THE APPENDICULAR MYOLOGY OF THE SANDHILL CRANE, WITH COMPARATIVE REMARKS ON THE WHOOPING CRANE

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UNTIL recently, very little had been published on the myology of the cranes. Fisher and Goodman (1955) described in detail the myology of the Whooping Crane (*Grus americana*); they also dissected one Little Brown Crane (*G. c. canadensis*). I began a myological study of the Sandhill Crane (*G. canadensis tabida*) at the suggestion of Dr. L. H. Walkinshaw, whose interest in the biology and taxonomy of the cranes is well known. For the first specimen of this subspecies, I am indebted to Dr. Wallace Grange of Babcock, Wisconsin. After the death of this captive bird, it was frozen immediately; I dissected it during the month of April, 1955. During February, 1956, two additional frozen specimens became available. These birds were killed by hunters during the latter part of October, 1955, in Jasper County, Indiana. For these specimens, I am indebted to Dr. Charles Kirkpatrick of Purdue University and to Russell Mumford of the University of Michigan.

Through the generosity of Dr. Fisher, I was permitted to study the Whooping Crane manuscript before I began my first dissection. After I had completed this work, Dr. Fisher and I discussed differences in interpretation of certain muscle complexes. These differences will be explained in the descriptions of the individual muscles, inasmuch as it was too late to make changes in the Whooping Crane manuscript.

There are two sets of muscle terminology currently in use in this country, that of Hudson (1937) and Hudson and Lanzillotti (1955) and that of Fisher (1946) and Fisher and Goodman (1955); I have included both sets of names. The muscles are discussed in the sequence used by Fisher and Goodman; they accepted Montagna's (1945) conclusions on the numbering of the hand digits, and, consequently, proposed new names for certain muscles (1955:39).

MYOLOGY OF THE WING

M. TENSOR PATAGII LONGUS (propatagialis longus)

Fisher and Goodman (1955:43) interpret the "elongately triangular belly" arising from the dorsal end of the furculum as belonging solely to M. tensor patagii brevis and state (p. 42) that "the only muscular origin" of the tensor patagii longus is that which "comes from the antero-palmar surface of M. biceps . . . ." In view of the traditional treatment of this complex by the British and German ornithologists, I believe that it is misleading to consider the slip from M. biceps brachii as M. tensor patagii longus (Fisher and Goodman, 1955: Fig. 17). Fürbringer and Gadow believed that both the tensor patagii longus and the tensor patagii brevis muscles were derivatives of M. deltoideus major; no one, to my knowledge, has suggested that either is a derivative of M. biceps brachii. In many birds (e.g., the cuckoos), the two tensors have a common origin and the bellies are separate only distally. In some birds, the two muscles are separate throughout.

Thus, there are two possible interpretations of this complex in the cranes. I prefer to interpret the belly arising from the furculum to be the fused bellies of Mm. tensores patagii longus et brevis (see also Mitchell, 1901: 641, "deltoides patagialis"). If one does not agree with this interpretation, then it is true, as Fisher and Goodman stated, that the only muscular origin for the tensor patagii longus is that derived from M. biceps brachii. This is, in part, an academic question, but it is important that the taxonomist recognize such differences of interpretation in myological studies so that these are not given erroneous taxonomic significance.

What Fisher and Goodman call the belly of M. tensor patagii longus is actually the *biceps slip*, a muscular slip widely used in taxonomic diagnoses. The biceps slip of Beddard is the *biceps propatagialis* of Gadow and Selenka (1891:255) and the *tensor accessorius* of Parker and Haswell (1947:441), Young (1950:427), and others.

In the Sandhill Crane, the origin of M. tensor patagii longus is essentially the same as that described for the Whooping Crane by Fisher and Goodman. The fleshy biceps slip (6-7 cm. long) arises from the coracoidal tendon of M. biceps brachii, becomes tendinous, and inserts on the elastic part of the tensor patagii longus tendon. A second origin is a small tendon, attached to the deltoid crest, which contributes to the tendons of insertion of both the tensor patagii longus and the tensor patagii brevis muscles. M. pectoralis, pars propatagialis, is a wide (2 cm.) aponeurosis, which is a continuation of the superficial layer of the fascial envelope which surrounds the insertion of M. pectoralis. This aponeurosis fuses with the distal end of the belly of the tensor patagii brevis and gives rise to parts of the tendons both of the tensor patagii longus and brevis.

The main area of insertion of the tensor patagii longus is on the extensor process of the carpometacarpus, but slips extend into the manus to fuse with its fascia and with the bases of the alula quills and their coverts. Fisher and Goodman (1955:68) stated that in the Whooping Crane, a part of M. abductor alae digiti II (= abductor pollicis) arises from the inserting tendon of M. tensor patagii longus. This is not true in the Sandhill Crane. I found no branches of the longus tendon extending to the elbow; such branches were found in *G. americana*, but not in *G. c. canadensis*, by Fisher and Goodman.

M. TENSOR PATAGII BREVIS (propatagialis brevis)

This muscle is weakly developed, having a belly about 9 cm. long and 2 cm. wide; the belly extends to the middle of the deltoid crest. It arises primarily from the dorsal end of the furculum, but has a small attachment to the acromion process of the scapula. Its main tendon is reinforced, as described above, by tendinous slips arising from the deltoid crest and from pars propatagialis of M. pectoralis.

The main tendon of insertion passes distad toward the elbow and expands into a thin band (2 cm. wide), which fuses, in part, with the tendon of origin of pars anconalis of M. extensor metacarpi radialis, and then passes proximad to attach to the distal end of the humerus, adjacent to the origin of pars anconalis. The rest of the brevis tendon (1 cm. wide) passes posteriad over the forearm muscles and extends the entire length of the forearm, sending slips to the bases of the feathers; distally, it attaches to the os ulnare. Fisher and Goodman (1955:43) state that in *G. c. canadensis* "the wide tendon continues posteriorly over the surface of the wing to insert on the tendon of origin of the wide anterior and superficial part [= M. flexor digitorum sublimus] of M. flex. carpi ulnaris." The tendon does not do so in *G. c. tabida* and it is difficult for me to see how the brevis tendon, located on the dorsal surface of the forearm, could pass posteroventrad through the secondaries and their coverts to insert on Mm. flexor digitorum sublimus or flexor carpi ulnaris, which are located on the posteroventral surface of the forearm.

Fisher and Goodman (1955:43) noted that in one specimen of the Whooping Crane "M. tens. pat. brevis . . . has a divided tendon of insertion; in the other birds the tendon is single." Unilaterally in one of my specimens of *G. c. tabida*, the tendon has three strong components connected by weak fascia. The most proximal of the three components, in part, passes proximad to insert on the lateral epicondyle (ectepicondylar process) of the humerus (without being connected with the tendon of M. extensor metacarpi radialis) and, in part, fuses with the middle band. The latter expands into a broad aponeurotic sheet, which passes posteriorly over Mm. extensor digitorum communis and flexor metacarpi radialis, and has attachments proximally to the tendon of M. scapulotriceps and to the lateral epicondyle (between the origins of Mm. extensor digitorum communis and extensor metacarpi radialis). This aponeurosis extends the entire length of the forearm, fuses with the antebrachial fascia, sends slips to the bases of the feathers, and attaches to the os ulnare. The most distal of the three components of the brevis tendon inserts on the tendon of pars anconalis of M. extensor metacarpi radialis, about 1 cm. proximal to the origin of its fleshy fibers.

M. PECTORALIS

In the Sandhill Crane this is a single muscle and is not divided, as in the Whooping Crane, into superficial and deep layers. Fasciculi from the deep surface of the belly, however, do insert by a broad aponeurosis on the tendon of origin of M. biceps brachii. In the Sandhill Crane, M. pectoralis arises from approximately the inferior third of the carina, from the posterior and anterolateral parts of the body of the sternum, and from nearly the entire length of the clavicle. I found no origin from the "tracheal enclosure." The muscle inserts on the ventral surface of the deltoid crest (pectoral crest of Shufeldt, 1890:70). Pars propatagialis is entirely aponeurotic; its attachments were described above (p. 283).

M. SUPRACORACOIDEUS

M. STERNOCORACOIDEUS

M. CORACOBRACHIALIS POSTERIOR

All are similar in origin and insertion to these muscles in the Whooping Crane (Fisher and Goodman, 1955:46–48).

M. LATISSIMUS DORSI

There are a few minor differences in this complex between *G. americana* and *G. canadensis tabida*. In the latter, the origin seems to be less extensive. In the Whooping Crane, pars anterior arises from (all?) the "thoracic" (= dorsal) vertebrae (Fisher and Goodman, 1955: 48). In the Sandhill Crane, it arises by an aponeurosis (anteriorly) and by fleshy fibers from the neural spines of the first four dorsal vertebrae; pars anterior is a thin fleshy band, about 5 cm. wide at its origin, and about 3 cm. wide (2 cm. in the captive bird) at midlength. Pars anterior has a fleshy insertion (5 cm. wide) on the humerus, beginning about 4 cm. distal to the junction of the deltoid crest and the articular head; this insertion is immediately posterior to the humeral attachment of M. triceps, scapular head (= M. scapulotriceps = M. triceps scapularis).

Pars posterior, in the Sandhill Crane, arises by an aponeurosis from the neural spines of the last three (Nos. 4, 5, and 6) dorsal vertebrae, from the fascia covering the anterior edge of M. extensor iliotibialis anterior (= sartorius), and by an aponeurosis attached to the anterior edge of the ilium. Pars posterior inserts on the humerus by a small, flat tendon, immediately proximal to the insertion of pars anterior, and posterior to the uppermost portion of the scapulotriceps anchor. In *G. americana* pars posterior

"attaches to the deep side of the anterior part but also inserts on the humerus beneath the fleshy insertion of the anterior portion."

Fisher and Goodman (1955:48) state that the dermal component (M. latissimus dorsi metapatagialis) may or may not be present in the Whooping Crane. I found a minute dermal component bilaterally in one specimen, unilaterally in a second specimen, but not at all in a third specimen of the Sandhill Crane.

MM. RHOMBOIDEUS SUPERFICIALIS ET PROFUNDUS

These two muscles are similar in the two cranes, but the origins and insertions are less extensive in *G. c. tabida.* M. rhomboideus superficialis arises by an aponeurosis from the first five dorsal vertebrae. Fisher and Goodman (1955:51) point out that the entire aponeurosis of origin of this muscle "is a caudal extension of the aponeurosis of M. cucullaris, hals pt.." M. rhomboideus superficialis inserts on all but the caudal 3 cm. of the scapula in the Sandhill Crane. M. rhomboideus profundus arises from the neural spines of the last cervical and the six dorsal vertebrae; it inserts on the caudal 10 cm. of the scapula.

In both cranes, an unusual feature is that M. rhomboideus profundus is larger than M. rhomboideus superficialis.

M. CORACOBRACHIALIS ANTERIOR

This is a well developed fleshy muscle (about 6 cm. long) located on the ventral aspect of the shoulder; the belly does not cover the anterior edge of the humerus. It arises mostly by fleshy fibers from the dorsal surface of the head of the coracoid, anterior to the origin of M. biceps brachii, and from the deep surface of the biceps tendon. The insertion is as described by Fisher and Goodman (1955:51).

M. DELTOIDEUS MINOR

In *G. americana,* M. deltoideus minor has a single head; in *G. c. tabida* it arises inside the triosseal canal by two heads: a ventral head from the medial process (procoracoid) of the coracoid and from the coracoclavicular membrane; a dorsal head from the ventral margin of the acromion process of the scapula. (The ventral head corresponds, in part, to a small accessory head of M. supracoracoideus present in some birds; such an accessory head, when present, however, inserts on the tendon of M. supracoracoideus.) In *G. c. tabida,* the two heads fuse and insert distal and posterior to the insertion of M. supracoracoideus; none of the fibers insert on the tendon of that muscle. As in *G. americana,* M. deltoideus minor conceals anterodorsally the tendon of M. supracoracoideus.

M. PROSCAPULOHUMERALIS (scapulohumeralis anterior)

See the descriptions of Mm. subscapularis and "proscapulohumeralis brevis."

M. SUBSCAPULARIS

The muscle that Fisher and Goodman (1955:52–53) and Fisher (1946:584) call M. proscapulohumeralis is actually the external head (pars externa) of M. subscapularis.

M. subscapularis is similar in the two cranes and, in fact, exhibits the same general structure in all genera I have dissected. In *G. c. tabida* it arises by two typical heads: pars externa and pars interna. The inserting tendon of M. serratus anterior passes between the two heads. The external head arises from an area 3 cm. long on the lateral surface of the scapula, beginning immediately caudal to the glenoid lip. The internal head, which is larger, arises from the medial surface of the scapula over an area about 5 cm. long. Insertion is on the capital groove and internal tuberosity of the humerus (as described in detail for *G. americana* by Fisher and Goodman, 1955:53).

"M. PROSCAPULOHUMERALIS BREVIS"

As Fisher and Goodman (1955: 53) state, this muscle is "very easily overlooked, for

it lies between the posterior edge of M. delt. major and the most proximal part of the scapular head of M. triceps." Furthermore, Fisher wrote (letter, May 5, 1955) that it "was not found uniformly in the Whooping Cranes." I found this muscle bilaterally in one specimen of the Sandhill Crane, unilaterally in a second, and not at all in a third. The muscle is so small and delicate, however, that it might be destroyed by shot or be so mutilated in handling a poorly preserved specimen that one might not be aware that a separate muscle was involved at all.

In the Sandhill Crane this is a minute band of fleshy fibers 3 cm. long and only about 2 mm. wide. It arises from the ventral edge of the scapula just caudal to the glenoid fossa and *anteroventral* to the origin of M. scapulotriceps. It inserts by fleshy fibers, and not by a tendon as in the Whooping Crane, on the humerus about 0.5 cm. proximal to the insertion of M. latissimus dorsi, pars posterior, and lateral to the origin of M. humerotriceps (= triceps, internal and external heads = triceps humeralis). The area of insertion is on the plane of the inferior margin of the pneumatic fossa of the humerus, but is entirely lateral to the humerotriceps muscle.

As mentioned above (p. 285), the muscle which Fisher and Goodman call M. proscapulohumeralis is actually the external head of M. subscapularis. Thus, the name M. proscapulohumeralis is available for the rudimentary muscle discussed here. In the cranes, however, this muscle does not exhibit the relationships of M. proscapulohumeralis as I have seen them in representatives of other orders. In most genera, it arises posterior to the origin of M. scapulotriceps and inserts in the pneumatic fossa of the humerus, between the internal and external heads of M. humerotriceps. No muscle in the cranes meets these specifications. However, either the origin or the insertion of a muscle may migrate phylogenetically.

Mitchell (1901:644; 1915:415) discussed the considerable variation in development of M. proscapulohumeralis in gruiform birds, though he did not investigate the genus *Grus*. He stated that this muscle inserts on the humerus "near the forked origin" of M. humerotriceps (= anconaeus humeralis), as I have seen it in other genera. He noted also that "in *Otis* it is much reduced, and is attached to the humeral anchor" of M. scapulotriceps (= anconaeus scapularis). Fürbringer (1902:547 and Figs. 258–260) also described and illustrated M. proscapulohumeralis in genera in which it does not insert in the pneumatic fossa. In *Ciconia* and *Pelecanus*, for example, the muscle inserts proximal and/or anterior to most of the origin of M. humerotriceps. It seems likely, therefore, that in the genus *Grus*, the small muscle which Fisher and Goodman call "M. proscapulohumeralis brevis" is actually M. proscapulohumeralis. Its area of origin seems to agree with the origin in other gruiform birds, but its insertion differs slightly from that previously reported.

The muscle which Fisher (1946:587) called "M. proscapulohumeralis brevis" in the Cathartidae is M. proscapulohumeralis in that group.

M. DORSALIS SCAPULAE (scapulohumeralis posterior)

This muscle is typical in origin and insertion. In *G. c. tabida* it arises from the posterior 9 cm. of the blade of the scapula. (see also M. expansor secundariorum and Fig. 1.)

M. SERRATUS POSTERIOR (serratus superficialis posterior)

In the origin of this complex there are minor differences between the Whooping Crane and the Sandhill Crane, and, in the latter, the muscle is not separated into a superficial and a deep layer. It is so divided in the Whooping Crane. In the Sandhill Crane, the main belly is rectangular in shape, being about 3 cm. long and 4.5 cm. wide at its origin, primarily from the shafts and uncinate processes of true ribs numbers 3, 4, and 5; there is some fascial origin also from rib number 6. The insertion is almost exclusively by an

aponeurosis on the ventral edge of the posterior end of the scapula. In the Whooping Crane, the superficial layer arises from "ribs 4, 5, 6, and 7 and from fascia overlying the external layer of intercostal muscles." The deep layer arises from ribs 4, 5, and 6.

I found a large dermal component (= M. serratus superficialis metapatagialis) arising primarily from the lateral surface of true ribs numbers 4 and 5 and from the intercostal fascia. The belly terminates in the metapatagium opposite the posterior margin of the humeral feather tract. From this area, a fibrous tendon continues distad along the surface of M. expansor secundariorum almost to the elbow.

M. SERRATUS PROFUNDUS

This complex is similar in the two cranes. In the Sandhill Crane it arises by fleshy fasciculi from the lateral surface, near the angle, of true ribs numbers 1, 2, and 3, and from the transverse process of the last cervical vertebra.

M. SERRATUS ANTERIOR (serratus superficialis anterior)

As is true of the preceding two muscles, there are minor differences in origin between the Whooping and Sandhill cranes. In the latter, the serratus anterior is a small muscle arising by three fleshy slips, one each from the first three true ribs and from the fascia covering the intercostal muscles. The dense aponeurosis of insertion passes upward between the two heads of M. subscapularis and inserts on the ventral edge of the scapula, beginning a short distance caudal to the glenoid lip.

M. SUBCORACOIDEUS

This muscle has a single belly in the cranes. In *G. c. tabida* it is a very small triangular-shaped muscle, 4 cm. long and 1 cm. in maximum width at its origin from the anteromedial surface of the coracoid, just dorsal to the middle of that bone. The tendons of Mm. subcoracoideus and subscapularis insert adjacent to each other on the humerus, and in one wing they fused at the insertion.

M. BICEPS BRACHII

This muscle exhibits the same relative development in the two cranes. In *G. c. tabida* the small belly (about 14 cm. long) lies in the proximal two-thirds of the arm. The tendon is ossified near the distal end of the humerus, but not at the insertions on the radius and ulna. The larger tendon inserts on the radius. The biceps slip is present (see M. tensor patagii longus).

M. DELTOIDEUS MAJOR

This muscle is similar in the two species, but the dermal component described for *G. americana* (Fisher and Goodman, 1955:57) is absent in *G. c. tabida*. In the latter, the belly of deltoideus major is about 12 cm. long and extends slightly less than half way down the humerus. The fibers of insertion are in contact posteriorly with the humeral anchor of M. scapulotriceps. The primary origin of the deltoideus major is on the dorsolateral surface of the scapula, and there is a secondary origin, by a flat aponeurosis (7 mm. wide) from the blade of the scapula as described by Fisher and Goodman for the Whooping Crane. In the Sandhill Crane, this aponeurosis is attached about 3 cm. caudal to the posterior glenoid lip and the origin of M. scapulotriceps, and dorsal to the anteriormost fibers of M. dorsalis scapulae. I did not find an os humeroscapulare and Fisher and Goodman did not mention it.

M. TRICEPS (triceps brachii)

This complex is similar in the two cranes. In *G. c. tabida* there is a strong aponeurotic connection or anchor (1.5 cm. long and 1.5 cm. wide) between the anterior surface of the scapular head (= M. scapulotriceps) and the humerus. The humeral attachment of this band begins about 3 cm. distal to the head of the humerus and lies immediately an-

terior to the insertion of pars anterior of M. latissimus dorsi. M. humerotriceps arises from the entire inferior margin of the pneumatic fossa of the humerus and is not distinctly divided into an external and an internal head. A few fasciculi arise from the bicipital crest anterior to the area of insertion of M. dorsalis scapulae. An ossified tendon forms on the ventral margin of the belly near the middle of the arm. Fleshy fibers arise almost to the level of the distal end of the humerus, but the insertion on the ulna is exclusively by a wide tendon. The tendon of insertion does not contain a sesamoid. (See discussion of M. anconaeus coracoideus.)

M. BRACHIALIS

This muscle is typical in origin, relations, and insertion.

M. EXPANSOR SECUNDARIORUM

Fisher and Goodman did not mention this muscle, but it certainly must be present and well developed in *G. americana.*

In *G. c. tabida,* M. expansor secundariorum (Fig. 1) is a well developed, roughly triangular-shaped muscle about 10 cm. long and 3 cm. wide at its base posterior to the elbow. This is a smooth muscle, which inserts primarily on the calami of secondaries numbers 17 through 23 and on the skin containing several of the distal tertials; a fibrous band, connected primarily to the humero-ulnar pulley, attaches to number 16. The belly extends over one-third the way up the arm, where fasciculi are attached to the skin forming the dorsal layer of the metapatagium. The muscle has two tendons of origin. The distal origin is by a flat tendinous band attached to the medial epicondyle of the humerus, distal to the origin of M. pronator brevis; this origin, apparently, has not been described for the cranes previously. A second tendon is formed at the apex of the belly in the metapatagium. This tendon runs proximad through that skin fold and pierces the lowermost semitendinous fibers (which function as a pulley) of M. dorsalis scapulae, about 2 cm. from the insertion of that muscle. In the axilla, the tendon bifurcates about 3 cm. proximal to the pulley. The larger, ventral branch of the tendon has its major attachment to the medial corner of the sternocoracoidal process of the sternum; the smaller, dorsal branch passes dorsomesiad to attach to the ventral edge of the scapula, near its articulation with the procoracoid. Fürbringer (1902:572) called the tendon extending from the scapula to the sternum the "sterno-coraco-scapulare internum" ligament; Newton (1896: 608) called it simply the "sterno-scapular ligament."

M. ANCONAEUS CORACOIDEUS

This muscle was first described by Fürbringer (1902:576, and earlier papers). For a recent discussion of M. anconaeus coracoideus see Berger (1956:159). In the Sandhill Crane (Fig. 1), the belly of this muscle is about 4.5 cm. long, but only about 1 mm. in maximum width. It arises by a tendon from the "scapular" tendon of M. expansor secundariorum. Distally the belly of M. anconaeus coracoideus gives rise to a second tendon, which inserts on the tendon of M. scapulotriceps near the distal end of the humerus. This is a striated muscle, as previously noted by Fürbringer. Fisher and Goodman do not mention this muscle in the Whooping Crane.

M. EXTENSOR METACARPI RADIALIS

This muscle is similar in the two cranes. In the Sandhill Crane, pars anconalis is a spindle-shaped muscle (about 6.5 cm. long), whose fleshy fibers begin about 5.5 cm. from the proximal surface of the olecranon process and about 1 cm. distal to the area where a part of the tensor patagii brevis tendon fuses with the tendon of origin of pars anconalis. Two tendons, interconnected by fascia, are present. The anterior tendon represents one tendon of insertion of M. tensor patagii brevis; the posterior tendon, the ori-

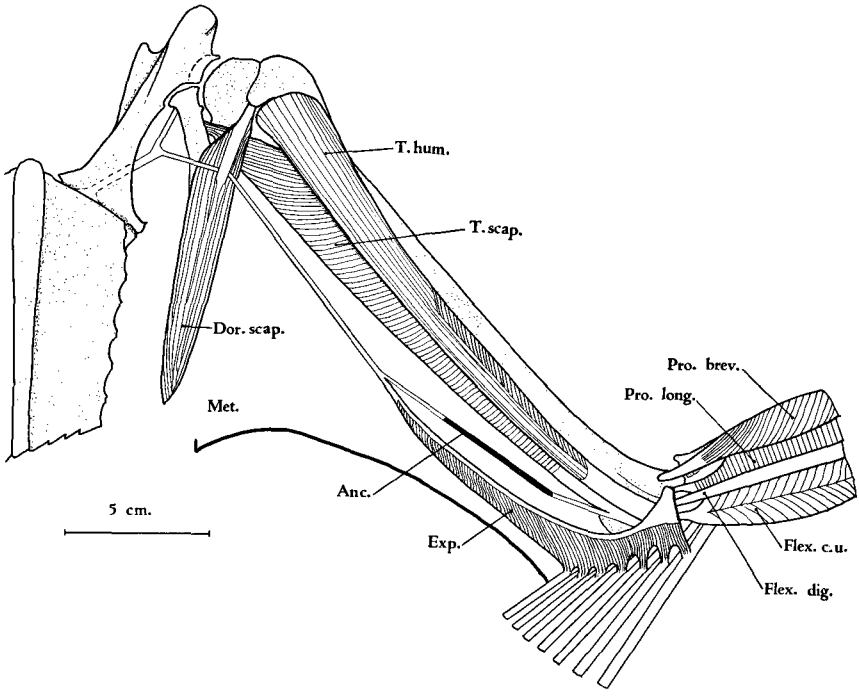

FIG. 1. Ventral view of certain muscles in the proximal region of the wing of *Grus canadensis tabida* to show relationships of Mm. expansor secundariorum and anconaeus coracoideus. The distal end of the humerus is distorted in order to show the triceps tendon and the origin of forearm muscles. Not shown is the fascial extension of the flexor digitorum sublimus tendon, which invests the superficial surface of M. flexor carpi ulnaris. Explanation of symbols: Anc., anconaeus coracoideus; Dor. scap., dorsalis scapulae; Exp., expansor secundariorum; Flex. c. u., flexor carpi ulnaris (humero-ulnar pulley not shown); Flex. dig., tendon of origin of flexor digitorum sublimus; Met., metapatagium; Pro. brev., pronator brevis; Pro. long., pronator longus; T. hum., humerotriceps; T. scap., scapulotriceps.

gin of pars anconalis. Both tendons are attached to the lateral epicondyle of the humerus. Pars palmaris is developed as illustrated for the Whooping Crane by Fisher and Goodman (1955: Fig. 16). The fleshy belly is about 7.5 cm. long. Pars anconalis and pars palmaris each give rise to separate tendons, which fuse to form a single ossified tendon of insertion. In addition to the usual insertion on the extensor process of the carpometacarpus, part of the tendon fuses with the tendon of M. extensor longus digiti II (= extensor pollicis longus), as in the Whooping Crane.

M. EXTENSOR DIGITORUM COMMUNIS

In the Sandhill Crane, this is a small, spindle-shaped muscle (8-9 cm. long), which is located in a little more than the proximal third of the forearm. The tendon bifurcates near the base of the pollex. The shorter branch inserts on the posterodorsal edge of digit II (= pollex), about 0.5 cm. from the proximal end of that bone. Fisher and Goodman

(1955: Fig. 20) illustrated this branch in the Whooping Crane, but described it (p. 60) as inserting on the "third finger." In *G. c. tabida* the longer tendon is ossified and inserts on the anterobasal corner of the proximal phalanx of digit III (of Montagna and Fisher and Goodman), or digit II (of Hudson), after passing through a fibrous pulley. I found no branch inserting on metacarpal II (I) as described and illustrated for the Whooping Crane by Fisher and Goodman (1955:60 and Fig. 20).

M. SUPINATOR BREVIS (supinator)

There are no important differences between the two species in the development of this muscle. In the Sandhill Crane the belly (about 8 cm. long) extends about one-third the length of the radius, i.e., nearly as far distad as M. pronator brevis. The muscle arises by a tendon from the lateral epicondyle of the humerus; some fleshy fibers also arise from the tendon of origin of M. extensor digitorum communis.

M. FLEXOR METACARPI RADIALIS (extensor carpi ulnaris)

This muscle exhibits similar relationships in the two cranes. In the Sandhill Crane it is a very small, spindle-shaped muscle 13 cm. long, but it is only about 0.5 cm. in maximum width. It arises from the distal end of the humerus in common with, and superficial to, the anconeus tendon. Fleshy fibers arise from this tendon 5 to 6 cm. from its humeral origin. As in the Whooping Crane, there is an aponeurotic attachment to the proximal end of the ulna. The muscle inserts near the base of the intermetacarpal space; the tendon of insertion is ossified.

M. PRONATOR BREVIS AND M. PRONATOR LONGUS (pronator sublimus and pronator profundus)

These two muscles have the same relationships as in *G. americana*. M. pronator longus (belly 10 cm. long) extends distad further than M. pronator brevis (belly 8 cm. long), but extends less than half way down the forearm. M. pronator brevis extends slightly more than one-third the length of the radius; it inserts primarily by an aponeurosis, beginning 4 cm. from the proximal end of the radius and extending to within 13.5 cm. of the distal end of that bone. The two muscles insert on about the same areas in *G. c. tabida* and *G. americana*: M. pronator longus over an area about 7 cm. long; M. pronator brevis over an area 4 to 5 cm. long.

M. EXTENSOR LONGUS DIGITI II (extensor pollicis longus)

This muscle exhibits the same relative development in the two birds. In the Sandhill Crane, it arises from the radius (for a distance of 6 cm.) and from the ulna (for a distance of only 2 cm.). The ulnar origin begins immediately distal to the biceps insertion. The small belly (about 13 cm. in overall length) is located in about the proximal half of the forearm; it is rounded distally, but is a flat muscle-sheet proximally and posteriorly. The tendon is ossified, except near the insertion, where it fuses with the tendon of M. extensor metacarpi radialis; the common tendon inserts on the extensor process of metacarpal II (I).

M. ANCONEUS (anconaeus)

This muscle is similar in the two species. In the Sandhill Crane it arises by a very large tendon, much larger than the tendons of Mm. extensor digitorum communis or supinator. The belly (about 13 cm. long) extends distad slightly more than half the length of the ulna, and thus inserts on somewhat more than the proximal half of that bone.

M. EXTENSOR LONGUS DIGITI III (extensor indicis longus)

Relative to the size of *G. americana* and *G. c. tabida* and to the development of this muscle in genera of other families, M. extensor longus digiti III might almost be considered rudimentary in the cranes. In the Sandhill Crane this muscle has a very small, spindle-shaped belly 12 cm. long but only about 3 mm. in maximum width. It arises

from the posterior surface of about the distal half of the radius in the Sandhill Crane and from the "middle third" of this bone in the Whooping Crane (Fisher and Goodman, 1955:64). It inserts on the distal phalanx of digit III (II).

M. FLEXOR DIGITORUM PROFUNDUS

This muscle has similar relationships in the two species. The relatively poorly developed belly (10 cm. long) in the Sandhill Crane is limited to less than the proximal half of the ulna. It has a V-shaped origin at the inferior margin of the insertion of M. brachialis; the origin extends to the origin of M. flexor carpi ulnaris brevis. The tendon of insertion is ossified except where it passes around the distal end of the ulna and into the manus; it inserts on the anteroventral corner of the distal phalanx of digit III (II). Thus, this muscle inserts on that phalanx *proximal* to the insertion of M. flexor digitorum sublimus.

M. FLEXOR DIGITORUM SUBLIMUS

Fisher and Goodman do not discuss this muscle, though they describe it as the "anterior part" of M. flexor carpi ulnaris. Shufeldt (1890:141) and Fisher (1946:598) also interpreted this complex in a similar manner. This "anterior part" is the flexor digitorum sublimus muscle as I have seen it in other genera and as it is described by Gadow and Selenka (1891:278). Though it might be considered rudimentary in the cranes, it definitely is present. The situation is confused because most of the muscle-complex is tendon and aponeurosis.

The strong tendon of origin (Fig. 1) arises from the distal end of the humerus, posterior to the origin of M. pronator longus, as described for the Whooping Crane by Fisher and Goodman (1955:66). From the posterior edge of this tendon, a thin but extensive aponeurosis passes posteriad to attach to the ulna; distally, the tendon inserts, in part, on the anterobasal corner of the os ulnare (os cuneiform), but has several small slips, which pass into the manus to fuse with the deep fascia on the palmar surface. These relationships are found both in *G. americana* and *G. c. tabida*. The rudimentary, bipinnate, fleshy belly (about 10 cm. long) of the flexor digitorum sublimus muscle arises from the anterior surface of the aponeurosis and from the deep surface of the main humeral tendon. The fleshy fibers begin about 4 cm. distal to the humerus. The small, ossified tendon of insertion of the sublimus muscle is entirely separate from the main (humeral) tendon, which inserts on the anterior edge of the ulnare; the latter attachment represents an accessory insertion of this complex and is not found in all families of birds. The sublimus tendon becomes fibrous as it passes around the anterior surface of the ulnare (anterior to the tendon of M. flexor carpi ulnaris and posterior to the accessory tendon of the sublimus muscle) and into the manus, where again it becomes ossified. The tendon passes distad along the anterior surface of the carpometacarpus and inserts primarily on the anterior edge, about mid-length, of the distal phalanx of digit III (II), but there is a fascial continuation to the tip of that phalanx. The flexor digitorum sublimus tendon, therefore, has a more distal insertion than the flexor digitorum profundus tendon. Fisher and Goodman (1955:66–67) also described this insertion in their discussion of the "anterior part" of M. flexor carpi ulnaris; see also Fisher, 1946:606 and Fig. 13.

M. FLEXOR CARPI ULNARIS

If one excludes the anterior part (= M. flexor digitorum sublimus) as described by Fisher and Goodman (1955:65–67), this muscle exhibits about the same development in *G. americana* and *G. c. tabida*. In *Grus* and apparently in all other birds, M. flexor carpi ulnaris arises by a very strong tendon from the medial (internal) humeral condyle and immediately passes through a strong humero-ulnar pulley. I have never seen any

departure from this relationship. In the Sandhill Crane the belly is relatively poorly developed. The bulk of the belly (total length about 15 cm.) is located in the proximal third of the forearm, though a small bundle of fleshy fibers accompanies the tendon almost to the distal end of the ulna. The strong, ossified tendon of insertion forms on the anterior surface of the belly at about the junction of the first and second fourths of the forearm; it inserts on the posterobasal portion of the ulnare. As in the Whooping Crane, the "superficial fasciculus of the posterior part" of M. flexor carpi ulnaris "attaches to the fascia over the bases of the feathers arising from the proximal two-thirds of the ulnar length" (Fisher and Goodman, 1955:67); in the Sandhill Crane, a small tendon forms from this posterior belly and also inserts on the base of the ulnare.

M. FLEXOR CARPI ULNARIS BREVIS (ulnimetacarpalis ventralis)

This is a well developed muscle, similar in the two cranes. In the Sandhill Crane the belly (about 12.5 cm. long) arises from slightly more than the distal half of the ulna. It has the typical relationships to the origin of M. flexor digitorum profundus.

M. ABDUCTOR ALAE DIGITI II (abductor pollicis)

This muscle, apparently, is similar in the two cranes. In each it has both a palmar and an anconal head. In the Sandhill Crane, as in all other genera I have dissected, the palmar belly arises from the tendon of insertion of M. extensor metacarpi radialis. Fisher and Goodman (1955:68) state that in *G. americana* this head arises from "the base of the extensor process" and by "tendinous fibers from the inserting tendon of M. tens. pat. longus." This is not true for the Sandhill Crane: the palmar head arises only from the tendon of M. extensor metacarpi radialis. There is a strong insertion of M. tensor patagii longus on the extensor process, but the tendon then fans out to become continuous with the deep fascia of the manus on both its dorsal and palmar surfaces. On both surfaces, this fascia passes superficially over the two heads of the abductor alae digiti II, but none of the fibers of this muscle arise from the tendon of tensor patagii longus.

The anconal head of the abductor alae digiti II arises from the extensor process; it inserts on the anterior corner of the base of digit II (pollex). The palmar head inserts by fleshy and tendinous fibers on the anterior edge of digit II in its basal half.

M. ADDUCTOR ALAE DIGITI II (adductor pollicis)

This muscle is well developed in the cranes. In the Sandhill Crane it arises by a flat aponeurosis about 1 cm. wide from metacarpal III (II). The bulky belly passes anteriad to insert on most of the posterior surface of digit II (pollex).

M. FLEXOR DIGITI IV (flexor digiti III)

This is a weakly developed muscle in the cranes. In the Sandhill Crane the belly is 3 cm. long and less than 0.5 cm. wide.

M. FLEXOR BREVIS DIGITI IV (flexor brevis digiti III)

This structure in the cranes is composed mostly of connective tissue (Fisher and Goodman, 1955:68). I agree with Hudson that it would be better to consider this not as a separate muscle, but simply as a distal part of the preceding muscle.

M. ABDUCTOR MINOR DIGITI III (abductor digiti II)

I have never seen such a muscle. In all birds that I have dissected, this structure is a ligament connecting the carpometacarpus with digit III.

M. FLEXOR METACARPI BREVIS

This muscle is absent in *G. americana* and in *G. c. tabida.* Hudson and Lanzillotti (1955:35 and 43) suggest that this name "be dropped from the literature" inasmuch as this muscle represents a distal head of M. extensor indicis longus (extensor longus

digiti III). Data which I have obtained suggest that this head may be of taxonomic use in some families. I think, therefore, that it would be convenient to retain the name flexor metacarpi brevis for indicating the presence or absence of this small muscle.

M. INTEROSSEUS DORSALIS

This muscle is similar in the two cranes. In the Sandhill Crane, it inserts primarily on the base of the distal phalanx of digit III (II); a small tendon continues to the tip of the digit.

M. INTEROSSEUS VENTRALIS (interosseus volaris)

In *G. americana* this muscle inserts on "the posterior aspect of phalanx 2, about three-fourths of the way out its length" (Fisher and Goodman, 1955:69). The insertion is similar in *G. c. tabida*, but the tendon is also anchored to the base of the distal phalanx of digit III (II).

M. EXTENSOR BREVIS DIGITI II (extensor pollicis brevis)

This very small muscle (belly about 1.5 cm. long) is developed as illustrated for the Whooping Crane by Fisher and Goodman (1955: Fig. 18).

M. ABDUCTOR MAJOR DIGITI III (abductor indicis)

This muscle is similar in the two species. In the Sandhill Crane, the muscle is mostly tendinous, though a few fleshy fasciculi arise at the level of the pisiform process. The ossified tendon forms at about the junction of the proximal and middle thirds of the carpometacarpus; the insertion is typical. The very small, deep head, described for *G. americana* by Fisher and Goodman is present in *G. c. tabida*.

M. FLEXOR DIGITI II (flexor pollicis)

Similar in the two cranes, this small (1.5 cm. long), fleshy muscle arises from the base of the carpometacarpus and inserts on the posterobasal corner of digit II (pollex) in the Sandhill Crane.

M. FLEXOR METACARPI POSTERIOR (ulnimetacarpalis dorsalis)

This is a poorly developed muscle with a belly 3.5 cm. long. In general, it has the same relationships as described by Fisher and Goodman (1955:70), except that in *G. c. tabida* the two smaller heads are mostly tendinous bands.

Myology of the Leg

M. EXTENSOR ILIO-TIBIALIS LATERALIS (iliotibialis)

This extensive muscle is similar in the two cranes. In the Sandhill Crane it arises by an aponeurosis from the entire anterior iliac crest and from all but the caudal 1 cm. of the posterior iliac crest. Some of the origin posteriorly is by fleshy fibers. It is throughout a thin sheet of muscle, but the posterior edge is the thickest. As Fisher and Goodman (1955:76) pointed out, "the fibers in the center of the muscle are less than half as long as those of the anterior and posterior edges." The distal half of the central part of the muscle is aponeurotic and is fused with the underlying muscles. The extensor ilio-tibialis lateralis muscle conceals from superficial view the anterior and superior half of M. extensor ilio-fibularis (= biceps femoris), but it does not conceal the bellies of Mm. flexor cruris lateralis and flexor cruris medialis.

M. EXTENSOR ILIO-TIBIALIS ANTERIOR (sartorius)

In the Sandhill Crane, this muscle arises primarily by an aponeurosis shared with pars posterior of M. latissimus dorsi from the neural spine of the last dorsal vertebra and from the anterior 5 cm. of the median dorsal ridge of the synsacrum. In the Whooping Crane, there is no origin from the last dorsal vertebra. In general, however, the muscle exhibits the same configuration in the two cranes. In the Little Brown

Crane, Hudson (1937:17) found the origin from the "anterior edge of the ilium only." The insertion in the Sandhill Crane is as described by Fisher and Goodman (1955:79).

M. PIRIFORMIS (gluteus medius et minimus)

As stated by Fisher and Goodman (1955:79), this muscle is similar in the two cranes, but it is "more strongly developed" in *G. c. canadensis*. In *G. c. tabida* it is a triangular-shaped muscle, 2 cm. wide at its base (origin) and about 4 cm. long. It inserts on the femur by a flat tendon anterodistal to the insertion of M. gluteus profundus (= iliotrochantericus posterior).

M. GLUTEUS PROFUNDUS (iliotrochantericus posterior)

Similar in the two cranes, none of the fibers of this muscle arise directly dorsal to the acetabulum, this area being pre-empted by the origin of M. gluteus medius et minimus (= piriformis).

M. ILIACUS (iliotrochantericus anterior)

This muscle is similar in the two cranes. Its relationships to M. iliotrochantericus medius are described below. (See Fisher and Goodman, 1955: Figs. 29 and 30.)

M. ILIOTROCHANTERICUS MEDIUS

Gadow and Selenka (1891:142) and Hudson (1937:60, 69) reported that they did not find this muscle in the genus *Grus*, but Fisher and Goodman (1955:123) found it in *G. americana* and *G. c. canadensis*. I found it bilaterally in two specimens and unilaterally in a third specimen of *G. canadensis tabida*. This muscle and M. iliotrochantericus anterior are separate at their origins only; the bellies fuse distally and insert by a common, wide (1.5 cm.) aponeurosis. In the right hip of one specimen, the iliotrochantericus anterior and iliotrochantericus medius muscles are completely fused, so that this complex is represented by a single muscle-mass, arising from the same area, however, occupied by both muscles in the other dissections. The fusion of these two muscles is an example of the general tendency toward fusion of muscles which arise from adjacent areas and whose fibers are parallel. The common tendon inserts on the femur just distal to the insertion of M. iliotrochantericus posterior. Though there are two distinct tendons of insertion for the three iliotrochanterici muscles, there is an almost continuous line of insertion for a distance of 3 cm., beginning on the trochanter.

MM. VASTUS LATERALIS AND VASTUS MEDIALIS (femoritibialis externus and medius)

There are no significant differences in this complex between the two cranes; see, however, the discussion of "M. femoritibialis externus" below.

M. EXTENSOR ILIO-FIBULARIS (biceps femoris)

This muscle is similar in the two cranes. In the Sandhill Crane the well developed belly arises mostly by fleshy fibers from all but the posterior 1 cm. of the posterior iliac crest. The strong tendon inserts on the fibula 4 cm. distal to the proximal articular surface of that bone.

M. FLEXOR CRURIS LATERALIS (semitendinosus and accessorius semitendinosi)

This complex exhibits a similar configuration in the two cranes. In the Sandhill Crane the semitendinosus muscle arises from approximately the posterior 1 cm. of the posterior iliac crest. The raphe which separates the semitendinosus from the accessory semitendinosus continues downward between pars media and pars interna of M. gastrocnemius to become continuous with the tendon of that muscle; the raphe is ossified about the middle of the belly of M. gastrocnemius. In its course between the two heads of that muscle, the raphe is accompanied by a small fleshy belly, the "distal accessory" head of Fisher and Goodman.

As in the Whooping Crane, there are two distinct parts to the accessory semitendinosus

muscle (Fisher and Goodman, 1955:83). The more proximal part inserts by fleshy fibers on the posterior surface of the medial condyle and the intercondylar region (popliteal region) of the femur, immediately proximal to the common origin of Mm. flexor hallucis longus, flexor perforatus digiti III, and flexor perforatus digiti IV, and the tendon of origin of M. gastrocnemius, pars media. The attachment to the femur is nearly transverse in direction, rather than vertical, as in many birds. The more distal part of the accessorius muscle (distal accessory head) passes lateral to the tendon of insertion of M. flexor cruris medialis (= semimembranosus) and does not insert on the belly of M. gastrocnemius, pars media, as it does in the Whooping Crane.

M. FLEXOR CRURIS MEDIALIS (semimembranosus)

This muscle is similar in the two cranes. The tendon of insertion is intimately fused with the raphe of the accessory semitendinosus and pars media of M. gastrocnemius, just before the latter fuses with the internal head of the gastrocnemius. The muscle inserts by a thin aponeurosis (2.5 cm. long and about 1.5 cm. wide) on the tibiotarsus, beginning about 3 cm. distal to the proximal end of that bone. In the Whooping Crane the tendon inserts "some five centimeters from the proximal end" of the bone.

M. CAUDOFEMORALIS (piriformis)

Fisher and Goodman (1955:85 and 123) emphasized the amount of variation they found in this complex. They found both pars caudofemoralis and pars iliofemoralis in two specimens of the Whooping Crane, but only pars iliofemoralis in a third specimen. In one dissection, they found three parts to the muscle.

I found both parts to this muscle in three specimens of the Sandhill Crane. Pars iliofemoralis is a very thin, triangular sheet of muscle, 2 cm. wide at its base, where it arises primarily by an aponeurosis from the ventral surface of about the middle third of the posterior iliac crest; the belly is approximately 6 cm. in length. It inserts by a fleshy band (about 5 mm. wide) on the lateral surface of the femur, beginning about 3.5 cm. distal to the trochanter and 1 cm. distal to the insertion of M. ischiofemoralis.

Pars caudofemoralis has a small spindle-shaped belly, 8 to 9 cm. long and only about 6 mm. in maximum width. It arises by a small tendon (3 cm. long, but only 0.5 mm. in diameter) from the fascia covering the depressor muscles of the tail; I found no direct bony attachment on the pygostyle. This tendon passes through a bony notch at the most caudal end of the projecting posterior iliac crest; the tendon is held in the notch by a ligament, which completes a fibro-osseous canal. The muscle inserts by a long, flat tendon (2 cm. long and 2 mm. wide) about 3 cm. distal to the trochanter and directly medial to the insertion of pars iliofemoralis.

M. FLEXOR ISCHIOFEMORALIS (ischiofemoralis)

This muscle is well developed in these cranes. In the Sandhill Crane it inserts on the femur about 1 cm. proximal to the insertion of M. caudofemoralis (see above). There is a striking difference in the relationships of the tendons of insertion of M. ischiofemoralis and the two parts of M. caudofemoralis in the Whooping Crane as described and illustrated by Fisher and Goodman (1955:86 and Figs. 30 and 31). They state that M. ischiofemoralis inserts "posterior to and between the insertions of the two parts of M. caudofem." In no genus have I seen the condition illustrated in Fisher and Goodman's Figure 31. In the Sandhill Crane, pars caudofemoralis inserts medial to pars iliofemoralis.

MM. ADDUCTOR SUPERFICIALIS ET PROFUNDUS (adductor longus et brevis)

These two muscles exhibit about the same relative development in the two cranes. M. adductor profundus is entirely fleshy at its origin in the Sandhill Crane and I did

not find a conspicuous "heavy layer of tendon" covering the medial surface of this muscle such as Fisher and Goodman (1955:88) described for the Whooping Crane. The glistening muscular fascia is well developed, however.

M. AMBIENS

Fisher and Goodman (1955:88–89) called attention to the differences in termination of the ambiens tendon in *G. americana* and *G. c. canadensis*. In the former, the ambiens tendon serves as the "principal, if not sole, origin for M. flex. perf. dig. II, although there is strong fascial interconnection between the origins of Mm. flex. perf. dig. II, III, and IV, and in one instance there is actually a branch of the main ambiens tendon that goes to the tibiotarsus." In the Little Brown Crane, "M. ambiens connected distally to the small lateral head of M. flex. perf. dig. III. It had little connection with M. flex. perf. dig. II and none with M. flex. perf. dig. IV."

In the Sandhill Crane, I found that the ambiens muscle arises primarily by a flat tendon from the pectineal process. The small, spindle-shaped belly is 6 to 8 cm. long and less than 1 cm. in maximum width. Distally, a very small tendon (1 mm. wide) forms and has the usual course through the patellar ligament. The tendon then passes distad medial to the biceps tendon and serves as the primary origin for the lateral head of M. flexor perforatus digiti III; the ambiens tendon does not give rise to any other muscle.

M. FEMORITIBIALIS INTERNUS

There are minor differences between the Whooping and the Sandhill cranes in development of this muscle mass and I found variation in the pattern in the three specimens I dissected. In one right leg, the muscle was indistinctly divided into two heads. In another right leg, one long and two short heads were present; each gave rise to a tendon and the three tendons fused for a common insertion. In the other dissections, there were two distinct heads. The posterior or long head arises from the posteromedial surface of the femur, beginning a short distance proximal to the area of insertion of M. iliacus; the origin is fleshy as far as the medial condyle. The short or distal head arises from a small area (about 2 cm. long) on the anteromedial surface of the femur, just above the medial condyle. The small tendon from the latter head fuses with the patellar ligament and with the tendon of the long head; the combined tendon inserts on the medial corner of the tibiotarsus at the base of the inner cnemial crest.

"M. FEMORITIBIALIS EXTERNUS"

As Fisher and Goodman (1955:89–90) imply, there is some confusion concerning the muscle they consider under this name and their M. vastus lateralis. Fisher (1946: Table 42) stated that his M. vastus lateralis was a synonym for M. femoritibialis externus of Gadow and Selenka (1891:154) and Hudson (1937:20). This muscle was discussed earlier by Fisher and Goodman on page 81.

The muscle which Fisher and Goodman call "M femoritibialis externus," I believe is simply a distal head of their vastus lateralis (= femoritibialis externus). I considered this head a part of M. femoritibialis externus in the cuckoos (Berger, 1953:68 and Fig. 6); it was illustrated, but not given a special name. Mitchell (1901:647 and Text-fig. 79) also called attention to this distal part in gruiform birds. In the Sandhill Crane, the distal head of M. femoritibialis externus arises from the posterior and lateral surfaces of the distal half of the femur, posterior to the more distal origin of Fisher and Goodman's vastus lateralis. The tendon of the distal head fuses, in part, with the patellar ligament, but the strongest portion of the tendon passes distad to insert on the outer cnemial crest of the tibiotarsus.

Fisher and Goodman (*loc. cit.*) also state that Gadow and Selenka's (1891:155) "M. femoritib. medius is apparently lacking . . . or is fused to M. femoritib. ext." in the Whooping Crane. However, Fisher (1946: Table 42) placed his M. vastus medialis in synonymy with Gadow's femoritibialis medius, which Fisher and Goodman described on pages 81 and 82. The discussion by Gadow and Selenka (1891:155) of the origin of the femoritibialis complex is not entirely clear, but points out that the femoritibialis medius passes directly to the patella, and, in many birds, the fleshy fibers do insert on the proximal surface of that sesamoid (see Hudson, 1937:20; Berger, 1953:68).

M. OBTURATOR EXTERNUS

Fisher and Goodman (1955:90) said that "Hudson (1937:28) stated that M. obt. ext. had two distinct parts in *G. canadensis*; our dissection of this species showed the separation to be superficial only."

In the Sandhill Crane, also, this muscle may be a single mass or may be partially separated into two heads. It is a broad band of fleshy fibers with a nearly continuous origin from the anterodorsal and anteroventral margins of the obturator foramen. The belly conceals much of the tendon of M. obturator internus. The externus has a broad fleshy insertion (1 cm. wide) on both sides (proximal and distal) of the tendon of M. obturator internus.

M. OBTURATOR INTERNUS

This muscle is triangular in shape. It does not arise inside the pelvic cavity, as it does in *Porzana* and *Coua*. The fibers converge to a tendon, which emerges through the obturator foramen and inserts on the posterolateral surface of the femur, less than 1 cm. from the trochanter.

M. PSOAS (iliacus)

This is a flat, fleshy band about 4 cm. long and 0.5 cm. wide. It arises from the ventral edge of the ilium about 1 cm. anterior to the acetabulum. It inserts by fleshy fibers on the femur for a distance of 1 cm., beginning 1 cm. distal to the neck of the femur, just proximal and somewhat posterior to the origin of M. femoritibialis internus. Fisher and Goodman (1955:90) said that "the condition described by Fisher (1946:670) for the cathartid vultures is found" in the Whooping Crane.

M. GASTROCNEMIUS

The three heads of this complex are, in general, similar in the two cranes. The following specific points may be mentioned for the Sandhill Crane.

Pars externa arises from the lateral condyle of the femur, as described by Fisher and Goodman (1955:91). The tendon of origin is, in part, fused to the biceps loop.

Pars interna has an extensive origin from the medial surface of the inner cnemial crest and from the patellar ligament. In fact, the fibers of M. sartorius and part of those of pars interna insert and arise, respectively, from a tendinous raphe separating the two muscles.

Pars media arises by a flat tendon from the intercondylar (popliteal) area of the femur, just proximal to the common tendon of origin for the long flexors. Fleshy fibers begin about 3 cm. from the femoral origin of the tendon. In the left leg of one specimen, I found an *accessory medial head*. This head (5 cm. long, but less than 1 cm. wide at the origin) arises from the posterior surface of the medial condyle of the tibiotarsus. The belly passes lateral to the inserting tendon of M. semimembranosus and anterior to the tendon of the distal accessory belly of M. accessorius semitendinosi. The belly tapers to a minute tendon, which fuses with the fascia covering the deep surface of pars externa (gastrocnemius) in the area where this head fuses with pars media.

M. PERONEUS LONGUS

Similar in the two cranes, this is a well developed muscle, which conceals all of M. tibialis anterior. The strong tendon of insertion forms as ossified radiating bands on the superficial surface of the belly. The tendon inserts on the tendon of M. flexor perforatus digiti III, 4 cm. distal to the proximal end of the tarsometatarsus. (See also Mitchell, 1913:1053.)

M. TIBIALIS ANTERIOR

Similar in general configuration in the two cranes, the femoral head (whose tendon is ossified) is almost equal in bulk to the tibial head in the Sandhill Crane. The common, ossified tendon bifurcates at the insertion on the tarsometatarsus, about 2 cm. from the proximal end of that bone, but the two tendons insert adjacent to each other.

M. FLEXOR PERFORANS ET PERFORATUS DIGITI II

In general, this muscle is similar in the two cranes. In one specimen of *G. c. tabida*, the belly was not bipinnate. Fisher and Goodman (1955:94) found this muscle "not clearly bipinnate" on one side of a specimen of *G. c. canadensis*. The total length of the belly is about 8 cm.; fleshy fibers extend further distad in the anterior half of the belly. The tendon of insertion is calcified in the region of the crus and tarsometatarsus, but not over the intratarsal joint. Fisher and Goodman found fusion between the tendons of Mm. flexor perforans et perforatus digiti II and flexor perforatus digiti II in *G. c. canadensis* (see also Mitchell, 1901:653), but not in *G. americana*. I did not find such fusion in *G. c. tabida*. The tendon of M. flexor perforans et perforatus digiti II perforates the tendon of M. flexor perforatus digiti II and is perforated by the tendon to digit II of M. flexor digitorum longus, as described by Fisher and Goodman (1955:94).

M. FLEXOR PERFORANS ET PERFORATUS DIGITI III

This muscle has a small (10 cm. long) bipinnate belly. The tendon perforates and is perforated. Hudson (1937:42) and Fisher and Goodman (1955:97) found a vinculum connecting the tendon of this muscle with the tendon of M. flexor perforatus digiti III in *G. c. canadensis*, but Fisher and Goodman did not find such a vinculum in *G. americana*. This vinculum is present in *G. c. tabida*. The vinculum is short (about 0.5 cm. long), but strong, and is located about 3 cm. from the distal end of the tarsometatarsus.

M. FLEXOR PERFORATUS DIGITI IV

The origin and insertion of this muscle in the Sandhill Crane are similar to those described for the Whooping Crane by Fisher and Goodman (1955:96). My specimens also exhibited the peculiar lateral head, which passes distad lateral to the biceps tendon before fusing with the medial head. The bulk of the muscle lies medial to the biceps tendon. Mm. flexor perforatus digiti IV, flexor perforatus digiti III, and flexor hallucis longus have a common origin, fleshy and tendinous, from the intercondylar area of the femur. This common origin is located just distal to the insertion of the accessory semitendinosus muscle and lateral to the origin of pars media of the gastrocnemius.

M. FLEXOR PERFORATUS DIGITI III

In the Sandhill Crane, the posterior head arises as described for the Whooping Crane by Fisher and Goodman. The much smaller lateral head is, in part, a direct continuation of the ambiens tendon, but a long (7 cm.), flat tendinous band, attached proximally to the head of the fibula, fuses with the ambiens tendon, just proximal to the origin of the fleshy fibers of M. flexor perforatus digiti III. This tendinous band is intimately associated with the lateral head of M. flexor perforatus digiti II. The fleshy fibers of the lateral head of M. flexor perforatus digiti III begin about 8 cm. distal to the proximal end of the fibula. There is a well developed vinculum between the tendon

of this muscle and the tendon of M. flexor perforans et perforatus digiti III. The tendon of insertion is perforated by both of the deep flexor tendons.

M. FLEXOR PERFORATUS DIGITI II

This muscle is as decribed for the Whooping Crane by Fisher and Goodman (1955: 97–98). Both heads are present in the Sandhill Crane. The lateral head (about 4.5 cm. long) arises by fleshy fibers from the patellar ligament and associated fascia and from the tendinous band mentioned above. This head is not connected with the ambiens tendon. The medial, or deep, head, about the same length, arises by a flat tendinous band from the femoral tendon of origin of M. flexor perforatus digiti III (part of the tendon is calcified). The inserting tendon of flexor perforatus digiti II is perforated by the tendon of flexor perforans et perforatus digiti II, although the bulk of the tendon inserts on the lateral side of the proximal phalanx, as described by Fisher and Goodman (1955:98).

M. FLEXOR HALLUCIS LONGUS

The origin of this muscle in the Sandhill Crane is the same as Fisher and Goodman (1955:98) described for the Whooping Crane. The relatively small belly (15 cm. long) extends about half way down the tibiotarsus, but it is one of the best developed muscles on the posterolateral aspect of the crus. The tendon of insertion in the Sandhill Crane differs in that it does not pass through a bony canal in the hypotarsus (see also Hudson, 1937:69); it does pass through such a canal in the Whooping Crane (Fisher and Goodman, 1955:99). Fisher and Goodman have pointed out that "in most birds there is some sort of a connection between" the tendons of Mm. flexor hallucis longus and flexor digitorum longus, "but Hudson (1937:48) did not find fusion of them in *Grus* [*c.*] *canadensis* (nor did we); he noted only a vinculum between them, as was the case in one of our Whooping Cranes." In one of my specimens of the Sandhill Crane, however, most of the tendon of flexor hallucis longus fused with the tendon of flexor digitorum longus in the distal one-fourth of the tarsometatarsus. Only a very small branch of the hallucis tendon continued directly to the hallux; this tendon was not ensheathed by the tendon of M. flexor hallucis brevis. Fisher and Goodman also were unable to demonstrate such a perforation of the brevis tendon in *G. americana.* In a second specimen of *G. c. tabida* the tendon of flexor hallucis longus did not fuse with the tendon of flexor digitorum longus, but they were connected by a strong vinculum (representing over half of the hallucis tendon), 4 cm. proximal to the distal end of the tarsometatarsus; the remainder of the hallucis tendon inserted on the hallux. In a third specimen, the two tendons were connected by a weak vinculum (2.5 cm. long), but the hallucis tendon retained its integrity throughout. Mitchell (1901:654) illustrated the considerable intergeneric variation in the pattern of these two deep plantar tendons in several gruiform birds.

M. FLEXOR DIGITORUM LONGUS

In the Sandhill Crane, the belly (13.5 cm. long) of this muscle is slightly shorter than the belly of M. flexor hallucis longus (15 cm.). The lateral head is the larger; the medial head is short and small. The tendon of this muscle alone passes through the single bony canal in the hypotarsus. The insertion is typical.

M. PERONEUS BREVIS

This muscle is poorly developed in the cranes (see Mitchell, 1913:1053). In the Sandhill Crane, the belly is 13.5 cm. long, but it is less than 0.5 cm. wide. The origin begins at the level of insertion of the biceps tendon, as in the Whooping Crane. The insertion is typical (see Fisher and Goodman, 1955:99–100).

M. EXTENSOR DIGITORUM LONGUS

The belly of this muscle is about 14 cm. long, but only 1 cm. in maximum width at the head of the tibiotarsus. The tendon of insertion passes through a bony canal at the distal end of the tibiotarsus, but it is held in place by a ligament on the proximal end of the tarsometatarsus. The general development is the same as described for the Whooping Crane by Fisher and Goodman (1955:100).

M. POPLITEUS

Typical in origin and insertion in the Sandhill Crane, this small muscle is about 2 cm. long and 1.3 cm. wide. It arises on the fibula, inserts on the tibiotarsus.

M. PLANTARIS

This is a very small muscle in the Sandhill Crane. Its belly is about 7 cm. long, but only about 0.7 cm. in maximum width at the proximal end of the tibiotarsus. The minute tendon inserts on the medial corner of the tibial cartilage.

The short toe muscles are very poorly developed in the Cranes (Fisher and Goodman, 1955:102), although I found remnants of the following eight muscles in both legs.

M. EXTENSOR HALLUCIS LONGUS

This is relatively a very small muscle, 5 to 6 cm. long and with a maximum width of but 2 to 3 mm. It seems to arise exclusively from the fascia covering the anteromedial surface of the intratarsal joint. The tendon inserts on the medial side, and not on the dorsal surface, of the distal phalanx of the hallux.

M. EXTENSOR PROPRIUS DIGITI III

This muscle is rudimentary. I found a few fleshy fibers on the anterior surface of the distal half of the tarsometatarsus, but much of the muscle seems to be represented by semitendinous fibers.

M. EXTENSOR BREVIS DIGITI IV

This muscle also is rudimentary. Tendinous and fleshy fibers arise from about the distal third of the tarsometatarsus. The tendon is about 1 mm. wide; it passes through a bony canal between the trochleae for digits III and IV to insert on the medial surface of the base of the proximal phalanx, digit IV.

M. ABDUCTOR DIGITI II

The 3 cm.-long belly is composed of fleshy and tendinous fibers. It arises from the medial surface of the distal end of the tarsometatarsus. The tendon inserts on the medial side of the base of the proximal phalanx of digit II.

M. FLEXOR HALLUCIS BREVIS

This is a minute muscle, 3 to 4 cm. long and with a maximum width of about 3 mm. It arises primarily from the medial surface of the hypotarsus. It has a thin, hair-like tendon about 0.3 mm. wide. It inserts on the base of the hallux and is not perforated by the tendon of M. flexor hallucis longus.

M. ADDUCTOR DIGITI II

This muscle is typical in origin and relationships. The belly is 4 cm. long and 4 mm. in maximum width. It arises at the proximal end of the tarsometatarsus, immediately inferior to the hypotarsal area. The hair-like tendon is about 0.3 mm. wide. It inserts on the dorsomedial surface of the base of the proximal phalanx, digit II.

M. LUMBRICALIS

This muscle shows the poorest development of any of the short toe muscles, and I did not find it in all dissections. When present, it consists of scattered fleshy and

tendinous fibers, located at the distal end of the tarsometatarsus. These insert primarily on the cartilaginous pads for digits III and IV.

M. ABDUCTOR DIGITI IV

This is another minute muscle, having a length of about 4.5 cm. and a maximum width of 3 mm. The tendon is less than 0.5 mm. wide, but it expands distally and inserts on the lateral side of the base of the proximal phalanx of digit IV.

M. ADDUCTOR DIGITI IV

This muscle is not present in the Sandhill Crane, nor in the Whooping Crane (Fisher and Goodman, 1955:102).

SUMMARY

Only two of the 47 major wing muscles are absent in *Grus americana* and in *G. canadensis tabida*: Mm. flexor metacarpi brevis (see page 292) and entepicondylo-ulnaris. Pars propatagialis M. cucullaris (= "dermo-tensor patagii" of Shufeldt, 1890, but not of Fisher, 1946: 574) also is absent. The os humeroscapulare (see page 287) is absent in both cranes. The following similarities of wing muscles in the two cranes deserve special mention: The biceps slip arises from the coracoidal tendon of M. biceps brachii and has a typical insertion on the tendon of insertion of M. tensor patagii longus. Mm. tensores patagii longus et brevis are represented by a single fused belly. M. scapulotriceps has a strong aponeurotic anchor extending from the anterior edge of the belly to the humerus. M. flexor digitorum profundus has a more proximal insertion on digit III (of Fisher) or digit II (of Hudson) than M. flexor digitorum sublimus. The latter muscle, though its belly is very small, is present and similar in each. M. proscapulohumeralis is present in both cranes. M. subcoracoideus has a single head. The tendon of insertion of M. serratus anterior passes between the two heads (pars externa and pars interna) of origin of M. subscapularis. M. deltoideus major has the usual origin from the dorsolateral surface of the scapula and also has an accessory tendinous origin from the scapula caudal to the glenoid fossa. M. expansor secundariorum is well developed in *G. c. tabida* and undoubtedly in *G. americana*. The rudimentary M. anconaeus coracoideus is present in *G. c. tabida* and probably in *G. americana*. M. adductor alae digiti II (adductor pollicis) is an exceptionally well developed muscle, whereas Mm. flexor digiti IV (III), abductor major digiti III (abductor indicis), and flexor metacarpi posterior are poorly developed. M. latissimus dorsi metapatagialis is inconstant in both species.

The following differences between *G. americana* and *G. c. tabida* were noted in the wing muscles: M. pectoralis is divided into a superficial and a deep layer in *G. americana*, but not in *G. c. tabida*. The origins of Mm. latissimus dorsi, rhomboideus superficialis, and rhomboideus profundus are less extensive in *G. c. tabida* than in *G. americana*. There is a dermal component to M. deltoideus major in *G. americana*, but I did not find one in *G. c. tabida*. M.

deltoideus minor apparently has a single head in *G. americana;* it has two heads in *G. c. tabida.* M. serratus posterior is divided into a superficial and a deep layer in *G. americana,* but not in *G. c. tabida.* There are minor differences in the origins of all three serrati muscles. M. abductor alae digiti II (abductor pollicis) has two heads in both cranes; the anconal head arises from the extensor process of the carpometacarpus, the palmar head from the tendon of insertion of M. extensor metacarpi radialis. Fisher and Goodman (1955:68) state that in *G. americana* the palmar head arises, in part, by "tendinous fibers from the inserting tendon of M. tens. pat. longus"; it does not do so in *G. c. tabida.*

I doubt the existence of any separate muscle which might be called "M. proscapulohumeralis brevis." I agree with Hudson and Lanzillotti (1955:43) that M. flexor brevis digiti IV (III) probably is best considered simply a distal part of M. flexor digiti IV (III); that M. abductor indicis brevis is a deep fasciculus of M. abductor major digiti III (abductor indicis); and that M. abductor minor digiti III (abductor digiti II) is a ligament—I know of no bird in which there is a muscle in this position.

The leg muscle formula in the Sandhill Crane is ABC(±)DXYAmV. Mm. iliotrochantericus medius (C) and iliotrochantericus anterior are fused in some specimens. Hudson (1937:69) gave the formula for the Little Brown Crane (*G. c. canadensis*) as ABDXYAmV; I assume that the two iliotrochanterici muscles were fused in his specimen. In two specimens of the Whooping Crane, Fisher and Goodman found the formula to be ABCDXYAm; though they added V to the formula on page 124, they stated (page 97): "we did not find any vinculum between the tendons of M. flex. perf. dig. III and M. flex. perf. et perf. dig. III." In a third Whooping Crane, the formula was BCDXYAm.

The following features common to the Whooping and the Sandhill cranes deserve mention: The accessory semitendinosus muscle has two well developed heads. M. iliotibialis has a large aponeurotic portion in the center of its distal half. Mm. vastus lateralis (= femoritibialis externus) and vastus medialis (= femoritibialis medius) are similar in both cranes; M. vastus lateralis has two distinct heads of origin, one proximal and one distal.

In the Sandhill Crane the tendon of M. ambiens gives rise only to the lateral head of M. flexor perforatus digiti III; in the Whooping Crane the ambiens tendon serves as the "principal, if not sole, origin for M. flex. perf. dig. II." In the Sandhill Crane, M. flexor ischiofemoralis inserts on the femur proximal to the areas of insertion of both parts of M. caudofemoralis. In the Whooping Crane M. flexor ischiofemoralis inserts "posterior to and between the insertions of the two parts of M. caudofem." (Fisher and Goodman, 1955:86); this is a most unusual relationship for these tendons. Fisher and Goodman

(1955:94) found fusion of the tendons of Mm. flexor perforans et perforatus digiti II and flexor perforatus digiti II in *G. c. canadensis*, but not in *G. americana*; I did not find fusion of these two tendons in three specimens of *G. canadensis tabida*. In the Sandhill Crane, only the tendon of M. flexor digitorum longus passes through a bony canal in the hypotarsus; in the Whooping Crane the tendons of flexor digitorum longus and flexor hallucis longus pass through bony canals in the hypotarsus (Fisher and Goodman, 1955:99). I found considerable variation in the amount of fusion between the tendons of Mm. flexor digitorum longus and flexor hallucis longus (see page 299). Unilaterally in one Sandhill Crane, I found an accessory medial head, arising from the proximal end of the tibiotarsus, of pars media, M. gastrocnemius.

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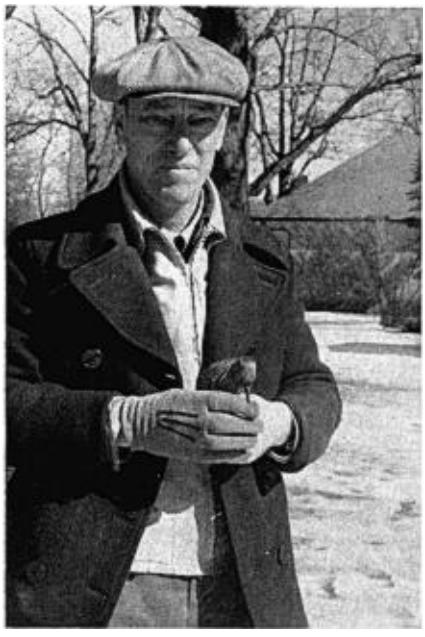

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