Morphology of the antebrachial musculature of the American kestrel, Falco sparverius (Aves)

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Abstract. The antebrachial musculature of the American kestrel (Falco sparverius) is described. This fills a gap in the avian morphology literature, and provides a reference for future comparative, functional and systematic studies. A table of synonyms-homologs is provided for each muscle as a reference frame for over 100 years of avian anatomical literature.

Key words: Morphology – Antebrachial musculature – American kestrel

Introduction

Studies of the forelimb musculature of birds have been undertaken for over a century. Many of those studies have used muscular anatomy across a number of avian taxa to assess systematic relationships within or between groups (e.g., Leach 1914; Swinebread 1954; Berger 1955, 1956a, 1968, 1969; Hudson and Lanzillotti 1955, 1964; Hudson et al. 1969; Van den Berge 1970; Jollie 1977; Raikow 1977, 1978; Rossier 1980; Schreweis 1982; Zusi and Bentz 1984; McKirick 1985). Fewer studies, however, have examined the anatomy of the avian forelimb to understand its use in flight (e.g., Sy 1936; Fisher 1946; Bannasch 1986; Dial et al. 1991). In particular, muscles of the forearm have received little attention (but see Nair 1954; Dial 1992a). Since the distal end of the wing, an oscillating limb, is reduced in mass (see Hildebrand and Hurley 1985), the distal musculature is reduced as well. Therefore, the majority of attention has been given to the muscles responsible for wing upstroke and downstroke, the pectoralis and supracoracoideus (Goslow et al. 1989).

Descriptive studies must form the basis of functional studies (Raikow 1985), and this paper provides a description of the musculature of the forelimb of the American kestrel (Falco sparverius), as a basis for future functional studies of the avian wing.

American kestrels are the smallest members of the North American Falconidae, and are widespread across the continent. An anatomical description of the forearm of this species (or genus) is not presently available. For purposes of discussion, the anatomy will be compared with other works on related species. In their study of the Corvidae, Hudson and Lanzillotti (1955) made occasional references and comparisons to the Prairie falcon, Falco mexicanus, and provided an illustration of the dorsal view of the superficial forelimb (their figure 33). Berger (1956a) examined the appendicular myology of the Pygmy falcon (Polihierax semitorquatus) in order to determine its relationships within the Falconidae. Jollie (1977) produced an extensive work on the anatomy and phylogeny of the Falconiformes, which is incomplete with reference to the forearm muscles, and is not functional in scope. Fisher's (1946) study on the appendicular anatomy of the New World vultures provides a basis for comparison with species specialized for gliding, even though the Carthartidae are not considered to be closely related to the Falconiformes (Sibley and Ahlquist 1990). In addition, tables of muscle synonyms/homologs of the antebrachial muscles are provided to permit an accurate comparison with a vast anatomical literature spanning well over 100 years.

In a recent paper (Meyers 1992a), I presented the shoulder and brachial muscles of the American kestrel as a basis for functional and comparative studies. Here I present a description of the antebrachial musculature of Falco sparverius as a baseline for functional and systematic studies.

Materials and methods

Anatomical material for dissection was obtained from the American Museum of Natural History (AMNH 10258, 10259) and

Gustav Fischer Verlag Jena
also from the Macdonald Raptor Research Centre (MRRC). Specimens from MRRC were obtained frozen and were fixed in 4% formalin. All material was stored in 2% phenoxethanol. Skeletal material was obtained from AMNH (12020, 15809).

Dissections of three male specimens were performed under a Wild M-5 stereomicroscope with a camera lucida (drawing tube), at magnifications of 6×, 12× and 25×. An iodine solution (Bock and Shear 1972) was used to help contrast muscle from connective tissue.

Anatomical nomenclature is from *Nomina Anatomica Avium* (NAA, Baumel et al. 1979) unless otherwise stated. Names of processes and fossae to which muscles attach are given descriptively and are then referred to by their NAA name.

Figures were prepared by tracing the dissection with a camera lucida or Mitsubishi video printer. The outline was then enlarged to cover a surface of 20×30 cm. This drawing was compared to the original specimen (dissection or skeletal element), corrected and detailed. Final drawings were traced in ink and labelled.

**Observations-Anatomy**

Muscles of the antebrachium are described relative to the avian anatomical position with the wing in extension. Thus for forearm muscles, the leading edge is cranial and the trailing edge is caudal. They are presented in a proximal to distal order. Included in each description is general orientation, origin, insertion, function based on attachments, and comparisons (where possible) with related species (Hudson and Lanzillotti 1955; Berger 1956).

**M. pronator superficialis (PS)**

*M. pronator superficialis* lies proximally on the ventral antebraconch, superficial to *M. pronator profundus*. It extends from the distal humerus to the radius.

![Diagram of *Falco sparverius* showing muscle attachments](image)

**Table 1. Synonyms of *M. pronator superficialis***

<table>
<thead>
<tr>
<th>Synonym</th>
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</thead>
<tbody>
<tr>
<td><em>Pronator brevis</em> Vaughan 1876; Shufeldt 1890; Leach 1914; Kaupp 1918; Burt 1930; Chamberlain 1943; Fisher 1946; Berger 1953, 1954, 1955, 1956a, c, d; Swinebread 1954; Fisher &amp; Goodman 1955; Fujikata 1959; Harvey et al. 1968</td>
</tr>
<tr>
<td><em>Entepicondylo-radialis sublimis</em> sy 1936</td>
</tr>
<tr>
<td><em>Flexor antibrachii radialis superficialis</em> Kuroda 1960</td>
</tr>
</tbody>
</table>

PS arises tendinously from a small, crescent-shaped area on the caudo-ventral surface of the distal humerus, just proximal to the humeral origin of *M. expensor secundarium* (Figs. 1, 5). PS fans out distally from its origin and inserts by mixed fleshy and tendinous fibers onto the cranial border of the ventral aspect of the proximal one-third of the radius (Fig. 2). The insertion lies superficial to the insertion of *M. pronator profundus* (Fig. 5).

PS, in addition to *M. pronator profundus*, is in a position to pronate the antebraconch. Berger's (1956) description for *Polihierax* corresponds to that for *Falco*.

**M. pronator profundus (PP)**

*M. pronator profundus* lies proximally on the ventral surface of the antebraconch, deep to *M. pronator superficialis*. It extends from the distal humerus to the radius.

![Diagram of *Falco sparverius* showing muscle attachments](image)

**Fig. 1.** Left humerus of *Falco sparverius*, showing muscle attachments.

a) dorsal view  b) ventral view

**Fig. 2.** Left radius and ulna of *Falco sparverius*, showing muscle attachments.

a) dorsal view  b) ventral view

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Table 2. Synonyms of M. pronator profundus


Pronator longus: Vaughan 1876; Shufeldt 1890; Leach 1914; Kaupp 1918; Burt 1930; Chamberlain 1943; Fisher 1946; Berger 1953, 1954, 1955, 1956a, c, d; Swinebroad 1954; Fisher & Goodman 1955; Fujioka 1959; Harvey et al. 1968; Koch 1973

Pronator profundus s. longus [Mm. entepicondylus-radiales]: Gadow & Selenka 1891

Entepicondylus-radialis profundus: Sy 1936

Flexor antibrachii radialis profundus: Kuroda 1960

Table 3. Synonyms of M. extensor metacarpi radialis


Extensor metacarpi radialis longior: Shufeldt 1890; Leach 1914; Kaupp 1918

Extensor metacarpi radialis longus: Vaughan 1876; Leach 1914; Burt 1930; Fujioka 1959

Extensor carpi radialis: Chamberlain 1943; McLeod et al. 1964

Extensor carpi radialis longus: Fujioka 1959

Extensor carpi radialis superficialis: Harvey et al. 1968

Extensor metacarpi ulnaris: Gadow & Selenka 1891

Extensor metacarpi ulnaris (radialis?): Marshall 1905

M. extensor digitorum communis (EDC)

M. extensor digitorum communis is a dorsal pinnae muscle of the antebrachium, and extends from the distal humerus to the ulula and major digit.

EDC arises from a V-shaped aponeurosis, the apex of which is attached to a process on the lateral epicondyle of the distal humerus (Figs. 1, 4). This attachment lies between the origins of M. extensor carpi radialis and M. extensor carpi ulnaris. The leg of the 'V' on the cranial side of the forearm is shared by the origin of M. supinator. The caudal ped of the 'V' lies deep to the fascial support of the secondary feathers, and gives off its own fascia to some of the secondaries.

M. extensor metacarpi radialis (EMR)

M. extensor metacarpi radialis is one of the largest antebrachial muscles in Falco, and lies along the cranial border of the forearm. It has a complex internal architecture and is visible from both dorsal and ventral aspects.

EMR arises from a process on the lateral aspect of the distal humerus (Proc. supracondylaris dorsalis). It has the most proximal origin of the antebrachial muscles. The superficial fibers of origin are tendinous, whereas the deeper ones are fleshy. The tendinous fibers continue distally a short distance, providing an insertion site for the tendon of M. propatagialis pars brevis (Fig. 4). The fusiform belly extends along the proximal belly of the radius. At about midway of the length of the radius, EMR gives rise to a very thick tendon (the thickest of the antebrachium).

The tendon of EMR extends distally and passes through a ligamentous tendon loop at the level of the radial carpal (Os radiale). It inserts onto the proximal surface of the processus extensorius of the carpometacarpus (Fig. 3).

EMR is likely to be an extensor of the manus, but may also assist forearm flexion if the wrist joint is fixed. Nair (1954) observed two bellies to this muscle in the kite, Milvus, and suggested that these were to prevent over-fatiguing of this muscle during soaring in this species.

Fig. 3. Left manus of Falco sparverius, showing muscle attachments.

a) dorsal view  b) ventral view
M. supinator (Su)

M. supinator is a short, parallel-fibered muscle lying on the dorsal aspect of the proximal antebrachium. It extends from the distal humerus to the proximal radius.

Table 5. Synonyms of M. supinator

<table>
<thead>
<tr>
<th>Synonym</th>
<th>Author(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Supinator brevis</td>
<td>Shufeldt 1890; Leach 1914; Kaupp 1918; Burt 1930; Fisher 1946; Berger 1953, 1954, 1956c; d; Swinebread 1954; Fisher &amp; Goodman 1955; Harvey et al. 1968</td>
</tr>
<tr>
<td>Supinator antibrachii</td>
<td>Kuroda 1960</td>
</tr>
<tr>
<td>Supinator medialis</td>
<td>Chamberlain 1943; Fujikoa 1959</td>
</tr>
<tr>
<td>Ectepicodonto-ulnaris</td>
<td>Gadow &amp; Selenka 1891; Beddard 1898; Marshall 1905; Sy 1989</td>
</tr>
</tbody>
</table>

Su arises from the cranial leg of a "V"-shaped tendon shared by M. extensor digitorum communis. The apex of the "V" arises from the lateral epicondyle of the humerus in between the origins of M. extensor metacarpal radii and M. extensor carpi ulnaris (Fig. 1). Su extends cranio-laterally towards the antebrachium, and inserts onto the proximal one-fifth of the dorsal surface of the radius (Fig. 2).

Su is in an anatomical position to supinate the forearm. However, with most of the movement of the forelimb restricted in rotational planes, Su may more likely function as a stabilizer of the elbow joint.

M. ectepicodonto-ulnaris (EU)

M. ectepicodonto-ulnaris is a parallel-fibered muscle lying on the dorsal surface of the antebrachium. It lies deep to M. extensor digitorum communis, and extends from the distal humerus to the ulna.

Table 6. Synonyms of M. ectepicodonto-ulnaris

<table>
<thead>
<tr>
<th>Synonym</th>
<th>Author(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ectepicodonto-ulnaris</td>
<td>Gadow &amp; Selenka 1891; Beddard 1898; Marshall 1905; Sy 1936; Settemeim 1959; Hudson et al. 1969; Vanden Berge 1970; Bauemel et al. 1979; Schreimeier 1982; Weinstein et al. 1984; Zusi &amp; Bentz 1984; McKiritch 1985; McGowan 1986; Dial 1992a, b; Meyers, this study</td>
</tr>
<tr>
<td>Anconaeus</td>
<td>Shufeldt 1890; Leach 1914; Kaupp 1918; Fisher 1946; Berger 1953, 1954, 1956c, d; 1960, 1968; Swinebread 1954; Fisher &amp; Goodman 1955; Goodge 1957; Sullivan 1962; George &amp; Berger 1966; Harvey et al. 1968; Robinson 1970</td>
</tr>
<tr>
<td>Supinator lateralis</td>
<td>Chamberlain 1943; Fujikoa 1959</td>
</tr>
</tbody>
</table>
EU arises tendinously from the lateral epicondyle of the humerus. The origin lies distal to the origins of Mm. supinator and extensor digitorum communis (Figs. 1, 4). EU extends distally and inserts onto a broad area on the cranio-dorsal surface of the proximal one-half of the ulna, and onto a dense sheet of connective tissue extending cranially from the ulna (Fig. 2). M. flexor digitorum profundus takes origin from the ventral surface of this incomplete "interosseous membrane". Superficial fibers of the tendinous origin of EU provide origin for the tendon of M. extensor carpi ulnaris.

Probably a joint stabilizer, EU may also assist in forearm flexion.

**M. extensor metacarpi ulnaris (ECU)**

M. extensor carpi ulnaris is a parallel fibered muscle on the caudal border of the dorsal antebrachium. It lies deep to M. extensor digitorum communis and extends from the distal aspect of the humerus to the proximal carpometacarpus.

ECU arises tendinously from the surface of the tendon of M. epectrocondylo-ulnaris. The belly is anchored to the ulna (Figs. 2, 4) and extends distally and gives off a flat tendon at about the level of the tendon of M. extensor metacarpi radialis (Fig. 4). The tendon lies deep and caudal to the tendon of M. extensor digitorum communis and passes through a tendon loop just proximal to the wrist articulation (Fig. 4). The tendon of ECU crosses over the wrist joint and passes over a dense ligament of the carpometacarpus. ECU inserts onto the proximal aspect of the dorsal surface of the carpometacarpus at the level of the ulnar insertion of M. extensor digitorum communis (Figs. 3, 4).

ECU, although called an extensor by homology (see George and Berger 1966) is probably a flexor of the manus.

**Table 7. Synonyms of M. extensor metacarpi ulnaris**

<table>
<thead>
<tr>
<th>Source</th>
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</thead>
<tbody>
<tr>
<td>Extensor metacarpi ulnaris: Gadow &amp; Selenka 1891; Beddard 1898; Marshall 1905; Kuroda 1960; George &amp; Berger 1966; Berger 1968; Evans 1969; Vanden Berge 1975; Raikow 1977, 1985; Baume et al. 1979; Rosser 1980; Schreweis 1982; Zusi &amp; Bentz 1984; McKirrick 1985; McGowan 1986; Meyers, this study</td>
</tr>
<tr>
<td>Flexor metacarpi radialis: Shufeldt 1890; Leach 1914; Kaupp 1918; Burt 1930; Fisher 1946; Berger 1953, 1954, 1956w, p, 1960; Nair 1954; Fisher &amp; Goodman 1955</td>
</tr>
<tr>
<td>Flexor metacarpi radialis: Swinebread 1954</td>
</tr>
<tr>
<td>Flexor metacarpi ulnaris: Sy 1936</td>
</tr>
<tr>
<td>Flexor carpi radialis: Fujioka 1959</td>
</tr>
<tr>
<td>Flexor metacarpi longus: Harvey et al. 1968</td>
</tr>
<tr>
<td>Ulnaris lateralis: Chamberlain 1943</td>
</tr>
</tbody>
</table>

**M. flexor digitorum superficialis (FDS)**

M. flexor digitorum superficialis, a muscle of the ventral forearm, extends from the distal humerus to the major digit. It is partly covered ventrally by M. flexor carpi ulnaris.

**Table 8. Synonyms of M. flexor digitorum superficialis**

<table>
<thead>
<tr>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flexor digitorum superficialis: Fujioka 1959; Berger 1960, 1968; Sullivan 1962; George &amp; Berger 1966; Evans 1969; Vanden Berge 1975; Raikow 1977, 1985; Baume et al. 1979; Rosser 1980; Schreweis 1982; Zusi &amp; Bentz 1984; McKirrick 1985; McGowan 1986; Meyers, this study</td>
</tr>
<tr>
<td>Flexor digitorum sublimus: Berger 1953, 1954, 1956d</td>
</tr>
<tr>
<td>Flexor metacarpi ulnaris: Burt 1930; Stegmann 1978</td>
</tr>
<tr>
<td>Flexor carpi ulnaris cranialis: Harvey et al. 1968</td>
</tr>
<tr>
<td>Flexor carpi ulnaris, anterioiusmuscle: Swinebread 1954</td>
</tr>
<tr>
<td>Anterior part of Flexor carpi ulnaris: Fisher &amp; Goodman 1955</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source</th>
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<tbody>
<tr>
<td>[part of Flexor carpi ulnaris: Shufeldt 1890</td>
</tr>
</tbody>
</table>

FDS arises from the deep surface of the Lig. humerocarpale as well as from a fascia which extends from FDS (deep to M. flexor carpi ulnaris) to the bases of the secondary feathers. About two-thirds distally down the ulna, FDS leaves the Lig. humerocarpale and becomes tendinous. This tendon disappears deep to the Lig. humerocarpale near the ulnar carpal (Os ulnare) and passes over the ventral surface of the wrist joint (Fig. 5). FDS runs along the cranio-ventral border of the carpometacarpus (with the tendon of M. flexor digitorum profundus) and inserts onto the distal end of the cranio-ventral corner of the proximal phalanx of the major digit (Fig. 3).

FDS is believed to extend the manus and major digit (Raikow 1985).

**M. flexor carpi ulnaris (FCU)**

M. flexor carpi ulnaris is the largest muscle of the ventral antebrachium, and is probably the most complex muscle in the forearm of *F. spavarietus*. It lies superficially on the caudal aspect of the ventral antebrachium, and sends fleshy and tendinous fibers to the secondary feathers.

FCU arises from the medial epicondyle of the humerus, and is the most distal of those muscles arising from that region (Fig. 1). A sesamoid is present in the short, thick tendon of origin. The muscle is much thicker than the tendon, and continues distally towards the wrist. The main portion of FCU (pars cranialis) inserts by a thick, strong tendon onto the ulnar carpal (Figs. 2, 5).

Along the caudal border of the muscle, a thin muscular belly (pars caudalis) gives off tendinous slips to each of the secondary feathers (Fig. 5). This band continues to the wrist and inserts onto the Os ulnare as well, dorsally to the insertion of pars cranialis.

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Table 9. Synonyms of M. flexor carpi ulnaris


*Flexor carpi-ulnaris*: Kuroda 1960

*Flexor carpi ulnaris caudalis*: Harvey et al. 1968

*Flexor carpi ulnaris, posterior muscle*: Swinebroad 1954

*Flexor carpi ulnaris s. entepicondyllo-carpalis*: Gadow & Selenka 1891

*Flexor metacarpi ulnaris*: Vaughan 1876; Dial 1992a

FCU is probably the chief flexor of the manus, and pars caudalis probably functions to “flex” the secondary feathers as well.

M. flexor digitorum profundus (FDP)

M. flexor digitorum profundus is a deep antebrachial muscle and lies between the radius and ulna on the ventral aspect of the forearm.

FDP arises from the middle portion of the medial one-half of the ulna and adjacent interosseus ligament. It takes its origin from the ligament about one-half way to the radius (Fig. 2). A portion of FDP origin extends along a thin area just caudal to the insertion of M. brachialis (Fig. 2). The muscle belly becomes visible ventrally just cranial to the lig. humerocarpale about midway along the length of the forearm. The tendon of FDP passes through a fibrous loop at the metacarpal-alular phalanx border (Fig. 4) and continues distally over the tendon of M. flexor digitorum superficialis. FDP inserts onto the proximal aspect of the ventral surface of the distal phalanx of the major digit. The tendon is ossified in AMNH 15809.

Raikow (1985) gives this muscle's function as a flexor of the wrist and an extensor of the major digit.

Table 10. Synonyms of M. flexor digitorum profundus


*Extensor digiti tertii manus medialis*: Harvey et al. 1968

M. extensor longus digiti majoris (ELDM)

M. extensor longus digiti majoris is a thin muscle lying between the radius and ulna. Whereas the belly is visible ventrally, the insertion is visible from the dorsal surface.

ELDM arises from most of the middle third of the caudal border of the radius (Fig. 2). Proximally, it lies between the insertion of M. pronator profundus and the origin of M. extensor longus aluææ. The proximal one-third of ELDM is covered by the two pronators. ELDM becomes tendinous just proximal to the wrist joint, and passes dorsally in between the radius and ulna. The flat tendon emerges on the dorsal surface of the ulna, and passes over the bifurcation of the tendon of M. extensor digitorum communis (Fig. 4). ELDM crosses over the tendon of M. extensor digitorum communis cranial to where that tendon lies in the sulcus tendineus (Fig. 4). Just prior to the carpometacarpal-major digit articulation, ELDM passes through a tendon loop. A sesamoid is present in the tendon cranial to the articulation. ELDM inserts onto a tubercle on the cranio-proximal aspect of the terminal phalanx of the major digit (Fig. 3).

Table 11. Synonyms of M. extensor longus digiti majoris

*Extensor longus digiti majoris*: Vanden Berge 1975; Raikow 1977, 1985; Baumel et al. 1979; Rosser 1980; Schreweix 1982; Weinstein et al. 1984; McKenzie 1985; McGowan 1986; Meyers, this study


*Extensor indicis longus & flexor metacarpi brevis*: Fisher 1946

*Extensor indicis medius longus*: Sullivan 1962

*Extensor longus digiti III*: Fisher & Goodman 1955; Berger 1956c; Robinson 1970; Lucas & Stettenheim 1972

*Extensor digiti longus*: Kuroda 1960

*Extensor digiti tertii longus*: Fujitake 1959

*Extensor digiti tertii manus lateralis*: Harvey et al. 1968

*Extensor of the third digit*: Chamberlain 1943

A small muscular slip (pars distalis) arises by a very thin tendon from the connective tissue of the wrist and attaches to the tendon of ELDM by its own short, thin tendon. ELDM is probably an extensor of the manus.

Both Hudson and Lanzillotti (1955) and Berger (1956) briefly mention this muscle. Berger calls the pars distalis M. flexor metacarpi brevis.

M. ulnometacarpalis ventralis (UV)

M. ulnometacarpalis ventralis is a relatively large muscle located on the ventral surface of the forearm. It is covered superficially by M. flexor digitorum profundus and extends from the ulna to the carpometacarpus.
Table 12. Synonyms of *M. ulnometacarpalis ventralis*

*Ulnometacarpalis ventralis*: Raikow 1977; Baumel et al. 1979; Rosser 1980; McGowan 1982, 1986; Zusi & Bentz 1984; McKitrick 1985; Raikow 1985; Meyers, this study

*Ulno-metacarpalis ventralis*: Koch 1973


*Ulni-metacarpalis ventralis*: Gadew & Selenka 1891; Beddard 1898; Sy 1936; Stegmann 1978

*Ulni metacarpalis ventralis*: Marshall 1905; Nair 1954

*Ulnometacarpalis ventralis*: Goedege 1957


*Flexor carpi ulnaris brevior*: Shufeldt 1890; Leach 1914; Kaupp 1918; Burt 1930

*Extensor carpi obliquus*: Chamberlain 1943; Harvey et al. 1968

*Extensor carpi ulnaris*: Fujioka 1959

UV arises from a chevron-shaped region on the ventral surface of the distal half of the ulna (Fig. 2). It gives off a thick tendon which passes over the ventral surface of the wrist joint, deep to Mm. extensor metacarpi radialis and extensor longus alulae (Fig. 5). The tendon passes over to the dorsal surface of the wrist, and inserts onto the dorsal surface of the proximal carpometacarpus, just proximal to the origin of M. extensor brevis alulae (Fig. 3).

UV may be an extensor of the manus.

![Fig. 5. Ventral view of musculature of the antebrachium and manus of *Falco sparverius*. Feathers removed, Mm propatagialis pars brevis and pectoralis propatagialis cut.](image)

**M. ulnometacarpalis dorsalis (UD)**

M. ulnometacarpalis dorsalis is a short muscle lying caudo-dorsally at the wrist joint. It extends from the distal ulna to the proximal carpometacarpus and primary feathers.

UD arises from an oval area on the dorsal surface of the distal ulna, and fans out towards the proximal carpometacarpus. One part of UD inserts onto a depression on the caudo-dorsal aspect of the proximal carpometacarpus, proximally to the intermetacarpal space and caudal to the origin of M. interosseus dorsalis (Fig. 3). A second part of UD inserts by numerous slips onto the bases of the retinaculum of the primary feathers (Fig. 4).

Table 13. Synonyms of *M. ulnometacarpalis dorsalis*

*Ulnometacarpalis dorsalis*: Baumel et al. 1979; Rosser 1980; McGowan 1982, 1986; Zusi & Bentz 1984; McKitrick 1985; Raikow 1985; Meyers, this study

*Ulno-metacarpalis dorsalis*: Koch 1973


*Ulni-metacarpalis dorsalis*: Gadew & Selenka 1891; Beddard 1898; Sy 1936; Stegmann 1978

*Ulni metacarpalis dorsalis*: Marshall 1905

*Ulnometacarpalis dorsalis*: Goedege 1957


*Flexor metacarpi caudalis*: Harvey et al. 1968

*Flexor metacarpi brevis*: Shufeldt 1890; Leach 1914; Kaupp 1918; Burt 1930

*Flexor aductor of the fourth digit*: Chamberlain 1943

*Flexor digitalis quarti longus*: Fujioka 1959

UD is in a position to stabilize the wrist joint, but may also affect some flexion at this articulation. It also can aid in flexion of the proximal primary feathers.

Hudson and Lanzillotti's (1955) description for *F. mexicanus* corresponds to that in *F. sparverius*.

**M. extensor longus alulae (ELA)**

M. extensor longus alulae is a relatively long and thin muscle extending from the radius and ulna to the carpometacarpus. It is visible on the dorsal surface of the forearm.

ELA takes origin from a narrow area on the proximal one-half of the caudal surface of the radius, just distal to the insertion of M. supinator and also from the ventral surface of the proximal ulna, cranial to the insertion of M. brachialis (Fig. 2). The two bellies join about midway along the length of the radius. Halfway along its length, ELA becomes tendinous. The thin tendon passes through two tendon loops near the wrist, and ELA crosses the wrist joint cranio-dorsally. ELA inserts onto the extensor process of the carpometacarpus caudally to the insertion of M. extensor metacarpi radialis (Fig. 3).

ELA is in a position to extend the manus, (in concert with M. extensor metacarpi radialis), but is probably not large enough to affect much movement.

Berger (1956) described two origins for ELA, from the proximal ulna as well as from the second quarter of the radius. ELA presents a nomenclatural enigma, as it does not attach to the ulnar digit in *Falco*, nor in many other species (George and Berger 1966).
Table 14. Synonyms of M. extensor longus alulae

<table>
<thead>
<tr>
<th>Extensor longus alulae:</th>
<th>Vander Berge 1975; Baumel et al. 1979; Rosser 1980; Schreiweis 1982; Zusi &amp; Bentz 1984; McKitrick 1985; Raikow 1985; McGowan 1986; Meyers, this study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extensor longus alulae:</td>
<td>Raikow 1977</td>
</tr>
<tr>
<td>Extensor pollicis:</td>
<td>Beddard 1898</td>
</tr>
<tr>
<td>Extensor longus digitii II:</td>
<td>Fisher &amp; Goodman 1955; Berger 1956c</td>
</tr>
<tr>
<td>Extensor ossis metacarpi pollicis:</td>
<td>Shufeldt 1890; Leach 1914; Kaupp 1918; Burt 1930</td>
</tr>
<tr>
<td>Extensor indicis longus:</td>
<td>Sullivan 1962</td>
</tr>
<tr>
<td>Extensor carpi radialis profun dus:</td>
<td>Harvey et al. 1968</td>
</tr>
<tr>
<td>Extensor carpi radialis brevis:</td>
<td>Fujioka 1959</td>
</tr>
<tr>
<td>Extensor digitorum indicis proprius:</td>
<td>Vaughan 1876</td>
</tr>
<tr>
<td>Extensor metacarpi ulnaris:</td>
<td>Nair 1954</td>
</tr>
</tbody>
</table>

M. interosseus ventralis (IV)

M. interosseus ventralis is a pinnate muscle which lies in the deep aspect of the intermetacarpal space. It is visible in dorsal view, and lies deep and distal to M. interosseus dorsalis. In *Falco* it is the larger of the two interosseus muscles.

IV arises fleshily from the distal two-thirds of the dorsal rim of the intermetacarpal space, and from the entire rim on the ventral surface (Fig. 3). It gives off a tendon at the distal border of the intermetacarpal space, which passes in between the minor digit and the proximal phalanx of the major digit (Fig. 4). IV inserts onto the caudo-dorsal aspect of the distal tip of the distal phalanx of the major digit (Figs. 3 – 5).

IV is in a position to retract the terminal phalanx, but may function to resist a protractile force on the phalanx.

Hudson and Lanzillotti’s (1955) figure of this muscle in *F. mexicanus* shows a similar insertion onto the major digit.

Table 15. Synonyms of M. interosseus ventralis

<table>
<thead>
<tr>
<th>Interosseus ventralis:</th>
<th>Chamberlain 1943; Fisher &amp; Goodman 1955; Kuroda 1960; Berger 1956c; Harvey et al. 1969; Vander Berge 1975; Raikow 1977, 1985; Baumel et al. 1979; Rosser 1980; Schreiweis 1982; Weinstein et al. 1984; Zusi &amp; Bentz 1984; McKitrick 1985; Meyers, this study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interosseus palmaris:</td>
<td>Shufeldt 1890; Gadow &amp; Selenka 1891; Beddard 1898; Marshall 1905; Leach 1914; Kaupp 1918; Burt 1930; Sy 1936; Fisher 1946; Berger 1953, 1954, 1956d, 1960, 1968; Swinebread 1954; Fujioka 1959; Sullivan 1962; George &amp; Berger 1966; Lucas &amp; Stettenheim 1972; Koch 1973; Stegmann 1978</td>
</tr>
<tr>
<td>Interosseus palmaris:</td>
<td>Robinson 1970</td>
</tr>
</tbody>
</table>

M. interosseus dorsalis (ID)

M. interosseus dorsalis is a pinnate muscle lying in the dorsal aspect of the intermetacarpal space, and is visible in dorsal view. ID lies proximally to M. interosseus ventralis, where it overlies that muscle’s origin. In *Falco* it is the smaller of the two interosseus muscles.

Table 16. Synonyms of M. interosseus dorsalis


ID arises fleshily from the cranial and caudal borders of the proximal one-third of the dorsal interosseus space (Fig. 3). It gives rise to a tendon midway along the interosseus space, which passes through a ligamentous loop at the carpometacarpus-major digit articulation (Fig. 4). ID inserts onto the dorso-lateral aspect of the proximal end of the distal phalanx of the major digit (Fig. 4).

ID is in a position to elevate the terminal phalanx of the major digit. It may function to counteract a depressor force on this element, possible during wing elevation.

Hudson and Lanzillotti’s (1955) figure of this muscle in *F. mexicanus* shows a similar insertion onto the major digit.

M. extensor brevis alulae (EBA)

M. extensor brevis alulae is a small, pinnate muscle which lies at the alular joint on the dorsal surface of the wrist. It crosses from the carpometacarpus to the alular phalanx.

Table 17. Synonyms of M. extensor brevis alulae

<table>
<thead>
<tr>
<th>Extensor brevis alulae:</th>
<th>Vander Berge 1975; Baumel et al. 1979; Rosser 1980; Zusi &amp; Bentz 1984; Raikow 1985; McGowan 1986; Meyers, this study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extensor pollicis:</td>
<td>Stegmann 1978</td>
</tr>
<tr>
<td>Extensor brevis digitii II:</td>
<td>Fisher &amp; Goodman 1955; Berger 1956c</td>
</tr>
<tr>
<td>Extensor indicis brevis:</td>
<td>Sullivan 1962</td>
</tr>
<tr>
<td>Extensor digitii secundis manus:</td>
<td>Harvey et al. 1968</td>
</tr>
<tr>
<td>Extensor of the second digit:</td>
<td>Chamberlain 1943</td>
</tr>
<tr>
<td>Abductor indicis:</td>
<td>Fujioka 1959</td>
</tr>
<tr>
<td>Extensor metacarpi radialis longus [sic]:</td>
<td>Burt 1930</td>
</tr>
<tr>
<td>Extensor proprius pollicis:</td>
<td>Leach 1914</td>
</tr>
</tbody>
</table>
ELA arises from a sulcus on the cranio-dorsal surface of the carpo-metacarpus, caudo-lateral to the extensor process of the carpometacarpus (Figs. 3, 4). The short muscle belly converges to a short tendon which inserts onto the cranio-proximal corner of the alular digit (Figs. 3, 4).

EBA is in a position to extend, and possibly elevate the alula. It probably functions in this capacity with M. abductor alulae.

Hudson and Lanzillotti’s (1955) figure of EBA in *F. mexicanus* corresponds to that in *F. sparverius*.

**M. abductor alulae (ABA)**

M. abductor alulae is a relatively large muscle lying on the ventral surface of the wrist. It spans the alular joint.

ABA arises from the ventral surface of the tendon of M. extensor metacarpi radialis, just prior to that muscle’s insertion. The belly passes around the extensor process of the carpometacarpus, beneath the associated wrist ligaments (Fig. 5), and crosses the alular joint. ABA inserts fleshily onto a sulcus on the ventral aspect of the proximal alular digit (Fig. 3). A very thin tendon continues from the muscle belly to the tip of the alular digit in specimen AMNH 10258 (Figs. 3, 5).

<table>
<thead>
<tr>
<th>Table 18. Synonyms of M. abductor alulae</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Adductor alulae</em>: Vanden Berge 1975; Baunel et al. 1979; Rosser 1980; Zusi &amp; Bentz 1984; McKirrick 1985; Raikow 1985; McGowan 1986; Meyers, this study</td>
</tr>
<tr>
<td><em>Adductor alulae</em>: Raikow 1977</td>
</tr>
<tr>
<td><em>Adductor indicis</em>: Sullivan 1962; Robinson 1970; Lucas &amp; Stettenheim 1972</td>
</tr>
<tr>
<td><em>Adductor alae digit I</em>: Fisher &amp; Goodman 1955; Berger 1956c</td>
</tr>
<tr>
<td><em>Adductor digiti secundi manus</em>: Harvey et al. 1968</td>
</tr>
<tr>
<td><em>Extensor proprius pollicis</em>: Shufeldt 1890; Kaup 1918; Burt 1930</td>
</tr>
<tr>
<td><em>Extensor indicis</em>: Fujioka 1959</td>
</tr>
</tbody>
</table>

ABA is in a position to extend/abduct the alula. It may also be able to depress the alula.

Berger (1956) described a fleshy and tendinous origin from the tendon of M. extensor metacarpi radialis. His description of the insertion corresponds to that in *F. sparverius*.

<table>
<thead>
<tr>
<th>Table 19. Synonyms of M. adductor alulae</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Adductor alulae</em>: Vanden Berge 1975; Baunel et al. 1979; Rosser 1980; Weinstein et al. 1984; Zusi &amp; Bentz 1984; McKirrick 1985; Raikow 1985; McGowan 1986; Meyers, this study</td>
</tr>
<tr>
<td><em>Adductor alulae</em>: Raikow 1977</td>
</tr>
<tr>
<td><em>Adductor indicis</em>: Sullivan 1962; Robinson 1970; Lucas &amp; Stettenheim 1972</td>
</tr>
<tr>
<td><em>Adductor alae digit I</em>: Fisher &amp; Goodman 1955; Berger 1956c</td>
</tr>
<tr>
<td><em>Adductor digiti secundi manus</em>: Harvey et al. 1968</td>
</tr>
<tr>
<td><em>Flexor brevis pollicis</em>: Shufeldt 1890; Leach 1914; Kaup 1918</td>
</tr>
<tr>
<td><em>Flexor indicis</em>: Fujioka 1959</td>
</tr>
</tbody>
</table>

ADA arises from the cranio-dorsal aspect of the proximal carpometacarpus, just distal to the alular condyle (Fig. 3). The short, parallel-fibers insert at a narrow point along the caudal aspect of the midshaft of the alular digit (Fig. 3).

ADA is an adductor of the alula, and may be aided by the alular tendon of *M. extensor digitorum communis* (Figs. 3, 4).

**M. adductor digiti majoris (ADM)**

M. adductor digiti majoris is a relatively long pinnate muscle lying along the cranio-ventral border of the carpometacarpus. It is visible ventrally, and is partly covered by the retinaculum of the wrist primaries (ulnocarpometacarpal aponeurosis) and the tendons of *Mm. flexor digitorum profundus* and *flexor digitorum superficialis*.

<table>
<thead>
<tr>
<th>Table 20. Synonyms of M. adductor digiti majoris</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Adductor digiti majoris</em>: Vanden Berge 1975; Raikow 1977, 1985; Baunel et al. 1979; Rosser 1980; Schreiweis 1982; McKirrick 1985; McGowan 1986; Meyers, this study</td>
</tr>
<tr>
<td><em>Adductor major digit I</em>: Fisher &amp; Goodman 1955; Berger 1956c</td>
</tr>
<tr>
<td><em>Adductor digiti I</em>: Kuroda 1960</td>
</tr>
<tr>
<td><em>Adductor medius</em>: Sullivan 1962; Robinson 1970; Lucas &amp; Stettenheim 1972</td>
</tr>
<tr>
<td><em>Adductor digiti tertii</em>: Fujioka 1959</td>
</tr>
<tr>
<td><em>Extensor digiti tertii manus distalis</em>: Harvey et al. 1968</td>
</tr>
</tbody>
</table>

ADM arises fleshily from a crescent-shaped region on the cranio-ventral surface of the carpometacarpus, including the proximal and ventral rim of the intermetacarpal space and pisiform process. Some tendinous fibers also arise from the ventral corner of the proximal alular digit, next to the insertion of *M. flexor alulae* (Figs. 3, 5).
Fibers from ADM converge to form a strong tendon which inserts onto the cranio-ventral aspect of the proximal phalanx of the major digit (Fig. 3).

Although in a position to abduct the major digit, action of ADM is restricted due to the relatively immobile carpometacarpal-major digit articulation. It may function to resist a retractive force acting on the major digit.

M. flexor alulae (FA)

M. flexor alulae is a very small, narrow muscle located on the ventral surface of the wrist. FA spans the ventral aspect of the alular articulation and lies between the tendon of M. flexor digitorum profundus and M. abductor alulae.

Table 21. Synonyms of M. flexor alulae

| Flexor alulae: Vanden Berge 1975; Baumel et al. 1979; Rosser 1980; Raikow 1985; McGowan 1986; Meyers, this study |
| Flexor indicis: Sullivan 1962 |
| Flexor digiti II: Fisher & Goodman 1955; Berger 1956c |
| Flexor digiti secundi manus: Harvey et al. 1958 |
| Adductor indicis: Fujioka 1959 |

FA arises from the proximal carpometacarpus, cranial to the pisiform process and proximal to the origin of M. abductor digiti majoris. FA has a fleshy insertion onto the caudo-ventral process of the alular digit, in common with two wrist ligaments just proximal to the alular tendon of origin of M. abductor digiti majoris (Figs. 3, 5).

Although probably too small for any major function, FA may assist M. adductor alulae in adduction of the alular digit. It may also have a slight depressive action.

M. flexor digiti minoris (FDM)

M. flexor digiti minoris is a small parallel-fibered muscle lying on the caudal border of the carpometacarpus. It is the only muscle attaching onto the minor digit.

FDM arises fleshy from a small area on the caudo-ventral surface of the proximal carpometacarpus (Fig. 3). Its fibers extend along the caudal border of the carpometacarpus, and FDM inserts by mixed fleshy and tendinous fibers onto a process on the caudo-proximal corner of the minor digit (Figs. 3–5).

FDM probably does not affect much movement to the minor digit, but may be involved in assisting flexion of the major digit. It may also function with M. interosseus ventralis in resisting a protractive force on the manus.

| Table 22. Synonyms of M. flexor digiti minoris |
| Flexor digiti minoris: Vanden Berge 1975; Raikow 1977, 1985; Baumel et al. 1979; Rosser 1980; Schreiweis 1982; Weinstein et al. 1984; Zusü & Bentz 1984; McKitrick 1985; McGowan 1986; Meyers, this study |
| Flexor minimi digiti: Shufeldt 1890 |
| Flexor minimi digiti + Flexor minimi digiti brevis: Leach 1914; Kaupp 1918; Burt 1930 |
| Flexor digiti IV: Fisher & Goodman 1955; Berger 1956c; Robinson 1970; Lucas & Stettenheim 1972 |
| Flexor digiti quarti: Sullivan 1962 |
| Flexor digiti quarti brevis + abductor digiti quarti proprius: Fujioka 1959 |
| Flexor digiti quarti manus longus: Harvey et al. 1968 |
| Flexor longus muscle of the fourth digit: Chamberlain 1943 |

Discussion

This study provides an anatomical basis of forelimb structure for future comparative and functional studies. Clearly, function can only be inferred by anatomy. Recently, Dial (1992a, b) used stimulation, electromyography and kinematics to address the function of the antebibrachial muscles during different modes of flight in the pigeon. He found that in the pigeon, M. extensor metacarpi radialis stabilizes the wrist during non-ascending flight, M. extensor digitorum communis maintains wrist extension during "back-flick" of upstroke, and Mm. flexor carpi ulnaris and extensor metacarpi ulnaris stabilize the wrist in steady-state flight. Additional stimulation and electromyographic studies are needed to assess the in vivo function of the remainder of forelimb muscles.

In addition to a traditional role in moving joints, the distal wing muscles may have different functional roles. For example, muscles may not "move a joint" as much as they may function to resist an antagonistic movement. Thus, a muscle such as interosseus ventralis may not only (if at all) function to retract phalanx I but may resist a protractive force imparted by the wing in flight. In addition, antebibrachial muscles may function to stabilize joints, prevent disarticulations, or decelerate rapidly moving limb segments. Current functional techniques make answering these questions a reality in the near future. Furthermore, these muscles may possess muscle spindles (see Maier 1983; Meyers 1992b) and may function as sensors to detect limb proprioception and relative state of contraction. Thus we may be forced to re-evaluate our understanding of muscles as simply movers of bones.

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anatomical specimens. E. Brainerd and K. Liem made the video printer available. This study was completed in partial fulfillment of the PhD degree in the Program in Ecology and Evolutionary Biology at Brown University.

Abbreviations:

ABA  M. abductor alulae
AD   alular digit
ADA  M. adductor alulae
ADM  M. abductor digitii majoris
BB   M. biceps brachii
Br   M. brachialis
CM   carpometacarpus
C    M. coracobrachialis cranialis
D    M. deltoideus major
EBA  M. extensor brevis alulae
ECU  M. extensor carpi ulnaris
EDC  M. extensor digitorum communis
ELA  M. extensor longus alulae
ELDM M. extensor longus digitii majoris
EMR  M. extensor metacarpal radialis
ES   M. expansor secundarius
EU   M. ectepicondylo-ulnaris
FA   M. flexor alulae
FCU  M. flexor carpi ulnaris
FDM  M. flexor digitii minoris
FDP  M. flexor digitorum profundus
FDS  M. flexor digitorum superficialis
ID   M. interosseus dorsalis
IMS  intermetacarpal space
IV   M. interosseus ventralis
L    M. latissimus dorsi pars caudalis
LH   Lig. humerocarpale
MaD  major digit
MiD  minor digit
OR   Os radiale
OU   Os ulnare
P    M. pectoralis
PL   M. patagialis longus
PP   M. pronator profundus
PPL  M. pectoralis patagialis pars longa
PPL-PL M. pectoralis patagialis pars longa + M. patagialis longus
PS   M. pronator profundus
R    radius
Su   M. supinator
T    M. triceps
U    ulna
UCA  ulnocarporeemial aponeurosis
UD   M. ulnometacarpalis dorsalis
UV   M. ulnometacarpalis ventralis

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