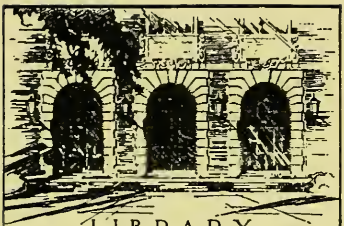

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CONTENTS

The Myology of the Whooping Crane, *Grus americana*

HARVEY I. FISHER and DONALD C. GOODMAN

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The Myology of the Whooping Crane, *Grus americana*

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Preface

The Whooping Crane, *Grus americana* (Linnaeus), has long been an interesting species of the American avifauna. Its size and color, its stately bearing, and its "whooping" call have made it noteworthy. In recent years its rarity and the consequent publicity have caused increased attention from ornithologists and the general populace.

Robert P. Allen (1952) has gathered all the information available for the species and has emphasized the dwindling population. In 1940 only 33 individuals were known. It is possible to be fairly accurate about the numbers because all the birds now winter in a limited area in Texas which has been set aside as the Aransas National Wildlife Refuge, and because these large, white birds are there obvious to any observer. From 1940 there was seemingly a gain of about one bird every three years until 1949, when the total population numbered 37, including two captives. The species has decreased since. With such a low rate of net increase as has been observed and with most losses occurring on migration where protection is difficult, it is perhaps not too pessimistic to regard the Whooping Crane as a nearly extinct species. Its fate may depend in part upon an educational program extending from the Slave Lake region of Canada to the Gulf Coast of the United States. This program might reduce losses such as occurred when two birds died during the fall migration of 1952; one of these had been shot. The loss of these two birds within one month nullified the probable increase of the preceding six years, if we can indeed expect but one individual to be added to the population in every three-year period.

This rarity was one of the reasons the senior author initiated an anatomical study in 1948. Only scattered notes about the morphology of the Whooping Crane can be found in the literature, and most of these are incidental to work on other species. The monographs by Blaauw (1897) and Blyth (1881) on the cranes only mention structure and give nothing of importance to this study. Lowe (1931a and 1931b) published anatomical studies of some gruiform species but nothing in detail on *Grus americana*. The same may be said of Mitchell's papers of 1901 and 1915. Coues (1874), Roberts (1880), Forbes (1882) and many others have noted the invasion of the sternum by the trachea. Ridgway and Friedmann (1941) and Beddard (1898) have summarized some of the known anatomical features of the genus. The latter publication, despite much myological information on other species of the genus, is marked by the absence of any data for the Whooping Crane. Hudson (1937) has reported on the muscles of the leg of *Grus canadensis*. Fürbringer (1888) included the wing musculature of *Anthropoides paradisea* in his monograph, and Gadow (1891) in his myological section referred to *Grus,* and sometimes specifically to *G. leucogeranus* and to *G. canadensis.* A few other minor references to specific information on the genus and species will be discussed where pertinent. Thus it is evident that published information on the structure of *G. americana,* particularly the myology, is virtually nil. With this in mind, it was felt that the species should not disappear, as did the Passenger Pigeon and others, without more complete knowledge of its structure.

Purely from the standpoint of the anatomist working with birds, it was desirable to have a complete myological study. To date there is but one such study of any avian species, Shufeldt's myology of the Raven (1890). Kaupp (1918) has discussed the myology of the chicken, but the treatment is very abbreviated. There are, of course, comparative and descriptive studies of the muscles of various regions of the avian body, but it is impossible to find in any language any other detailed study of all the muscles of one species. It is even impossible to use several papers to piece together for a species a complete work of this nature.

Related to this reason for the study is the fact that the nomenclature of the muscles in birds is in a state of confusion. By careful study of the papers on the different regions, we have tried to introduce a common, stabilizing element into the confusion in naming muscles. In no sense, however, can this study be considered as of primary importance in the homologizing of muscles; our specimens were too few to permit detailed studies of the innervation in most regions.

Another, perhaps the initial, stimulus for our work was the availability in 1948 of the first specimen, incomplete though it was, preserved in alcohol.

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Contents

List of Illustrations

Materials

Preserved specimens, other than skins, of Whooping Cranes are even fewer than the living birds. For example, the senior author, in gathering material for an osteological study of the genera *Grus, Balearica,* and *Anthropoides,* could not locate a single complete skeleton of *Grus americana* and only two that were reasonably complete. Most osteological specimens consist of one or a few bony elements. There is an unverified report that the Senkenberg Museum in Frankfurt has complete skeletons of a male and a female that died in captivity, but we have not been able to check this. It is our belief that the three birds used in this study were the only ones preserved as alcoholic specimens.

In the fall of 1948 the first specimen was received from the United States Fish and Wildlife Service through the courtesy of Mr. Robert P. Allen and Dr. John W. Aldrich. It had been skinned, and the head was missing, as were the entire wing and the leg distal to the knee. For shipment from Texas to the United States National Museum the carcass was frozen. At the museum it was preserved in 70 per cent alcohol for shipment to the University of Illinois. The following information concerning this specimen is taken from a letter of January 18, 1949, to Harvey I. Fisher from Robert P. Allen:

> It is not known when this individual received the original wound that broke the bones of the left wing. It was first noted in December, 1947, when my notes read: "Dec. 14, 1947—Ground inventory. Note on the 'Summer Pair': evidently both of these birds have injured left wing." This was on the Aransas National Wildlife Refuge near Austwell, Texas, where most of the surviving Whoopers winter. This "pair" (They may be merely companions) had spent the summer, and it was now presumed that failure to migrate was a result of injured wings that prevented flight.
>
> A certain percentage of the Texas flock lives outside the refuge area and are subject to illegal shooting by waterfowl hunters in the nearby bays.
>
> This pair became accustomed to whole yellow corn bait as the winter advanced and by this means were kept on Long Pond on the refuge and away from the shore of the Intercoastal Waterway, where they often fed on blue crabs (*Callinectes sapidus*), mud shrimps (*Callianassa*) and other small invertebrates of the region, as well as killifishes, these items comprising their normal winter food. However, on March 14th I left for Louisiana to investigate the status of two captive Whooping Cranes we were holding there and did not return until March 20th. During this brief period the two injured Cranes presumably wandered once more to the shore of the Waterway.
>
> On March 24th this individual of the pair was found lying down on the edge of Salada Pond. Dried blood (at first thought to be dried mud) was noted on its neck and upper breast. When I tried to approach, it walked in labored manner towards Mustang Slough. The next morning, with the help of refuge personnel, the bird was captured. Left wing was hanging heavily, breath was labored, bird thin and weak. We carried it to headquarters, phoned for a vet but the bird died at 11:30 A.M.

With Russel Clapper's assistance the bird was skinned and it was discovered that the neck had been pierced by a bullet, apparently from a .22 calibre rifle. Trachea was shattered and wound clotted. Examination also showed that the old wound had broken humerus completely, the ends being separated by weight of wing so that healing was impossible. The ulna was shattered.

The following measurements were made before skinning:

Weight at time of death	10 lbs. 5 ounces.	
Culmen	133 mm.	
Wing	619 mm.	
Tibia	329 mm.	
Tarsus	278 mm.	
Mid-toe (to "heel")	138 mm.	
Hind toe	30 mm.	
Outside toe	110 mm.	
Inside toe	87 mm.	
Palmation (relaxed)	24.5 mm.	(depth)
Palmation (extended)	38 mm.	
Spread	2209 mm. (87 inches)	
T. L. (contour)	1289 mm.	
T. L. (chord)	1257 mm.	
Base of tarsus (circum.)	1 & ⅞ inches.	
Extreme width of track	7 inches	

Brains weighed 314 grams.

Bird lice, eyeballs and oil gland were sent to Dr. Aldrich in separate containers.

The skeletal remains of this specimen are now No. 347355 in the series of the United States National Museum. Dissection showed it to be a female.

The second specimen (KU No. 31198) was found October 31, 1952, by Mr. Thane S. Robinson. The location was 8.5 miles south of Sharon, Barber Co., Kansas. Mr. Robinson telephoned Dr. E. Raymond Hall who notified Dr. Clarence Cottam of the United States Fish and Wildlife Service. Employees of this service picked up the crippled crane that same day and transported it by truck to Mineral Wells, Texas, where it died November 1. The carcass was then taken to San Antonio. On November 6 the now frozen specimen was flown by pilot Hanson to Topeka, where it was secured by Drs. Tordoff and Hall.

Measurements of this female, taken before skinning, include:

Weight—13.25 lbs.
Chord of wingspan—7 ft.
Chord of wing—612 mm.
Arc of wing—632 mm.
Tarsus—309 mm.
Middle toe with claw—132 mm.
Exposed culmen—152 mm.
Bill from ant. end nostril—90 mm.
Angle of gonys to tip of mandible (= length of gonys in Baldwin, etc.)—66 mm.

No physical injuries could be found when the bird was skinned by Tordoff and Fisher, or even when it was dissected. There was no evidence that the bird had been shot.

In late November, 1952, we received a report that a bird had been shot in Canada and transported to Texas. It subsequently died, was frozen, and shipped to us December 1, 1952. We skinned this female and sent the skin to the National Museum of Canada. The skeleton is preserved at Southern Illinois University. The history of the bird is pieced together in the following excerpts from letters to Harvey I. Fisher:

From Mr. Fred Bard—March 6, 1953:

To review the events that took place when we were notified of the capture of a wounded Whooping Crane at Griffin, Saskatchewan. The bird was apparently seen a week or two earlier by Mr. Orville Blosser, a nephew of Mr. P. E. Barlow of Griffin, a farmer, who saw and caught the Crane on October 30th. The Crane was apparently walking around in a stubble when he spotted it quite early in the morning. He pursued it with the truck, chasing it into a willow bluff in the field. He threw his coat over the bird and picked it up. The bird was placed in the back of his truck and he drove to Weyburn, where he contacted Mr. Jim Mahoney of the Weyburn Branch of the Fish and Game League. Mr. Mahoney 'phoned me reporting the capture of a bird and that it had been injured. I instructed him to call in a veterinarian and do whatever they could for the bird.

When Mr. Lahrman and I lifted the bird from the crate and placed it on the straw, we noticed one leg badly twisted and on examination found the socket joint to be completely through the skin and twisted around in the wrong way. I then contacted Dr. H. L. Watson, a physician and surgeon who agreed to come out and examine the bird. That evening Dr. Watson checked the joint. I had in the meantime set it as best I could and put it in splints. The joint seemed to be properly set and Dr. Watson sutured the tendons and the skin covering the joint; antiseptics were used and the damaged leg joint placed in a cast.

The bird was fed from time to time. The first feeding was a little water, and the next fresh goldeneye fish. It seemed to take these reasonably well, and in a few hours seemed to look somewhat brighter. Later attempts were made with wheat soaked in water, and some milk with aureomycin given by Dr. Watson.

On Sunday afternoon the plane, dispatched from Minnesota with Ross Hanson as the pilot, left Regina with the injured bird for San Antonio Zoo. Mr. Ralph Stueck of Abernathy offered to accompany the bird on this trip to feed and water it and so relieve the pilot of these duties.

From Mr. Rossalius C. Hanson—February 6, 1952:

Mr. Bard, or his associates, picked up the crippled Whooper from a rancher in the vicinity of Weyburn, Sask. The bird, at that time, had a crippled left wing and broken left leg. The wing injury appeared to be a shot wound, while the leg injury was believed sustained during capture by the rancher. He had an M.D. work on the bird and they amputated the wing at the wrist and set the leg in a cast. The bird was treated with penicillin and oral aureomycin. At the time I picked up the bird it had a bad rattle in its throat, indicating a respiratory condition. This may have been due partially to the administering of the oral aureomycin with a syringe and on the other hand it may have been an outcome of the bird's lowered resistance.

During the flight from Regina to San Antonio the bird was force-fed, but regurgitated most of the food during the trip. It retained some meat particles fed it on the second day of the trip. Soaked wheat and eggs were not retained. The bird was picked up on Nov. 2, by myself at Regina, and deposited at the San Antonio Zoo on Nov. 4. No drugs were administered during the flight. The bird was in a very weakened condition at the start and during the flight did not show any improvement.

I delivered the bird to Mr. Fred Stark, Director, San Antonio Zoo, San Antonio, Texas and he administered to the bird from then on.

From Dr. Clarence Cottam—December 24, 1952:

Unfortunately, I do not have the exact date it died, but it was within a day or so of November 6.

No measurements of significance could be made from this last specimen which was badly emaciated and had a wing amputated at the wrist as well as a broken leg.

Acknowledgments

Our appreciation goes to Mr. Robert P. Allen of Tavernier, Florida, for preserving the original specimen which was the major impetus in initiating this work, and to Dr. John W. Aldrich of the United States Fish and Wildlife Service for sending the specimen to the senior author. Dr. Harrison Tordoff and Dr. E. R. Hall of the Museum of Natural History, University of Kansas, were responsible for our receiving the second specimen. Dr. Tordoff aided the senior author in skinning the bird in such a way as to make possible the preservation of a complete skin and a complete skeleton. He also supplied measurements and other data. Mr. Thane S. Robinson first located this bird in the field.

We wish to thank the Canadian government for granting permission for us to retain the carcass of the Saskatchewan bird. Dr. Clarence Cottam of the United States Fish and Wildlife Service made all the arrangements. Acknowledgment of aid rendered is also due Mr. Orville Blosser of Griffin, Saskatchewan, Mr. Fred G. Bard, director of the Provincial Museum of Saskatchewan, Mr. Rossalius C. Hanson of Winona, Minnesota, and Mr. Fred W. Stark, director of the San Antonio Zoo and Aquarium. All these individuals took part in the capture or care of this bird.

Dr. Robert W. Storer of the Museum of Zoology, University of Michigan, kindly sent a Little Brown Crane to us.

Mr. Charles A. McLaughlin of the Zoology Department, University of Illinois, inked and labeled the final drawings, and we are grateful for his skill and patience.

Finally we express our gratitude to the Research Board of the Graduate College, University of Illinois, for enabling the junior author to participate in the work in 1952 and 1953. His contribution as a research assistant was in part the result of financial support by the Board.

Methods

Dissection proceeded very slowly and copious notes were taken on all organ systems. We attempted to gather all possible information. However, having only three specimens, it was not possible to treat all systems completely; some structures were invariably displaced and ruptured in work on other features. For example, innervations in the head region could not be studied without destroying muscles, and it was not simply a matter of taking off a layer of muscle and the attendant nerves. Life-size, or in many instances twice life-size, scale drawings were made as we dissected.

One major difficulty was that all specimens had been frozen before we received them. In frozen condition the tissues are very brittle and easily broken by any strain; such breakage was sometimes extensive in the neck, axillary, and pubic regions. Often it was necessary to study all three specimens to obtain a clear picture of the muscles in a region.

In general, the procedure was as follows: As the first bird was dissected, notes and drawings were made. Subsequent work on the other birds was compared with these notes and drawings. Any variations between individuals or between sides of the same individual were recorded in notes and drawings. Finally, a rough manuscript was prepared and checked against all dissection notes and drawings. The final drawings represent composites in part, for we have tried in most instances to illustrate the "usual" condition, but all the illustrations are made from specimens of *Grus americana* and to accurate scale.

As discussed previously, the nomenclature of avian muscles is difficult. With one exception (M. dermoglossus), we have not introduced any new names. We have tried, by careful study and comparison, to use the most appropriate names already in literature. For names of muscles in the wing, tail, and leg we have followed Fisher (1946), who prepared comparative tables of their nomenclature. For the rest of the muscles we have included similar lists of names at the beginning of the appropriate section. The order of discussion of muscles in each section follows the sequence of listing in the table.

The osteological terminology follows Howard (1929).

Both authors have been active in all aspects of this anatomical study. No part can be said to be entirely the work of either one. Any part first done by one of us has been checked in detail by the other, on the same or subsequent specimens.

Muscles of the Skull and Jaws

The muscles are listed here in the sequence followed in the text.

M. dermo-temporalis
M. dermo-temporalis—Shufeldt (1890:5-6)
part M. cranio-cervicalis—Edgeworth (1935:283)

M. cucullaris, caput portion
M. cucullaris, kopftheil—Fürbringer (1888:1056), Gadow (1891:107-109)
M. complexus—Gadow (1891:107-109), Shufeldt (1890:263-286), Palmgren (1949:194-195)
M. complexus—Boas (1929:189-193)

M. biventer cervicis
M. biventer cervicis—Shufeldt (1890:270-272), Gadow (1891:107-109), Boas (1929:161-164)
M. biventer—Palmgren (1949:194)

M. splenius capitis and *M. splenius accessorius*
M. rectus capitis posticus major—Shufeldt (1890:268-270)
M. rectus capitis posticus—Gadow (1891:112)
M. splenius capitis—Boas (1929:164-169), Palmgren (1949:194-195)

M. depressor mandibulae
M. biventer maxillae—Shufeldt (1890:18-19)
M. digastricus s. depressor mandibulae—Gadow (1891:318-319)
M. depressor mandibulae—Edgeworth (1935:109), Hofer (1950)

M. rectus capitis lateralis
M. rectus capitis anticus minor—Shufeldt (1890:265-266)
M. rectus capitis anticus minor s. lateralis—Gadow (1891:120-121, pl. 18a)
M. rectus capitis lateralis—Boas (1929:194), Palmgren (1949:202)

M. rectus capitis superior
M. rectus capitis lateralis plus M. trachelo-mastoideus—Shufeldt (1890: 289-290). Shufeldt must have been partly in error in thinking that the M. longus lateralis cervicis et capitis of Gadow was the same as these muscles of Shufeldt's description. These muscles may correspond in part to the capitis part of Gadow's muscle. The remainder of M. longus lateralis cervicis et capitis compares well with the M. obliquus colli slips described and figured by Shufeldt.
part M. spinalis cervicis plus part M. longus lateralis cervicis et capitis—Gadow (1891:110, 116-117)
M. rectus capitis superior—Boas (1929:195-196)

M. rectus capitis ventralis
lateral part
not described: ?part M. flexor capitis inferior—Shufeldt (1890:267-268)
part M. rectus capitis anticus major s. medialis—Gadow (1891:120, pl. 18b)
M. rectus capitis ventralis—Boas (1929:194-195), Palmgren (1949: 202-203)
medial part
part M. flexor capitis inferior—Shufeldt (1890:267-268)

part M. rectus capitis anticus major s. medialis—Gadow (1891:120)
M. rectus capitis ventralis—Boas (1929:194-195), Palmgren (1949: 202-203)

M. flexor colli brevis
?part M. rectus capitis lateralis—Shufeldt (1890:289)
? M. lateralis colli—Gadow (1891:119)
M. flexor colli brevis—Boas (1929:196-197)

M. flexor colli profundus
?part M. longus colli (inferior oblique part?)—Shufeldt (1890:287-288)
part M. longus colli anticus—Gadow (1891:118-119)
M. flexor colli profundus—Boas (1929:197)

M. adductor mandibulae externus superficialis
part M. temporal—Shufeldt (1890:16)
parts 1 and 2 M. temporalis—Gadow (1891:320-321)
part M. adductor mandibulae externus—Edgeworth (1935:58-60)
M. adductor mandibulae externus superficialis—Lakjer (1926:45-46), Hofer (1950:438-468, fig. 15, A. e. sf. and A. e. sf. b.)

M. adductor mandibulae externus profundus
part M. temporal—Shufeldt (1890:16)
?part 3 M. temporalis—Gadow (1891:322)
part M. adductor mandibulae externus—Edgeworth (1935:58-60)
M. adductor mandibulae externus profundus—Lakjer (1926:46), Hofer (1950:464)

M. adductor mandibulae medius
part M. temporal plus M. pterygoideus externus—Shufeldt (1890:16, 20-21)
M. ethmo-maxillaris plus M. quadrato-maxillaris—Gadow (1891: 322-323)
? M. adductor mandibulae posterior plus ? M. pseudotemporalis profundus—Lakjer (1926:54-55, 63-65)
part M. adductor mandibulae medius—Edgeworth (1935:58-59)
?deep part M. pseudotemporalis (M. quadrato-mandibularis)—Hofer (1950:478)

M. adductor mandibulae externus medialis
part M. temporal plus M. masseter—Shufeldt (1890:16)
parts 1, 2 and ?3 M. temporalis—Gadow (1891:320-322)
part M. adductor mandibulae externus—Edgeworth (1935:58-60)
M. adductor mandibulae externus medialis—Lakjer (1926:46), Hofer (1950:438-468)

M. pseudotemporalis
part M. temporal—Shufeldt (1890:16)
M. spheno-maxillaris—Gadow (1891:323)
M. pseudotemporalis superficialis—Lakjer (1926:63-65)
part M. adductor mandibulae medius—Edgeworth (1935:277)
? superficial part M. pseudotemporalis—Hofer (1950:468-477)

M. pseudotemporalis bulbi
M. pseudotemporalis bulbi—Lakjer (1926:figs. 124, 127)

M. pterygoideus ventralis
part M. pterygoideus internus—Shufeldt (1890:20)
part Mm. pterygoidei—Gadow (1891:323-325)
ventral part M. adductor mandibulae internus—Edgeworth (1935:58, figs. 605c, 607)
M. pterygoideus ventralis—Lakjer (1926:65-67), Hofer (1950:481-495)

M. pterygoideus dorsalis
- part M. pterygoideus internus—Shufeldt (1890:20)
- part Mm. pterygoidei—Gadow (1891:323-325)
- dorsal part M. adductor mandibulae internus—Edgeworth (1935:58, fig. 605c)
- M. pterygoideus dorsalis—Lakjer (1926:65-67), Hofer (1950:481-495)

M. protractor pterygoideus
- ?part M. entotympanicus—Shufeldt (1890:19-20)
- part 4b M. temporalis (M. orbito-pterygoideus)—Gadow (1891: 319-323, pl. 27 fig. 4)
- M. protractor pterygoideus—Lakjer (1926:23-25), Hofer (1950: 432-438)
- part M. spheno-pterygo-quadratus—Edgeworth (1935:57)

M. protractor quadratus
- ?part M. entotympanicus—Shufeldt (1890:19-20)
- part 4a M. temporalis (M. orbito-quadratus)—Gadow (1891:319-323, pl. 27 fig. 4)
- M. protractor quadratus—Lakjer (1926:23-25), Hofer (1950:432-438)
- part M. spheno-pterygo-quadratus—Edgeworth (1935:57)

M. dermo-temporalis

Figure 1 shows M. dermo-temp. arising from the same fascial layer that forms part of the origin of M. depress. mandib. This fascia is attached to the outer face of the opisthotic process, posterior and dorsal to the external auditory meatus. From the origin the muscle, which is about 3.5 centimeters in length, courses postero-dorsad across the anterior part of M. rectus cap. lat., the most dorsal part of M. geniohy., and the side of the middle of the length of the caput part of M. cucullaris to insert on the skin near the mid-dorsal line over the articulation between the second and third cervical vertebrae.

M. cucullaris, caput part

It may be observed in figures 1 and 4 that the cephalic part of M. cucullaris lies dorsally on the neck just posterior to the head but passes postero-ventrad to assume a lateral and even a ventral position at the posterior end of cervical vertebra number 4. It is a thin sheet of muscle with much aponeurotic connection to the underlying muscles and, in the dorsal midline, to its counterpart of the opposite side.

Origin.—Although there is much fascial connection posteriorly, particularly in the dorsal half of the neck, the primary origin is from the diapophysis of the fourth cervical vertebra. It is difficult to be more specific regarding the origin because of the intimate relationship of fascial elements in this area.

Insertion.—Anteriorly the muscle attaches to the most superficial part of the occipital crest from the midline laterad. The medial part of the insertion is immediately superficial to the insertion of M. biventer cerv., and the lateral part to the insertion of M. splenius cap. (fig. 4).

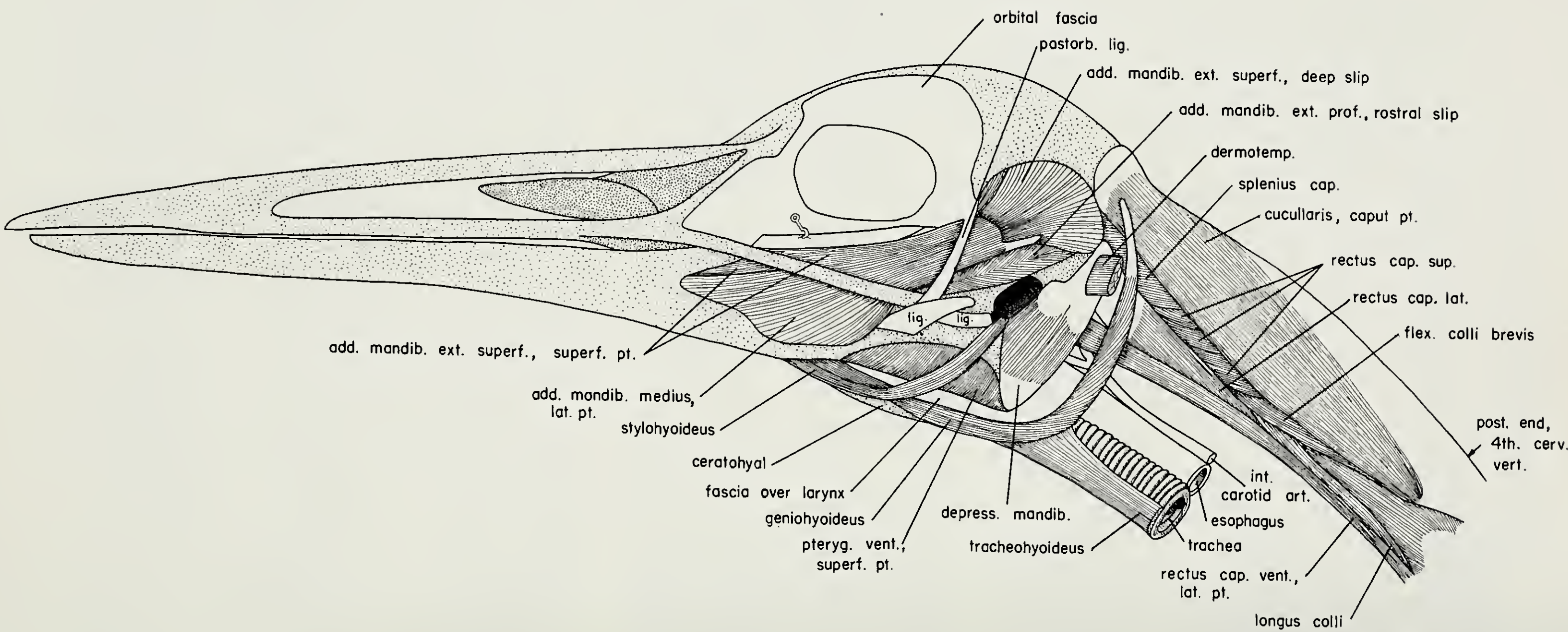


Fig. 1. Lateral view of the superficial muscles of the head and throat, and vertebral muscles associated with the head.

M. biventer cervicis

The long, attenuated muscle is fleshy in the anterior 4 centimeters of its length but at the posterior end of the second cervical vertebra a long, thin tendon is formed (fig. 3). The tendon goes posteriorly on the neck just lateral to the midline. Anteriorly the muscle lies between the sheets of muscle making up the caput part of M. cucullaris and M. splenius cap. In the middle of the length of the twelfth cervical vertebra the tendon becomes fleshy and forms a belly of the same proportions as the anterior belly. The posterior belly extends to the middle of the fifteenth vertebra, where a tendon is again formed.

Origin.—The posterior end of the tendon just mentioned arises from the anterior edge of the neural crest of the sixteenth cervical vertebra and is closely associated with other muscles attaching here.

Insertion.—Tendinous and fleshy insertion is made on the occipital crest just lateral to the midline and deep to the insertion of the cephalic part of M. cucullaris; it is about 0.5 centimeter wide (fig. 4).

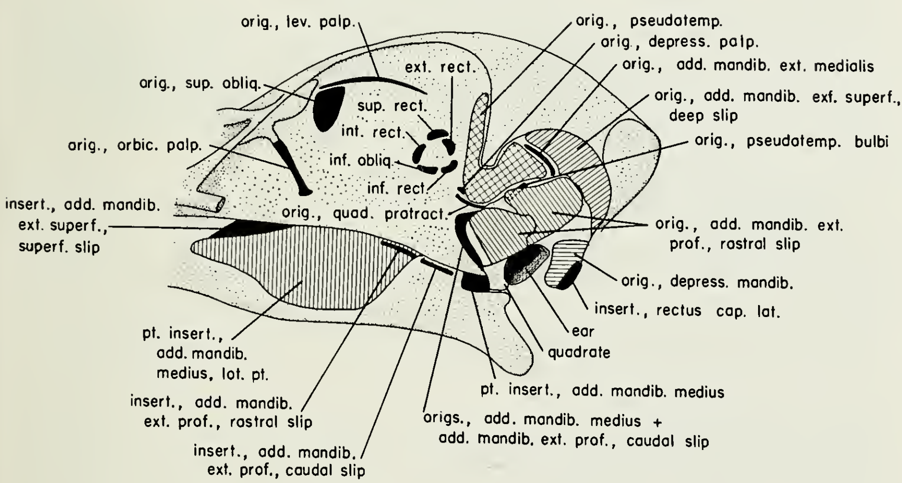


FIG. 2. Diagram of the muscular attachments on the skull and lower jaw.

M. splenius capitis

The thick, triangular belly lies on the dorso-lateral part of the vertebral column over the atlas and axis (figs. 1, 3). It is, for the most part, covered by the caput part of M. cucullaris and M. biventer cerv. The antero-ventral portion of the muscle lies just beneath the insertion of M. rectus cap. lat., while the postero-lateral edge covers parts of Mm. splenius access. and rectus cap. sup.

Origin.—There is fleshy and tendinous origin from the side of the neural crest of the axis and from fascia overlying the atlas and extending to the foramen magnum. On the axis the origin is dorsal to the middle of the belly of M. splenius access. and to the Mm. interspinales arising from the antero-ventral part of the crest (fig. 3).

Insertion.—A wide line of fleshy insertion (fig. 4) is present in the dorsal part of the occipital region and extends ventro-laterally on to the base of the opisthotic process. At its ventral end the insertion is medial to the insertion of M. rectus cap. lat. and the dorso-lateral part of the origin of M. depress. mandib. and is almost continuous with the heavy, medial origin of this same muscle.

M. splenius accessorius

Although the muscle does not connect directly with the skull, it is included here because it is apparently a part of the splenius complex (figs. 3, 5). It is a flat band which is covered anteriorly by M. splenius cap. and which overlies the anterior end of the M. spinalis cerv. complex; it runs from the third cervical vertebra to the atlas. The dorsal edges of the second and third fasciculi of M. rectus cap. sup. lie under the ventral border of the anterior half of M. splenius access.

Origin.—The lateral surface of the neural crest of the third cervical vertebra provides fleshy and tendinous origin.

Insertion.—The insertion is primarily tendinous on the posterior surface of the most ventral and lateral extent of the atlas (fig. 5), and contiguous with the ventral edge of the interspinales muscles.

M. depressor mandibulae

In figure 1 the muscle may be seen to lie across the suspension of the lower jaw; the medial part of the muscle is best illustrated in figure 7. Posteriorly and distally the lateral and medial parts are inseparably fused, but the inserting tendon of M. rectus cap. lat. forms the separation in the dorsal part. Deep to the medial part is the ligamentum mandibulae.

The antero-ventral edge is in contact with M. pteryg. vent., and M. stylohy. arises just anterior to the anterior edge of the belly of M. depress. mandib. Above the origin of M. stylohy., M. depress. mandib. is separated from the external auditory meatus only by the membrane lining this canal. It would seem that any swelling of the belly, as when the muscle contracts or the posterior end of the mandible arcs dorsad, would tend to close the opening of the ear. The dorsal fascial part of the lateral portion is in part covered by M. dermo-temp.

Origin.—The extent of the origin from the postero-lateral area of the occipital region and the posterior face of the opisthotic process may be observed in figures 2 and 4. On the lateral surface of the process the origin is tendinous and fleshy, but it goes dorsad as a tendinous aponeurosis to the level of the deep slip of M. add. mandib. ext. superf. From the most ventral and medial tip of the opisthotic process, a strong tendon forms a major part of the origin of the deeper, medial portion of the muscle; in fact, many of the tendinous fibers pass through the fleshy belly and thus go from origin to insertion and serve as a ligament.

Insertion.—The superficial and most ventral part of the insertion is tendinous on the postero-ventral corner of the lateral surface of the mandible. The primary insertion is fleshy on the entire area of the posterior end of the mandible, bordered anteriorly by the posterior end of M. pteryg. vent. (fig. 1).

M. rectus capitis lateralis

The asymmetry visible in the Mm. recti cap. vent. is not so evident in the present muscles. On the left side the belly of M. rectus cap. lat. is intimately connected with the deep lateral edge of the belly of M. rectus cap. vent., probably as a secondary effect of the asymmetry of the latter

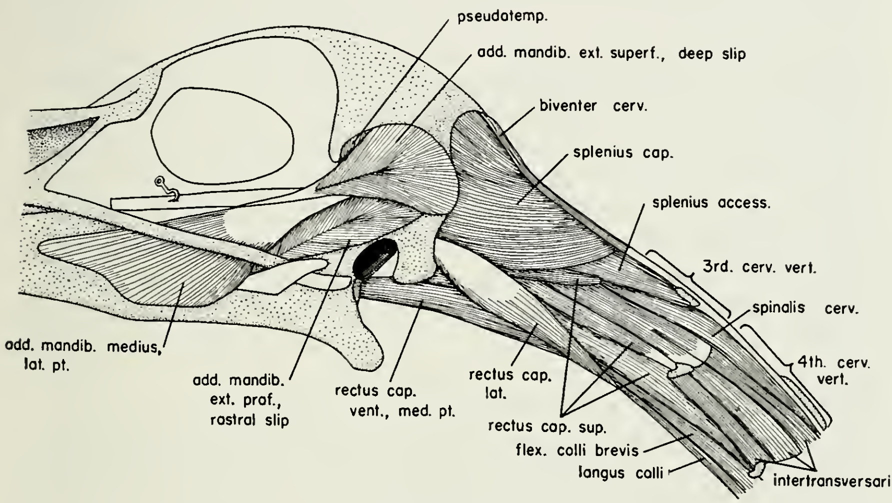


FIG. 3. Lateral view of a second layer of muscles of the head and the anterior vertebral region.

muscle. On the right these two recti muscles are separate and distinct. In lateral view the single slip of M. rectus cap. lat. emerges from the neck musculature just dorsal to the lateral part of M. rectus cap. vent. (figs. 1, 3, 7) and ventral to the various slips of M. rectus cap. sup.

Origin.—There is fleshy and fascial origin from the ventro-lateral corners of the hypopophyses of cervical vertebrae 3 and 4.

Insertion.—A heavy tendon attaches to the posterior face of the base of the opisthotic process, deep and posterior to the lateral origin of M. depress. mandib. (figs. 2, 3, 4) and superficial in part to the most lateral edge of M. splenius cap.

M. rectus capitis superior

The muscle complex to be considered consists of five different fasciculi which arise from the first five cervical vertebrae and extend to the ventro-lateral region of the head (figs. 1, 3, 5, 6, 7). They are arranged serially so that the most dorsal goes anteriorly from the atlas and the most ventral and posterior slip comes from the fifth vertebra. From this description it is apparent that the slips increase in length from anterior to posterior in the series. In lateral and dorsal view the bundles are variously covered by M. splenius cap., the caput part of M. cucullaris, and M. rectus cap. lat. On the ventral side they are deep to the latter muscle and to the lateral part of M. rectus cap. vent.

Origin.—Fasciculus number 1, the most anterior and dorsal, arises from the most lateral extent of the anterior surface of the postzygopophyseal area of the atlas. Number 2 comes from the same part of the postzygopophyseal process of the axis, but its origin goes forward on a mid-lateral line on the body of this vertebra. The same part of vertebra 3 gives rise to slip 3 which is twice as large as slips 2 and 4; the origin is completely tendinous and continues anteriorly across the joint between vertebrae 2 and 3. There is fleshy origin from the ventro-lateral corner of the centrum of vertebra 2 and beneath the origin of the second part of the muscle complex. Part number 4 has fleshy and tendinous origin from the lateral tip of the transverse process of vertebra 4; the origin is closely interconnected with the fascia giving rise to the Mm. intertransversarii. Bundle 5 arises fleshily from the anterior edges of the posterior zygopophyseal processes of vertebrae 3 and 4 and from a mid-lateral line on the centrum of vertebra 4; there is also tendinous origin from the anterior edge of the transverse process of vertebra 5. The deep surface of this fifth part of M. rectus cap. sup. gives off a small slip antero-mediad.

Insertion.—The four most anterior slips insert tendinously and in common on the lateral three-fourths of the length of the posterior edge of the basitemporal plate (figs. 4, 8). The fifth and by far the largest slip inserts tendinously on the most antero-lateral corner of the axis and the postero-lateral aspect of the atlas. There is heavy fascia covering the articulation between the first two cervical vertebrae and attaching anteriorly to the base of the skull; the fifth slip uses this as part of its insertion. Hence the functional insertion of the slip is at least in part on the middle of the posterior edge of the basitemporal plate.

M. rectus capitis ventralis

The muscles of the two sides are not symmetrically arranged; on each side of the ventral aspect of the neck the muscle consists of a medial and a lateral part. On the left side the posterior end of the lateral portion extends fleshily to the caudal end of the fifth cervical vertebra; on the right side it goes only to the fourth vertebra. This asymmetry is also visible in the medial parts of the muscles; the left goes to the fourth vertebra and the right to the third. The variation between sides is apparently correlated with the position of the trachea. Superficial to the caudal end of the right M. rectus cap. vent. the trachea moves from its position on the right side of the neck to a ventral location (fig. 9).

In figure 7 it may be observed that the lateral part is superficial to M. rectus cap. lat. and is separated from its opposite member by the paired veins; this separation is only superficial, for along the posterior two-thirds of their dorsal edges the muscles meet in the midline. Where the two medial parts are side by side they are inseparable. Although in their posterior parts the lateral and medial slips are distinct, they are more or less fused opposite and anterior to the region of M. depress. mandib. (figs. 1, 3, 7).

Origin.—The left lateral part comes from the hypopophyses of cervical vertebrae 4 and 5 (sometimes 6 as well) and from the midventral line of the centra between these hypopophyses. The anterior end of this line is continuous with the posterior end of the line of origin of the medial part, which latter origin continues on this line to the base of the skull.

The right lateral part takes its principal origin from the hypopophysis of vertebra 4 but may extend on to number 5. The medial part on this side is similar in its origin to that on the left except that it goes posteriorly only as far as the hypopophysis of the third vertebra.

Insertion.—The lateral parts of this pair of muscles insert tendinously on the posterior surface of the occipital process (fig. 8), and the medial parts attach fleshily to the entire area of the basitemporal plate (figs. 7, 8). There may be tendinous insertion at the apex of the basitemporal plate.

M. flexor colli brevis

Topographically the muscle could be considered as slips of the M. rectus cap. sup. complex (figs. 1, 3, 5, 6). However, its anterior end does not reach to the head. Consequently, functionally at least, it is a separate muscle. It lies posterior and ventral to the most posterior slip of the superior rectus group and is just dorsal to the cephalic end of M. longus colli. In its passage antero-ventrally it traverses the most ventral and lateral parts of the Mm. intertransversarii present here.

Origin.—The origin is in three parts. The most anterior comes from the ventro-lateral corner of the entire length of the axis, beneath the anterior end of the posterior fasciculus of M. rectus cap. sup., and from the anterior end of the third cervical vertebra. Origin 2 is on the lateral end of the transverse process of the fifth vertebra, virtually in common with, but deep to, the origin of the posterior parts of M. rectus cap. sup. The last origin is tendinous from the end of the transverse process of the sixth vertebra and is superficial to the ventral edge of the Mm. intertransversarii (fig. 6).

Insertion.—The most anterior insertion is fleshy on the dorso-lateral edge of the anterior end of the most posterior slip of M. rectus cap. sup., which in turn attaches primarily to the atlas. The other slips of this flexor insert, one above the other, on the most posterior area of the transverse process of the third cervical vertebra. At its insertion the more posterior of these parts is fused with the anterior part of M. longus colli (fig. 6).

M. flexor colli profundus

This group of fasciculi (fig. 6) has sometimes been considered a part of M. longus colli. It does in fact replace M. longus colli on vertebrae 2 and 3 and coexists with this muscle on vertebrae 4 and 5. There are six distinct bundles of fibers constituting M. flex. colli prof., which is the deepest of the ventral muscles in the anterior part of the neck.

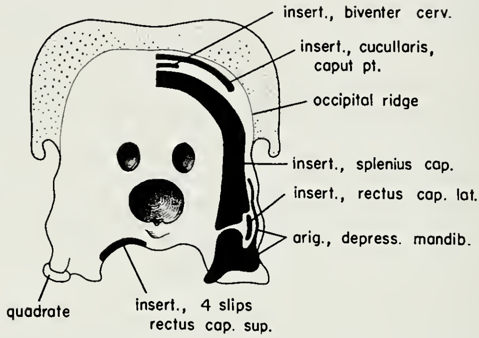


FIG. 4. Diagram of the muscular attachments on the posterior end of the skull.

Origin.—The anterior part (slip 1) arises fleshily from the lateral part of the antero-ventral surface of the transverse process of vertebra 3. Slip 2 comes from a more medial and posterior part of the same process (fig. 6). Number 3 takes fleshy origin from the antero-ventral edge of the transverse process of the fourth vertebra and from the ventro-lateral corner of the centrum of the third vertebra. The fourth slip, counting from the anterior end of the complex, originates as a fleshy and tendinous belly from the transverse process and anterior part of the centrum of vertebra 5 and from the side of the posterior end of the centrum of the fourth vertebra. Bundles 5 and 6 come from the ventral surface of the antero-lateral corner of the sixth vertebra, and to a lesser degree from the same surface of the postero-lateral corner of vertebra 5 (fig. 6).

Insertion.—Slips 1 and 2 insert fleshily on the ventral part of the anterior end of the axis (fig. 6); the attachment of number 1 is dorso-anterior to that of number 2. Number 3 goes tendinously to the posterior end of the hypopophysis of the axis. Four inserts tendinously on the postero-lateral corner of the hypopophysis of the third cervical vertebra. Number 5 attaches to the same place on the fourth vertebra, in common with the second most anterior slip of M. longus colli. Slip 6 inserts on the same area of vertebra 5.

M. adductor mandibulae externus superficialis

The nomenclature of the muscles of the adductor and pterygoideus groups is in a state of vast confusion, despite the major studies by Lakjer

(1926), Edgeworth (1935), Fiedler (1951), and Hofer (1951). Because of interspecific variation and lack of agreement between previous workers it is virtually impossible to assign names with confidence. We agree with Beecher (1951:415) that "the jaw musculature appears confusing when fully labelled . . . ." We have not, with our few specimens, conducted any independent investigations of homologies, and we only use the existing names (pp. 7-9).

The most superficial of the adductors is M. add. mandib. ext. superf., which has two parts—a superficial and a deep layer. The outer layer does not always cover the dorsal part of the deep layer (fig. 1), lies just beneath and somewhat posterior to the eye, and is parallel and anterior to M. add. mandib. ext. prof. At its antero-ventral extent it is immediately anterior to the outer part of M. add. mandib. medius. The deep pinnate fasciculus of M. add. mandib. ext. superf. (figs. 1, 3) in some specimens is the most superficial muscle of the upper part of the temporal fossa; Mm. pseudotemp., add. mandib. ext. medialis, and add. mandib. ext. prof. are deep to it. In its distal part the muscle is covered by the superficial part of M. add. mandib. ext. superf. and by the lateral part of M. add. mandib. medius.

Origin.—The superficial layer originates from the fascia overlying the middle of the length of the deep layer and from a tendon which passes beneath the postero-ventral part of the deep layer to attach to the posterior rim of the temporal fossa. The deep part comes fleshily from an extensive area of the dorso-posterior region of the temporal fossa (fig. 2).

Insertion.—The superficial fasciculus inserts tendinously and fleshily on the dorso-lateral edge of the mandible for a distance of 1 centimeter, starting just anterior to the anterior edge of the dorsal part of the insertion of the external part of M. add. mandib. medius. (figs. 2, 7). This attachment continues forward, on the dorsal rim of the mandible, to the region of the junction of the maxillary and quadratojugal bones where it ends on the connective tissue in the corner of the mouth. Laterally the insertion is dorsal to the anterior part of the insertion of the external portion of M. add. mandib. medius.

Immediately ventrad to the postorbital process of the skull, the bipinnate belly of the deep slip forms a calcified tendon (fig. 3) which inserts on the coronoid process of the mandible between the two layers of M. add. mandib. medius (fig. 5). The insertion is posterior to the insertion of the superficial slip.

M. adductor mandibulae externus profundus

The muscle has two parts—a rostral and a caudal (figs. 1, 3, 5). Other than the posterior part of M. add. mandib. medius (?M. add. mandib. post. of Lakjer, 1926) this is the most posterior of the external adductor muscles. It is posterior and in antero-ventral part deep to M. add. mandib. medius. The dorsal end of the rostral part is covered by the deep slip of

M. add. mandib. ext. superf. and in turn completely covers the caudal part. The rostral slip is bipinnate (figs. 1, 3) and the caudal slip simple (fig. 5).

Origin.—Figure 2 shows the fleshy origin of the rostral slip from the postero-ventral area of the temporal fossa and from the dorso-lateral surface of the orbital process of the quadrate. Beneath the fleshy origin there are several strong bands of calcified tendon which extend from origin to insertion; some of these come from the antero-dorsal part of the suprameatic process.

The anterior edge of the orbital process of the quadrate provides fleshy origin for the caudal slip (fig. 2); the area is limited to the ventral half of this edge, for the posterior slip of M. add. mandib. medius arises from the dorsal half and is continuous and inseparable from the dorsal end of the caudal part of this profundus muscle.

Insertion.—The rostral slip inserts tendinously on the dorso-lateral corner of the mandible, beneath the middle of the orbital fossa, deep and dorsal to the insertion of the main, external body of M. add. mandib. medius, and anterior to the insertion of the caudal fasciculus. The posterior end of the line of attachment is 2 centimeters from the posterior end of the mandible. See figure 2 for an illustration of both insertions.

M. adductor mandibulae medius

As we understand the conformation of the muscle, it consists of a medial and a lateral part, which together make this the largest of the jaw adductors. The lateral part may be seen external to the mandible (figs. 1, 3, 7), and the medial slip is beneath the eye as the deepest of all adductors in this area (figs. 5, 7, 8). The lateral part is, in its dorsal half, deep to the superficial fasciculus of M. add. mandib. ext. superf. Its disto-anterior edge is in contact, on the outer surface of the mandible, with this superficial fasciculus; its posterior border is over the M. add. mandib. ext. prof. In some specimens the postero-ventral corner is in contact with the superficial part of M. pteryg. vent. The lateral and medial parts are separated on the dorsal ridge of the mandibular ramus by the insertions of both fasciculi of M. add. mandib. ext. superf. and by that of the rostral bundle of M. add. mandib. ext. prof. (figs. 2, 5).

Origin.—A calcified tendon from the postero-ventral part of the squamosal bone, but primarily from the post-temporal process of this bone, constitutes the origin of the lateral part (fig. 3). The tendon is deep to the ventral edge of the deep part of M. add. mandib. ext. superf. and immediately dorsal and superficial to the upper edge of the rostral slip of M. add. mandib. ext. superf. The medial part arises fleshily from the dorsal part of the lateral face and from the anterior surface of the orbital process of the quadrate (fig. 2); the medial area of this process provides some fleshy origin. The dorsal part of the fleshy origin is overlaid by heavy fascia. Since M. pseudotemp. inserts on the dorso-medial edge of the medial part, it should probably be considered a part of the origin.

Insertion.—The lateral part inserts directly on the external surface of the mandible by means of muscular fibers; the region of insertion includes all that part of the mandible covered by the muscle in figures 1 and 3. (See also fig. 2). The medial part of M. add. mandib. medius at-

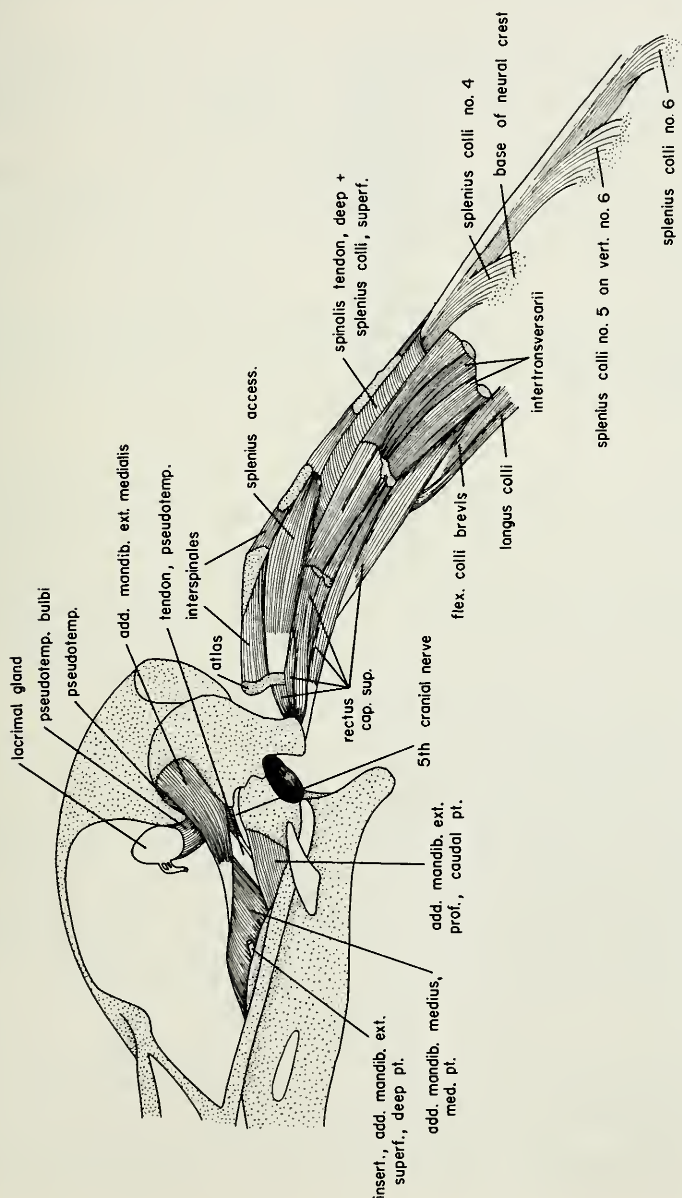


FIG. 5. Lateral view of the deep muscles of the head and a third layer of muscles in the anterior vertebral region.

taches fleshily to the inner side of the mandibular ramus in that depression beginning posteriorly at the internal articular process and going anteriorly to the region of the surangular. At its posterior end the insertion extends dorso-laterad on the mandible just anterior to the articular facets; this latter extension may correspond to the insertion of M. add. mandib. post. of Lakjer. In lateral aspect the wide, inserting tendon of M. pseudotemp. crosses the medial part and attaches to the medial side of the mandible.

M. adductor mandibulae externus medialis

As may be seen in figure 5, this is the deepest of the muscles of the adductor group in the temporal fossa; it is superficial only to M. pseudotemp. and to the origin of M. pseudotemp. bulbi (fig. 2).

Origin.—It arises tendinously from a narrow line in the temporal fossa, between the dorso-posterior part of the origin of M. pseudotemp. and the antero-dorsal section of the origin of the deep slip of M. add. mandib. ext. superf. (fig. 2).

Insertion.—At the postero-ventral corner of the orbital fossa the thin band of muscle becomes tendinous and inserts as a weak aponeurosis or dense fascia on the connective tissue covering the dorso-medial border of M. add. mandib. medius (fig. 5).

M. pseudotemporalis

Although this is the deepest of the muscles in the temporal fossa, the anterior corner of the dorsal end of its thick belly is visible superficially (figs. 1, 3). In cross-section the belly is triangular; at the ventral end of the post-orbital process the belly is crossed superficially by the belly of M. pseudotemp. bulbi. Edgeworth (1935:277) included M. pseudotemp. as part of his M. add. mandib. medius. However, in the Whooping Crane it is a very distinct muscle as Lakjer (1926:63-65) has indicated. We were not able to find the two parts described by Lakjer.

Origin.—The origin is well depicted in figure 2; usually it is fleshy but in one instance aponeurotic origin was also found.

Insertion.—At the postero-ventral corner of the eye, the heavy belly gives way to a strong, flat, calcified tendon which goes ventrad superficial to the medial part of M. add. mandib. medius (fig. 5). The tendon inserts on the middle of the width of the mandible, about 3 centimeters from the posterior end of the bone. Thus the insertion is covered medially by the insertion of the medial layer of M. add. mandib. medius.

M. pseudotemporalis bulbi

The thin band of M. pseudotemp. bulbi lies ventral to the post-orbital process, deep to M. add. mandib. ext. medialis and superficial to the middle of the belly of M. pseudotemp. (fig. 5).

Origin.—The origin is fleshy and tendinous from the middle of the ventral part of the temporal fossa, posterior to the origin of M. pseudotemp., and deep to the anterior edge of the origin of the rostral slip of M. add. mandib. ext. prof. (fig. 2).

Insertion.—There is fleshy insertion on the fascia beneath the postero-ventral corner of the lacrimal gland (fig. 5). A second insertion, tendinous, comes from the muscle immediately ventral to the lacrimal gland and attaches to the connective tissue at the postero-ventral corner of the eye.

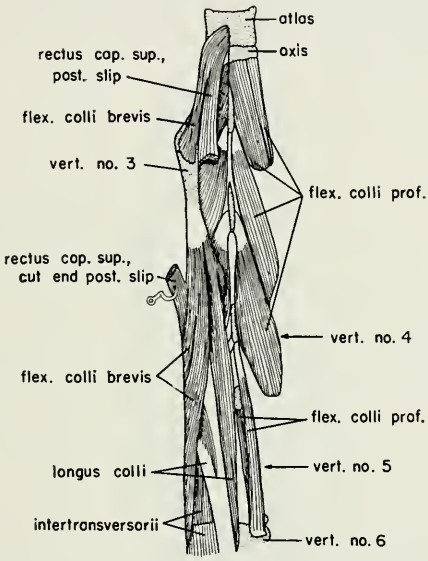


FIG. 6. Ventral view of the deep muscles of the anterior vertebral region.

M. pterygoideus ventralis

Edgeworth (1935) synonymized all of Lakjer's pterygoideus muscles with the muscle he called M. adductor mandibulae internus. Embryologically the entire muscle mass may be a single unit but, as Lakjer has shown, it breaks into a number of distinct, well-defined muscles which are variously developed in the different groups of vertebrates and which show major differences between some related species. It is of course easiest to combine all these into one unit, but this makes descriptive treatment of the variations an arduous task and leads to a glossing-over of the quite manifest diversities and separate entities of this complex of muscles. We have, therefore, retained as a matter of convenience the terms—M. pterygoideus ventralis and M. pterygoideus dorsalis. And since these pterygoideus muscles are composed of several fasciculi in the Whooping Crane, we designate these subdivisions as lateral and medial parts.

The pterygoid muscles are in three layers in the Whooping Crane—a ventral, which is itself in two layers, and a dorsal stratum. The superficial ventral layer is undivided, but the deep, ventral part exists as lateral and medial slips. The dorsal layer is similarly separated into lateral and medial fasciculi; this sheet is here designated as M. pteryg. dors. Both ventral sheets are called M. pteryg. vent.

In figure 7 both layers of M. pteryg. vent. are shown, as is the division of the deep layer into lateral and medial parts. The superficial layer is the outermost muscle of the ventral surface, crossed only by the small belly of M. stylohy. and a branch of the facialis vein. Its posterior end is marked by contact with M. depress. mandib. (fig. 1). The postero-medial

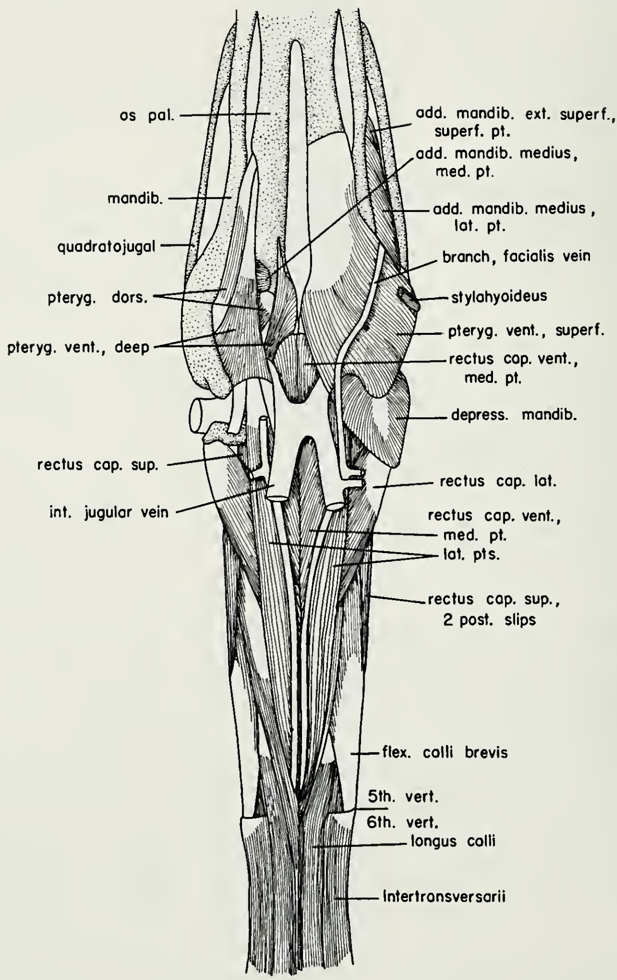


FIG. 7. Ventral view of the muscles of the jaw and the anterior vertebral region. On the left side of the jaw region the superficial layer of M. pteryg. vent. and M. depress. mandib. have been removed. Note the asymmetry of M. rectus cap. vent.

edge overlies the anterior end of the medial bundle of M. rectus cap. vent. Anteriorly it covers the posterior two-thirds of the length of the os palatine and all of the second and more dorsal layer of M. pteryg. vent. After removal of the superficial sheet, which is strongly bipinnate on its deep aspect, the two fasciculi of the deeper layer are evident (fig. 7). The lateral slip extends forward from the inner side of the posterior end of the mandible; it is superficial to the insertion of the lateral part of M. rectus cap. vent. on the occipital process on the lateral area of the basitemporal plate. Along the ventro-lateral edge of the wing of the palatine, it is superficial to the parts of M. pteryg. dors. The medial fasciculus of the deep layer of M. pteryg. vent. goes antero-mediad from the posterior end of the mandible, bordered medially by the anterior end of the medial part of M. rectus cap. vent. and laterally being superficial to the insertion of the medial part of M. pteryg. dors. (fig. 7).

Origin.—The superficial layer is overlaid anteriorly by a strong, silvery aponeurosis which forms part of the origin from the ventral area of the palatine, and particularly from the medial edge. Deep to this aponeurotic origin there is strong fleshy origin from the entire ventral concavity of the palatine. The lateral part of the deep sheet arises tendinously from the posterior half of the lateral corner of the palatal wing; the medial part of this layer comes fleshily from the posterior end of the palatine (fig. 7) and passes posteriorly over M. protract. pteryg.

Insertion.—The superficial muscle attaches fleshily on the outer face of the posterior part of the mandible, on all that part of this bone covered by the muscle in figure 1. Medial to this insertion is a thin line of tendinous insertion going dorsad on the inner aspect of the mandible and between the origin of the lateral, deep fasciculus and the medial part of the insertion of M. depress. mandib.

The lateral, deep fasciculus of M. pteryg. vent. inserts fleshily on the medial face of the mandible in an area delimited posteriorly by the insertion of M. depress. mandib., ventrally by the ventral edge of the mandible, and dorsally in its anterior extent by the ventral edge of the lateral slip of M. pteryg. dors. The medial bundle of the deep layer goes to the internal articular process as mixed fleshy and tendinous fibers (fig. 7).

M. pterygoideus dorsalis

The two slips comprising the muscle are illustrated in figure 7; the medial one is best shown in figure 8. The lateral fasciculus lies antero-dorsad of the lateral part of M. pteryg. vent.; its dorsal surface is in contact with the medial aspect of the medial part of M. add. mandib. medius. The more medial slip of M. pteryg. dors. is deep to the second layer of M. pteryg. vent. and is in part superficial to M. pteryg. protract. (fig. 8).

Origin.—The lateral part has tendinous and fleshy origin from the entire dorso-lateral surface of the palatine as far anterior as the most anterior part of the origin of the superficial layer of M. pteryg. vent. shown in figure 7. At this point, which is 6 or 7 centimeters from the posterior end of the palatine, the origin continues dorso-mediad and ends about 12 millimeters above the most ventral border of the palatal alae.

The medial slip of M. pteryg. dors. arises tendinously and fleshily from the ventral and antero-lateral edges or surfaces of the anterior end of the os pterygoid (fig. 8). The strong tendon shown overlying the insertion is superficial only.

Insertion.—The lateral belly sends a partly calcified tendon, 1 centimeter wide, to the medial face of the mandible. This site is anterior to the insertion of the medial part of this same muscle, is immediately ventral to the medial insertion of M. add. mandib. medius, and is covered posteriorly by the insertion of the deep, lateral part of M. pteryg. vent. (fig. 7). The medial slip attaches fleshily to the medial aspect of the posterior end of the mandible, and deep to all other attachments; its anterior border is marked by the posterior end of the insertion of the medial part of M. add. mandib. medius (fig. 8).

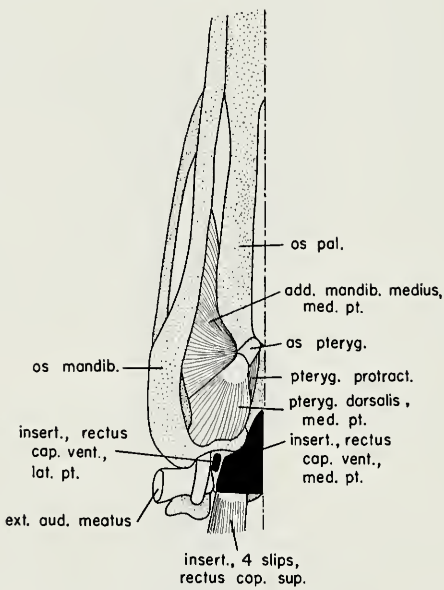


FIG. 8. Ventral view of the deep muscles of the posterior end of the skull and jaw.

M. protractor pterygoideus

Figure 8 shows some of the relationships of the muscle. It is a small belly lying along the medial side of the os pterygoid and between this bone and the antero-lateral border of the basitemporal plate. It is largely covered by the medial slip of M. pteryg. dors. and by the medial slip of the second layer of M. pteryg. vent.

Origin.—The posterior end of the belly arises, primarily as fleshy fibers with a few superficial tendinous fibers interposed, from the most lateral protuberance of the basitemporal plate, which point lies at the level of the posterior end of the quadrate.

Insertion.—There is a fleshy insertion, with some superficial fascial connection, on the medial and dorsal surfaces of the anterior third of the length of the pterygoid bone.

M. protractor quadratus

The very thin belly of this muscle, which is only 8 millimeters wide, comes from the antero-ventral edge of the temporal fossa and from the postero-ventral part of the orbital fossa (fig. 2). It inserts on the posterior edge of the most medial part of the orbital process of the quadrate. The insertion is thus opposite the posterior part of the quadrate origin of the rostral slip of M. add. mandib. ext. prof. The anterior part of the muscle is immediately deep to the heavy belly of M. pseudotemp.

Muscles of the Tongue Region

M. constrictor colli
  ? M. digastric in pt. *or* M. platysma myoides—Shufeldt (1890:6-7, 21-22)
  pt. M. cucullaris *or* M. constrictor colli—Gadow (1891:214-216, 306)
M. intermandibularis
  M. mylohyoideus—Shufeldt (1890:24-26), Moller (1930:670, 691, 709)
  M. mylo-hyoideus ant.—Gadow (1891:304-307), Mudge (1903:247-257)
  M. intermandibularis—Edgeworth (1935:61)
M. geniohyoideus
  M. genio-hyoideus—Shufeldt (1890:27), Gadow (1891:313), Mudge (1903:261-262)
  M. kerato-mandibularis—Moller (1930:669, 692, 708)
  M. branchiomandibularis—Edgeworth (1935:61)
M. stylohyoideus
  M. stylohyoideus—Shufeldt (1890:26-27), Gadow (1891:305-307), Mudge (1903:253-257)
  ant. pt. M. mylo-hyoideus post.—Gadow and Mudge (*loc. cit.*)
  M. hyo-mandibularis lat.—Moller (1930:670, 691, 710)
  M. gularis—Edgeworth (1935:109, 281-282)
M. genioglossus
  M. genio-glossus—Gadow (1891:314), Mudge (1903:262), Moller (1931: 119, fig. 9)
M. dermoglossus—new name
M. ceratoglossus—lateralis and *inferior* (*superior* absent in *G. americana*)
  M. cerato-glossus—Shufeldt (1890:30-33), three parts Gadow (1891: 315-316) and Mudge (1903:214-232)
  M. kerato-hyoideus—Moller (1930:671, 692, 710)
M. hypoglossus rectus
  pt. M. depressor glossus—Shufeldt (1890:30)
  M. hypoglossus rectus—Gadow (1891:317), Mudge (1903:246-247)
M. hypoglossus obliquus
  pt. M. depressor glossus—Shufeldt (1890:30)
  M. hypoglossus obliquus—Gadow (1891:317), Mudge (1903:246-247)
M. thyroglossus
  med. fibers M. sterno-hyoideus—Shufeldt (1890:29-30)
  M. thyreo-glossus—Gadow (1891:309)
  M. thyroglossus—Mudge (1903:235-245)
M. thyrohyoideus
  lat. fibers M. sterno-hyoideus—Shufeldt (1890:29-30)
  M. thyreo-hyoideus—Gadow (1891:307-312)
  M. thyrohyoideus *plus* accessorius—Mudge (1903:232-234)
M. tracheohyoideus
  ant. pt. M. cleido-tracheales—Shufeldt (1890:9-10)
  M. tracheo-hyoideus—Gadow (1891:307-312), Moller (1930:671, 692, 710)
  pt. M. sterno-hyoideus—Mudge (1903:258-261)

M. tracheolaryngeus superior
ant. pt. M. tracheo-lateralis—Shufeldt (1890:47-48)
M. tracheo-laryngeus superior—Gadow (1891:309)
M. tracheolaryngeus inferior
post. pt. M. tracheo-lateralis—Shufeldt (1890:47-48)
M. tracheo-laryngeus inferior—Gadow (1891:309)
M. sternotrachealis
M. sterno-trachealis—Shufeldt (1890:49-52), Gadow (1891:729-730)
M. thyroarytenoideus
M. thyreo-arytenoideus—Shufeldt (1890:45-47)
M. apertor laryngis—Gadow (1891:718)
M. dilatator laryngis—Edgeworth (1935:285, 440)
M. constrictor glottidis
M. constrictor glottidis—Shufeldt (1890:45)
M. sphincter laryngis—Gadow (1891:718)
M. constrictor laryngis (dorsal portion) or M. constrictor dorsalis—Edgeworth (1935:285, 440)
M. serpi-hyoideus of Gadow (1891:305-307) and Mudge (1903:253-257) is absent in the Whooping Crane, as is *M. cerato-hyoideus* of Shufeldt (1890: 27-29), Gadow (1891:316), and Mudge (1903:262-263)

M. constrictor colli and M. intermandibularis

Apparently the only remaining part of the ventral constrictor sheet in the Whooping Crane is represented by a thick aponeurosis having only a few contractile fibers. The aponeurotic layer lies between the posterior ends of the mandibles and extends forward nearly to the base of the tongue. It goes posteriorly to the level of the 6th or 7th cervical vertebra and there blends in with the fascia around the trachea and the ventrolateral part of the cervical musculature.

The anterior edge of the part corresponding to M. constrictor colli is marked by the posterior end of the basihyal bone. The few contractile fibers present are in a transverse band across the posterior half of the urohyal. Another diffuse band occurs across the anterior half of the length of the basihyal and probably represents the posterior edge of a vestigial M. intermandib.

M. stylohy. (figs. 1, 7, 10), which is also a derivative of this primitive constrictor sheet of muscle, is a distinct muscle and will be described shortly. It seemingly is the remainder of the sheet lying between M. constrictor colli and M. intermandib.

On either side the fibers of M. constrictor colli arise from the posteroventral part of the mandible and from the fascia which overlies the insertion of M. depress. mandib. and is just postero-ventral to the origin of M. stylohy. The fasciculus here termed M. intermandib. attaches to fascia about 2 centimeters antero-ventrad of the origin of M. stylohy.

M. geniohyoideus

This is a large band of muscle which extends from the posterior end of the epibranchial cartilage to the inner surface of the mandible. In the Whooping Crane it consists of but one fasciculus (figs. 1, 9, 10) which has, in the middle of its length, some interconnection with M. dermogl. in one of two specimens.

Origin.—There is fleshy origin from the entire circumference of the

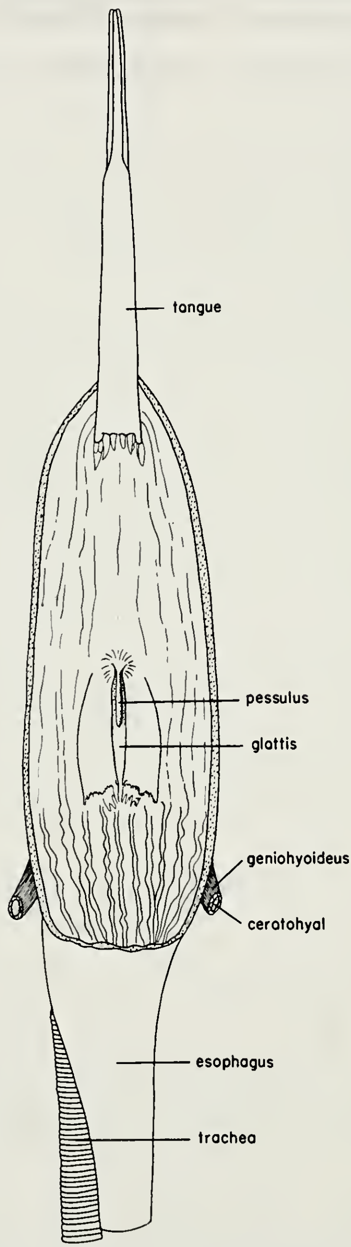


Fig. 9. Dorsal view of the tongue and the floor of the pharynx. The stippled area represents a cut edge of the wall.

epibranchial cartilage and from the dorsal and lateral surfaces of the posterior half of the length of the ceratohyal. Because of the variable development of the posterior extent of the epibranchial and ceratohyal, between specimens and even between the two sides of the same individual, the posterior part of the origin of M. geniohy. is also variable. The greatest development of the horn of the hyoid apparatus is shown in figure 1; in the other extreme, the posterior end barely reaches the level of the postero-dorsal corner of the mandible.

Insertion.—From the anterior end of its origin the muscle goes anteriorly and somewhat laterally to insert fleshily on the inner surface of the mandible. This attachment is opposite the basihyal, or about 7 centimeters anterior to the posterior end of the mandible. The anterior end of the insertion is marked by the most anterior end of the insertion of M. add. mandib. medius on the lateral surface of the mandible.

M. stylohyoideus

The band of muscle termed M. stylohy. here represents the anterior part of the posterior mylohyoideus sheet. The posterior part of this sheet, termed M. serpi-hyoideus by several authors (see page 27), could not be found in the Whooping Crane.

M. stylohy. is a thin and narrow muscle lying superficially on the lateral face of the posterior part of the jaw and on the ventral surface of M. pteryg. vent. It crosses M. geniohy. and goes anteriorly alongside the ceratohyal bone (fig. 1).

Origin.—The disto-anterior part of the opisthotic process (fig. 1) gives tendinous origin primarily, while there is strong fleshy and tendinous origin from the middle of the postero-lateral corner of the mandible.

Insertion.—The fleshy and fascial attachment is to the most antero-lateral surface of the ceratohyal. The anterior end of the insertion is marked by the articulation between the ceratohyal and basihyal bones (fig. 10).

M. genioglossus

This muscle is a fleshy, widely triangular body which in ventral view is covered by M. geniohy., by M. stylohy., and by M. dermogl. In figure 10, M. geniohy. has been cut and pulled laterally.

Origin.—There is a fleshy origin from the inner side of the mandible, dorsal to the middle of the width of the mandible. The site of the origin is dorsal to the mandibular attachment of M. geniohy.

Insertion.—From this relatively short and narrow line of origin the muscle fans out as it goes ventro-mediad. Posterior to the entoglossum there is fleshy insertion on the tissues forming the floor of the mouth. The insertion continues anteriorly from the base of the entoglossum for one-half the length of this structure. Anterior to M. hypogl. obliq. the muscles of the two sides meet in the ventral midline of the entoglossum (fig. 10),

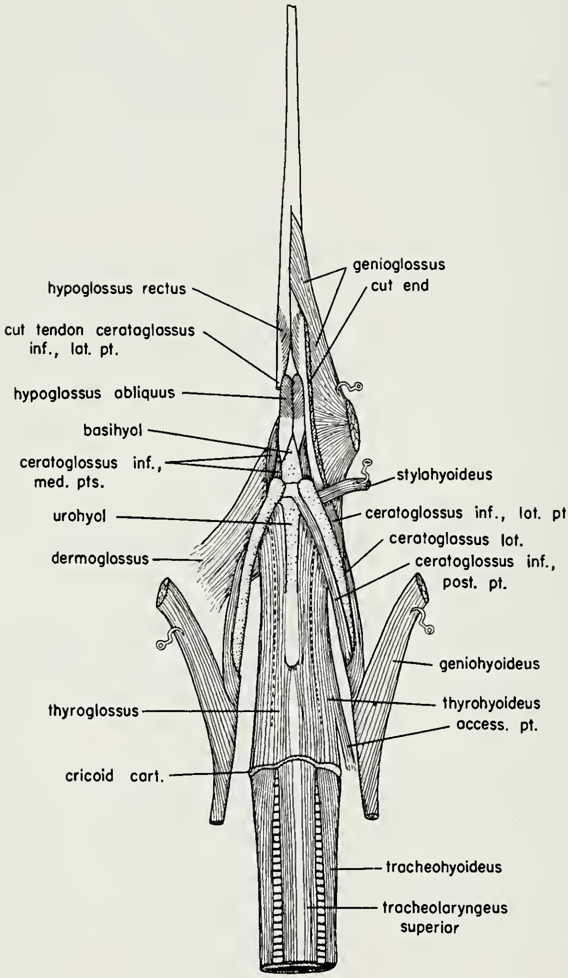


FIG. 10. Ventral view of the musculature of the tongue and the anterior part of the trachea.

covering M. hypogl. rectus and inserting on the entoglossum. Throughout its length the insertion is in intimate contact with the floor of the mouth.

M. dermoglossus

We have been unable to find in the literature any muscle that is topographically similar to this one, and because we were unable to determine its innervation in our specimens, we have simply used the descriptive name, M. dermoglossus (fig. 10). Judging from its position and insertion, the muscle may correspond to a superior slip of M. ceratogl., which has moved its origin from the ceratohyal bone to the skin and connective tissue immediately surrounding this bone. The absence of a true M.

ceratogl. sup. in the Whooping Crane might be further indicative of this interpretation.

Origin.—The fascia on the external surface of the side of the pharynx, dorsal to the ceratohyal and medial to the middle of the length of the belly of M. geniohy., gives rise to the rather indistinct lateral end of the muscle.

Insertion.—The fibers go antero-mediad, but mostly anteriorly, to insert as mixed fleshy and fascial fibers on the dorso-lateral corner of the anterior end of the basihyal. This location is lateral and anterior to the insertion of M. thyrohy. and deep and medial to the lateral part of the insertion of M. hypogl. obliq.

M. ceratoglossus lateralis

Figure 10 shows the belly of this muscle paralleling and bordering the lateral side of the anterior half of the length of the ceratohyal. The anterior part of it is covered by the lateral and medial parts of M. ceratogl. inf. Posteriorly the end of the muscle on the ceratohyal is marked by the anterior edge of M. geniohy. In one specimen, M. ceratogl. lat. received a few fibers which came from the dermal end of M. dermogl.

Origin.—There is fleshy origin from the ventro- and dorso-lateral surfaces of the ceratohyal anterior to the most anterior part of the origin of M. geniohy.

Insertion.—The dorsal and somewhat lateral surface of the anterior end of the basihyal and the postero-ventral and lateral corner of the entoglossum receive fleshy fibers.

M. ceratoglossus inferior

As may be observed in figure 10, M. ceratogl. inf. consists of three major divisions in *Grus americana*—lateral, medial, and posterior; the medial may in turn be composed of two parts. The medial and lateral divisions span the articulation between the ceratohyal and basihyal, and the inserting end of M. stylohy. crosses the ventral side of the lateral part. M. ceratogl. lat. is superior to both the medial and lateral parts of M. ceratogl. inf. in the anterior half of its length. The medial part (or parts) is approximately half the length of the latter fasciculus.

The posterior slip of M. ceratogl. inf. was present in definable form in but one of the three specimens. It lies on the inner face of the ceratohyal bone, opposite M. ceratogl. lat.

Origin.—The lateral part comes fleshily from the anterior 2 centimeters of the lateral surface of the ceratohyal, except that the most anterior 4 millimeters of this surface give fleshy origin for the medial part of the inferior division. The posterior division arises as fleshy fibers, adjacent and anterior to the origin of M. ceratogl. lat. from the medial surface of the ceratohyal.

Insertion.—At the level of the posterior end of the basihyal the lateral part forms a tendon which passes anteriorly across the ventral aspect of the medial belly and the insertion of M. hypogl. obliq. Opposite the posterior end of the entoglossum the tendon is attached to and forms the origin of M. hypogl. rectus (fig. 10). The most anterior extent of the tendon, and the actual tendinous insertion, of the lateral part of M. ceratogl. inf. is 0.5 centimeters anterior to the posterior end of the entoglossum and on the ventro-lateral corner of this structure. This insertion thus lies at the anterior end of M. hypogl. rectus and is covered ventrally by M. geniogl.

The insertion of the medial part is fleshy on the ventro-lateral edge of the middle third of the basihyal, deep to M. hypogl. obliq. and posterior to the insertion of M. dermogl.

The posterior part inserts on the fascia overlying the joint between the urohyal and basihyal elements.

M. hypoglossus rectus

The Mm. hypogl. rectus and hypogl. obliq. would seem to be parts of the same sheet of muscle. However, as may be seen in figure 10, the fibers of the two lie nearly at right angles to each other. Both are covered ventrally by the medial part of M. geniogl.

Origin.—Mudge (1903:247) noted that there was little variation in M. hypogl. rectus and gave its origin, for all forms (parrots) he dissected, as the postero-lateral process of the entoglossum. In the Whooping Crane the origin is consistently from both the postero-lateral process and the tendon of the lateral part of M. ceratogl. inf.; the latter part of the insertion is always the major part, only a few fibers coming from the described position on the entoglossum.

Insertion.—From the lateral attachment the fibers go antero-mediad for a short distance and eventually fade into a strong, tendinous aponeurosis which continues anteriorly on the ventral surface of the entoglossum to the middle of the length of this structure. This aponeurosis is also the one on which the Mm. geniogl. meet in a superficial, midline raphe.

M. hypoglossus obliquus

As is shown in figure 10, the paired muscles of this name lie on the ventro-lateral surface of the anterior end of the basihyal and extend forward on to the posterior end of the entoglossum. Laterally they are deep to the tendon of the lateral part of M. ceratogl. inf. and to M. geniogl.; posteriorly they are medial and superficial to the one or two slips of the medial fasciculus of M. ceratogl. inf.

Origin.—There is tendinous and fascial origin from the ventro-lateral corner of the posterior half of the length of the basihyal. Caudally this origin may be very attenuated.

Insertion.—It is strongly fleshy on a longitudinal line on the posterior end of the ridge forming the ventro-lateral corner of the entoglossum. This line is continuous with, but posterior to, the line of insertion of the tendon of the lateral part of M. ceratogl. inf.

M. thyroglossus and M. thyrohyoideus

These muscles extending from the posterior rim of the cricoid cartilage to the basihyal bone are considered together because in only one of three specimens was there any very obvious separation into a lateral M. thyrohy. and a medial M. thyrogl. The two names which include the "thyro" are retained here only through our desire to add no more confusion to the nomenclature of muscles; since there is no thyroid cartilage in birds, the use of the term is misleading. The paired masses (fig. 10) lie on the ventral surface of the larynx, separated from each other anteriorly by the urohyal bone. Posteriorly, in the mid-ventral line, only fascia separates the thyroglossal muscles of the two sides.

If we regard the lateral part as M. thyrohy., we may then designate as M. thyrohy. access. (Mudge, 1903:232) the small slip which comes off the postero-lateral part. The posterior ends of M. thyrogl. and M. thyrohy. are superficially continuous with M. tracheolar. sup. and M. tracheohy. This continuity is, however, represented by only a few fibers and is but another indication of the fact that these four muscles represent the anterior end of the more primitive sheet of muscle considered as M. sternohy.

Origin.—The muscles originate from the ventral and lateral surfaces of the posterior end of the cricoid cartilage. There is, however, close fascial connection to the cricoid cartilage throughout the distance that the muscle traverses the cricoid. The part designated as M. thyrohy. access. arises primarily from the fascia of the floor of the mouth and pharynx just lateral to the glottis, but may get some fibers from the postero-dorsal rim of the cricoid.

Insertion.—The insertion of the fused mass is largely tendinous on the anterior end of the lateral surface of the basihyal, deep to the insertion of M. dermogl. The anterior part of the course of the muscle is covered by the medial and lateral parts of M. ceratogl. inf.

M. tracheohyoideus

The part of the primitive M. sternohy. lying posterior to the cricoid and on the lateral surface of the trachea forms this muscle (fig. 10). It is several times as large as M. tracheolar. sup. and extends posteriorly from the cricoid for about one-third the length of the neck (about 14 centimeters in our specimens). A thin fasciculus comes from the dorso-medial corner of the anterior end and passes to the dorsal surface of the larynx (fig. 12). We found no convolutions or circumtracheal windings such as Steinbacher (1934, 1935) reported in some woodpeckers.

Origin.—At its posterior end the muscle arises from the skin and from

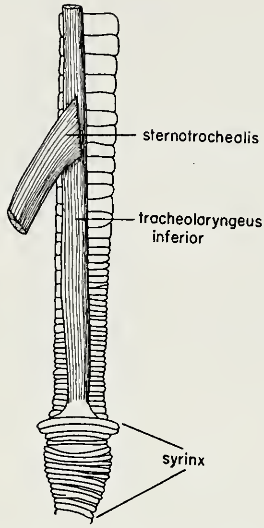


FIG. 11. Lateral view of the left side of the posterior part of the trachea and the syrinx.

the fascia between the trachea and the vertebral column. This dermal attachment is here considered the origin because primitively the posterior end of the muscle was connected to the sternum.

Insertion.—The main body of the muscle inserts on the ventral, lateral, and dorsal surfaces of the posterior end of the cricoid (fig. 10). The small slip formed anteriorly crosses the surface of M. thyroaryt. on the dorsal side of the larynx and inserts fleshily on the dorso-lateral corner of the posterior end of the arytenoid cartilage (fig. 12).

M. tracheolaryngeus superior

Figure 10 shows the muscle on the ventral side of the trachea, immediately lateral to the midline and separated from the same muscle of the opposite side by fascia only; in fact, the two almost seem to be continuous in the midline. M. tracheolar. sup. with M. tracheolar. inf. formerly constituted a continuous band from sternum to larynx. In birds the middle part of the length of this band has disappeared entirely or in part. This gives rise to considerable and frequent variations in length of the two parts. In one Whooping Crane (no. 2) M. tracheolar. sup. extended posteriorly 10 centimeters from the cricoid cartilage, and in another (no. 3) only 4 centimeters.

Origin.—The ventro-lateral surfaces of three or four tracheal rings provide fleshy origin.

Insertion.—The medio-ventral edge of the posterior rim of the cricoid cartilage receives the fleshy anterior end of the muscle (fig. 10).

M. tracheolaryngeus inferior

As was indicated above, there is considerable variation in the anterior extent of this muscle. In one specimen (no. 2) the anterior end of this muscle was 11 centimeters posterior to the cricoid cartilage and, except for a gap of 1 centimeter, formed a direct continuation of M. tracheolar. sup. In specimen number 3 the anterior end was 4 centimeters posterior to the cricoid but was on the dorso-lateral part of the trachea; thus in this specimen there seems to have been a dorsad movement away from the posterior end of M. tracheolar. sup. However, as it went toward the lower end of the trachea the muscle shortly assumed the usual mid-lateral position.

From this variable site anteriorly M. tracheolar. inf. continues caudally to the syrinx (fig. 11). (Because we did not wish to destroy the sternum, which is extensively penetrated by the trachea, the muscle could not be followed throughout its length.) The muscle was present in the same relative position when the trachea entered and when it emerged from the sternum; it was, therefore, assumed to be continuous. Some increase in size is apparent in the muscle from the lower cervical region to the syrinx. Opposite the coracoid bone the longitudinal fibers of this muscle surround the insertion of M. sternotrach.

Origin.—The mid-lateral or occasionally the dorso-lateral parts of the tracheal rings give fleshy origin.

Insertion.—Two or three tracheal rings anterior to the syrinx the muscle forms a thin aponeurosis which fans out to attach to somewhat more than the middle half of the dorso-ventral length of the first syringeal ring (fig. 11). M. tracheolar. inf. does not give rise to any other syringeal muscles in the Whooping Crane; see Miskimen (1951:497-504) for a recent discussion of the relations of this muscle (her M. tracheo-lateralis) to other muscles of the syrinx in passerine birds.

M. sternotrachealis

This is one of the few names that has been used consistently by avian anatomists. In addition to those workers listed on page 27, Mayr (1931: 337) and Miskimen (1951:497, 504) used the name M. sterno-trachealis. The entire muscle is only 6 centimeters long and but 5 or 6 millimeters wide (fig. 11). It arises from the most dorsal part of the dorsal or inner face of the sterno-coracoidal process of the sternum. It extends antero-dorsad to insert on the middle of the side of the tracheal rings opposite the coracoid, some 5 centimeters anterior to the syrinx. The insertion is fleshy and is surrounded, or nearly so, by the fibers of M. tracheolar. inf.

The extrinsic syringeal muscles noted by Beddard (1898:368) as coming from the angle of the first rib must have been the Mm. sterno-tracheales.

M. thyroarytenoideus

This muscle is to be found on the dorsal side of the larynx (fig. 12). It virtually covers this surface, being separated from its counterpart of the opposite side by the glottis and parts of the arytenoid cartilage. M. constrictor glottidis is deep to this muscle. Posteriorly M. thyroaryt. is in contact, on the cricoid cartilage, with the dorsal part of the insertion of M. tracheohy. and is covered by the slip of this muscle that inserts on the posterior crest of the arytenoid cartilage.

Origin.—In general the fibers can be said to arise fleshily from the posterior edge of the cricoid and from the posterior half of the length of the dorso-lateral edge of the lateral cricoid.

Insertion.—The fibers pass antero-medially to insert fleshily on the lateral surface of the entire length of the arytenoid cartilage (fig. 12).

M. constrictor glottidis

The muscle is completely hidden from dorsal view by M. thyroaryt. (fig. 12) on the larynx and the most anterior extent of M. tracheohy. It lies on the dorsal surface of the cricoid cartilage and the lateral part of the arytenoid.

Origin.—Fleshy origin is provided by the dorsal and lateral surfaces of the medial or middle cricoid cartilage.

Insertion.—From this origin the fibers fan out anteriorly and somewhat laterally. The primary insertion lies in the connective tissue anterior and lateral to the anterior apex of the arytenoid cartilage. Some fibers of the most lateral part of the belly may insert on the middle of the length of the dorso-medial rim of the lateral cricoid cartilage.

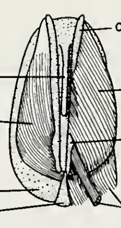


Fig. 12. Dorsal view of the larynx and the musculature surrounding the glottis. Mm. tracheohy. and thyroaryt. have been removed on the left side.

Muscles of the Orbit and the Ear

M. orbicularis palpebrarum
  M. orbicularis palpebrarum—Shufeldt (1890:52-53)
  M. orbicularis—Gadow (1891:445)
  ?M. tensor periorbitae—Lakjer (1926:135)
  part M. constrictor palpebrae inferioris—Edgeworth (1935:275)
M. levator palpebrae superioris
  M. levator palpebrae superioris—Shufeldt (1890:55-56)
  M. levator palpebrae—Gadow (1891:445)
M. depressor palpebrae inferioris
  M. depressor palpebrae inferioris—Shufeldt (1890:56-57), Gadow (1891:445), Lakjer (1926:135)
  part M. constrictor palpebrae inferioris—Edgeworth (1935:275)
M. quadratus nictitantis
  M. quadratus nictitantis—Shufeldt (1890:57)
  M. quadratus membranae nictitantis—Gadow (1891:443)
M. pyramidalis nictitantis
  M. pyramidalis nictitantis—Shufeldt (1890:57-58)
  M. pyramidalis membranae nictitantis—Gadow (1891:443-444)
M. obliquus superior
M. obliquus inferior
M. rectus superior
M. rectus inferior
M. rectus externus
M. rectus internus
  } all in common use in vertebrates: Shufeldt (1890:58-61), Gadow (1891:442-443)
M. tensor tympani—Shufeldt (1890:62-63), Gadow (1891:462)

No variations from the usual pattern in birds were found in any of the eye muscles. In figure 2 the origins are indicated, and figure 13 shows the insertions. The only attachments not shown are: the maxillojugal part of the origin of M. orbic. palp., which was removed with the skin, as was the insertion of this muscle on the lower eyelid; the insertion of M. lev. palp. on the upper eyelid, removed with skin; the insertion of

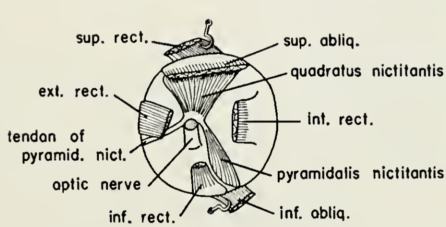


Fig. 13. The muscles of the eyeball as seen from the medial side of the eye. Only Mm. pyramidalis nict. and quadratus nict. are completely shown; all other muscles have been cut near their insertions.

M. depress. palp., removed with lower lid; and the insertion of M. pyramidalis nict. on the nictitating membrane.

M. tensor tympani, if present in the ear region, was destroyed in skinning.

Muscles of the Wing

Most of the names of the muscles of the wing follow Fisher (1946:607-611), who has compared his nomenclature with that of earlier workers. However, Montagna (1945) demonstrated that the digits of the avian hand are numbers II, III, and IV rather than I, II, and III as in most current literature. Thus is settled, at least to our satisfaction, the hundred-year-old controversy. Names of certain of the wing muscles must be changed to avoid confusion. Below, the old names are given in brackets following the new names. The new names were chosen after consultation with a number of anatomists. We here list, in the sequence in text, the names used; this should facilitate use, as in general the muscles are treated in the sequence of removal from the specimen.

M. tensor patagii longus
M. tensor patagii brevis
M. pectoralis
M. supracoracoideus
M. sternocoracoideus
M. coracobrachialis posterior
M. latissimus dorsi
M. cucullaris, hals part
M. rhomboideus superficialis
M. rhomboideus profundus
M. coracobrachialis anterior
M. deltoideus minor
M. proscapulohumeralis
  and M. subscapularis
M. proscapulohumeralis brevis
M. dorsalis scapulae
M. serratus posterior
M. serratus profundus
M. serratus anterior
M. subcoracoideus
M. biceps
M. deltoideus major
M. triceps
M. brachialis
M. extensor metacarpi radialis
M. extensor digitorum communis
M. supinator brevis
M. flexor metacarpi radialis
M. pronator brevis
M. pronator longus
M. extensor longus digiti II
  [extensor pollicis longus]
M. anconeus
M. extensor longus digiti III
  [extensor indicis longus]
M. flexor digitorum profundus
M. flexor carpi ulnaris
M. flexor carpi ulnaris brevis
M. abductor alae digiti II
  [abductor pollicis]
M. adductor alae digiti II
  [adductor pollicis]
M. flexor digiti IV
  [flexor digiti III]
M. flexor brevis digiti IV
  [flexor brevis digiti III]
M. abductor minor digiti III
  [abductor digiti II]
M. flexor metacarpi brevis
M. interosseus dorsalis
M. interosseus ventralis
M. extensor brevis digiti II
  [extensor pollicis brevis]
M. abductor major digiti III
  [abductor indicis]
M. flexor digiti II
  [flexor pollicis]
M. flexor metacarpi posterior

M. tensor patagii longus

The complex topographical relationships of this muscle may be observed in figures 16 and 18. The intricate mechanism has three major sources of origin (figs. 16, 18 and described below) from the shoulder

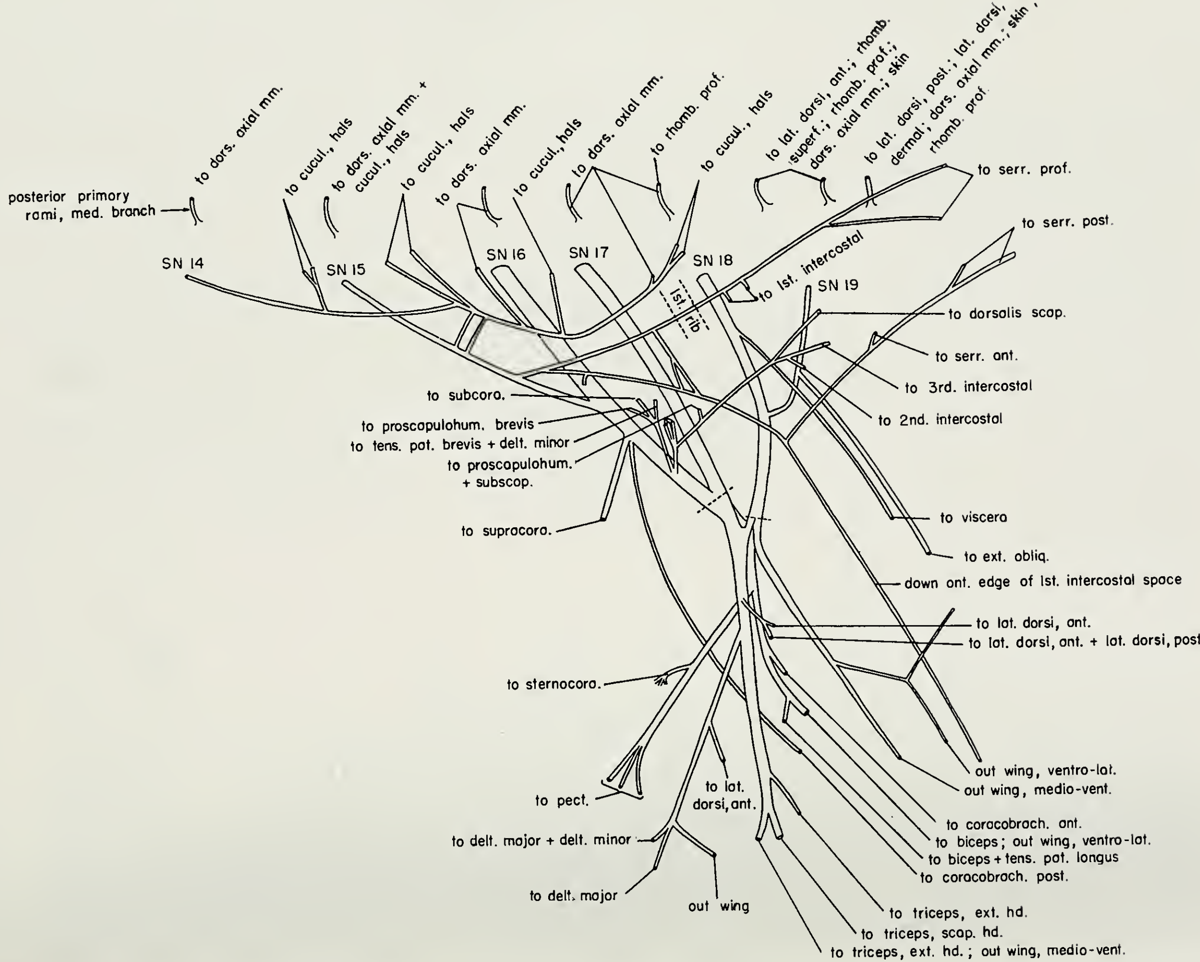


FIG. 14. Dorsal view of the brachial plexus of the right side of specimen number 1 to show source of innervation of certain muscles. Com-
... with figure 15 to observe variation from side to side in same specimen. *Note:* In both figures dotted lines across main nerve trunks

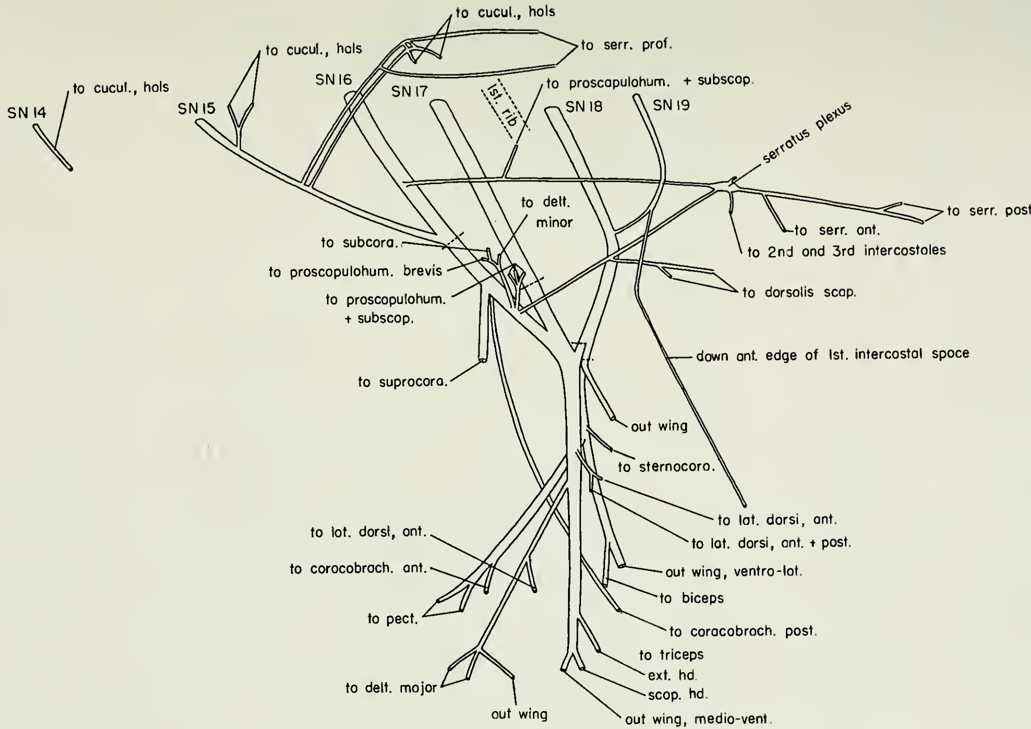


Fig. 15. Dorsal view of the brachial plexus of the left side of specimen number 1 to show the innervation of certain muscles. Compare with figure 14.

region. Halfway out the humeral length these three parts form a wide elastic tendon (fig. 16) which almost immediately subdivides. Both the latter subdivisions send inelastic tendons to the region of the elbow. The subdivided elastic tendons are 10 centimeters long, and they fuse distally to form an inelastic tendon which courses to the wrist in the anterior edge of the patagium, passes through the tendinal groove in the antero-distal surface of the radius, and goes to the metacarpus. Such complexity in the tendinous arrangement is apparently not present in *Balearica pavonina* (Mitchell, 1901). Our specimens of *americana* do not agree with the statements of Lowe (1931a, 1931b) that the tensor tendons are simple and represent an "archaic" condition. In *G. canadensis* we found no complicated system of slips to the wrist.

The ventral division of N. brachialis longus sends a twig to this muscle from the branch serving M. biceps (fig. 14).

Origin.—The most anterior source is by a non-elastic tendon from the anterior edge of the tendon of M. tens. pat. brevis at the junction of this latter tendon with its belly. The middle origin is a strong elastic tendon arising from the distal end of the anterior surface of the deltoid crest of the humerus and at approximately the middle of the length of M. delt. major. The only muscular origin is the posterior one (figs. 16, 17, 18) which comes from the antero-palmar surface of M. biceps at the level of the middle of the deltoid crest. Beddard (1898) described a similar, but tendinous, origin in *Anthropoides virgo*, and Gadow (1891:255) listed this bicipital muscular origin as typical of *Grus*. We found it in *G. canadensis*. Its tendinous origin is in common with that of M. biceps and deep to the fleshy superficial part of M. pect. The anterior and middle sources of origin unite to form an inelastic tendon which shortly joins the tendon of the posterior and muscular origin.

Insertion.—The major and usual insertion is on the most antero-proximal part of the extensor process of metacarpal II, palmar to the insertion of M. extens. longus dig. II (figs. 16, 18, 20, 21). The six inelastic tendons extending posteriorly from the wide elastic tendon in the middle of the patagium attach to the broad fascial covering of the anconal aspect of the elbow and forearm.

The presence of elastic tendon in the origin and in the middle of the length of the primary tendon of insertion suggests that there may perhaps be little muscular action involved in the functioning of this muscle. When the forearm is extended, the elastic tendons in the inserting tendon and in the origin would hold the patagium taut. With the wing partly or completely flexed, the small muscular belly of the origin might aid in tightening the patagium. In line with the view that a muscle can contract to one-third or one-half the length of the relaxed belly, it is difficult to see how this muscle, which is so short in relation to the length of the inserting tendon, could do much effective work when the forearm is even partly flexed. Flexion of the hand would automatically tense the entire complex of this muscle.

M. tensor patagii brevis

The elongately triangular belly lies on the antero-dorsal aspect of the shoulder (figs. 16, 18, 22, 25) just anterior to M. delt. major, dorsal to the proximal part of M. pect., and anconal to the middle and posterior origins of M. tens. pat. longus. The belly is one-fourth the humeral length; at the level of formation of this tendon there are wide aponeurotic attachments to the deltoid crest of the humerus. The muscular origin of M. tens. pat. longus also arises here.

A branch of the 16th spinal nerve (fig. 14) passes across the dorsal proximal surfaces of Mm. delt. major and minor and penetrates the deep side of the proximal part of the belly. In one bird, and only on the right side, a second innervation was present; it came from the superior division of the plexus.

Origin.—The origin is mixed fleshy and tendinous from the lateral face of the most dorsal part of the furculum. There is wide fascial connection proximally to the surface of M. cucullaris, hals pt., and antero-ventrally to the surface of M. pect.

Insertion.—The origin of part of M. tens. pat. longus should be considered one insertion of M. tens. pat. brevis, for, with the forearm extended, contraction of the latter muscle would tense M. tens. pat. longus. Lowe (1931b) listed as one feature of the Gruidae the absence of any "wristward slip." To us this slip to M. tens. pat. longus constitutes a "wristward slip"; we also found this in the Little Brown Crane. The principal insertion is, however, by a wide, flat tendon which passes down the antero-anconal edge of the upper wing musculature and moves out somewhat distally in the patagium to insert widely on the strong fascia over the elbow (fig. 18). Within this fascial attachment is a particularly strong band of fascia that inserts on the tendon of origin of M. extens. meta. rad., pars anconalis. This connection to the origin of M. extens. meta. rad. in effect serves M. tens. pat. brevis as an insertion on the ectepicondyle of the humerus. Perhaps this posterior band of fascia in the attachment is comparable to the "inner division" of Lowe, who found this division absent in *Balearica* but present in chicks of *Grus grus.* In *G. 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 of M. flex. carpi ulnaris. It is of interest that M. tens. pat. brevis in one specimen (fig. 16) has a divided tendon of insertion; in the other birds the tendon is single (fig. 18).

M. pectoralis

This, the largest muscle of the body, is easily separated into superficial and deep portions. These are so distinct they will be considered sepa-

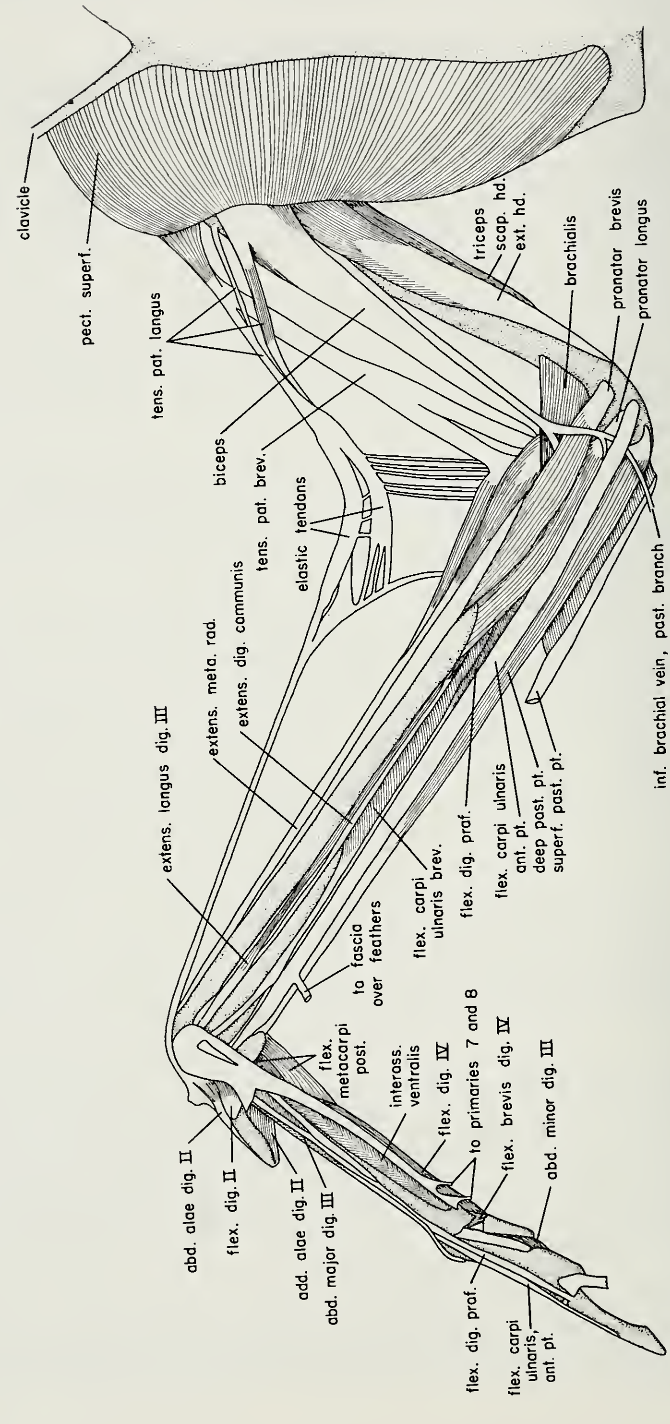


FIG. 16. Ventral view of the superficial muscles of the breast and wing of the right side.

rately. Beddard (1898:366) found this double layer in *Bugeranus carunculatus* and *Balearica pavonina.* In *Grus canadensis* we found the two parts to be hardly separable; the deep part is weakly developed. Innervation is from branches of the inferior trunk of N. brachialis longus (figs. 14, 15).

Superficial part.—The position and relationships are well shown in figures 16 and 25. There it may be seen that on the ventral side of the body this muscle is superficial to the origins of Mm. biceps, triceps, and tens. pat. longus; in figures 17 and 29 the relations with the deep layer and with M. supracoracoid. may be observed.

Origin.—It is entirely fleshy from that part of the sternal plate not used by M. supracoracoid., except that there is a small posterior part not utilized by either muscle. A major part of the fleshy origin is from the lateral surface of the keel and the furculum as far antero-dorsally as the coracoid. At the postero-dorsal edge of the belly the origin extends dorsally on to M. ext. obliq.

Insertion.—Although there are some tendinous fibers, the insertion is primarily fleshy on the palmar side of the deltoid crest of the humerus. The distal part of the insertion is on a rounded papilla at the distal end of the deltoid crest, by a wide, thick tendon which extends to the area of insertion by passing beneath and through the fleshy insertion on the deltoid crest. We found the insertion in *canadensis* to be fleshy except for an underlying sheet of connective tissue extending from origin to insertion; the poorly developed deep part of the muscle inserts on this sheet.

Deep part.—There was considerable variation in the conformation of this layer. The left side of the bird whose right side is depicted in figure 17 showed a more "normal" or usual situation. The fibers were nearly at right angles to the axis of the tendon of origin of Mm. biceps and tens. pat. longus, and not parallel to it as shown in figure 17. On the left side the blood vessels and nerves perforated the posterior edge of this deep part, as they usually do, and they did not lie outside as shown in the drawing.

Origin.—In one-half of the dissections origin is from the most ventral part of the tracheal enclosure at the anterior end of the sternum and from fascia lying between this enclosure and the furculum. There is also some fibrous and fascial origin from the surface of M. supracoracoid. In the instance figured the origin was from the surface of the anterior half of M. supracoracoid. with only slight origin from the tracheal enclosure; this condition of the origin is to be found in the remainder of the dissections.

Insertion.—In no specimen did this deep part insert on anything other than the tendon of origin of Mm. biceps and tens. pat. longus. There is no attachment to the tubercle on the deltoid crest of the humerus, where this part of the pectoralis complex frequently inserts. As has been described, there is tendinous insertion on this papilla, but it comes from an inseparable part of the superficial layer. Insertion on the originating tendon of M. biceps, rather than directly on a more distal part of the humerus itself, would seem to decrease the effectiveness of action, and the only possible function when the arrangement is as shown in figure 17 is a bracing of the coracoid.

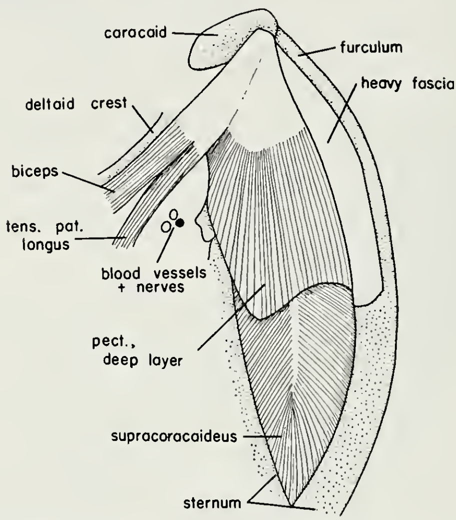


FIG. 17. Ventro-lateral view of the deep breast muscles to show variation in direction of fibers of the deep part of M. pect. and its unusual insertion.

M. supracoracoideus

This is the deepest of the pectoral muscles (figs. 17, 29) and is of pinnate structure. The anterior half of the fleshy belly is immediately beneath the deep part of M. pect. but is separated from it by a heavy aponeurotic sheet extending from the furculum to the coracoid, and the posterior half is deep to the superficial part of M. pect. Just posterior to the sternocoracoidal articulation, nerves and blood vessels enter the middle of the length of the dorsal edge of the belly after emerging from a foramen in the coracoid. The nerves are branches of the trunk of N. brachialis longus, but they come off proximal to the area of formation of the inferior and superior trunks. Thus it can only be noted that the fibers may come from either the 15th or 16th spinal nerves or from both.

Although the superficial pinnate structure of the muscle is as shown in figure 29, this pinnate part constitutes less than one-third of the bulk of the muscle. The deeper two-thirds consist of fibers which form a tendon along the dorsal edge of the belly. The two tendons fuse opposite approximately the middle of the coracoidal length.

There is a fleshy anterior part of the muscle which is identical to that described for cathartids by Fisher (1946:579), except that it continues dorsad up through the triosseal canal and inserts on the tendon of the main part of the M. supracoracoid., beneath the belly of M. delt. minor (fig. 19).

Origin.—Fleshy origin comes from all the surfaces of the keel and the sternal plate covered by the belly (fig. 29). This extends anteriorly on to the proximal half of the anterior face of the coracoid and to the most anterior extent of the bony tracheal enclosure formed by the sternum. The anterior fleshy part arises from the medial edge of the coracoid, the lateral surface of the furculum, and the fascial sheet between the coracoid and the furculum.

Insertion.—A strong tendon emerges from the dorsal end of the triosseal canal, passes distally beneath M. delt. minor, and attaches to the anconal surface of the external tuberosity of the humerus.

M. sternocoracoideus

The tripartite belly of this muscle lies anterior and superficial to the sternal part of the second rib, deep to the anterior edge of M. ext. obliq., and superficial to the outer layer of the intercostal muscles (fig. 29). There is always innervation from the same inferior trunk of N. brachialis longus that goes to the great pectoral muscles (figs. 14, 15); there may be a second nerve from the fused trunk formed by nerves 15 and 16.

Origin.—The dorsal fasciculus arises as mixed fleshy and tendinous fibers from the antero-lateral surfaces of the second rib, and the more ventral band comes from the posterior edge of the second sternal rib and the antero-lateral surfaces of the third sternal rib. The anterior bundle arises fleshily from the entire length of the sternocoracoidal process of the sternum, deep to the belly of M. coracobrach. post.

Insertion.—There are also three parts to the insertion. The more posterior and superficial insertion is mixed fleshy and tendinous on the posterior edge of the sternocoracoidal process of the coracoid. The deeper insertion here is tendinous on the most dorsal aspect of the sternocoracoidal process of the sternum. The most anterior bundle of the belly inserts by means of fleshy and tendinous fibers in the usual sternocoracoidal impression on the coracoid.

M. coracobrachialis posterior

The heavy, fleshy belly is bipinnate and lies on the proximo-lateral surface of the coracoid, but as it extends dorsally it curves around to lie on the posterior surface of the shaft of the coracoid. The antero-lateral part of the belly is in contact with M. supracoracoid. and the middle and proximal parts of the belly cover most of the distal parts of M. sternocoracoid. (fig. 29). Blood vessels and nerves emerging from the chest cavity send branches to the superficial surface of the dorsal part of the belly. Innervation is by a branch from the fused 15th and 16th spinal nerves prior to the separation into superior and inferior divisions (fig. 14), and sometimes from the inferior division.

Origin.—The origin is fleshy from the lateral half of the antero-lateral face of the proximal one-half of the coracoidal length and extends medially and dorsally on to the postero-lateral aspect of the coracoid. In the middle of the coracoidal length the free belly is separated from the bone by a large vein which comes proximally around the head of the humerus.

Insertion.—The tendon inserts on the internal tuberosity of the humerus.

M. latissimus dorsi

This muscle usually consists of three parts lying on the superficial aspect of the interscapular region and extending from the vertebral column to the humerus (figs. 18, 22, 25). The posterior band is deep to the anterior bundle, where they cross, and the dermal component, if present, may be superficial to the posterior band or may be a caudal division of this band. These two conditions of the dermal fasciculus are shown in figures 18 and 22; the left side of the bird whose right side is shown in figure 18 did not have any dermal muscle in this region. The variation in size of this dermal part may be seen by comparing figures 18 and 22. Gadow (1891:228) found no pars metapatagialis in *G. leucogeranus*. Our specimen of the Little Brown Crane showed the condition illustrated on the right side of figure 22.

The innervation is complex. The most dorsal part of the anterior belly often receives branches of the 19th and 20th posterior primary rami which come out through the fleshy sheet of M. rhomb. superf. The 21st posterior primary ramus sends twigs to the posterior part of M. lat. dorsi and to the dermal component (fig. 14). In this same figure and in figure 15 it may be observed that various twigs of the superior division of N. brachialis longus serve this muscle complex.

Origin.—The anterior part arises by a thin aponeurosis 7 centimeters wide from the neural crests of the thoracic vertebrae. This origin (figs. 18, 22) is just superficial to the origin of M. rhomb. superf. Another aponeurosis, starting approximately 1 centimeter posterior to the anterior one and going caudad to the fascial origin of M. extens. ilio-tib. ant., forms the origin for the posterior band of M. lat. dorsi. There may also be fascial origin from the connective tissue overlying the costal musculature. In some instances the origin of the posterior band is deep to the origin of the dermal part, but this seems to be less frequent in occurrence than is the formation of the dermal component as a fasciculus of the posterior band. The posterior edge of M. lat. dorsi, post. pt., just covers the caudal end of the scapula.

Insertion.—The anterior part inserts fleshily on a narrow line, some 5 centimeters long, beginning about four centimeters from the proximal end of the humerus. The belly enters the musculature of the upper arm palmar to the scapular head of M. triceps and anconal to the entrance of M. lat. dorsi, post. pt.

The tendon of this latter part of the muscle attaches to the deep side of the anterior part but also inserts on the humerus beneath the fleshy insertion of the anterior portion.

M. cucullaris, hals part

This band of muscle, some 9 centimeters wide, lies over the anterior part of the cervico-thoracic region (figs. 18, 22, 25) and extends to the shoulder. Posteriorly the muscle is in contact with M. rhomb. superf. and distally with Mm. pect., tens. pat. brevis, and delt. major. The posterior part of the muscular sheet overlies the anterior edge of M. rhomb. prof. Anteriorly on the neck the muscular fibers are smaller and more widely spaced. Branches from the combined 14th and 15th spinal nerves and posterior primary ramus 15 go to this muscle (figs. 14, 15). In some instances, nerves to this muscle may come from the 14th and 15th prior to the fusion of the nerves.

Origin.—A thin aponeurosis from the most dorsal part of the neural crests of vertebrae 18, 17, 16, and the posterior part of 15 provides the origin for the muscle (figs. 18, 22).

Insertion.—The posterior part of the muscle, consisting of shorter fibers, inserts fleshily and tendinously on the most anterior centimeter of the dorso-medial edge of the scapular head and is perforated by blood vessels and nerves emerging from the triosseal canal. The insertion anteriorly and ventrally continues to be largely fleshy, but with some obvious fascial connections, on the antero-medial edge of the furculum. Attachment to the furculum continues ventrad to within 4 centimeters of the furcular symphysis.

It is of interest that the ventral portion of the hals part of M. cucullaris, between the clavicle and the trachea, is very closely adherent to the underlying clavicular air sac. There is wide aponeurotic origin from the fascia overlying the lateral surface of the base of the neck. The short muscular fibers originating here are only one-third the length of those in the main belly. It would seem, therefore, that the sparse and thin belly dorso-anteriorly and the complete absence of the dorsal two-thirds of the existing antero-ventral fibers indicate a considerable reduction in the anterior extent of this muscle.

M. rhomboideus superficialis

The short but wide belly of this muscle lies between the scapula and the vertebral column, deep to M. lat. dorsi, and at its anterior edge superficial to M. rhomb. prof. (figs. 18, 22). The fibers fan out somewhat, as they pass laterally. The innervation is through the posterior primary rami of spinal nerves 19 and 20 (fig. 14).

Origin.—An aponeurosis from the neural crests of all vertebrae from

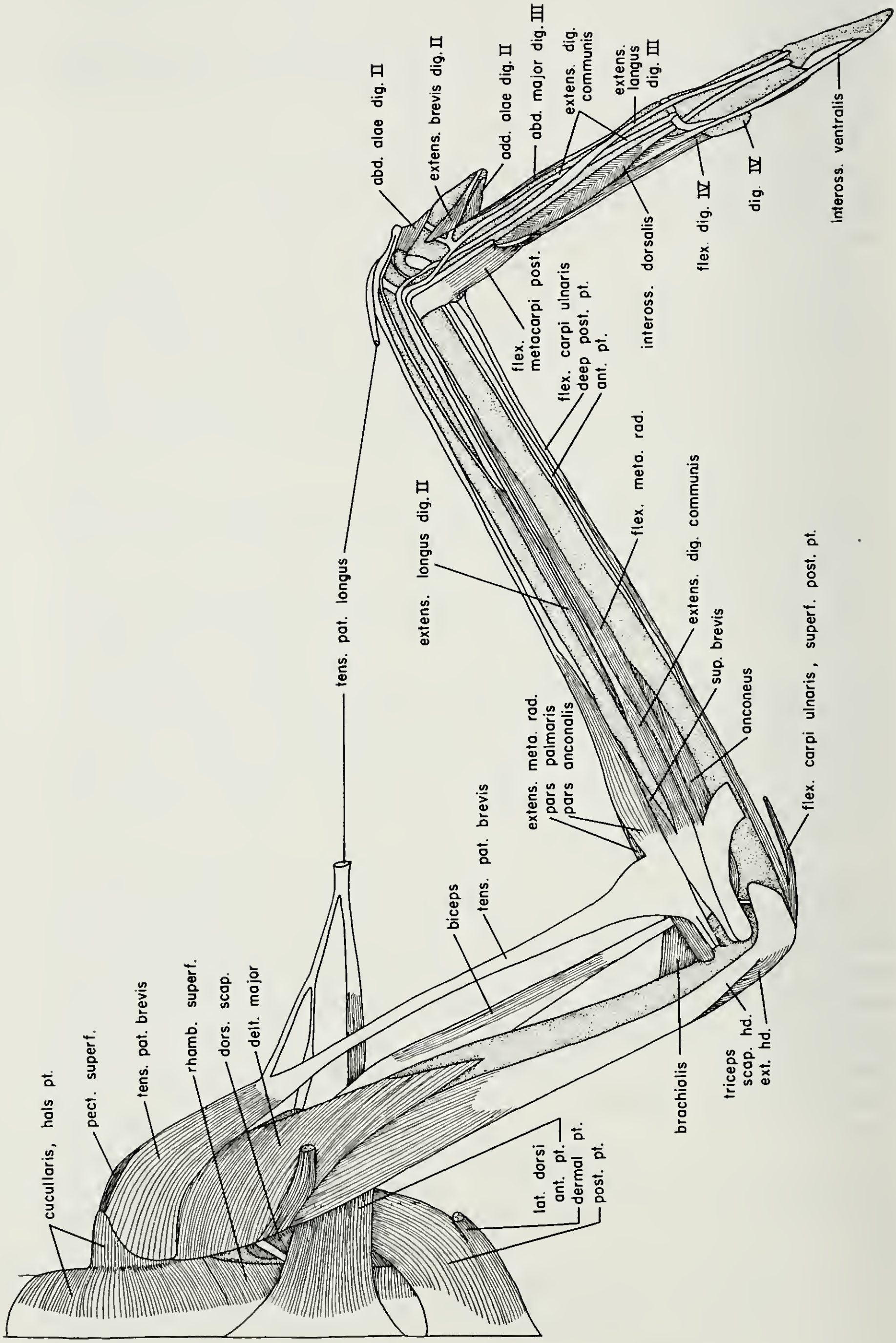


FIG. 18. Dorsal view of the superficial musculature of the right shoulder and wing. For details of the tendinous complex of M. tens. pat. longus see figure 16.

number 19 to the most anterior extent of the sacrum forms the origin. In some birds the posterior three or four centimeters of the width of the muscle are tendinous from the origin to the scapula and are strongly connected to the underlying M. rhomb. prof. The entire aponeurosis of origin is a caudal extension of the aponeurosis of M. cucullaris, hals pt.

Insertion.—Mixed fleshy and tendinous fibers, mostly fleshy in the anterior part and completely tendinous posteriorly attach to the dorsal border of the scapula. This insertion extends posteriorly from the caudal edge of the insertion of M. cucullaris to the distal tip of the scapula.

M. rhomboideus profundus

This is an extremely wide and thin sheet of muscle, deep to the hals part of M. cucullaris and to M. rhomb. superf.; it extends from the posterior end of the 16th vertebra to the last vertebra in front of the sacrum. The fibers run somewhat posteriorly as they go laterad from the vertebral column to the scapular blade (fig. 22). Innervation is from the posterior primary rami numbers 18 to 21, inclusive (fig. 14).

Origin.—The origin is by a narrow aponeurosis from the dorsal crests of vertebrae 17 to 22 (fig. 22) and deep to the origins of M. cucullaris, hals pt., and M. rhomb. superf. This origin is also closely applied to the underlying longitudinal spinales muscles.

Insertion.—Fleshy fibers attach to the entire length of the dorso-medial edge of the scapular blade. In some specimens the anterior one-half of the insertion is partly tendinous in this position, and the posterior half gradually encroaches on the medial surface of the scapula until, at the tip of the blade, the entire width of the medial face is utilized as an area for insertion.

M. coracobrachialis anterior

The heavy muscular band constituting this muscle lies anteriorly on the shoulder, between the coracoid and the humerus (figs. 22, 29), and deep to the distal end of M. pect. and to the origin of M. tens. pat. brevis. The postero-dorsal part of the belly is in contact with M. delt. minor. On the palmar side the tendon of origin of M. biceps covers M. coracobrach. ant., which in turn lies just superficial to the palmar ligament of the shoulder joint.

Innervation may come from the inferior branch of N. brachialis longus going to M. biceps (fig. 14) or from the inferior branch serving the great pectoral muscles (fig. 15).

Origin.—Fleshy and tendinous fibers arise from the antero-dorsal part of the coracoid; only tendinous origin comes from the tendon of origin of M. biceps, and the two tendons are inseparable ventrally.

Insertion.—The insertion is superficially and anteriorly fleshy on the palmar surface of the humerus. The area extends distally as far as the distal end of the bicipital crest, but is delimited posteriorly by the bicipital furrow and the proximal part of the base of the deltoid crest. Thus the insertion is deep to the insertion of the superficial part of the M. pect. and is bordered antero-proximally by the insertion of the fleshy anterior part of M. supracoracoid.

M. deltoideus minor

In figures 19 and 22 it may be seen that this small finger of muscle is the deepest of all muscles on the dorsal side of the shoulder joint. It lies between the scapulo-clavicular articulation and the humerus. It closely invests the tendon of insertion of M. supracoracoid. (fig. 19). The principal innervation is from the same branch of N. brachialis longus superior that goes to M. delt. major, but usually there are branches from the undivided trunk of spinal nerves 15 and 16 that go to M. delt. minor and to M. tens. pat. brevis (figs. 14, 15).

Origin.—Tendinous origin anteriorly comes from the most dorsal coraco-clavicular ligament. Posteriorly there is fleshy origin from the most anterior part of the middle of the scapular head and from the lateral surface of the clavicle.

Insertion.—Proximal to the insertion of M. delt. major on the deltoid crest of the humerus, there is fleshy attachment to the anterior edge of the deltoid crest. In its distal part the insertion, which begins immediately distal to the external tuberosity, laps over on to both the anconal and palmar edges of the crest and completely hides from antero-dorsal view the insertion of M. supracoracoid.

M. proscapulohumeralis and M. subscapularis

The bellies of these two contiguous muscles are more nearly separate in the Whooping Crane than in the cathartid vultures described by Fisher (1946:584). Except at the extreme anterior edge the bellies are covered by M. dorsalis scap. M. proscapulohum. may be regarded as the lateral, superficial fasciculus which is separated in its proximal half from the underlying band (M. subscap.) by the inserting tendon of M. serr. ant. (fig. 19). M. proscapulohum. may cover M. subscap. completely, as illustrated, or the latter muscle may be visible in its most posterior extent just superficial to M. serr. prof.

The innervation may be provided from the combined trunk of the 15th and 16th spinal nerves, prior to the division into dorsal and ventral branches (fig. 14), from only the 16th trunk by the branch going to the serratus plexus (fig. 15), or from a combination of these two sources. It thus seems apparent that the 16th spinal nerve could be the origin of the nerve fibers in each instance.

Origin.—The proscapulohumeral part arises fleshily from the ventral edge of the second and third fifths of the length of the scapular blade and from the ventral half of the lateral face of the second fifth of the scapula. M. subscap. takes fleshy origin from most of the width of the medial surface of this bone in the second and third fifths of its length.

Insertion.—Distal to the tendon of insertion of M. serr. ant. it is impossible to distinguish two separate bellies, and their insertion is, therefore, in common. The insertion is primarily tendinous, but with some fleshy attachments, on the posterior border of the proximal one-half of the capital groove on the anconal surface of the humerus and extending on to the internal tuberosity anterior and dorsal to the insertion of M. subcoracoid.

There is strong, almost tendinous, fascial connection between the deep, distal part of the belly and the underlying ribs 2 and 3. This might be considered a part of the insertion.

M. proscapulohumeralis brevis

This is a very thin band of muscle extending from the scapula to the anconal surface of the proximal part of the humerus. It 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. At its origin it is but 1 centimeter wide, and gradually narrows down to a tendon some 2 millimeters wide. The entire length is only 3.5 centimeters.

The innervation is from the combined trunk of the 15th and 16th nerves. Sometimes it is from a twig which emerges from the center of M. proscapulohum. and passes to M. proscapulohum. brevis from beneath the scapular head of M. triceps. In other instances the innervation is from the same branch that serves Mm. tens. pat. brevis and delt. minor. This variation is not as great as might be thought at first, however, for it can be seen in figures 14 and 15 that in either case the twigs come from the same dorsal part of the nerve trunk.

Origin.—Mixed fleshy and tendinous fibers arise from the dorso-lateral face of the neck of the scapula, deep and posterior to the fleshy scapular origin of M. delt. major and just anterior to the scapular origin of M. triceps. The more lateral and deeper part of the muscle takes origin from the ventral edge of the scapular neck. This deeper origin is entirely tendinous, and the tendon is continuous with the tendon of insertion.

Insertion.—The fleshy fibers of the origin insert on the tendon just described, and this tendon then passes to the distal end of the medial crest of the humerus. It attaches here, posterior to part of the insertion of M. delt. major and proximal to the most proximal part of the origin of the external head of M. triceps.

M. dorsalis scapulae

The heavy, triangular belly of this muscle passes laterally from the scapula to the humerus (figs. 22, 25, 29). It is hidden from dorsal view by the latissimus dorsi complex of muscles, and in turn it covers Mm. proscapulohum. and subscap. The antero-distal edge of the belly is posterior to M. delt. major, while the postero-ventral border of the distal part is dorsal to the large blood vessels and nerves emerging from the axilla and superficial to the belly of M. serr. ant. (fig. 29).

The nerve which serves M. proscapulohum. and which arises from the combined 15th and 16th spinal nerves sends a twig to M. dorsalis scap. before breaking up into several branches which pass to the intercostal musculature (figs. 14, 15). In at least one instance the nerve giving rise to the twig to M. dorsalis scap. continued to the serratus plexus.

Origin.—There is fleshy origin from the entire length and width of the outer surface of the scapular blade, except in the distal 3 centimeters of scapular length where the origin is from only the ventral half of the width.

Insertion.—Superficially there is a strong ensheathing tendon which attaches to the proximal anconal edge of the bicipital crest; the deeper part is fleshy to the same area.

M. serratus posterior

This muscle consists of two major parts—a superficial and a deep layer—but the superficial sheet has a separable dermal component along its anterior edge (fig. 25). Although the fundamental condition of this superficial sheet is the same in the birds we dissected, there is considerable variation in the dermal fasciculus. In one specimen of *americana* and in *G. canadensis* it was approximately four times as large as it is shown in the drawing. The fibers of all parts are aligned in practically the same direction, but those of the deep layer are shorter (fig. 25). The contractile part of the deep layer is nearly twice the width of the superficial belly. At their dorsal ends the superficial and deep layers are separated by the postero-proximal part of M. dorsalis scap.

Nerves may come to this group of muscles from the serratus plexus and from the common trunk of spinal nerves 15 and 16 (figs. 14, 15). Sometimes only one and sometimes both these sources seem to be utilized, but in all instances Mm. serr. post. and serr. ant. are served by the same branch and M. serr. prof. is innervated by a branch from the 15th nerve.

Origin.—The superficial layer arises by a wide aponeurosis from the external surfaces of ribs 4, 5, 6, and 7 and from fascia overlying the external layer of intercostal muscles (fig. 25). This origin is ventral to the uncinate processes and immediately ventral and superficial to the origin of the deep layer (figs. 25 and 29), which is confined to ribs 4, 5, and 6 and the intervening costal musculature but which in some cases extends anteriorly on the rib basket to the posterior edge of rib 3. The aponeuroses of the two layers are distinctly separate.

Insertion.—The posterior half of the insertion of the superficial portion is widely tendinous to that part of the external surface of the tip of the scapular blade not occupied by the origin of M. dorsalis scap. The anterior half is on the dorso-lateral edge of the scapula and dorsal to the origin of M. dorsalis scap. (fig. 25). The dermal component attaches fleshily to the skin at the caudal end of the scapular feather area. A broad tendon to the posterior 4 centimeters of the ventral edge of the scapula forms the insertion of the deep layer (figs. 19, 29); the anterior part of this insertion is separated from that of the superficial layer by the origin of M. dorsalis scap.

M. serratus profundus

Three rather indistinct slips of this muscle lie dorso-medial to the scapula; only two are visible in lateral view (fig. 19). A fourth slip lies ventro-medial to the distal half of the scapular blade (fig. 19). The dorsal margin of the first three fasciculi is closely attached to the latero-ventral edge of the spinales muscles along the vertebral column. Dorsally these fasciculi are covered by M. cucullaris, hals pt., and by M. rhomb. prof. The fourth finger of muscle is hidden laterally by M. subscap. and M. dorsalis scap.

Nerve branches of the 15th spinal nerve go to the dorsal and ventral surfaces of all the slips (figs. 14, 15).

Origin.—Three distinct areas give tendinous origin, but there is much fascial interconnection. The most anterior of the three dorsal slips comes from the ventro-lateral anterior corner of the transverse process of the 18th vertebra. The second slip arises from the lateral surface of the most proximal part of the blade of rib 1, and the third fasciculus from the same area of rib 2. The first, or most anterior, slip is the largest. The ventro-medial part of this muscle comes fleshily from the posterior edge of rib 2 (fig. 19) and approximately one centimeter ventral to the origin of the third slip of the dorso-medial group.

Insertion.—All the slips insert as fleshy fibers on the medial surface of the scapular blade, and the ventro-medial finger of muscle also attaches to the ventral edge of the scapula. The length of the area of insertion is from four centimeters distad of the scapular head to within two centimeters of the caudal end of the scapula.

M. serratus anterior

In striking contrast to the other serratus muscles, M. serr. ant. has but one simple fasciculus. It courses antero-dorsad from the rib basket to the scapula, in its passage going between the bellies of Mm. proscapulohum. and subscap. (figs. 19, 25, 29). Source of the innervation is from a nerve formed by branches of the 15th and 16th spinal nerves. It may go to this muscle prior to entering the serratus plexus (fig. 14), or a nerve from the plexus may pass to the muscle (fig. 15).

Origin.—The second and third and occasionally the fourth ribs, at the level of the uncinate processes, and the intercostal musculature here (figs. 19, 25, 29) furnish fleshy and aponeurotic origin.

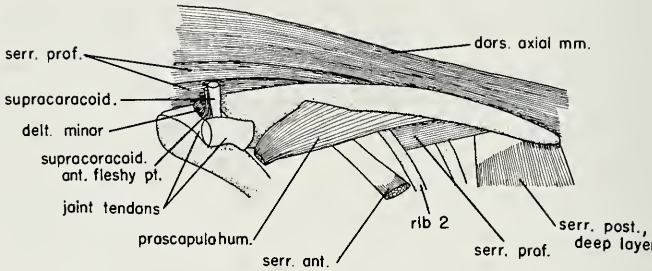


FIG. 19. Lateral view of the deep muscles of the shoulder.

Insertion.—The band-like tendon of insertion separates the fleshy bellies of Mm. proscapulohum. and subscap. before attaching to the ventral edge of the scapular blade some nine centimeters from the distal end of the scapula. This insertion is about one-third of the way caudad on the scapula.

M. subcoracoideus

This is a small, weak muscle arising fleshily from the postero-internal corner of the coracoid, at the level of the procoracoid, and extending to the humerus. Tendinous insertion on the humerus is on the proximal face of the internal tuberosity immediately posterior to the insertion of Mm. proscapulohum. and subscap.

A nerve from the combined 15th and 16th roots goes to this muscle. The nerve may (fig. 14) or may not be produced before the trunk forms dorsal and ventral divisions; if the nerve comes off after this separation, it is always from the dorsal division (fig. 15) and thus indicates this source in all instances.

M. biceps

The anterior edge of the deeper musculature of the upper arm is formed by the long, thin belly and tendon of M. biceps (figs. 16, 18, 29). Dorsally and anteriorly it is covered by the humeral muscles and the tensors; ventrally, the large pectoral muscle hides it proximally. Thick, tendinous fascia closely ensheaths much of the contractile tissue. Near the distal end of the belly and on its ventro-anterior edge a tendon diverges to provide the origin of the only belly of M. tens. pat. longus (fig. 16). A variation of this relationship between the two muscles is shown in figure 17, in which it may be seen that the two simply have a common, tendinous origin which is intimately connected to the insertion of the deep layer of M. pect.

A branch of N. brachialis longus inferior enters the deep side of the belly (figs. 14, 15).

Origin.—A tendon 1.5 centimeters wide comes from the bicipital area of the ventro-anterior corner of the lateral face of the coracoid. This tendon always forms a part of the origin, but is not invariably used as well for origin of M. tens. pat. longus and as insertion by part of M. pect., as indicated in figure 17. (See the descriptions of these muscles for other relationships). The larger head of origin of M. biceps is tendinous from the bicipital crest of the humerus; this head may receive twigs from N. brachialis longus superior. The two heads fuse completely one-third of the way distad on the humerus.

Insertion.—A tendon is formed about five-sixths of the way out the humerus; almost immediately it bifurcates to form two rounded tendons as it enters the antero-palmar part of the muscles of the forewing. Entrance is made just palmar to the entrance of N. brachialis longus superior and the superior brachial blood vessels. The two tendons are anconal to the insertion of M. brachialis. The insertion of the more anconal tendon is on the bicipital tubercle about one centimeter from the proximal end of the radius. Attachment by the other tendon is in the usual position on the ulna and some 2 centimeters from the proximal end of the olecranon process.

M. deltoideus major

Figures 18 and 22 show the position of the muscle. It lies on the medio-anconal surface of the proximal half of the upper arm, bordered anteriorly beneath M. tens. pat. brevis by M. delt. minor. About one-third of the way distad along the posterior edge of M. delt. major a dermal component arises and passes antero-dorsad to the skin (dermal component not found in Little Brown Crane). Deep to the origin of this dermal slip, and coming from the middle of the thickness of the posterior edge of the main belly is a tendon 3 millimeters wide. This tendon goes across the scapular head of M. triceps and M. dorsalis scap. (fig. 18) to attach to the dorso-lateral face of the scapula about one-third of the distance posteriorly on the scapula.

Anteriorly directed twigs from N. brachialis longus superior enter the middle of the posterior side of the belly, after emerging from beneath the scapular head of M. triceps. Usually there are distinct twigs going to the anterior and posterior parts of the belly (figs. 14, 15). Another branch of one of the twigs continues anteriorly to serve M. delt. minor (fig. 14).

Origin.—It is fleshy from the dorso-lateral surface of the scapular head, anterior to the origin of the scapular part of M. triceps, and posterior to that part of M. delt. minor which comes from the scapula. At its dorso-medial edge there is some origin from the dorsal end of the clavicle. The tendon, previously described, to the blade of the scapula might also be considered as part of the origin.

Insertion.—The distal end of the belly tapers to a point (fig. 18) on the anconal surface of the humerus. The insertion is thus fleshy and embraces all of the proximal half of the anconal surface exclusive of the bicipital area and that region lying proximal to a line drawn between the external tuberosity and the ligamental furrow. The posterior edge of the insertion is marked in the middle of its length by the wide aponeurosis which the scapular head of M. triceps sends to the anconal surface of the humerus; distally the posterior edge is next to the anterior edges of the fleshy origins of the internal and external heads of M. triceps.

M. triceps

The various heads of this muscle form the entire posthumeral musculature of the wing (figs. 16, 18, 22, 25, 29). On the dorsal aspect of the wing, M. triceps is covered proximally by M. delt. major, and on the palmar side of the wing by M. biceps and M. pect. Three muscles constitute M. triceps—the scapular, the external, and the internal heads.

The belly of the scapular head extends nearly to the distal end of the humerus. On the mid-anconal surface of this head and opposite the distal half of the deltoid crest, a strong band of connective tissue connects to the anconal surface of the humerus. Proximally the scapular and external heads are separated by the main trunk of N. brachialis longus superior and by major blood vessels passing to the wing.

The external head lies along the entire postero-anconal surface of the humerus. It is a heavy bipinnate muscle which has the bulk of its contractile structure limited to the proximal half of the humeral length; some few fibers continue distad nearly to the elbow. Distally the bellies of the external and internal heads are intimately connected. It seems, in fact, as though the internal head is a distal continuation of the anterior half of the pinnate structure of the scapular head. Thus the fibers of the internal head extend disto-posteriorly from the anterior edge of the anconal surface of the humerus to a separate tendon of insertion which is formed anterior to the tendon of the external head. In their distal extent the fibers change direction to insert on the common tendon utilized by all the heads.

All innervation is from the N. brachialis longus superior (figs. 14, 15). The branch to the scapular head is separate from the branch that goes to both the internal and external heads.

Origin.—The origin of the scapular head of M. triceps is from a dorsoventral line 1.5 centimeters wide which lies on the posterior edge of the head of the scapula and just posterior to the origin of M. delt. major. This is a mixed fleshy and tendinous origin. There is also strong fascial origin from the anterior edge of the proximal part of M. dorsalis scap.

The external head arises fleshily from the posterior half of the anconal surface of the humerus from the proximal part of the bicipital surface distad to the beginning of the distal third of the humeral length. This includes part of the origin of the internal head, the rest of which has previously been described.

Insertion.—The strong, band-like tendon formed at the level of the humeral condyles contributes to, or at least is attached to, the joint membrane but continues distally to insert on the anconal surface of the ulna in an obliquely antero-posterior line some 3 centimeters long and 1.5 centimeters from the proximal end of the ulna (fig. 18).

M. brachialis

The origin, insertion, and relations of the muscle are as described by Fisher (1946:591). (Most of these features may be seen in figures 16, 18, 20, 21.)

M. extensor metacarpi radialis

The long, slender fusiform bellies of the muscle form the anterior edge of the musculature of the forewing (figs. 16, 18, 20, 21). The pars anconalis forms its belly about four centimeters distad on the forewing, and its belly extends to the middle of the radial length. The belly of the pars palmaris lies in the proximal third of the radial length, anterior and ventral to the pars anconalis, and anconal to the inserting tendon of M. biceps and the major blood vessels and nerves entering the forearm musculature. Pars palmaris is twice as large as pars anconalis. M. tens. pat. brevis inserts widely on the originating tendon of the anconalis part of M. extens. meta. rad. (fig. 18).

A branch of N. brachialis longus inferior sends twigs to the two bellies. The palmaris is entered in the middle of its posterior surface and the anconalis in the middle of its palmar face.

Origin.—Pars anconalis may originate from the ectepicondylar prominence of the humerus as two small flat tendons (fig. 18). One of these tendons has perhaps been usurped from the inserting tendon of M. tens. pat. brevis, for the tendon in this latter muscle is in part continuous with this origin. In one specimen the origin was by but one tendon. Pars palmaris takes mixed fleshy and tendinous origin from the same prominence but proximal and palmar to the origin of the pars anconalis; the tendinous part of the origin is limited to the palmar side and is covered anconally by the fleshy origin (fig. 18).

Insertion.—The calcified tendon of the anconalis part fuses to the posterior edge of the calcified tendon of the pars palmaris at the distal end of the radius to form a common uncalcified tendon of insertion. This tendon continues across the anterior surface of the wrist and deep to the tendon of M. tens. pat. longus. Just before attaching to the proximal side of the tip of the extensor process of metacarpal II, this tendon fuses with the inserting tendon of M. extens. longus dig. II (figs. 18, 20, 21).

M. extensor digitorum communis

The bipinnate belly is restricted to less than the proximal half of the radial length and is in a superficial, anconal position (figs. 16, 18). The belly is triangular in cross-section, and its bipinnate structure is visible only on its deep surface.

As the posterior branch of N. brachialis longus superior passes distally

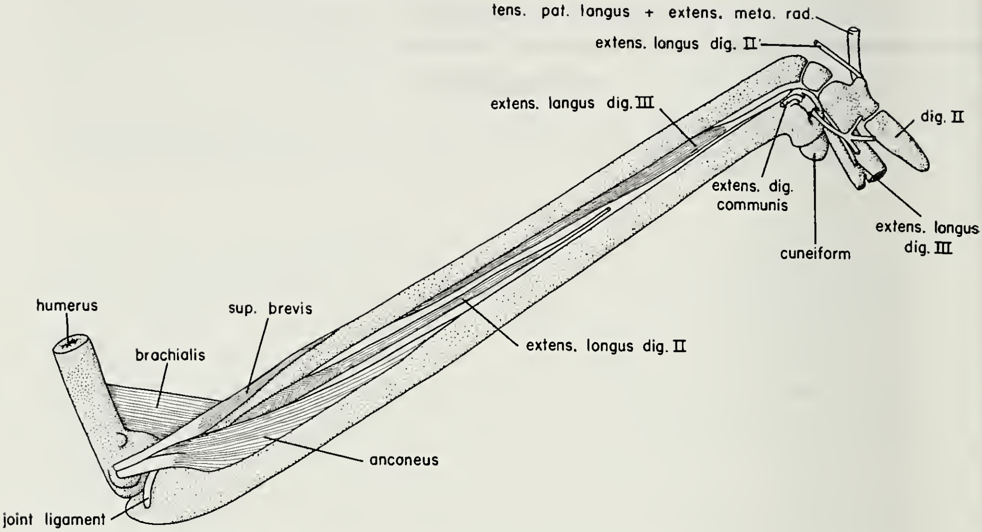


FIG. 20. The deep musculature of the right forewing as observed in dorsal view.

between the bellies of the present muscle and M. anconeus it sends twigs to each.

Origin.—Superficially the origin is strongly tendinous in common with Mm. anconeus and sup. brevis (fig. 18). Deep to the distal half of this tendon and extending out one-third the length of the radius, there is fleshy origin from the posterior side of the radius. It is this origin which makes the muscle bipinnate on its deep side.

Insertion.—Just before the middle of the length of the forearm is reached, a small round tendon is formed. It passes distally along the antero-anconal corner of the ulna, deep to the tendon of M. flex. meta. rad., and in its own tendinous canal over the anconal surface of the external condyle of the ulna. In the drawing of this region (fig. 18) the tendons have been somewhat displaced to show their continuity from forearm to hand. The tendon of M. extens. dig. communis is actually the only one to cross the anconal face of the ulnar condyle; all other tendons pass through the tendinal groove on the distal end of the ulna (fig. 20).

Once across the wrist joint the tendon goes disto-anteriorly on the metacarpus and crosses superficially the tendon of insertion of M. extens. longus dig. III. Opposite the base of digit II a tendon comes off anteriorly and at right angles to the main tendon to send a proximal branch to the distal anconal surface of metacarpal II, beneath the origin of M. extens. brevis dig. II, and a distal branch to the postero-anconal edge of the third finger, beneath the middle of the belly of M. extens. brevis dig. II (fig. 18). In one specimen only the distal branch, to the third finger, was present. Tension on this anteriorly directed branch would adduct this finger, but the more proximal attachment to metacarpal II would apparently function only to hold the main tendon in its anconal position on the metacarpus.

The chief inserting tendon continues distally in a bony groove on the antero-anconal edge of metacarpal III, passes beneath the tendon of M. extens. longus dig. III, and goes to its insertion in the middle of the proximal, anconal edge of phalanx 1 of digit III (fig. 18).

M. supinator brevis

The small bipinnate belly is located in the proximal one-fourth to one-third of the antero-anconal surface of the radius (figs. 18, 20, 21).

It lies anterior to the belly of M. extens. longus dig. II and anconal to M. brachialis. The most proximal part of its belly is separated from the radius by a large branch of N. brachialis longus superior which sends a twig into the palmar surface of this muscle.

Origin.—In figure 20 the tendinous origin from the ectepicondylar prominence of the humerus may be observed to be just proximal to the origin of M. anconeus. This origin is also connected to that of M. extens. dig. communis; in some instances (fig. 18) there is a common tendon of origin.

Insertion.—As soon as the muscle leaves the humerus it sends fleshy fibers to the most proximal end of the anconal surface of the radius and even to the joint ligaments. Farther distally the origin fans out to insert fleshily on the anterior surface as well. The muscle is greatly attenuated at its distal end and attaches only to the anterior surface of the radius (figs. 20, 21).

M. flexor metacarpi radialis

This is the most superficial of the anconal muscles lying between the radius and the ulna (fig. 18). Its long, fundamentally bipinnate belly is in the second to fifth sixths of the ulnar length, deep proximally to M. extens. dig. communis and superficial to M. anconeus.

The same anterior branch of N. brachialis longus superior serves this muscle and M. extens. dig. communis.

Origin.—In figure 18 the tendinous origin from the most distal part of the face of the ectepicondylar prominence may be seen. Of special interest is the wide vinculum or aponeurosis which passes posteriorly from the distal end of the originating tendon to insert on a longitudinal line on the postero-anconal corner of the ulna, just anterior to the row of papillae for the secondary feathers.

Insertion.—The round tendon, formed five-sixths of the way out the forewing, continues distad along the antero-anconal surface of the ulna, through the tendinal groove on the distal end of the ulna, and inserts on the fused area of metacarpals III and IV. The attachment is at the proximal anconal end of the intermetacarpal space and adjacent to the antero-distal corner of the insertion of M. flex. metacarpi post. (fig. 18).

M. pronator brevis

On the palmar surface of the elbow (fig. 16) the fusiform belly is located posterior to M. extens. meta. rad., pars palmaris, and anterior and superficial to M. pronator longus. The proximal part of the belly passes between the major branches of the inferior brachial vein. Its anconal edge meets M. sup. brevis on the anterior edge of the radius.

Several twigs from the anterior branch of N. brachialis longus inferior enter the deep side of the muscle after emerging beneath the insertion of M. pronator longus. However, the largest nerve to this muscle comes from beneath the tendon of origin of M. pronator longus and goes into the middle of the most proximal part of the deep surface of the belly of M. pronator brevis.

Origin.—A wide, flat tendon comes from the most proximal part of the internal humeral condyle, palmar and proximal to the proximal end of the palmar articular ligament. The origins of the pronator muscles are separate (fig. 16).

Insertion.—Mixed fleshy and tendinous fibers attach on a line 5 centimeters long on the antero-palmar corner of the radius and starting about 5 centimeters from the proximal end of the radius. The anterior border of this insertion is marked by the insertion of M. sup. brevis.

M. pronator longus

The belly lies in the proximal third of the palmar surface of the forearm (fig. 16); its anterior edge is deep to M. pronator brevis and its posterior border deep to the anterior, tendinous part of M. flex. carpi ulnaris. The bellies of the two pronators are separated by a vein that passes to M. flex. dig. prof., which is beneath M. pronator longus. N. brachialis longus inferior provides innervation.

Origin.—A wide, strong tendon comes from the middle of the medial surface of the internal humeral condyle, deep to the origin of the superficial anterior part of M. flex. carpi ulnaris (fig. 16).

Insertion.—The insertion is 7 centimeters wide and consists of fleshy and fascial fibers attaching to the postero-palmar surface of the radius posterior to the insertion of M. pronator brevis.

M. extensor longus digiti II

The very slender bipinnate belly lies within the proximal half to two-thirds of the radial length (figs. 18, 20, 21). At its proximal end the muscle is located on the palmar side of the forewing and deep to M. anconeus, but it gradually moves to an anconal position in the middle of the length of the forewing. Here it is in part deep to M. extens. dig. communis and anterior to M. flex. meta. rad. From this anconal position posterior to the radius it sends a tendon obliquely antero-distad through the tendinal groove of the radius and then to the anterior edge of the wrist.

In the proximal part of the belly, the anterior branch of N. brachialis longus superior may be found imbedded in the deep surface. Two twigs from this branch enter the deep, anterior surface of the belly.

Origin.—The origin is widely fleshy from the posterior surface of the radius, starting just distal to the insertion of M. biceps and continuing half way out the radius. Just distal to the ulnar insertion of M. biceps there is a short, narrow and fleshy origin from the middle of the anterior face of the ulna. This ulnar connection provides origin for the posterior half of the pinnate structure which is most apparent in the proximal half of the belly's length (fig. 21).

Insertion.—The small tendon of insertion lies superficially on the antero-anconal edge of the wrist just posterior to the tendon of M. extens. meta. rad. Immediately proximal to the insertion on the extensor process of metacarpal II, these two tendons fuse (figs. 18, 20, 21).

M. anconeus

The position and topographical relationships of this muscle may be observed in figures 18, 20, and 21. The belly is not completely bipinnate and is covered by a heavy, silvery sheath of fascia. The same branch of N. brachialis longus superior, that serves M. extens. longus dig. II, sends twigs to the antero-palmar edge of this muscle.

Origin.—A tendon from the ectepicondylar prominence of the external humeral condyle furnishes an attachment for the fleshy fibers (fig. 20).

Insertion.—As soon as the belly is formed just distal to the humero-ulnar articulation, short proximal fibers insert fleshily on the anterior and anconal faces of the ulna. This fleshy insertion continues distad to end in an attenuated point about halfway out the ulna (fig. 20).

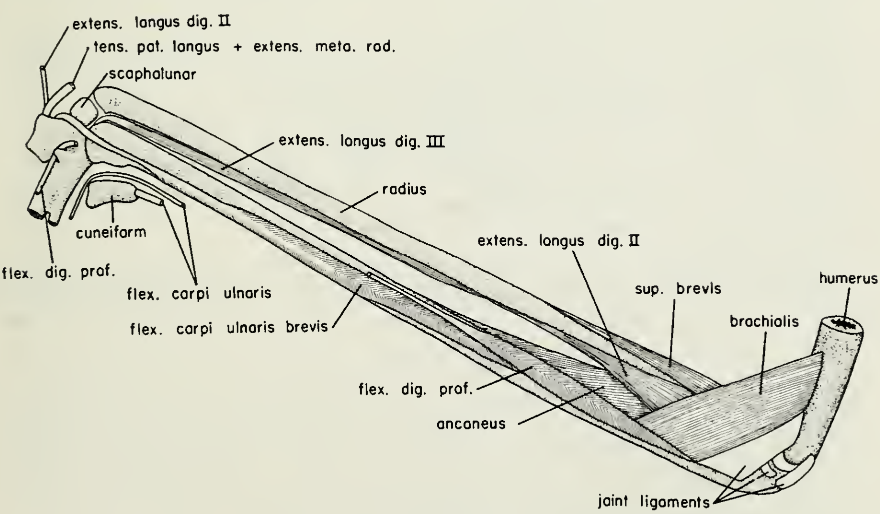


FIG. 21. The deep musculature of the right forewing as seen in ventral view.

M. extensor longus digiti III

The long, slender, pinnate belly is located in the distal two-thirds of the posterior surface of the radius. It may extend to the end of the forewing as contractile tissue (fig. 21) or it may lack several centimeters of attaining this distal position (figs. 16, 20). The proximal third of the belly is in contact with the distal part of the belly of M. extens. longus dig. II, but in figure 20 the two have been separated for greater clarity in delineation. N. brachialis longus superior (the anterior branch) supplies the innervation.

Origin.—Fleshy origin is from the posterior surface of the radius in the middle third of this bone's length (figs. 20, 21).

Insertion.—The uncalcified tendon formed at or near the distal end of the forewing passes through the tendinal groove on the end of the ulna, in its own fibrous sheath. On the anconal surface of the metacarpus and opposite the base of the index finger, this tendon passes beneath the tendon of M. extens. dig. communis (fig. 20). Near the middle of the metacarpal length the tendon crosses superficially the tendon of M. extens. dig. communis and takes up an anterior position which it maintains to its insertion on the antero-anconal corner of the base of phalanx 2 of digit III.

M. flexor digitorum profundus

Figures 16 and 21 illustrate the general position of this muscle on the forewing. It is the deepest of the muscles of the palmar aspect of the proximal third of the ulna. Mm. pronator longus, flex. carpi ulnaris, and usually flex. carpi ulnaris brevis must be removed to bring it into view from the palmar side of the wing. Innervation is from the anterior branch of N. brachialis longus inferior.

Origin.—Fleshy origin from the postero-palmar surface of the ulna extends from the most distal extent of the distal, superficial joint ligament (fig. 21) to the proximal end of the origin of M. flex. carpi ulnaris brevis, which is approximately one-third of the distance out the ulna.

Insertion.—The tendon goes distally on the palmar surface of the ulna, posterior to the tendon of M. flex. carpi ulnaris brevis and just anterior to the tendinous anterior part of M. flex. carpi ulnaris (fig. 16). It crosses the wrist joint beneath the wide, superficial sheath over this joint, hooks around the anterior aspect of the pisiform process of the metacarpus (fig. 21), and passes beneath the strong ligament connecting the pisiform process and the distal end of the radius. As it passes the process it is in part covered by the belly of M. flex. dig II. The tendon courses distad on the antero-palmar corner of metacarpal III, superficial to M. abd. major dig. III, crosses superficially the tendon of M. flex. carpi ulnaris, ant. pt., in the distal half of the metacarpus, and inserts on the anterior palmar edge of the base of phalanx 2 of digit III (fig. 16).

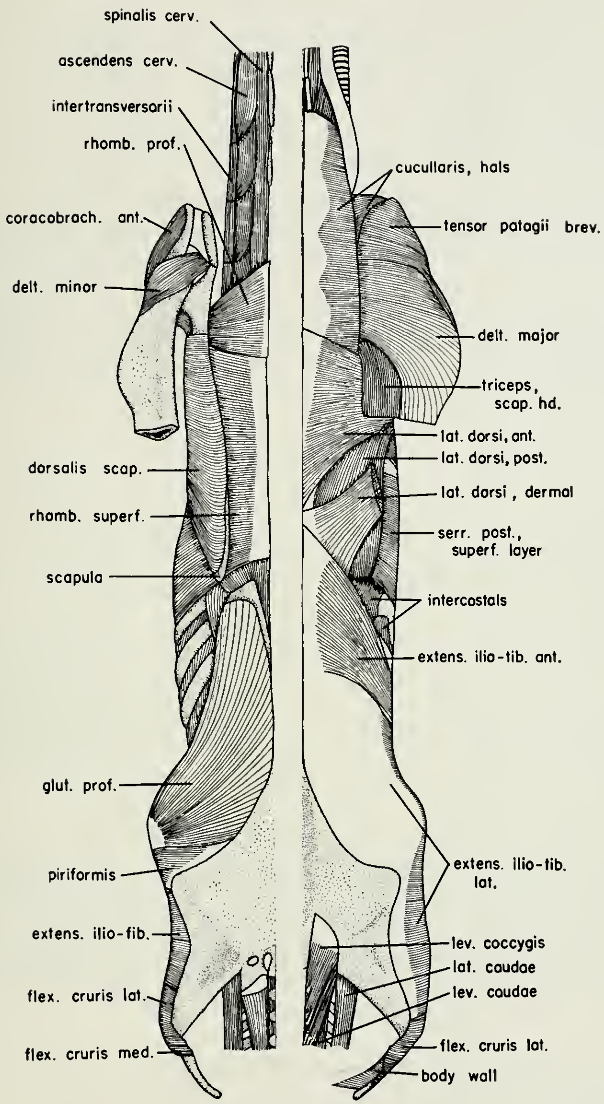


FIG. 22. The musculature of the body in dorsal view. Superficial muscles are shown on the right side and a second layer on the left side.

M. flexor carpi ulnaris

As Fisher (1946:598) found in the American vultures, this muscle consists of three quite distinct parts—an anterior belly which is completely covered on the palmar side by a wide tendon, and a posterior part which has two subdivisions.

The anterior part (fig. 16) is the most superficial of all muscles on the palmar side of the ulna. No contractile fibers are visible on the surface; indeed, this anterior fasciculus may be entirely tendinous except for a few fibers at the proximal end which form a pinnate belly 0.5 centimeters wide and 4.5 centimeters long. This was the condition found on three of the four sides dissected; on one side of one bird the belly was 0.75 centimeters wide and 14 centimeters long. This belly is deep to the superficial tendon and forms its own minute tendon which passes distally beneath the superficial tendon and finally fuses with it at the proximal end of the os cuneiform. The anterior branch of the inferior brachial vein is closely associated with the small tendon throughout the latter's length. The proximal half of the length of the posterior edge of the superficial tendon is connected by a strong aponeurosis to a line on the ulna, which is just posterior to the ulnar papillae for the major under-coverts of the secondaries.

Two elements comprise the posterior part; they lie on the postero-palmar edge of the ulna (figs. 16, 18). The anterior and deeper belly is by far the larger and is of bipinnate structure with the tendon of insertion being formed primarily along its anterior border. In the proximal half of the length of this belly there is strong, fleshy connection to the more superficial and posterior element. This posterior part may be seen as a wide band of aponeurotic tendon which extends posteriorly and distally to fan out over the bases of the feathers growing posteriorly from the forewing. All the contractile fibers lie anterior to this tendon (fig. 16).

Innervation of all three parts comes from N. brachialis longus inferior; each part has a separate twig which enters the deep proximal surface of each belly.

Origin.—The wide tendon of the anterior part arises as the most palmar and centrally located of all the tendons attaching to the medial surface of the internal humeral condyle. This site is immediately proximal to the tendinous origin of the deep division of the posterior part (fig. 16). The very small belly, previously described as deep to the superficial tendon of the anterior part, takes fleshy origin from the deep surface of the tendon.

A round tendon from the most distal extent of the medial face of the internal humeral condyle (fig. 16) provides the origin of the deep bundle of the posterior part of M. flex. carpi ulnaris. The superficial and posterior belly of this part takes fleshy origin from the proximal half of the posterior border of the deep belly of the posterior part.

Insertion.—As mentioned above, the small, deep tendon and the superficial tendon of the anterior part fuse at the proximal end of the os cuneiform. The major part of this combined tendon inserts broadly on the postero-proximal edge of the cuneiform (figs. 16, 18, 21). However, a small tendon, seemingly a structural continuation of the tendon of the small belly but, because of the fusion, now a functional part of the entire superficial part of M. flex. carpi ulnaris, goes distally through the tendinal groove on the anterior surface of the cuneiform (fig. 21) and continues out the palmar side of metacarpal III, along the posterior border of M. abd. major dig. III and later beneath the tendon of M. flex. dig. prof., to insert on the antero-palmar edge of phalanx 2 of digit III (fig. 16). Some 3 centimeters proximal to the insertion on the cuneiform a branch of the superficial tendon passes postero-distad to attach to the strong fascial coverings of the palmar side of the manus and to the fascia around the bases of the feathers.

The deep bundle of the posterior part of the muscle inserts widely and strongly on the most proximal part of the cuneiform. This insertion is closely attached or fused to the insertion of the superficial anterior part. The superficial fasciculus of the posterior part attaches to the fascia over the bases of the feathers arising from the proximal two-thirds of the ulnar length.

M. flexor carpi ulnaris brevis

The bulk of this muscle is in the distal two-thirds of the length of the forewing, but the tendon of insertion may be formed at the beginning of the distal third of the ulna (fig. 16) or farther distad, as at the level of the posterior end of the cuneiform (fig. 21).

The middle of the anconal edge of the belly receives nerve fibers from N. brachialis longus inferior.

Origin.—Fleshy origin comes from that part of the ulna covered by M. flex. carpi ulnaris brevis in figure 21.

Insertion.—The tendon passes to the wrist across the palmar surface of the ulna and deep to the ligament between the radius and the pisiform process of the metacarpus. At the disto-palmar edge of the scapholunar it goes anconally over the proximal anterior part of the anconal carpal trochlea to insert widely on the antero-anconal border of this trochlea. Just before it inserts, the tendon goes beneath the tendons of Mm. extens. longus dig. II, extens. meta. rad., and tens. pat. longus.

M. abductor alae digiti II

Figures 16 and 18 demonstrate the presence of palmar and anconal components in this muscle. The palmar element is anterior to M. flex. dig. II, and the anconal part is nearly in contact with the posterior part of M. extens. brevis dig. II. Thus both sides of the extensor process are covered by this muscle. Anteriorly the bellies are in contact, but the extensor process separates them posteriorly.

The usual avian position of this muscle is on the palmar aspect of the metacarpus. Even though the anconal belly is the larger in the Whooping Crane, the innervation for both bellies comes from the inferior nerve which crosses the surface of M. flex. dig. II. This perhaps indicates that the anconal muscle represents an anterior part of the palmar belly, which part has secondarily moved to an anconal location.

Origin.—The palmar belly has an extensive origin, for such a small muscle, of fleshy and tendinous fibers from the most proximal part of the base of the extensor process and tendinous fibers from the inserting tendon of M. tens. pat. longus. The origin on the anconal side is entirely fleshy from the extensor process.

Insertion.—Anterior and proximal to the articulation of digit II the two distinct heads fuse and continue across the joint to attach to the antero-palmar edge of the proximal half of the index finger. The insertion on the anconal aspect does not extend as far distally.

M. adductor alae digiti II

In *Grus americana* (figs. 16, 18) the muscle is the same as Fisher (1946: 600) described for cathartid vultures.

M. flexor digiti IV

This muscle may be found along the posterior edge of the distal two-thirds of the metacarpus (figs. 16, 18). Proximally it is in contact with the distal end of M. flex. meta. post., and anconally the anterior border touches M. inteross. dorsalis. The end of the median branch of N. brachialis longus inferior provides the innervation.

Origin.—There is fleshy origin from the posterior side of the distal two-thirds of metacarpal IV. In addition there is intimate connection on the palmar side with the fascial overlay shown in figure 16.

Insertion.—The primary attachment is fleshy on the postero-proximal surface of the base of digit IV. However, the bases of the primary feathers are in contact with the anconal face of this muscle and there is much fascial connection with the quills of these feathers.

M. flexor brevis digiti IV

The very small belly of the muscle may be seen in figure 16 to be located on the palmar aspect of the articulation of digit IV. Although there are muscle fibers present, as shown by studies of its cross-section, it is mostly connective tissue. It seemingly represents an anterior distal division of M. flex. dig. IV.

M. abductor minor digiti III

A large tendon, shown in figure 16, is in the proper position for this muscle and probably constitutes the major remnant. There are, however, contractile fibers running antero-distally from the anterior edge of digit IV to the posterior edge of phalanx 1 of digit III and in part to the above tendon. These fibers could exert an insignificant flexing action on digit III, and then only when digit IV is held rigidly. Any abducting function must have been lost when the major part of the muscle became completely tendinous.

M. flexor metacarpi brevis

Not present in the Whooping Crane.

M. interosseus dorsalis

This long, attenuated, bipinnate muscle is visible superficially on the anconal aspect of the metacarpus (fig. 18). Its belly is limited to the proximal three-fourths of the intermetacarpal space and is separated from M. inteross. ventralis by the anterior branch of N. brachialis longus superior which serves both muscles.

Origin.—The anterior fibers of the pinnate structure take fleshy origin from a narrow line along the postero-anconal edge of metacarpal III. Posterior fibers take similar origin from a line on the antero-anconal border of metacarpal IV.

Insertion.—The inserting tendon passes in its own tendinous sling across the joint between the metacarpus and digit III and goes antero-distally to insert on the anterior anconal corner of the base of phalanx 2 of digit III. Its area of attachment is immediately posterior to the insertion of M. extens. longus dig. III.

M. interosseus ventralis

The bipinnate belly of this muscle occupies all of the palmar aspect of the intermetacarpal space (fig. 16). Its postero-palmar edge is in contact with the sheet of fascia extending distally from the wrist. N. brachialis longus superior (ant. branch) supplies the innervation.

Origin.—The anterior half of the pinnate structure takes fleshy origin from the postero-palmar edge of metacarpal III, and the posterior part from the antero-anconal edge of metacarpal IV. The belly of the muscle emerges on the anconal side of the manus and continues distad between the bellies of M. inteross. dorsalis and M. flex. dig. IV (fig. 18). There is, however, no origin distal to the intermetacarpal space.

Insertion.—The tendon which is formed opposite the base of digit III runs across the antero-anconal surface of digit IV and along the posterior edge of the anconal face of the phalanges of digit III to attach to the posterior aspect of phalanx 2, about three-fourths of the way out its length.

M. extensor brevis digiti II

Figure 18 shows the small muscle lying superficially on the anconal aspect of digit II. In some instances its proximo-anterior corner is in contact with M. abd. alae dig. II. M. add. alae dig. II is palmar and distal to the anterior edge of the belly.

Origin.—Mixed fleshy and tendinous fibers arise from the angle formed by the fusion of metacarpals II and III. The origin is superficial to, but intimately interconnected with, the insertion of M. extens. dig. communis on the distal end of metacarpal II.

Insertion.—A tendon extends to the tip of the distal anconal aspect of digit II. This tendon is superficial to the insertion of M. extens. dig. communis on digit II.

M. abductor major digiti III

M. abd. major dig. III is located on the antero-palmar corner of metacarpal III (figs. 16, 18). It is bipinnate and may have two more or less distinct bellies proximally; but these unite in a common tendon about halfway out metacarpal III. The tendons of Mm. flex. dig. prof. and flex. carpi ulnaris (ant. pt.) lie on the palmar surface of the belly.

Origin.—Fleshy origin for the more proximal fasciculus comes from the palmar surface of the base of metacarpal III, distal to the pisiform process, and from the fused area of metacarpals II and III. This latter site of origin is deep to the belly of M. flex. dig. II and posterior to the origin of M. add. alae dig. II. The deeper head, when present, arises from the antero-palmar aspect of metacarpal III.

Insertion.—From 1 to 3 centimeters proximal to the base of digit III the entire muscle becomes tendinous, passes obliquely forward across the joint, and inserts on the antero-palmar corner of the base of phalanx 1, digit III (fig. 16). The insertion thus often lies beneath the wide inserting tendon of M. extens. longus dig. III.

M. flexor digiti II

There is no variation from the description given for cathartids by Fisher (1946:604). See figure 16.

M. flexor metacarpi posterior

Three fingers of muscle comprise this complex which is to be found on the posterior surface of the wrist (figs. 16, 18). The posterior branch of N. brachialis longus superior provides all the innervation. All three fasciculi arise tendinously, and in common, from an arc-shaped line on the anconal surface of the external ulnar condyle. The most posterior of the fingers passes straight distad to begin fleshy insertion on the posterior surface of metacarpal IV about one-third or one-fourth of the distance out the metacarpal. This insertion is only about 1.5 centimeters long; its distal extent is marked by the most proximal part of the origin of M. flex. dig. IV.

The second and smaller belly, which in figure 16 is immediately palmar to the posterior belly, has a tendinous insertion on the posterior surface of metacarpal IV just proximal to the fleshy insertion of the posterior belly. The smallest bundle of muscle is the most anterior part shown in figure 16. It is largely tendinous, the belly being very short, but it has a mixed fleshy and tendinous insertion on the posterior edge of the fused metacarpals III and IV about 2 centimeters proximal to the intermetacarpal space.

Muscles of the Tail

The names of the muscles of the tail follow Fisher (1946:636); a partial synonymy may be found there. We here list, in the sequence in text, the names used; the muscles are discussed in the sequence of easiest removal from the specimen.

Mm. adductor rectricum
M. levator coccygis
Mm. interspinales
M. levator caudae
M. lateralis caudae
M. depressor caudae
M. levator cloacae
M. depressor coccygis
M. lateralis coccygis
Mm. intercoccyges
M. caudofemoralis—considered with muscles of leg (page 85)

Mm. adductor rectricum

Although the general description given by Fisher (1946:627) for cathartids is applicable to the Whooping Crane, there are some differences in insertion. In the crane, fibers originating from the lateral face of the most medial rectrix pass to the *dorsal* surface of the second most medial rectrix and also to the third. This insertion probably results from the fact that the second rectrix lies somewhat below, or ventral to, the other tail feathers (figs. 23, 24).

M. levator coccygis

Figures 22, 23, and 25 show the several fasciculi of this muscle located on either side of the vertebral column in the caudal region. Dorsally a heavy fascial aponeurosis covers the entire muscle. This aponeurosis originates as a continuous sheet from the tips of the transverse processes beneath M. lev. coccygis and emerges dorsally between Mm. lev. caudae and lat. caudae. After emerging it curves toward the midline to attach to the neural crests of the vertebrae. M. lev. coccygis is superficial to the proximal two-thirds of M. lev. caudae (figs. 22, 23).

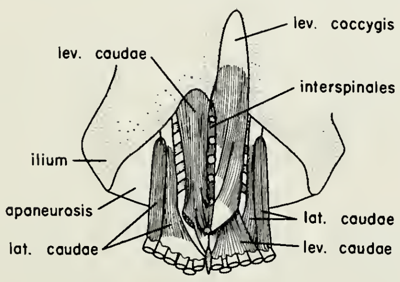


Fig. 23. Dorsal view of the muscles of the tail. On the left side M. lev. coccygis and the distal insertion of M. lev. caudae have been removed.

Origin.—Anteriorly the origin is entirely tendinous from the dorsal surface of the sacrum, beginning anteriorly at the level of a line between the two antitrochanters. The origin extends posteriorly on to the transverse process of the first free caudal vertebra, but is fleshy in the caudal half of its length.

Insertion.—The three fingers of the belly have separate insertions. The most medial inserts on the lateral surface of the dorsal spine of the third free caudal vertebra. The middle bundle goes to the same position on the fourth vertebra, and the lateral fasciculus, with its tendon sometimes nearly twice the size of the two former ones, goes to the fifth free vertebra, just anterior to the pygostyle. Although these insertions are mostly tendinous, there are fleshy fibers on their deep sides. The tendon of the most lateral bundle of muscle passes beneath the uropygial gland.

In one specimen there was a fourth part—a deep portion coming fleshily from the outer two bundles, opposite the second free vertebra, and inserting tendinously on the lateral face of the pygostyle just anterior to the haemal canal.

Mm. interspinales

These are the small, fleshy muscles present between the neural spines of cervical vertebrae 1 through 6, of vertebra 17 posteriorly to the sacrum, and of the caudal vertebrae and between the hypopophyses of the caudal vertebrae (figs. 23, 29). The dorsal interspinales of the tail are definitely paired; a space may often be found in the midline between the muscles of the right and left sides. This separation is not evident on the ventral muscles or on most of the cervical ones. Despite the fact that they can only function when the vertebrae are movable, these muscles are fleshy between the last two fused vertebrae of the sacrum. There are even ligaments extending farther anteriorly, which probably represent vestiges of the dorsal interspinales muscles. The series present from cervical vertebra 17 posteriorly to the sacrum shows much diminished size caudally. Posteriorly they are present, dorsally and ventrally, between successive free caudal vertebrae and between the last vertebra and the pygostyle. In the caudal region they are in part deep to the medial edge of M. lev. coccygis, but in turn they are superficial to the medial edge of M. lev. caudae.

The innervation in the tail comes from that branch of the caudal nerve (formed from sacral nerves 7, 8, and 9, fig. 27) which also serves Mm. lev. coccygis and lev. caudae. There may also be a branch from the sciatic nerve.

M. levator caudae

The proximal two-thirds of the muscle is hidden from dorsal view by M. lev. coccygis (fig. 23). The long, finger-like belly is located lateral to the neural spines of the caudal vertebrae and dorsal to their transverse processes. That distal part of the muscle visible in superficial, dorsal view fans out laterally over the bases of the rectrices and covers the medial extension of M. lat. caudae. The lateral surface of M. lev. caudae is covered by the aponeurosis described with M. lev. coccygis.

Origin.—Fleshy origin comes from the posterior edges of the ilium and of the transverse process of the penultimate fused caudal vertebra, and from the dorsal surfaces of the transverse processes of the last fused vertebra and the first three unfused vertebrae of the tail. There is also some fleshy origin from the fascia lying between the transverse processes.

Insertion.—At the level of the fourth free vertebra, the medial part of the muscle is superficially divided into three superimposed fasciculi. The most proximal of these inserts fleshily and tendinously on the neural spine of the fourth free vertebra just beneath the insertion of M. lev. coccygis. The second finger goes to the same position on the fifth free vertebra, and the most distal and deepest of these three fasciculi sends a tendon to the antero-lateral corner of the pygostyle (fig. 23). The undivided and main part of the belly continues distad to fan out over the ventro-lateral surfaces of the major upper-coverts and the dorsal surfaces of the five more medial rectrices; in figure 23 the coverts, which are literally buried in the distal end of the muscle, have been removed.

Inasmuch as the oil gland is situated superficially over the area where M. lev. caudae emerges from beneath M. lev. coccygis and over the broad insertion of M. lev. caudae on the coverts, it is not too surprising that there are fibers of M. lev. caudae which insert directly on the fascia of this uropygial gland.

M. lateralis caudae

Two separate parts comprise the muscle (fig. 23) which is on the dorso-lateral aspect of the tail. The more lateral part is a long, rounded belly along the lateral edge of the dorsum of the tail; the medial is a broader band whose lateral edge is deep to the lateral finger of this muscle and whose distal end is deep to M. lev. caudae. The ventro-lateral border of the lateral fasciculus is in contact with M. depress. caudae.

Origin.—The lateral belly arises as fleshy fibers from the aponeurosis between the caudal vertebrae and the medio-posterior edge of the ilium (fig. 23). The origin does not extend anteriorly as far as the ilium, but it does in part overlie the tendinous and fleshy origin of the medial belly which comes from the postero-medial edge of the ilium and from the above-mentioned aponeurosis. This medial part also takes fleshy origin from the transverse processes of the last fused vertebrae and the first three unfused caudal vertebrae.

Insertion.—The lateral part inserts fleshily on the dorsal and partly on the lateral surface of the most lateral rectrix. The medial belly fans out toward the midline and passes distally between the bases of the major upper-coverts and the rectrices. Some muscular fibers and tendinous strands are sent to the coverts, but the major attachment is to the dorsal surfaces of the quills of the rectrices; superficially the latter insertion is aponeurotic, but strong fleshy fibers are present beneath. Two small tendons are sent to the proximo-lateral surface of the neural spine of the pygostyle (fig. 23).

M. depressor caudae

M. depress. caudae is present as a wide, flat band on the superficial aspect of the lateral part of the ventrum of the tail (fig. 23). Medially it is bordered by the cloacal region and by M. lev. cloacae. It is superficial to M. depress. coccygis, but the proximal three-fourths of its antero-lateral edge are covered by the origin of M. flex. cruris med.

Origin.—Most of the posterior edge of the ilium, the dorso-posterior edge of the ischium, the ischio-pubic aponeurosis, the pubis posterior to the end of the ischium, and the lateral two-thirds of the interpubic ligament furnish fleshy origin. In the medial region of the tail the muscles of either side come within 1 centimeter of each other.

Insertion.—As the wide band of muscle leaves its origin it begins to narrow sharply, until it is only 1 centimeter wide at its insertion on the ventral surfaces of the outer two rectrices. In the lateral extent of this fleshy attachment there is intimate contact with the ventro-lateral fibers of the insertion of the lateral part of M. lat. caudae.

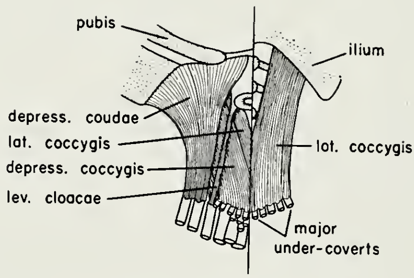


Fig. 24. Ventral view of the muscles of the tail. On the right side of the drawing Mm. depress. caudae, lev. cloacae, and depress. coccygis have been removed.

M. levator cloacae

The narrow but long belly is visible on the ventral side of the tail, parallel to the distal two-thirds of the medial edge of M. depress. caudae and lying in the same plane (fig. 24). The 2-millimeter-wide belly crosses the ventral face of M. depress. coccygis as it passes from its fleshy attachment on the ventral surfaces of the under-coverts of rectrix four, and primarily on this rectrix, to a mixed tendinous and fleshy connection on the dorso-lateral corner of the cloaca (fig. 24).

M. depressor coccygis

This muscle consists of a wide and flat belly which, in its proximal part, is immediately deep to Mm. depress. caudae and lev. cloacae and which, throughout its length, is superficial to the lateral border of M. lat. coccygis (fig. 24). Dorsal to the cloaca a ligament passes laterally on each side, goes through the belly of either M. depress. coccygis, and attaches to the most posterior tip of the ilium.

Origin.—Fleshy origin comes from the same area as that of M. depress. caudae but deeper. However, there is also fleshy attachment to the ventral side of the aponeurosis (fig. 24) extending from the posterior extent of the ilium ventro-posteriorly to the ischio-pubic ligaments.

Insertion.—It is fleshy on the ventral surfaces of the bases of the under-coverts beneath rectrices one to four (fig. 24). In the midline, ventral to the last two free vertebrae and to the pygostyle, the muscle is in contact with its counterpart of the opposite side, but the two muscles do not fuse in a midline raphe.

M. lateralis coccygis

M. lat. coccygis is the deepest of the muscles on the ventral surface of the tail (fig. 24). Judging by the size of this thick and wide belly, it is also the most powerful. The distal half of the belly is covered by a heavy, strong layer of fascia which is closely applied to the belly and forms a part of the insertion.

Origin.—Fleshy origin comes from the postero-internal border of the ilium and from the ventral surfaces of the transverse processes of all the free caudal vertebrae.

Insertion.—On the deep, medial edge of the belly there are two fasciculi which insert on the ventro-lateral faces of the hypopophyses of the last two free vertebrae. There is strong, fleshy connection to the ventro-proximal part of the pygostyle, proximal and ventral to the articulation and the haemal foramen. There is a variable number of small, deep tendons which insert on the lateral face of the pygostyle distal and dorsal to the articular area. Superficially the major insertion is fleshy on the ventral surfaces of all the under-coverts, except the most lateral; this connection to the bases of the under-coverts is deep and proximal to the insertion of M. depress. coccygis on these feathers.

Mm. intercoccyges

These muscles as figured by Fisher (1946:633), described by Shufeldt (1890:315-317), and called the Mm. intertransversarii (in part) by Gadow (1890:115), were not present as distinct entities in the Whooping Crane. They may have been represented as some of the distal and deep fasciculi of M. lat. coccygis.

M. caudofemoralis

This muscle is considered with the musculature of the hind leg (page 85).

Muscles of the Leg

The names of the muscles of the leg follow Fisher (1946:694-696), who compared his nomenclature with that of earlier workers. We here list, in the sequence in text, the names used; this should facilitate use, as in general the muscles are treated in the sequence of removal from the specimen.

M. extensor ilio-tibialis lateralis
M. extensor ilio-tibialis anterior
M. piriformis
M. gluteus profundus
M. iliacus
M. ilio-trochantericus medius
M. vastus lateralis
M. vastus medialis
M. extensor ilio-fibularis
M. flexor cruris lateralis
M. flexor cruris medialis
M. caudofemoralis
M. flexor ischiofemoralis
M. adductor superficialis
M. adductor profundus
M. ambiens
M. femoritibialis internus
M. femoritibialis externus
Mm. obturator externus and internus
M. psoas
M. gastrocnemius
M. peroneus longus
M. tibialis anterior
M. flexor perforans et perforatus digiti II
M. flexor perforans et perforatus digiti III
M. flexor perforatus digiti IV
M. flexor perforatus digiti III
M. flexor perforatus digiti II
M. flexor hallucis longus
M. flexor digitorum longus
M. peroneus brevis
M. extensor digitorum longus
M. popliteus
M. plantaris
M. extensor proprius digiti III
M. extensor brevis digiti III
M. extensor hallucis longus
M. abductor digiti II
M. extensor brevis digiti IV
M. adductor digiti II
M. flexor hallucis brevis
M. abductor digiti IV

M. extensor ilio-tibialis lateralis

This is the most superficial lateral muscle of the hip (figs. 22, 25). It is a thin sheet of triangular shape, bordered anteriorly by M. extens. ilio-tib. ant. and posteriorly by Mm. extens. ilio-fib. and flex. cruris lat. The fibers in the center of the muscle are less than half as long as those of the anterior and posterior edges. The anterior part of the muscle is innervated from the femoral nerve; the posterior part is served by a peroneal twig (fig. 28, nos. 15, 21). In each instance the nerve enters between the first and second thirds of the length of the respective part and is accompanied by blood vessels. Thus the muscle has a double innervation and circulatory supply—one anterior and one posterior to the femur.

Origin.—A broad, double aponeurotic sheet covers the entire ilial region and forms a common origin for Mm. extens. ilio-tib. lat. and ant. M. extens. ilio-fib. also takes origin from the deeper part of this aponeurosis. The deep part of the sheet is very fibrous, almost tendinous;

bands of fibers radiate anteriorly, dorso-anteriorly, and dorsally from the antitrochanteric region to form strengthening bands in the origin. Anteriorly the aponeurosis covers Mm. glut. prof. and piriformis; posteriorly it hides the proximal part of M. extens. ilio-fib. The ultimate attachment of the muscle under consideration is, by means of this aponeurosis, to the entire length of the anterior and posterior iliac crests (fig. 22).

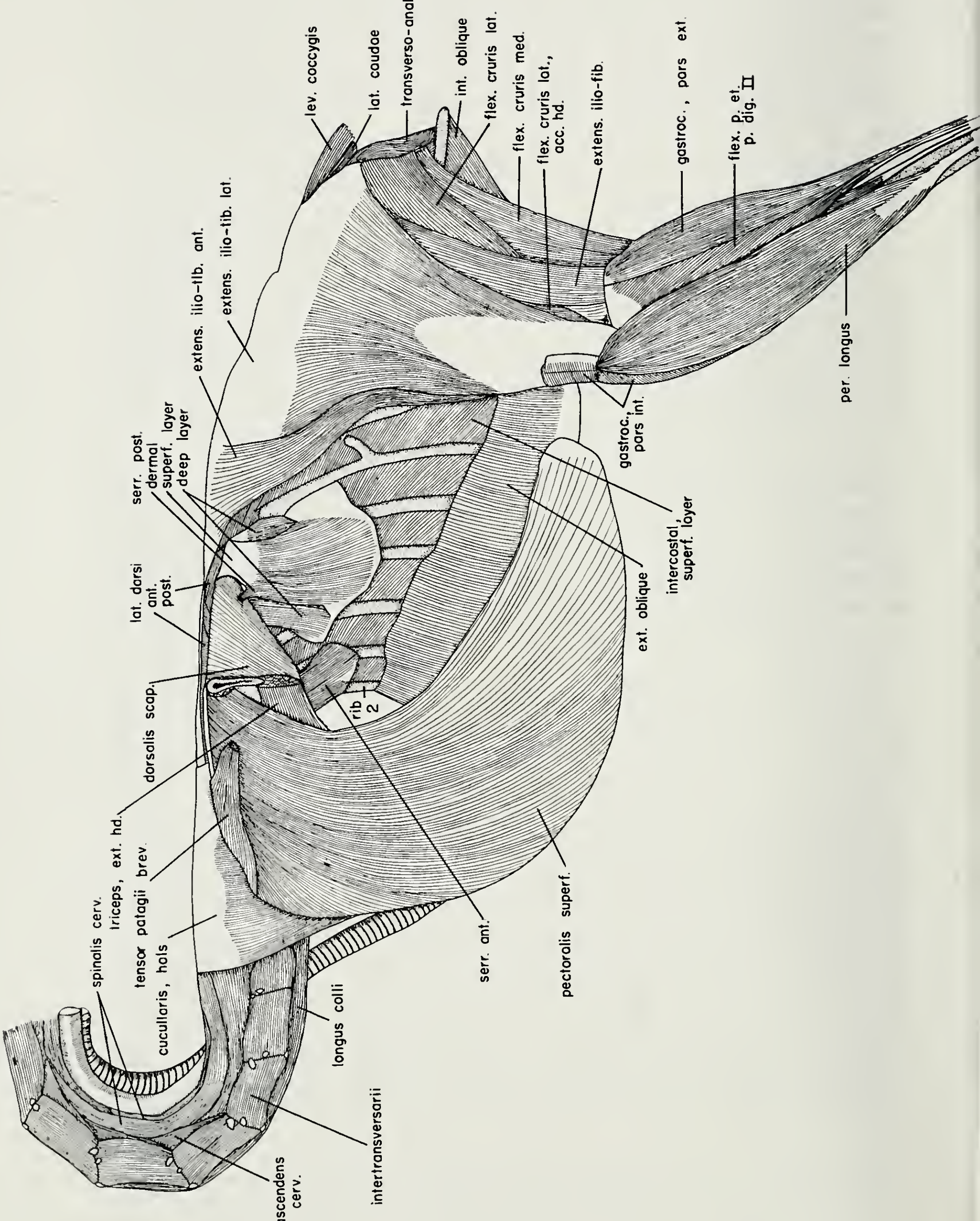
Insertion.—Just above the knee, the anterior fleshy part of this muscle joins the posterior edge of M. extens. ilio-tib. ant. to form a common, diamond-shaped sheet of insertion. M. vastus lat. fuses strongly with the deep surface of this sheet, which sheet in turn is a major component of the patellar tendon. It is quite noticeable that the anterior part of the sheet inserts on the patellar tendon; the posterior portion of the aponeurosis sends strong fibers of connective tissue directly to the rotular crest and to the anterior surface of the outer cnemial crest, in addition to its patellar contribution.

M. extensor ilio-tibialis anterior

Forming the anterior edge of the hip and thigh musculature, this heavy band of muscle (figs. 22, 25) moves from an antero-lateral position proximally to an antero-medial location at the distal end of the femur. It is bordered posteriorly and laterally by M. extens. ilio-tib. lat., to which its postero-distal border is fused. On the medial side of the thigh (fig. 26) M. extens. ilio-tib. ant. is immediately superficial to Mm. ambiens and vastus med.

Innervation is from the same branch of N. femoralis that serves the anterior part of M. extens. ilio-tib. lat. (fig. 27; fig. 28, nos. 4-6, 15). There is variation in the blood supply to this muscle. In one specimen a branch of the femoral artery emerged from beneath M. glut. prof. and entered the fleshy origin of M. extens. ilio-tib. ant., and a second femoral artery divided to send two branches, one to the middle and another to the distal part of the belly of the muscle. In two specimens, only the branches of the second femoral artery were present. A different branch of this same femoral vessel goes to the anterior part of M. extens. ilio-tib. lat. Hence, as regards topographical relationships of nerves and blood vessels, the anterior portion of M. extens. ilio-tib. lat. is more closely tied in with M. extens. ilio-tib. ant. than it is with its own posterior part.

Origin.—Superficially the origin is aponeurotic from the anterior part of the iliac crest, anterior to, but continuous with, the origin of M. extens. ilio-tib. lat. (figs. 22, 25). The origin extends medially, by aponeurosis, to the neural crests of the posterior lumbar vertebrae. There is fleshy origin from the entire width of the ilial blade antero-dorsal to the origin of M. glut. prof. (fig. 29). In *G. canadensis* the origin is similar to the aponeurotic origin just described; we did not find the primary origin to be from the anterior end of the ilium as did Hudson (1937).


lev. coccygis
lat. caudae
transverso-analis
int. oblique
flex. cruris lat.
flex. cruris med.
flex. cruris lat., acc. hd.
extens. ilio-fib.
gastroc., pars ext.
flex. p. et p. dig. II
per. longus
gastroc., pars int.
intercostal, superf. layer
ext. oblique
pectoralis superf.
serr. ant.
rib 2
extens. ilio-tib. ant.
extens. ilio-tib. lat.
serr. post.
dermal
superf. layer
deep layer
lat. dorsi
ant.
post.
dorsalis scap.
triceps, ext. hd.
tensor patagii brev.
spinalis cerv.
cucullaris, hals
longus colli
intertransversarii
ascendens cerv.

Insertion.—The fleshy insertion on the medial side of the patellar tendon is covered medially by the most proximal fleshy head of origin of the pars interna of M. gastroc. On the lateral surface of the knee the aponeurosis of insertion is superficially continuous with that of M. extens. ilio-tib. lat., but there is a round tendon here which apparently forms the main lateral insertion of M. extens. ilio-tib. ant. This tendon runs through the patellar tendon, deep to, and sometimes fused with, the inserting tendon of M. femoritib. int., and inserts on the base of the inner cnemial crest just medial to the rotular crest.

M. piriformis

This small triangular muscle (figs. 22, 29, 30, 31) is in the second layer of hip muscles, deep to M. extens. ilio-tib. lat. The innervation (fig. 28, no. 34) comes from an anteriorly directed twig coming out of the ilio-ischiatic fenestra; the twig continues cephalad to serve the posterior part of M. glut. prof. In *G. canadensis* M. piriformis is more strongly developed than in *G. americana.*

Origin.—Mixed fleshy and tendinous from the iliac crest in the 4 centimeters just anterior to the antitrochanter. The anterior part of this origin overlaps the posterior edge of the origin of M. glut. prof.

Insertion.—At the level of the femoral trochanter a flat tendon is formed; it passes distally over the outer face of the femur to insert between the insertions of M. iliacus and M. caudofem.

M. gluteus profundus

This muscle lies in the anterior ilial fossa deep to Mm. extens. ilio-tib. ant. and lat. and immediately superficial to Mm. iliacus and ilio-troch. med. Posteriorly the muscle is covered by M. piriformis, and there is a strong fascial aponeurosis covering M. glut. prof. (figs. 22, 29). Innervation is in two parts—posteriorly a twig from the sciatic nerve serves the posterior part of M. glut. prof. and M. piriformis, and anteriorly a recurrent branch of N. femoralis goes to the anterior part of M. glut. prof. and to M. ilio-troch. med. (fig. 28, nos. 1, 2, 34, 35).

Origin.—Superficially, a heavy aponeurosis from the anterior iliac crest forms part of the origin, but the main portion of the origin is fleshy from the entire ilial fossa posterior to the origin of M. extens. ilio-tib. ant. and anterior to the acetabulum (fig. 29). Ventrally this area is limited by the heads of Mm. iliacus and ilio-troch. med.

Insertion.—The inserting tendon is formed as the muscle passes over the antero-dorsal part of the femoral trochanter. Attachment is to a curved line on the lateral face of the trochanter, anterior to and partly covered by the insertion of M. piriformis and just proximal to the insertion of M. ilio-troch. med.

M. iliacus

This muscle (figs. 29, 30) forms the antero-ventral border of the pelvic

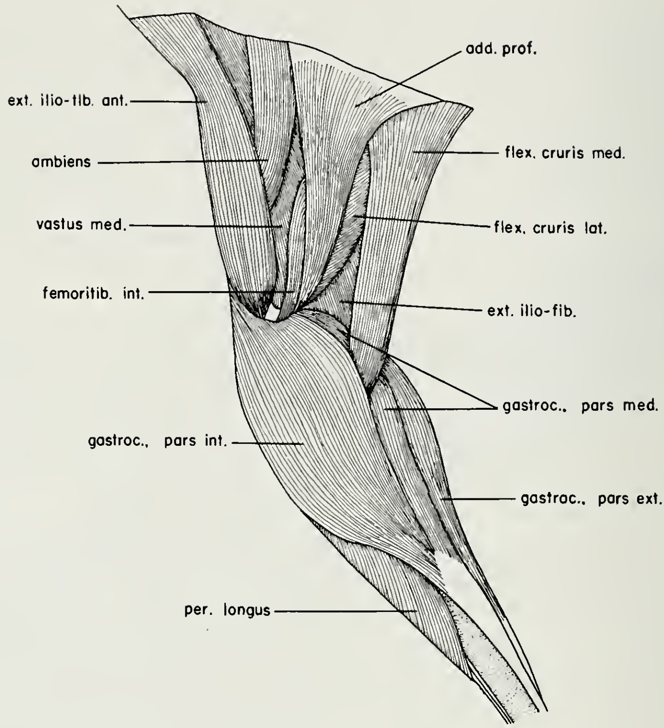


FIG. 26. Medial view of the superficial muscles of the hind leg.

musculature going to the femur. Innervation is from N. femoralis by a branch coming off just distal to the branch that serves part of M. glut. prof. and M. ilio-troch. med. (fig. 28, no. 3). In one specimen, twig No. 4 of figure 28 went to M. iliacus rather than to M. extens. ilio-tib. ant.

Origin.—The fleshy, but partly tendinous, origin extends along the entire ventral edge of the ilium from a point 1 centimeter from the anterior end to within 1 centimeter of the acetabulum; the latter centimeter is occupied by M. ilio-troch. med.

Insertion.—The major part of the attachment is tendinous on a line 1.5 centimeters long on the middle of the outer surface of the femur, continuous proximally with the line of insertion of M. ilio-troch. med. (fig. 30). As may be noted in the illustration, there are a few fleshy fibers covering the tendon of insertion, but this fleshy insertion is of minor significance.

M. ilio-trochantericus medius

This is the deepest of the pelvic muscles anterior to the femur and seems to be a posterior extension of the sheet forming M. iliacus (fig. 30). The nearly uniform width of this muscle is, on its anterior edge, continuously in contact with the posterior edge of M. iliacus. In some instances a branch of N. femoralis emerges between these muscles and passes to M. glut. prof. (fig. 28, no. 2). As may be seen in figure 28 (no. 1), a recurrent branch of N. femoralis serves this muscle. Gadow (1891: 142) said this muscle was absent in *Grus*, and Hudson (1937:13, 60) did not find it in *Grus canadensis*, but it was present in our specimens of both species.

Origin.—Fleshy and 1 centimeter wide from the ventral edge of the ilium immediately anterior to the acetabulum.

Insertion.—Tendinous on the lateral surface of the femur just proximal to the insertion of M. iliacus (fig. 30) and distal to the insertion of M. glut. prof.

M. vastus lateralis

The long, thick, and rounded belly of this muscle lies deep to Mm. ilio-tib. lat. and ant. and forms the major bulk of the second layer of muscles on the anterior surface of the thigh (fig. 29). The distal half of the posterior part of the belly is closely adherent to the deep surface of the overlying M. extens. ilio-tib. lat. At the level of the middle of the length of the femur M. vastus lat. and M. vastus med. become inextricably fused. Blood vessels enter the middle of the proximal ends of the two parts, as do branches of nerves coming from N. femoralis (fig. 28, nos. 7-11). There is much variation in the number and position of nerves going to this muscle complex—numbers 7 and 8 may go to the lateralis part or 7 may go to the medialis and 9 then to the lateralis.

M. vastus medialis

The belly extends farther proximally than does the belly of M. vastus lat. and lies on the antero-medial surface of the femur (fig. 30). The medial surface is crossed in the middle of its length by M. ambiens (fig. 26).

Origin of vastus complex.—Lateralis.—The most proximal part of the fleshy origin overlies the insertion of M. iliacus on the outer surface of the femur (fig. 29). The fleshy origin occupies the lateral surface of the second and third sixths of the femoral length. On the posterior face of the femur the fleshy origin with some connective tissue components continues distally as far as the proximal part of the origin of M. femoritib. ext. On the anterior femoral surface the origin extends distally to the distal third of the femoral length. Posteriorly these origins are bounded by part of the insertion of M. add. superf., and anteriorly by the intermuscular line which continues distad from the trochanteric ridge.

Medialis.—The mixed fleshy and tendinous origin is from the hollow in the anterior face of the femur, medial to the trochanteric ridge. Short fibers of the medialis arise tendinously from the length of the trochanteric ridge to within 4 centimeters of the distal end of the femur. At this level the linear aponeurotic origin ceases and the origin becomes widely fleshy from the anterior and medial surfaces of the femur. The finger or bundle of muscle formed by this latter fleshy origin is nearly or completely separate from the lateralis and medialis portions and is perhaps comparable to the M. vastus intermedius or M. vastus femoris of other authors. It lies between the medialis and lateralis parts, and, although contributing to the usual vastus part of the patellar tendon, it may send a small, nearly distinct tendon directly to the patella.

Insertion of vastus complex.—All parts of the vastus enter into the formation of the patellar tendon, but it is possible to find thickenings of this tendon which correspond to the various components of the vastus. These thickened bands within the patellar tendon extend from the lateralis and medialis parts to the cnemial crests of the tibia; the one from the intermedius goes to the patella. However, in three of the six dissections the insertion of the intermedius part was fleshy on the patella.

M. extensor ilio-fibularis

This heavy muscle is a member of the second layer on the lateral surface of the thigh, lying deep to M. extens. ilio-tib. lat., posterior to M. vastus lat., and anterior and superficial to the flexor cruris group (figs. 22, 25, 29). The width of the belly decreases distally, and a tendon is formed in the region of the knee. This tendon passes into the posterior surface of the upper tibial musculature (figs. 31, 33, 34, 35). The upper part of the belly is separated from the underlying muscles by a nerve which goes posteriorly to serve M. flex. cruris lat. Blood vessels accompanied by nerves enter the belly in two places—proximally at the level of the pubis and distally just above the formation of the inserting tendon. Both nerves serving this muscle come from the peroneal trunk (fig. 28, nos. 23, 26).

Origin.—There is fleshy origin from a narrow line on the posterior iliac crest from the antitrochanteric region to the anterior edge of the origin of M. flex. cruris lat. (figs. 22, 29). Lateral to the head of the femur there is an aponeurotic origin that covers the posterior edge of M. piriformis; in this same region there is very close attachment to the deep aponeurotic origin of M. extens. ilio-tib. lat.

Insertion.—The heavy inserting tendon passes through the characteristic tendinous loop, the proximal medial end of which is attached to the proximal end of the external femoral condyle (fig. 33) and the distal lateral end to the most lateral proximal part of the flexor attachment area on the femur. The third arm of this loop, as described by Hudson (1937:25 and fig. 3), is not present as such. In its place is a strong vinculum which is 2 centimeters wide and passes to the tendinous origin of the several flexor muscles posterior to the knee (fig. 33); this vinculum is in part covered laterally by M. flex. perf. et perf. dig. II. We found this same vincular arrangement in *G. canadensis*, but part of the most distal edge of the vinculum continued anteriorly to attach to the anterior edge of the fibula. Accompanying the tendon of insertion through the loop is N. peroneus. N. tibialis enters the shank musculature distal to the insertion of M. extens. ilio-fib. which is on the outer face of the fibula and some 5.5 centimeters distad from its head.

M. flexor cruris lateralis

This is a long band of muscle lying deep in the posterior part of the thigh and extending from the posterior pelvic and caudal regions to the knee (figs. 22, 25, 26, 29, 31). In cross section the muscle is nearly triangular, the shape apparently being due to crowding by M. flex. cruris med. on the deep side and by M. extens. ilio-fib. on the lateral side. In the knee region this band is joined by the fibers of the proximal accessory part of M. flex. cruris lat. which comes from the femur. The junction of the two parts is marked by a tendinous raphe which, at its distal end, forms the inserting tendon.

The distal accessory head is inseparable from the proximal accessory head in the region proximal to the raphe. The distal part is recognizable only because its fibers do not impinge on the raphe; they continue distally to form a wide tendon inserting on the pars media of M. gastroc. and on the underlying muscles.

Innervation of the main head is on its antero-lateral surface, in the upper half of the belly's length, by a branch of the same short crural nerve that serves Mm. flex. cruris med., caudofem., and depress. caudae (fig. 28, nos. 29, 30, 31); this nerve crosses the lateral surface of the two parts of M. caudofem. Opposite the proximal accessory part of the muscle two twigs from N. tibialis serve the two inseparable bellies of the accessory parts.

Origin.—The origin is fleshy from the posterior 2 centimeters of the posterior iliac crest deep to the origin of M. extens. ilio-fib. and just dorsal to the tendon of pars caudi-fem. of M. caudofem. (figs. 22, 25, 29). Other origin in this region takes place by means of fascia overlying the origin of M. flex. cruris. med., the disto-lateral and dorsal surfaces of the pubis, and the body wall dorsal to the pubis. The proximal accessory head arises fleshily from a 3-centimeter-long line in the proximal part of the popliteal region. Farther distally the origin (probably of the distal accessory segment) becomes aponeurotic and tendinous from the medial surface of the internal condyle of the femur. In lateral view, this origin is deep to the tendinous loop for M. extens. ilio-fib.

Insertion.—The tendon coming from the raphe at the junction of the main and proximal accessory heads usually inserts on the wide tendon of insertion of M. flex. cruris med. at the surface of the shank musculature. As described previously, the tendon of the distal accessory head inserts on the posterior surface of the pars media of M. gastroc., posterior to

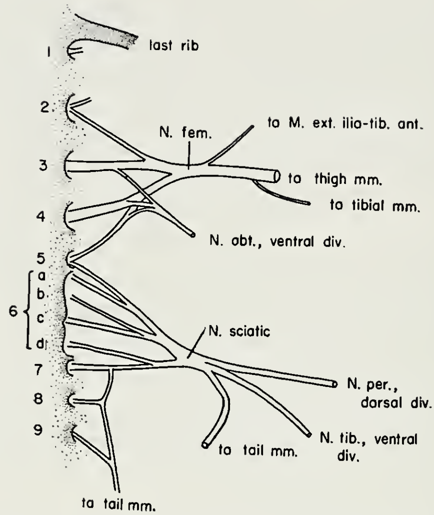


Fig. 27. Ventral view of the left sacral plexus to show the composition and the disposition of the major nerve trunks. The numerals refer to points of emergence of nerves between diapophyses.

the inserting tendon of M. flex. cruris med. The insertion is about as figured by Fisher (1946:667).

M. flexor cruris medialis

This is the deepest and most posterior of the thigh muscles (figs. 22, 25, 26, 29). Medially it is covered only on its most proximal anterior corner by M. add. prof. Its proximo-lateral surface is covered by M. flex. cruris lat. At the upper end of the anterior edge of the belly a short crural nerve enters this muscle from between M. caudofem. and M. flex. ischiofem. This is essentially as diagrammed in figure 28 (no. 31) except that no. 31 in the figure comes off farther distad. This variation in level of branching is found from specimen to specimen within a species. In one specimen the bifurcation of the nerve serving the two parts of the flexor cruris complex occurred inside the pelvis.

Origin.—Fleshy from the ventro-posterior corner of the ischium, from the fascia between the pubis and ischium, and from the entire lateral face of the pubis posterior to the adductor muscles and extending to within 2 centimeters of the caudal end of the pubis (fig. 22). There is strong fascial connection throughout the fleshy origin.

Insertion.—As the muscle passes to the tibial musculature a thin, wide, and strong inserting tendon is produced. Almost immediately the tendon of the main and proximal accessory heads of M. flex. cruris lat. inserts on this wide tendon; in one instance only a vinculum formed this connection between the tendons. The combined tendons then pass into the shank musculature to insert on a longitudinal line on the antero-internal corner

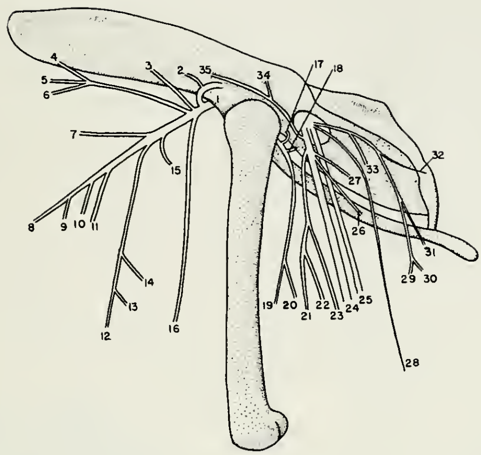


FIG. 28. Semidiagrammatic lateral view of the sacral plexus of the Whooping Crane to show the distribution of nerves to the various muscles.

1. ilio-troch. med.
2. glut. prof.
3. iliacus
4, 5, 6. extens. ilio-tib. ant.
7, 8. vastus lat.
9, 10, 11. vastus med.
12, 13. femoritib. int.
14. ambiens
15. extens. ilio-tib. lat.
16. tibial musculature
17. obt. ext.
18. obt. int.
19. add. prof.
20. add. superf.
21, 22. extens. ilio-tib. lat.
23. extens. ilio-fib., lower pt.
24. femoritib. ext. and tibial muscles of peroneal nerve
25. lower tibial muscles of tibial nerve
26. extens. ilio-fib., upper pt.
27. flex. ischiofem.
28. tibial musculature
29, 30. flex. cruris lat.
31. flex. cruris med.
32. depress. caudae
33. caudofem.
34. piriformis
35. glut. prof., post. pt.

of the tibial shaft some 5 centimeters from the proximal end of the tibiotarsus. In some dissections we found fleshy and tendinous insertions on the pars interna and pars media of M. gastroc.

M. caudofemoralis

In figures 30 and 31 it may be observed that both the pars caudifemoralis and pars ilio-femoralis may be present in the Whooping Crane, as previously reported by Beddard (1898:367). Hudson (1937:22) found these two parts to be separate in *Grus canadensis*. In one specimen of *G. americana* (fig. 30) three bands made up the proximal part of this complex. In another specimen the two typical parts were present (fig. 31), and so widely separate that a wide area of M. flex. ischiofem. was visible between them. The accessory part (pars ilio-fem.) was by far the larger; it was deep to Mm. extens. ilio-fib. and flex. cruris lat. and laid between the crural nerves going to the flexor cruris muscles and those to the adductor muscles. Beddard (*loc. cit.*) found but a "feeble accessory part" in *G. americana*, and Gadow (1891:161) indicated that *only* the accessory part was present in *Grus*. Our third specimen showed only a typical pars ilio-fem. as Gadow reported. Thus three very distinct conditions of this muscle were present in the specimens we had.

Both parts of the muscle are innervated by a branch of the nerve going to the Mm. flex. cruri (fig. 28, no. 33).

Origin.—The pars caudi-femoralis arises from the most ventral tip of the pygostyle as a tendon which courses latero-ventrad to pass through the ischial notch; immediately it forms a narrow, thin band of fleshy muscle. The pars ilio-fem. comes fleshy in its anterior two-thirds from a line along the most ventral part of the posterior iliac crest deep to the origins of Mm. extens. ilio-fib. and flex. cruris lat. The posterior third to half is aponeurotic (fig. 31).

Insertion.—Pars caudi-fem. when present inserts tendinously on the outer face of the femur some 4 or 5 centimeters from the proximal end of the femur. This is an insertion distinct from that of the pars ilio-fem., even in that instance shown in figure 30, in which there was some fleshy fusion of the bellies of the three parts. The pars ilio-fem. inserts widely and fleshily some 2 to 4 centimeters distad from the proximal end of the femur and on its postero-lateral surface; this insertion is anterior and partly proximal to that of M. flex. ischio-fem. and posterior to the insertion of M. piriformis (figs. 30, 31). In that specimen in which pars caudi-fem. was absent, pars ilio-fem. had its insertion 1.5 centimeters distal to the insertion of M. flex. ischio-fem.

M. flexor ischiofemoralis

This is the deepest of the post-femoral muscles arising from the ischium. Its antero-dorsal edge is covered by the pars ilio-fem. of M. caudofem. (figs. 30, 31) and its ventral edge by the pars caudi-fem. In its distal third to half, a heavy, silvery, tendinous sheath overlies the surface of the belly. The peroneal nerve sends a branch to the middle of the deep surface of the belly (fig. 28, no. 27).

Origin.—Fleshy from virtually the entire lateral surface of the ischium posteriorly from the ilio-ischiatic fenestra to a point just beneath the widest extension of the posterior iliac crest. At its caudal end the origin may be limited by the tendon of origin of pars caudi-fem. of M. caudofem.

Insertion.—Tendinous on the postero-lateral part of the femur, some 3 centimeters distad, and posterior to and between the insertions of the two parts of M. caudofem. (fig. 31).

M. adductor superficialis

This heavy, entirely fleshy band of muscle lies on the medial side of the posterior part of the thigh (figs. 30, 31) and is deep only to M. add. prof. on the internal surface (fig. 26). The principal innervation comes from N. obturator and enters the upper half of the deep surface of the belly (fig. 28, no. 20), but a twig from a branch of N. peroneus (the branch to M. ischiofem., fig. 28, no. 27) may enter the lateral surface of the belly in company with the blood vessels supplying this muscle.

Origin.—Fleshy from the most ventral edge of the ischium, starting 1 centimeter posterior to the acetabulum and continuing caudad for one-half the length of the ischium. On the inner side the origin is aponeurotic

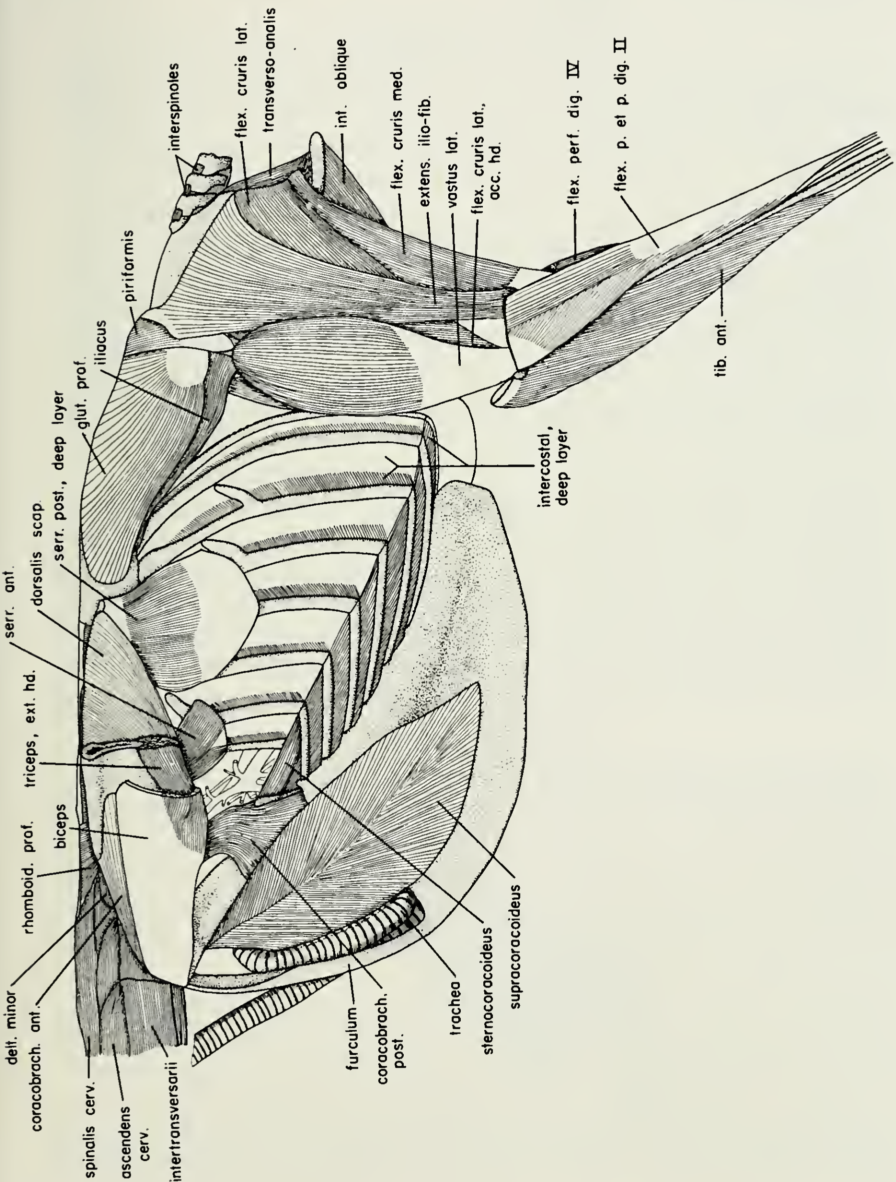


Fig. 29. Lateral view of the musculature, showing a second layer of muscles on the breast, body wall, and hind leg.

from the fascia between the ischium and the pubis and from a thin line on the dorso-lateral edge of the pubis.

Insertion.—The insertion is usually entirely fleshy on the postero-internal edge of the femur distad from the level of insertion of pars caudi-fem. of M. caudofem. to the most posterior part of the origin of M. femoritib. ext. in the popliteal area. In lateral view the distal part of the insertion is covered by M. femoritib. ext., and the proximal part by the ventral part of M. caudofem.

M. adductor profundus

On its medial surface this muscle is completely enveloped from origin to insertion in a heavy layer of tendon (figs. 26, 30, 31). This condition is present also in *canadensis*. Its lateral surface is largely covered by M. add. superf. N. obturator supplies the innervation (fig. 28, no. 19).

Origin.—This starts 1 centimeter posterior to the acetabulum, immediately deep to M. add. superf., and continues caudad to within 4 centimeters of the posterior tip of the pubis. The anterior half is mixed fleshy and tendinous superficially, but is entirely tendinous on the medial side from the ventral edge of the ischium and the fascia between the ischium and the pubis. The posterior half of the origin is primarily from the outer face and ventral edge of the pubis, the posterior third being completely tendinous. Most of the fleshy fibers of the posterior part of the muscle arise from the lateral surface of this tendon.

Insertion.—The insertion, laterally fleshy and medially tendinous, starts 5.5 centimeters from the proximal end of the femur and extends distally on this bone to the popliteal region. The medial tendinous part of the insertion extends to the internal femoral condyle along a narrow line medial to the popliteal region. Thus the insertion lies on the mid-posterior surface of the femur, bordered medially by the origin of M. femoritib. int. and laterally by the insertion of M. add. superf.

M. ambiens

This thin but relatively wide band of muscle lies on the medial side of the thigh (fig. 26) and extends antero-distad, superficial to M. vastus med. as seen in medial view. Two-thirds of the way down the thigh a small tendon is formed (fig. 32). This tendon passes disto-laterally through the patellar tendon deep to the insertion of M. extens. ilio-tib. ant. The same branch of N. femoralis serves M. ambiens and M. femoritib. int. (fig. 28, nos. 12, 13, 14).

Origin.—Widely fleshy from the region of the pectineal process on the pelvis. Hudson (1937:16) found the origin in *Grus canadensis* to be only partly fleshy, and we noted only tendinous origin in this species.

Insertion.—After passing through the patellar tendon (fig. 34), the inserting tendon of M. ambiens fuses imperceptibly into the originating tendon of M. flex. perf. dig. II; thus M. ambiens forms 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 our one example of 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.

M. femoritibialis internus

Lying along the medio-posterior surface of the distal two-thirds of the femur is this bipinnate muscle. In lateral view (fig. 32) it appears to consist of two parallel fingers of muscle. (See fig. 26 for medial view.) Its innervation is from the branch of N. femoralis that also passes to M. ambiens (fig. 28, nos. 12, 13).

Origin.—Usually the fleshy origin begins one-third of the way down the femur and extends to within 1 centimeter of the proximal end of the internal condylar ridge. This is contrary to the statement of Gadow (1891:156) that in *Grus* the origin is limited to the distal half of the femoral length. Hudson (1937:21) found the origin in *G. canadensis* to extend into the proximal fifth of the femoral length, and this was the condition in one of our specimens of *G. americana* and in the specimen of *G. canadensis*. The medial side of this origin is heavily aponeurotic from the intermuscular line on the posterior surface of the femur.

Insertion.—At the level of the distal end of the femoral condyle the muscle abruptly converges into a heavy tendon, the anterior third of which may form part of the patellar tendon and the posterior two-thirds go beneath the origin of the pars interna of M. gastroc. to insert on the inner cnemial crest of the tibiotarsus. At its area of insertion and just proximally, the inserting tendon of M. femoritib. int. provides part of the origin of several flexor muscles.

M. femoritibialis externus

Gadow (1891:155) noted the presence of three slips to what he called

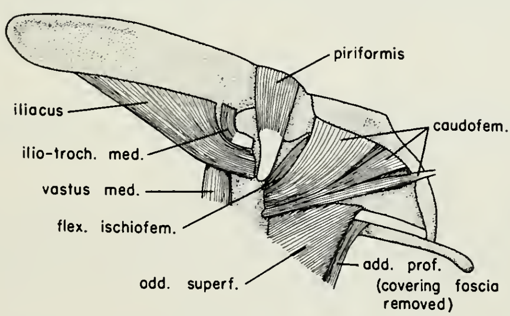


FIG. 30. Lateral view of the deep muscles of the thigh. Compare with figure 31 to note variation in M. caudofemoralis.

M. femoritibialis. We have above described for the Whooping Crane the muscle that corresponds to his M. femoritib. int. His M. femoritib. medius is apparently lacking in this species or is fused to M. femoritib. ext.; Hudson (1937:20-21) noted the fusion of the medius and externus portions in a number of species, but intimated the presence of separate medius and externus slips in *Grus canadensis*. Fisher (1946:667) figured a muscle in the position of the externus in cathartid vultures but did not describe it.

In *Grus americana*, M. femoritib. ext. is a broadly triangular muscle located in a deep position on the outer face of the distal half of the femur and extending across the lateral surface of the knee joint (fig. 31). Proximally the belly is superficial to the distal end of M. add. superf. As the muscle passes to the shank it crosses the origins of Mm. flex. hallucis long. and flex. perf. et perf. dig. III and part of M. tib. ant. The innervation comes from N. peroneus (fig. 28, no. 24) and enters the posterolateral edge of the muscle, with the accompanying blood vessels.

Origin.—The origin is widely fleshy from the lateral face of the femur, extending proximally from the proximal end of the external condylar crest to approximately the middle of the length of the femur. Proximally the origin is on the lateral face of the femur, but it is on the anterior surface distally. The deep part of the distal half of the origin is aponeurotic from the lateral edge of the popliteal region (fig. 31).

Insertion.—Part of the insertion is on the patellar tendon, but the anterior two-thirds of the insertion forms a separate tendon to the distolateral tip of the outer cnemial crest of the tibiotarsus. Just before the patellar component fuses with the patellar tendon, M. flex. perf. et perf. dig. II takes part of its origin from the deep side of this component.

Mm. obturator externus and internus

These muscles (fig. 32) are as described by Fisher (1946:671) for the Black Vulture, except that no tibial innervation was found for M. obt. int. See figure 28, nos. 17 and 18, for the innervation in the Whooping Crane. 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.

M. psoas

The condition described by Fisher (1946:670) for the cathartid vultures is found in this crane.

M. gastrocnemius

The three parts of this muscle form a nearly continuous covering on the anterior, medial, and posterior sides of the upper half of the tibiotarsus (figs. 25, 26). Except for their common insertion the three heads are distinct and will be discussed separately.

Pars externa

The pars externa forms the posterior border of the shank musculature, lying posterior and superficial to M. flex. perf. et perf. dig. II. Its medial edge borders the pars media. Halfway down the tibiotarsus there is considerable fusion between the fleshy bellies of the pars externa and the pars media. Three-fifths of the way down the tibiotarsus the tendon of insertion is formed. This courses down the posterior side of the tibiotarsus and is joined on its medial edge two-thirds of the way down the tibiotarsus by the common tendon of the pars interna and pars media.

Origin.—This origin is separated from that of the pars media by the inserting tendon of M. extens. ilio-fib. and by N. peroneus. The primary origin is tendinous from the flexor attachment on the external surface of the distal end of the femur. There is also tendinous and some fleshy origin from the lateral femoritibial ligaments and from the underlying tendons of origin of other flexor muscles.

Pars interna

Lying on the medial and anterior surfaces of the shank, this heavy and wide muscle, the largest of the three gastrocnemius components, is superficial to M. per. longus (figs. 25, 26). Proximally its fleshy belly curves around the anterior surface of the patellar tendon and extends on to the inserting tendon of M. extens. ilio-tib. lat. On its postero-medial edge, pars interna is separated from pars media and from M. plantaris by the common band of insertion of Mm. flex. cruris lat. and med. The tendon of this part joins the anterior edge of the tendon of the pars media about halfway down the postero-medial corner of the shank. This combined tendon then continues distally just anterior and medial to the tendon of the pars externa (fig. 26).

Origin.—Fleshy from the antero-lateral surface of the patellar tendon and from the medial surface of the inner cnemial crest of the tibiotarsus, anterior and distal to the inserting tendon of M. femoritib. int. Distal to this tendon and continuing throughout the upper third of the length of the shank there is additional fleshy origin from the tendons of the underlying muscles.

Pars media

The long, narrow belly lies superficially on the medial side of the shank between the pars externa and pars interna (fig. 26), but separated from the former by the inserting tendon of M. flex. cruris med.

Origin.—The popliteal region of the femur gives tendinous origin posterior and proximal to the tendons of origin of all the other muscles arising here. At the level of the entrance of the major blood vessels and nerves into the shank, this tendon becomes the fleshy belly.

Insertion of M. gastrocnemius.—Two-thirds of the way down the tibiotarsus the combined tendon (calcified) of the pars media and pars interna fuses to the medial edge of the inserting tendon of the pars externa to form the common calcified tendon of insertion. This passes distally down the posterior surface of the tibiotarsus and across the intratarsal joint, where it is bound to the bones by heavy fascia. As it moves across this joint it becomes much wider and aids in formation of the so-called "tibial" cartilage on the posterior side of the joint. This tendon, now twice as wide as above the joint, continues over the posterior surface of the hypotarsus, to the edges of which there is strong vincular attachment. Thus, this superficial tendon of M. gastroc. in effect forms an investing sheath over the deeper-lying tendons on the hypotarsus and the region immediately distad. The tendon narrows and thins out rapidly until it is no longer discernible as a definite tendon in the last third of the tarsometatarsal length. Between the distal end of the hypotarsus and the distal end of the tendon there is relatively weak insertion on the ridges on either side of the posterior metatarsal groove. It seems clear that the primary insertion is that on the hypotarsus.

Innervation.—N. tibialis serves all three parts. A branch from behind the tibiotarsus emerges just distal to the inserting tendon of M. flex. cruris med. and sends a twig beneath the pars media to the pars interna. Another twig comes up toward the surface between the pars media and pars externa; a bifurcation sends a branch to the belly of each of these muscles.

M. peroneus longus

On its medial side the belly of M. per. longus is covered by the pars interna of M. gastroc. Laterally the posterior edge of M. per. longus is superficial to M. flex. perf. et perf. dig. II (figs. 25 and 26). In figure 25 the belly, which is limited to the proximal half of the shank's length,

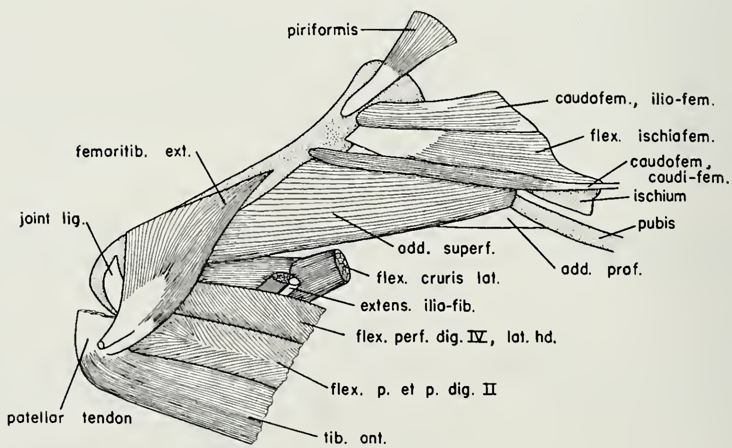


FIG. 31. Lateral view of the deep muscles of the thigh and the second layer of shank muscles; only M. gastroc. has been removed in the latter region.

is displaced posteriorly to show the bipinnate structure which is even more apparent on the deep surface. Innervation comes from the prefibular branch of N. peroneus.

Origin.—Fleshy from the space between the inner and outer cnemial crests, from the external face of the inner cnemial crest, and from the anterior surface of the outer cnemial crest. Part of this origin is inseparable from that of M. flex. perf. et perf. dig. II. All along the postero-medial edge of the belly there is aponeurotic origin from the intermuscular line on the medial surface of the tibiotarsus; this aponeurosis continues proximally on the anterior edge of the inner crest. On its lateral margin the muscle has both fleshy and tendinous origin from the muscles underlying its proximal two-thirds.

Insertion.—The calcified tendon formed in the middle of the shank's length goes distally along the postero-lateral corner of the tibiotarsus to the intratarsal joint. At the level of the external tibial condyle a vinculum 1.5 centimeters wide comes off posteriorly and passes medially to attach to the connective tissue sheath surrounding the extensor tendons as they pass through the intercondylar sulcus; this sheath is continuous from the proximal end of the sulcus to the proximal end of the hypotarsus, and it contains the tibial cartilage. The tendon that continues distally across the intratarsal joint is only 3 millimeters wide and much thinner than the tendon above the bifurcation. On the lateral surface of the joint the tendon is enclosed in its own sheath, and on the hypotarsus it lies in the most lateral bony groove, beneath the investing tendon of M. gastroc., and anterior to all other tendons on the latero-anterior part of the hypotarsus. The tendon finally inserts on the lateral edge of M. flex. perf. dig. III approximately one-fourth of the way down the posterior surface of the tarsometatarsus.

M. tibialis anterior

The bipinnate belly of this muscle lies in the second layer on the anterior surface of the upper half of the shank (figs. 29, 31, 33). It is almost completely covered by M. per. longus, and laterally is just anterior and in part deep to M. flex. perf. et perf. dig. II. A branch of N. peroneus goes to the anterior head and two or three branches pass to the femoral head.

Origin.—The pinnate nature of this muscle seemingly comes about through the fusion anteriorly of the edges of the two heads of origin. The anterior head arises fleshily from the antero-lateral surface of the tibiotarsus between the two cnemial crests, sometimes by tendon from the most proximal antero-lateral corner of the fibular head, and tendinous from the edge of the rotular crest. The femoral head takes tendinous origin from the usual position on the disto-anterior face of the external femoral condyle. This head is unusually well developed proximally;

fleshy fibers surround the tendon of origin to within less than a centimeter of the attachment to the femur.

Insertion.—The calcified tendon is formed between the bellies of the two parts of the muscle, approximately in the middle of the shank, and lies on the mid-anterior surface. Just above the tibial condyles the tendon passes through a wide, tendinous loop across the tendinal groove, and continues distally on to the tarsometatarsus where it attaches to the usual tubercle on the mid-anterior face of this bone.

M. flexor perforans et perforatus digiti II

The anterior part of the very thin bipinnate belly of the muscle is visible superficially between M. per. longus and the pars ext. of M. gastroc. on the outer side of the upper part of the shank (fig. 25). In figure 29 it may be seen that the pinnate structure is somewhat peculiar in some specimens; the anterior part is typical, but the fibers proximally insert on the fleshy fibers of the posterior part and these latter fibers extend straight distad to attach to the tendon. This conformation of the muscle was also present in *G. canadensis,* but on one side of our specimen the muscle was not clearly bipinnate. The belly anteriorly is a third to half as long as the shank and posteriorly only one-fifth to one-fourth as long. A typical development of this muscle is shown in figure 34. Innervation comes from N. tibialis just lateral to the insertion of M. extens. ilio-fib. and enters the posterior belly.

Origin.—Mixed fleshy and tendinous from the deep surface of the patellar tendon and from the postero-lateral side of the outer cnemial crest just anterior to the fibular head. There is tendinous attachment, along with other flexors, to the usual flexor origin on the outer surface of the external femoral condyle. In all its length proximal to the insertion of M. extens. ilio-fib. there is strong fleshy connection with the underlying muscles.

Insertion.—Below the most distal extent of the anterior part of the belly the tendon deep to that of M. gastroc. narrows abruptly and continues across the posterior face of the intratarsal joint. Over the joint the inserting tendon of M. flex. perf. et perf. dig. II is the most medial of the third layer of tendons. In the hypotarsus it has its own bony groove, the most medial of all, and in this position courses down the posterior side of the tarsometatarsus just beneath the tendon of M. gastroc. and later goes beneath the tendon of M. flex. perf. dig. II, which it perforates at the level of the base of the first phalanx of digit II. Mitchell (1901: 653) stated that there may be fusion between these two tendons. We found none in *G. americana,* but there was fusion here in *G. canadensis.* The tendon is immediately perforated by M. flex. dig. longus. This perforation is unequal—the medial part is larger and sends a strong branch to the medial corner of the base of phalanx 2. The two usual and superficial tendons continue distad to insert on either ventral corner of the base of the claw.

M. flexor perforans et perforatus digiti III

Only the posterior edge of this muscle is visible when M. flex. perf. et perf. dig. II is in place. The bipinnate belly is limited to the proximal third to half of the tibial length (figs. 33, 35). N. tibialis supplies a branch to the deep side of the middle third of the belly.

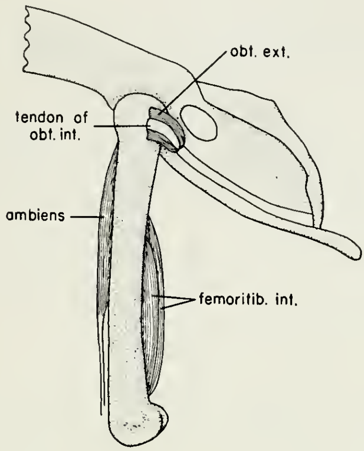


Fig. 32. Lateral view of the deepest muscles of the hip and thigh.

Origin.—This muscle can be said to take origin from all the surrounding structures. There are some fleshy elements but tendinous origin predominates. Usual sources of origin are: patellar tendon; deep side of M. femoritib. ext.; vinculum from tendinous loop for M. extens. ilio-fib.; flexor area on external femoral condyle; postero-lateral edge of outer cnemial crest of tibiotarsus; deep posterior surface of M. flex. perf. et perf. dig. II; and aponeurotic from the fibular head and shaft. Hudson (1937:46) and we did not find a fibular shaft attachment of this muscle in *Grus canadensis.*

Insertion.—The calcified tendon, formed about one-third of the way down the lateral side of the shank, crosses to a mid-posterior position in the intercondylar sulcus, passing alone through a connective tissue canal. It continues distad beneath the gastrocnemius tendon to the base of digit III. The perforations of and by the tendon are as described by Hudson (1937:46) and Fisher (1946:676), except that its perforation by M. flex. dig. longus occurs opposite phalanx 1 of digit III, rather than phalanx 2. Actual insertion is on the joint fascia between phalanges 2 and 3 and on the proximal ventral corners of phalanx 3.

M. flexor perforatus digiti IV

The tendon of insertion of M. extens. ilio-fib. divides the proximal part of the belly into lateral and medial heads of origin (figs. 33, 35). This is also true for *Grus canadensis* (our specimen and Hudson, 1937:43). Just distal to this separating tendon the two heads fuse to form the pinnate belly which extends two-fifths of the way down the tibiotarsus and forms the posterior edge of the shank beneath the pars externa of M. gastroc. Both heads are innervated by N. tibialis, but by different branches.

Origin.—The superficial finger of the lateral head arises tendinously from the flexor area on the femur and from the vinculum of the M. extens. ilio-fib. loop. This femoral origin of the lateral head seems to be unusual. The more usual origin in birds is represented in this species by a very short (2 cm.) band of fleshy fibers coming off the deep side of the middle of the length of the superficial part. This fleshy origin is from the fibular head.

The medial head is mixed fleshy and tendinous from the proximal part of the popliteal area, but there is also extensive fleshy and tendinous interconnection with the posterior surface of M. flex. hall. longus and the posterior head of M. flex. perf. dig. III.

Insertion.—There is a very close relationship between the calcified tendon of this muscle and that of M. flex. perf. dig. III. In the region of the intratarsal joint the latter tendon encloses the one of the present muscle anteriorly and laterally, and both pass through the same calcified canal in the hypotarsus. The tendon of M. flex. perf. dig. IV continues down the postero-lateral aspect of the tarsometatarsus to the tarsal malleolus for digit IV. At the base of phalanx 1 the tendon is perforated by that of M. flex. dig. longus. Two deep branches are immediately inserted on either ventral corner of the distal end of the basal phalanx. A single main tendon continues out the ventral surface of the digit, sends another deep tendon to the distal end of phalanx 2, and finally inserts on the distal end of phalanx 3 and the proximal end of phalanx 4.

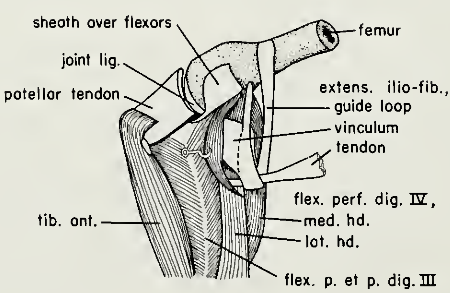


FIG. 33. Details of the relation of the muscles of the upper shank to the mechanism of insertion of M. extens. ilio-fib., in lateral view. M. flex. p. et p. dig. II has been removed with complex of M. gastroc.

M. flexor perforatus digiti III

Two distinct yet fleshily interconnected bellies form this muscle (figs. 34, 35). The lateral head is limited to the proximal half of the tibiotarsal length, and its belly to the second fourth of this length. The posterior and more proximal belly lies on the postero-medial aspect of the shank and is about twice the size of the lateral head. Halfway or more down the length of the lateral head, this head sends fibers postero-internally to fuse with the antero-lateral edge of the posterior head. A trunk of the tibial nerve runs distally between and deep to the two heads and sends twigs to each.

Origin.—The lateral head has with M. flex. perf. dig. II a common origin from the inserting tendon of M. ambiens, but there is tendinous attachment to the head of the fibula. The posterior head arises tendinously from the mid-popliteal area, but there is so much fascia in common with the other muscles here that no more definite area can be defined. There is much fleshy connection with the medial head of M. flex. perf. dig. IV.

Insertion.—Just above the intercondylar sulcus, the small uncalcified tendon of the lateral head fuses to the large calcified tendon of the main head. As it crosses the intratarsal joint the tendon is wide and uncalcified. One-sixth of the way down the tarsometatarsus the tendon of M. per. longus attaches to the lateral edge of the now bony tendon of M. flex. perf. dig. III. Continuing down the posterior surface of the tarsus to the base of digit III, the tendon is perforated opposite phalanx 1 by the tendons of Mm. flex. perf. et perf. dig. III and flex. dig. longus. The two tendons thus formed insert on either ventral corner of the distal end of phalanx 1.

In the Whooping Crane we did not find any vinculum between the tendons of M. flex. perf. dig. III and M. flex. perf. et perf. dig. III. Hudson (1937:42) noted a vinculum in *G. canadensis*, and we found one in our dissection of this species. While such intrageneric variation seems unlikely on the basis of past studies, our dissections were carefully done and we do not believe we overlooked any such vinculum in *G. americana*.

M. flexor perforatus digiti II

The bifurcated belly lies in the upper third of the postero-lateral surface of the tibiotarsus. The smaller head is the deeper one and is parallel to the lateral head of M. flex. perf. dig. III. The more superficial main head is a rounded belly lying immediately lateral to the insertion of M. extens. ilio-fib. and to Mm. per. brevis and flex. dig. longus. Innervation comes from the tibial nerve.

Origin.—The small, deep head arises fleshily from the tendon of origin of the lateral head of M. flex. perf. dig. III, which is also the inserting tendon of M. ambiens. The main head, which is apparently the more constant one in birds, comes from the deeper parts of the patellar tendon

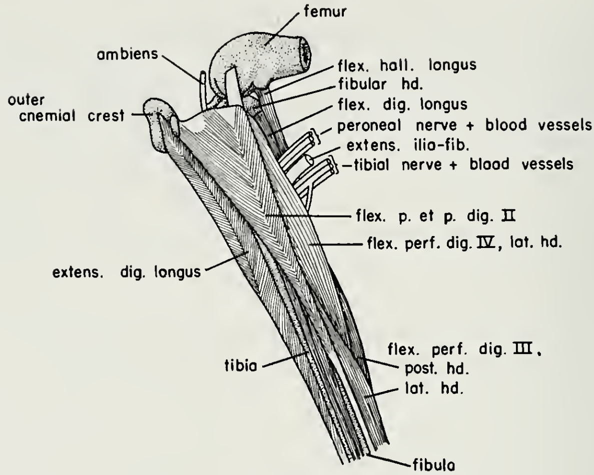


Fig. 34. Lateral view of the muscles of the upper shank after removal of Mm. gastroc., tib. ant., and femoritib. ext.

in the region of the fibular head. No direct connection to the usual site of origin, the flexor area of the external femoral condyle, was found.

Insertion.—The two bellies fuse fleshily about one-third of the way down the shank and produce a narrow, calcified tendon which extends distad to cross the intratarsal joint in its own fascial canal. Continuing down the leg, the tendon is immediately superficial to the tendon of M. extens. dig. longus on the posterior surface of the tarsus. The principal insertion is on the palmar cartilage ventral to the trochlea for digit II and on the postero-ventral and lateral corner of the base of phalanx 1 of digit II. At the insertion this tendon is perforated, but the lateral ramus thus formed is by far the largest and inserts on phalanx 1 as described above. The medial branch is very small and inserts on the medial corner of the phalanx. In fact, one might say that perforation does not occur here, and that the perforating tendons, those of Mm. flex. perf. et perf. dig. II and flex. dig. longus, simply lie medial to the tendon of M. flex. perf. dig. II.

M. flexor hallucis longus

As may be observed in figures 34 and 36, this muscle consists of a long, narrow belly lying posterior to M. flex. dig. longus in the deep posterior musculature of the upper half of the shank. N. tibialis sends a branch to the deep anterior surface of the belly just above the region of insertion of M. extens. ilio-fib.

Origin.—From the most lateral part of the popliteal region come fleshy and tendinous fibers. There is also tendinous origin from the femoral part of the joint capsule. No evidence of two heads of origin was found, but between the first and second thirds of the tibial length there usually are several small, fleshy attachments (origins) from the tibiotarsus; in only one dissection were these absent.

Insertion.—The inserting tendon passes down the postero-lateral length of the tibiotarsus and across the intratarsal joint as the deepest of all tendons in this lateral position. Below the hypotarsus, which the tendon traverses in its own bony canal, the tendon moves medially to lie just superficial to the centrally located tendon of M. flex. dig. longus. Eight centimeters above the distal end of the tarsometatarsus the tendons of the two muscles fused in one of our specimens of *americana*. (See M. flex. dig. longus for the details of this insertion.) In most birds there is some sort of a connection between these two tendons, but Hudson (1937:48) did not find fusion of them in *Grus canadensis* (nor did we); he noted only a vinculum between them, as was the case in one of our Whooping Cranes. When the two tendons are distinct, M. flex. hall. longus inserts in the usual position on digit I.

M. flexor digitorum longus

The bipinnate belly is limited to the proximal half of the shank (figs. 34, 36). Innervation is from the tibial nerve.

Origin.—The bifurcated head of origin is as figured by Fisher (1946: 682); his figure 21 is a posterior view, rather than anterior as labeled. Laterally the origin is fleshy from the postero-distal half of the fibular head and continues down to the last fourth of the fibular length. A narrow line on the tibiotarsus, adjacent and parallel to the fibular origin, also gives fleshy origin to this muscle. The most proximal part of the medial origin is beneath the distal end of M. popliteus and separated from the lateral head by tibial nerves and blood vessels. A longitudinal line on the proximal third of the postero-medial corner of the tibiotarsus provides further fleshy origin for the medial head.

Insertion.—The calcified tendon, formed in the middle of the tibiotarsal length, shortly crosses to a mid-posterior position on the shank. As it goes over the intratarsal joint it is in the most medial group and is the deepest of all tendons here, being immediately beneath that of M. plantaris. After passing through a bony canal in the hypotarsus, the tendon forms three rami about 5 centimeters above the tarsometatarsal malleoli. Before these branches are formed the tendon is joined by that of M. flex. hall. longus. The common branches characteristically perforate the other flexors as they pass to the digits. A fourth and extremely small ramus extends to the base of digit I, but we could not find that it perforated M. flex. hall. brevis. The insertions of the rami to digits II, III, and IV are as described for the Black Vulture by Fisher (1946:681).

M. peroneus brevis

The belly of M. per. brevis consists of the usual fleshy fibers, but there are also many tendinous fibers extending from origin to insertion (fig.

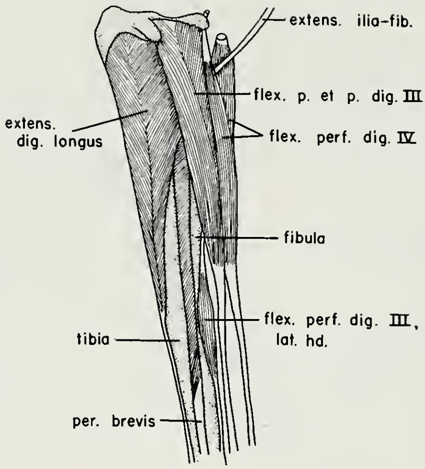


FIG. 35. Antero-lateral view of the third layer of muscles in the upper shank.

35). The long, narrow, semi-pinnate belly extends distally along the lateral and anterior surfaces of the fibula from the insertion of M. extens. ilio-fib. to the beginning of the middle or to the last third of the tibiotarsal length in both *G. americana* and *G. canadensis*. The peroneal nerve trunk which lies deep to this muscle sends a twig to the fibular surface of its belly. Mitchell (1913:1053) found M. per. brevis to be very weak in *Grus, Anthropoides,* and *Balearica*.

Origin.—The origin is mixed fleshy and tendinous from the anterior and lateral faces of the fibula distal to the insertion of M. extens. ilio-fib. and continues on the tibiotarsus distal to the end of the fibular spine. Distal to the fibular crest of the tibia, in those dissections in which the belly extends this far, there is fleshy origin in a narrow area bordered anteriorly by an intermuscular line and posteriorly by the fibula.

Insertion.—The calcified tendon passes along the antero-lateral corner of the tibiotarsus. Just above the tibial condyles it passes through a strong loop of connective tissue. Here the tendon widens and thickens to pass across the lateral surface of the external tibial condyle and to insert on the proximo-lateral edge of the hypotarsus. We found no interconnections between this tendon and that of M. per. longus or the tibial cartilage.

M. extensor digitorum longus

Limited to the upper third to half of the tibiotarsal length, the belly of this muscle is bipinnate and elongately triangular (fig. 35). It is the deepest of the muscles on the anterior side of the shank, lying just lateral to the intermuscular line on the antero-medial edge of the tibiotarsus. As the prefibular branch of N. peroneus crosses the lateral face of the tibia, above the fibular crest and deep to the fibula, a twig enters the postero-lateral surface of this muscle.

Origin.—There is fleshy origin from the outer surface of the inner cnemial crest, from the distal edge of the outer cnemial crest, from the intervening area distal to the rotular crest, and from a triangular area on the upper one-third of the anterior face of the tibiotarsus. Below the middle of the belly there may be a small slip of origin coming from the overlying M. tib. ant. On its medial edge the belly is closely attached by aponeurosis to the intermuscular line.

Insertion.—The tendon is calcified above and below the intratarsal joint, but not across the joint itself; this is true for all tendons crossing this articulation. From its antero-lateral position at the region of its formation, the tendon moves distad and mediad to pass through a fibrous loop and then a bony canal just above the malleolar region. It crosses the medial edge of the intratarsal joint, goes down the antero-medial corner of the tarsometatarsus, and finally comes to lie in the middle of the anterior side of this bone. Nine centimeters above the metatarsal malleoli the tendon bifurcates, and the lateral ramus thus formed bifurcates about 3 centimeters from the distal end of the tarsometatarsus. The area between the various branches is a continuous sheet of white connective tissue, but the above-described tendons are clearly visible. The single, most medial branch passes medially to the base of digit II. There it passes through a fibrous loop and continues distally along the antero-medial edge of the basal phalanx to insert in part on the distal end of this phalanx, but continuing out to attach to the dorso-medial aspect of the claw. The middle branch, formed on the metatarsus, and the aponeurotic sheath pass straight out to the base of the first phalanx of digit III. The tendon crosses to the digit lateral to the malleolus for digit III and goes out the antero-lateral surface. There is strong fascial connection to the base of the first phalanx of digit IV as the ramus passes to digit III. On this latter digit the points of insertion are the distal ends of phalanges 1 and 2 and the fascia over phalanx 3. The variable and diffuse areas of attachment to this digit and to digit IV show agreement with *Grus*

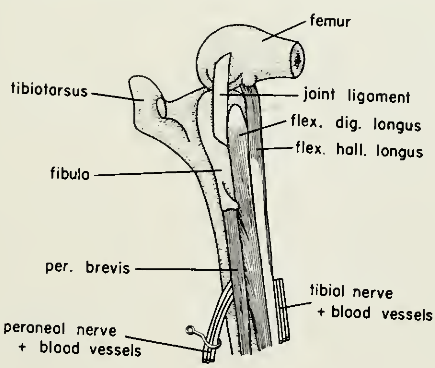


FIG. 36. Lateral view of the deepest muscles of the upper tibial region.

canadensis as described by Hudson (1937:33). The most lateral branch of the main tendon, the one going to digit IV, courses directly over the anterior surface of the malleolus for the fourth toe and inserts broadly on the most proximal end of the basal phalanx, but continues distad to insert on the distal ends of phalanges 1, 2, and 3 and on the anterior fascia over phalanx 4.

M. popliteus and
M. plantaris

Both these muscles are as described for cathartid vultures. (See Fisher, 1946, pp. 683 and 687, respectively.)

The Whooping Crane shows evidence of great reduction in the small tarsometatarsal muscles going to the toes. M. extens. prop. dig. III and M. extens. brevis dig. III exist only as remnants; only a few extremely short, proximal fibers remain of the former and a sheet of connective tissue represents the latter. For the general topographical relationships of these muscles in birds, the reader is referred to Hudson (1937:88, 89) and Fisher (1946:687). Mm. extens. hall. longus, abd. dig. II, and extens. brevis dig. IV are as described by the latter author, except that the insertion of the first muscle is on the base of phalanx 1 in *G. americana*. Mm. add. dig. II, flex. hall. brevis, and abd. dig. IV are also of the conformation described by him. M. add. dig. IV is not present in *G. americana* and *G. canadensis*.

Muscles of the Body Wall

M. obliquus abdominis externus
M. obliquus externus abdominis—Shufeldt (1890:301-302)
M. obliquus abdominis externus—Gadow (1891:126-127)
M. obliquus abdominis internus
M. obliquus internus abdominis—Shufeldt (1890:303)
M. obliquus abdominis internus—Gadow (1891:127-128)
M. rectus abdominis
M. rectus abdominis—Shufeldt (1890:303-305) and Gadow (1891:130-131)
M. transversus abdominis
M. transversalis abdominis—Shufeldt (1890:305-306)
M. transversus abdominis—Gadow (1891:128-129)
Mm. intercostales externi and interni
Mm. triangularis sterni, Mm. intercostales, and Mm. appendico-costales —Shufeldt (1890:295-301)
Mm. costi-sternalis, Mm. quadratus lumborum, Mm. intercostales externi and interni and Mm. interappendicular costarum—Gadow (1891:122-126)
M. transverso-analis
M. transversus perinei—Shufeldt (1890:312)
M. transverso-analis—Gadow (1891:129-130)

M. obliquus abdominis externus (external oblique)

This thin band of muscle covers the outer surface of the ventral fourth to third of the length of the ribs (fig. 25). Its ventral edge is beneath the dorsal edge of the superficial part of M. pect. Anteriorly its belly covers the origin of M. sternocora., and at its dorso-anterior corner is nearly in contact with the ventral end of M. serr. ant. In general, the muscle can be said to extend posteriorly from the second rib to within 3 centimeters of the most distal end of the pubic bones.

On the rib basket the muscle is superficial to the Mm. intercost. ext., on the lateral part of the abdomen to M. obliq. abdom. int., and on the ventral part of the abdomen to M. rectus abdom. Frequently the direction of the fibers may be more nearly vertical than is shown in figure 25.

The ventral attachment of the fibers is fascial to the costal margin of the sternum beneath M. pect., and posteriorly it is by an aponeurosis to the midline raphe of the abdomen. This aponeurosis posterior to the sternum narrows gradually until at the posterior end of the muscle the fleshy fibers of either side nearly meet in the midline. The posterior edge of the muscle, composed of very short fibers, is attached by a wide aponeurosis to the ventral edge of the pubis and to the interpubic ligament.

The dorsal attachment of M. obliq. abdom. ext. is aponeurotic to the external faces of the ribs and to the fascia overlying the outer layer of intercostal muscle. This aponeurotic connection, which has been removed in figure 25, extends dorsad nearly to the uncinate processes. The greatest dorsal extent occurs anteriorly where the aponeurosis may cover and connect with the origin of M. serr. ant.

M. obliquus abdominis internus

The thin layer of this muscle covers the space between the last rib and the distal ends of the pubes (figs. 25, 29). Its fibers are directed antero-ventrally at a 45-degree angle with the vertebral column; thus they lie at nearly a 90-degree angle with the long axis of the last rib. M. obliq. abdom. ext. covers the ventral one-third of the muscle. The ventral edge of the internus is in contact with the dorsal edge of M. rectus abdom., and it is in part superficial to M. trans. abdom.

Origin.—Aponeurotic origin comes from the ventral edge of the pubis, from the pectineal process, or just anterior to it, caudad to within 2.5 centimeters of the posterior end of the pubis. There is close interconnection between this aponeurosis and the one that provides origin for M. trans. abdom.

Insertion.—There is fleshy connection with the postero-lateral border of the last rib. This insertion is limited ventrally by the articulation between the vertebral and sternal parts of the rib, and it extends dorsad some 8 centimeters.

M. rectus abdominis

The broad, thin band of belly is located between the posterior end of the sternum and the pubis and is just lateral to the midline. It is usually about 4 or 5 centimeters wide, is deep to M. obliq. abdom. ext., and is superficial to M. trans. abdom. Its dorso-lateral border is next to the ventral edge of M. obliq. abdom. int. Only a midline raphe separates the right and left Mm. recti abdom.

Origin.—The posterior two-fifths of the muscle are completely aponeurotic and come from the distal 2.5 centimeters of the pubis and from the interpubic ligament.

Insertion.—Superficially the insertion on the posterior end of the sternal plate is aponeurotic, but fleshy fibers make up the bulk of this attachment. There is also some fleshy insertion on the posterior edge of the sternal part of the last rib.

M. transversus abdominis

The belly is the deepest of all muscles of the abdomen posterior to the sternum; its deep surface is in contact with the peritoneum. Dorsally it is deep to M. obliq. abdom. int., and ventrally to M. rectus abdom. The sheet of contractile tissue extends from the sternum posteriorly to the pubis, dorsally to the pectineal process of the pelvis, and anteriorly beneath the sixth, seventh and eighth ribs. The fibers in this broad muscle run nearly at right angles to the vertebral column, but their ventral ends curve somewhat posteriorly.

Origin.—The anterior part of the origin is by fleshy fingers which come from the deep surfaces of the last three ribs; the area of attachment is 4 or 5 centimeters dorsal to the junction of the vertebral and sternal parts of the ribs. Posteriorly this origin is aponeurotic from the ventral edge of the pubis deep to, but closely connected with, the origin of M. obliq. abdom. int. However, in the most posterior 5 centimeters of the pubic length the origin is muscular.

Insertion.—In the ventral midline a raphe from the posterior end of the sternum to the interpubic ligament forms the insertion for the M. trans. abdom. of either side.

Mm. intercostales externi (intercostal superf. layer)
and Mm. intercostales interni (intercostal, deep layer)

In the region of the vertebral ribs the intercostal musculature is composed of two layers (figs. 25 and 29). On the sternal ribs only the superficial layer is found (fig. 29); if the deep layer is present at all in this area it is apparently represented by a sheet of fascia closely applied to the deep side of the superficial intercostal muscles. With this exception the intercostal muscles are characteristic in configuration and position, being present in all intercostal spaces.

The fibers of the superficial layer go obliquely antero-dorsad and attach fleshily to the edges of the ribs. Two modifications associated with this layer are to be found near the uncinate processes in both the Whooping and the Little Brown Crane. On the outer face of the base of each uncinate process is a small, distinct fasciculus (not shown in the drawings) which extends dorso-anteriorly to attach to the postero-ventral edge of the tip of the next most anterior uncinate process. Also present are triangular sheets of aponeurosis, weaker in *canadensis* than in *americana,* which go from the antero-dorsal edge of each uncinate process to the posterior edge of the same rib and extend some 2 or 3 centimeters dorsad of the union of the uncinate process with its rib. These sheets of connective tissue are figured for the Raven by Shufeldt (1890: 293, fig. 73) and for *Colymbus septentrionalis* by Gadow (1891, plate 18a, fig. 1). The small fingers of muscle differentiated over the uncinate processes are not mentioned by Gadow, as far as we can determine, but they may correspond to the Mm. appendico-costales of Shufeldt (1890: 298-299, and fig. 73).

The deep layer of the intercostal muscles is much more fascial in content than the superficial layer (fig. 29). The fibers are directed antero-ventrad and thus lie nearly at right angles to the fibers of the outer or external layer. The muscles are limited to the vertebral rib part of the thoracic basket.

M. transverso-analis

The thin sheet of contractile and connective tissue constituting this muscle forms the body wall posterior to the pelvis (figs. 25, 29). It arises from the deep corner of the postero-medial edge of the ilium, from the transverse processes of the last two fused vertebrae in the pelvis, and from the posterior border of the ilium. It attaches ventrally to the dorsal medial edge of the distal end of the pubis and to the interpubic ligament. The muscles of the two sides meet in a midline raphe ventral to the cloaca.

Muscles of the Vertebral Column

The muscles of the vertebral column are listed below in the order of discussion in the text.

M. spinalis cervicis
  part M. longus colli posticus—Shufeldt (1890:272-275)
  M. spinalis cervicis superior, post. slips of M. spinalis dorsi, and ? part M. multifidus-semispinalis—Gadow (1891:110-114)
  M. spinalis cervicis—Boas (1929:148-158)
Mm. splenii colli
  part M. longus colli posticus—Shufeldt (1890:272-275)
  ?ant. slips M. spinalis cervicis (superior)—Gadow (1891:110)
  Mm. splenius colli—Boas (1929:164-170)
Mm. dorsales pygmaei
  ?part M. longus colli posticus—Shufeldt (1890:272-275)
  ?M. spinobliquus cervicis of M. spinales complex—Gadow (1891:110-111)
  Mm. dorsales pygmaei—Boas (1929:158-161)
M. spinalis thoracis
  M. longissimus dorsi—Shufeldt (1890:278-281)
  M. longissimus dorsi and ?part M. multifidus-semispinalis—Gadow (1891: 106, 113-114)
  M. spinalis thoracis—Boas (1929:148-158)
M. longus colli
  M. longus colli anterior—Shufeldt (1890:285-288)
  M. longus colli anticus—Gadow (1891:118-119)
  M. longus colli (ventralis)—Boas (1929:179-188)
M. scalenus
  M. scalenus medius—Shufeldt (1890:297-298)
  M. scalenus—Gadow (1891:124-125)
Mm. ilio-costales
  part M. sacro-lumbalis—Shufeldt (1890:276-278)
  part M. ilio-costalis—Gadow (1891:106-107)
Mm. levatores costarum
  Mm. levatores costarum—Shufeldt (1890:298) and Gadow (1891:123-124)
Mm. ascendentes cervices
  M. obliquus colli—Shufeldt (1890:281-284)
  M. cervicales ascendens—Gadow (1891:107)
  M. ascendens cervicis—Boas (1929:170-176)
Mm. ascendentes thoraces
  ?part M. sacro-lumbalis—Shufeldt (1890:276-278)
  ?part M. ilio-costalis—Gadow (1891:106-107)
  M. ascendens thoracis—Boas (1929:170-176)
Mm. intertransversarii
  part Mm. intertransversales—Shufeldt (1890:294-295)
  part Mm. intertransversarii plus ?part M. longus lateralis cervicis et capitis —Gadow (1891:115-117)

Mm. intertransversarii—Boas (1929:176-177)

Mm. inclusi

med. part Mm. intertransversales—Shufeldt (1890:294-295)

Mm. intertuberculares (part of Mm. intertransversarii anteriores)—Gadow (1891:116, 121)

Mm. inclusi—Boas (1929:177-179)

Mm. intercristales

Mm. interarticulares—Shufeldt (1890:292-294)

Mm. rotatores s. obliquo-transversales—Gadow (1891:114)

Mm. intercristales—Boas (1929:188-189)

Mm. obliquo-transversales

M. obliquo-transversales—Shufeldt (1890:294)

M. transverso-obliquus—Gadow (1891:106)

part M. ascendens cervicis—Boas (1929:170)

Mm. interspinales - discussed with muscles of the tail (p. 72)

M. interspinales—Shufeldt (1890:291-292), Gadow (1891:114-115), and Boas (1929:189)

M. spinalis cervicis and M. splenius colli

It was impossible for us to make a single drawing of this complex of the dorsal spinal musculature. Therefore, the system is first separated into cervical and thoracic parts—M. spinalis cervicis and associated muscles and M. spinalis thoracis. Because of the interconnections of the first part, several drawings and diagrams were prepared; but even these do not make clear the multitudinous ramifications and anastomoses. Boas (1929: plate 11) has illustrated the complex in *Ardea cinerea;* comparison with this will perhaps aid.

The Whooping Crane shows much the same condition of the muscle-complex as exhibited by *Ardea cinerea,* except that the main tendon of origin in the crane is from the dorsal crest of the 18th vertebra. The tendon is fleshy, to a limited degree, on its deep side in the region of the 16th and 17th cervical vertebrae; but it becomes increasingly contractile opposite the 14th and forms its main belly between this vertebra and number 9.

Four fleshy fasciculi come off the deep side of the main spinalis muscle; the most anterior of these goes to the M. ascendens cerv. going to cervical vertebra 13 (fig. 39) and the remaining three to vertebrae 14, 15, and 16, respectively. In addition to these fleshy bands, there are five separate tendons from the deep lateral side of the main muscle; they attach to the Mm. ascendentes cerv. which insert on vertebrae 12 to 8 (fig. 39).

There are eight distinct slips of M. splenius colli on each side (fig. 5). The most posterior arises from the ninth cervical vertebra and the others from succeeding, more anterior vertebrae. Each slip arises beneath the tendon of the main spinalis cervicis muscle and goes anteriorly and dorsally to attach to M. spinalis cerv. Between vertebrae 5 and 9, M. spinalis cerv. covers the Mm. splenii colli, but anterior to the fifth vertebra the slips of Mm. splenii colli emerge between the tendons of the spinalis cervicis muscles of the two sides and cover the tendon in dorsal view. The most anterior of the bellies of Mm. splenii colli is the largest, and there is a gradual diminution in size posteriorly.

The Mm. dorsales pygmaei are also intimately related to M. spinalis cerv. In the Whooping Crane they are as shown by Boas for *Ardea cinerea* except that there are six of them, one arising from each vertebra from 15 to 10, inclusive. Thus, compared to this heron the extra M. dorsalis pygmaeus in the Whooping Crane seems to lie at the anterior end of the series. Arising from the mid-dorsal part of the vertebrae, the slips pass anteriorly to insert on the lateral part of the vertebrae—skipping one vertebra in their passage. The slip coming from vertebra 11, for example, inserts on vertebra 9 (fig. 40).

In one specimen we found a second trunk of M. spinalis cerv. arising from vertebra 16 and attaching to the most anterior accessory fleshy fasciculus of the main belly of M. spinalis cerv. It did not receive or send out any additional slips. Boas indicated the attachment of M. dorsalis pygmaeus to such slips; in our species these pygmaeal muscles insert on the accessory fasciculi arising from the main tendon.

Origin.—The main tendon of M. spinalis cerv. originates from the anterior end of the neural crest of vertebra 18 (fig. 37). The accessory tendons and fasciculi, opposite vertebrae 18 to 15, arise from the main tendon. M. splenius colli in each instance comes from the lateral surface of the base of the neural spine of the vertebrae (nos. 9-2). Mm. dorsales pygmaei originate fleshily from the anterior edge of the most medial part of the ridge extending postero-laterally from the mid-dorsal line of the centrum on to the dorsal surface of the postzygopophyseal process. This origin is immediately medial to and from the same line as the origin of the Mm. intercristales (fig. 40).

Insertion.—The primary tendon of M. spinalis cerv. attaches to the posterior edge of the lateral half of the postzygopophyseal process of the axis. The accessory tendinous slips and the most anterior fleshy fasciculus (shown in fig. 39) insert on the Mm. ascendens cerv., and through them on the posterior edge of the dorsal surface of the postzygopophyseal processes of vertebrae numbers 13 to 8. As may be observed in figure 40, the lateral edge of the inserting tendon forms part of the insertion of the Mm. obliquo-trans. The bundles of Mm. splenii colli insert on the main tendon of M. spinalis cerv. opposite vertebrae 8 to 2, but the most anterior bundle also inserts directly on the postzygopophyseal process of the axis.

The small slips here designated as the Mm. dorsales pygmaei show a graduated series of insertions. Posteriorly in the series the attachment is to the anterior end of the fleshy accessory slips of the main tendon of M. spinalis cerv. This insertion moves anteriorly and laterally by successive steps until it is located lateral to, but in common with, the insertion of the

Mm. intercristales on the postzygopophyseal process (fig. 40); this is apparent from vertebra 11 or 12 anteriorly.

M. spinalis thoracis

Figure 37 shows the muscle as a posterior extension of the dorsal, spinal musculature. In the midline the muscles of the two sides are separated only by the neural processes of the vertebrae from number 18 posteriorly. In the region above ribs 5 and 6 the ventral edge of M. spinalis thoracis is in contact with the superficial posterior part of M. ilio-costalis. Anterior to this region it overlies the dorsal edges of the various slips of the Mm. ascendentes thoraces. Superficially the muscle is covered by a heavy aponeurosis. Four separate bundles may be distinguished but there is much interconnection, especially in the latero-ventral extent (fig. 37).

Origin.—The origin of all four parts is superficially tendinous and aponeurotic, but anteriorly the tendons and aponeuroses become shorter and broader and there is more fleshy belly. The greater development of fleshy bellies anteriorly may correspond to the greater flexibility of the vertebral column, which increases anterior to the synsacrum. The most posterior belly arises from the lateral side of the dorsal process of the most anterior, fused vertebra in the pelvis and also from the dorso-anterior edge of the ilial blade. The next fasciculus anterior comes from the lateral surface of the same vertebra. There is no distinct origin from the second vertebra anterior to the pelvis. The third bundle, from the posterior end of the series, originates from the third vertebra anterior to the ilium. From the region of vertebrae 4 to 7 anterior to the pelvis there is continuous origin for the anterior fasciculus. Laterally, all these heads of origin fuse into a continuous belly.

Beneath these origins, there is continuous fleshy origin from the lateral part of the base of the dorsal processes of all these thoracic vertebrae; the fleshy origin is strongest posteriorly and extends laterally on to the dorsal side of the bases of the transverse processes.

The lateral border of the belly formed in these ways is in intimate contact with, and even fused to, the underlying Mm. intertransversarii, ascendentes thoraces, and obliquo-trans.

Insertion.—There is tendinous attachment to the postero-lateral corners of the dorsal crests of vertebrae 19 to 17, inclusive. The most anterior end of the lateral fleshy belly inserts fleshily on the posterior edge of the postzygopophyseal processes of vertebrae 16 and 15; these areas are deep to the slips of the Mm. ascendentes cerv.

M. longus colli

The extremely intricate and complicated muscle known as M. longus colli lies on the ventral side of the neck and extends from the 21st vertebra to the 3rd cervical vertebra. Posteriorly the various bellies increase in

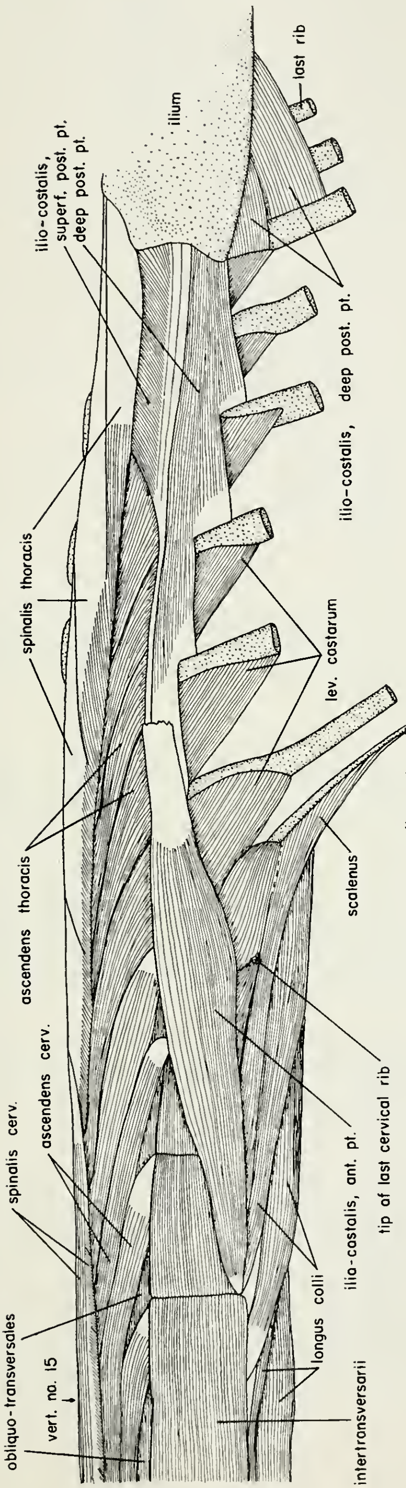


FIG. 37. Lateral view of the superficial muscles of the left side of the vertebral column.

actual size, and in apparent size by interfusion, until they are fairly large (fig. 38). Opposite vertebra 16 one may find four distinct fasciculi (figs. 37, 38). Opposite vertebra 17 the middle two slips fuse, and just posterior to this vertebra they fuse to the most medial belly. Thus, at the level of vertebrae 18, 19, and 20, two bellies are evident; only the most lateral and unfused belly continues posteriorly to vertebra 21.

Rather than try to describe the multitudinous origins and insertions, we have prepared a diagram (fig. 38). In it the solid lines indicate fleshy fasciculi, and the dotted ones tendinous insertions. The solid, curved lines to the left of the fasciculi are fleshy origins from the vertebrae opposite them. The anterior ends of the dotted lines represent insertions on the vertebrae opposite them. In general, it may be said that there is tendinous insertion on vertebrae 16 to 3, inclusive, and that there is fleshy origin from vertebrae 21 to 5, inclusive.

Specifically the origin is from the middle of the length of the midventral line of the centrum. Posteriorly, from vertebrae 21 to 17 the origin is from a wide line on the entire length of the centra and from the anterior faces of the hypopophyses. The insertion is on the posterior edge of the tip of the transverse processes of vertebrae 16 to 3; in figure 6 it can be seen that the insertion here is medial to, but in common with, the insertion of part of M. flex. colli brevis. Posterior to this latter muscle the insertion is superficial and more or less in common with the insertion of the Mm. intertransversarii.

M. scalenus

The muscle (fig. 37) lies just anterior to the first rib and lateral to the posterior bellies of M. longus colli. Its anterior end is deep to the anterior part of M. ilio-costalis, and the postero-dorsal part of its length is more or less fused to the M. lev. costarum on rib number 1.

Origin.—Tendinous and fleshy origin comes from the most postero-ventral corner of the diapophysis of the 16th vertebra, from the surface of the Mm. intertransversarii, and in small extent from the cervical rib of vertebra 18.

Insertion.—Fleshy insertion is on the anterior edge of the distal half of the length of the blade of rib number 1, and immediately ventral to the finger of M. lev. costarum on this rib.

M. ilio-costalis

Although this muscle is a nearly continuous structure in the area in which it lies, it may most easily be discussed as three rather distinct bundles (fig. 37). Alongside the neck and dorsal to M. scalenus is the most anterior belly. Dorsal to the bases of ribs 2 to 6 is a posterior part which is divided into superficial and deep parts.

The anterior belly is a flat band extending from the base of the third rib to the 16th vertebra; it is the most superficial muscle here, after the

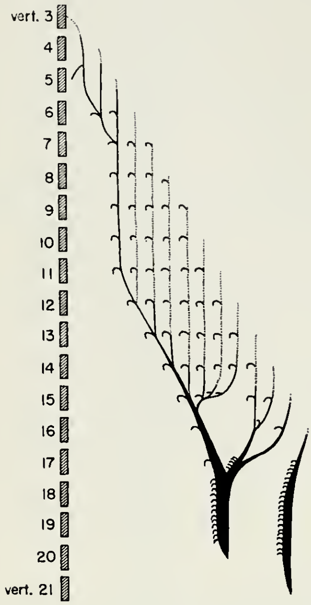


FIG. 38. Diagram of M. longus colli of right side. Solid lines represent fleshy parts; dotted lines indicate tendons. All free ends, whether of solid or dotted lines, indicate attachments to the vertebrae opposite them. *Note:* The parts have been spread laterally; in life they are superimposed for the most part.

wing and its associated musculature are removed. Immediately deep to it are parts of Mm. ascendentes cerv. and intertransversarii on the dorsal border, and parts of Mm. lev. costarum, scalenus, and longus colli ventrally.

The superficial, posterior part of M. ilio-costalis (fig. 37) is ventral to the posterior part of M. spinalis thoracis and overlies the more caudal slips of Mm. ascendentes thoraces. Its ventral, tendinous border is in part fused with the deep, posterior part of M. ilio-costalis the dorsal edge of which it covers.

The dorsal fourth of the width of the deep, posterior belly is covered, as just explained, and constitutes the main contractile part of this fasciculus. The ventral edge thins and fans out over the bases of the respective ribs (fig. 37). The extreme posterior end of this part of the muscle is ventral to the ilium and lies over the bases of the last ribs.

Origin.—The anterior slip shows its segmental nature in its origin. Superficially there is completely tendinous origin from the surface of the anterior tendons of the posterior parts, but the transverse processes of the first three thoracic vertebrae provide tendinous and fleshy origin on the deep side. In each instance the origin is from the dorso-lateral surface of the tip of the transverse process and extends ventro-laterally on fascia nearly to the tubercle of the respective rib.

The superficial, posterior part has its origin on a calcified tendon which forms part of the origin of M. spinalis thoracis. Posteriorly the anterior edge of the ilium gives aponeurotic origin. The deep, posterior part has its primary fleshy and tendinous origin from the anterior edge of the ilial blade, but there are additional tendinous origins from the tips of the transverse processes of ribs 3 to 6. The fibers arising from the processes go dorso-laterally to join the deep side of the main body of the muscle. The more ventral and posterior slips arise fleshily from the antero-ventral edge of the ilium, ventral to the origins of Mm. glut. prof. and iliacus; these fingers of muscle are superficial to the most posterior parts of M. lev. costarum and to the external costal muscles.

Insertion.—The anterior bundle of M. ilio-costalis attaches fleshily and tendinously in three places—the posterior edge of rib 1, beneath the middle of the belly of M. lev. costarum; the posterior border of the greatly inflated transverse processes of vertebrae 17 and 16 (these insertions mingle inseparably with the fibers of Mm. intertransversarii); and aponeurotic and fascial on the most antero-ventral corner of the transverse process of vertebra 16.

The superficial, posterior part forms a calcified tendon along its ventral edge; the tendon passes forward to insert on the postero-dorsal corner of the tip of the transverse process of thoracic vertebra number 3.

A series of insertions are present for the deep, posterior belly. The most ventral and posterior slips attach fleshily to ribs 7, 8, and 9. As the main body of this part passes forward, successive tendinous insertions are made on the posterior edges of ribs 6 to 2. The insertions become progressively weaker anteriorly until only a narrow and thin aponeurosis goes to the second rib (fig. 37).

M. levator costarum

Figure 37 shows most of the nine parts of this muscle; size of the individual slip decreases posteriorly. At the anterior end of the series a few fibers going to the last cervical rib might be considered the most anterior extent of the muscle, but they have been here allied with parts of Mm. intertransversarii. This anterior region is deep to the anterior part of M. ilio-costalis and just dorsal to M. scalenus. Posteriorly the slips are increasingly covered by the slips of the posterior part of M. ilio-costalis until, at the end of the rib basket, the last two fasciculi are completely hidden in lateral view.

Origin.—In each instance an individual slip arises, largely fleshily but with some tendinous fibers intermixed, from the most ventro-lateral part of the diapophysis of a thoracic vertebra.

Insertion.—The fibers go ventro-posteriorly at a 45-degree angle with the vertebral column and attach to the base of the corresponding rib. The most extensive area of insertion is the anterior edge of the base of each

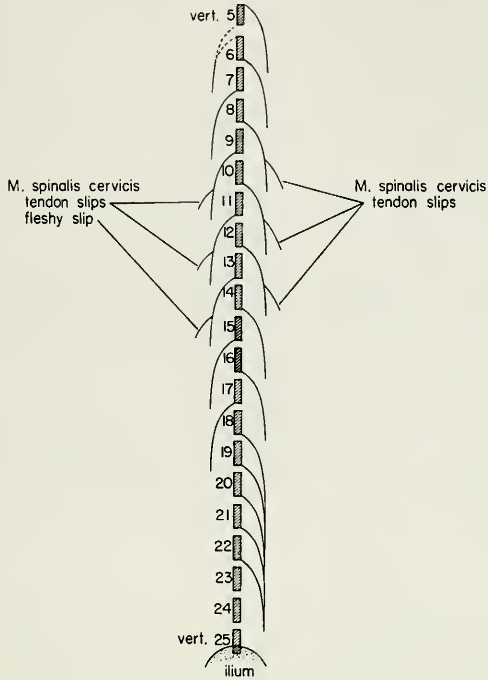


FIG. 39. Diagram of the attachments of Mm. ascendentes and the relationship to certain parts of M. spinalis cerv.

Note: All slips shown belong to the right side; those on the left were moved there for greater clarity.

rib, but as shown in figure 37 the dorsal part of the insertion in many cases encroaches upon the lateral surface of the rib. This latter extent is most evident for the most anterior slip, which entirely covers the base of the first rib and ventrally fuses with M. scalenus.

Mm. ascendentes

We cannot in our descriptive treatment follow Boas (1929) who grouped all the ascendentes muscles and the Mm. obliquo-transversales. In the Whooping Crane we distinguish as separate parts the cervical and thoracic divisions of the ascendentes muscles—calling them Mm. ascendentes cervices and Mm. ascendentes thoraces, respectively—as well as the distinct bundles known as Mm. obliquo-trans.

The ascendentes muscles are located on the dorso-lateral aspect of the vertebral column, ventral to the spinalis complex and dorsal to the Mm. intertransversarii (figs. 22, 25, 29, 37), which latter muscles may overlap the posterior ends of the ascendentes slips. Figures 37 and 40 show that the Mm. ascendentes largely cover the Mm. obliquo-trans. The series is complete and regular from the 25th vertebra (the one fused to the pelvis) to the anterior end of the second cervical vertebra (fig. 37). We could find no break in the series such as Boas (1929:170-176) has described for several series and figured for *Larus*. The diagram (fig. 39) shows the attachments between the vertebrae; in general the slip arising from one vertebra traverses the length of the next two vertebrae anteriorly before inserting. That is, a slip originating on the anterior end of vertebra 18 traverses 17 and 16 to insert on the posterior end of 15. Anterior to vertebra 10 some of the slips may branch to insert on two different vertebrae, but there seems to be little constancy in this variation. In the Whooping Crane the fasciculi arising from vertebrae 5, 4, and 3 go only to the next anterior vertebra; for example, that from 4 goes to vertebra 3, and the most anterior one, that from vertebra 3 goes to the axis. The slips inserting on vertebrae 22 to 18 have a common lateral belly which arises from vertebrae 25 to 21, inclusive.

A variation was noted in one specimen. The slip arising from vertebra 16 was joined by an equally large finger coming from the muscle originating on the 18th vertebra. The combined bundle was then fused in usual fashion with the most anterior fleshy accessory fasciculus of M. spinalis cerv.

The manner of interconnection of the Mm. ascendentes with M. spinalis cerv. has been described in connection with the latter muscle and is shown in figure 39. There is a progressive increase in size of the individual muscles as one observes the series from anterior to posterior.

Origin.—In general the origin is fleshy and tendinous from the anteroventral aspect of each transverse process; in the anterior part of the cervical series the origin may extend medially on to the centrum. In the posterior end of the thoracic series the origin is likewise from the transverse process, but a continuous origin, even between vertebrae, is made possible by utilization of the calcified ligaments connecting the transverse processes of successive fused vertebrae present here.

Insertion.—The insertions are mixed fleshy and tendinous in all instances and are on the dorsal surfaces of the postzygopophyseal processes immediately superficial and anterior to the insertions of the Mm. obliquotrans., and, as has been described, in common with certain slips of M. spinalis cerv. (fig. 39).

Mm. intertransversarii

This series of muscles is present from the posterior end of the axis posteriorly throughout the length of the neck and the first two thoracic vertebrae (figs. 3, 5, 6, 7, 22, 25, 29, 37, 40). They constitute the outer muscular layer of the ventro-lateral quadrant of the neck. Dorsally they overlie the ventral ends of the Mm. ascendentes and obliquo-trans. Ventrally they are in contact with the lateral face of M. longus colli. Posterior to the second thoracic vertebra, their position is occupied by calcified ligaments; even those slips between the last cervical and the first and second thoracic vertebrae are much reduced.

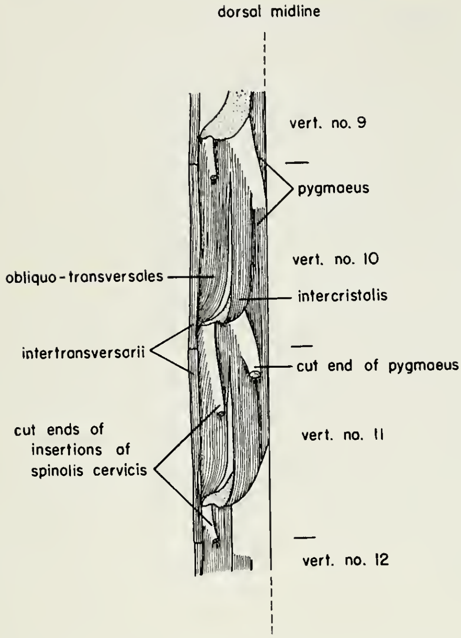


Fig. 40. Dorsal view of the deep muscles of the left side of the neck.

They originate on the distal, anterior edges of the transverse processes and the parapophyses and course forward to insert on the distal, posterior edge of the transverse processes and the parapophyses of the next vertebra anterior to the one of origin.

Mm. intercristales

The intercristales muscles are easily visible (fig. 40) throughout the neck region, from the axis posteriorly. The individual slips are smaller in the lower neck region, and only small, irregular vestiges are present in the anterior thoracic region. It seems likely that the decreased motility of the vertebrae as they are more and more tightly fused into the synsacrum is correlated with the elimination of the muscles in that region.

Where the Mm. interspinales are present, they separate the Mm. intercristales of the two sides. The Mm. dorsales pygmaei, where present, are also involved—the Mm. intercristales being just lateral and partly deep to them.

At their posterior ends the muscles arise from the dorsal surface of the medial half of the postzygopophyseal crest and insert fleshily and tendinously and in common with the Mm. obliquo-trans. and Mm. dorsales pygmaei on the posterior edge of the postzygopophyseal process of the next vertebra anterior to the one of origin (fig. 40).

Mm. obliquo-transversales

As was indicated for Mm. intertransversarii and Mm. intercristales, the individual slips decrease in size at the posterior end of the series and are not present posterior to the second or third thoracic vertebra. It may be true, however, that in all these instances the muscles in this region are simply reduced and fused with the overlying musculature to such an extent that their separate identities are indistinguishable. The details of their topographical relationships are illustrated in figures 37 and 40.

Origin.—The Mm. obliquo-trans. arise fleshily from the lateral part of the anterior surface of the postzygopophyseal processes and from the fascia overlying the articulation. At their origin and indeed for almost half their length they are closely connected to the Mm. intertransversarii.

Insertion.—The anterior attachment is mainly fleshy but with some deep tendinous parts on the dorsal surface of the next anterior postzygopophyseal process. The medial edge of the inserting end is fused with the fleshy fibers of the Mm. intercristales. This insertion is deep and posterior to the insertion of the ascendentes muscles and is partly in common with the accessory fasciculi of M. spinalis cerv. (fig. 40). Some lateral fibers of the Mm. obliquo-trans. insert on the inserting tendons of the accessory fasciculi.

Discussion

It is not practical to attempt a summary of many aspects of this largely descriptive study. Nevertheless, several particulars have been impressed on the authors during their work. One of these is the great variability that may exist in the conformation of muscles and, apparently, in the pathways of nerves to the muscles. This variation is found between the two sides of a single Whooping Crane, between individuals of this species, between the Whooping Crane and the Little Brown Crane and, judging from the literature, between various species of the genus *Grus*.

Although we here have emphasized this variation in internal structures, it is likely that a similarly detailed study of external features would show as great a degree of diversity. The view that internal anatomical features are more variable than the external ones most frequently used by taxonomists is untenable. It has perhaps arisen on the one hand from lack of information that could be supplied by anatomists and on the other by lack of knowledge of what has been demonstrated anatomically. Too often the anatomist has been content with dissection of one or two specimens; that of course could be a criticism of this work, but no more birds were available and we have tried to show the magnitude of variation present in only three specimens of *Grus americana.* We did not have a sufficient sample for detailed statistical treatment.

In this discussion we shall limit ourselves to an enumeration of some of the more significant findings.

The muscles of the skull show little individual variation. The pair of muscles known as M. rectus capitis ventralis is asymmetrical, and to a lesser degree so is M. rectus capitis lateralis. The asymmetry is apparently correlated with the position of the trachea, which moves from a ventral to a lateral position on the neck at the level of the posterior half of these muscles. M. cucullaris is so reduced in the middle of its length that two parts—caput and hals—are distinguishable.

The primitive ventral constrictor sheet of muscle across the floor of the mouth and throat is nearly gone. A few transverse fibers at the level of the urohyal bone are designated as M. constrictor colli, and a few across the anterior half of the basihyal are termed M. intermandibularis. Because of variable development of the epibranchial and ceratohyal bones, there is some variation in the development of the muscles, primarily in M. geniohyoideus.

The posterior part of the primitive mylohyoideus sheet of muscle, called M. serpihyoideus by many authors, is absent. A muscle for which we could find no previous description is described as M. dermoglossus. It may correspond to a superior slip of M. ceratoglossus, which we could not find in *Grus americana.*

M. hypoglossus rectus takes its main origin from the inserting tendon of the lateral part of M. ceratoglossus inferior; only minor origin comes from the entoglossum. Mm. thyroglossus and thyrohyoideus are essentially a continuous layer and an M. thyrohyoideus accessorius is present. M. tracheohyoideus has no circumtracheal windings. The lengths of M. tracheohyoideus, M. tracheolaryngeus superior, and M. tracheolaryngeus inferior vary greatly; this seems to be correlated with general reduction in the muscles of the middle of the cervical length.

We found no important variation, individual or interspecific, in the muscles of the eye and the body wall.

Other than those already mentioned, we noted few differences in the muscles of the vertebral column. There is sometimes a variation in the number of fasciculi present in M. spinalis cervicis and in the Mm. dorsales pygmaei. The Mm. ascendentes and obliquo-transversales are distinct muscles, and the insertions of the former vary in being on one or two vertebrae. The Mm. intercoccyges could not be found in our specimens. Mm. intercristales, and in fact most of the dorsal spinal muscles, show strong development anteriorly, as part of the mechanism of the long neck, but these muscles are sharply reduced and fused together in the thoracic region; they are vestigial or absent in the synsacral area.

In the wing the tendons for the tensor muscles of the patagium are complex and do not represent a simple archaic condition. There is an inner division to the inserting tendon of M. tensor patagii brevis. In both species M. biceps gives rise to a fleshy finger of origin for M. tensor patagii longus. M. deltoideus major has a dermal component in *G. americana,* but this fasciculus was not present in *G. canadensis.* The dermal slip of M. latissimus dorsi is variable in size and may be absent. M. serratus posterior also has a finger which passes to the skin and is greatly variable.

The major breast muscle, M. pectoralis, is usually divisible into superficial and deep parts. The deep part shows considerable variation in the direction of its fibers and in the extent of its development; it may insert only on the tendon of origin of M. biceps and M. tensor patagii longus. In three of our six dissections of the Whooping Crane, M. pectoralis utilized the well developed tracheal enclosure for part of its origin.

The brachial plexus, though an important anatomical feature, has not been considered by many investigators. In addition to other things this study sought to contribute to the knowledge of the brachial plexus of *Grus americana*, with notes on the variation between individuals and the two sides of the same individual.

Variation between the sides of one individual of *Anser cinereus* has been figured by Fürbringer (1888: Taf. IX, Nos. 7-8). The differences between the right and left sides in our study (see figures 14 and 15) are of approximately the same scope as those noted for *Anser cinereus.*

One difference found between the right and left sides in two specimens was that spinal nerve 14 entered the brachial plexus by joining spinal nerve 15 on the right side, while on the left this spinal nerve innervated M. cucullaris, hals part, without joining the brachial plexus.

Variations found solely in specimen number 1 were: the dorso-ventral division occurring before the junction of spinal nerves 16 and 17 on the left side and at their junction on the right side; dorsal plexi being formed by branches of spinal nerves 15 and 16 on the left side only; an extra innervation to M. proscapulohumeralis from a proximal branch of spinal nerve 15 on the left side only; M. coracobrachialis anterior innervated through the inferior division but by a twig from the branch going to M. biceps on one side and by one going to M. pectoralis on the other.

In specimen number 3, a branch of the fused spinal nerves 15 and 16 innervated M. coracobrachialis posterior on the right side, but this same branch went to M. sternocoracoideus on the left. There was less variation found in the brachial plexi of specimen number 3 than in those of number 1.

The differences in brachial plexi between individuals of *Anser cinereus* were also figured by Fürbringer (*op. cit.*: Taf. IX, Nos. 9-12) and of *Columba livia* (*op. cit.*: Taf. X, Nos. 17-20). The variations occurring between our specimens number 1 and 3 are discussed in the text under the muscle concerned, but for the sake of clarity these variations were not included in the figures.

The extent of variation between individuals is of no greater scope than that variation found to exist between the sides of an individual. For example, on both sides of specimen number 3, spinal nerve 16 divides before its junction with 17; a branch is formed at this point of division and courses to spinal nerve 17. At the point of fusion of spinal nerve 17 and the branch of 16, nerve 17 forms a dorsal and a ventral division. This structure is intermediate to those previously described for the two sides of specimen 1. Further examples of individual variations were: a second innervation to M. tensor patagii brevis from the superior division was found only in specimen number 3; a separate branch of the inferior division, just distal to its formation, goes to M. coracobrachialis posterior and to M. sternocoracoideus; no such branch was found in specimen number 1. Although M. sternocoracoideus is innervated through the inferior division in this specimen, no definite branch of this division was found to go to M. coracobrachialis posterior.

The brachial plexi of specimen number 3 are most like that of figure 14, which may be considered as the more usual condition.

The short muscles extending from the tarsometatarsus to the digits of the foot are much reduced and M. adductor digiti IV is absent in both species.

M. flexor perforans et perforatus digiti II is variable in its structure. When it is bipinnate, the posterior half may be atypical, and the muscle in some individuals is not even bipinnate. There was fusion of the tendons of M. flexor perforans et perforatus digiti II and M. flexor perforatus digiti II in *G. canadensis,* but this connection was not found in *G. americana.* The fusion is so clear in the Little Brown Crane it would be unlikely that a similar condition in the Whooping Crane would be overlooked. M. flexor perforans et perforatus digiti II has no direct origin from the flexor area of the external femoral condyle, as is usual.

M. flexor hallucis longus may have only one head of origin. The heads of origin of M. flexor perforatus digiti IV are separated by the inserting tendon of M. extensor ilio-fibularis. The loop for the inserting tendon of this latter muscle is identical in the two species but is not typical; the third arm is a vinculum to the tendons of origin of several muscles on the lateral face of the tibiotarsus.

M. peroneus brevis has connective tissue fibers extending from origin to insertion and is well developed in the two species, contrary to past reports in the literature.

M. femoritibialis medius could not be found as a separate entity in the Whooping Crane. The proximal and distal accessory heads of M. flexor cruris lateralis are not distinct except at their distal ends.

We could find, for pars caudifemoralis of M. caudofemoralis, no attachment to caudal vertebrae other than to those incorporated in the pygostyle. It was noted that when this part of the muscle is absent, the insertions of the pars iliofemoralis and of M. flexor ischiofemoralis are farther distad on the femur. M. ambiens has a widely fleshy origin in *americana* and a narrow, tendinous origin in *canadensis.* Except for the variations noted, our dissections agree with Hudson's characterization (1937:69) of the myology of the hind leg of the Gruiformes.

In his papers of 1873 and 1874, Garrod set up a system of symbols for easy designation of certain muscles in the thigh of birds. He believed these particular muscles were of considerable value in setting up major taxonomic categories, and he based this thinking upon the results of hundreds of dissections. Although subsequent research has revealed a number of inadequacies in this system, and it is realized that the sum-total of all characteristics of the animal must be considered, it is still worthwhile to review our limited findings in the light of Garrod's muscle formulae and the modifications proposed by Hudson (1937).

Symbols Used

A = M. femoro-caudal of Garrod, the pars caudifemoralis of M. piriformis of Hudson and the pars caudifemoralis of M. caudofemoralis of this study.

B = the accessory part of M. femoro-caudal of Garrod, the pars iliofemoralis of M. piriformis of Hudson and the pars iliofemoralis of M. caudofemoralis of this study.

X = M. semitendinous of Garrod and Hudson and M. flexor cruris lateralis of this study.

Y = the accessory part of M. semitendinous of Garrod and Hudson and the accessory part of M. flexor cruris lateralis of this study.

Hudson has proposed the following symbols for additional muscles he regards as of significance:

C = M. ilio-trochantericus medius of Hudson and this study.

D = M. glutaeus medius et minimus of Hudson and M. piriformis of this study.

Am = M. ambiens

V = vinculum between inserting tendons of M. flexor perforatus digiti III and M. flexor perforans et perforatus digiti III.

On the basis of his dissections, apparently of *Grus antigone* and *Anthropoides virgo*, Garrod (1873:640 and 1874:123) gave his myological formula of the Gruidae as ABXY + ambiens. Gadow (1891:161) stated that only the iliac part (B) of M. caudofemoralis was to be found in *Grus*, species not noted. However, Gadow (1893:181) agreed with the formula ABXY + ambiens for *Anthropoides* and *G. antigone*, but noted that A was much reduced in the latter. He also found A and B to be absent in *Balearica*. Mitchell (1901:647-648) noted " . . . some Cranes alone display both muscles," referring to the two parts (A and B) of M. caudofemoralis, and he found A always absent and B present or absent in *Balearica chrysopelargus*, now *B. p. regulorum*. He regarded V as characteristic of the Gruidae. Beddard (1898:367) gave the formula for all *Grus*, except *G. leucogeranus*, as ABXY+. For *Balearica pavonina* he listed BXY+, and for *Balearica regulorum* and *G. leucogeranus* it was XY+ only. He found in *G. americana* only a minute A and a small B, but X and Y were present. Ridgway and Friedmann (1941:6) repeated the view that the presence of a "femorocaudal muscle" is characteristic of the Gruidae except *Balearica*. Hudson (1937:60, 69) gave the formula ABXY for *Grus canadensis* and could not find M. ilio-trochantericus medius in his single specimen. Gadow (1891:142) did not find this latter muscle in *Grus*, but we found it in both *americana* and *canadensis*.

In *Grus americana,* according to our work, the formula ABCDXYAmV would apply to birds 1 and 2, but A was absent in the third specimen. It must be noted that considerable variation was present in the relative development of the two parts of M. caudofemoralis (p. 85) and that the vinculum may be so little developed as to be easily overlooked.

Thus it is impossible with the information at hand to set up any definite formula for the family Gruidae, or apparently even for the genera *Grus* and *Balearica* as now known. One would not expect intraspecific variation of the sort we noted or that found by Mitchell and Beddard in *Balearica; regulorum* and *pavonina* are at present considered to be races of *B. pavonina.* The variation of *G. leucogeranus* from the *Grus* line is not unexpected, for this crane also differs in many other ways. The presence or absence of M. ilio-trochantericus medius cannot be used as a gruine characteristic; it was present in all our specimens, but, as noted above, may be absent in *G. canadensis* (*cf.* Hudson) and perhaps other species of *Grus* (*cf.* Gadow).

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