

A STUDY OF THE STRUCTURE OF THE HUMERUS IN THE CORVIDAE

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The identification of the bones of fossil and Recent passerine birds has for long presented a difficult problem. As a step toward facilitating this kind of identification it was decided that an attempt would be made to construct a key to certain of the members of the family Corvidae (crows, jays, and magpies) based on humeral configuration. The humerus was selected because of its variation among the passerines and its relative abundance in fossil deposits. After a survey of the literature on the myology of the shoulder girdle of the Corvidae, it was apparent that a more detailed study of the muscles of the head of the humerus would have to be made before a critical analysis of configuration could be undertaken. The writer wishes to express his appreciation to Dr. Alden H. Miller for his continued interest and criticism of the work.

GLOSSARY

To enable precise reference to characters, some new terms (marked with an asterisk) were coined, and to avoid confusion all terms which have been employed in reference to the humerus are here defined (fig. 50).

- Bicipital crest. Internal (ventral) margin of bicipital surface.
 Bicipital furrow. Depression medial to palmar ridge.
 *Bicipital groove. Oblique groove for blood vessel on bicipital surface.
 Bicipital surface. On palmar side of head, delimited laterally by palmar ridge, proximally by ligamental furrow, and distally by the point of contact of bicipital crest with shaft.
 Capital groove. Groove between internal tuberosity and head.
 *Capital shaft ridge. Ridge running to head from tubercle at proximal end of shaft line.
 *Deltoid ridge. Faint ridge forming medial limit of insertion of *M. deltoideus* on anconal surface; distal portion lateral to latissimus ridge usually absent.
 *Deltoid surface. Area between deltoid ridge and pectoral crest; area of attachment of *M. deltoideus superficialis longus lateralis*, lateral part.
 External tuberosity. Tuberosity at proximal margin of pectoral crest; *Mm. supracoracoideus* and *deltoideus profundus brevis* insert thereon.
 *Fossa I. Pneumatic fossa.
 *Fossa II. Fossa between pneumatic fossa and capital shaft ridge.
 Head. Articular surface at proximal end.
 Internal tuberosity. Tuberosity separated from head by capital groove; insertions of *Mm. coracobrachialis posterior*, *subcoracoideus*, *subscapularis*.
 *Latissimus ridge. Ridge on anconal surface of insertion of *M. latissimus dorsi anterior*; adjacent and medial to posterior end of deltoid surface.
 *Medial bar (=median crest). Bar or partition from internal tuberosity to floor of fossae; lies between fossae when two are present, or forms medial limit of fossa I.

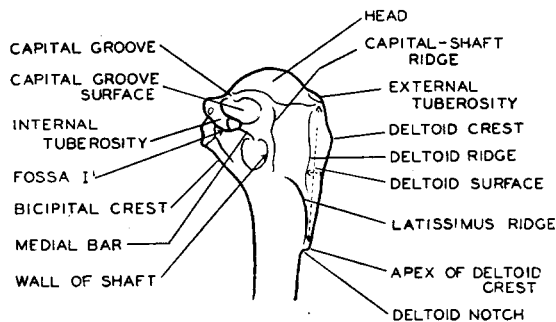


Fig. 50. Anconal view of head of corvid humerus.

- *Palmar ridge. Ridge on palmar surface which forms medial limit of area of insertion of *M. pectoralis superficialis*.
- Pectoral crest (=deltoid crest). External (dorsal) margin of deltoid surface.
- Pectoral crest, apex of. Distal prominence of pectoral crest.
- *Pectoral notch. Notch between apex of pectoral crest and shaft.
- *Pectoral surface. Area of insertion of *M. pectoralis superficialis*, limited medially by palmar ridge.
- *Shaft line. Anconal apex of shaft.
- *Shaft, wall of. Surface of shaft between floor of fossae and shaft line.

MYOLOGY

The topographical relationships of the brachial muscles throughout the Corvidae exhibit but slight variation. The following descriptions are of the single representative species, the crow (*Corvus brachyrhynchos*) and were derived from four dissections. The muscles were identified on the basis of innervation (fig. 51).

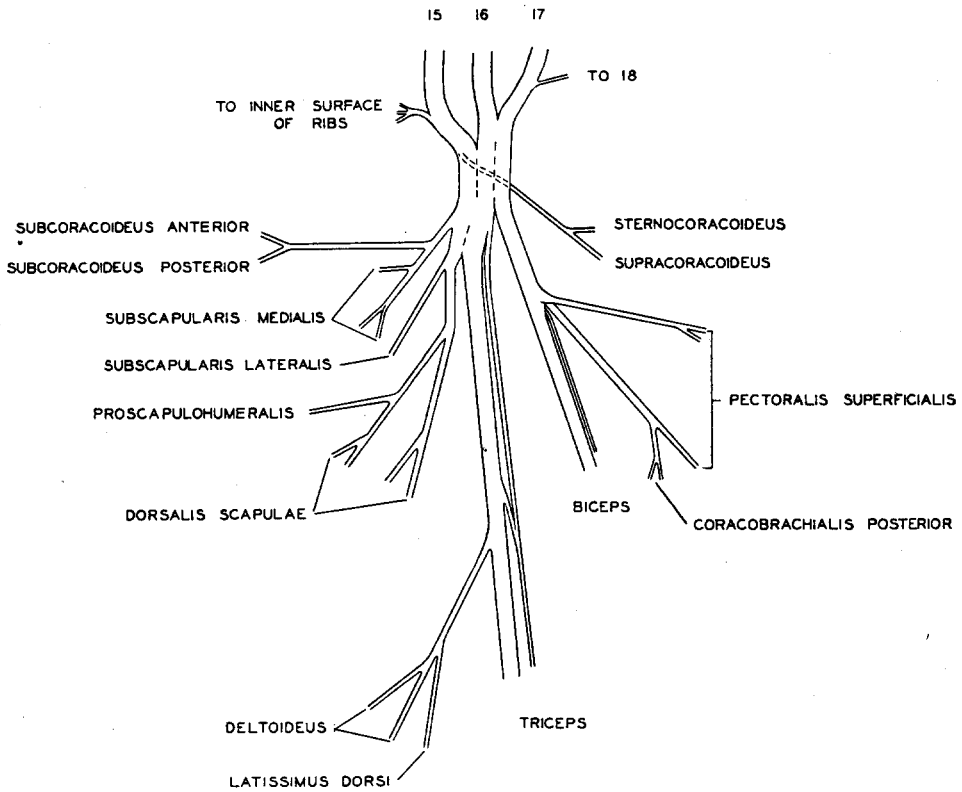


Fig. 51. Brachial plexus of *Corvus brachyrhynchos*.

The desirability of designating avian muscles in terms of those of other tetrapods has been recognized by several workers. For this reason the terminology used here is that of Howell (1937) which takes into account the most advanced views on muscle homology. Gadow (1891), Fürbringer (1902), Shufeldt (1890), and Burt (1930) were used for additional reference.

Drawings of the sternum, furcula, coracoid, scapula and humerus of *Corvus brachyrhynchos* were made with a dioptograph. Areas of origin and insertion of the muscles on

the humerus were taken at the time of dissection and plotted on the drawings of the bones.

Thoracodorsal matrix.—*M. latissimus dorsi anterioris*. Origin: thoracic vertebrae—spines of third and anterior one-half of fourth. Insertion: humerus—on latissimus ridge of anconal aspect. Innervation: by a twig from *N. deltoideus* rather than a separate branch from *N. thoracodorsalis* as in *Gallus*.

M. latissimus dorsi posterior. Origin: thoracic vertebrae—apex of spines of fifth, sixth, seventh, and eighth by light fascia; fascia of *M. sartorius*—light fascia along posterior margin of proximal portion of muscle. Insertion: *M. latissimus dorsi anterior*—on fascia of dorsal surface at contact of two slips; humerus—by a weak tendon on small tubercle at distal limit of capital shaft ridge. This is also point of attachment of ligament from os humeroscapularis. Innervation: by bifurcation of twig supplying *M. latissimus dorsi anterior*.

Axillary matrix.—*M. dorsalis scapulae*. Origin: scapula—lateral surface of posterior three-fifths of blade. Insertion: humerus—ventral to pneumatic fossa on margin of bicipital crest by a strong tendon; area clearly defined on bone. Innervation: *N. dorsalis scapulae*.

M. deltoideus; occurs in three main divisions. (1) *Superficialis longus medialis*. Origin: clavicle—dorsal surface. Insertion: distal to humerus; is in contact with humerus but has no additional origin or insertion thereon. (2) *Superficialis longus lateralis*; originates as two distinct parts: (a) Lateral part. Origin: scapula—small tendon immediately posterior to origin of *pars profunda brevis* and by fibers from triangular area on dorsal surface adjoining neck of scapula; humerus—deltoid surface and by a few fibers along a line from deltoid crest posteriorly toward ectepicondyle. (b) Medial part. Origin: Os humeroscapularis and ligaments of shoulder joint. Lateral and medial parts unite one-half length of humerus distally. (3) *Profundus brevis*. Origin: scapula—oval-shaped area between furcular and coracoidal articular surfaces, deep to anterior part of *superficialis longus lateralis*. Insertion: humerus—on external tuberosity superficial to insertion of *M. supracoracoideus*. (*Pars profunda longa*, described by Howell as occurring in *Gallus*, is lacking in corvids.) Innervation: *N. deltoideus*.

M. proscapulohumeralis. Origin: scapula—crest of one-fourth of blade immediately proximal to origin of *M. dorsalis scapulae*. Insertion: humerus—on rounded scar on distal portion of floor of pneumatic fossa. Innervation: by twig from proximal branch of *N. dorsalis scapulae*. This innervation might lead one to conclude that *M. proscapulohumeralis* is more closely associated with *M. dorsalis scapulae* than with *M. subscapularis* as suggested by Howell.

M. subscapularis. Origin: scapula—proximal two-fifths of lateral surface of blade, the two distinct parts of muscle separated axially by origin of slip of *M. serrati*. Insertion: humerus—by a

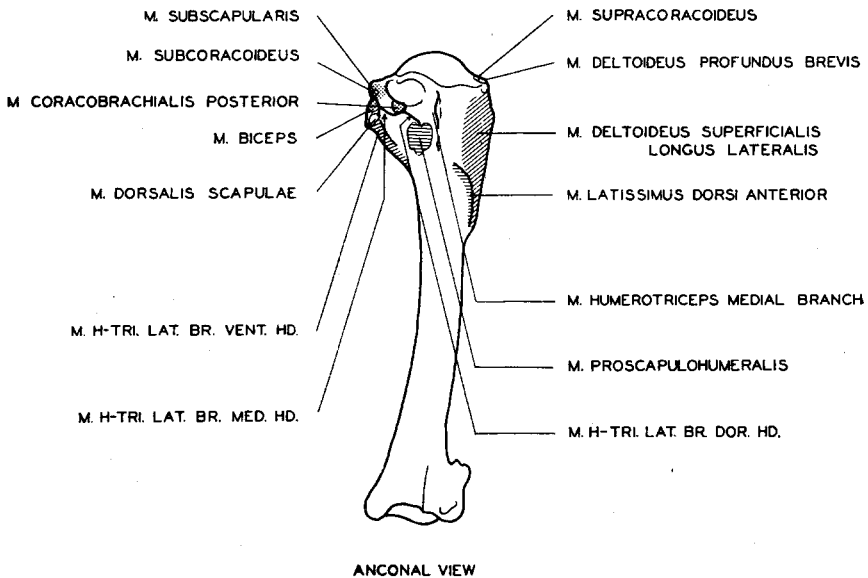


Fig. 52. Humerus of *Corvus brachyrhynchos*, x1, showing areas of muscle attachment on proximal end.

common tendon on internal tuberosity immediately distal to tendon of *M. subcoracoideus*. Innervation: medial portion innervated by a dorsal branch of *N. subcoracoideus*. Lateral portion, contrary to the findings of Howell in *Gallus*, not innervated by twig of this dorsal branch but by separate branch from base of *N. dorsalis scapulae*; this latter branch arises immediately distal to base of *N. subcoracoideus*.

M. subcoracoideus; consists of two parts, anterior and posterior, with widely separated origins and common insertion. (1) Anterior part. Origin: coracoid—oval area on dorsal surface posteriorly adjacent to glenoid facet; fibers closely adherent to ventral portion of *M. subscapularis* near insertion of latter. Innervation: *N. subcoracoideus*, anterior twig. (2) Posterior part. Origin: coracoid—inner surface of base medial to sternocoracoidal impression, with lateral margin of muscle adjacent to medial margin of impression. Innervation: *N. subcoracoideus*, posterior twig. The posterior part unites with the anterior part two-thirds length of coracoid anteriorly. Common insertion: humerus—tendon on margin of internal tuberosity ventrally adjacent to insertion of *M. subscapularis*.

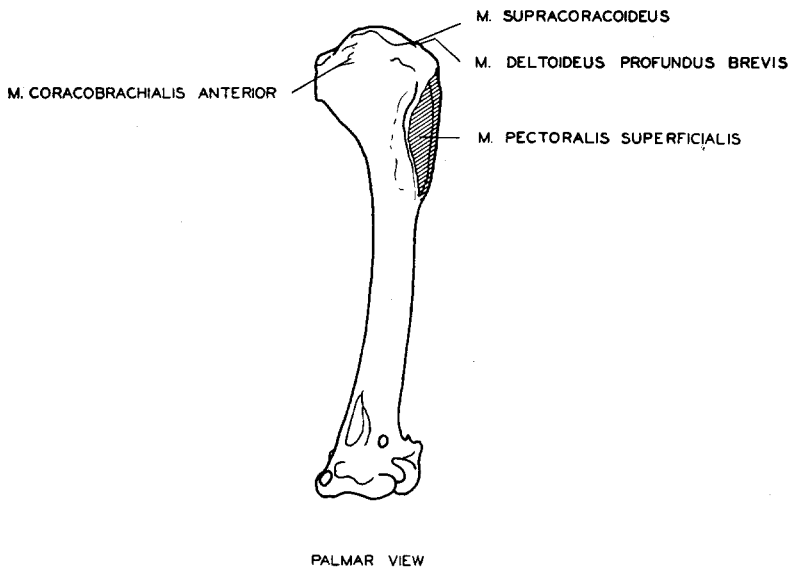


Fig. 53. Humerus of *Corvus brachyrhynchos*, x1, showing areas of muscle attachment on proximal end.

Brachio-antebrachial group.—*M. triceps*; made up of two distinct portions, *scapulotriceps* and *humerotriceps*. (1) *Scapulotriceps* (not considered since it is not directly related to morphology of head of humerus). (2) *Humerotriceps*; originates as two main branches, lateral and medial, with common insertion: (a) Lateral branch, composed of three digitations; ventral head—proximal portion of bicipital crest immediately lateral to *M. dorsalis scapulae*, extending distally around tendinous insertion of latter; medial head—from lateral (ventral) edge of pneumatic fossa, joining ventral head 2 mm. distally at posterior margin of insertion of *M. dorsalis scapulae*; dorsal head—from proximal wall of lateral one-half of fossa, joining united lateral and medial heads short distance distal to their union. Lateral branch attached to ventral margin of humerus from its origin distally about three-fourths length of bone; attachment consists of a few fibers on a line along which indistinct ridges may be visible. (b) Medial branch—single head from wall of shaft and posterior portion of capital groove between internal tuberosity and capital shaft ridge adjacent to head of humerus; indentation present at site of origin; few fibers attach along "line of shaft"; attachment extends three-fourths length of bone and fine lines or ridges may occur on bone. The lateral and medial branches unite one-half length of humerus distally. Insertion: ulna—by a common tendon. Innervation: *N. radialis*.

Pectoralis matrix.—*M. pectoralis superficialis*. Origin: carina—area adjacent to margin; sternal plate—narrow area along posterior margin, and a few fibers lightly adherent to posterolateral surface of sternal plate; membrane covering sternal notch—surface of membrane and posterior sternal process;

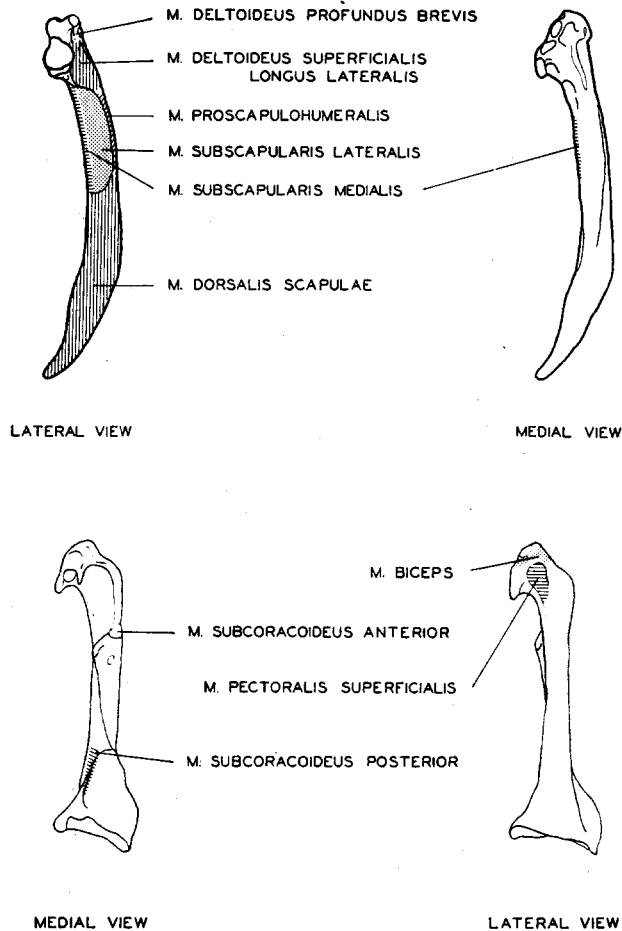


Fig. 54. Scapula (above) and coracoid (below) of *Corvus brachyrhynchos*, x1, showing areas of origin of muscles.

lateral body surface—light fascia attached from surface of ribs adjacent to posterior sternal process and from fascia of adjacent muscles; clavicle—anterior, lateral, and posterior surfaces, extending from furcular process anterodorsally one-half length of bone; dorsal to this point limited to anterior and lateral surfaces; coracoid—broad tendon from anterolateral surface of head; coracoclavicular membrane—ventral posterior portion. Insertion: humerus—pectoral surface. Innervation: N. pectoralis.

Anterior coracoid matrix.—M. supracoracoideus. Origin: ventral manubrial spine—entire lateral surface; carina—area not occupied by M. pectoralis superficialis; sternal plate—anterior surface; posterolateral boundary a line from postlabial ridge to posterior end of carina where origin of M. pectoralis superficialis reaches sternal plate. Insertion: humerus—on external tuberosity by strong tendon; scar medial to that of M. deltoideus profundus brevis. Innervation: N. supracoracoideus which arises proximally from N. 14.

Posterior coracoid matrix.—M. coracobrachialis posterior. Origin: coracoid—posterolateral surface (posterolateral crest) of ventral two-fifths; sternum, postlabial ridge—by fascia over M. sternocoracoideus (M. subclavius, Shufeldt) to postlabial ridge; to slight extent from fascia of M. sternocoracoideus. Insertion: humerus—on crest of internal tuberosity by strong tendon. Innervation: by twig arising from N. pectoralis, farther distally than in *Gallus*.

M. coracobrachialis anterior. Origin: anterior surface of dorsal ligament, which extends from head of coracoid to palmar surface of head of humerus near M. pectoralis superficialis. Insertion:

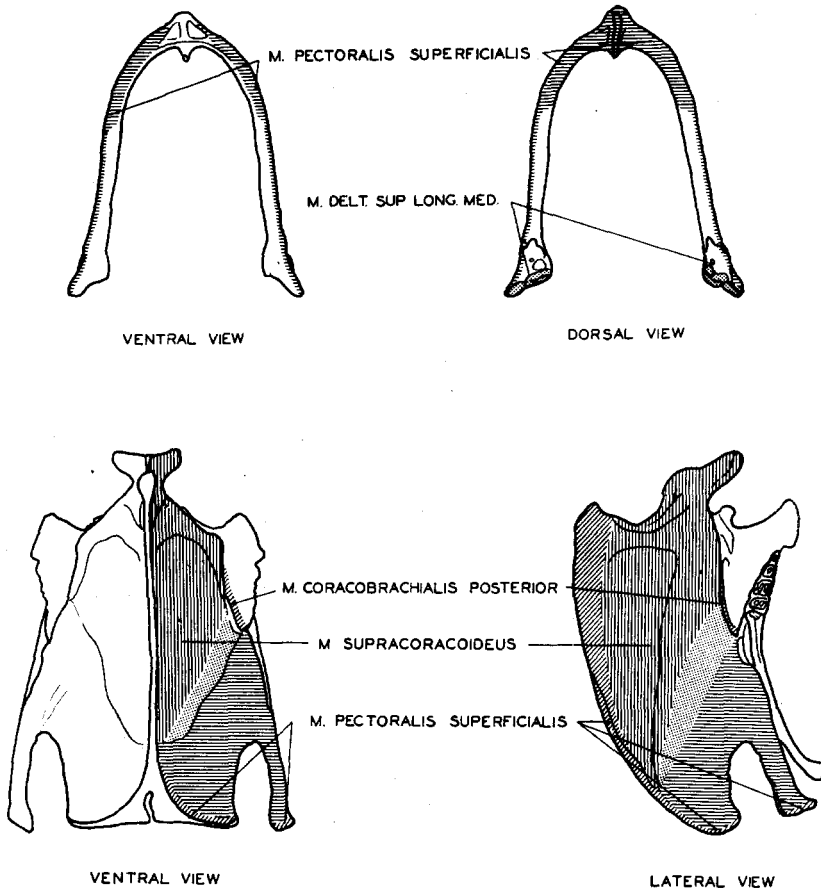


Fig. 55. Furculum (above) and sternum (below) of *Corvus brachyrhynchos*, x1, showing areas of origin of muscles.

humerus—thin fascia on palmar surface medial to dorsal ligament. Innervation: not observed. This muscle in *Corvus brachyrhynchos* is small and indistinctly defined.

Brachio-antebrachial group.—*M. biceps.* Origin: coracoid—lateral surface of dorsal end by broad tendon; humerus—lateral margin of pneumatic fossa by flat tendon. Insertion: ulna. Innervation: branches of common flexor nerve.

OSTEOLOGY

A comparison of the configuration of the humerus in members of the Corvidae shows the high degree of uniformity that one would expect in a family which is a natural group. When the range of individual variation is established, it is clear that the several genera, and particularly their respective species, can be distinguished from one another only by minor differences in configuration.

An attempt has been made to construct the key to the humeri of available genera and species of corvids on an absolute rather than a comparative basis. Measurements of the humerus are used as the basis for the primary divisions of the family. The various measurements are:

1. Length: the maximum length from the head to the condyles.
2. Width of head: the maximum width from the external tuberosity to the margin of the proximal portion of the bicipital crest.

3. Distal width: the maximum width between the prominences of the ectepicondyle and the entepicondyle.
4. Minimum shaft diameter: the minimum diameter measured between the surface on a line from the bicipital crest to the entepicondylar prominence and the surface on a line from the deltoid crest to the ectepicondylar prominence.

TABLE 1
Average minimum and maximum measurements of humeri of corvids in millimeters

	Number measured	Length	Width of head	Distal width	Minimum shaft diameter
<i>Corvus corax</i>	6	89.0 (82.1-101.7)	25.6 (23.6-27.7)	21.2 (19.0-24.7)	7.8 (6.7-8.9)
<i>Corvus cryptoleucus</i>	6	71.0 (68.2-73.5)	20.8 (20.2-21.6)	17.4 (17.0-17.8)	6.3 (6.0-6.8)
<i>Corvus brachyrhynchos</i>	25	63.6 (56.0-71.0)	17.9 (16.0-20.6)	15.9 (14.1-17.9)	5.7 (5.0-6.3)
<i>Pica pica hudsonia</i>	17	43.7 (41.9-47.9)	12.3 (11.8-13.4)	11.2 (10.6-12.1)	3.7 (3.5-4.3)
<i>Pica nuttalli</i>	10	43.3 (41.1-44.0)	12.2 (11.3-13.0)	11.0 (10.4-11.7)	3.7 (3.5-4.2)
<i>Nucifraga columbiana</i>	10	38.2 (36.0-39.8)	11.5 (10.4-12.1)	10.3 (10.0-10.5)	3.4 (3.3-3.6)
<i>Aphelocoma sieberi</i>	4	38.5 (37.0-39.1)	11.0 (10.9-11.2)	9.9 (9.8-10.1)	3.2 (3.0-3.3)
<i>Cyanocitta stelleri</i>	39	34.0 (31.6-36.7)	10.2 (9.5-10.8)	8.9 (8.4-9.4)	3.0 (2.7-3.4)
<i>Cyanocitta cristata</i>	9	33.0 (31.9-34.7)	10.0 (9.7-10.4)	8.8 (8.5-9.2)	2.9 (2.7-3.2)
<i>Cyanocephalus cyanocephalus</i>	13	34.3 (32.2-35.9)	10.7 (10.3-11.2)	9.1 (8.7-9.6)	3.0 (2.8-3.3)
<i>Aphelocoma californica</i>	35	31.1 (28.9-33.5)	9.1 (8.2-9.7)	8.2 (7.5-8.6)	2.7 (2.4-2.9)
<i>Perisoreus canadensis</i>	12	30.2 (28.8-31.8)	9.0 (8.6-9.5)	7.9 (7.5-8.2)	2.6 (2.5-2.8)

Plottings of frequency distribution of measurements makes it obvious that for certain species the number of individuals used was insufficient to suggest correctly the range for the species. This situation had to be taken into account in setting limits of size groups in the key.

After a survey of the family, six features of the configuration of the head of the humerus, each of which varied among the different species, were chosen for possible use as key characters. These characters are:

1. The presence or absence, and the degree of development, if present, of a small concavity adjacent to the margin of the head of the humerus at the point of origin of the medial branch of *M. triceps*.
2. Configuration of the internal tuberosity at the point of tendinous insertion of *M. coracobrachialis posterior*: the degree of prominence of this shoulder, its shape (angular or rounded), and the curvature of its proximal margin.
3. The completeness of the fossa, and the size and shape of the fenestra. For orientation in description of the shape, this fossa was viewed from the distal end of the humerus with the internal tuberosity above it; the apex of the fenestra is thus directly below the tuberosity.
4. The deltoid crest, whether rounded or straight when viewed from anconal aspect.
5. The straightness of the capital groove, the shape of its basin and the presence or absence of a ridge at the medial end of the groove.
6. The presence or absence of a groove at the base of the medial bar (medial margin of *M. proscapulothumeralis*).

A summary of the development of these characters is given in table 2. The numbers in parentheses show the proportionate occurrence of the respective characters. For example, 8:10 means the "character" is present in the proportion of eight out of ten individuals.

TABLE 2

	Concavity at margin of head (origin medial branch, <i>M. triceps</i>)	Shelf on internal tuberosity at insertion of <i>M. coracobrachialis posterior</i>		
		Prominence	Shape	Margin
<i>Corvus corax</i>	None (10:10) Slight depression (4:10)	Distinct (10:10)	Angular	Straight proximally (8:10)
<i>Corvus brachyrhynchos</i>	None (10:10) Slight depression (5:10)	Distinct (6:10); Medial margin indistinct (4:10)	Angular, oval	Medially convex
<i>Corvus cryptoleucus</i>	None (10:10) Slight depression (2:10)	Distinct (10:10)	Angular	Medially convex
<i>Pica pica</i>	None (10:10)	Distinct (8:10)	Round, oval	Rounded
<i>Pica nuttallii</i>	None (10:10) Slight depression (6:10)	Distinct (10:10)	Angular, square	Medially indistinct, straight
<i>Nucifraga columbiana</i>	None (10:10)	Distinct (6:10)	Oval, angular	Proximally indistinct; slopes to internal tuberosity
<i>Aphelocoma sieberi</i>	Slight (10:10)	Distinct (8:8)	Oval, angular	Proximally indistinct; slopes to internal tuberosity
<i>Cyanocitta stelleri</i>	Slight (7:10) None (3:10)	Indistinct (9:10)	Round, oval	Proximally indistinct; slopes to internal tuberosity
<i>Cyanocitta cristata</i>	Prominent (2:10) Slight (6:10) None (2:10)	Indistinct (10:10)	Round, oval	Proximally indistinct; slopes to internal tuberosity
<i>Cyanocephalus cyanocephalus</i>	Slight (10:10)	Indistinct (10:10)	Round, oval	Proximally indistinct; slopes to internal tuberosity
<i>Aphelocoma californica</i>	Slight to prominent (10:10)	Distinct (10:10)	Round, oval or rounded square	Straight, round
<i>Perisoreus canadensis</i>	None (4:10) Slight (6:10)	Distinct	Angular at medioproximal margin	

	Fossa I		Pectoral crest	Capital groove		Groove at base of medial bar
	Completeness	Fenestra		Straightness	Ridge	
<i>Corvus corax</i>	Incomplete	Small; oval or chordate medially	Rounded (8:10); straight medially (2:10)	Straight (10:10)	None	None
<i>Corvus brachyrhynchos</i>	Incomplete	Small; oval, rectangular, triangular	Straight (6:10); slightly rounded (4:10)	Straight (2:10)	Slight, rounded (4:10)	None
<i>Corvus cryptoleucus</i>	Incomplete	Small; oval, or rounded square	Straight (8:10); slightly rounded (2:10)	Straight (8:10)	None	None
<i>Pica pica</i>	Incomplete (varies widely)	Small (5:10) to large (5:10)	Slightly rounded; medially nearly straight	Curved (10:10)	Slight (2:10)	Present (10:10)
<i>Pica nuttallii</i>	Incomplete (7:10), varies	Small (3:10) to large (7:10)	Slightly rounded	Curved (9:10)	Slight (2:10)	None (8:10)
<i>Nucifraga columbiana</i>	Incomplete	None (1:10) Small (4:10); Large, odd-shaped (5:10)	Rounded (7:10); straight (3:10)	Curved (10:10)	Slight (3:10)	Slight, obscure (3:10)
<i>Aphelocoma sieberi</i>	Incomplete (2:8)	Small (1:8) Large 7:8); rounded laterally, straighter medially	Straight (6:8) Concave (2:8)	Slightly curved (8:8)	None (7:8)	Slight (2:8)
<i>Cyanocitta stelleri</i>	Complete (10:10)	Large, round, rectangular; notch at apex (7:10)	Straight (6:10); slightly concave (2:10), slightly convex (2:10)	Straight (7:10)	Present (10:10), varies in prominence	Slight, round (4:10)
<i>Cyanocitta cristata</i>	Complete (8:10)	Small to large; rounded, rectangular	Straight (2:10); slightly convex (8:10)	Straight (4:10)	Present (8:10), varies in prominence	Slight, round (4:10)
<i>Cyanocephalus cyanocephalus</i>	Incomplete (4:10)	Small to large; notch at apex (8:10)	Straight, or nearly so (7:10)	Curved (10:10); forms groove in head (9:10)	Prominent (10:10)	Slight (4:10)
<i>Aphelocoma californica</i>	Complete (9:10)	Large; as wide as high	Slightly concave (7:10); straight (3:10)	Curved (9:10)	Slight (8:10)	Present (9:10)
<i>Perisoreus canadensis</i>	Complete (7:8)	Large, wider than high	Rounded (6:8)	Curved (10:10)	Slight to indistinct	Present (6:10)

KEY TO THE HUMERI OF CERTAIN NORTH AMERICAN CORVIDS

Only those species represented by four or more individual skeletons are included; nevertheless some of the characters in use may not prove to be valid when larger series are examined.

- A. Length more than 55 mm.; shaft 5.0 mm. or more in diameter; width of head more than 15 mm.
 B. Length more than 80 mm.; width of head more than 23 mm.; distal width more than 18.5 mm.
Corvus corax
- BB. Length less than 80 mm.; width of head 15.0-22.0 mm.; distal width 13.5-18.5 mm.
 C. Bicipital furrow distinct; surface between furrow and palmar ridge perpendicular or nearly so.
Corvus brachyrhynchos
- CC. Bicipital furrow absent or broad and indistinct; surface between furrow and palmar ridge not perpendicular, but sloping.
Corvus cryptoleucus
- AA. Length less than 55 mm.; shaft less than 4.5 mm. in diameter; width of head less than 15 mm.
 B. Length more than 41 mm.
 C. Groove present at base of medial bar; area of insertion of M. coracobrachialis posterior not set off sharply from surface of internal tuberosity
Pica pica hudsonia
- CC. No groove at base of medial bar; area of insertion of M. coracobrachialis set off sharply from surface of internal tuberosity.
Pica nuttallii
- BB. Length less than 41 mm.
 C. Length 36.0 mm. or more.
 D. No concavity present at origin of medial branch of M. triceps; pneumatic fossa broadly rounded beneath internal tuberosity, angular or narrowly rounded next to shaft surface, and rounded laterally.
Nucifraga columbiana
- DD. Concavity present at origin of medial branch of M. triceps (if no concavity distal width less than 10.0 mm.); fossa angular or narrowly rounded beneath internal tuberosity, broadly rounded next to shaft surface, and straight laterally.
 E. Length of deltoid surface more than 4.5 times its width, length of bone 37.0 mm. or more, distal width more than 9.5 mm.
Aphelocoma sieberi
- EE. Length of deltoid surface less than 4.5 times its width, length of bone less than 37.0 mm.; distal width less than 9.5 mm.
Cyanocitta stelleri
- CC. Length less than 36.0 mm.
 D. Distance from plane of bicipital surface to anconal apex of internal tuberosity more than 4.5 mm.
 E. Distal end of palmar ridge (palmar aspect) parallel to pectoral crest, or approaches apex of pectoral crest at low angle (usually less than 25 degrees at point of juncture).
Cyanocitta stelleri
- EE. Distal end of pectoral ridge not parallel to pectoral crest, approaching apex at high angle (usually more than 25 degrees at point of juncture).
 F. Bicipital margin of floor of fossa with acute ridge, not rounded; medial bar relatively straight in anconal view.
Cyanocitta cristata
- FF. Bicipital margin of floor of fossa with rounded ridge, not acute; medial bar concave distally in anconal view.
Cyanocephalus cyanocephalus
- DD. Distance from plane of bicipital surface to anconal aspect of internal tuberosity less than 4.5 mm.
 E. Pneumatic foramen rounded, as wide as high.
Aphelocoma californica
- EE. Pneumatic foramen compressed, wider than high.
Perisoreus canadensis

DISCUSSION

In the course of the study of the Corvidae, other passerine families were examined with a view to determining the general limits of variation of the fossae of the head of the humerus within the Passeriformes. In addition, the "lower" orders of Aves were surveyed superficially in an attempt to ascertain "primitive" and "advanced" conditions of the fossae.

In all groups of birds, except a part of the passerines, only one fossa is present. As one examines the orders in the sequence set forth in the A. O. U. Check-list (1931), a tendency toward an increase in size and depth of this single fossa (Fossa I) is readily apparent. This general tendency toward enlargement, as one proceeds from the primi-

tive to the advanced orders, indicates that the *M. humerotriceps* becomes progressively more important functionally, since its diameter is reflected in the size and depth of the fossa. In the following discussion of the passerines the term "primitive" is used to refer to the part of the order that is similar to the lower orders of birds in that only Fossa I is present in the head of the humerus. Since both Fossa I and II are present only in a part of the Passeriformes, and since Fossa II is present only in those passerines capable of vertical flight, this latter part of the order is considered to be "advanced."

In the primitive group of passerines which have but one fossa (Fossa I), the fossa varies from shallow and incomplete to deep and complete. In some of the more advanced families of the "primitive group" a concavity occurs medial to Fossa I, but the proximal wall of this concavity is thick and not translucent as in the "advanced group." All of the members of the "advanced group" have both Fossa I and II present. In the lower families of the advanced group Fossa II is small and completely separated from Fossa I by the medial bar. This bar is shortened in the higher families so that it does not extend distally into the floor of the fossae; thus I and II are united. With the reduction of the medial bar there occurs an increase in the thickness of the crista of the head; apparently this thickening is to maintain rigidity.

The degree of completeness of Fossa II is correlated with the area of cross section of the medial branch of *M. humerotriceps*. In the Corvidae and other passerine families of the "primitive group" this branch is smaller than the lateral branch and is usually less than one-third the diameter of the latter. In the "advanced group" the medial branch varies from one-half to approximately the same diameter as the lateral branch. The maximum development of the medial branch is present in the fringillids. In this family of passerines vertical flight is most highly developed. The exact role that the *M. humerotriceps* plays in vertical flight is not clear at the present writing, but since the muscle is the only extensor of the elbow joint, its increase in size and length obviously results in an increase in the ability of the individual to extend the outer wing. This increase in the speed and strength of the extension is apparently correlated with vertical flight. The wing is semiflexed at the beginning of the down stroke and the extension of the outer wing is reached at the termination of the down stroke. A rapid and forceful extension near the completion of the stroke, accompanied with rotation of the humerus, may aid the outer wing muscles to snap the hand and finger portions of the wing downward. Rotation of the humerus is necessary when a bird leaves its perch and flies directly upward with its body axis in a vertical direction. The recovery is made with the wing in a semiflexed position. The afore-mentioned rotation is mainly the result of the action of *Mm. pectoralis superficialis*, *dorsalis scapulae* and *proscapulo-humeralis*.

It is of interest to note that the presence of the medial fossa (Fossa II) transfers the line of stress from an oblique direction in relation to the line of the shaft of the humerus to a position parallel to the line.

Such families as the Tyrannidae, Alaudidae, Cotingidae, Corvidae, and the divergent Hirundinidae fall into the "primitive group," while in the "advanced group" the Fringillidae, Thraupidae, Icteridae, Ploceidae, and Compothlypidae occur. Some genera of the Mimidae are "primitive," others "advanced," with respect to the humerus. It is of interest to note that in young individuals of *Agelaius phoeniceus* there is but one fossa present (Fossa I), whereas in the adult both Fossa I and II have developed.

Obviously it is not possible to establish a "phylogenetic series" within the family Corvidae based on a single character. It seems advisable, however, to note the relationships as suggested by the characters of the head of the humerus so that future workers may compare their interpretations derived from other characters.

A shallow pneumatic fossa (Fossa I) with no concavity or depression at the margin of the head (origin of the medial branch of *M. triceps*) is considered to be generalized. In the more specialized condition the pneumatic foramen is deep, and a concavity occurs near the margin of the head at the point of origin of the medial branch of *M. triceps*.

Based only on the characters of the head of the humerus and primarily on the degree of development of the pneumatic fossa, the order of the members of the family from generalized toward specialized is:

Corvus corax. Raven.
Corvus cryptoleucus. White-necked Raven.
Corvus brachyrhynchos. American Crow.
Pica pica hudsonia. American Magpie.
Pica nuttallii. Yellow-billed Magpie.
Nucifraga columbiana. Clark Nutcracker.
Cyanocephalus cyanocephalus. Pinyon Jay.
Cyanocitta cristata. Blue-jay.
Cyanocitta stelleri. Steller Jay.
Aphelocoma sieberi. Arizona Jay.
Aphelocoma californica. California Jay.
Perisoreus canadensis. Canada Jay.

The relationship between the genera is diagrammed in figure 56. The point at which the branch terminating in *Cyanocephalus*, *Cyanocitta*, and *Aphelocoma* arises may

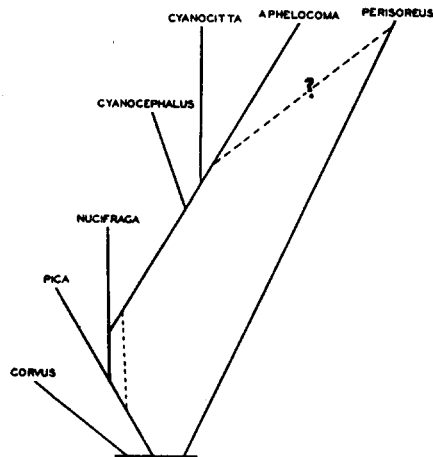


Fig. 56. Diagram showing relationship of certain genera of corvids based on configuration of head of humerus.

well be placed too far from the base of this limb, but the affinities are toward *Nucifraga*. The relationship of *Perisoreus* is uncertain as indicated, but its humeral similarity to *Aphelocoma* is clear.

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