. In Tables 19-20 various comparisons are made (similar to those of Gadow or Fürbringer). The groups of the falconiforms are compared one with another and with four genera of other orders. Each group is represented by a symbol, used when the muscle is distinctive. When two or more groups have comparable muscles, the symbol of one of the groups is used for all (A in preference to the other symbols among falconiforms).

The preparation of such tables presents the problem of ascertaining whether the condition of a muscle in one group falls into the expected limits of variation of another or whether it is sufficiently distinct to be regarded as unique. The decision is an arbitrary one and these comparisons are, therefore, subjective. I have tried to be conservative and have indicated some characters as shared that other workers might feel are distinctive.

The use of such a table of comparisons is misleading in that the relative value of a detail may vary from insignificant to important and yet constitute a unit character in either case. For example, in Table 20, the cathartid seems to be more closely related to *Gallus* than to *Fregata*, but the cathartid and *Gallus* exclusively share only 4% of features while the cathartid and



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triceps brachii	A	S	A	A	A	Fr	A	Fr
pectoralis	C	S	A	A	A	C	A	A
suprascoracoideus	C	A	A	A	A	A	A	A
coracobrachialis longus	C	A	A	F	A	C	F	A
biceps brachii	A	S	A	A	A	S	A	A
tensor fascia latae	C	S	A	A	A	Fr	A	C
iliofibularis	C	A	A	A	A	A	C	C
gluteus maximus	A	A	P	A	A	A	A	P
piriformis	C	A	A	A	A	A	A	C
rectus femoris	A	A	A	A	A	A	A	K
vastus lateralis	A	A	A	A	A	A	A	K
biceps femoris et semimembranosus	C	S	A	A	A	A	A	A
pars lateralis	C	C	A	A	C	A	A	C
pars medialis	A	A	A	A	A	A	A	A
semitendinosus	A	S	A	A	A	A	A	A
gracilis et adductor longus	C	S	P	A	A	C	A	K
adductor brevis et magnus	A	A	P	A	A	A	A	K
obturator externus								
pars internus	A	S	A	A	A	A	A	A
pars externus	A	A	P	A	A	P	A	A
caudiliofemorialis	A	S	A	A	A	A	A	A
gastrocnemius	C	S	A	A	F	Fr	B	F
plantaris pars accessorius	C	C	A	A	A	A	A	C
soleus	C	A	A	A	C	A	A	C
flexor digitorum superficialis	C	S	P	A	A	A	A	K
vinculum between tendons of								
pars perforatus digiti III	C	S	A	A	Fr	Fr	Fr	K
and pars perforans et perforatus								
digiti III	C	S	P	A	A	Fr	P	K
flexor hallucis longus	C	S	P	A	A	Fr	P	K
flexor digitorum longus	C	C	A	A	C	A	B	C
deep flexor tendons	C	S	C	A	F	C	A	K
insertion of tibialis anterior	C	P	P	A	F	P	B	A
peroneus longus	C	C	P	A	A	C	P	C
peroneus brevis	A	A	P	A	A	A	A	A
extensor digitorum brevis								
pars hallucis	C	C	A	A	A	C	B	A
pars extensor digiti III	C	C	A	A	C	C	B	A
pars adductor-extensor								
digiti IV	C	A	A	A	A	C	A	K

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interossei plantaris  
 pars abductor digiti IV  
 flexor hallucis brevis  
 \* \* \* \* \*  
 Table 20. Summary of Table 19 in which the number of points of agreement or disagreement between types, and the number of unique features of each type is expressed in terms of percentage of the total number of features compared. To the right and above are indicated the percentage of features in which the different groups (or genera) disagree one from the other. Diagonally down the center is the percentage of features unique to each group (within the materials compared). In the lower left hand area, the percentage of features shared exclusively by any two groups (a measure of similarity). The symbols are as in Table 19.

	C	S	P	A	F	Fr	G	B	K
C	$\frac{19.6}{1.8}$								
S	69.7	$\frac{31.8}{1.8}$							
P	1.8	1.8	$\frac{8.9}{1.8}$						
A	0	1.8	1.8	$\frac{1.8}{5.4}$					
F	0	1.8	0	$\frac{12.5}{0}$					
Fr	10.0	2.	0	0	$\frac{18.0}{2.}$				
G	4.	2.	0	0	0	$\frac{14.}{0}$			
B	0	0	4.	0	0	0	$\frac{14.}{2.}$		
K	0	0	0	0	0	2.	0	$\frac{28}{2.}$	

*Fregata* share 10%. On the basis of features I judge to be most significant, the cathartid and *Fregata* are much closer to each other than either is to *Gallus*, but such a relationship is not indicated by the table.

From the tables the following conclusions are suggested:

1. The different groups of the falconiforms, including *Pandion* as a separate entity, show about the same number of differentiating features as do species of other orders. No close interrelationships are indicated.
2. The cathartid and sagittariid types stand out as distinctly different from each other and the other groups (or genera).
3. The accipitrid (with or without *Pandion*) has few unique features and exclusively shares none with the other groups with which it is usually placed.
4. The suborder Falcones, compounded of the accipitrid, pandionid, and falconid types, cannot be defined on the basis of sharing myological peculiarities any more than it is definable osteologically or by ptilosis.

The first of these items is actually put to the test in a discussion of the others. The second implies that we are not dealing with "primitive Accipitres;" it suggests independent divergence. In contrast, the cathartid suggestively agrees with *Fregata*. There appears to be a positive affinity here which is not indicated among the falconiforms. *Sagittarius* shows evident specialization but not from an accipitrid or falconid type. Nor does it seem likely that the falconid or accipitrid could stem from the sagittariid type. A common ancestor for all could not be viewed legitimately as a member of any of these groups.

As to the third item it should be explained that separation of *Pandion* from the accipitrid does not essentially alter measurement of the degree of dissimilarity or similarity of the latter. The value of separation lies in the idea that the extreme of a group can show a degree of independence similar to that of an unrelated species.

The accipitrid shows few unique features and, therefore, can hardly share many with *Pandion*. One might say that most of the features which are plastic have been altered in *Pandion*; those that are not, are shared in a variety of ways with the accipitrid and other groups. The distinctiveness of *Pandion* is somewhat reduced by the variation from the basic accipitrid type observed in the pernin and elanin kites. These do not bridge the gap; rather they demonstrate the plastic nature of the aberrant structures.

The comparison between the owl and accipitrid is much the same in terms of percentage of dissimilarity, but this is not the whole story. The differences are more significant; further, some of the special features distinguishing the owl (particularly

in dermal musculature) are not among those evaluated.

The assumed common ancestry of the accipitrid and falconid finds no support in myology. The hind limb musculature, which should show some evidence of convergence, beyond the increased size of the shank muscles (for grasping), instead falls into two clear-cut styles, which do not overlap. Nor can one be derived from the other. The style of the falconid can be considered the more primitive (having a *soleus* and *medial semimembranosus*); it cannot be any more successfully compared with the sagittariid or the cathartid type than with the accipitrid.

Myologically the cathartids can be split into two subfamilies, the first containing *Cathartes* and *Coragyps* and the second the larger condors. This division is founded on the presence or absence of the *caudiliofemoralis* and the presence of a single or double tendon for the *obturator externus*. The myological constancy of this group (many minor variations exist) can act as a model for the amount of variation to be expected in the subfamily and family. If anything, the range of variation is less than that expected in a family (Fisher, 1946:709-710).

Some of the present subfamilies of the Accipitridae are not represented in the dissection material, but pertinent facts can be added to those already known. *Pandion* is usually considered to be most closely related to the pernins, but comparisons of musculature indicate little essential agreement. Points of similarity are few but include close agreement on the muscles of the abdominal wall and the heavier whiter tendons of the *extensor digitorum longus*. The tendons of *Pandion* mark the extreme, whereas *Chondrohierax* and *Aviceda* are halfway toward the usual accipitrid condition. *Elanus* has a shank that superficially resembles that of *Pandion*. The pernins appear to differ by the absence of the *rectus femoris (ambiens)*, less modified abdominal muscles, and more distinct bellies for the superficial flexors of the shank.

*Elanus*, including *Gampsonyx* (and *Chelictinia*), stands out as a peculiar genus by virtue of the insertion of the *rectus femoris* into the lateral part of the superficial flexor of the shank; the form of the bellies of the superficial flexor; the *caudiliofemoralis* arising by a narrow tendon from the ventral, anterior point of the pygostyle (appears to arise more forward than in others); the very weak *peronaeus longus*; and the fairly thick and white *extensor digitorum longus* tendon, which resembles those of *Pandion*, *Chondrohierax*, and *Aviceda*. The shank musculature resembles *Pandion* in its molding, indicating a powerful leg and foot in this small hawk.

The aegyptiins (only *Necrosyrtes* and *Torgos* examined) have a peculiar *caudiliofemoralis*, which resembles that of *Pandion* in its long insertion tendon. The dermal muscles of this group are particularly well developed. *Neophron* Garrod, 1873:635, fig. 3) differs from *Necrosyrtes* in the form of the *caudiliofemoralis*, resembling the typical accipitrid. The myology of such genera as *Gyps* and *Gypaëtus* (Nitzsch, 1863; 1866) appears to differ little from that of the typical accipitrid. Myologically the aegyptiins are not supported as a subfamily.

*Aquila (Uroaëtus)*, *Buteo*, *Circus*, *Accipiter*, and *Ictinia* show little difference as compared one with another. A myological description of one suffices for all. *Gymnogenys*, which is well marked osteologically, differs little (Beddard, 1889) from this central array of accipitrid species.

Although there is marked uniformity among the falconids, the Falconinae and Polihieracinae appear to differ in that the *pars internus* of the *flexor hallucis brevis* is lacking, the *peronaeus longus* is small and does not overlap the *tibialis anterior* (a feature shared with *Herpetotheres* as a specialization), and the nerve of the *semitendinosus* passes lateral to the *pars medius* of the *biceps femoris et semimembranosus* rather than through the belly. *Polihierax* is peculiar in the rectus tendon passing medial to the insertion of the *iliofibularis*, rather than lateral, and in the resultant reorganization of the superficial flexor muscle origin. Furthermore this genus has a small slip of the *soleus* fused with the *gastrocnemius*. Both of these features represent advances over the primitive style, a change which is in agreement with the specialization implied by the reduced body size in this group.

*Herpetotheres* and *Micrastur* resemble the Polyborinae in the reduction of the *pars pectoralis* of the cutaneous maximus and the development of the throat musculature; they differ (from all) in that the *soleus* is partly fused with the medial part of the *gastrocnemius*. These two genera differ markedly in details of their tarsometatarsal musculature and in the development of the *peronaeus longus*.

The Polyborinae are well marked by the style of the *tensor patagii brevis* tendon, which resembles that of the accipitrid in its division into two parts. This is possibly a retention of a more primitive style in contrast to the unbranched condition observed in other falconids.

## VISCERAL ANATOMY

### Introduction

Four groups of characters are considered here; these are the convolutions of the gut, the presence of both ovaries and their relative development, the main arteries in the region of the heart, and the syrinx. The first and third of these are investigated most easily in fresh specimens and with more difficulty in preserved materials.

### Comparative Anatomy

#### Gut

Gadow (1879, 1889; Gadow and Selenka 1891) described the convolutions of the gut and a system for their analysis. He described various loops and classified the relationships of the arms of the first four of these loops into several categories. He (1889:309) pointed out that the accipitrids tend to have five or six intestinal loops and these are orthocoelous (arms relatively straight) with a tendency to teleogyrous (ends of loops curled) or mesogyrous (irregular spiraling of loop).

The convolutions of the gut were studied in a different manner by Mitchell (1896, 1901). He pinned out the gut on a flat surface and recorded its relationships to the mesentery and to the hepatic portal vein and its branches. Mitchell's system has considerable merit and was used as recently as 1938 by Al-Hussaini in his study of the Aegyptian kite.

In order to compare the guts of the different falconiforms certain introductory concepts are of value (fig. 197). These involve both the basic plan and the finer details of the gut. In its simplest form the gut is a straight tube from stomach to cloaca. Among most birds two segments of the simple gut have retained their original positions and these are the stomach and the large intestine. The falconiform's stomach has increased in length and its left wall has bulged out posteriorly, leaving the pylorus at a point on its right, dorsal aspect. The stomach is differentiated only poorly into an anterior proventriculus and a posterior, saclike ventriculus. The stomach walls are distensible and in preserved specimens the shape of this organ varies greatly. Gadow's (Gadow and Selenka 1891:641) comments on the comparative form of the stomach are useless, if one has only preserved materials.

The large intestine is relatively straight although it may show minor kinks which correlate with its distention by food. It is proportionally short but with the shortening of the body cavity of the bird (as compared with the long bodies of primitive vertebrates) its anterior end is separated from the pylorus by less than its length.

The small intestine is the part of the gut in which elongation has taken place. The small intestine is usually thrown into four major loops: the duodenal, meckelian, supraduodenal and precolonic (supracaecal of Al-Hussaini). These loops can be identified by convenient reference points.

The duodenal loop is a typical "closed" loop, that is, the descending limb (section passing posteriorly) parallels and lies close to the ascending limb. It arises at the pylorus and passes posteriorly along the dorsal, right aspect of the ventriculus. It extends around the posterior curve of the stomach and then projects into the body space or is thrown into a small coil (telogyrous state of Gadow). When coiled the distal end curls forward and dorsally in an anti-clockwise fashion as viewed ventrally. The ascending limb lies dorsally and follows the course of the descending one; at the level of the pylorus it passes dorsally and medially, close to the dorsal body wall.

From this anterior, "body wall," position the meckelian loop begins and the greater part of the length of the gut is involved in this section. This loop at its midpoint, broadly speaking, may show a "vitelline" diverticulum which appears as a small out-pocketing or merely as a thickening, or spot, on the wall of the gut. This diverticulum marks the point of attachment of the gut to the yolk sac. This diverticulum can best be seen in fresh material and is, in fact, difficult to locate in preserved specimens unless it actually projects from the gut wall. This loop is of the "open" type and its ascending limb ends on or near the dorsal midpoint of the ventriculus and may, or may not,

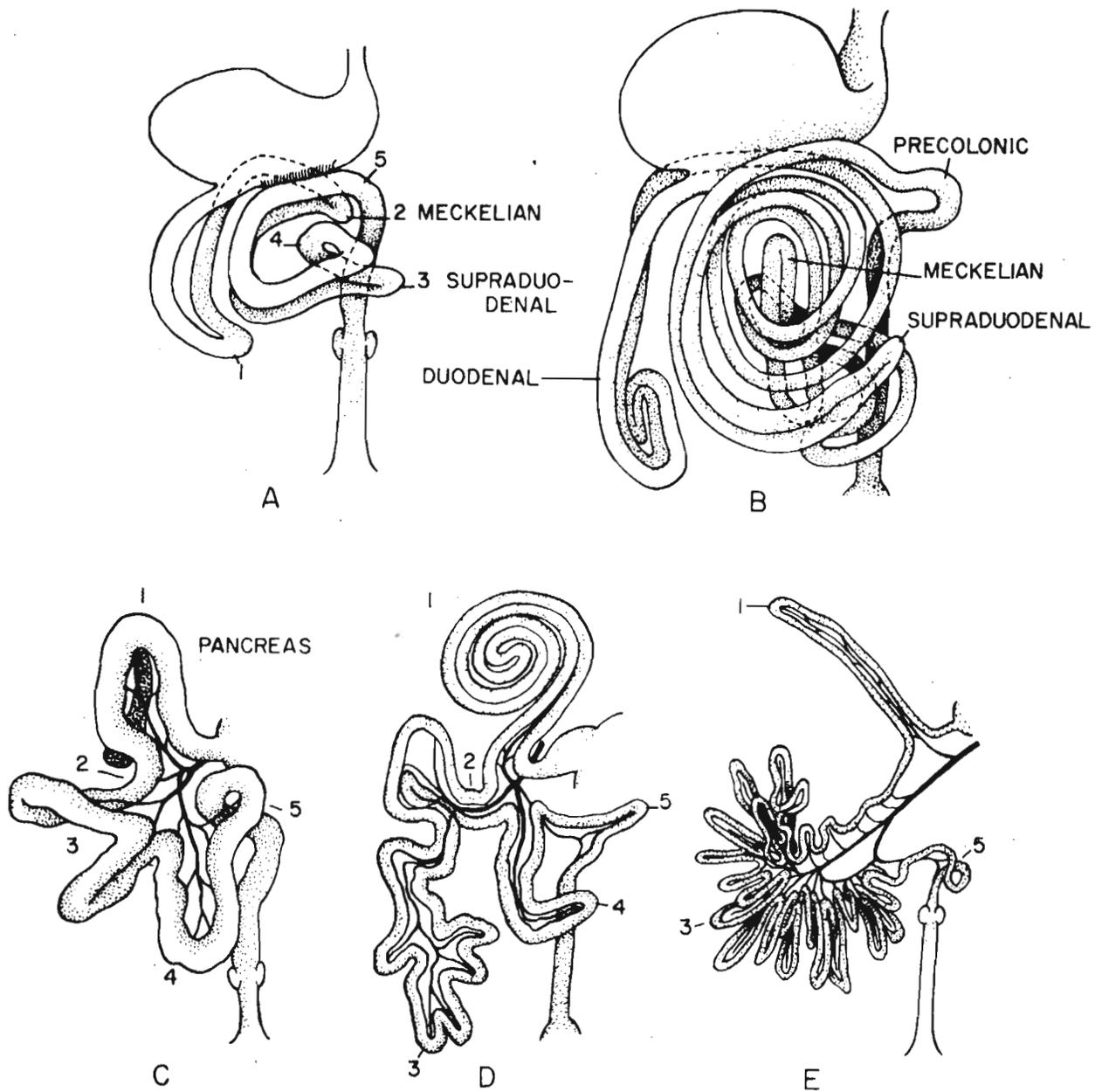


Fig. 197. Two styles of illustrations of the convolutions of the intestine A. and C, *Elanus caeruleus*; B and D, *Coragyps atratus*; E. *Pandion haliaetus*.

be bound to the stomach wall. The meckelian division may be asymmetrically disposed or spiralled (mesogyrous, as opposed to regular spirals, cyclocoelous) with the midpoint lying dorsally and centrally. This loop is essentially undeveloped in *Elanus*.

The supraduodenal loop is a closed loop arising in the region of the dorsal wall of the ventriculus; it may be bound to the stomach wall. Its descending limb passes posteriorly, laterally (to the left) and ventrally to form a half circle, its distal end being directed in an anti-clockwise coil as viewed ventrally or projecting dorsally and anteriorly. The distal end of this loop may pass between the stomach and the end of the duodenal loop (*Falco*, *Polyborus*, *Coragyps*). The ascending limb passes dorsal to the descending and is always bound to the stomach wall for a short distance.

The meckelian and supraduodenal loops in their simplest state encircle an area of mesentery in which branches of the hepatic portal vein lie. These loops usually have secondary loops, which in turn may be thrown into small tertiary ones.

From this point of attachment to the stomach, the gut passes to the left and dorsally as the precolonic loop. This portion generally has irregular folds and kinks and usually there is a single, small open loop. This loop may be essentially lacking (*Elanus*) or there may be a compounded one (*Circus*). The section ends at the beginning of the large intestine.

The large intestine at the point of transition usually has a pair of lateral diverticula of varying size. Diverticula are lacking in the cathartids and there is no easily identifiable point where the small intestine leaves off and the large intestine begins.

Other features of the gut are worthy of comment at this point. The liver is bilobed, the two parts being of about equal size and disposed symmetrically to either side and below the proventriculus. The right lobe is attached to the dorsal body wall by a posterior medial projection which encloses the post cava. A large gall bladder is present and there are two bile ducts, one from the gall bladder and a second from the region of anastomosis of the two liver lobes. The bile ducts enter the small intestine in the region of the distal end of the duodenal loop. The pattern of the bile and pancreatic ducts probably could not be used for the characterization of groups.

The spleen is poorly to well developed; it is located in the dorsal mesentery of the stomach, anterior to the curve of that part of the gut attached to the stomach wall between the supraduodenal and precolonic loops.

The tongue is well developed in all of the falconiforms. The cathartids have the dorsal lateral margin of the tongue denticulate (fig. 198). The falconiforms all have expanded the esophagus into a crop. The crop is highly distensible and cases are often cited of carrion-feeding types being unable to fly because of their gorged condition. *Cathartes* (not *Coragyps*) is peculiar in having a dense, hairlike, mass at the pyloric exit of the stomach.

In comparing the various groups of falconiforms, there are no great differences between them. The accipitrids show the

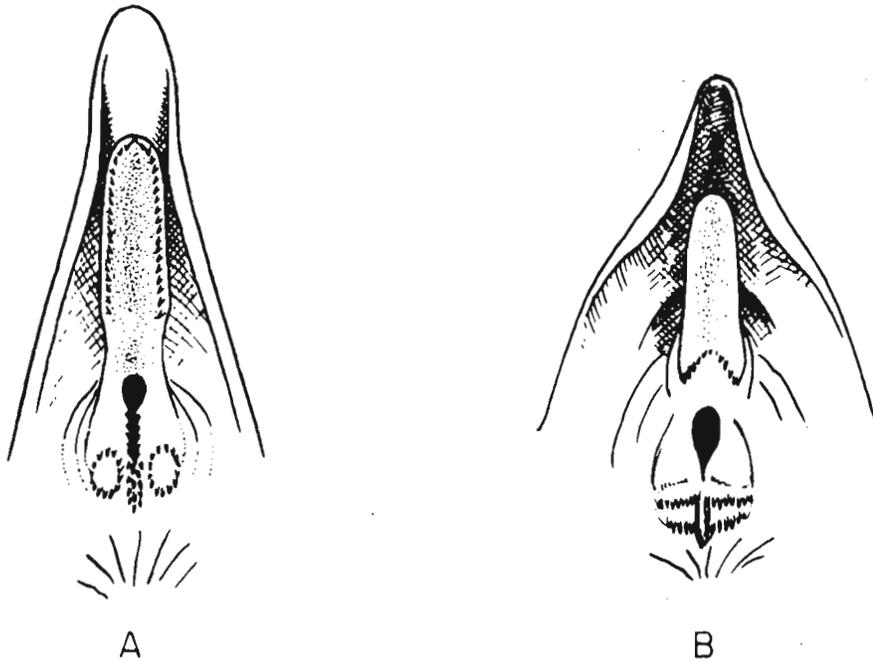


Fig. 198. Dorsal views of tongue and lower jaw of A. *Coragyps atratus*, B. *Buteo jamaicensis*.

greatest diversity as expected in view of the number of species. Subfamilies could not be differentiated with the materials at hand.

The simplest gut is that of *Elanus* 197) in which the duodenal loop can almost be considered open. The meckelian loop is scarcely more than simple. The region between the meckelian and supraduodenal loop is slightly open (like the duodenal). A precolonic loop is absent, the gut showing only a slight propensity for kinking.

*Aviceda* is not too distant from *Elanus* but has typical, closed duodenal and supraduodenal loops. The meckelian loop is better developed and is asymmetrically disposed in the body cavity. *Accipiter striatus* is as simple as *Elanus* with the exception that a distinct precolonic loop is present and the first and third loops are closed. The extreme of complexity is found in *Circus* in which the meckelian loop is spirally disposed, approaching the form found in *Falco* or in the cathartid. The spiral arrangement of the meckelian loop probably varies in its perfection in different individuals. In general, the meckelian loop of the accipitrids is asymmetrically disposed.

The length of the gut, which largely affects the meckelian section, is variable. *Circus* has the longest gut in proportion to its body size. The guts of *Torgos*, *Necrosyrtes*, and *Haliaeetus* are also long (see comments of Gadow 1891:643). The length of the gut is correlated with the amount of looping and, usually, the propensity for mesogyrous disposition.

*Pandion* is distinctive in that a recognizable supraduodenal loop is absent and the enormously elongated meckelian section is

divided into a large series of closed, straight, secondary loops (20-25 in number). *Haliaeetus* has a somewhat similarly elongated meckelian section but its secondary loops are not as closed and both the supraduodenal and precolonic loops are strongly developed. In *Haliaeetus*, elongation has also involved the duodenal loop which shows secondary folding whereas in *Pandion* elongation has involved mainly the meckelian section. *Pandion* also shows a proportionally longer large intestine and a very large, kidney-shaped spleen. Gadow's (Gadow and Selenka 1891:642-644) comments on *Pandion* appear to be based upon a single specimen in which the disarrangement of the digestive track led him to record several points not substantiated by my specimens, nor to be expected in such a bird.

The falconids are quite like the accipitrids. *Falco* has the meckelian loop coiled, whereas the gut of *Polyborus* is irregularly disposed. In both *Falco* and the cathartid the base of the meckelian loop is closely appressed and bound by loose connective tissue to the dorsal wall of the stomach. This does not seem to be the case in the accipitrid. The accipitrid and falconid are generally similar but appear to differ in the development of the spleen.

The cathartid differs in the form of the tongue, a family criterion at best; it also differs in the consistent and fairly symmetrical coiling of the meckelian section and the absence of the colonic caeca. The relationships of spleen, liver and stomach are somewhat at variance with the accipitrid picture (such as the usual appearance of a semidistinct pyloric section to the stomach in the accipitrid).

On the basis of the gut there are three poorly defined groups: accipitrid-falconid, *Pandion*, and cathartid (*Sagittarius* not seen). The gut of the falconiforms shows a much wider range of variation than that of the tubinares, although the latter have a somewhat more consistent diet than the falconiforms, according to some.\*

#### Gonads

Stanley and Witschi (1940) and Rand (1942) have supplied much of the information on bilateral ovaries in the falconiforms, (Table 21).

Apparently the cathartids never show a right ovary and thus mark a more modified stage than other groups. *Pandion* also has no right ovary. The kites tend to lack a right ovary and the largest, most specialized forms such as the vultures are similar. In such species as *Buteo jamaicensis* or *Aquila chrysaetos* the right ovary may be lacking or present. *Accipiter* and *Circus* agree in the strong development of both ovaries and stand in

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\* Forbes (1881:17) notes that, "The Tubinares as a group agree very closely together in the form of stomach and intestines possessed by them, which have peculiarities not occurring in any other groups of birds, and it is only in the variations in form and structure of the tongue, in the nature of the armature of the mucous membrane of the mouth, and in the presence or absence of caeca that the various forms differ in any important degree from each other."

Table 21. Occurrence and relative development of the right ovary in the falconiforms.

Classes		
A	Right ovary more than half the size of the left.	
B	Right ovary one-fourth to one-half the size of the left.	
C	Right ovary less than one fourth of the left but present.	
D	No distinct right ovarian rudiment.	
Species	No. examined	Class
Cathartid		
<i>Cathartes aura</i>	7	D
Sagittariid		
<i>Sagittarius serpentarius</i>	1	A
Accipitrid		
<i>Aviceda subristata</i>	3	C-D
<i>Henicopernis longicauda</i>	4	C-D
<i>Chondrohierax uncinatus</i>	1	C
<i>Milvus migrans</i>	6	C-D
<i>Haliastur indus</i>	1	C
<i>Accipiter gentilis</i>	6	A
<i>Accipiter novaehollandiae</i>	10	A
<i>Accipiter poliocephalus</i>	1	B
<i>Accipiter fasciatus</i>	2	A
<i>Accipiter cooperii</i>	16	A
<i>Accipiter melanochlamys</i>	2	A
<i>Accipiter nisus</i>	42	A-B
<i>Accipiter striatus</i>	4	A-B
<i>Accipiter cirrhocephalus</i>	3	A
<i>Circus cyaneus</i>	19	A
<i>Circus pygargus</i>	3	A
<i>Circus aeruginosus</i>	1	A
<i>Circus spilonotus</i>	2	A
<i>Circus approximans</i>	1	A
<i>Buteo jamaicensis</i>	23	C-D
<i>Buteo lineatus</i>	6	C
<i>Buteo buteo</i>	7	C-D
<i>Buteo platypterus</i>	4	C-D
<i>Parabuteo unicinctus</i>	2	C
<i>Harpyopsis novaeguineae</i>	2	C-D
<i>Hieraaëtus morphnoides</i>	2	C-D
<i>Aquila chrysaëtos</i>	3	C-D
<i>Necrosyrtes monachus</i>	1	D
<i>Pandion haliaetus</i>	2	D
Falconid		
<i>Falco peregrinus</i>	10	B-C
<i>Falco cenchroides</i>	1	B
<i>Falco tinnunculus</i>	2	B-C
<i>Falco sparverius</i>	8	A-B-C
<i>Ieracidea berigora</i>	2	B-D
<i>Herpetotheres cachinnans</i>	1	C
<i>Milvago chimachima</i>	1	C

strong contrast to the buteonin and aquilin subgroups.

The right ovary in *Accipiter* has been demonstrated as functional at least in one case by Stieve (1924). He observed a specimen of *Accipiter gentilis* in which two ovulated follicles were found in the left and one in the right ovary; the bird was sitting on three eggs. (The egg had passed from the right ovary down the functional left oviduct.) The right oviduct is either absent or extremely vestigial in all birds.

Stanley and Witschi (1940) pointed out that in the Accipitrinae the ovaries are nearly the same size in the resting phase but with activity the left becomes larger and is better developed. Their data do not confirm this contention.

Embryological studies (Stanley and Witschi, 1940) show that the number of germ cells in the splanchnopleure is equal on either side at early stages but as a result of secondary migration these cells become concentrated on the left side. The left side appears to have a greater attractive power for these cells in later stages and as a result produces a larger left ovary, sometimes to the total elimination of the right. Stanley (1937) stated that lack of development of the right ovary is not due to failure of any one part to develop but to a deficiency of inductors in the embryonic gonad site. Stanley and Witschi (1940) pointed out that some birds are unique in that the right gonad is composed only of the medullary portion. The right oviduct disappears by secondary atrophy of an originally well-developed embryonic structure.

These same workers stated that species with small right ovaries tend to have a reduced right testis. The observations in my study do not support this premise; there is individual variation ranging from a right testis half the size of the left to a right testis considerably larger than the left. Most males tend to have a slightly larger left gonad regardless of the ovary condition. A male of *Coragyps* had the right testis about two-thirds the size of the left whereas in a specimen of *Cathartes* the left testis was just larger than the right. In *Torgos*, *Buteo*, *Milvus*, *Daptrius*, and *Micrastur* the two testes were roughly equal. In a single adult male goshawk the left testis was just a bit larger.

#### Arteries in Region of Heart

The circulatory system of the falconiform is generally the same as that described by Gadow and Selenka (1891), Beddard (1898: 48-57) or Hyman (1942:351-358, for the pigeon). Garrod (1873) was the first to attempt a systematic investigation of a part of the circulatory system. He described several patterns of the carotids and indicated their occurrence in different groups of birds. The subject of carotids had only incidental consideration until Glenny reopened discussion of the "main arteries in the region of the heart" (Glenny, 1955, for summary of a series of papers) with the view that their taxonomic importance had not been fully evaluated.

Glenny described a ligamentous vestige of the left fourth (systemic arch), a ligamentous vestige of the right sixth arch connection to the dorsal aorta (ductus botalli or ductus

arteriosus when a lumen is present and ligamentum botalli or arteriosus when the lumen is lacking), and ligamentous vestiges of the dorsal components of the third (carotid) arch connected with the systemic arches (ductus caroticus on right side and ductus shawi on the left) which serve the dorsal aspect of the syrinx and esophagus.

The arteries in the region of the heart are fairly similar in the falconiforms, (type A-1 of Glenny, 1955:562). Glenny (1941) described the arteries in the golden eagle and red-tailed hawk. He found a ligamentum botalli on the right side in both species. In most species, a recognizable right ligamentum botalli could not be found; it was (fig. 199) well developed in

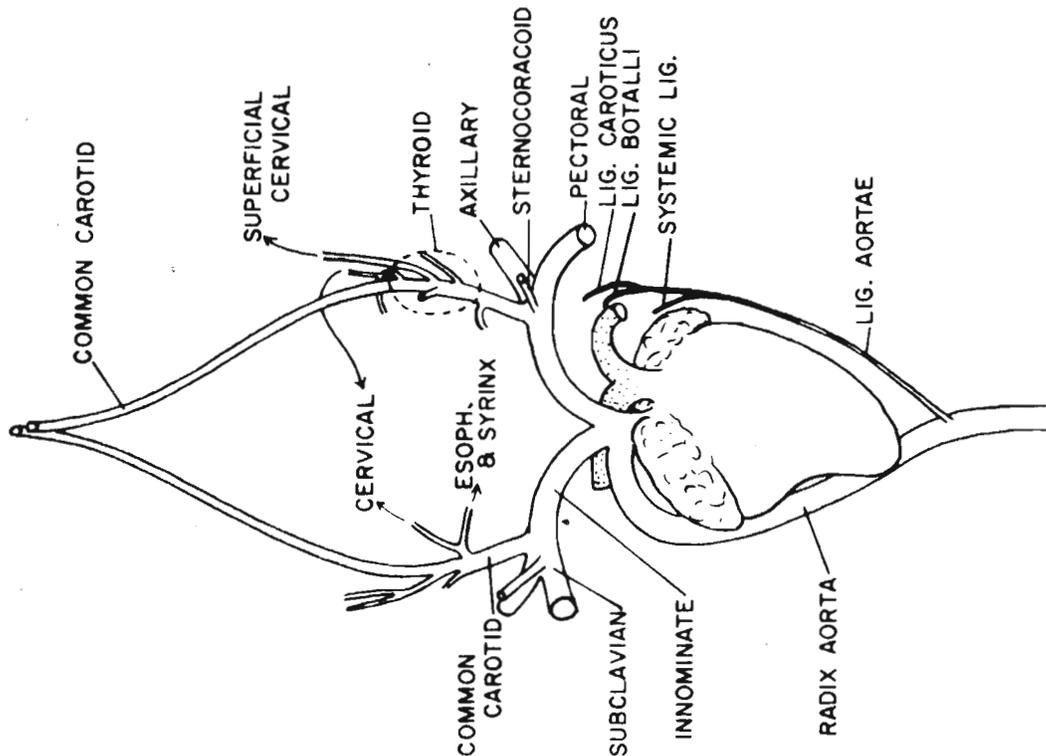


Fig. 199. Ventral view of heart and main vessels of *Pandion haliaetus*.

a specimen of *Haliaeetus leucocephalus*. Glenny's description of the left fourth vestige did not apply to the specimens I examined; there was a distinct connection of this vestige by a thread of tissue to the left pulmonary artery at a point just outside the lung. This connection is the left ligamentum botalli. In the species I examined, there were vestiges of the ligamentum caroticus on the left side. From these dissections, it is apparent that there are usually bilateral ducti botalli (or arteriosis) and vestigial systemic connections for the more anterior arches, at least on the left side.

Among the falconiforms (fig. 199) the bilateral innominate vessels each give rise to an anteriorly and dorsally directed common carotid and a laterally directed subclavian stem which

almost immediately divides to form several smaller vessels: anterolaterally and anteriorly directed axillary artery, and a laterally directed pectoral artery which almost immediately forms several branches.

The common carotid, a short distance from the innominate, gives rise to arteries which parallel the course of the vagus nerve, extend dorsomedially to the muscles of the neck and on the right side only, medially to the syrinx and esophagus. The region of the carotid from which these branches spring lies dorsal to the thyroid gland. Probably small branches come off both common carotids to the esophagus but these could not be distinguished in the uninjected specimens. The carotids of either side pass medially and forward between the two bands of the longus colli muscles; the left carotid comes to lie superficial to the left.

The right systemic arch lies just dorsal to the base of the right innominate and usually does not show as viewed ventrally. It curves dorsally, medially, and posteriorly, passing just anterior to the right pulmonary artery at the point where that vessel enters the right lung. It reaches the dorsal midline just at the level of the apex of the heart and here it is joined by the ligamentous vestige of the left arch. Just posterior to this point, it gives off a ventrally directed coeliac artery from its right side and further posteriorly a median-arising and ventrally directed superior mesenteric artery.

The accipitrids and falconids examined all showed a well-developed, left systemic vestige connected to the dorsal aorta; and the cathartids showed a much smaller one. The falconids differed in that they lacked a distinct and separate artery from the right carotid to the esophagus and syrinx. In *Falco* there was such a vessel but it appeared to be a division of the "cervical" branch (same in the cathartids, *Pandion*, and *Necrosyrtes*). On the basis of the carotids there were slight differences in the details of the pattern of the cathartids as compared with the others. *Pandion* was quite similar to the accipitrid.

Among the falconiforms, sufficient differences are not yet known to make a practical contribution to systematics.

#### Syrinx

The syrinx of the falconiforms (fig. 200) has been studied by Beddard, and little can be added to his accounts of this structure (1898--pp.475-476, for accipitrids and falconids; p. 479, for *Pandion*; p. 480, for *Sagittarius*; pp. 481-482, for cathartids; also 1903). Alden Miller (1937:204-205) has discussed reference points for comparing the syrinx of different species. As in his account, the pessulus is used here as the key, although it probably is not constant in its position. Forbes (1882:32) assumed that the position of the insertion of the intrinsic muscles was constant and that the number of bronchial semi-rings could be determined from the insertion. An examination of his figures shows insertions on the first or second, third, fourth, fifth and ninth bronchial semi-rings and also an asymmetric insertion in the case of *Pagodroma nivea*

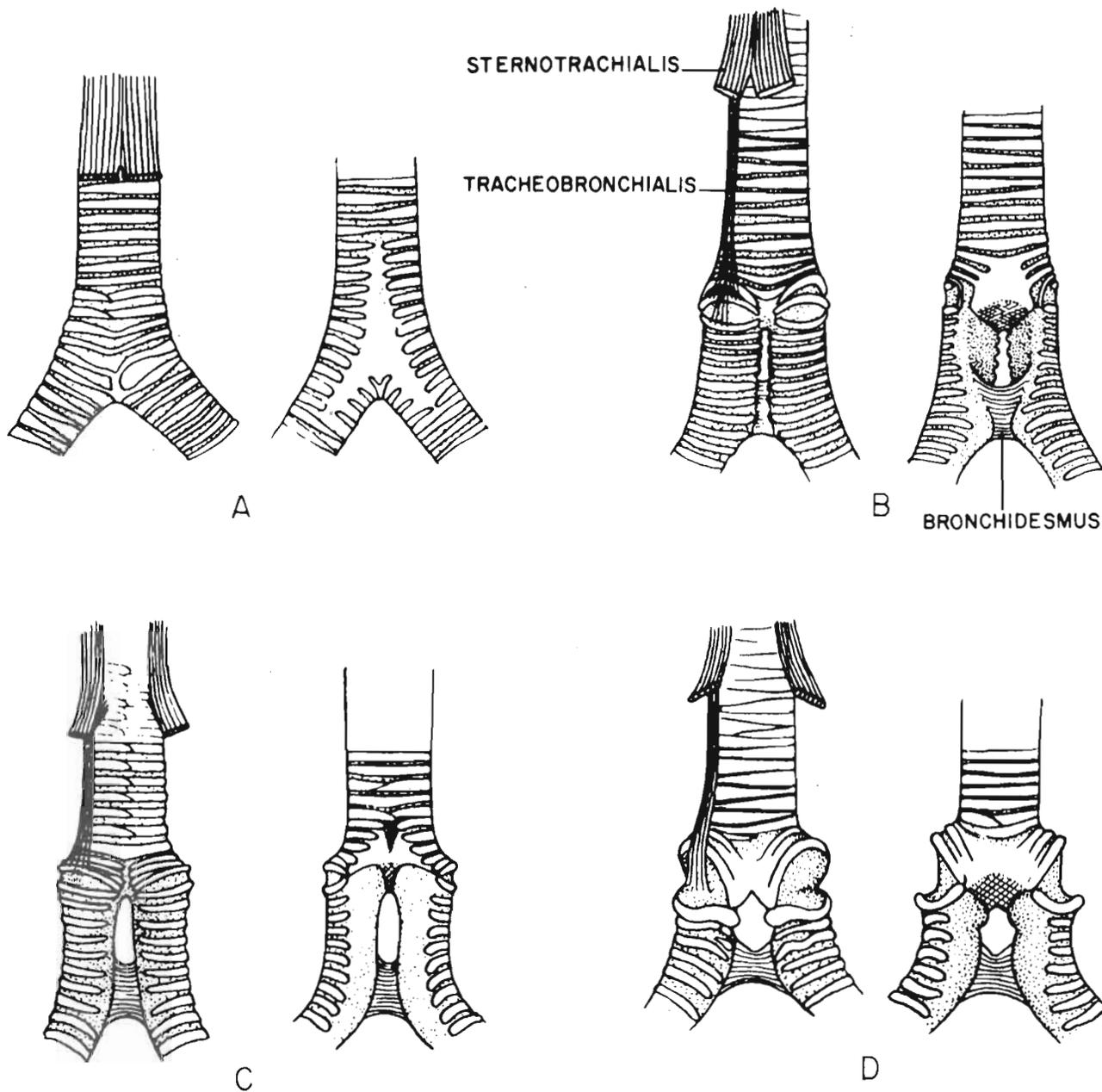


Fig. 200. Dorsal (right) and ventral (left) views of syrinx of  
 A. *Cathartes aura*, B. *Pandion haliaetus*, C. *Elanus caeruleus*, D.  
*Polyborus cheriway*.

(figures 13-14, p. 35). Miller (1937) found irregularities of insertion involving both symmetry and the number of the bronchial semi-rings.

The simplest syrinx among the falconiforms is that of the cathartid (fig. 200A). There is no well-defined syringeal box; there is a small pessular band which passes between the bronchi at their origin from the trachea. In *Cathartes* and *Coragyps* two tracheal rings are involved in the formation of the "syrinx." Unlike all other falconiforms the medial posterior aspect of the bronchus from the pessulus distally is not membranous (lacking the medial tympaniform membrane), although the semi-rings are thinner in this region. The dorsal aspect of the distal end of the trachea and the proximal half of the bronchi are membranous, or at least present a gap in the rings on this surface. A bronchidesmus is wanting. The syrinx of the condors as described by Beddard (1903) agrees with these observations.

In general, the trachea and bronchi of the cathartids are more membranous and less rigid than in the others and show the simplest condition. The *tracheobronchialis* muscles and lateral and medial tympaniform membranes are lacking. The situation in the cathartid marks either the beginning or the end of the syrinx. It can be assumed that the primitive bird had a syrinx, and that it has degenerated in the cathartid. These birds are essentially voiceless.

The syrinx of the accipitrid is of the tracheobronchial type (fig. 200B, C). The trachea ends at the "voice box" which is made up of the last few fused or semi-fused rings of the trachea. The bronchi are separated by a narrow bar, the pessulus, which bears the semilunar membrane on its interior surface. The first bronchial rings are incomplete medially, thus forming a medial tympaniform membrane on each bronchus. The tympaniform membrane is widest at the pessulus (the entire medial aspect of the bronchus) and tapers gradually to a point just outside the lung. The second and third semi-rings of the bronchi are usually in contact at their ends (ventrally and dorsally) and separated at their midpoints to form an ovoid membrane, a lateral tympaniform membrane (the interannular membrane of Beddard). The bronchi, near their origin, are connected by a membranous sheet, the bronchidesmus of Beddard, which extends from the level of the fourth or fifth bronchial semi-ring to the level of the distal end of the medial tympaniform membrane.

All the species examined (Table 17) have a distinct syringeal box, although in *Elanus* it is weakly developed. The second and third bronchial semi-rings usually enclose a lateral tympaniform membrane, but in *Necrosyrtes* there is scarcely a distinguishable gap. The tracheobronchialis muscles insert typically upon both the second and third bronchial rings. In some genera (*Buteo* and *Elanus*) the insertion upon the third semi-ring may be reduced to a membrane or be lacking. The medial tympaniform membranes of *Elanus* are nearly in contact at the anterior end of the bronchidesmus whereas in most accipitrids and *Pandion* they are distinctly separated. The syrinx of *Dryotriorchis* (Beddard, 1903, fig. 18) is most peculiar and divergent; it lacks completely the lateral

tympaniform membrane and has the intrinsic muscles inserting on the fifth semi-ring.

*Pandion* (fig. 200B) agrees well with the pernin or the typical accipitrid. On the basis of the structure of the syrinx one could assume that the call was like that of the accipitrid and such is the case.

The falconid syrinx differs in that the first bronchial semi-ring is always fused into the syringeal box and the second closely appressed to it; the lateral tympaniform gap is well developed and ovoid in shape, and the *tracheobronchialis* muscles insert upon the second bronchial semi-ring or beyond this on the middle of the lateral tympaniform membrane.\*

The syrinx of *Sagittarius* is briefly characterized by Beddard (1898:480) as, "A strong box is formed by the last tracheal ring, and the intrinsic muscles are attached to bronchial semi-ring 2." From the description this syrinx appears to be as distinctive as that of the falconid or accipitrid.

In lacking the syrinx, the cathartids contrast sharply with the other groups. The syrinx of each of the remaining groups--accipitrid, falconid and (?) Sagittariid--is distinctive.

*Pandion* cannot be distinguished from the accipitrid by the form of this structure but the sternotracheal muscles inserts asymmetrically on the ventral aspect of the trachea (as in *Carpophaga*, Beddard 1898:310, fig. 157) rather than laterally.

The range of variation of the syringes within the falconiforms appears to exceed that found in the owls or tubinares. Within each of the subdivisions, accipitrid, falconid, etc., variation is no greater and, if anything, less than that in the tubinares

#### Air Sacs

Al-Hussaini (1938) has described the air sacs of *Milvus* and those of the cathartid were described by Bignon (1889). Gilbert (1939) described this system in the bird and supplied a bibliography. Forbes (1881:32) described variation in the air sacs of the tubinares which involved bilateral interclavicular air sacs in most of the Procellariidae as compared with the fused single sac in *Pelecanoides* and the Oceanitidae. Watson (1883) described the uniformity of the air sacs of the Spheniscidae (single interclavicular sac). Waterman and Eddy (1942) have

\* \* \* \* \*

\* Beddard (1898:475-476) described the falconid syrinx thoroughly, "Much like the syrinx of *Falco* is that of *Hieracidea berigora*; I can, indeed, detect no differences. So too *Tinnunculus alaudarius* and *Erythropus vespertinus*. In *Milvago chimango* and *M. chima-chima* the syrinx is at first sight perfectly similar, but the intrinsic muscles only just get beyond the first bronchial semi-ring [second bronchial semi-ring]. In *Herpetotheres cachinnans* this divergence from the normal falconine syrinx is carried still further, the intrinsic muscle being attached to the first semi-ring.

"The syrinx of *Polyborus brasiliensis* is an exaggeration of the falconine type. The first and second bronchial semi-rings are very prominent and wide apart, thus leaving a very spacious intrannular membrane, to which the intrinsic muscles are attached."

made a comparative study of five domestic species.

#### Summary and Conclusions

The visceral anatomy of the falconiforms like the other anatomical aspects suggests that the falconiforms are composed of four distinct groups. Lack of relationship is shown by the sharing of various characters with other, unrelated, species of different orders. The study of visceral anatomy is as yet only poorly documented but deserves further investigation.

#### EXTERNAL FEATURES

External features have been the main taxonomic interest of ornithologists. A sharply hooked bill, relatively small head in proportion to the body, relatively large size, strong wings and tail, and usually, powerful, grasping feet with long curved claws have identified the falconiforms. Minor differences in the shape of the bill, shape of nostril, proportions of wing and tail length, type of scalation of tarsus, proportion of tarsus to wing, tail, middle toes, or length of claw are characters for the separation of genera and species. The choice of those to be used in each case has been left to the taxonomist. As a result no two groups are characterized by the same features and the individuality of each description is presumed to be as unique as the species or group described.

The external features used to describe falconiforms are reviewed here only in a general way and without reference to the voluminous literature, which, to a certain extent, is summarized by Swann (1924-45) and Friedmann (1950). Although it is assumed that external features will continue to be useful at the subfamily or family level, it is not the purpose of this discussion to argue the relative merits of characters or to improve on existing descriptions at any taxonomic level, below that of the family.

This account is based on an examination of skins of all the species of the falconiforms with the exceptions of *Leptodon forbesi* (probably an aberrant *Leptodon palliatus*), *Leucopternis polionota*, and *Haematornis asturina*.

#### Comparative Anatomy

##### Head

The bill of the falconiforms shows a wide range of variation in proportions and yet there is basic uniformity within each group. That of the cathartid is most distinctive. It shows only a superficial agreement with that of the other groups in its hooked tip; it compares better with that of the Anhimidae or some galliforms. The cathartid bill is long, relatively wide, and tends to be well rounded and inflated. It is peculiar in its high palatal arching, deep tomium, lack of a well-differentiated cere, wide-open nasal vestibule (which acts as an external naris), and the perforate nasal septum. This type is unique among birds in the open vestibule. Among the falconiforms it is almost matched by that of *Neophron*, *Necrosyrtes*, and *Gyps*. The closest approach to the naked, soft-skinned cere is that of *Neophron*, but

in this genus the nostril and the imperforate septum are distinctly accipitrid. The bill and cere color of the cathartid varies but it is not yellow.

The accipitrid bill is usually short and stout, the culmen curves from the cere to the tip. The shape in the accipitrid can vary with specialization; it is weakly hooked and gallinaeous in appearance in *Pernis* and extremely elongated and hooked in *Rostrhamus* (and in *Helicolestes*). There are minor variations in the angle between cere and culmen; the extremes, among the not obviously modified forms, are illustrated by *Accipiter striatus* and *Aquila chrysaetos*. The greatest range of interspecific (or intraspecific?) variation is found in the hook-billed kites of the genus *Chondrohierax* (fig. 201).

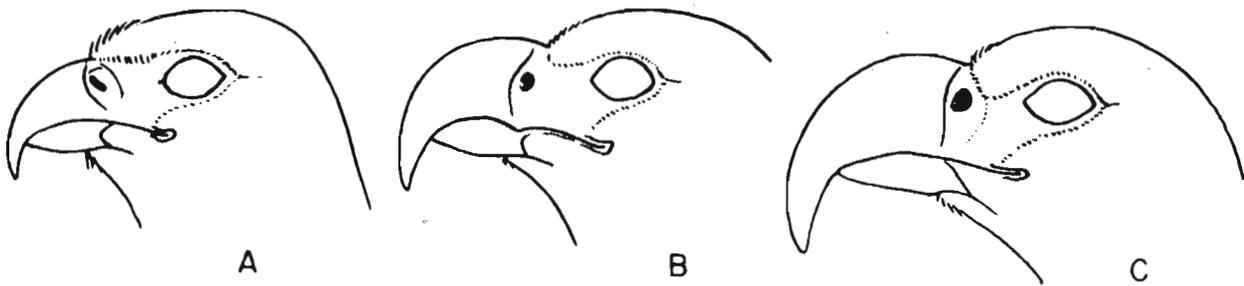


Fig. 201. Bill form in the genus *Chondrohierax*. A. *C. uncinatus*, B. *C. wilsonii*, C. *C. megarhynchus*.

The upper part of the bill usually is smoothly sheathed from cere to tip, but, in *Gypaëtus*, there is an indication of a suture from the nostril toward the tip (fig. 202), a line similar to

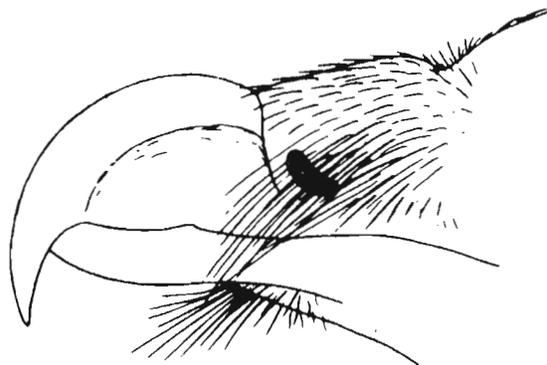


Fig. 202. Bill and cere region of *Gypaëtus barbatus*.

that observed in many other kinds of birds. This crevasse is not well marked in all specimens of *Gypaëtus*, but is distinguishable in most. *Machaerhamphus* is unique in that the culmen is thin and drawn upward.

The tomium varies from straight to rounded, "toothed" or notched. *Aviceda* and *Harpagus* have two "teeth" while *Ictinia* has a single *Falco*-like "tooth". The tomium is subject to heavy wear, like the tip of the bill, and as a result shows a wide range of variation in some species. Notched tomia may be nothing but a broken edge while curved tomia may occur in species which usually have straight edges. Tothing of the tomium is correlated with the underlying bone structure in *Falco*, or the production of a thicker section in the bill sheath which wears out to form the "tooth".

The bill is usually bluish black or horn colored. It is yellow in the larger species of *Haliaeetus* and *Torgos tracheliotus*. The African subspecies of *Milvus migrans* have a yellow bill in contrast to the black one of the typical subspecies. *Aquila verreauxi* and *A. audax* show some yellow and orange toward the base and tomium as do many species of some genera (*Butastur*, etc.). Color in the bill is related to food and shows seasonal as well as individual and geographic variation, as does the eye (Jollie, 1947).

The accipitrid cere is usually yellow but ranges to bluish gray in *Pandion*. It is a soft, somewhat inflated region covered by flakey skin with a waxy finish. In *Gypaëtus* (fig. 202), the cere is largely covered with bristles, except immediately around and anterior to the nostril; in this way it is like that of the falconid. In all other accipitrids, the cere is naked. The nostril is set in the cere and varies from a horizontal slit, overhung by a lip in *Pandion* to a round or vertically ovoid opening.

The accipitrid cere fades into the skin of the bristled lores. In some of the pernins and in *Machaerhamphus*, the loreal region is covered with numerous, small, pennaceous feathers. Transitional stages between the plumed and bristled lores are shown by other pernins.

The bill of the falconid varies from the quail-like one of *Milvago* to the short, strongly-hooked one of *Microrastur* or *Falco*. *Falco* is peculiar in its shortened, pug face and resultant modification of the vestibular folds. The "tooth" of the bill of *Falco* is lacking in the Polyborinae and Herpetotherinae; it is almost matched by that of *Ictinia*. The bill may be whitish, yellowish, or horn as in the accipitrids.

The cere is like that of the accipitrid in coloration but somewhat distinct in form and usually covered by bristles. The bristles are least evident in *Falco* and *Polyborus*. The nostril tends to be round or bluntly triangular and rimmed by an elevation of skin (except in the Herpetotherinae where only the dorsal margin projects). *Polyborus* is the extreme in nostril form (fig. 118B). The vestibular fold shows at the nostril opening; its tip appears as a distinct central tubercle in *Falco*. The lores are always bristled.

Sushkin (1905:63) described the horny palate of the falcon as ridged whereas that of the accipitrid is not. A palatal ridge is present in all of the falconiforms but it is most strongly and uniformly developed in the falconids (figs. 60, 107).

*Sagittarius* agrees with the accipitrid in most details: the cere is yellow, the nostril ovoid (fig. 79A), the lores are

covered with bristles. However, a vestibular fold is lacking.

The outline of the feather margin on the mandible was identified by Sushkin (1905:63) as characteristic. In the accipitrid, the side of the ramus is feathered to the horny sheath but the ventral edge is unfeathered for a short distance posteriorly; thus there is a distinct indentation or line between the lateral feathers and those of the throat. Such an indentation is lacking in the Falconinae and Polihieracinae but is present in the Herpetotherinae. The reduced face and chin feathering of the Polyborinae obscures it.

Many accipitrids have crests on the head, and similar crests appear in many groups of birds. The form is quite variable and within a genus (*Hieraaëtus*) a crest may be present or absent. Any evidence of a crest is lacking in the cathartid (head feathering reduced also in the natal stage) whereas *Sagittarius* has long crest feathers which hang well down onto the neck. None of the falconids has a well-marked crest, although *Herpetotheres* has a broad nuchal one. Among vulturine species, the head feathering is strongly reduced.

The face may have brightly colored areas or be uniformly colored red or blackish in the vulturine species. The most highly modified head cover is that of *Sarcoramphus*. *Torgos* has large lateral lappets of skin on the neck. *Vultur* has wattles at the chin and a large fleshy caruncle on the top of the head in the adult. *Sagittarius* is unique in its well-developed eye lashes. *Micrastur* and *Circus* have facial ruffs much like the owl. These seem to be correlated with a large external ear, at least in *Circus* and the owls.

#### Wing and Tail

Proportions have been commonly used for differentiation: the length of the wing as compared with the tail or the length of the exposed part of the primary feathers and the position of the tips of the primaries in relation to the tail. These proportions are highly variable. Such genera as *Elanus*, *Gampsonyx*, *Chelictinia*, *Elanoides*, *Machaerhamphus*, *Ictinia*, and *Harpagus* are shaped like a pigeon. More hawklike but with pointed wings (i.e., tip primaries longest) are *Milvus*, *Haliastur*, and *Ictinaëtus*. Rounded, blunt-tipped wings are found in some kites (*Rostrhamus*, *Chondrohierax*, *Leptodon*) and some falconids (*Herpetotheres*, *Micrastur*) as well as being the mode in most of the accipitrids and all of the cathartids and *Sagittarius*. The long-winged form (and way of flight) of *Pandion* cannot be matched in any other falconiform but it is suggested by *Gypaëtus*.

A wing formula is based on which primary feather is longest and the descending order of lengths of the others. Within one genus (*Aquila*), the formula may vary considerably; within a species, it may not be constant (*Falco rusticolus*, *Buteo polysoma*).

The notching of the primaries has been discussed as a functional feature by Saville (1957). As a taxonomic feature it has been used to separate the mainland subspecies of *Buteo polysoma* from *Buteo poecilochrous*. Notching is observed in all falconiforms (weakest in *Chelictinia*) but it is also found in other birds as well.

The tail ranges from deeply forked in *Chelictinia* and

*Elanoïdes* to square or rounded; from short in *Terathopius* to long and floppy (like that of a magpie) in *Erythrotriorchis*, *Eutriorchis*, *Driotriorchis*, and *Urotriorchis*. The tails of species of a single genus may be square, rounded, or wedged (*Euplectes*--Delacour and Blanc, 1933-1934). The basic proportions of wing and tail may vary within a species (fox sparrow, Linsdale, 1928). As a result primarily of variation in tail length, such closely related genera as *Pernis* and *Elanoïdes* or *Chondrohierax* differ markedly in proportions. The same is the case in comparing *Rostrhamus* with *Helicolestes*, but otherwise they are so similar that they can be considered congeneric. On the other hand, the close resemblance of *Chelictinia* and *Elanoïdes* or *Neophron* and *Necrosyrtes* appears to be due to convergence.

The almost exclusive use of body proportions has been the weakest point in systematic work and has resulted in many unnatural associations (well illustrated by Swann's work).

#### Hind Limb

*Sagittarius* is unique in having very long, cranelike legs. Among the accipitrids, the legs may be fairly long and thin (*Accipiter*, *Circus*, *Gymnogenys*, *Geranospiza*, *Hypomorhphus*, etc.) or shorter and thick (*Stephanoaëtus*, *Harpia*, *Pithecophaga*). The shortest legs in proportion to body length occur in the kites (*Elanoïdes*, *Chondrohierax*, *Elanus*, etc.). Among the cathartids, the fossil *Neocathartes* had long legs (intermediate toward *Sagittarius*) as did some more recent forms; the living species have relatively short legs. The falconids are like the average accipitrid. Compton (1938) pointed out that the thigh of the osprey and cathartid is more closely attached to the trunk than in other falconiforms. This peculiarity is approached in *Sagittarius* and the aegyptiins.

The length of the tibiotarsus has been compared with that of other leg and foot segments but an accurate measurement can only be based on the bone. The length of the tibial plumes has sometimes been used (subspecies of *Aquila chrysaëtus*). In *Sagittarius*, the cathartids, and *Pandion*, these do not extend beyond the heel; in most accipitrids and falconids they do. The shank is feathered at least to the heel in all falconiforms.

The length of the tarsometatarsus has been used for proportions within the limb as well as compared with that of the wing, tail, or exposed primaries. Utilization of such proportions may reveal significant points at the species level (Friedmann, 1950).

The proportions of the toes and claws are variable. *Accipiter* and *Astur* were separated on the basis of the length of the middle toe as compared with the outer toe. Analysis of this proportion indicated that there was every gradation between the short- and long-toed species. Correlation of toe proportions (also as related to tarsometatarsal length) with feeding habits has been made in the cases of several species of *Falco* (see Stresemann, 1927-34:465-466). The evidence indicates the possibility of short- and long-toes species being parallel adaptive variations in several lines.

Peculiar to certain accipitrid species is the fact that the outer toe is shorter than the inner (Ridgway, 1874:83--*Ictinaëtus*,

*Gymnogenys*, and *Geranospiza*). The cathartids stand apart in having a short and weak hind toe, while the anterior toes are relatively long and slim, indicating little grasping power. *Sagittarius* has short thick toes and a foot which compares well with that of the accipitrid. The toes of the falconid are proportionally longer and thinner than in the typical accipitrid, but exceeded by some species of *Accipiter* which show "parallel", bird-catching modifications. The pads marking the penultimate joint of the anterior toes are better developed in falconids (matched in some species of *Accipiter*, least marked and almost cathartid-like in *Polyborus*). There is no absolute gap between the accipitrid and falconid in toe details but the feet of most, if not all, species indicate to which group they belong; the vulturine species are most nearly alike.

The form of the claws is one of the primary features of the falconiforms, although the cathartids must be considered exceptions. They range from blunt and straight (cathartids, *Polyborus*) or long and straight but sharply pointed (*Ictinaëtus*) to well-curved and powerful weapons as in most species of accipitrids. The grooving on the under surface as well as the form of the edges is used taxonomically. Ridgway (1874) and Friedmann, (1950) noted the lack of a ventral groove in the *Elaninae*.

The cathartids and *Sagittarius* have well-developed membranes between the second and third and the third and fourth digits whereas the accipitrid and falconids have only the latter one.

(Table 22). A membrane is lacking in *Pandion* and is much reduced

Table 22. Squamation of the tarsometatarsus among falconiforms.

Cathartid	finely scaled	inner and outer membranes
Sagittariid	coarsely scutellate	inner and outer membranes
Accipitrid		
Pandion	finely scaled	no membrane
Elanin	finely scaled	slight outer membrane
Aviceda	coarsely scaled	slight thick outer membrane
other genera of perninae	from scaled to weakly scutellate	outer membrane
Machaerhamphus	finely to coarsely scaled	outer membrane
Ictinia	scaled to scutellate	outer membrane
Milvus	coarsely scaled to scutellate	outer membrane
Rostrhamus	scutellate	outer membrane
Haliaeetus	scaled or scutellate	outer membrane
Icthyophaga	coarsely scutellate	outer membrane
Gypaëtus	scaled	outer membrane
Neophron	scaled	outer membrane
Circaëtin	scaled	outer membrane
Aegyptiin	scaled	outer membrane
Aquilin	feathered all around	outer membrane

Accipitrin ( <i>Buteo</i> , <i>Accipiter</i> , etc.)	scutellate to coarsely scutellate--some feathered	outer membrane
Circus	scutellate	outer membrane
Falconid		
Herpetotheres	scaled	outer membrane
Micrastur	scaled or scutellate	outer membrane
Polyborin	weakly scutellate	outer membrane
Polihieracin	weakly scutellate	outer membrane
Falconin	weakly scutellate	outer membrane

\* \* \* \* \*

in the elanins and *Aviceda*.

Among the falconiforms there is a continuous range of variation from a finely reticulate (scaled) cover of the tarsometatarsus to scutellate or nearly booted ones (Table 22 and fig. 203). Scutes appear to be formed by the fusion of scales of the reticulate cover. The size and number of scutes is related to the size and thickness of the limb, and the amount of flexion and protection required. The primitive, fairly large bird, probably had a reticulate pattern which has been modified in smaller species, or where added protection was needed (large ratites and some long-legged types), to a partially scutellate (or ocreate one--see Boetticher, 1929).

The cathartid belongs to the primitive array of large species with a reticulate cover. *Sagittarius* (fig. 204) has a scutellate cover fore and aft; posteriorly the scutellae extend down nearly to the hind toe. The accipitrids range from perfectly reticulate to almost perfectly scutellate with some fusion of the scutes posteriorly to form an imperfect ocrea. Within one species the extremes may occur, as in the large species of *Haliaeetus* and in the species of *Milvus* or *Ictinia*. Although the pattern of scales or scutes is variable, the falconids generally have only three scutes above the toes on the anterior aspect of an otherwise reticulate tarsometatarsus.

The tarsometatarsus is feathered in some of the accipitrids. It is feathered all around in *Ictinaeetus*, *Aquila* (*Uroaetus*), *Hieraaetus*, *Cassinaetus*, *Spizaetus*, *Spizastur*, *Oroaetus*, *Lophaetus*, *Stephanaeetus*, *Polemaetus* (i.e., the aquilins), or it has a series of scutes up its posterior aspect in *Buteo lagopus*, *Buteo regalis*, and some specimens of *Buteo hemilasius*. The feathered tarsometatarsi of the aquilins and species of *Buteo* are parallel developments from the primitive scaled condition.

The coloration of the tarsometatarsus and foot is of no value. It ranges from bright red in some species (*Sarcogyps*, and some species of *Falco*) to slate gray or blackish. The feet and lower leg of most accipitrids and falconids are yellow like the cere. *Sagittarius* has flesh-colored legs and feet whereas those of the cathartids range from pinkish white to black. Light-colored legs (as the cere and the skin around the eyes) sometimes vary with age, the diet, sex, and time of year.

Plumage Coloration

The patterns of plumage coloration of the various types of falconiforms can be characterized (coloration of the face, bill, and foot have already been mentioned). The cathartids tend to

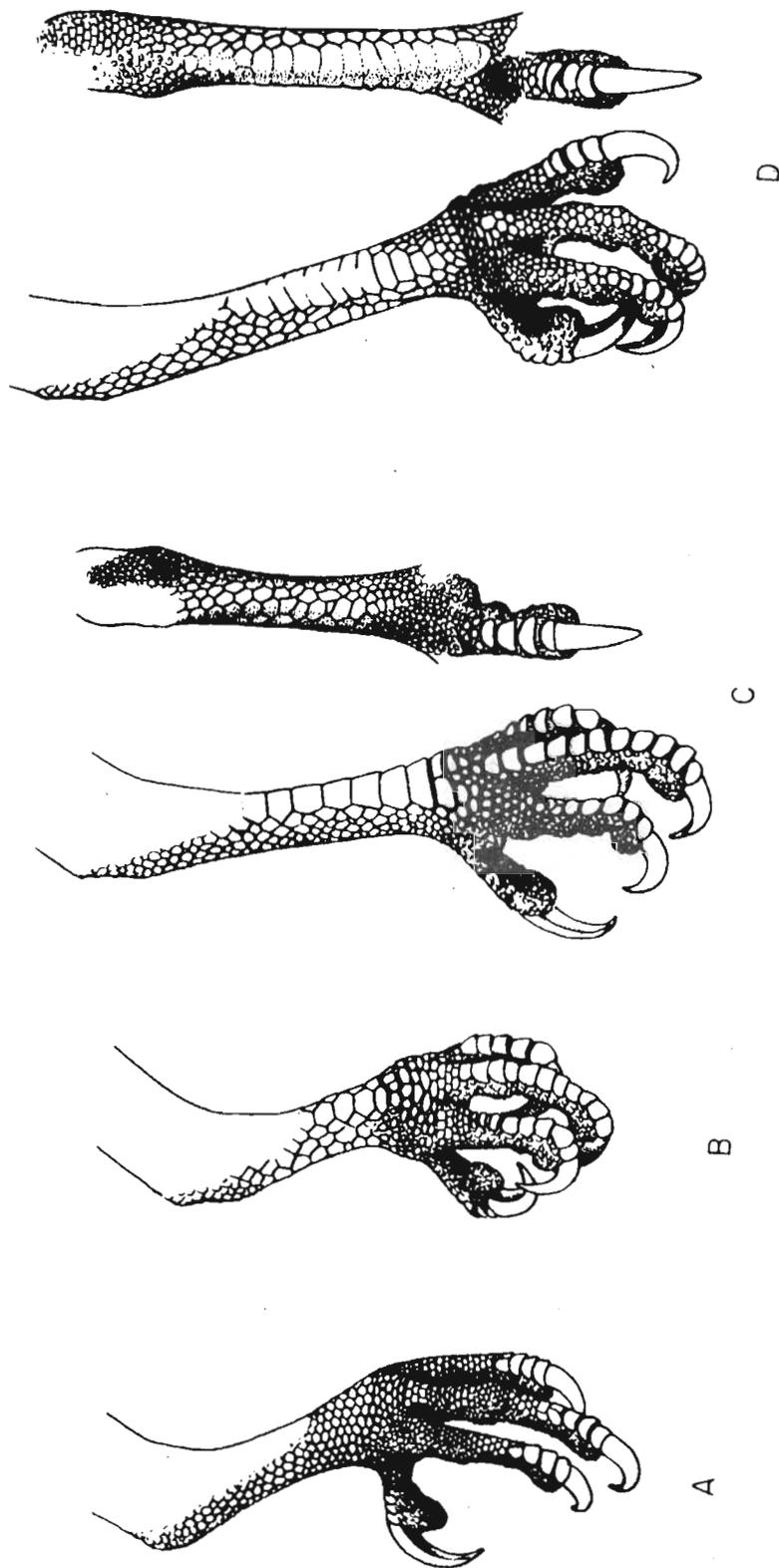


Fig. 203. Anterolateral views of tarsometatarsi and feet of A. *Elanus caeruleus*, B. *Aviceda subcristata*, C. *Milvus migrans*, D. *Buteo jamaicensis*. Posterior views to right in C and D.

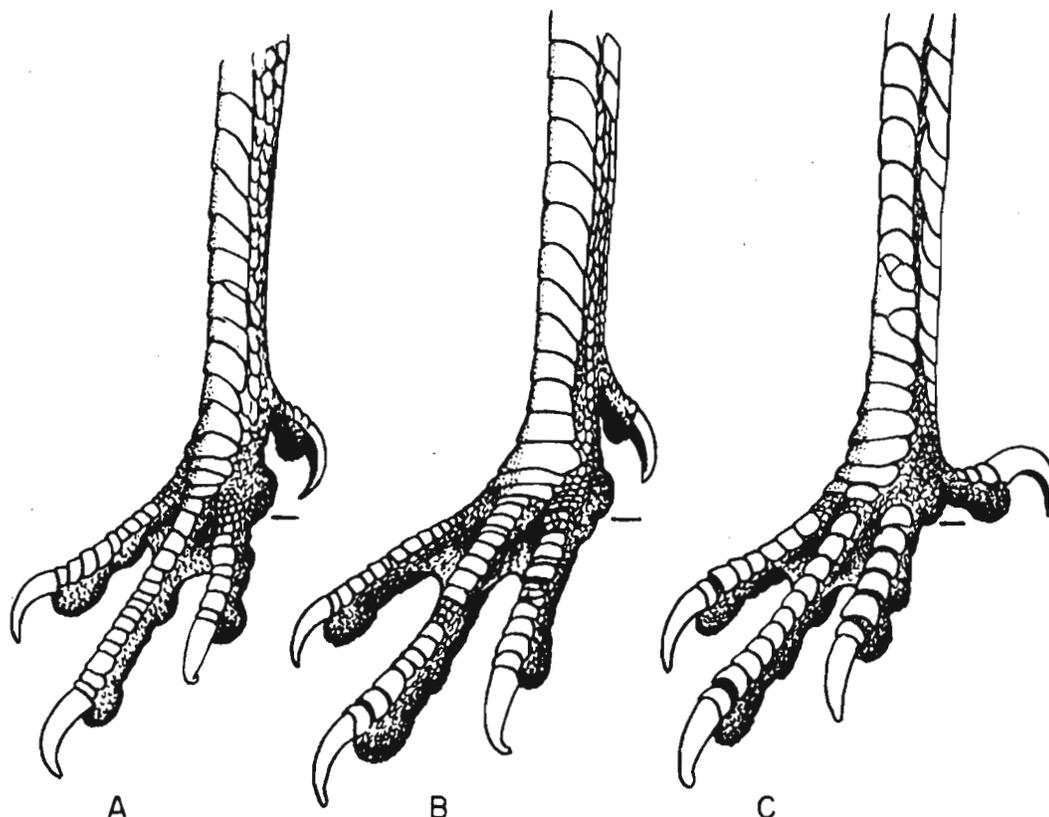


Fig. 204. Anterolateral views of distal end of tarsometatarsi and feet of A. *Sagittarius serpentarius*, B. *Cariama cristata*, and C. *Chunga burmeisteri*.

have solid black plumages and resemble their relatives in the Pelecaniformes and Procellariiformes in this respect. The strong odor of skins of these orders also suggests interrelationship. The plumage pattern of *Sarcoramphus* is the extreme in the reduction of pigmentation. However, the young are black. The condors have white areas in the wing. The cathartids are such a small group that the plumage possibilities can only be assumed to parallel those observed in the procellariiforms or pelecaniforms.

A hypothesis on the evolution of coloration can be stated. The primitive coloration was probably barred brown with or without iridescence. From this three basic types of modifications arose: modification of pattern itself (*viz.*, stripes for bars), general dilution of pigmentation to white locally or over much of the body, or increased pigmentation to solid black (which may then be diluted to white in part). Combinations of these have occurred although one or the other is predominant. Black or black and white plumages thus represent an extreme just as does the light-colored or white plumage.

*Sagittarius* has a similar color pattern in young and adult which can be described as regional dilution and intensification of color. There is no real similarity to the cathartid but only

the suggestion that the two groups may have stemmed from a uniformly colored ancestor.

The accipitrids and falconids are similar in having a primarily barred plumage pattern. The more finely-barred pattern seems to be the more primitive; the tendency for reduction in the number and increase in width of bars in the adult indicates the direction of modification. A barred pattern may be lost in most parts of the plumage through intensification of pigmentation, but frequently appears at the base of the primaries. The convergence between *Pseudogyps* or *Trigonoceps* and the condors should be noted. The large vulturine species (not including *Gypohierax*) as a group and the species of *Haliaeetus* and *Aquila* show modification toward solid coloration. This is not evidence of common ancestry but rather a convergence that might have adaptive value. *Gypohierax* and *Neophron* are an opposite extreme with largely white plumages.

The "primitive" species of the accipitrids, the kites, frequently show highly modified plumages: the elanins might be chosen as the most extreme, followed by some pernins. The most primitive patterns are found in *Buteo*, *Accipiter*, and closely related genera suggesting their more recent radiation from a relatively unspecialized ancestral type. As would be expected, adult plumages are more modified than the juvenile; in some species of the the primitive core the juvenile pattern has shifted toward the modified adult type. In what appear to be advanced plumages, there has been a loss of barring or at least a submergence of the bars into the generally darkened plumage. Where the number of bars has been reduced in certain species, some feathers may be more advanced than others. As an example, in *Accipiter badius* the central tail feathers may show four broad bars and the outer ones seven. Within one species there are different levels of pattern differentiation (*Buteo lineatus* and *Circus aeruginosus*).

The accipitrids as a group show certain peculiarities of plumage markings such as the broadly barred underparts (emphasis or intensification) of certain kites, *Circaetus*, etc; the median black throat stripe (Table 23) found in almost all subgroups ex-  
 \* \* \* \* \*  
 Table 23. Occurrence of a median throat stripe among accipitrids. Probably variants of other species have been overlooked in compiling this list.

<i>Machaerhamphus alcinus</i>	young and adult
<i>Aviceda jerdoni</i>	young and adult
<i>Aviceda subcristata</i>	young and adult
<i>Aviceda madagascariensis</i>	variants
<i>Leptodon palliatus</i>	young
<i>Pernis apivorus</i>	variants
<i>Harpagus bidentatus</i>	young and adult
<i>Harpagus diodon</i>	young and adult
<i>Accipiter trivirgatus</i>	young and adult
<i>Accipiter virgatus</i>	young
<i>Accipiter griseiceps</i>	young

Accipiter haplochrous	young
Accipiter eichhorni	young
Accipiter cooperii	rare variant
Urotriorchis macrourus	young
Dryotriorchis spectabilis	young and adult
Spilornis rufipectus	variants
Spizaëtus alboniger	young and adult
Spizaëtus cirrhatus	young
Spizaëtus nipalensis	variants
Kaupifalco monogrammicus	young and adult
Butastur teesa	young and adult
Butastur indicus	young and adult
Butastur liventer	young
Butastur rufipennis	young and adult
Buteo nitida	young
Buteo magnirostris	young
Buteo platypterus	young

\* \* \* \* \*  
 cept the Elaninae and the vulturine species; the choice of color for the barring of the underparts, usually reds and grays; and the tendency to gray and white plumages.

The falconids do not show the complete accipitrid pattern, although *Micrastur* is indistinguishable from, and shows the same kinds of variations as, *Accipiter*. The falconids tend to have finer barring of the body plumage than the accipitrid and this barring shows parallel modifications. Ridgway (1874:75) remarked that in *Micrastur* "The number of tail-bands cannot be relied on as a specific character, since there is a great variation in this respect among different individuals of the same species. Thus, *semitorquatus* has in some specimens only four bands, and in others as many as seven; *ruficollis* has four to six; *leucauchen* has six to seven, and *concentricus* three to four. The number is greater in the young plumage than in the adult."

Among the falconids the most primitive pattern appears to be that of *Milvago*. Each of the subfamilies shows stages of differentiation from this type with extremes reached in *Herpetheres*, *Polyborus cheriway*, and *Polihierax semitorquatus*. The falconinae have sexual dimorphism of pattern in some species, generally a differentiated adult plumage, and all have a moustache mark or marks.

Both the accipitrid and falconid have striking examples of parallel pattern development. The extremely close similarity between *Accipiter pectoralis* and *Spizaëtus ornatus* or between *Falco albigularis* and *Falco deiroleucus*, along with the basic uniformity (or conservatism) of pattern throughout the accipitrids or falconids, suggests that only a few genetic factors are involved and that these remain in fairly stable combinations.

#### Summary and Conclusions

External characters, as indicated here, are no more conclusive than internal features in determining the subdivisions of the subdivisions of the falconiforms, but like the internal

features there is a suggestion of independent origin for the several groups.

The cathartid shares the webbing of the toes with *Sagittarius* but also with many other birds (fig. 204). *Sagittarius* differs in the scutellation of the tarsus, the form of the foot and bill and in its general body form. The cathartid can be compared better with selected aspects of the procellariiforms and pelecaniforms.

Comparison of *Sagittarius* and the ciconiiform (preferably a stork) finds little agreement--even the plumage pattern cannot be linked effectively. The stork has a reticulate tarsus, which might not be considered of great importance in some cases, but here it seems to be significant. The only conclusion is that there is no identifiable common ancestor for the cathartid and Sagittariid, certainly none which could be identified as belonging to either of these types.

The accipitrid and falconid types do not intergrade in any way suggestive of significant common ancestry although a certain amount of convergence is evident. *Micrastur* and *Herpetotheres* have been confused with the accipitrid but can be differentiated on the basis of the bristled cere and the form of the nostril rim. Details of the feet are useful but not conclusive. In any case, they appear to be specialized end types rather than relict primitives in most of their external features.

*Pandion* differs markedly from the average accipitrid and represents an extreme in nostril details, plumage pattern, squamation of foot and toes, and general texture and size of the feathers. If this genus is identified as a specialized accipitrid, it supplies a working limit for variation within such a type.

In view of *Pandion* and on the basis of external features, the falconid and accipitrid could have a common ancestor although the degree of similarity (and lack of intergradation) does not necessitate this.

#### PHYLOGENY WITHIN THE FALCONIFORM GROUPS

##### Introductory Remarks

Before considering the question of the interrelationships of the four falconiform types described and evaluated in the previous sections or the place of each of these groups in a phylogenetic scheme for birds, it is necessary to speculate on evolution within the class and within each of the types. The direction or trends of change that have occurred in each structural unit should be defined so that comparisons will take on added meaning. The possibility for error is great, but the results of the examination of several anatomical systems should reinforce each other; i.e., the sequence of events as indicated by pterylosis will support that suggested by the skeletal system (reciprocal illumination of Hennig).

As an evolutionary starting point let us start with a hypothesized ancestral bird. To be called a bird, an organism must have certain features. Among them the following seem important:

feathered\*; warm blooded; four-chambered heart\*\*; lung of tubular structure and air sacs which extend throughout the body; true bill with horny sheath, teeth lacking\*\*\*; lacrimal, supraorbital, postorbital, epipterygoid, and ectopterygoid missing from skull; mesethmoid well developed; lateral ethmoid present; large orbitosphenoid (laterosphenoid or pleurosphenoid) present; orbit large and confluent with the antorbital fenestra in front (loss of lacrimal?) and the tympanic recess behind; loss of contact between the squamosal and quadratojugal; relative enlargement of cranium (related to increased activity and agility); mandible without teeth (see footnote bottom of page); presence of a meckelian fenestra and absence of a coronoid; neck relatively long, trunk short, and tail abbreviated; thoracic cavity enclosed by ribs articulating with a ventral, keeled sternum; pelvis large, attached to a large number of synsacral vertebrae, ilium, ischium and pubis extending posteriorly behind the acetabulum; anterior appendage modified as wing, digits II, III, and IV present, digit V vestigial; hind limb well developed for bipedal stance; four-toed foot designed for perching or walking; a fused tibiotarsus in the shank, fibula reduced distally; tarsometatarsal components fused, first metatarsal developed only distally and articulating with tarsometatarsus; and, lastly, many details of myology, particularly the great development of *pectoralis*. Any animal which does not fit this definition cannot properly be called a bird. For example, *Archaeopteryx* should be viewed as too similar to the reptile and not modified enough to be a bird.

This definition is not adequate, as regards many of the details described in this account, and needs to be enlarged upon. The following additions seem to be appropriate.

Pterylosis: feathers well developed and differentiated on most parts of the body (showing specialized forms correlated with functions); aftershaft well developed; pterylosis pigeon-like, the ventral tract undivided on the breast; only the protegmen present; 11 primaries in the wing, carpal remex with covert present, wing diastataxic (Steiner, 1918).

Skull: palate dromaeognathous (upper bill involving both premaxilla and maxilla; the latter more so than in the Neognathae; maxillopalatines not touching at the midline but in contact with the vomer, which is flattened in the plane of the palatal surface; median nares to either side of the posterior portion of the vomer; pterygoid large, a unit structure, in contact with the vomer anteriorly and supported medially and near its posterior end by a large basipterygoid process; palatines relatively small); prefrontal well developed with a distinct supraorbital process; palatines relatively small); prefrontal well developed with a distinct supraorbital process; nasal opening holorhinal or incisorhinal (new term--the opening forms an acute angle dorsoposteriorly).

\* \* \* \* \*

\* pennaceous structure gives supporting area for flight.

\*\* left systemic arch lost.

\*\*\* teeth of *Hesperornis* may be a case of neoteny, an adaptation for fish capture correlated with loss of flight and diving habit; *Icthyornis* may also be a case of adaptation for fishing.

Mandible: anterior splenial fused with dentary (*see*, Jollie, 1957a); no (?) coronoid.

Body skeleton: 14-15 cervicals; 9 vertebrae between main brachial and pelvic nerve roots; long synsacrum of 10-15 vertebrae; short caudal series of about seven units; ribs well developed with uncinat processes; sternum large with deep keel, two deep incisions in posterior margin; coracoid with simple head and distinct distal expansion at articulation with sternum, small procoracoid process; clavicles fused ventrally, small round head in contact with coracoid and a thin extension extending back to contact scapula; scapula thin and blade-like, pointed posteriorly; pelvis formed of ilium, ischium and pubis fused at the acetabulum, separate behind this vertical; ilium extending length of pelvis, attached to the transverse processes of the synsacral vertebrae; no prepubis.

Limbs: claws on second (most anterior) and third digits of wing; two bones in the carpal region with a sesamoid anteriorly for the tensor patagii longus tendon.

Myology: belly of *ceratoglossus* lies above insertion of *transversus hyoideus*; dermal muscles weakly developed; *tracheobronchialis* inserts on second and/or third bronchial semi-ring; *expansor secundariorum* present; *latissimus dorsi* with two parts; *teres major* small; *teres minor* small, arising from the anterior margin of the scapula (and clavicle?); deltoid two parted, one part serving the propatagium and its *tensor patagii brevis* tendon diffuse (not distinct bands); *biceps* slip to propatagium present; *triceps* with *pars axillaris*; *pectoralis* a single mass with outer and deep insertions; *tensor fascia latae* arising along entire dorsal iliac margin; *rectus femoris (ambiens)* present and inserting through patellar sheath into superficial digital flexor mass; *biceps femoris et semimembranosus* inserts through "accessorius"; *caudiliofemoralis* with caudal and iliac origins; *plantaris* two parted, the *pars tibialis* incorporated into the *gastrocnemius* sheet; *soleus* present and well developed; *flexor digitorum superficialis* subdivided into five *perforans* and *perforatus* parts; the deep flexor tendons fused throughout much of the length of the tarsometatarsus; *tibialis anterior* covered largely by the *peronaeus longus*.

Viseral Anatomy: gut looped and fairly long; stomach simple (as in the falconiforms); caeca present but small; only the left ovary and oviduct developed (perhaps vestige of right); testes equally developed; both carotid arteries developed and together in the hypapophysial canal (Glenny, 1955), vestiges of other vessels in the region of the heart; syrinx of simple tracheobronchial type (much as in the accipitrid) with slight medial and lateral tympaniform membranes; full number of pulmonary air sacs present and penetrating bones; air spaces of head (from nasal passage and middle ear) also present.

External anatomy: in proportion and size about like *Archeopteryx*; tail shortened and composed of 12 feathers; form adapted for easy progression (walking) on the ground, or jumping from branch to branch in the tree; wing not utilized in climbing other than as a balancer; bill somewhat longer than deep and hooked at the tip; covered by a plated rhamphotheca composed of

four or more pieces above and seven below (Jollie, 1961); nostril midway along the length of the bill; simple vestibular fold and slightly rolled nasal tubinal; olfactory chamber with small fold or rolled tubinal; plumage well developed and with smooth outer surface, brown colored, with darker cross bands; foot and tarsometatarsus covered with fine scales (reticulate).

The primitive bird, as described here, did not differ markedly from living types except for its intermediate condition in some anatomical features. If this is an accurate description of the avian archetype we can conclude that most living groups (families in some cases, orders in others) have all progressed equally far from this starting point in one feature or another. Not one of the existing groups can be considered as more primitive than others unless comparisons are based upon specific features. The ostrich is more primitive than many types in terms of its large basipterygoid processes but more modified in the large gap between pterygoid and vomer.

In order to consider the direction of evolution within the falconiform groups, we must have an understanding of the basic adaptive radiation within birds. For this we can hypothesize that the primitive body form was retained in some birds but underwent modification in others along three basic lines: (1) cursorial habit coupled frequently with increase in size and loss of power of flight; (2) swimming habit involving pterylotic changes, webbed feet, and slightly increased size; (3) arboreal habit involving shortening of leg and no change or a decrease in size.

These basic routes of hind limb specialization were accompanied by modifications in flight. An aquatic type could become flightless (*Hesperornis* or Spheniscidae), or highly modified for flight (frigate-bird). These locomotor specializations were primarily for securing food and are also reflected in bill, head, and neck form. Once started on one of these paths there was some changing of direction; i.e., a swimmer could become a wader or take to the shore to become distinctly cursorial.

Birds of an aquatic habit (swimmers, pelagic sea birds, waders, and shore or marsh species) were most abundant in the period of the first radiation of birds because of the greater abundance of food. The land environment did offer possibilities for scavengers and predators. At first food included small reptiles, the eggs or young of larger forms, mammals or leftovers from a dinosaur's meal while along the shores carrion was always available; later with the appearance of flowering plants and insects a much more varied food supply (including fruits) was available and radiation of small species (particularly passeriforms) to exploit fully these sources followed.

#### The Cathartid (Cathartoid) Type

The primitive cathartid modified the ancestral pterylosis by adding a metategmen and reducing or losing the aftershaft. A solid plumage coloration of a dark brownish black was achieved before the origin of this group and was continued with little change throughout its history. The palate was schizognathous (in the true sense of the term), the maxillopalatines were well

developed and spoon-like, the medial surface being nearly vertical. The prefrontal was free, basipterygoid processes were present, and the pterygoid developed a joint at its midpoint as a result of fusion with the palatine. The cranium was less rounded than in living types, the upper bill somewhat shorter. The vestibule opened widely through the external naris and the vestibular fold was reduced or lost. The body skeleton was fairly primitive, but the coracoid was strengthened as a result of increase in size; the sternum had two posterior emarginations. In their myology this group was modified. The *pectoralis* became divided into two separate layers. (A tendency for this complete division is shared with the entire swimming line suggested above.) Also the *teres minor* developed a *pars internus*.

*Neocathartes grallator* approaches the archetype of this group, an archetype quite similar to that of the stercorariid, procellariiform, pelecaniform, ciconiiform, and sagittariid types. The main doubt as to the propriety of this association stems from the fact that the first three groups have a webbed foot whereas the others do not. The reduced hind toe of the cathartid suggests that the foot may have been webbed, but this specialization was lost with the move to the shore and land where they continued their scavenging way of life.

Perhaps *Neocathartes* had longer legs and shorter wings than the prototype, since these could be specializations for shore-living. It is possible that the swimming prototype may have passed through a vulturine wading stage toward its present habit. The possibility of a fossil "cormorant" being present already in the Cretaceous would argue against a basal position for this Eocene fossil (Wetmore 1951b:53). In any case, *Neocathartes* is probably much like the ancestor of the present cathartid species.

Of the living and well-known fossil species, *Cathartes* and *Coragyps* retain more of the primitive features. In these, it can be assumed that the bill is elongated, head feathering reduced, external naris lost (along with the vestibular fold), prefrontal fused to the orbit margin, the cranium more rounded, and most units of the body skeleton retaining a suggestion of the ancestral, swimming proportions.

The condors showed marked specialization in terms of size, in pterylosis, in plumage and body coloration. In this group the greatly elongated rostrum, the prominent exoccipital and basiparasphenoid processes, the form of the cranium and its superficial overlay of bone along with its relationship to the neck all denote specialization. *Sarcoramphus* is intermediate between *Cathartes* and *Vultur* in many respects (but not in plumage coloration). *Gymnogyps* is more modified than *Vultur*, and its trend in skull modification is carried even further in *Breagyps*.

Morphologically the fossil *Gymnogyps amplus* (Fisher, 1947) and living *Gymnogyps californianus* intergrade and probably represent subspecies in time. (Howard, 1947, expressed the same opinion.) The variability of the fossil form is explained by the long period during which the remains were deposited. It is probable that many of the tar pits were open and actively collecting at widely separate times and, in the opinion of Howard (conversation), for only relatively short times. Fisher (1947) stressed

the gap in measurements, but the gap exists only when averages are considered; further, the modern population is small and might conceivably show a reduced range of variability because of strong environmental selection on a dying species.

The evolution of the cathartidae (fig. 205), including the

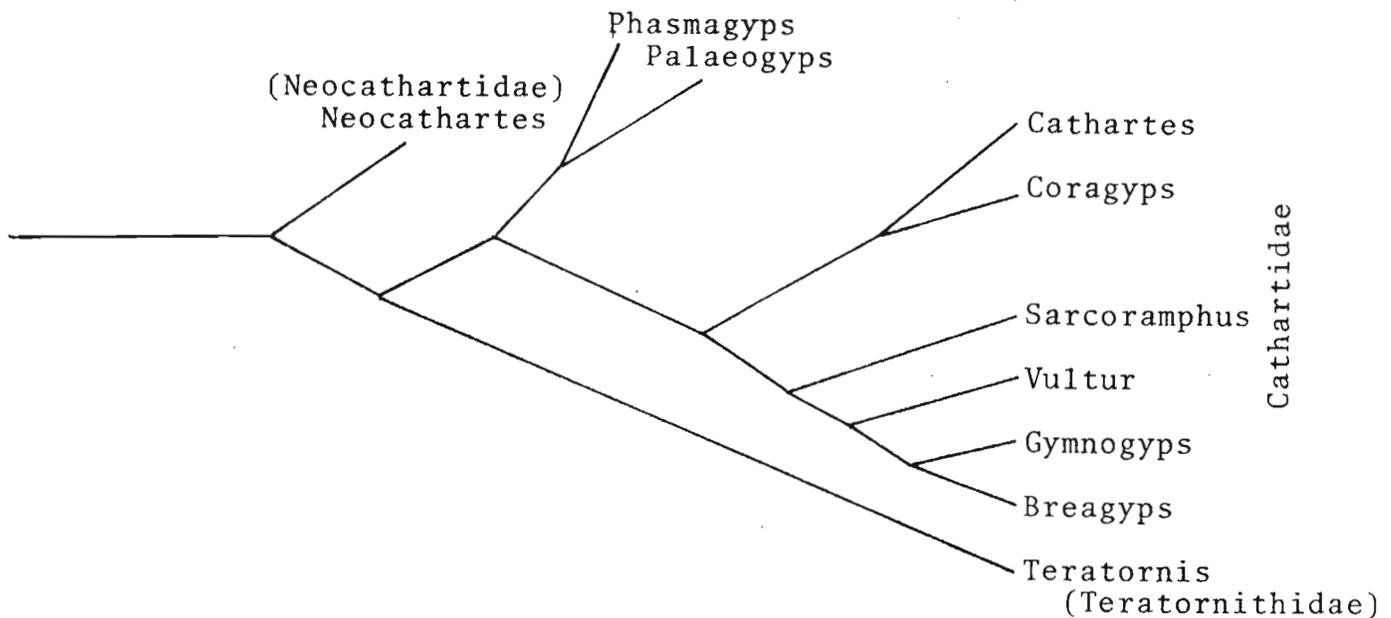


Fig. 205. The phylogeny of the cathartids.

Oligocene *Phasmogyps patritus* and *Palaeogyps prodromus*, has been schematically illustrated by Fisher (1944:294, fig. 47). He indicated (p. 293) that *Breagyps clarki* was ancestral to *Gymnogyps* and *Vultur*. Such a view is hardly tenable inasmuch as *Breagyps* was a contemporary of *Gymnogyps* and as such could not be ancestral (see Howard, 1952). *Breagyps* with its much elongated rostrum, is a more extreme specialization than *Gymnogyps* and is thus even further from the ancestral type. The amount of change evident in comparing Pleistocene fossils with modern forms suggests that divergence of the condors took place in the Pliocene.

The most extreme cathartid in some respects is *Teratornis merriami*. The rostrum is highly modified, the interorbital septum is imperforate, and the olfactory capsule reduced in size. The pectoral girdle and the sternum are modified in parallel fashion to those of *Fregata* and *Diomedea*. In its pterylosis and myology *Teratornis* may have gone further than the condors. This giant vulture also retains certain unmodified features, such as the configuration of the cranium and quadrate and the tarsometatarsus. The retention of such features suggests an early divergence of this line from that giving rise to the living cathartids.

*Teratornis incredibilis* (Howard, 1952) was described from a "cuneiform" (radiale) bone. It does not seem worthwhile to specu-

late on the nature of a species known from a single wing element.

Thus, comparison of the condors, or *Teratornis*, with other types of birds can only be misleading since, as the most specialized cathartids, they can resemble other groups only through convergence.

European fossils which have been identified as belonging with this group are too poorly known to be allocated. Cracraft and Rich (1972) commented on the Tertiary (Eocene, Oligocene of France) occurrence of European cathartids, *Eocathartes*, *Plesiocathartes*, *Diatropornis* (*Tapinopus*), and *Amphiserpentarius*. Relative to the first of these they conclude (p. 273) that several features "strongly suggest that *Eocathartes* is a cathartid vulture. Unfortunately, neither Lambrecht's discussion nor his figures is sufficiently detailed to construct a generic diagnosis." Wetmore (1955:54) reached a similar conclusion. *Plesiocathartes europaeus* (Gaillard, 1908:41-44) is based on a part of the shaft and the distal trochleae of the tarsometatarsus. In size this fossil is much smaller than known cathartids, and in details of structure shows nothing that can be used to link it conclusively with this group. It is of a generalized form suggestive of several groups of birds. The hypotarsus, which might improve the identification, is missing.

*Diatropornis ellioti*, from the same formation as *Plesiocathartes* (Gaillard, 1908:48-51, fig. 8), is known from the complete tarsometatarsus and the distal end of the tibiotarsus. It probably is a cathartid, but identification as such needs confirmation from other parts of the skeleton.

Cracraft and Rich (1972:275) identified the tibiotarsal fragment of *Amphiserpentarius schlosseri* (Gaillard, 1908:45-47, fig. 7) as a cathartid but again the evidence is inconclusive.

Failure to identify these fossils positively as cathartids limits the range of this group to the New World and suggests that it developed in a fashion paralleled by an Eurasian counterpart, the aegyptiins. Should these fossil genera prove to be cathartids (*Diatropornis* probably is) the probability remains high that they entered Europe from North America since here is where most of cathartid evolution appears to have occurred.

#### The Sagittariid Type

This monotypic genus has no real fossil history. In terms of this study, *Amynoptilon robustum* (Milne-Edwards, 1867071) does not compare well enough with the living representative to be considered related (see fig. 127).

It can be assumed that the ancestor of *Sagittarius* had the following features: maxillopalatine processes fused at midline, vomer a vertical plate between the internal nares, basipterygoid processes well developed and functional; prefrontal with large supraorbital process but no supraciliary, the body skeleton and limbs much like those of the ancestral cathartid except the foot modified for clutching, myology also like the ancestral cathartid, pterylosis unmodified from the primitive avian, metategmen and aftershaft present.

The modern species compared with the ancestor, is modified in the following manner: crane-like form with its attendant modi-

fications of osteology (form of sternum or pelvis--shared with *Cariama* and storks); pterylosis (i.e., separation of axillary and sternal tracts, a trend indicated in the storks); specialized color pattern; feather crest; and scutellate tarsometatarsus.

This genus probably represents an independent line established at the first radiation of birds. A wading (or cursorial type) with legs of medium length gave rise to two lines, one of which acquired a long stabbing bill (the ciconiiform) the other which developed a shorter, hooked bill (sagittariid) and a foot modified for capture of small vertebrates by grasping. The latter line gradually developed a more-and-more raptorial appearance. Along with, or after, the acquisition of the bill type, the legs became progressively more stilt-like as an adaptation for a particular style of feeding. This history thus presumes a relationship with the Ciconiiformes, one which involves some degree of parallel development with the Ciconiidae.

#### The Accipitrid Type

This type is represented in the Upper Eocene by the tarsometatarsus of *Palaeohierax gervaisi* (Milne-Edwards, 1869-1871), but it is not until the Oligocene remains of *Paleoplancus sternbergi* (Wetmore, 1933) or *Buteo grangeri* (Wetmore and Case, 1934) that other parts of the skeleton, including the skull, are represented. The fossil remains fit well into the range of variation shown by living species; there is no evidence of transition with any other type of bird.

From the fossils and from the comparative anatomy of the accipitrid group we can describe the archetype as follows: hooked upper bill, perhaps longer than that of the average living species; the cranium rounded and fairly large; supraorbital process of prefrontal large (and ? with a superciliary); the palate weakly desmognathous; the vomer a vertical plate between the internal nares; the basipterygoid processes vestigial; the pterygoid jointed at its middle, the anterior part fused to the palatine; the mandible without a meckelian fenestra; the coracoid strengthened and expanded distally; the head of the clavicle drawn back; the sternum with a single pair of incisions; the pelvis strengthened through further fusion and covering over of the spaces between the transverse processes of the synsacral vertebrae; the foot and tarsometatarsus altered for clenching food, the latter with two calcaneal processes separated by a deep flexor groove (like *Gypohierax* or *Palaeohierax*); ventral feather tract altered by the slight separation of an axillary band; a metategmen present and the aftershaft retained; primitive plumage color pattern of bars altered dorsally and in the wings and tail by reduction in the number of cross bars and strengthening of their pigmentation; the under surface lighter with some feathers cross-barred or striped.

The history of the group can be described as one involving a direct conversion of the ancestral type toward a more specialized predator (in opposition to the view of a close relationship with the Ciconiiformes). The ancestral type retained its walking habit, but increased its power of flight. Its adaptations to the original food source, carrion, involved development of a shorter,

stronger, hooked bill and grasping feet (both serving in tearing up food for swallowing). This type of bill and foot was a preadaptation for increasing vulturine efficiency and also for seizing and killing smaller animals, including birds. Active radiation was quickly followed by radiation away from the scavenger ancestral type. The latter was represented at any time in the history of the group by only a small number of species, since this way of life could supply only a small number of niche specializations, and there was little geographical isolation within Eurasia-Africa for such birds.

The radiation of this group from the ancestral type can be approached only through the existing species. Various genera can be linked with each other at several levels of differentiation, some of which might be identified as subfamilies, others as species cores or supergenera. The trunk and main branches of the phylogenetic tree can only be surmised. The best approach seems to start from the well-defined generic groups and work back through time, showing the different levels of interrelationship as far as is possible.

The Aegypiinae offer a starting point since they represent the assumed primitive way of life (fig. 206). Actually, the very large species of this array must be considered as highly specialized in terms of size and plumage coloration. Unfortunately, these vulturine species are not anatomically well known in spite of the fact that all of them have been dissected at one time or another. It is evident from the study of osteology, however, that the present subfamily Aegypiinae (Peters, 1931) is an undefinable array within which there is a well-marked core of species, the aegypiins (see p. 30).

The aegypiins probably radiated during the Pliocene into the present group of species. This radiation occurred as a result of the abundance of large herbivores. The group is characterized by having an ossified lateral vestibular wall which outlines the external naris; in lacking a superciliary; in having a well-developed, pointed supraorbital process; and in sharing details of coracoid, sternum, tarsometatarsus, and pterylosis. The members of this group physically resemble, in some respects, the large eagles of the genus *Aquila* but this could be the result of need for strength in tearing up the bodies of the large mammals on which they feed. Attributing this similarity to convergence is in agreement with the conclusion that *Aquila* is a genus of some age and modification.

The aegypiins can be placed in three supergenera. The first includes two pairs of genera: *Torgos* (*tracheliotus*) and *Aegypius* (*monachus*), *Trigonoceps* (*occipitalis*) and *Sarcogyps* (*calvus*). The first pair of species differs markedly from one another in coloration and in details of external appearance, such as the shape of the nostrils or the lappets of the former; in its skull *Torgos* has a more rounded cranium, the supraorbital process of the prefrontal bent down more into the orbit, the antorbital process heavier, the bill higher and more inflated, the nasal process of the premaxilla wider and the maxillopalatine processes somewhat more fused at the midline. In spite of the marked differences,

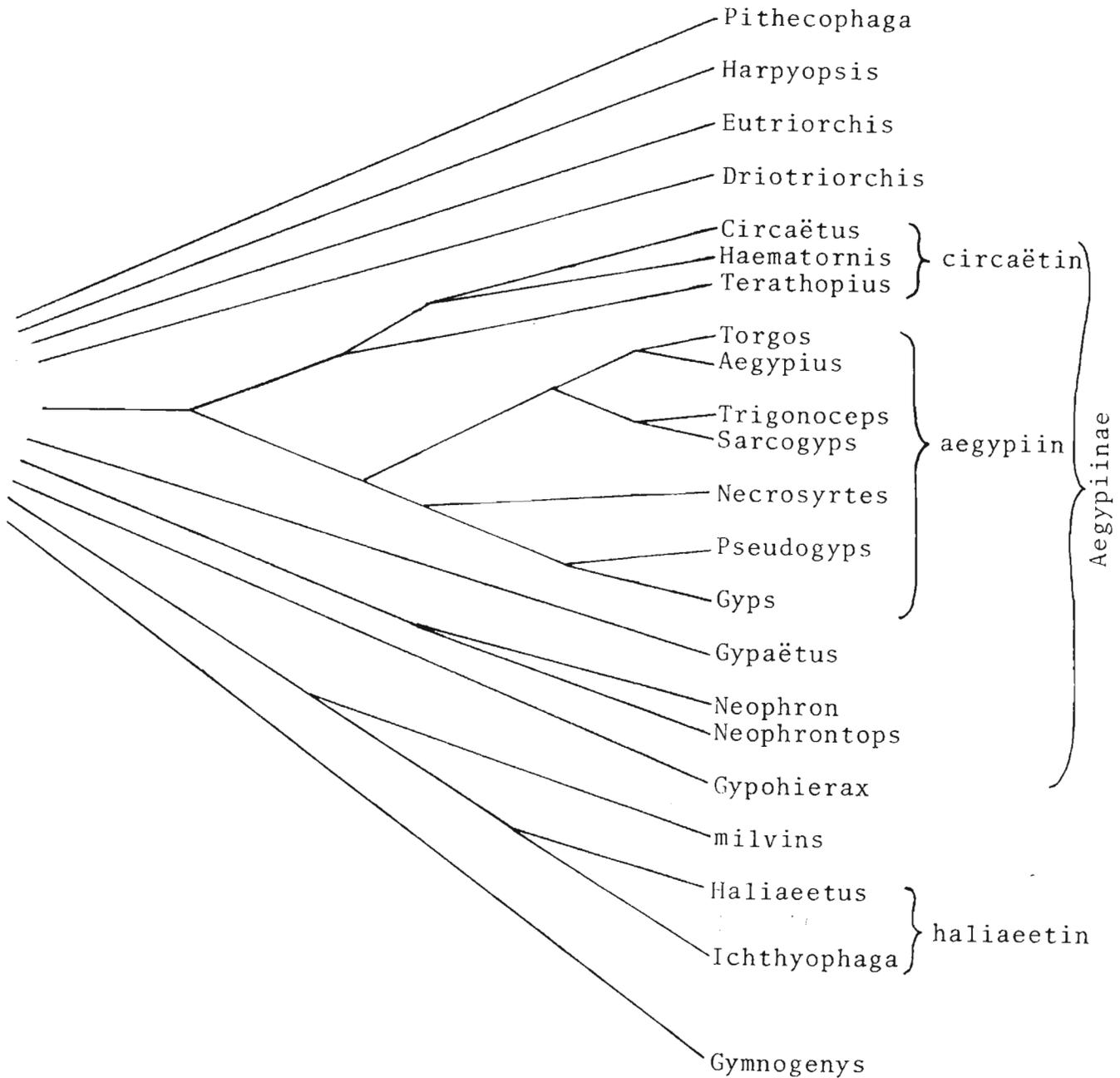


Fig. 206. The phylogeny of the aegyptiins and somewhat similar genera.

the degree of similarity is such that one must conclude that these genera are geographic representatives of a not-too-ancient species, which in its appearance was closer to *Aegyptius*.

The same sort of relationship exists between the species of *Sarcogyps* and *Trionoceph*. The former is more primitive in coloration but more specialized in osteological detail. The differences between these species are of a greater magnitude

than those between the larger vultures.

These two pairs of species appear to be derivatives of a common ancestor which existed in the not-too-distant past. The time of separation might be indicated by making these species congeneric; certainly placing them in a single supergenus is not out of order.

The second supergenus contains the species of *Pseudogyps* and *Gyps*. *Gyps* is the more modified type. The elongated bill, schizognathous form of palate, reduction of vomer, shape of the cranium, elongated basiparasphenoid and exoccipital processes, orientation of skull on neck (angle of base and back of skull), elongated neck and shortened trunk all denote specialization (see fig. 97 for convergence to *Gymnogyps*). The dilution of coloration can also be cited.

The third supergenus contains only *Necrosyrtes monachus*. The exact affinities of *Necrosyrtes* cannot be stated, but it appears to be a member in good standing of the small-headed vulture group, which also contains the supergenus *Gyps*. In coloration there has been intensification of general tone with submergence of barring; the head form is highly altered but the size and general proportions are primitive.

*Neophron* and *Necrosyrtes* possess certain superficial resemblances but disagree in detail. The former lacks the vestibular ossifications, has a reduced supraorbital process of the prefrontal, an ossified vomer and a perforate interorbital septum. The base of the skull is somewhat inflated and differs in details. The sterna are unlike, and there is a lack of fundamental agreement in details of the tarsometatarsus. Details of the ventral feather tract separate these genera as does the plumage coloration of the adult (highly modified from the blackish, primitive plumage of the immature). *Neophron* is "kite-like" in many respects, while *Necrosyrtes* compares better with the other aegyptiins. Assuming some kind of close relationship, such disagreement is unexpected; assuming convergence, it is to be expected. The latter view has been adopted here.

To make the problem of the relationship between *Neophron* and *Necrosyrtes* even more interesting, a third fossil genus (from North America) must be considered. *Neophrontops americanus* is more like *Neophron* than the aegyptiin. These three genera are similar in general form with the cathartid, *Coragyps*, suggesting that the shape of the head and bill has a strong adaptive value for a specific vulturine niche.

The other species currently included in the subfamily by Peters (1931) have no apparent close relationship. *Gypaëtus barbatus* is a widespread Eurasian-African relict, probably of considerable age and highly modified in terms of size, ptilosis, and plumage coloration. It differs so markedly from the aegyptiin type that only convergence can be assumed for those few features they share.

*Gypohierax angolensis* could be a very old species, descended with little change from the Cretaceous or Eocene accipitrid (based on similarity to *Palaeohierax* or *Palaeoborus umbrosus*, see Howard, 1932:70-71). The white coloration of the adult (modified from the blackish juvenal plumage) suggests great age or a long

independent history. In its plumage coloration and stages, *Gypohierax* agrees with *Neophron perenopterus*.

Since *Gypaëtus*, *Gypohierax*, and *Neophron* cannot be positively associated with each other or with any other species groups, they are considered here as independent lines going back to the first radiation of the accipitrid type.

Also of uncertain relationship are the haliaëetins (*Ictin-aëtus*, *Haliaeetus*, and *Ichthyophaga*). These eagles are probably closely related to the vulturins, but such a tie is as much speculation as anything else.

The circaëtins resemble the aegyptin in having the lateral vestibular wall ossified, the calcaneal processes on a medial ridge, a rectilinear pelvis, and a reticulate tarsus. They disagree primarily in having a superciliary. *Terathopius* is in many respects intermediate between the circaëtins and the aegyptins, suggesting a close tie among these generic cores. The problem is one of whether all should be in one subfamily, or two. If two, the disposition of *Terathopius* is difficult to decide.

The circaëtin core may, or may not, include *Driotrionchis spectabilis* and *Eutrionchis astur*. The former has a fairly advanced style of coloration whereas the latter is quite primitive in this respect. Both have a finely scaled tarsus and a modified shape (long tail), particularly the latter. Both appear to be very old species, or at least they are very different from any other kind of hawk. In this case, and in many of those yet to be discussed, there are no physical features known at the present, other than general appearance, which can be used to support relationship.

Another core of species, based upon one feature and little else, is that of the aquilins (fig. 207). The feathered tarsometatarsus (feathered all around) marks this group, the species of which at present are distributed among a dozen genera. Many of the species are large and powerful and in terms of proportions are distinct from one another. Osteologically the group is marked by the strong contours of the skull, the strong bill, and (usually) the flat rather than folded bridge of bone over the olfactory nerve. The body skeleton is powerful and relatively uniform within the group; the tarsometatarsus is particularly characteristic (fig. 131). The pterylosis of this group is marked by the presence of small pennaceous feathers on the crop region. In coloration there is a trend among the smaller species for a white undersurface marked with streaks or spots. The smaller species appear to be the less modified.

Figure 207 shows the genera included in this array and their hypothetical interrelationships in time. The genus *Spizaëtus* is shown as having two parts, in the New and Old World, which resemble each other as much through convergence, as through common ancestry.

Very close to the aquilin group is the accipitrid, which is made up of three cores or supergenera: buteogallin, buteonin, and accipitrid (fig. 208). These three cores, along with several genera, which cannot be more exactly placed, share a more recent ancestor than that which gave rise to the aquilin. Of this array the Central and South American species of the buteogallin super-

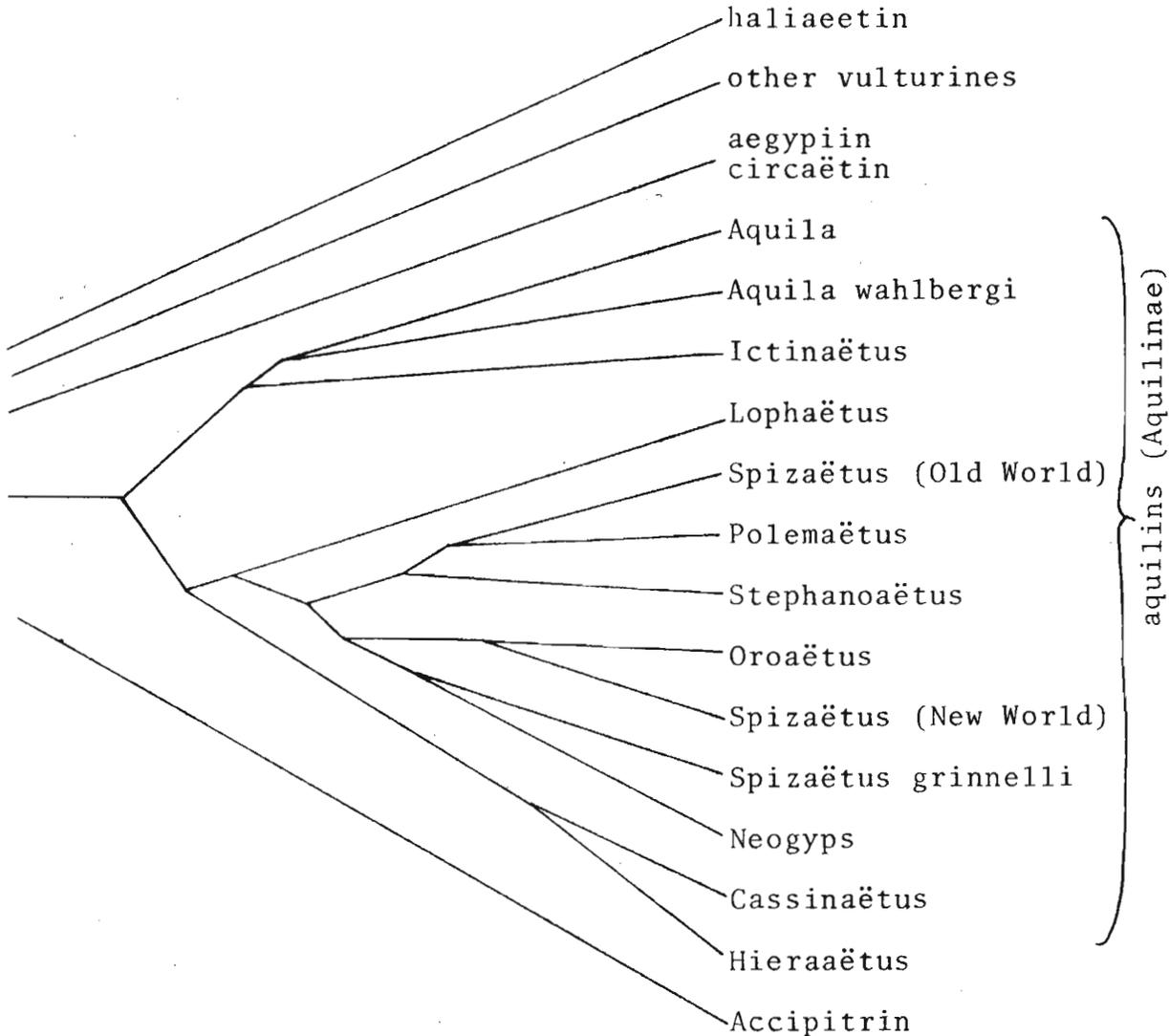


Fig. 207. The phylogeny of the aquilins in relation to somewhat similar genera and generic cores.

genus appear to retain more of the primitive features, a statement that is more of a hope than a defensible hypothesis. Probably the usual trend in this array has been a reduction in size with the smallest species (of *Accipiter* and *Buteo*) being the more recently developed.

The buteogallin core is well marked in terms of plumage pattern, the long tarsometatarsus, and other osteological details. This group includes *Heterospizias meridionalis*, a species usually placed closer to *Accipiter* than *Buteo*. The tarsometatarsus of this group is like that of *Titanohierax gloveralleni* and *Calohierax quadratus* from the recent cave deposits of the Bahama Islands (Wetmore, 1937) or *Hypomorphnus enecta* from the Middle Miocene of Nebraska (Wetmore, 1923).

The buteonin core intergrades with the buteogallin and the

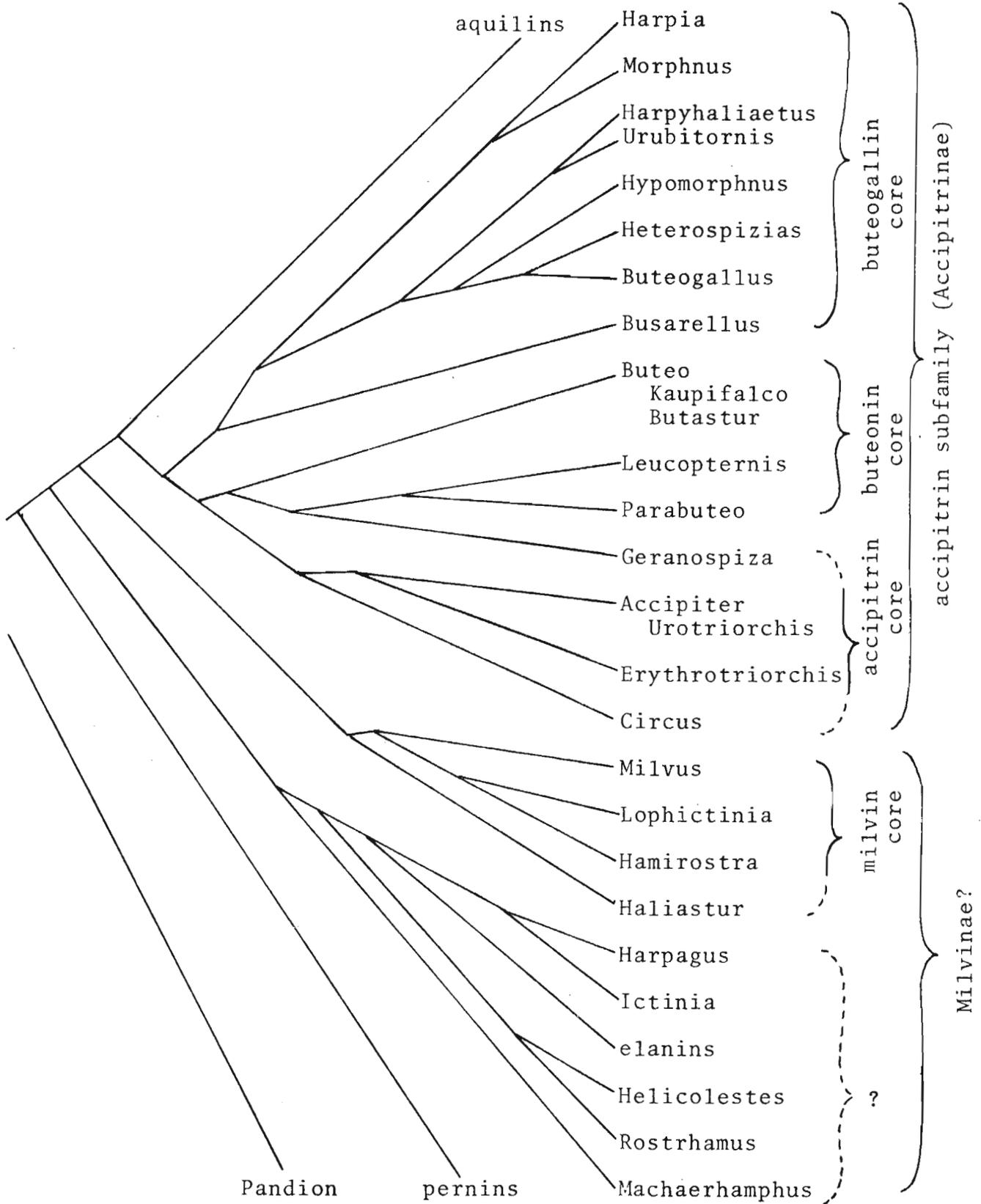


Fig. 208. The phylogeny of the accipitrins in relation to their next of kin. The elanins include *Elanus*, *Gampsonyx* and (?) *Chelictinia*.

accipitrin. It consists of shorter-legged, broader- and longer-winged species. It is best developed in the New World, suggesting its origin here, but with a limited dispersal into the Old World where competition with members of the aquilin and accipitrin groups may have restrained it. The species of this core are intermediate in size but probably average smaller than the ancestral form. *Buteo fuscescens*, the largest species, is probably larger than the ancestral type.

To differentiate the buteonin core from that of *Accipiter*, *Erythrotriorchis*, and *Urotriorchis* is difficult. On the basis of average proportions one can say that the accipitrin core species have shorter, narrower wings and a longer tail than those of the buteonin core, and the tarsometatarsus and toes are longer and slimmer. An average difference in shape of bill might also be cited. In all features, however, the two groups appear to intergrade perhaps due to adaptive convergence.

Of the accipitrin core species, *Erythrotriorchis radiatus* appears to preserve more of the primitive features of the group. In its proportions and coloration it is very close to *Accipiter burgersi*. *Erythrotriorchis doriae* is less like *Accipiter* and can be compared with the milvins.

The genus *Circus* appears to be an early derivative of *Accipiter* in which the outer ear and the underlying bones have been greatly altered. The convergence to *Micrastur* in the facial ruff should be noted. The age of *Circus* is well shown by the tendency toward pale gray plumages and sexual dimorphism of pattern and coloration in some species.

The milvin genera (fig. 208) continue this series toward the kites. They share the reddish, cross-barred, or streaked plumage pattern with *Busarellus*, *Buteogallus*, *Eutriorchis*, *Erythrotriorchis*, and some species of *Circus*. As the milvins cannot be properly defined, the inclusion of the species of *Haliastur* must be considered provisional. This group marks the transition from the scaled (primitive) to the scutellate tarsus found in most of the members of this array.

Somewhat more distant and showing strong specialization in size (small) and feeding habit are the other "kites". These might be placed in a kite subfamily, but this would be an artificial catch-all. Differing least from the accipitrin type are *Ictinia* and *Harpagus*. These distinctly colored species with a notched tomium are close to the elanins in shape, size and plumage coloration.

The elanins mark an extreme of modification from the primitive type both in terms of plumage pattern (young and adult), and in myological details of the hind limb. Osteologically they are also distinctive in the separation of maxillopalatines, reduction of ossification in the nasal vestibules, and the form of the tarsometatarsus.

*Rostrhamus* and *Helicolestes* are geographic representatives of a single ancestral type, highly modified in shape of the bill, body proportions, and in plumage coloration. Without detailed study it is only possible to guess as to the next of kin of these species but their placement with other kites is probably not

incorrect.

*Machaerhamphus* is an extreme type without apparent close relatives. To place it closer to the elanin than to other kites is to assume that the open palate is of significance. Other skull features might be used to separate these. The distinctive features suggest a long and independent history for this species.

The pernin genera form the last and one of the most distinct species groups. The prefrontal is reduced, the supraorbital process is shortened, and the superciliary lost. The orbit is very large with reduced margins and all of the processes of the skull are reduced. The tarsometatarsus varies but may involve calcaneal canals for the flexor tendons. Certain features of the sternum and pectoral girdle resemble the aegyptian, i.e., primitive. Some of the details of myology (the superficial flexor muscle of the shank and lack of the *rectus femoris*) represent modification away from the primitive. External similarities in bill form, foot and tarsometatarsal cover, plumage patterns, and the tendency for small pennaceous feathers covering the lores and base of bill mark this group. All of these features suggest a long independent evolutionary history, which might be diagrammed as in figure 209. Much of the resemblance between this group

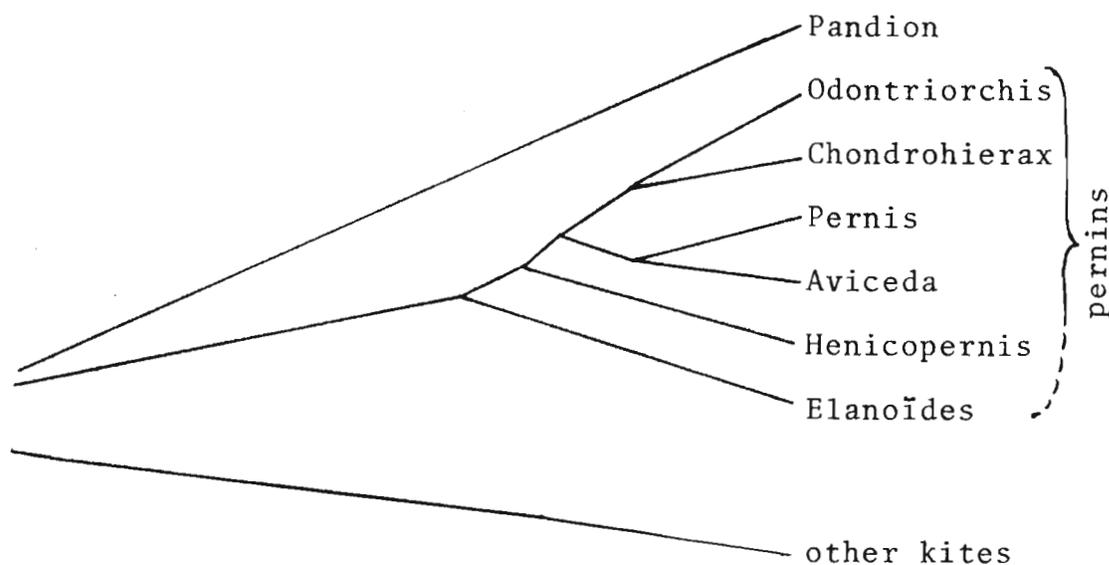


Fig. 209. The phylogeny of the pernins and their next of kin.

and the elanin (modified plumage pattern, superficial flexor muscle details, and *rectus femoris* insertion) may be due to parallel changes in the two lines.

The last, and most distinctive species of the accipitrid type, is *Pandion haliaetus*. It usually has been placed in a separate family or a distinct suborder (see Table 2). This species differs in its ptilosis, osteology, and myology so drastically that it must either be excluded from the Accipitridae or recognized as representing the extreme of allowable variation within a family. The similarity of *Pandion* to the pernin kites

has frequently been remarked, but upon testing it is found to be very unconvincing. It seems best to leave *Pandion* as the sole representative of a subfamily of great age but limited as to its biological success in terms of speciation. (The single species is cosmopolitan except for South America at the present time.)

From the above discussion, most of the genera of the Accipitridae can be seen to fall into four large subfamilies: the Aegyptiinae, Aquilinae, Accipitrinae, and Perninae. To this can be added the small subfamilies Haliaeetinae, Elaninae, and Pandioninae. The Elaninae can be enlarged doubtfully, to include *Ictinia* and *Harpagus* and, even more doubtfully, *Machaerhamphus*. *Elanoïdes* might be cited as intermediate between elanin and pernin. This leaves several genera standing alone: *Gymnogenys*, *Gypohierax*, *Neophron*, *Gypaëtus*, *Pithecophaga*, *Harpyopsis*, *Eutriorchis*, *Driotriorchis*, and *Machaerhamphus*. Recognition of each of these as distinct subfamilies is perhaps not proper, but for the present this is necessary. Some of these genera (with the exceptions of *Gymnogenys*, *Pithecophaga*, *Harpyopsis* and *Machaerhamphus*) might be included with the Aegyptiinae but to do so would soon draw in the kites and before long all of the accipitrids.

Such a large number of subfamilies is not out of accord with the history of birds as described by Wetmore (1951b:63). He suggests that birds were most abundant in the Miocene and Pliocene. During the ice age severe reductions occurred both in terms of numbers and of species. During the interglacial periods and after the ice retreated for the last time there was some reradiation and an increase in number of species but also further extinctions. A dozen or so subfamilies does not seem too excessive when we consider that only remnants of a once widely diversified family are represented by living species.

#### The Falconid Type

The archetype of this group must be constructed without fossil assistance since it is a conclusion of this study that the Miocene *Falco ramenta*, described by Wetmore (1936), cannot be identified as belonging with this group. However, the basic similarity of the component species makes this task somewhat simpler than it might otherwise be.

The following attributes seem reasonable: skull not unlike that of the primitive accipitrid, differing in the ossification of the vestibular walls, in the detailed relationship of the premaxillary palatal extensions and the medial ossified bar, in the minutia of the cranium and palate, and in the lack of superciliary, separately ossified anteropterygoid, and jugal; mandible with a meckelian fenestra; coracoid slim with rounded head and large procoracoid which nearly encloses the triosseal canal, distal end only slightly expanded and without a distinct sternocoracoid process; sternum with two deep notches posteriorly, keel deepest at the anterior end; several thoracic vertebrae fused, reduced number of vertebrae in synsacrum; pelvis broad with rounded contours; tarsometatarsus with inner calcaneal ridge extending much of length of bone, leg and foot not powerfully developed; ventral feather tract with strongly separated axillary

and sternal bands, vestigial connection between large axillary division and ventral tract at inner base of thigh, dorsally the primitive bilateral bands meet only in the caudal region, metategmen developed and the after shaft retained; color pattern much like that of the accipitrid (modified along similar lines in the evolution of the group); the lores and cere covered with bristles; tarsometatarsus reticulately scaled.

The history of this group can only be conjecture. It can be assumed to have developed from an arboreal line, the foot adapted to perching. Probably always weakly predaceous, this group fed on small organisms killed by nipping with the bill. The feet were used for holding prey, but they lacked the clenching power of the accipitrid. Radiation within the group was mainly a matter of perfection of predation styles with some species tending toward scavenging.

This group arose in the New World (South America?) to fill a predation niche not occupied, or only partially occupied, by the accipitrids. The most successful genus, *Falco*, with several different sizes of species, invaded the Old World and is now cosmopolitan.

Of the living genera, *Milvago* is most primitive in plumage coloration. This plumage feature is shared with *Polyborus lutosus*, *Ieracidea berigora*, and *Falco novaehollandiae* (and the immatures of many species of *Falco*). *Micrastur* and *Herpetotheres* represent old, relict species with specialized color patterns and a combination of specializations and primitive features. Particularly to be noted is the great alteration of the tarsometatarsus in *Micrastur* as compared with *Herpetotheres* or the other falconids. Alteration of this structure is also observed in the Polyborinae or *Spizapteryx*.

It is not really possible to identify one genus as the most primitive since all of the genera have undergone change with time (fig. 210). The difference between *Micrastur* and *Herpetotheres* is as great in some details (form of tarsometatarsus) as a comparison of either with *Falco*. Yet, for example, these genera are more alike and more specialized, in terms of the *soleus* muscle than either is like *Falco*. The various criteria suggest the great age of *Micrastur* and *Herpetotheres*. The large number of species of *Falco* suggest that this radiation occurred relatively recently and was due to some extent at least to the periodic ice ages of the Pleistocene. In the genus *Falco*, radiation has involved a general reduction in size.

#### THE PLACE OF THE FALCONIFORMS IN THE CLASS AVES

##### Introductory Remarks

Various sections of this study establish the view that the types found in the order Falconiformes are so dissimilar that their inclusion in a single order is undesirable. The evidence does not prove this conclusion, but limited comparisons in each system examined indicates that the degree of difference between these types is in each case at least as great as that between other orders. Within each of the falconiform groups there is a range of

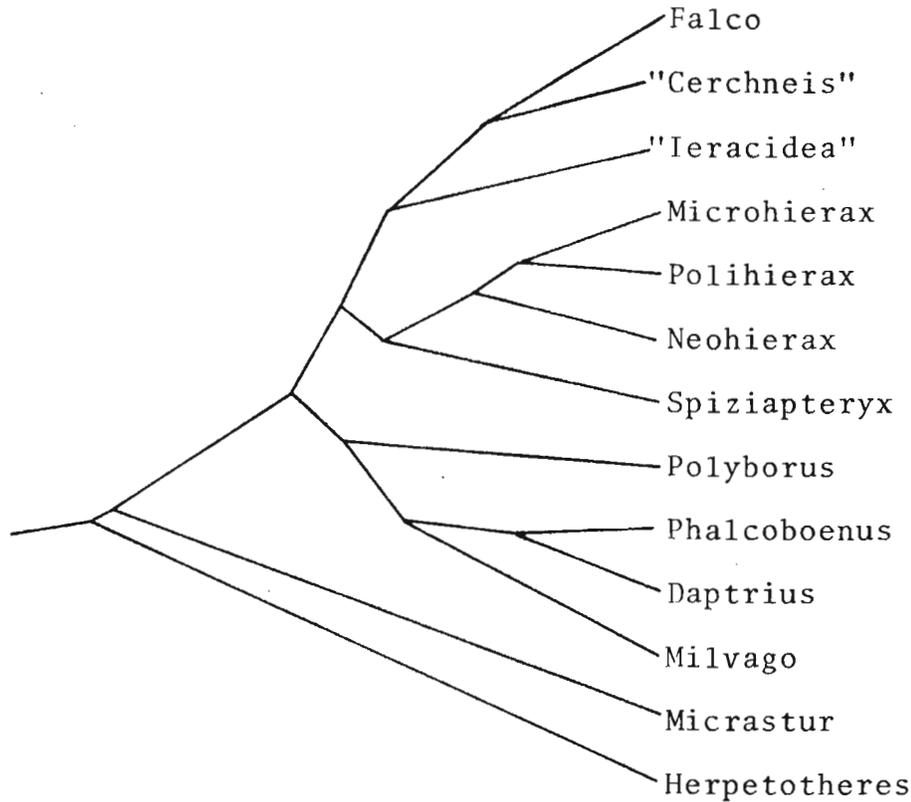


Fig. 210. The phylogeny of the falconids.

variation comparable to that of some orders and nowhere, in spite of the convergent forces which might be presumed to be in operation, is there conclusive overlapping of features. Where certain features are shared, they are of doubtful value. The question then becomes one of where do these types belong in the phylogeny of birds? Each of the groups can now be considered in the light of the broader results of this study.

#### The Cathartid Type

This type is the most distinct of the falconiforms. Its uniqueness does not appear to stem from specialization; rather it reflects a different heritage, a heritage which appears to be shared to a noticeable extent with the procellariiforms, pelecaniforms, ciconiiforms, and charadriiforms. On the basis of its morphological peculiarities, when compared with these types, it should be considered an independent order.

This type is represented in the upper Eocene by *Neocathartes grallator*. This fossil appears to be essentially like the living species and shows no greater resemblance to the other falconiform types than they do. The most aberrant member of this group is the Pleistocene species, *Teratornis merriami*. This huge bird appears to be greatly modified, away from the basic primitive style as typified by the smaller living species of *Cathartes* and *Coragyps*. Its modifications are paralleled to some extent in large species of related orders.

The suggestion by Ligon (1967) that the cathartids are a suborder of the ciconiiforms is rejected. I have reviewed each of the areas examined by Ligon but reached a different conclusion. The possible role of the cathartid as a precursor of the accipitrid or sagittariid types will be discussed under the next heading.

#### The Sagittariid Type

Many of the remarks concerning the cathartid and its next of kin apply equally well to this group, and any discussion of the origin of the accipitrid from a "ciconiiform" group (Garrod, 1874), or "Order Pelargornithes" Fürbringer, 1888) involves both types. First let us consider the degree of interrelationship and then the "primitiveness" of position of both groups.

The assumption of a relationship between the cathartid and sagittariid types cannot be confirmed by any of the morphological features described here. There is a superficial similarity in some details of the hind leg musculature, and the form of the tarsometatarsus but nothing more. Whatever features these two types share, as suggested by the description of their archetypes, these are very generalized structures shared probably with the entire aquatic array. Whereas the cathartid shows some evidence of vulturine specialization, the sagittariid, as compared with the ancestral type, is greatly modified in its head skeleton, pterylosis, and crane-like form. *Diatropornis ellioti*, known from several tarsometatarsi and the distal end of the tibiotarsus (Gaillard, 1908: Cracraft and Rich, 1972) could be considered "intermediate" in form but the evidence is far too weak to have real meaning. These tarsometatarsi might belong to a number of orders. Their small size suggests a fairly specialized species, well away from any stem position.

The suggestion (supported by the long-legged *Neocathartes*) that the primitive falconiform was a long-legged ciconiine does not seem very probable, although the ancestor was probably more cursorial, with longer legs, than many of the living species. Crane-like proportions are a specialization and, therefore, a matter of convergence in the several types sharing them (*Sagittarius*, cranes, cariamids, some ciconiiforms, flamingos).

Since the cathartid and sagittariid show little agreement, it is not likely that they represent remnants of a single primitive, predatory type, but more likely that they are separate evolutionary lines which have retained some features in common with other, equally distinct and separate lines such as the procellariiforms, ciconiiforms, pelecaniiforms, stercorariids, and possibly gulls.

The cathartid type as an ancestor of the accipitrid seems most unlikely. If the cathartid constitutes an effective vulturine type, which is suggested by its long history, it would seem probable that it could have evolved into some predatory form. Failure to become active predators is best explained as due to occupation of such niches by aggressive, well-adapted accipitrids. The contemporary evolution of these two groups is indicated by their structural differences, which must be considered as heritage rather than habitus.

*Sagittarius* as a living representative of the primitive accipitrid stem type, cannot be so easily dismissed. If the head skeleton is indicative of common ancestry, one can assume that the total predatory form (i.e., that of the accipitrid type) had already been fixed before their dichotomy. Such a conclusion does not agree with the stork-like body skeleton and the distinctive pterylosis and myology. The style of pterylosis (more specialized than that of the accipitrid) might easily be the result of the alteration of body form, for it is paralleled by changes among ciconiids. Certain features of the skeleton and myology appear also to be functional dictates of this body form (agreement with storks, cranes, and *Cariama*). However, whereas other stork-like types reveal their natural interrelationships in many details, *Sagittarius* does not. Even in terms of the head structure there is doubt as to an accipitrid relationship. This head type could be a functional convergence, a situation apparently paralleled by the falconid. The differences between the accipitrid and sagittariid types suggests that divergence occurred at such an early stage, that ordinal separation better expresses what must otherwise be anatomically meaningless.

#### The Accipitrid Type

If we assume that the accipitrid type shared a common ancestry with the sagittariid, it was not until after their divergence that the accipitrid differentiated into what has been described here. The constancy of pterylosis, osteology, and myology, measured in terms of the aberrant genus *Pandion*, suggests that this line stems back to the initial radiation of birds.

Fossil remains of accipitrids date back to the Upper Eocene. These agree well with living forms, and there is no evidence of gradation toward other types (orders) of birds, including *Sagittarius*. The fossils suggest that many primitive features have been retained in some of the vulturine genera, particularly *Gypohierax*. In size the early accipitrids were fairly large, larger perhaps than most of the modern species. Modification in this group has apparently involved an average decrease in size.

Whereas the cathartid and sagittariid show some similarity to a group of orders, the accipitrid type does not. The accipitrid is a radical departure in form of skull and tarsometatarsus and in myology, particularly that of the hind limb. The physical isolation of the accipitrid type suggests a long independent history.

The body plan of the accipitrid does not clearly indicate its ancestry, but one can assume that it came from a cursorial, vulturine type which was contemporaneous with a second type that eventually gave rise to the cathartiform, procellariiform, pelecaniform, ciconiiform, sagittariiform, sphenisciform, and charadriiform arrays. This ancestral type dates back at least to the Cretaceous.

#### The Falconid Type

The possible relationship between the accipitrid and the falconid types is the most difficult to discuss. It makes no

difference whether the problem is viewed in terms of the two types as derivatives of an intermediate ancestor or as products of a prototype belonging to one or the other of the present types (i.e., falconid type ancestral to accipitrid or vice versa). The lack of overlap between them does not agree with a theory of common ancestry. For example, if the style of pterylosis of the accipitrid is adapted for predation, then both types should share it. The question then is why are the two types so different? The same type of analysis of skull form, tarsometatarsus, and myological features reaches this same unalterable conclusion, viz., that the starting points of the two types were dissimilar and that any features shared (hooked bill, general shape of head, and body proportions) are convergent developments and adaptations to a way of life.

Sushkin (1905) and others have assumed that *Herpetotheres* or *Micrastur* is indeed intermediate between the accipitrid and falconid types, a conclusion not reached in this study. Any greater similarity between these genera and the accipitrid can be considered more as evidence of convergence than relationship, a degree of convergence much less than one might expect.

If the accipitrid and falconid types are not related in some direct way, where should one look for their next of kin? The hypothetical point of origin of the falconid can be based on an osteological similarity to owls, parrots, cuckoos and plantain eaters. It is doubtful that the pectoral girdle of the falconid would show convergence to that of such a diverse lot. Rather a more intimate relationship can be assumed between these groups than exists with types lacking this kind of pectoral girdle. In contrast, the pectoral girdle of the accipitrid resembles more the water bird type than the arboreal stem of the falconid.

The constant conclusion reached is that the falconid is more closely affiliated with other non-falconiform types of birds than the accipitrid. The past association of these types is based wholly on their predatory habit and not upon morphological similarities, other than those which are patently adaptive.

#### Summary and Conclusions

The order Falconiformes, as defined by Peters (1931), Mayr and Amadon (1951) and Wetmore (1960), has been examined in as much detail as possible in terms of its ptilology, osteology, myology, viscerology, and external features. Comparisons are examined in terms of demonstrating similarities or lack of similarity. The evolutionary trends of features are considered along with the idea of each species being a mosaic of features. The conclusion, suggestive or strongly reinforcing, of each of these anatomical accounts has been that the falconiforms is an artificial aggregation of species of four orders: Sagittariiformes, Cathartiformes, Accipitriformes, and Falconiformes. These orders are separated by morphological gaps as large as, or larger than, those separating many other orders. Whereas some of the present orders of birds can confidently be associated into even larger categories, the Accipitriformes stand alone as the earliest cursorial, scavenger-predatory line of birds. The Sagittariiformes

and Cathartiformes appear to be natural parts of a vast array of birds of aquatic or shore habitats whereas the Falconiformes (*sensu stricto*) belong with an arboreal array.

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For legend of Fig. 54, see page 80 - (p. 180 of Volume 2).

